A Superb Guide to Tropical American Bryophytes

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Guide to the Bryophytes of Tropical America

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Summary

This work provides descriptions, illustrations and keys to the 595 genera and 120 families of bryophytes (hornworts, liverworts, mosses) recorded from tropical America. The generic descriptions include data on the diversity, distribution, and ecology of the group within the Neotropics, important morphological characters, salient features of use in plant identification, as well as literature for species identification. The introductory section of the book provides a discussion of the main morphological features of the hornworts, liverworts, and mosses an overview of the different regions and habitats within the Neotropics and their characteristic bryophytes, information on how to collect and process bryophytes, a list of important herbaria in tropical America, a glossary of technical terms, and a bibliography. The following new names are proposed: *Amphilejeunea reflexistipula* (Lehm. & Lindenb.) Gradst. comb. nov., (*Cryptogynolejeunea reflexistipula* (Lehm. & Lindenb.) Schust.) and *Triandrophyllum eophyllum* (Schust.) Gradst. comb. nov. (*Olgantha eophylla* Schust.).

Resumen

La presente guía provee claves, descripciones e ilustraciones para los 595 géneros y 120 familias de briofitas (antocerotas, hepáticas, musgos) registrados para América tropical. Las descripciones incluyen datos sobre diversidad, distribución y ecología del grupo en el neotrópico, caracteres morfológicos importantes, rasgos salientes utilizados en la identificación de las plantas, así como literatura para la identificación de especies. La introducción provee una discusión de las características morfológicas más importantes de los antocerotas, hepáticas y musgos, una sección sobre las diferentes regiones geográficas y tipos de hábitats en el neotrópico y sus briofitas características, información sobre como colectar y procesar las briofitas, una lista de herbarios importantes en América tropical, un glosario de términos técnicos y bibliografía. Se proponen los siguientes nombres nuevos: *Amphilejeunea reflexistipula* (Lehm. & Lindenb.) Gradst. comb. nov. (*Cryptogynolejeunea reflexistipula* (Lehm. & Lindenb.) Schust.) and *Triandrophyllum eophyllum* (Schust.) Gradst. comb. nov. (*Olgantha eophylla* Schust.).

Table of contents

Preface

Due to its great variation in landscapes and climates, tropical America has a very rich and diverse bryophyte flora. There are nearly 4000 species of neotropical hornworts, liverworts, and mosses, nearly one third of the world diversity of bryophytes. Tropical America is also very rich in endemics, with 50 endemic genera of hepatics and 70 of mosses. Bryophytes not only constitute an important part of the total plant biodiversity in the Neotropics, they are also an important element of the tropical ecosystems, particularly montane rain forests where they serve as water reservoirs and prevent water from running off immediately down the slopes into streams. Most bryophytes are also very sensitive to ecological disturbances, in particular to changes in ambient air quality. When primary forests are disturbed by logging or other human activities, the damaging effects readily show up in the bryophyte composition. Bryophytes occur in most tropical ecosystems, including lowland rain forests, montane rain forests, páramos, punas, dry forests, savannas, etc., and they can be used in these ecosystems as biodiversity indicators. These plants broadcast early warning signals that alert us to the loss of biodiversity and ecosystem quality. Bryophytes are easy to collect. However, for the non-specialist they are not easy to identify. The lack of a good identification tool for tropical America stimulated the authors to consolidate the scattered information in the literature, to add to this their long-term field experience in the area, and to prepare a generic guide with appropriate attention to distribution and ecology of the bryophytes.

This book has been designed to serve as a practical introduction to the genera of bryophytes of tropical America, their morphology, distribution, ecology, and identification, and is meant for usage by people involved in teaching botany, ecology, and plant geography, as well as all those investigating neotropical bryophytes and their place and role in the natural environment. Since good scientific data on bryophyte ecology and floristics in the Neotropics are very scarce, we hope that the information provided in this work will be useful and will stimulate further bryological research in the area.

The book is structured as follows. General features of the bryophytes, including peculiarities in their morphology, life cycle, and important characters by which they can be identified, are discussed in the first part of the introduction. Technical terms in the keys and descriptions that may be unfamiliar to the user are explained here as well as in the glossary that follows the chapter on general features. The introductory section continues with an overview of bryophyte distribution and conservation in tropical America and with a description of the most important bryophyte habitats in the area. In order to guide the interested reader to further bryological information, the next section presents the most important bryological literature and addresses of important bryological herbaria in tropical America. Finally, collecting, processing, and storage of bryophytes are discussed.

In the descriptive part of this guide, keys, descriptions, and illustrations are provided for the orders, families, genera, and sometimes subgenera of the bryophytes of tropical America. It should be emphasized that the keys are primarily made for the identification of the neotropical genera of bryophytes and may not always work for other tropical regions. Those wishing to identify species should consult the publications on the individual genera cited in the text. Genera and families are treated in alphabetical order. All taxa are described except when the order or family is monotypic; in this case the subordinate family or genus description is omitted. The descriptions are usually kept brief and do not pretend to be comprehensive. Rather, special attention is given to the features of the plants that are important for their

recognition and identification. Nearly all genera are illustrated. The descriptions of the orders and families follow basically the same sequence as those of the genera but are usually more brief. Data on ecology of higher taxa are not given unless they are particularly characteristic of the group. Bibliographic references as well as morphological characters common to the order, the family, and the genus are usually not repeated for each taxonomic category.

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General features of the bryophytes

Bryophytes include nearly 15000 species in more than 1000 genera worldwide. Three main groups of bryophytes are recognized: the **liverworts** or **hepatics** (class Hepaticae), the **hornworts** (class Anthocerotae), and the **mosses** (class Musci). Differences between the three groups are shown in Table 1. Bryophytes are an ancient group of land plants that disperse by spores instead of seeds and have inhabited this planet for almost 300 million years, their origin dating back to the Devonian. The oldest fossils known of the bryophytes are in many respects similar to extant taxa and it is for this reason that bryophytes are sometimes looked upon as living fossils. In the evolutionary scale, the bryophytes occupy a place between the green algae and the vascular plants (ferns and seed plants). Much evidence points to mosses and liverworts being a branch of early vascular plant evolution, whereas hornworts may be placed “between“ green algae and vascular plants.
Bryophytes share with the green algae and the vascular plants the possession of chlorophyll as their primary photosynthetic pigment and starch as their principal food reserve. Unlike the algae, which are mostly aquatic, bryophytes and vascular plants are land plants. Their complex reproductive organs, consisting of spore- or gamete-producing cells surrounded by a **jacket of sterile cells**, and the retention of the zygote (= fertilized egg cell) within the female sex organ, developing into an **embryo**, are fundamental differences from the algae and are typical adaptations to life on land. The development of leaves and stems in most bryophytes and vascular plants is another distinctive feature separating them from the algae. Bryophytes are distinguished from the vascular plants primarily by their generally poorly developed water and food conducting systems (except Polytrichales), by the lack of roots and, most importantly, by their very different life cycle. In the vascular plants, the actual plant (the one that we see in the field) is the **sporophyte** or asexual generation; the gametophyte or sexual generation of the vascular plants is much reduced and often ephemeral. In bryophytes, however, the actual plant is the **gametophyte**. The sporophyte is usually much more reduced and attached to and largely dependent on the gametophyte during its development.
Bryophytes are plants of humid places; the availability of liquid water is essential for their development and metabolism. The gametophyte, for example, needs water to allow the motile, biflagellate **spermatozoids** or **antherozoids** (male sex cells) to swim to the female organ, where the egg is located. Due to the lack of roots and vessels, water transport is mainly external (ectohydric) except in certain thalloid liverworts and mosses that have a more or less well developed internal transport system. Bryophytes are typically **poikylohydric** plants, that is, their turgor depends on moisture in the environment. During dry periods, the plants dry up almost completely and may become dormant. When wetted, water is taken up rapidly by the plants and photosynthesis is resumed. The drought tolerance characteristic of bryophytes is shared with the lichens, many terrestrial algae, and small animals like tardigrads, nematodes, and rotifers that often live in association with bryophytes.

Life Cycle

Like vascular plants, the life cycle of the bryophytes is an alternation of two phases or generations (Fig. 1A), a **gametophyte** and a **sporophyte**. The dominant generation in the life cycle of a bryophyte is the gametophyte (the one that produces the gametes). The gametophyte originates from a spore produced by the sporophyte. Upon germination, the spore produces a so-called **protonema** from which one or more gametophytes arise.

The gametophytes are usually haploid (one set of chromosomes) and produce the sex organs or gametangia, **archegonia** (female) and **antheridia** (male). The gametangia are usually surrounded by specialized leaves or **bracts** or by other types of protective structures. A gametangium or group of gametangia together with its surrounding protective structure(s) is called the **gametoecium**; the male gametoecium is called the **androecium**, the female is called the **gynoecium**. The gametangia can be born on the same plant (**monoicous**) or on separate ones (**dioicous**) (Fig. 1B). When monoicous, the plants can be **autoicous** (gametangia on different shoots), **paroicous** (gametangia on the same shoot but separate), or **synoicous** (gametangia mixed in the same gametoecium). The dioicous and autoicous condition are common in all three groups of bryophytes, the paroicous condition occurs in liverworts and mosses and the synoicous condition is exclusive to mosses.

The archegonium is flask-shaped and consists of an enlarged basal portion or venter, where the **egg cell** is located, and an elongated upper portion or neck, that the **spermatozoids** penetrate to fertilize the egg cell. Once fertilization has occurred, a **zygote**, the sporophytic generation, is formed. After various cell divisions, the zygote develops a **foot** that penetrates into the gametophyte. The upper embryonic cells elaborate the rest of the sporophyte, the **capsule**, in which the spores are produced, and the **seta**, which raises the capsule above the gametophyte to enhance the dispersal of the spores. The spores are produced by **meiosis**; each diploid spore mother cell is divided into 4 haploid spores (a tetrad). When the capsule matures, the spores are liberated and the life cycle is completed. Unlike vascular plants, the sporophyte in bryophytes is dependent on the gametophyte and is relatively ephemeral.

For a more in-depth introduction to the morphology of bryophytes and aspects concerning their ecology, geography, genetics, physiology, and systematics, the following books may be consulted:

- Richardson, D. H. S. 1981. *The Biology of Mosses*. Blackwell Scientific Publications, Oxford.
- Schofield, W. B. 1985. *Introduction to Bryology*. Macmillan Publishing Co., New York.
- Schuster, R. M. 1966*. The Hepaticae and Anthocerotae of North America,* Vol. I. Columbia University Press, New York.
- Schuster, R. M. (ed.). 1983-84. *New Manual of Bryology*, Vols. 1, 2. Hattori Botanical Laboratory, Nichinan.
- Watson, E. V. 1971. *The Structure and Life of Bryophytes*, 3rd ed. Hutchinson University Library, London.

Table 1. Differences between liverworts, hornworts, and mosses.

	LIVERWORTS	HORNWORTS	
Plants	- leaves in 2-3 rows or without leaves	- without leaves	-
Branches	- developing from leaf initial cells or inner cells of stem, rarely from stem epidermis	-	-
Leaves	- originating from 2 initial cells (from 1 cell in Calobryales and Metzgeriales), undivided or lobed, without midrib	-	-

Cells	- with numerous chloroplasts - pyrenoid lacking - trigones usually present	- with 1-4 large chloroplasts, each with or without a pyrenoid - trigones lacking	-
Oil bodies	- usually present	- lacking	-
Rhizoids	- unicellular	- unicellular	-
Paraphyses	- usually lacking (sometimes present between antheridia)	- lacking	-
Sporophyte	- growing by an apical cell - during development entirely surrounded by a calyptra and other protective organs (perianth, marsupium, involucrum, etc.)	- growing by a basal meristem - during development partially surrounded by involucre, a calyptra lacking	- -
Spore maturatio	- synchronous, before elongation of seta	- asynchronous (seta lacking)	-
Capsule	- rounded to cylindrical, supported by a fragile, colorless seta (or seta lacking) - opens at once, by (1-)4 valves - lacking columella, stomata, and peristome; elaters present	- cylindrical to long filiform, seta lacking - opens gradually from top to bottom, by 2 valves - with columella, with or without stomata, peristome lacking; elaters present	- -
Protonema	- very small, thalloid, producing only 1 gametophyte	- very small, thalloid, producing only 1 gametophyte	-
Chemistry	- monoterpenes, sesquiterpenes and diterpenes; lunularic acid present	- terpenoids (?); lunularic acid lacking	-

LIVERWORTS

The liverworts or hepatics (class Hepaticae) include about 5000 species; an estimated 1350 species in 188 genera occur in the Neotropics. Although there are xerotolerant taxa, the majority of the liverworts are found in humid and shaded places. They occur in all environments, except marine ones. Some taxa can withstand total or partial submersion in creeks, rivers, or periodically flooded areas. Nevertheless, the great majority of the liverworts are terrestrial (including epiphytic and saxicolous) plants.
Liverworts are very diverse in structure and the species are morphologically often highly variable. There are two main types: **leafy** liverworts (Fig. 2A--B) and **thallose** liverworts (Fig. 2 C-G). When plants are prostrate, the lower surface, that may be in conact with the substrate, is referred to as **ventral**, the other as **dorsal**. The ventral surface is usually attached to the substrate by **rhizoids** consisting of a single, elongated cell. In erect plants, the terms dorsal and ventral may be difficult to use and are therefore sometimes replaced by **antical** and **postical**.

Leafy liverworts

Habit

The habit of the gametophyte of the leafy liverworts may be prostrate, ascending, erect, or (less frequently) pendent. Erect growing gametophytes often originate from a creeping, ± leaf-less shoot or **rhizome**.

Stem

The stem (Fig. 2B) of the leafy liverworts can be subdivided into three sectors or "merophytes", two lateral ones and one ventral one. Each merophyte may have a leaf attached to it, those of the ventral merophyte being the "underleaves“. The width of the ventral merophyte is a measure of the robustness of the stem. It is an important taxonomic character to classify the genera of the family Lejeuneaceae. The width of the ventral merophyte is expressed as the number of epidermal cell rows seen across the ventral surface of the stem, between and beyond the opposite bases of the underleaves.
The internal structure of the stem varies from homogeneous to being differentiated into a well-defined (outer) **cortex** and an (inner) **medulla** (Fig. 4E). The outer cortical layer is also called the epidermis. The cortex may consist of small, thick-walled cells in 1-3 layers (Fig. 15G) (often with brownish-pigmented walls), or of much enlarged, thin-walled cells. Following Schuster (1966), an enlarged, thin-walled cortex may be called a **hyalodermis** (Fig. 4E). The presence or absence of a differentiated cortex is an important generic character.

Branches and branching pattern

The branches may have ordinary vegetative leaves, tiny, scale-like leaves or no leaves at all. Branches with scale-like leaves are called **flagellae** (Figs. 20N, 58C), those without leaves are **stolons** (Figs. 22L, 25G). The leafless stolons usually originate from the ventral side of the stem, particularly towards the base of the stem, and may serve as a hold-fast for the plants (e.g., *Stephaniella*, *Odontoschisma*). Branching in the leafy liverworts is highly diversified and quite important in taxonomy. Following Crandall-Stotler (1972), there are two basic kinds of branches: **intercalary** (or thecal) branches and **terminal** (or athecal) branches (Fig. 3A-G).
Intercalary branches originate from inner cells of the stem and therefore have a small collar around the base. They tend to be at right angles from the stem and usually stand in

the axils of the leaves (or underleaves) except in the *Lejeunea*-type branch. There are four types of intercalary branches (Fig. 3A-D):

- ***Bazzania*-type**. branch originating from the ventral side of the stem, from underleaf axil.
- ***Plagiochila*-type**. branch originating from the lateral side of the stem, from leaf axil.
- ***Lejeunea*-type**. branch originating from the lateral side of the stem, from behind the leaf.
- ***Anomoclada*-type**. branch originating from the dorsal side of the stem.

Terminal branches originate from a leaf initial cell or from stem epidermis cells very near to the apex so that no collar is formed. They develop at 45-60 degrees to the stem. When originating from a leaf initial cell, the leaf associated with the branch is a half leaf. Three terminal branch types are distinguished in this book (Fig. 3E-G):

- ***Frullania*-type**. branch originating from a ventral leaf initial cell so that it replaces the ventral half of a leaf; the branch is therefore associated with a half leaf on its dorsal side.
- ***Kurzia*-type**. branch originating from a dorsal leaf initial cell and therefore associated with a half leaf on its ventral side.
- ***Radula*-type**. branch originating from a stem epidermis cell and therefore associated with an unmodified leaf.

In several families, **innovations** or branches originating directly below the perianth, can occur (see under **reproductive organs**).

Leaves

The leaves are generally arranged in three rows, two lateral rows (lateral leaves or "leaves") and a ventral row (**underleaves** or **amphigastria**), (Fig. 2A-B). The underleaves are usually smaller than the leaves and sometimes they are lacking altogether. The leaf position may be **transverse** *(*e.g., *Haplomitrium, Herbertus,* Fig. 3J-K), **incubous** (e.g., *Bazzania*, *Frullania*, Fig. 3L-M) or **succubous** *(*e.g., *Plagiochila, Lophocolea,* Fig. 3H-I). The leaf lamina is normally unistratose (rarely thicker at the base), without midrib (= costa), and may be undivided, lobed, to deeply dissected into filiform segments. The leaves may also be complicate-bilobed, that is, a bifid leaf with lobes folded together longitudinally (Figs. 41G, 59H, 66D). The segments may be unequal in size and the ventral or the dorsal one bigger than the other. Usually, the dorsal segment is the largest though there are exceptions like *Scapania* (Fig. 66H), in which the lobe or dorsal segment is smaller than the ventral one. The ventral lobe or **lobule** may have different forms and may be attached to the dorsal lobe by a small portion or along most of the ventral side of the lobe. In the Lejeuneaceae, the line of attachment between lobe and lobule is called the keel and the margin which is not attached to the lobe is called the "free margin" (Fig. 4F). Usually, there are one or several teeth along the "free margin" (Fig. 34G,I), the outermost one normally being the "apical tooth." A hyaline papilla is usually associated with the apical tooth, at the proximal (Fig. 4G) or distal (Fig. 4H) side of the tooth.

Leaf cells

The leaf cells may vary in shape from isodiametric to long rectangular and the cell walls may be uniformly thin or thickened, or may have collenchymatous thickenings called **trigones**. The shape of the trigones can be cordate (Fig. 35H), triangular (Figs. 44H, 47K) or stellate (Fig. 42D). The shape and number of these trigones are important taxonomic characters. The cells usually have chloroplasts and **oil bodies** when fresh. In some liverworts (*Bazzania*, *Herbertus*), the leaf lamina has rows of elongated cells in the

middle, resembling a midrib; this is the **vitta** (Figs. 58A, 26D,E). Unlike a true midrib, the vitta is only one layer in thickness.

Oil bodies

The oil bodies are unique organelles of the liverworts that are lacking in the mosses and the hornworts. The number, chemical composition, shape, and size of the oil bodies are variable. Nevertheless, these variations are very important in the taxonomy of the liverworts, particularly in the Metzgeriales and Jungermanniales. It should be noted that the characters of the oil bodies are always to be studied from fresh material. Upon drying of the plants, the oil bodies usually desintegrate or their morphology changes. Seen through the microscope, oil bodies in the cytoplasm appear to be colourless, rarely brownish (*Radula*) or sepia *(Calypogeia peruviana)*, and are homogeneous or segmented. Different types of oil bodies may be recognized. In neotropical hepatics, Gradstein et al. (1977) recognized four different types, *Massula*-type, *Bazzania*-type, *Jungermannia*-type, and *Calypogeia*-type (Fig. 4A-D).

- ***Massula*-type** oil bodies are homogeneous or divided into 1-4 segments, small in size (2-6 µm in length) and numerous, more than 8 per cell in midleaf cells. Oil bodies of this type are found in, e.g., *Anoplolejeunea, Brachiolejeunea, Porella*, and many Metzgeriales (Fig. 4A).
- ***Bazzania*-type** oil bodies are also homogeneous or 1-4-segmented, but are larger (4-15 µm long) and less than 8 per cell. This type of oil body is typical of *Bazzania* and *Symbiezidium* (Fig. 4B).
- ***Jungermannia*-type** oil bodies are finely segmented or "granular," made up of numerous minute globules (less than 1 µm in diameter). The oil body may become homogeneous upon degeneration, therefore its structure must be studied from fresh material. Size and number of oil bodies per cell vary. *Jungermannia*-type oil bodies occur in, e.g., Acrobolbaceae, Gymnomitriaceae, Jungermanniaceae, Lejeuneaceae, Scapaniaceae, etc. (Fig. 4C).
- ***Calypogeia*-type** oil bodies are coarsely segmented or „botryoidal" (like a cluster of grapes), made up of distinct globules exceeding 1 µm in diameter. The oil body usually decomposes into independent globules that in time disintegrate. Size and number of oil bodies per cell vary. The *Calypogeia*-type oil body occurs in *Calypogeia, Frullania, Herbertus*, *Lophocolea*, and many Lejeuneaceae (Fig. 4D).

Ocelli

In some members of the Lejeuneaceae, such as *Stictolejeunea* (Fig. 39G-I) and *Leptolejeunea* (Fig. 46M), and in *Frullania*, specialized leaf cells occur that have one very large oil body and lack chloroplasts, the so-called **ocelli**. The distribution of the ocelli within the plant is an important taxonomic character. In dry herbarium material ocelli may usually be recognized by their size, which may be larger or smaller than ordinary leaf cells.

Rhizoids

The majority of the leafy liverworts have rhizoids for attachment though there are some taxa (Calobryales) that lack them. The rhizoids in liverworts, unlike those of the mosses, are normally unicellular (rarely septate-multicellular). They usually originate from the ventral side of the stem (Fig. 2A), rarely from the lobules (*Radula*, Fig. 64N) or from leaf margins (*Metzgeria*, Fig. 69A). In some families rhizoids are scattered, in others they are arranged in bundles. When in bundles, rhizoids usually originate from the base of the underleaves or near to it. In epiphyllous taxa, rhizoids are often fused together to form a compact structure, an adhesive disk or **secondary rhizoid disk** (Figs. 39A, 53E).

Reproductive organs

Reproductive organs are produced from superficial cells of stems or branches. The antheridia are located in the axils of specialized leaves, the male bracts, on the main shoot or on specialized male branches. They are spherical or oval in shape and united to the stem by a thin stalk. In a few groups believed to be primitive (e.g., Herbertaceae), the antheridia may develop from axils of underleaves (Fig. 26H) or male bracteoles.

The archegonia lack paraphyses and are protected by bracts or bracteoles in one or more series, at the tip of long or short shoots. In many taxa the archegonia are, in addition, surrounded by a thin tubular organ, the **perianth** (Figs. 5A, 43B), located between the bracts and the archegonia and originating by fusion from 2-3 leaves. The perianth is usually very short before fertilization but becomes greatly enlarged after fertilization, emerging beyond the bracts and enveloping the young sporophyte. Sometimes the perianth develops without the occurrence of fertilization (commonly so in *Plagiochila*). The shape of the perianth, its ornamentation, the number of keels and their location (ventral or dorsal) and the way it is flattened (lateral, dorsiventral) are important characters in the taxonomy of the leafy liverworts (Fig. 5E-P).

In the Lejeuneaceae, the presence or absence of **innovations** (= branches originating directly below the perianth) and the leaf sequence of the innovations are important generic characters. As to leaf sequence, two different types of innovations are distinguished: **lejeuneoid** innovations, in which the basalmost leafy appendage is a lateral leaf (Fig. 4J), and **pycnolejeunoid** innovations, in which it is an underleaf (Fig. 4I). Sometimes, the first leaf and underleaf of the innovation are produced at nearly equal levels and the innovation leaf sequence may be difficult to determine. In this case the position of the underleaf relative to the leaf should be determined from subsequent series of leaf, towards the apex of the innovation.

Sporophyte

Unlike the mosses, the developing sporophyte is fully enveloped within the **calyptra** (= modified fertilized archegonium) until maturity. The calyptra generally remains very thin and inconspicuous, but in some cases it turnes into a thick, fleshy structure composed in part of stem tissue and partly of archegonial tissue. Such a **shoot calyptra** (Fig. 5B) occurs in the Calobryales, *Adelanthus*, *Anthelia*, and some members of the Metzgeriales. In some taxa, a tubular structure enveloping and protecting the developing sporophyte occurs that is entirely derived from stem tissue, the so-called **perigynium** (Fig. 5C-D). These perigynia may be erect (e.g., *Isotachis*, *Trichocolea*) or pendent (e.g., *Balantiopsis*, *Tylimanthus*, *Calypogeia, Gongylanthus*); when pendent, it is called **marsupium** (Figs. 5D, 15H). In plants having a shoot calyptra or perigynium, the perianth is normally lacking or greatly reduced.

The mature sporophyte is composed of an expanded **foot**, anchoring the parasitic sporophyte into the gametophyte; a stalk or **seta**; and a **capsule** (Fig. 4K). The seta is very short until the capsule is ripe; thereafter it elongates rapidly, within one or a few days, by elongation of its cells. The elongated seta is colorless and usually very delicate, remaining erect only by turgor pressure. The mature capsule is spherical or cylindrical and dehisces by four valves. The orientation of the valves in the unopened capsule is usually straight but in the Balantiopsidaceae and the Calypogeiaceae the valves are spirally twisted. The capsule wall is composed of many layers, the innermost layer usually having cells ornamented with nodular or ring-like thickenings that are very distinctive. The anatomy of the capsule wall and the pattern of thickening are important taxonomic features.

Spores and elaters
Within the mature capsules, there are **spores** and **elaters** (Fig. 4L-M). The latter are narrowly elongated, unicellular organs provided with one or more spirally thickened bands that may become compressed upon dehiscence of the capsule, causing rotation and movement of the elaters (hygroscopic movement). The function of the elaters is obviously to help release the spores from the capsule. In most leafy liverworts the elaters are free inside the capsule but in the Lejeuneaceae and the Jubulaceae they are attached to the top and the bottom of the capsule wall. When the capsule opens and the valves bend backwards, these attached elaters become considerably stretched. Suddenly, they break loose at their basal ends and usually swing into the air, thereby violently ejecting the spores. The explosive discharge of the spores in the Jubulaceae and some of the Lejeuneaceae (subfamily Ptychanthoideae) has been described as the "spiral-spring" mechanism by various authors (see Schuster, 1966a). The spores germinate into a tiny, thalloid **protonema** that may be globose, cylindrical, or discoidal in shape. A filamentous protonema, commonly found in the mosses, is very rare in liverworts. Germination is exosporic or endosporic; the latter type of germination is particularly characteristic of epiphytes (Lejeuneaceae, Jubulaceae, *Radula* spp., *Plagiochila* spp.). Each protonema gives rise to one new gametophyte, as different from mosses which have protonemata that may give rise to more than one gametophyte.

Vegetative reproduction
Leafy liverworts have a wide range of vegetative reproduction. Nearly every part of the gametophyte can become an asexual reproductive diaspore. Vegetative reproduction can take place by simple regeneration from leaf or stem cells or by specialized diaspores such as **gemmae** (Figs. 43G, 66G) produced on the surface or margins of leaves (Fig. 52K), caducous or fragmenting leaves, caducous branches (cladia), (Fig. 46L), etc. In some cases, like in the primitive Calobryales, vegetative reproduction has not been reported; in others (Gymnomitriaceae, Balantiopsidaceae, Antheliaceae), asexual reproduction occurs only on rare occasions.

Thalloid liverworts

Habit
Thalloid liverworts have a dorsiventrally flattened gametophyte or thallus, resembling more or less a green ribbon. The thallus is usually dichotomously branched (pinnate in *Riccardia*) and variable in its internal structure.

Thallus structure
In the Metzgeriales, the thallus is internally simple and multistratose throughout, or composed for most of its width of a single layer of cells (the thallus **wings**) while the central portion is multistratose, resembling a midrib (Figs. 69A,F; 71A,G). In the Marchantiales, the thallus is internally differentiated, having green, chlorophyllous tissue on the dorsal side, usually located in **air chambers** that open by specialized **pores** to the upper thallus surface (Fig. 72M,O); towards the ventral surface, the thallus of the specialized forms is made up colorless storage tissue. The walls of the air chambers are usually visible on the dorsal thallus surface as thin lines, forming a reticulate pattern. The pores are surrounded by concentric rings of cells (Fig. 73J). Thallus cells may have chloroplasts and oil bodies (Metzgeriales), or the oil bodies may be solitary in specialized cells (Marchantiales, Monocleales). The rhizoids are smooth or, in the Marchantiales, of two types: smooth and tuberculate; the latter having peglike projections on the inner walls

(Fig. 74L,M). The ventral surface is sometimes covered by **scales** (Fig. 72N) in 2 or more rows that may be colorless or with a deep purple to black coloration (e.g., *Marchantia, Ricciocarpus*).

Reproductive organs
The antheridia are produced on the thallus surface, naked or surrounded by an **involucre**, or inside the thallus, in special antheridial chambers. In *Marchantia*, the antheridial chambers are located on stalked receptacles, the **antheridiophores** (Fig. 76E,M). The antheridial chambers are below the upper surface of the antheridiophore and open to the exterior by a small pore.
The archegonia are on the thallus surface or embedded inside the thallus and are usually surrounded by an involucre. In some genera there are 2 involucres surrounding the archegonia (e.g., *Asterella*, *Pallavicinia*); the inner one is called the **pseudoperianth** (Fig. 72L,Q). The pseudoperianth develops only after fertilization and resembles the perianth of the Jungermanniales, but the latter originates from leaves whereas the pseudoperianth is of thalline origin. In the Aneuraceae, there is no involucre; the young sporophyte is surrounded by a fleshy **calyptra**. In the Marchantiales, the archegonia are often located on receptacles which may become stalked after fertilization, the **archegoniophores** (Fig. 76D,L). Juvenile receptacles bear archegonia in radial rows on the upper (dorsal) surface. Due to unequal growth of the cells at the disc center, as compared with those at the periphery, the archegonia are displaced towards the lower (ventral) surface of the receptacle. In some taxa *(*e.g., *Monoclea)* mucilage papillae are associated with the archegonia.

Sporophyte
The sporophyte of thalloid liverworts is basically similar to that of the leafy ones, but in the the Marchantiales and Sphaerocarpales the seta is very short or lacking, the elaters are sometimes absent and the mode of dehiscence of the capsule varies. In the Monocleales the capsule opens by 1 valve instead of 4, in the Metzgeriales by (1-)2-4 valves or irregularly, in the Marchantiales by means of a disc-like structure at the apex called the **operculum,** or irregularly. As in other liverworts, the capsule lacks a columella and stomata but the capsule wall is composed of only one layer of cells in the Monocleales, Marchantiales and Sphaerocarpales (of several layers in the other groups), During development, the sporophyte is enveloped and protected by the calyptra.

Spores and elaters
The mature spores vary considerably in size. In *Fossombronia*, *Sphaerocarpos*, and most of the Marchantiales they are often very large, thick-walled and with a richly ornamented outer surface (Figs. 68E, 77J-K). These large spores are excellently drought and frost resistant and may retain their ability to germinate for many years. The durability of the spores is obviously advantageous for dispersal and may explain why many thalloid liverworts have very wide geographical ranges. The pattern of spore surface sculpturing is usually of crucial importance for species identification. When released from the capsule, the individual spores are normally "free“ except in the genus *Sphaerocarpos* and some species of *Riccia*, in which they remain united in groups of 4 (tetrads) (Fig. 72I). The elaters are free within the capsule except in some members of the Metzgeriales, in which the elaters are attached like a brush to a small basal or apical stump of sterile tissue, the **elaterophore** (Fig. 2C). In Ricciaceae and *Sphaercarpos*, the sporophyte has been reduced and internalized within the thallus, lacks elaters and a seta, and has no special mechanism of capsule dehiscence. The spores are released by decay of the

capsule wall and the thallus around them. Germination of spores is like that in the leafy liverworts and is usually exosporic, rarely endosporic.

Vegetative reproduction

Vegetative reproduction may be by simple regeneration from thallus cells or by specialized diaspores, e.g., by gemmae produced at the apex of the thallus or in specialized flask-like *(Blasia)* or cup-like (*Lunularia*, *Marchantia*) structures, or by tubers produced on the underside of the thallus *(Cyathodium, Fossombronia)*.

HORNWORTS

The hornworts (class Anthocerotae) are the smallest class of the bryophytes, containing less than 100 species worldwide, in 8-9 genera. In the Neotropics there are probably no more than 30 species, in 7 genera. In the past hornworts have often been treated as a mere order of the Hepaticae because of their superficial resemblance to the thalloid liverworts. The numerous unique features in their morphology and ontogeny, however, indicate that the hornworts should be treated separatedly from the liverworts. Seven genera are recognized in tropical America. *Anthoceros, Phaeoceros, Notothylas, Folioceros, Leiosporoceros, Megaceros*, and *Dendroceros;* the first three are also distributed widely in temperate zones. Hornworts usually grow in rather open places on soil or rock; along rivers; on road banks; and in arable fields. *Dendroceros* and *Megaceros* can be found epiphytic on trees and rotten logs in humid montane forests.

Habit
The gametophyte of the hornworts is always thalloid, forming dark to light green rosettes with little internal tissue differentiation (Figs. 79A, 80B).

Thallus structure
The thallus grows from a wedge-shaped, 4-sided apical cell that rests in an apical notch. The thallus cells are thin-walled and usually have only 1 large, plate-like chloroplast (Fig. 79H), rarely 2-4 *(Megaceros)*. Each chloroplast is usually provided with a **pyrenoid**, a specialized organelle involved in the synthesis of starch found only in the hornworts and the algae. There are no oil bodies. The thallus margins are entire, lobed, sinuous, or, in the Dendrocerotaceae, strongly crispate. The rhizoids have thin walls and are quite smooth. The thallus is usually several layers of cells thick throughout, being barely attenuated towards the margins. In *Dendroceros*, however, the middle portion of the thallus is considerably thicker than the rest and differentiated into a discrete midrib. On the ventral side of the thallus there are small **air chambers** or **crypts** that are usually open to the outside via **pores**. These chambers contain symbiotic colonies of cyanobacteria of the genus *Nostoc*. The *Nostoc* colonies maintain a mutualistic association with the hornworts, fixing nitrogen from the air and in turn receiving carbohydrates from the hornwort plant. In some genera there are large schizogeneous **mucilage cavities** (formed by destruction of cells) inside the thallus, in addition to the small ventral chambers containing *Nostoc* colonies.

Reproductive organs
The antheridia are spherical and stalked, and are produced in groups or solitary in dorsal cavities of the thallus. The archegonia are individually immersed in the dorsal side of the thallus, their necks usually just emerging beyond the thallus surface. Unlike mosses and liverworts, the first division of the zygote is vertical, determining the bilateral symmetry characteristic of the hornwort sporophyte. The first zygote divisions produce, towards the basal part, the **foot** of the sporophyte, while the upper cells develop into a **capsule** that grows from a meristematic tissue at the base, the **intercalary meristem**. A seta is lacking.

Sporophyte
The capsule is an elongated, fusiform cylinder (Fig. 79A), with a wall composed of 4-5 layers of cells and with or without **pores** or **stomates** (Fig. 79B). When young, the capsule is protected by a sheet of cells produced by the gametophyte, the **involucre** (Fig. 80A). The involucre is torn by the gradual elongation of the capsule and usually remains at the base as a tube. In *Notothylas,* which has rather short capsules, the involucre (Fig. 80K)

surrounds almost the entire capsule until the spores are mature. Internally, the hornwort capsule has a central axis of sterile tissue, the **columella** (Fig. 79A), surrounded by sporogenous tissue. The sporogenous tissue produce spores and elaters. The elaters can be multicellular, branched, with irregularly thickened walls *(Anthoceros, Phaeoceros*), or unicelular, elongated, and with discrete spiral thickenings similar to those observed in the elaters of the liverworts. The multicellular elaters of *Anthoceros* and *Phaeoceros* are sometimes called **pseudoelaters** (Fig. 79E).
Spore maturation and capsule dehiscence in the hornworts is gradual (**asynchronous**), from the apex to the base where younger parts of the capsule and the intercalary meristem are located. Dehiscence is by two valves. The capsule walls may be hygroscopic and their torsion movements contribute to spore dispersal. The spores of the hornworts are usually richly ornamented on the outer surface, with distinct trilete marks (indicating the position of the spores in the tetrad) (Fig. 80E), except in the genus *Leiosporoceros* in which they are completely smooth, lacking any trace of a trilete mark (Fig. 80M). Spore germination is exosporic except in *Dendroceros*, which has large, multicellular spores due to endosporic germination.

Vegetative reproduction
In the hornworts this occurs usually by simple vegetative multiplication, related to decay of older portions of the thallus. In *Megaceros* reproduction by means of caducous thallus segments occurs and in some Mediterranean species of *Phaeoceros* tubers are produced that may germinate into new thalli under favorable conditions. The production of these tubers is apparently an adaptation to the dry climate where vegetative thalli, with the exception of the tubers, die back during prolonged dry periods.

MOSSES

The “Musci,” commonly called mosses, are the most complex group among the bryophytes, not only because of the morphology of their gametophyte but in particular because of the complex structure of the sporophyte. Worldwide, the mosses are estimated to include about 12800 species (a more realistic figure may be 8000 species), in 900 genera. It is estimated that there are about 2600 (2300-2950) species, in 400 genera, in tropical America. Mosses are generally drought-tolerant, more so than liverworts, but they occur mainly in humid and/or shaded places. In tropical America mosses can be found in all habitats, except submerged in the sea.
Mosses are a highly diverse class of plants and the species can be morphologically very different. Some members of the subclass Polytrichidae may be nearly one meter tall whereas *Micromitrium austinii* Aust. measures about half a millimeter in height. In the field, mosses can be readily distinguished from the liverworts by their spirally arranged leaves (Fig. 7C-D) and their sporophyte. Other distinguishing characters are presented in Table 1.

Habit
Based on the location of the sporophyte, mosses are divided in two artificial groups. acrocarpous mosses and pleurocarpous mosses. **Acrocarpous** mosses produce their archegonia and sporophytes terminally at the stem top using the apical cell, usually grow erect in tufts (not in mats) or turfs, and are little-branched (Fig. 6A-C). **Pleurocarpous** mosses produce their archegonia and sporophytes laterally on stems, are generally trailing or prostrate, and may form mats, wefts, or dense tufts; they can be pendent, dendroid, or frondose (Fig. 6D-J). Pleurocarpous and acrocarpous conditions can occur within the same families and are therefore not good taxonomic characters to separate families.

Stem
The internal structure of the stem in mosses may be homogeneous or, more often, consists of an outer epidermis, a cortex, and a central strand (Fig. 6K-M). Often, the cortex is further differentiated into an outer cortex of cells with strongly thickened, darkish-pigmented walls surrounding an inner cortex of larger, thin-walled cells. The central strand is very small or absent in some species, in others it is strong, up to one third the diameter of the stem. It resembles a primitive vascular bundle and often contains a few large, thick-walled water-conducting cells, the hydroids. The Polytrichidae possess the most highly developed stems, having, in addition to hydroids, some metabolite-conducting cells or “leptoids.“ The latter are analogous to the sieve elements of the higher plants.

Branches
As opposite of liverworts, branches in mosses are usually of a single morphological kind, the *Fontinalis*-type. These branches originate from cells of the stem epidermis, usually stand at an oblique angle with the stem and do not have a collar at the base.

Leaves
Leaves show many different features and are the most important aid in the identification of the species. They are usually arranged spirally around the stem or branches; sometimes they are 2-5 ranked (Fig. 7A-E). Leaf orientation varies considerably (Fig. 7). Many pleurocarpous species have **complanate** leaves (Fig. 7O), i.e., originating from all sides of the stem but flattened out in one plane like the frond of a fern. The complanate leaf orientation may be confused with the **distichous** condition (Fig. 7P); in the latter, however, the leaves do not arise from all sides of the stem but originate in two sharp ranks.

The basic parts of the moss leaf are shown in Fig. 8D-G. The shape of the leaf is variable as in liverworts, although in mosses they are **never lobed**. Leaf outline can be ovate, lanceolate, etc. (Fig. 8A), and the apex varies from obtuse or truncate to acuminate or aristate (Fig. 8B) At the base, the leaf is sometimes decurrent or ensheathing the stem (Fig. 8C). The leaf margin can be variably toothed or entire (Fig. 10C). Sometimes there is a distinct **border** along the leaf margin, made up of cells, in one or several layers, that differ in shape from the other laminal cells. The form of the leaf in cross section can also be an important aid in identification (Fig. 10B).
Generally, the leaf lamina consists of a single layer of cells with the exception of the nerve or **costa** (midrib) which, when present, is composed of narrow and elongated cells of several layers in thickness. The costa may be single or double, short or long, **percurrent** or **excurrent**, or absent (Fig. 9A-D). In cross section, the **costa** may be homogeneous or heterogeneous (Fig. 9E-F). In the latter case, there are usually groups of thick-walled cells with very small cell lumina, the **stereids**, and of one or two rows of large **guide cells** (Fig. 9F). In a few genera like *Leucobryum, Octoblepharum*, and *Leucophanes*, the leaf is **multistratose** and composed of a central layer of chlorophyllous cells, the **chlorocysts**, that are surrounded by one or more layers of hyaline cells with pores in the cell walls, the **hyalocysts** (= **leucocysts**) (Fig. 9G). In *Sphagnum* the leaves are of one layer of cells but here narrow chlorophyllous cells (chlorocysts) alternate with large, porate hyaline cells (hyalocysts) (Fig. 9L).
Some mosses have **paraphyllia**, i.e., extremely small, filamentous, leaflike structures that arise scattered over the stem surface (Fig. 21E). Their function is to increase the photosynthetic area and improve external water conduction. Similar structures are **pseudoparaphyllia** that are of more restricted occurrence and are confined to branch buds.

Leaf cells
The leaf cells vary considerably among mosses. Cell shape, cell size, and cell arrangement within a leaf can differ considerably between genera but also within a single leaf (e.g, from base to apex). Cell shape can range from quadrate to long and narrow (Fig. 10A). Cells along the leaf margin can be different, forming a **leaf border** (Fig. 9O-P), and at the lowermost part of the leaf in the corners a group of cells, the **alar cells**, can be differentiated (Figs. 9M-N, Q-S). These can be inflated and thick-walled or quadrate, forming a distinctive triangular area from the costa to the border of the leaf. Although in most cases cell walls are evenly thickened, they can be very narrow, thick (incrassate), sinuose, porose or ornamented by **papillae** (e.g., in many Pottiaceae) (Fig. 10D). A similar structure to papillae are **mammillae**, but here the cell lumen protrudes locally above the leaf surface (e.g., in *Philonotis*). Trigones, found in liverworts, are lacking in mosses.

Rhizoids
Unlike liverworts, the rhizoids of mosses are multicellular with oblique or diagonal transverse walls, often a brown color. The cell walls of rhizoids can occasionally be papillose.

Reproductive organs
The female organs or **archegonia** are flask-shaped, the male organs or **antheridia** are club-shaped (Fig. 1A). They are surrounded by sterile uniseriate filaments (**paraphyses**), are produced from superficial cells, either at the tip of elongated shoots (acrocarps) or from abbreviated branches in the leaf axils of the stems or branches (pleurocarps). Unlike liverworts, both sex organs can occur together in the same **gametoecium**; this condition is called synoicous (Fig. 1B). Archegonia and antheridia may be surrounded by protecting,

vegetative or modified leaves. These modified leaves constitute the **perichaetium** (associated with archegonia) and the **perigonium** (associated with antheridia), respectively. Perichaetia exhibit considerable variation and are sometimes employed as a diagnostic character.

Sporophyte

The sporophyte of mosses, like that of liverworts, consists of a **capsule**, **seta,** and **foot** (Fig. 1A). The **foot** penetrates the gametophyte and serves for support and for translocation of substances to the capsule**.** The **capsule** consists of a spore-bearing urn, often with a short or long neck, and a lid or operculum. The capsule is initially protected by tissue of the venter of the fertilized archegonium; this tissue remains on top of the developing capsule as a hood-like structure, the **calyptra** (Fig. 1A, 11O). **Cucullate** calyptrae are usually split or divided on one side, more often than not they are smooth and naked (devoid of hairs); **mitrate** calyptrae are not split, often short and cover the capsule in the form of a bishop's miter; **campanulate** calyptrae are longer and cover the capsule in the form of a bell. In most cases the capsule is elevated above the gametophyte by means of a **seta** to facilitate dispersal of spores. Unlike in liverworts, the seta elongates before the capsule matures and is usually made up of thick-walled cells which contribute to the maintenance of its erect position. The length of the seta varies considerably. In *Sphagnum* and *Andreaea* the seta is lacking and the capsule is elevated by a **pseudopodium**, a leafless prolongation of the gametophytic stem. Other features of note include whether the seta is erect or flexuose or variously curved, smooth or ornamented (usually roughened, papillose or rarely spinose).

The orientation of the capsules can be erect, inclined, horizontal, or pendulous (Fig. 11C-M). They may be immersed among the perichaetial leaves or highly exserted above them (Fig. 11A-B). The urn may be symmetric or asymmetric and curved, and occasionally it is ribbed or furrowed (Fig. 11C-J).

At the junction with the seta, the capsule may possess a short neck (Fig. 11L) which is sometimes expanded into an **apophysis** (or hypophysis). The epidermal cells of the urn, the **exothecial cells** (Fig. 11Q), show considerable variation in shape and wall thickness and these characters can also be of taxonomic value. **Stomata** (Fig. 11S) often occur in the lower portion, on the neck or distributed throughout the urn. They can be exposed (superficial) or embedded in the epidermal layer of the capsule (immersed) and are rarely modified beyond the typical two **guard cells** into four or more subquadrate shaped cells

The mouth of the capsule is usually covered by a lid-like structure, the **operculum** (Fig. 11N). When present, the operculum exhibits a limited amount of variation; it can be plane (nearly flat), convex or conic, apiculate, or short to long rostrate, with the beak erect or oblique. The operculum remains united to the capsule by a group of specialized cells, the **annulus** (Fig. 11T), which allow detachment of the operculum. It is often composed of several rows of obovate cells that can adhere to the urn mouth and calyptra, or are deciduous and revoluble. The annulus is best observed when an intact mature capsule is dissected and the operculum carefully removed. Mosses with a dehiscent operculum are referred to as **stegocarpous.** Mosses which lack an operculum and peristome and which release the spores by rupturing the urn cell walls are referred to as **cleistocarpous**.

The most distinctive part of the capsule is the **peristome,** a single or double circle of teeth around the mouth of the capsule, present in most of the genera. In some groups the teeth are made of up of whole cells (**nematodontous**) (Fig. 11R). In the majority of mosses they are made up of cell walls (**arthrodontous**) (Fig. 11T-Y). In the latter, the peristome teeth are composed of paired periclinal walls or lamellae which are differentially thickened. Nematodontous peristomes are mostly of 1 circle of teeth, arthrodontous peristomes may be of 1 circle (single) (Fig. 11T) or 2 circles (double) (Fig. 11U).

In a double arthrodontous peristome the outer circle of teeth is called the **exostome**; it always consists of 16 teeth (although sometimes they are fused in pairs). The inner circle, or **endostome**, is composed of basal plates (the basal membrane) and positioned on this is a series of 16 segments often alternating with reduced structures called cilia (1-5). The double peristome is referred to as **diplolepidous**. A single arthrodontous peristome is composed of 16 teeth that are entire or perforate, or divided partially to fully to the base, thus appearing as 32 segments or teeth. This type of peristome is referred to as **haplolepidous** and is in most cases homologous to the inner circle of a double peristome. Peristome teeth offer important diagnostic characters to separate the subclasses of the mosses (see below).
Inside the capsule sporogeneous tissue in which the spores are formed and a central cylinder of sterile tissue, the **columella** (Fig. 1A), can be observed. In the Polytrichidae the tip of the columella is expanded, forming a membranelike stucture, the **epiphragm** (Fig. 11P), that nearly closes the mouth of the urn. In the subclass Archidiidae the columella is lacking. The wall of the capsule may vary in thickness. Unlike liverworts, moss capsules lack elaters and the walls do not have ring-like or nodular thickenings.
Characters of the sporophyte are employed for subdividing the Musci into seven subclasses. In many cases the common name of the subclass refers to the salient capsule character.

1. **Andreaeidae** or “lantern mosses,“ release their spores through four longitudinal slits in the capsule, thereby looking like a lantern.
2. **Sphagnidae** or “peat mosses,“ have no seta but a pseudopodium instead and a capsule which, under gas pressure built up during spore maturation, throws off the operculum violently and shoots the spores in the air (“gun shot” mechanism).
3. **Tetraphidae** or “four-toothed mosses,“ with a nematodontous peristome of four teeth each made up of numerous dead cells. This subclass is not present in tropical America.
4. **Polytrichidae** or “hair-cap mosses,“ derive their name from a hairy calyptra (but hairs lacking in some genera). The capsule mouth is closed by an epiphragm and has a ring of 32 to 64 nematodontous teeth. Spores are released through openings between the teeth, like salt from a salt shaker.
5. **Buxbaumiidae** or “bug mosses,“ have a very large sporophyte and a very minute gametophyte, so that at a first glance only the sporophyte is visible. Bug mosses are unique in having a double nematodontous peristome.
6. **Bryidae** or “jointed-toothed mosses,“ by far the largest group are characterized by an arthrodontous peristome. The spores are released through the capsule mouth and spore release may be promoted by the hygroscopic movements of the peristome.
7. **Archidiidae** or “large-spore mosses,“ have no columella, lack a seta, and release their spores through disintegration of the capsule wall.

Spores
The spores are typically spherical and ornamented, although variation exists in shape and degree of surface ornamentation. The shape can also be irregularly ovoid or trilete and the surface smooth, papillose, spinose, or pitted. Spores may germinate immediately or may be dormant for a variable period of time (one or two days to several years). Upon germination, they develop a **protonema** that may be filamentous and branched or laminar (*Sphagnum*). In some mosses, the spore upon germination gives rise to a branched filamentous, green protonema, the **chloronema**, with transversal walls perpendicular to the main axis and many chloroplasts. From this phase, new cells are formed that bear fewer

chloroplasts and have transversal walls that are diagonal or oblique. This phase is known as the **caulonema**. From the latter protonematic phase arise the foliose gametophytes.

Vegetative reproduction

Vegetative reproduction is widely distributed among mosses. Like liverworts, almost any part of the gametophyte can serve as a vegetative diaspore. Vegetative reproduction allows rapid colonization of new habitats, contributes to increasing the size of populations and may enhance species distribution.

Two types of vegetative diaspores are known in mosses, **gemmae** and **propagules** (Fig. 9J-K). Gemmae are small globose, elliptic, or cylindric bodies of a few cells. They can be produced from various parts of the gametophyte such as the apices of the leaves (*Syrrhopodon, Streptopogon*), the costa (*Tortula papillosa*), the surface of the lamina (*Tortula amphidiacea*), and the rhizoids (*Leptobryum filiforme*). Propagules are reduced buds, branches, or leaves that serve as vegetative diaspores. Propagules are produced usually in the leaf axils; they are variable in shape and often numerous.

Bryophyte distribution and conservation in tropical America

Tropical America (= Neotropics) is located between the Tropic of Cancer and the Tropic of Capricorn, stretching from Central Mexico and Cuba southwards to Bolivia, Paraguay, and southeastern Brazil. The landscape of the Neotropics is extremely diversified, including such highly contrasting areas as the hot, tropical lowland rain forests of the Amazon Basin, the extensive cordilleran system of the Andes with ice-capped peaks arising to over 6000 m, the dry savannas and scrubby vegetation of the Brazilian Planalto region, and the lush tropical islands of the West Indies.

Table 2. Bryophyte diversity in tropical America.

	Families	Genera	Species
Mosses	76	400	ca. 2600
Hepatics	41	188	ca. 1350
Hornworts	3	7	ca. 30
Total	120	595	ca. 3980

Due to the great variation in landscapes, tropical America has an extremely rich flora. There are nearly 4000 species of bryophytes (2600 mosses, 1350 hepatics, 30 hornworts), in 595 genera and 120 families, or almost one third of the world´s total bryophyte diversity (Table 2). The largest families of mosses in the Neotropics, in terms of total number of species, are the Pottiaceae, Pilotrichaceae, Dicranaceae, Bryaceae, Fissidentaceae, Macromitriaceae, Sphagnaceae, Sematophyllaceae, Hypnaceae, and Orthotrichaceae. Speciose moss genera are *Breutelia, Bryum, Campylopus, Fissidens, Lepidopilum, Macromitrium, Sematophyllum, Sphagnum,* and *Syrrhopodon*. Among hepatics, the largest family in the Neotropics by far are the Lejeuneaceae with over 400 species in 70 genera. Important genera with high numbers of species include *Bazzania, Frullania, Metzgeria, Plagiochila, Radula, Riccardia,* and *Riccia*. Tropical America is also a world center of endemism, with about 80 endemic genera of mosses and over 50 in hepatics (Schuster 1990; Gradstein & Raeymaekers, 2000). Generic endemism in the Neotropics is more than 10 times as high as in Europe and North America.

Many different regions may be recognized in the Neotropics, each with its own characteristic flora. Following Gentry (1982) and others, the following regions are recognized (Fig. 12):

1. Mexico
2. Central America
3. West Indies
4. Chocó
5 Northern Andes
6. Central Andes
7. Amazonia
8. Guayana Highland
9. Brazilian Planalto
10. Southeastern Brazil

There is no comprehensive review of the bryological exploration of tropical America. It is evident, however, that bryological exploration in tropical America has been very uneven. Some areas, e.g., the West Indies, Guianas, and the Galapagos Archipelago, have

received much more attention than others. Even today there are still areas in the Neotropics without a single bryophyte record. A brief assessment of the general state of bryological exploration in the Neotropics was given by Delgadillo M. (1982) and Matteri (1985), of particular areas by, e.g., Churchill et al. (1995b), Gradstein (1995), and Griffin and Gradstein (1982) for the Andes, by Florschütz-de Waard (1990) and Gradstein and Hekking (1989) for the Guianas, and by Lisboa (1991) for the Amazonian area of Brazil.
In this chapter, brief descriptions are provided of the physiographic and bryological characteristics of the regions, together with a brief assessment of the importance of each region for bryophyte conservation (see also Box 1) and citation of important literature. References cited are of two kinds:1) important recent papers, which provide references to older literature, 2) older works that are still relevant. An important source of information that appeared after completion of the manuscript and could not be consulted is the following: S. Davis et al. 1977, Centers of Plant Diversity Vol. 3: the Americas. WWF, IUCN.
Conservation importance of the region is evaluated based on the occurrence of endemic genera (Table 3) and threatened species. Important sources on endemic genera are the papers by Delgadillo M. (1994) on neotropical mosses and by Schuster (1990) on hepatics. Three categories are recognized: "endemic genera," "subendemic genera," and "other characteristic genera" (Table 3), **Endemic genera** are only known from one single region in the Neotropics, **subendemic genera** are known from 2(-3) adjacent regions, **other characteristic genera** are known from one single region but occur also in other parts of the world.
Data on threatened species are from the papers by Gradstein (1992b) on threatened bryopytes of neotropical rain forests and by Delgadillo M. (1996) on endangered mosses of Mexico. Following Gradstein, two categories may be recognized. "endangered species," and "rare species." **Endangered species** are narrowly endemic species known from only a few (1-3) localities, in areas undergoing rapid deforestation, e.g., Mexico, Central America, the West Indies, western Ecuador, the outskirts of the Amazon Basin, the Andes, and Southeastern Brazil (Groombridge, 1992; Myers, 1983). **Rare species** are narrowly endemic species known from areas not threatened with immediate deforestation such as inner Amazonia and the Guianas, and species occurring over a wider range that are nowhere common. The number of known localities of "rare" species is usually less than 10.

Table 3. Number of genera and species, endemic genera, subendemic genera, and other characteristic genera of the neotropical regions. For explanation see text.

Region	**Number of genera / species** Hepatics	Mosses	**Endemic genera**	**Subendemic genera**
Mexico	124 / ?	286/891	H none M *Acritodon* *Anomobryopsis* *Curviramea* *Cygniella* *Florschuetziella* *Hymenolomopsis* *Nematocladia* *Pringleella*	H none M *Bryomanginia* *Dendropogonella* *Jaffeuliobryum* *Pseudopohlia* *Synthetodontium*

Central America	141 / 600	275/870	H none M *Ceuthotheca* *Fabronidium*	H *Campanocolea* *Fulfordianthus* *Lindigianthus* *Ruizanthus* *Szweykowskia* M *Bryomanginia* *Dendropogonella* *Hydropogonella* *Pseudopohlia* *Stenodictyum* *Synthetodontium*
West Indies	120/?	228/500	H *Amblyolejeunea* *Leiolejeunea* *Physantholejeunea* *Phycolepidozia* *Steereella* M *Diploneuron* *Hookeriopsis* *Teniolophora*	H *Cephalozia* subgen. *Macrocephalozia* M *Hyophiladelphus* *Macrodictyum* *Weissiodicranum*
Chocó	70 / ?	82/150	H *Luteolejeunea,* M none	H *Cephalozia* subgen. *Macrocephalozia* *Fulfordianthus* L*ejeunea* subgen. *Prionoc* M none
Northern Andes	145/800	270/ 1200-1400	H *Chaetocolea* *Leptoscyphopsis* *Myriocolea* *Platycaulis* *Pseudocephaloziella* *Rhodoplagiochila* *Paramomitrium* *Sphaerolejeunea* M *Allioniellopsis* *Gradsteinia* *Kingiobryum* *Sphagnum* Sect. *Cuculliforme* *Stenodesmus* *Timotimius*	H *Campanocolea* *Lejeunea* subgen. *Prionoc* *Mytilopsis* *Ruizanthus* *Szweykowskia* S*tephaniellidium* M *Callicostellopsis* *Dendrocryphaea* *Lindigia* *Stenodictyon*
Central Andes	105 / ?	265/ 1200-1400	H none M *Aligrimmia* *Coscinodontella* *Flabellidium* *Gertrudiella* *Koponenia* *Leptodontiella* *Mandoniella* *Polymerodon* *Pseudohyophila* *Schroeterella* *Sphagnum*	H *Stephaniellidium* M *Bryomanginia* *Callicostellopsis* *Dendrocryphaea* *Jaffueliobryum* *Lindigia* *Stenocarpidiopsis*

			Sect. *Inretorta* *Streptotrichum* *Trachyodontium*	
Amazonia	87/400	101/311	H *Cephalantholejeunea* *Neopotamolejeunea* *Protocephalozia* *Pteropsiella* *Schusterolejeunea* *Verdoornianthus* M *Colobodontium* *Hydropogon*	H none M *Hydropogonella* *Macrodictyum*
Guayana Highlan	89 / ?	95/200	H *Haesselia* *Vanaea* *Odontoseries* *Trabacellula* M *Holomitriopsis* *Steyermarkiella*	H *Mytilopsis* *Micropterygium* M none
Brazilian Planalto	61 / ?	116/ ?	H none M none	H none M none
Southeastern Bra	130 / ?	242/ ?	H *Pluvianthus* *Vitalianthus* M *Cladostomum* *Crumuscus* *Itatiella* *Moseniella* *Paranapiacabaea*	H *Bromeliophila* *Myriocoleopsis* M *Philophyllum*

Survey of the bryophyte regions

1. MEXICO

Mexico lies on the border of the temperate Northern Hemisphere and the Tropics, and is highly mountainous. In the north, the country is dissected by two large mountain ranges, the Sierra Madre Occidental and the Sierra Madre Oriental, running parallel to the coast and enclosing a high, semidesertic plateau. In the center of the country, in the area of Mexico city, these ranges are crossed by volcano chains - beyond, they run southwards as a single range. Only the eastern tip of the country, the Yucatan Peninsula, is a low-lying flat area. The highest elevation in Mexico is Pico Orizaba (5610 m).

Due to its location and elevational variation, Mexico contains an extremely diverse flora; the country is a meeting point of temperate and tropical elements. The tropical part, extending east of the Isthmus of Tehuantepetec (Oaxaca, Chiapas, Yucatan Peninsula) and covering about one third of the country, has evergreen rain forests and deciduous forests. The rain forests, once forming a corridor from Veracruz to Chiapas, have largely disappeared except in the south near the border of Guatemala (Selva Lacandona). Nowadays, deciduous forests occurring in areas with a pronounced dry season are the most common tropical forest type of Mexico.

Conservation importance.

Hepatics. The northernmost occurrence of many neotropical rain forest species is in Mexico. In terms of hepatics, the abundance of drought-tolerant thalloid hepatics is

particularly characteristic of the country. Mexico is the neotropical center of diversity of the family Aytoniaceae (*Asterella*, *Cryptomitrium*, *Plagiochasma, Reboulia)*. The occurrence of holarctic species reaching their southernmost distributional limits in the mountains of Mexico is a further characteristic of the Mexican bryophyte flora.
Mosses. Keeping in mind that only the southern half of the country lies within the neotropical realm, the composition of the flora appears to be a near equivocal mixture of elements of the Northern and Southern Hemispheres. Semi-xerophytic and xerophytic elements are a conspicuous component to the Mexican moss flora with such families as the Pottiaceae contributing significantly to the overall diversity, and to a lesser extent the Erpodiaceae and Grimmiaceae, among other families. Approximately 9% or 98 species of the mosses of Mexico are endemic and the following 14 endemic species were listed as endanged or in need of protection. *Acritodon nephophilus*, *Anomobryum tereticaule*, *Astomiopsis exserta*, *Brachymenium murale*, *B. saint-pierrei*, *Bryoceuthospora mexicana*, *Dicranum lophoneuron*, *Fissidens obscurocostatus*, *Floribundaria schenckii*, *Hymenolomopsis tolucensis*, *Jaffueliobryum arsenei*, *Oreoweisia mexicana*, *Pseudotaxiphyllum richardsii*, and *Synthetodontium pringlei* (Delgadillo M., 1996). Six further endemic species are only known from the original type collection.
Important literature.
Hepatics. Bourell (1992); Fulford & Sharp (1990); Gradstein & Váña (1994); Gottsche (1863).
Mosses. Bourell (1992); Cárdenas S. (1988); Delgadillo M. (1978, 1979, 1984, 1990, 1993, 1996), Delgadillo M. & Cárdenas (1995); Durán et al. (1992); Sharp et al. (1994).

2. CENTRAL AMERICA
Central America includes the countries of Guatemala, Belize, Honduras, El Salvador, Nicaragua, Costa Rica (including Cocos Island), and Panama. Highest elevations are Volcán Tajumulco, Guatemala, 4220 m; Mt. Chirripó, Costa Rica, 3820 m. Central America constitutes a narrow bridge between the giant landmasses of North America and South America and is made up of a chain of volcanos, many of which are still active. The eastern slopes of the mountains, bordering the Caribbean, are very moist due to their exposure to the moisture-laden trade-winds and are covered by evergreen rain forests. The western, Pacific slopes are normally drier, especially below 1000 m, being located in the rain shadow; they are mainly covered by deciduous woodlands and scrub. In the south however, towards the Chocó region, the Pacific coastal climate becomes wetter; moist evergreen forests are found here (e.g., Osa Peninsula, Costa Rica).
Central America is made up of two high mountain regions, a northern and a southern one, separated by the Nicaraguan depression. The northern part (Guatemala, Honduras) is characterized by the occurrence of many holarctic species reaching their southernmost limit of distribution here. The southern part (Costa Rica, Panama) is characterized by the great number of Andean taxa reaching their northernmost extent. The mountain forests of Central America are usually dominated by oak or in the north, by pine. Above the tree line, alpine vegetations called "zacatonal" in the north and "páramo" in the south occur.
Conservation importance.
Hepatics. With respect to total number of genera Central America is the second richest area in the Neotropics (141 hepatic genera recorded), surpassed only by the northern Andes. None of the Central American hepatic genera are endemic to the region, however. There are five subendemic genera, which occur mainly in the southern part of Central America, viz. Costa Rica and Panama. These countries have six endangered endemic species including the liverworts *Fulfordianthus evansii* and *Nowellia reedii,* and four species of mosses (see below).

Mosses. The Central American moss flora, with an estimated 267 genera and 870 species, is characterized by a predominately tropical element but with a significant number of north temperate taxa. Species endemism, based on the first volume of the Moss Flora of Central America (Allen, 1994) was estimated at ca. 10% (20 of 203 species) which implies that for the entire moss flora, about 80 to 90 species may be endemic to the region. Species that have been listed as rare or endangered include *Brymela tutezona* from Panama (now represented by several collections); *Syrrhopodon isthmi* from Panama, Colombia, and Ecuador (see discussion under Chocó); *S. theriotii,* and *Campylopus atlanticus*.

Important literature.

Hepatics. Dauphin (1999); Dauphin et al. (1998); Gradstein et al. (1994), Gradstein et al. (2000), Gradstein & Váña (1987); Herzog (1938a, 1951); Morales (1991); Sillet et al. (1995); Stotler et al. (1998); Whittemore & Allen (1996).

Mosses. The region is now being treated as a whole in a monograph entitled *Moss Flora of Central America* (Allen, 1994, 2000). The first volume of at least four was published in 1994, and the second volume will appear in the Fall of 2000. Previously checklists have been published for most of the seven countries, but all are now dated. The publication on the mosses of Guatemala by Bartram (1949), which served as the standard introductory text for students first learning neotropical mosses, is dated but still a very useful illustrated treatment. Keys to the genera of mosses from Costa Rica by Griffin and Morales (1983) is the only such treatment and useful throughout much of Central America. Other important references are: Allen & Snider (1983); Arrocha, (1992); Bartram (1928, 1929, 1932, 1934, 1950); Bowers (1970, 1974); Breen & Reese (1971); Crosby (1969a, 1971a, 1974); Crosby & Crum (1967); Crum (1950, 1952a, b, 1968); Crum & Richards (1984); Gradstein & Salazar Allen (1992); McQueen (1995); Morales & Griffin (1987); Reed & Robinson (1971); Salazar Allen & Crosby (1985); Salazar Allen et al. (1991); Sillett et al. (1995); Steere (1934, 1937, 1946); Steere & Chapman (1946); Townsend & Allen (1998); Winkler (1965); Wolfe & McQueen (1992).

3. WEST INDIES

The West Indies can be subdivided in two subregions: the Greater Antilles with the Bahamas, and the Lesser Antilles. The Greater Antilles comprise Cuba, Jamaica, Haiti, the Dominican Republic, Puerto Rico, and the Virgin Islands. Highest elevation: Pico Duarte, Dominican Republic, 3175 m. The Greater Antilles are a group of large, continental islands in the northern part of the West Indies that are remnants of an ancient landmass. There are no signs of volcanic activity. The islands have a very rich flora, reflecting the great diversity of habitats on the islands as well as their complicated geological history. The lowland areas are usually dry and covered by thorny bushes or woodland remnants; in the mountains there are luxuriant cloud forests. Alpine vegetation is restricted to the highest elevations of the Dominican Republic. The islands share many species with other neotropical regions and, additionally, with North America. The archipelago of the Bahamas has an origin different from that of the Greater Antilles and is usually treated as a separate subregion of it. However, the bryophyte flora of the Bahamas is not very rich and scarcely different from that of the Greater Antilles.

The Lesser Antilles comprise the Leeward islands (e.g. Saba, St. Eustatius, St. Kitts and Nevis, Montserrat, Antigua), Windward islands (Guadeloupe, Dominica, Martinique, St. Lucia, St. Vincent, Barbados, Grenada), Trinidad and Tobago, and the southern Dutch Antilles (Curaçao, Aruba, Bonaire). Highest elevations: La Soufrière, Guadeloupe, 1467 m; Morne Diablotin, Dominica, 1447 m; Mt. Pelée, Martinique, 1397 m. The Lesser Antilles are a group of small islands, mainly of volcanic origin unlike the Greater Antillean islands, are of oceanic origin and not remnants of an ancient landmass. They are disposed in an

arc between the northeastern angle of the South American continent and the eastern extremity of the Greater Antilles. The islands are covered by a lush vegetation - including scrub, savanna, montane rain forest, various coastal formations, etc. - that is heavily affected by the frequent hurricanes arising in the southern Atlantic Ocean.
Conservation importance.
Hepatics. The hepatic diversity of the West Indies includes about 120 genera. Five threatened species occur in the West Indies. A particularly critical area is eastern Cuba, which has at least two endangered taxa. *Drepanolejeunea senticosa* and *Nowellia wrightii.* It is also one of the few areas where the rare *Neurolejeunea catenulata* has been collected in recent years. The forests of Dominica, the wettest and most densely wooded island in the West Indies, are affected by hurricanes about once every 15 years and were seriously damaged in 1979 by Hurricane David. The genus *Phycolepidozia,* with only one known species, is endemic to the forests of Dominica and considered endangered. It was collected there first in 1966 and has not been sighted since. Another potentially endangered genus of the West Indies is *Amblyolejeunea,* known only from the lush cloud forests of the southwestern part of Basse Terre, Guadeloupe.
Mosses. Moss diversity of the West Indies is, as might be expected of insular floras, rather moderate; possibly on the order of 500 or less species. No estimate of the number of endemic species is available, but one may expect a figure of 5-10%. A significant number of endemic *Pilotrichum* species are found in the West Indies (Crosby, 1969); of 13 species occurring in the region, 10 are endemic.
Important literature.
Hepatics. Evans (1911); Fulford (1987); Gradstein (1989); Jovet-Ast (1947-50); Pagán (1942); Pócs (1988); van Slageren (1979).
Mosses. A treatment is now in preparation for the entire region by W. R. Buck (New York Botanical Garden), with the first volume of two, covering the pleurocarpous mosses, published in 1998. Previous floras and florulas for several of the islands include Guadeloupe (Foucault, 1977), Jamaica (Crum & Bartram, 1958), Puerto Rico (Crum & Steere, 1957), Saba and St. Eustatius (Wiersma, 1984). Other important references for the mosses are: Bartram (1955, 1956); Bescherelle (1876); Bizot (1965, 1973); Buck (1990a); Buck & Steere (1983); Crosby (1969b, 1970, 1971b); Crum (1965); Duarte B. (1973); Florschütz (1967); León (1933); Motito et al. (1992); Reese (1991); Russell & Miller (1977); Salto (1941); Sastre-De Jesús (1992); Sastre-De Jesús & Buck (1993); Schubert (1978); Serrano (1996); Steere (1985); Townsend (1994); Welch & Crum (1959, 1969); Zündorf (1989).

4. CHOCÓ

The Chocó includes the lowland regions, up to 500 m in elevation, along the Pacific coast of Ecuador and Colombia. It is the wettest region of the Neotropics, having an annual rainfall of over 10000 mm, and is largely covered by lowland rain forests. Endemism in the vascular plant flora is high. Due to the everwet climate, hepatics are much more prominent in the Chocó than mosses and account for almost 90% of the bryophyte cover in the forests (Frahm, 1994; Gradstein, in prep.). The flora of the region resembles that of southern Central America, many Chocó species reach their northernmost limit of distribution in Costa Rica, especially in the Osa Peninsula. Others extend northeastwards to the Napo region of Ecuador (e.g., *Fulfordianthus pterobryoides*, *Syrrhopodon isthmi*).
Conservation importance.
Hepatics. Nine threatened species occur in this floristically very rich area, including three endangered ones: *Drepanolejeunea spinosa* (Colombia), *Leptolejeunea tridentata* (Colombia), and *Spruceanthus theobromae* (Ecuador). No hepatic genera are endemic to the Chocó but *Fulfordianthus* and *Luteolejeunea* are subendemic, extending northwards to

Central America. Both are very common in the Chocó even though they have been little collected. Obviously, the region is underexplored and much more fieldwork is needed to properly assess the conservation importance of the hepatic flora.
Mosses. The number of mosses is unknown, but is not likely to exceed 150 species. The majority of species have been treated in a limited fashion by Churchill and Linares (1995). No moss genera are endemic to the Chocó. Only a few species are restricted to this region; these include from Colombia *Fissidens cylindrothecus*, *Holomitrium aberrans*, and *Lepidopilum permarginatum*; and finally from Ecuador and Colombia and confined to the premontane or higher montane belt *Schliephackea prostrata*. *Syrrhopodon isthmi*, previously listed as a potential Chocó element, is now also known from Napo province of Ecuador. Families that are well represented in the Chocó include the Calymperaceae, Fissidentaceae and Pilotrichaceae.
Important literature.
Hepatics. Gradstein (in prep.); Herzog (1955).
Mosses. Churchill & Linares C. (1995); Frahm (1994).

5. NORTHERN ANDES (including Galapagos Islands)
The northern Andes include the Andean mountains of Eastern Venezuela, Colombia, Ecuador, and northern Peru (north of 8° S), above 500 m. Highest elevations: Mt. Chimborazo, Ecuador, 6267 m; Sierra Nevada de Santa Marta, Colombia, 5775 m. The northern Andes are very complex geomorphologically and are made up of numerous snow-capped volcanos, covered with lush montane forests and humid alpine vegetation called "páramo." In Ecuador the Andes is made up of two distinct cordilleras, separated by a broad and densely inhabited interandean valley; in Colombia the cordilleras are split into three distinct massifs, the Eastern, the Central and the Western cordillera. The cordilleras of Colombia are separated from each other by two deep river valleys, the Río Magdalena in the east and the Río Cauca in the west. The interandean valleys are usually hot and dry, the outer slopes bordering Amazonia and the Pacific coast (Chocó) are usually very wet, becoming dry only in the northeast bordering the savannas (llanos) of NW Colombia and Venezuela, and in the southwest towards the Peruvian coast.
Because of the great climatic and elevational variation, the northern Andes has a highly diverse vegetation and flora. The montane forests and the páramo with its bizarre life-forms, including the stem-rosettes of the genus *Espeletia* (Compositae), are a center of diversity for many groups of plants. Unfortunately, much of the forest has been cleared or damaged and large parts have been put into cultivation for cattle grazing or altered into coffee plantations or potato fields.
The Galapagos Islands (highest elevation 1707 m) are treated here as a subregion of the northern Andes. The bryophyte flora of the archipelago is relatively well-explored and is composed of an interesting mix of species from the adjacent mainland of South America and from the Caribbean islands. Due to the rather mesic climate, typical rain forest taxa are scarce; drought-tolerant members of the Marchantiales and Jungermanniales predominate. Most of the bryophytes occur at higher elevations, in the montane woodlands. The deserted coastal areas are very poor in species and are mostly inhabited by thalloid hepatics and small acrocarpous mosses. Interestingly, endemism is higher in the dry coastal areas than in the montane habitats (Gradstein & Weber, 1982).
Conservation importance. The northern Andes is the richest region in the Neotropics in terms of species and endemic taxa. About 40000 species of flowering plants have been recorded, compared with 30000 in the Amazon Basin, an area 20 times larger than the northern Andes (Henderson et al., 1991). Since the northern Andes are now almost completely deforested, with less than 10% of the forests remaining (in contrast, about 88% of the Amazonian forests are still intact), this region is a priority area for conservation.

Hepatics. The northern Andes has the largest number of hepatic genera and the highest rate of endemism in the Neotropics (145 hepatic genera, of which 8 are endemic and 6 subendemic). Several endemic genera are from one or two collections. This suggests that much more work is still needed to arrive at a proper understanding of bryophyte diversity of the region. The area is rich in Gondwanalandic groups that have their widest expansion in temperate regions of the Southern Hemisphere, recurring at high elevations in equatorial regions. Endangered species include *Drepanolejeunea spinosa* (Colombia), *Sphaerolejeunea umbilicata* (Colombia), and *Myriocolea irrorata* (Ecuador). The latter species occurs on the lower slopes of the Ecuadoran Andes, bordering Amazonia, an area where the forest is under considerable pressure. *Myriocolea irrorata* and the moss *Fissidens hydropogon* were discovered more than a century ago and have not been collected since. An intensive field search in potentially suitable habitats is urgently needed to ascertain the continued existence of these rare taxa. Fifteen species of hepatics are endemic to the Galapagos Islands, among them 2 species of *Frullania*, 3 species of *Riccia* and several species of *Plagiochila*. There are no genera or subgenera unique to the archipelago.

Mosses. Moss diversity in the northern Andean countries (Venezuela, Colombia, Ecuador) is estimated at 1200-1400 species. Families that are notably diverse, as compared to the central Andes, include the Dicranaceae, Daltoniaceae, Pilotrichaceae, Sematophyllaceae, and Sphagnaceae. The páramo life zone contains approximately 543 species (Churchill & Griffin, 1999); a significant number of páramo mosses also extend downslope into the open montane forests. The Galapagos Islands, included here, contain about 103 species of mosses, six of which are considered endemic. There are about 370 species presently recognized as endemic to the northern Andes. How many of these will prove to be “good” species and endemic is difficult to determine; a reasonable estimate may be on the order of 200 or more. *Fissidens hydropogon* and *Lepidopilum grevilleanum* have both been proposed for the Red List (Tan et al. 1994); to that list should be added two Ecuadoran species, *Allioniellopsis cryphaeoides* and *Sorapilla sprucei*. Examples of selected taxa of note are: *Dendrocryphaea*, primarily distributed in southernmost South America with a single species in the Neotropics, *D. latifolia* from Colombia; *Eobruchia*, one from Ecuador, *E. ecuatoriana*, and another from southeast Brazil; and *Sorapilla* consisting of two species, one from Ecuador, *S. sprucei* (known only from the type collection) with a further species recorded from New Guinea.

Important literature.

Hepatics. Gradstein & Hekking (1979); Gradstein (1995, 1998, 1999); Gradstein & Weber (1982); Léon V. et al. (1998); Mägdefrau (1983); Schultze-Motel & Menzel (1987a); Schuster (1978-1991); Spruce (1884-1885); Uribe & Gradstein (1998); Wolf (1993a,b,c; 1995).

Mosses. Balslev & de Vries (1982, 1991); Bermúdez R. (1978); Castillo L. et al. (1994a,b); Churchill (1989, 1991, 1994, 1996), Churchill & Griffin (1999); Churchill & Linares C. (1995); Churchill et al. (1995a,b); Churchill et al. (2000); Cleef (1981); Gradstein & Weber (1982); Gradstein et al. (1989); Griffin (1975; 1977a,b; 1979a; 1982); Griffin et al. (1973); Linares C. (1988); Leerdam et al. (1990); López Figueiras (1976); Moreno (1992a,b); Pursell (1973, 1977); Pursell & Crusco de Dall’Aglio (1978); Ramírez Reyes & Bowers (1975); Ramírez Reyes & Crusco de Dall’Aglio (1981); Reenen & Gradstein (1984); Reese & Bermúdez R. (1980); Robinson (1986); Rudas & Aguirre C. (1990); Schultze-Motel & Menzel (1987); Steere (1948); Sturm & Rangel (1985); Weber (1993); Wolf (1993a,b,c, 1995).

Box 1. Conservation needs

A global "Action Plan" for the protection of endangered bryophytes and bryophyte habitats has been prepared by the Bryophyte Specialist Group of the International Union for the Study and Conservation of Nature, IUCN (Hallingbäck et al, 2000). The following is a short list of issues that may be taken into consideration when promoting bryophyte conservation in tropical America.

Inventories. Systematic collecting of bryophytes in tropical America started over 200 years ago. Areas that should receive inventory priority include large parts of the Chocó region, the northern Andes, the eastern slopes of the Andes, the hepatic flora of the Central Andes, portions of Amazonia, southeastern Brazil, and Central America. Based on these inventories, national or regional **Red Lists** can be developed.

Centers of Bryophyte Diversity. Taking into consideration that conservation action should focus on those areas which are the most important for their bryophytes, Centers of Bryophyte Diversity should be identified. These areas, if conserved, would safeguard not only the greatest number of species but also the evolutionary novelties.

Ecological Research. As indicated in the next chapter, bryophytes play an important role in tropical ecosystems. Nevertheless, very little ecological research, crucial to the sustainable management of these ecosystems, has been done. There is an urgent need for research on communites and succession - including studies of forest canopies and ecosystem disturbance - and of hydro-ecological research on bryophytes in moist tropical forests.

Training and Education. In order to facilitate inventories and ecological research, there is an urgent need to provide adequate training facilities to undergraduate and graduate students in tropical America and to promote the appointment of bryophyte taxonomists at botanical research centers in the area. This includes better access to the bryological literature and the establishment of bryological herbaria.

Bryological Herbaria. Herbaria are the botanical archives of biodiversity, and are crucial centers for taxonomical research, floristics, ecology, and all conservation actions. There is an urgent need to donate reference specimens or duplicates of collected material to these institutions and to hire well-trained personnel to maintain and study the collections.

Awareness promotion. Bryophytes are not well known to the public at large. Their presence and their role in tropical ecosystems should be displayed well and awareness-raising programmes, e.g., visitor trails in national parks highlighting bryophytes, videos, press coverage of bryological symposia, etc. should be promoted where possible.

Exploitation of bryophytes. More and more bryophytes are being harvested in the wild for horticultural or other purposes. So far this exploitation has not yet resulted in a documented threat to specific species or genera, but there is a need to monitor bryophyte exploitation and to exchange information on this issue. Restrictions on exploitation, at least in protected areas, may be necessary and *in vitro* cultivation should be promoted where feasible. Bryophytes are not listed on one of the appendixes of CITES (Convention on International Trade of Endangered Species); even so, monitoring of possible international trade should be considered.

Legal Protection of Bryophytes. In tropical America, endangered bryophytes species are not legally protected. Since such a strict protection of species is very difficult to enforce, habitat protection by means of designation of protected areas is an appropriate alternative for the conservation of most bryophytes.

6. CENTRAL ANDES

The Central Andes (or "southern tropical Andes" of some authors) include the Andean mountains of Peru south of 8° S, Bolivia, and northern Chiloe/Argentina, and are situated above 500 m. Here, the Andes reaches the widest and most complex section. It is composed of a series of mountain chains or cordilleras, reaching its highest elevation in the "Cordillera Blanca" of Central Peru (Huascaran, 6768 m, highest point in tropical America). A wide interandean valley or "altiplano" separating the two major cordilleras in southern Peru and Bolivia, at an elevation of about 4000 m, is the location of the Lago Titicaca, the largest high-mountain lake in the world. Probably the most striking feature of the Central Andes are the great contrasts in climate, the Pacific slopes being extremely dry and desertic while the Amazonian slopes are very green and covered by lush tropical montane vegetation. Above timberline, the climate is again relatively dry and the vegetation consists mainly of grasslands called "puna" (the northern part of Peru, north of 8° S, has humid "páramo" vegetation and is therefore included in the Northern Andes rather than in the Central Andes). In sheltered places, patches of arboreal vegetation dominated by *Polylepis* (Rosaceae) occur in these grasslands, especially at the base of steep-sided valleys. The large stem-rosette life forms (*Espeletia*) typical of the páramos of the northern Andes are completely absent in the puna.

Conservation importance.

Hepatics. The known hepatic flora of the Central Andes is rather poor as compared with other regions (105 genera, none endemic and only 1 subendemic), due possibly to the dry climate in large parts of the region but also to the lack of exploration. *Chonecolea andina* (known from Cuzco) is endemic and almost all neotropical records of the family Cleveaceae (*Athalamia*, *Mannia*, *Sauteria*) are from the Central Andes. The northern Andean endemic genus *Chaetocolea* reaches its southernmost limit of distribution in the humid mountains of northern Peru and is not (yet) known to occur in the Central Andes.

Mosses. The central Andean countries (Peru and Bolivia) are now estimated to contain about 1200 species. While many of the “endemics” will likely be synonymized, the region, particularly in Peru, still remains poorly explored and additional species will be recorded. The families Grimmiaceae and Pottiaceae, both well adapted to xerophytic environments such as the open montane and puna, are particularly rich in species and genera in the central Andes as compared to the northern Andes. At present there are about 417 endemic moss species recorded for the Central Andes. It is anticipated that at least half will likely prove to be synonyms or reflect a broader geographical distribution.

Important literature.

Hepatics. Hegewald & Hegewald (1985); Herzog (1916, 1920); Menzel (1984); Salazar Allen & Gradstein (1997); Schultze-Motel & Menzel (1987a).

Mosses. Churchill (1996); Churchill et al. (1995a,b); Churchill et al. (2000); Frey (1987); Hermann (1976); Herzog (1909, 1910; 1916, 1923); Lewis (1990, 1991); Menzel (1992); Menzel & Schultze-Motel (1987); Reese (1979); Schultze-Motel & Menzel (1987); Timme (1985); Young & León (1990).

7. AMAZONIA

Amazonia includes the vast, 8 million km² lowland area (below 500 m) drained by the Amazon and Orinoco river systems and covers parts of Brazil, Venezuela, Colombia, Ecuador, Peru, Bolivia, and the Guianas. The bryologically little known Orinoco basin is included here in Amazonia because there is no bryofloristic evidence separating the two. The Guianas, comprised by the three countries Guyana (formerly British Guiana), Suriname, and French Guiana, is also treated as part of Amazonia (Gentry, 1982) with exception of the areas above 800 m, which are part of the Guayana Highland. The

Guianas are bryologically one of the better known regions of the Neotropics and are (still) largely covered by undisturbed rain forests.
Conservation importance.
Hepatics. Although the total number of genera is not so high, Amazonia is an important center of diversity with 6 endemic hepatic genera. All these are terrestrial or rheophytic taxa, with the exception of the epiphytic genus *Verdoornianthus*. Inner and northern Amazonia, and the adjacent slopes of the Guayana Highland and the Andes are a center of endemism for lowland rain forest species. Seventeen endemic bryophyte species, most of them hepatics, have been identified as threatened. Since deforestation in many portions of Amazonia is not (yet) alarming, the threatened taxa are mostly classified as rare (Gradstein, 1992b). The hepatic flora of the Guianas is very similar to that of the rest of Amazonia but is slightly richer in genera. This richness is probably due to the somewhat more rugged topography, with numerous inselbergs (rising to about 800 m) as well sandstone-capped table mountains - remnants of the ancient Guayana shield - being present in the area. Almost 400 species have been reported (Gradstein & Hekking, 1989), the majority of them Lejeuneaceae, which is the most important bryophyte family in equatorial lowland areas. There are many more hepatics than mosses. In spite of this rich diversity, the hepatic flora of the Guianas is mainly made up of widespread species and has virtually no endemics. There are only 1-2 doubtful endemic species and one endemic variety (*Stictolejeunea balfourii* var. *bekkeri*).
Mosses. Moss diversity in Amazonia is relatively low. Although for any particular site as many as 40-50 species may be found, an increase in additional species from site to site is low; in other words species turnover is low between sites. The majority of the species are widespread in the Neotropics. Two families are conspicuously diverse in these equatorial lowland areas, Calymperaceae (*Calymperes*, *Syrrhopodon*) and Fissidentaceae (*Fissidens*). Additional diverse families include Pilotrichaceae and Sematophyllaceae, and less so the Dicranaceae, Hypnaceae, Leucobryaceae, and Macromitriaceae. The largest geographical region in the Neotropics, the Amazon Basin (in the strict sense) contains 311 species (Churchill, 1998). Four families, Pilotrichaceae, Calymperaceae, Fissidentaceae, and Sematophyllaceae, account for nearly 50% of the total Amazonian moss diversity. The Guianas (French Guiana, Guyana, and Suriname) contain 238 species (Florschütz-de Waard, 1990). Species endemism in the region is low, probably on the order of about 5% or less. Three species of *Calymperes* have been categorized as rare or endangered, *C. mitrafugax*, *C. platyloma*, and *C. smithii*.
Important literature.
Hepatics. Boggan et al. (1997); Cornelissen & Ter Steege (1989); Florschütz-de Waard & Bekker (1987); Gradstein & Hekking (1989); Gradstein et al. (1990); Griffin (1979b); Montfoort & Ek (1990); Spruce (1884-1885); Vital & Visnadi (1994); Yano (1984, 1989).
Mosses. Boggan et al. (1997); Buck (1990b); Churchill (1994, 1998); Churchill et al. (1992); Cornelissen & Ter Steege (1989); Florschütz (1964); Florschütz-de Waard (1986, 1990, 1996); Florschütz-de Waard & Bekker (1987); Griffin (1979b); Lisboa (1976, 1991, 1993); Montfoort & Ek (1990); Onraedt & Cremers (1980); Richards (1953); Yano (1981, 1989, 1995).

8. GUAYANA HIGHLAND

The Guayana Highland is made up of large, sandstone-capped table mountains or "tepuís" that are remnants of the ancient Guayana shield, stretching from eastern Colombia to Suriname, across the interior of Venezuela and Guyana (Pakaraima Mts). Highest elevations: Mt. Neblina, 3045 m; Mt. Roraima, 2772 m. The mountains are famous for their rich endemic vascular flora (Steyermark et al., 1995).
Conservation importance.

Hepatics. The number of hepatic genera (89) is rather low but endemism is high. In fact, the Guayana Highland is the second most important center of endemism in the Neotropics for hepatics with 7 endemic or subendemic genera, including highly evolved taxa such as *Haesselia* and *Trabacellula* (Cephaloziaceae), *Vanaea* (Jungermanniaceae) and *Odontoseries* (Lepidoziaceae). The region is also the center of diversity of *Micropterygium* (Lepidoziaceae), a neotropical genus of 18-19 species more than half of which are endemic to the Guayana Highland. The hepatic flora of these tepuís has been little investigated and there is probably still ample opportunity for discovery of new species and even genera.

Mosses. Moss diversity in the Guayana Highland is likewise relatively low, probably not exceeding 200 species, and endemism seems to be lower than in hepatics. There are 2 endemic genera, both belonging to the Leucobryaceae. *Holomitriopsis* and *Steyermarkiella*. Species endenism is not known, but anticpiated to be low with the exception of the genus *Sphagnum*. *Leucomium steerei* has been listed as threatened. The tepuís have attracted a number of field botanists, and in recent years many have been explored for mosses. Given the climate (cool and wet) and habitat conditions one might reasonably consider the summits ideal for mosses, but as noted by Buck (1988) moss diversity on the summits is low, probably not much beyond 70 species. Buck postulated that spores, gemmae, and propagula derived from the lowlands via prevailing winds from the south (Amazonia) consist of species ill-adapted for survival on these summits. Evidence in support of this theory is based on the presence of lowland and some highland species found in large sinkholes where conditions are more favorable.

Important literature.

Hepatics. Fulford (1967, 1971); Gradstein & Florschütz-de Waard (1989); Robinson (1986).

Mosses. Buck (1988); Gradstein & Florschütz-de Waard (1989); Pursell (1973).

9. BRAZILIAN PLANALTO

The Brazilian Planalto includes the vast cerrado-caatinga region lying between Amazonia and the moist Atlantic coastal region of SE Brazil. Geologically, the Planalto is part of the ancient Brazilian plateau, formed of Precambrian crystalline rock and separated from the ancient Guayana Highland region by the threshold through which the Amazon River flows. The region is relatively low and barely exceeds 1000 m in elevation. The climate is mostly arid and the vegetation exists of dry, thorny brush ("caatinga") in the north and savannas and deciduous woodlands ("cerrado") in the south. Only on the higher slopes exposed to the trade winds are rains more abundant, favoring some semi-evergreen forests, e.g., in the Chapada Diamantina (Stannard, 1995). These forests are like green oases in the midst of the caatinga and probably hold the greatest bryophyte diversity. Most of these moister forests have been cleared, however. The flowering plant flora of the dry vegetation of the Planalto are in large part endemic and very rich in species. The bryophyte flora, however, is expectedly rather poor. Terrestrial hepatics and acrocarpous mosses predominate; species of the moist rain forests may occur in local moist pockets and in gallery forests. The bryophyte flora is probably similar to that of the "llanos" of northern Venezuelan and Colombia, but too little is known to properly assess the bryofloristic affinities of the Planalto.

Conservation importance.

Hepatics. This dry region has the poorest hepatic flora of the neotropical regions, with only 62 hepatic genera recorded, none of which are endemic or subendemic. The drought-tolerant taxa *Chonecolea*, *Cylindricolea* and the thalloid *Cronisia*, *Cyathodium*,

Exormotheca, and *Notothylas* are of greatest floristic interest. The great importance of the region for conservation is its unique vascular flora.
Mosses. The moss flora, excluding the highlands, is semi-xerophytic and xerophytic, with a low species diversity. No genera are endemic to the planalto. The Chaco forest of Paraguay contain about 15 species. Genera characteristic or of particular note include *Erpodium*, *Helicophyllum*, *Jonesiobryum*, and *Rhachithecium*.
Important literature.
Hepatics. Vital (1974); Yano (1984, 1989, 1995).
Mosses. Yano (1981, 1989, 1995).

10. SOUTHEASTERN BRAZIL

The Atlantic coastal area of southeastern Brazil ("Mata Atlântica"), ranging from Pernambuco in the north to Santa Catarina and Rio Grande do Sul in the south, has a very humid climate with rains distributed almost throughout the year and frequent occurrence of fog. Because of the wet climate, an almost continuous band of evergreen rain forests once covered this area, flanked on the west by the dry, scrubby caatingas and cerrados of the Planalto region. The region is Brazil's most heavily populated area; for this reason, the Atlantic rain forests are under severe pressure and much of it has disappeared. In some mountain areas, however, these forests have been restored by large-scale reforestation projects. Some of these planted forests are quite luxuriant and species-rich, especially in epiphytes
The Atlantic coastal region has several parallel mountain ranges with cloud forests and páramo formations, the principal ones being the Serro do Mar extending from Rio Grande do Sul to Bahía and covered by cloud forests, and the Serro de Mantiqueira (São Paulo to Espírito Santo) with cloud forests and páramo formations. The highest elevations are in the Serro de Mantiqueira: Pico da Bandeira (2890 m), Serra Fina (2795 m), and Algulhas Negras in the Serra de Itatiaia (2787 m).
Conservation importance**.**
Hepatics. A rich bryophyte flora continues to exist in the forest remnants and secondary types of vegetation of the region. In number of hepatic genera, the region ranks third after the northern Andes and Central America. Two genera are endemic (*Pluvianthus, Vitalianthus*) and four are found within the Neotropics only in SE Brazil (widespread outside the Neotropics): *Balantiopsis*, *Saccogynidium, Southbya*, and *Sphaerocarpos* (Table 3). The area harbors at least five threatened species, including the endangered *Drepanolejeunea aculeata.*
Mosses. The number of moss species for southeastern Brazil is not known, or at least not readily accessible. It can be assumed, however, that this region is highly diverse. The primary contribution is derived from the tropical montane and southern subtemperate zones. No single region in the Neotropics would benefit more to have an updated, detailed specimen-based catalogue, or for that matter a moss flora. In addition to a significant number of endemic taxa (e.g., the genera *Cladastomum*, *Crumuscus* and *Paranapiacabaea*), southeast Brazil also contains a number of interesting disjunct species that are found in the Andes, Central America, West Indies, and of special note, the Paleotropics, in particular Africa. Several genera are only represented in the Neotropics from southeast Brazil and in the Eastern Hemisphere, including for example *Sclerodontium clavinerve* from Australia, and *Sphaerothecium reconditium* from Sri Lanka. One of the conspicuously diverse genera includes *Schlotheimia.* While requiring a careful study, this genus will likely remain highly diverse. *Campylopus gemmatus* is listed as an endangered species.
Important literature.

Hepatics. Hell (1967); Pôrto (1990), Pôrto et al. 1999; Schäfer-Verwimp (1989, 1991, 1992, 1996); Schäfer-Verwimp & Vital (1989); Schiffner & Arnell (1964); Yano (1984, 1989).
.Mosses. A useful treatment does exist for southernmost southeastern Brazil (Sehnem 1969-1980), however it now requires updating and careful examination of species concepts. Other references are. Pôrto (1990); Schäfer-Verwimp (1989, 1991, 1992); Schäfer-Verwimp & Vital (1989); Visnadi & Vital (1995); Yano (1981, 1989, 1995).

Box 2. Role of bryophytes in tropical ecosystems

Bryophytes have an important role to play at different levels within the environment, varying from the micro-environment of a tropical leaf to the entire landscape. They are among the first colonizers of bare substrates and play an important part in the initial development of soil. In several habitats such as bogs and mountain forests they form a major part of the biomass. Thick layers of bryophytes on trees and soil may reduce erosion by absorbing large quantities of rain water. On a smaller scale, bryophytes have been shown to play a role in nitrogen fixation in the environment, for example, in the soil and on individual leaves in the rain forest.

Bryophytes play a crucial role in the water retention of tropical ecosystems. Large loads of epiphytic bryophytes (mostly liverworts) in the montane cloud forests or "mossy forests" are particularly effective in storing large amounts of water. Studies of the water storage capacity of these bryophytes have revealed that they can store on average 5 times, with a maximum of about 25 times their dry weight. An important percentage of the rainfall is captured by these bryophytes, which may be as high as 20-40% in forests with a "mossy" canopy. Part of the water evaporates back into the atmosphere, whereas the surplus drips gradually down along the trunks or freely to the ground. By holding the rainwater in and between the tissues of the plants, the bryophyte layer serves as a water reservoir, preventing water from running off immediately down to rivers and streams. Owing to their luxuriant bryophyte vegetation, the tropical mountain forests may thus serve as a water reservoir for the surrounding land and for areas down slope. Similarly, peatlands in the páramos, made up of *Sphagnum* species, also store large amounts of rainwater and function as water reservoirs.

Bryophytes may serve as a substrate for other plants and offer shelter to small animals (frogs, lizards, snails, arthropods, etc.). Many tiny orchids grow in the moss carpets covering the branches in the tree crowns and are therefore called "moss epiphytes." The moist environment created by the bryophytes is also quite favorable to the establishment and growth of important groups of micro-organisms, such as the nitrogen-fixing blue-green algae. In a tropical rain forest, it has been shown that the nitrogen fixation on living leaves by blue-green algae is proportional to the biomass of the tiny epiphyllous liverworts covering these leaves.

Finally, bryophytes may can be used as bio-indicators of pollutants since they lack conductive tissues to take up water from the substrate and do not have a protective leaf cuticle like flowering plants. Consequently, there is free entrance of solutions and gases to most of the living cells of the plants. Upon rewetting, bryophytes can absorb pollutants through the leaves and accumulate them in large amounts. Owing to their sensitivity to changes in the humidity of the ambient air and to water quality, and their often relatively slow growth, bryophytes are very good bioindicators of small changes in climatic or environmental conditions and, indirectly, of disturbances in the ecosystem. It is for these reasons that bryophytes are often used in several countries as bioindicators for monitoring air pollution and changes in water quality of lakes and rivers. By mapping the distribution of sensitive bryophyte species or genera an assessment can be made of the habitat quality; by mapping the accumulation of pollutants in bryophytes, the availability of these pollutants in the environment can be measured.

In spite of their usefulness as bioindicators, bryophytes have scarcely been used in the tropics for this purpose. The reason for their neglect is obviously the lack of basic information on recognition and habitats (Buck & Thiers, 1989; Frahm & Gradstein, 1990). The available data are mostly scattered in numerous specialized journals, or hidden on herbarium labels or in the notebooks of the collectors.

Bryophyte habitats in tropical America

The main habitats of bryophytes in tropical America are the different types of rain forest (including mountain rain forests), the dry forests, and the tropic-alpine habitats. páramo, puna, and zacatonal. This chapter provides brief descriptions of the general ecological features of these habitat types and their characteristic bryophytes (see also Box 2). Special attention is given to taxa characteristic of undisturbed habitats, in view of their importance as indicators of the ecosystem quality (Box 3).

RAIN FORESTS

Rain forests, taken in a broad sense to include "wet forests," "moist forests," and "montane forests," are a principal habitat for bryophytes in the tropics. These are evergreen forests occurring in areas with a rainfall distributed more or less equally over the year and surpassing 2000 mm annually. In areas with a prolonged dry season of over 3 months duration and lower annual precipitation, rain forests are replaced by dry forests ("deciduous forests," "seasonal forests"), and savannas. Evergreen montane forests are also treated as rain forests, even though the humidity in these forests is often determined by the frequent occurrence of clouds and mist rather than by high rainfall (hence their name "cloud forest" or "mist forest").
Rain forests occur in all neotropical floristic regions, except in the llanos of Colombia and Venezuela and the dry regions of Brazil and Paraguay. In the Brazilian Planalto, shrubby *cerrado* and *caatinga* vegetation prevail, with elements of the rain forest appearing in moist isolated pockets and in gallery forests bordering rivers.
Structure and floristic composition of tropical rain forests vary considerably and many different types have been distinguished. In mountain regions, different types of rain forest occur on the slopes of the mountains. Using the elevational distribution patterns of bryophytes and other ecological parameters, Frahm & Gradstein (1991) recognized the following altitudinal rain forest types or belts.

- Lowland rain forest (0 - 300/500 m)
- Submontane (= premontane) rain forest (300/500 - 1000/1400 m)
- Lower montane rain forest (1000/1400 - 2000/2500 m)
- Upper montane rain forest (2000/2500 - 3000/4000 m)
- Subalpine rain forest (above 3000/4000 m)

The elevational limits of these belts change based on local variations in climate, especially air humidity and direction of winds at the base of the mountains. Windward slopes adjacent to oceans or large extensions of lowland rain forest receive more moisture than leeward slopes bordering semi-desert vegetation. As a consequence, the belts are lower on windward slopes then on leeward slopes. Moreover, the elevation of the forest belts decreases towards higher latitudes and is higher on continents than on islands.
The bryophyte flora of tropical rain forests changes significantly with elevation. Different taxa often occur in the different forest belts. Similar trends may be observed among flowering plants but as these are much more speciose than bryophytes and have much narrower ranges, elevational diversity patterns in flowering plants are usually more difficult to assess. Owing to the relatively modest number of species and genera, their usually very wide geographical ranges, possibly due to their greater antiquity, and the great variation in biomass, bryophytes are very useful indicators of life zones and forest types in tropical mountain regions (Frahm & Gradstein, 1991).

Diversity of hepatics and mosses varies considerably in the different rain forest belts. In hepatics, diversity in terms of number of genera is highest in the submontane and lower montane belts, lowest in the subalpine (and alpine) belt. The lowland and upper montane belts are intermediate as regards generic diversity. Species richness is highest in the upper montane forest. In mosses, maximum diversity is in the upper montane belt, the lower montane belt is second highest in species diversity, followed by the alpine belt. In general, the páramo appears higher in diversity than the much drier puna, although that remains to be documented. Wet or moist lowland forests are relatively species-poor in mosses; they are richer in liverworts.

The differences between high and low regional species diversity is found not just in the total number of species (gamma diversity) but also in the number of additional species recorded from further inventoried localities within a region or zonation (beta diversity). Lowland species diversity, for example in the Amazon Basin, may be relatively high for a specific site (alpha diversity); however, fewer additional species may be encountered when other localities are sampled. The opposite is true for upper montane and transitional montane-alpine, here species turn-over is high.

Most bryophytes in the rain forests are epiphytes. In dense forest, epiphytic bryophytes do not grow in a random fashion. Different genera and species are found on tree bases, trunks, branches, twigs, living leaves, or on logs in various stages of decay. Some occur exclusively in the moist, shaded understory of the forest and the lower portions of the canopy, others are found only in the drier, outer portions of the forest canopy high above the ground. Some occur in both habitat types. Following Richards (1984), these ecological groups are called "shade epiphytes" (or "understory epiphytes"), "sun epiphytes" (or "canopy epiphytes"), and "generalists." The shade epiphytes are least adapted to desiccation and are most seriously affected by forest disturbance and deforestation (Gradstein, 1992a,b). About 20% of the hepatic genera are shade epiphytes of virgin forests that do not occur in secondary forest or plantations and seem to vanish when the forest canopy is opened up. A special group of shade epiphytes are the species growing on decaying wood (logs, branches fallen from the canopy, and old, rotten trunk bases) and on living leaves, the epiphylls. They also seem to be very sensitive to deforestation; this has scarcely been investigated, however.

The occurrence of bryophytes on living leaves is characteristic of tropical rain forests (Richards, 1984). In areas with a prolonged dry season, growth on the cutinized, water-repellent leaf surfaces is usually impossible except in local moist pockets near waterfalls, in canyons, and in coastal areas with frequent mists. Many different species have been recorded from leaves but only few are exclusive (or almost exclusive) to this habitat, the majority of them also occurring on bark or other substrates. "Typically" epiphyllous bryophytes are mostly hepatics of the family Lejeuneaceae (subfam. Lejeuneoideae), in addition a few species of *Radula* (sect. "*Epiphyllae*") and *Crossomitrium* (mosses) seem to be exclusive to leaves. They are small, usually pale-colored plants that grow tightly to the leaf surface by means of adhesive discs made up of fused rhizoids. Other adaptations of typical epiphylls are the common incidence of rapid, asexual reproduction by gemmae and the retention of juvenile morphological features in the adult plant (paedamorphosis), e.g., in Cololejeuneae and in *Radula yanoella* Schust. The shortened, rapid life cycles of these plants are explained as adaptations to their survival in the relatively ephemeral habitat (Gradstein, 1997).

Terrestrial bryophytes are rather uncommon in lowland rain forests but occur more frequently in montane forests, due to the presence in these forests of humus-rich soils favorable for the establishment of terrestrial species. They may occur on earth banks inside the forest, especially in light gaps, at forest margins, and also on roadside banks, in

ditches, along creeks and rivers, etc. The open habitat sites are particularly rich in mosses.

Rain forests once occupied large areas in tropical America; in many places they have now been logged or cleared and converted into plantations and farmlands, or replaced by secondary forests, scrubland or savannas. Large tracts of undisturbed lowland rain forest nowadays remain only in Amazonia, in the Guianas, and in the Pacific coastal lowlands of Colombia (Chocó). Relatively small areas of forest exist in Central America and Mexico, especially along the Caribbean side of the region, and along the Atlantic coast of Brazil. In the West Indies, lowland rain forests have virtually disappeared (see Box 3).

Box 3. Bryophytes as forest disturbance indicators

Bryophytes, because of their abundance in tropical rain forests, are affected by disturbance of the forests. Recent studies indicate that the floristic changes due to deforestation may be very large, depending on the amount of damage inflicted upon the forest. In monocultures and other areas with large-scale farming methods and total clearance of the forest, the forest flora is much more impoverished than in areas of shifting cultivation and small-scale damage to the forest. Thus, it has been found that plantations of exotic tree species may harbor less than 10% of the bryophyte flora of the adjacent virgin rain forest. Secondary forests with a more diversified tree flora, however, may retain 50-70% of the bryophyte species of the undisturbed forest.

It has been shown that the shade epiphytes of the forest, occurring primarily in the undergrowth of the forest, are more seriously affected by the disturbance than those that are growing in the high canopy (Gradstein 1992a,b). The reason is that shade epiphytes are less well adapted to desiccation, therefore they are the first to disappear when the forest canopy is opened up. Sun epiphytes, on the other hand, are adapted to relatively dry micro-habitats and have, predictably, better survival chances. They may "come down" from the high canopy in open, logged forests and establish themselves nearer to the ground in secondary habitats or in plantations. Generalists may also be expected to have better survival chances.

Epiphyllous bryophytes also appear to be particularly sensitive to disturbance of the forest because of their preference for sheltered habitats.

Clearcutting results in the immediate loss of many forest bryophytes. After 25 years of forest regeneration, however, at least some species may have returned (Gradstein 1992a). How bryophytes fit into secondary succession of the rain forest remains largely unknown. Generalizations are dangerous as there are many different kinds of rain forests and bryophyte richness varies considerably.

For the purpose of conservation, genera exclusive to virgin forests are crucial ones. They are the ones that are most seriously threatened by rain forest destruction and may serve as bioindicators of habitat quality. Genera restricted to virgin forest include several very rare, endemic taxa, known from only a single or very few collections (e.g., *Haesselia*, *Phycolepidozia*, *Sphaerolejeunea*, *Temnoma*, *Vanaea*) as well as some common ones. It appears that indicators of lowland forests are much more numerous than of montane forests, for reasons that are not clear. Possibly this discrepancy is explained by the much smaller area that remains of undisturbed montane forests in the Neotropics as compared with lowland forests (see Churchill et al., 1995a; Henderson et al. 1991).

1. Lowland rain forests

Lowland rain forests are found from sea level to the foot of the mountains, up to 300/500 m. Above, they are replaced by submontane (= premontane) and montane forests. Bryophytes are not very conspicuous in lowland forests and mostly grow as epiphytes on bark or living leaves, forming appressed, smooth mats; soil and rock are less inhabited. Hepatics are usually more numerous than mosses, the majority being members of the Lejeuneaceae, which may account for up to 70% of total hepatic diversity. Other hepatic families represented in the lowland forest include Radulaceae, Jubulaceae, Plagiochilaceae, Lepidoziaceae, and the thalloid Aneuraceae and Metzgeriaceae. These families usually have only few species in the lowland forest and are more speciose at higher elevations.
Mosses are represented primarily by four families, Calymperaceae, Fissidentaceae, Pilotrichaceae, and Sematophyllaceae, accounting for as much as 45% of the total moss diversity. Other families include the Macromitriaceae, Hypnaceae, and Leucobryaceae; however nearly half of the families found in the lowlands are often represented by only 1-2 species in each.

Characteristic bryophytes of lowland rain forests
Shade epiphytes Hepatics. *Archilejeunea parviflora,* ***Echinocolea asperrima***[1], ***Fulfordianthus evansii*** (Central America), ***Haplolejeunea*** (Guianas; trunk bases)*, Lejeunea* spp., ***Lejeunea* subgen. *Otigoniolejeunea*,** *Luteolejeunea* (Chocó), *Plagiochila* spp. Various epiphyllous Lejeuneaceae, including *Cyclolejeunea* spp., ***Leptolejeunea*** spp. (restricted to undisturbed forest except *L. exocellata* and *L. elliptica*), ***Prionolejeunea*** spp., ***Rhaphidolejeunea****,* etc. Mosses. *Calymperes* spp., *Cyrto-hypnum* spp., *Lepidopilum* spp. (esp. *L. polytrichoides*, *L. surinamense*), *Leucomium strumosum*, *Fissidens* ssp. (e.g., *F. guianensis*), *Mniomalia viridis*, *Phyllodon truncatulus*, *Phyllodrepanium falcifolium*, *Syrrhopodon* spp., *Taxithelium planum.*
Sun epiphytes Hepatics. *Acrolejeunea, Archilejeunea auberiana, Frullania* (e.g., *F. nodulosa*), *Lopholejeunea, Mastigolejeunea, Pycnolejeunea, Schiffneriolejeunea amazonica, Thysananthus, Verdoornianthus* (Amazonia). Mosses. *Groutiella* spp., *Henicodium geniculatum*, *Holomitrium* (e.g., *H. arboreum*), *Macromitrium* spp.
Generalist epiphytes Hepatics. *Ceratolejeunea* spp., *Cheilolejeunea, Lejeunea* spp., *Radula flaccida* (epiphyllous)*, Symbiezidium.* Mosses. *Crossomitrium* spp. (frequently epiphyllous), *Neckeropsis* spp. *Octoblepharum* spp., *Zelometeorium* spp.
Decaying wood Hepatics. *Aneura* spp.*,* ***Arachniopsis****, Calypogeia*, *Lophocolea martiana*, *Micropterygium*, *Odontoschisma falcifolium,* ***Prionolejeunea****, Riccardia* spp., ***Trachylejeunea****,* ***Zoopsidella***. Mosses. *Callicostella* spp., *Isopterygium* spp., *Leucobryum* spp., *Pilosium chlorophyllum*, *Sematophyllum* (e.g., *S. subsimplex*), *Taxithelium planum*, *Trichosteleum* spp.
Soil and rock

[1] bold face: species restricted to or characteristic of undisturbed habitats (virgin forest indicator)

Hepatics. *Arachniopsis*, *Calypogeia miquelii* (= *C. amazonica*), *Notothylas*, *Protocephalozia*? (N. Amazonia). Mosses. *Dicranella* spp. (e.g., *D. hilariana*), *Fissidens* spp., *Philonotis* spp., *Splachnobryum obtusum.*
Creeks and rivers Hepatics. Characteristic rheophytes occuring in lowland rain forest areas include members of the families Lejeuneaceae and Cephaloziellaceae. Rheophytic hepatics often have special morphological features such as a creeping rhizome, thick stems and "superfertility" (Thiers, 1988). They include the Amazonian endemics ***Cephalantholejeunea, Marsupidium gradsteinii, Neopotamolejeunea***, and ***Schusterolejeunea***, furthermore ***Kymatocalyx rhizomatica*** (Central America), and the widespread but overlooked ***Stictolejeunea balfourii.*** Mosses. *Hydropogon fontinaloides* - Amazon Basin (epiphytic associated with inundated forests), *Hydropogonella gymnostoma* - Amazon Basin and Panama. Rheophytes seem to occur mainly in regions covered with primary rain forest and thus may be good indicators of undisturbed habitats.

2. Submontane rain forests

Submontane (= premontane) forests are confined to the lower slopes of the mountains, usually occurring at elevations between 300/500 - 1000/1400 m. Bryophytes are somewhat more conspicuous than in lowland forests and include more robust, erect or pendent forms. Submontane forests also differ from the lowland forests by the appearance of montane taxa, mostly of the lower montane forests. Submontane forests are usually mist-affected and this, in addition to the slight decrease in temperature, is the main reason why the bryophyte flora of submontane forest differs from that of lowland forest.

Characteristic bryophytes of submontane rain forests
Shade epiphytes Hepatics. *Bryopteris filicina, Colura* sect. *Harmophyllum*, ***Colura clavigera*****,** *Dactylolejeunea* (W. Indies), *Fulfordianthus pterobryoides* (Chocó), *Luteolejeunea* (Chocó), ***Phycolepidozia*** (Dominica), ***Physantholejeunea*** (W. Indies), *Vitalianthus* (E Brazil). Mosses. Pterobryaceae, *Schliephackea* (*S. prostrata* - Chocó), *Syrrhopodon* spp., *Isodrepanium lentulum*, *Phyllogonium* spp. (to upper montane), *Stenodictyon* spp.
Sun epiphytes Hepatics. *Cystolejeunea*, *Frullania* spp., *Lepidolejeunea eluta*, *Marchesinia*. Mosses. *Groutiella* spp.
Decaying wood, including humus and leaf litter Hepatics. *Anomoclada, Calypogeia*, ***Mnioloma, Cephalozia*** **subgen.** ***Macrocephalozia*** (= *Fuscocephaloziopsis*), ***Haesselia*** (Guayana Highland), *Lophocolea connata, Micropterygium* spp., ***Nowellia*** (decorticated wood), ***Pallavicinia***, *Trabacellula* (Guayana Highland). Mosses. *Amblytropis* spp., *Brymela* spp., *Mesonodon*, *Thamniopsis* spp. (particularly *T. undata*).
Soil and rock Hepatics. *Alobiella*, *Alobiellopsis*, *Arachniopsis*, *Calypogeia*, *Kymatocalyx*. Mosses. *Dicranella* spp., *Fissidens* spp.

Creeks and rivers Hepatics. *Alobiella*, *Kymatocalyx*, ***Myriocolea*** (Ecuador), *Myriocoleopsis* (SE Brazil). Mosses. *Sematophyllum* spp. (to upper montane).

3. Lower montane rain forests

The lower montane forests, occurring at elevations between 1000/1400 - 2000/2500 m, usually have a much more luxuriant bryophyte vegetation than the submontane and lowland forests. Thick carpets of bryophytes, especially hepatics, may be found on trunks and branches; road banks, usually almost bare at lower altitudes, may be densely covered by bryophytes. Numerous taxa not found at lower elevations appear in lower montane forests, especially in the shaded understory. Many of these occur also in upper montane forests. A striking feature of montane forests, as compared with lowlands forests, is the much greater number of bryophyte families, which is about 2-3 times higher than in the lowlands. Among hepatics, the genera *Plagiochila, Bazzania,* and *Herbertus* are very prominent and represented by numerous species. Other important hepatic genera are *Lepidozia, Leptoscyphus, Lophocolea, Trichocolea*, and the thalloid *Dumortiera, Metzgeria, Monoclea*, *Riccardia*, and *Symphyogyna*. Diversity of *Lejeuneaceae*, although still the most important family in terms of species-richness, decreases with elevation and accounts for about 45% of total hepatic diversity in the lower montane forest, 30% in the upper montane forest and 20% in the subalpine forest (Gradstein, 1995).

Mosses appear to be well adapted to low or moderate levels of disturbance, this is particularly true in the montane region (lower and upper montane). Open montane areas interspersed with secondary forests are exceptionally rich in mosses, which likely exceeds the diversity found in undisturbed forests at comparable elevations. Rather numerous genera of Dicranaceae and Pottiaceae are very common in the open montane environment. Genera such as *Bartramia*, *Breutelia*, *Bryum*, *Campylopus*, *Ceratodon*, *Ctenidium*, *Dicranum*, *Hypnum*, *Leptodontium*, *Pilopogon*, *Pogonatum*, *Rhacocarpus*, *Rhodobryum*, and *Thuidium*, often form thick mats and tufts, sometimes in pure stands. Corticolous or lignicolous species of mosses are represented by the Cryphaeaceae (principally *Cryphaea* and *Schoenobryum*), Hypnaceae (*Mittenothamnium*), Meteoriaceae (*Meteoridium*, *Meteorium*, *Papillaria*), Prionodontaceae (*Prionodon*), and Thamnobryaceae (*Porotrichum*). An inconspicuous community, usually composed of few individuals and thus readily overlooked, is found on branches and twigs of low or shrubby trees; characterístic genera include *Cryphaea*, *Daltonia*, *Entodon*, *Lepidopilum*, *Orthotrichum*, *Streptopogon*, and *Zygodon*.

Characteristic bryophytes of lower montane rain forests
Shade epiphytes Hepatics. ***Blepharolejeunea saccata***, ***Echinocolea dilatata,*** *Heteroscyphus*, ***Jubula***, ***Leiolejeunea*** (Jamaica)***,*** *Lophocolea connata, Radula stenocalyx*, ***Sphaerolejeunea*** (Colombia), *Taxilejeunea sulphurea*, *Trichocolea* spp. Mosses. *Adelothecium bogotense*, *Acidodontium* spp., *Neckera* spp. (all to upper montane).
Sun epiphytes Hepatics. *Adelanthus* spp., *Brachiolejeunea leiboldiana*, *Diplasiolejeunea* spp., *Dicranolejeunea, Frullania riojaneirensis*, *Herbertus* spp., *Kurzia* spp.,

Leptoscyphus spp., *Marchesinia robusta*, *Pluvianthus* (SE Brazil), *Cheilolejeunea inflexa*, *Syzygiella* spp., *Tylimanthus laxus*, ***Vanaea*** (Guayana Highland). Mosses. *Holomitrium* spp., *Macromitrium* spp., *Zygodon* spp.
Generalist epiphytes Hepatics. *Bazzania* spp., *Drepanolejeunea* spp., *Lepidozia* spp., *Metzgeria* spp., *Omphalanthus* spp., *Plagiochila* spp., *Porella brasiliensis*, *P. swartziana*, *Radula* spp. Mosses. *Prionodon* spp., *Squamidium* spp. (to upper montane).
Decaying wood Hepatics. *Aneura pinguis* (also on rock), *Bazzania* spp., *Calypogeia* spp., *Cephalozia* spp., Geocalycaeae, **Haplomitrium**, *Lepidozia* spp., *Nowellia* spp., *Odontoschisma* spp., *Megaceros*, *Monoclea* (also on rock), *Riccardia andina*, *R. cervicornis*, *Symphyogyna brogniartii*, *Telaranea*. Mosses. *Trachyxiphium* spp.
Soil and rock Hepatics. *Alobiella husnotii, Alobiellopsis dominicensis* (mostly Caribbean), *Anthoceros* spp., *Dumortiera hirsuta*, *Marchantia* subgen. *Chlamidium, Iwatsukia* spp. (mostly Guayana Highland), *Kymatocalyx* spp., *Monoclea gottschei, Neesioscyphus* spp., *Odontoseries chimantana* (Guayana Highland), *Paracromastigum bifidum*, *Phaeoceros* spp., *Reboulia hemisphaerica, Riccardia fucoidea*. Mosses. *Atrichum polycarpum.*
Creeks and rivers (also upper montane) Hepatics. *Jungermannia decolor, Nardia succulenta*. The latter species is particularly characteristic of seepage areas and springs and is often common on steep, dripping roadside banks where the water is rich in minerals. In addition, *N. succulenta* may grow on the edges of hot sulphur springs and fumaroles and is a good indicator of hot volcanic soil or rock. Mosses. *Platyhypnidium aquaticum* (to alpine).
Open montane (also upper montane and alpine) Mosses. *Breutelia* spp., *Campylopus* spp., *Ctenidium* spp., *Leptodontium* spp., *Thuidium* spp.

4. Upper montane rain forests

Upper montane forests are mainly found in the high Andes and on the high mountains of Central America, at elevations from 2000/2500 m to near the forest line at 3000/4000 m. The number of species and biomass of bryophytes is even higher than in the lower montane forests and all trees and branches are thickly covered by bryophytes, especially hepatics. Upper montane forests are therefore often called "mossy forests." A further characteristic is the conspicuous terrestrial layer of bryophytes, due to the presence of organic, humus-rich soils in these forests. Characteristic hepatics of upper montane forests include *Frullania convoluta*, *Lepicolea pruinosa*, and *Scapania portoricensis* (also subalpine). Most upper montane forests are disturbed by human activities; indicator species of undisturbed forest are unknown.

Characteristic bryophytes of upper montane rain forests
Epiphytes Hepatics. *Acrobolbus*, *Bazzania* spp., *Frullania convoluta, Herbertus* spp., *Lepicolea pruinosa*, *Macrolejeunea pallescens*, *Porella* spp., *Plagiochila* spp.,

Scapania (*Macroscapania*) *portoricensis, Steereochila*, *Syzygiella anomala*, *Szweykowskia*. Mosses. *Daltonia* spp., *Macromitrium* spp., *Pilotrichella flexilis, Symblepharis lindigii*, *Zygodon* spp. (all to subalpine).
Decaying wood Hepatics. *Temnoma.* Other characteristic genera are shared with the lower montane forests (see above). A bryophyte community rich in holarctic species (e.g., *Anastrophyllum hellerianum*, *Cephalozia catenulifera*, *Jamesoniella autumnalis, Lophozia longiflora*, *Nowellia curvifolia*) occurs on rotting logs in upper montane pine forests of Mexico and Guatemala (Gradstein & Váña, 1994).
Soil and rock, including leaf litter and humus Hepatics. ***Athalamia*** (Central Andes), *Calycularia* (Mexico), *Chaetocolea* (N Andes), *Diplophyllum*, *Eopleurozia* (N. Andes and Guayana Highland), *Mannia* (Central Andes), *Sauteria*, *Targionia*. Mosses. *Diplostichum longirostre*, *Pyrrhobryum mnioides*, *Rhodobryum* spp. (to alpine).
Creeks and rivers: see lower montane rain forest
Open montane (to subalpine) Mosses. *Brachythecium* spp., *Bryoerythrophyllum* spp., *Caribaeohypnum polypterum*, *Diplostichum*, *Polytrichadelphus* spp.

5. Subalpine rain forests

Subalpine forests are dwarf forests near timberline. They occur at elevations above 3000 m in the Andes and Central America. Above timberline, they are replaced by alpine formations such as páramo and puna. The elevation of the subalpine forests varies with the location of the timberline and their extent is heavily determined by human activities. Bryophytic biomass may reach peak values in subalpine forest but species diversity is lower than in upper montane forest due to the more simple forest structure. Another characteristic feature is the lessening of substrate preferences of bryophytes. Species growing as epiphytes at lower elevations may occur here also on soil or rock.
Subalpine forests are different from the dwarf "elfin forests" occurring at low elevations on the summits of islands (e.g., in the West Indies) or on the peaks of lower mountains or ridges. These forests resemble subalpine forest by their low canopy and tortuous tree trunks, but their species composition is very different and more similar to that of the lower montane (or upper montane) rain forest.

Characteristic bryophytes of subalpine rain forests
Epiphytes Hepatics. *Bazzania placophylla*, *Campanocolea, Herbertus serratus*, *Leptoscyphus cuneifolius*, *Lindigianthus*, *Plagiochila corniculata*, *Platycaulis*? (Venezuela), *Rhodoplagiochila* (Venezuela). Mosses. *Chorisodontium* spp., *Lepyrodon tomentosus*, *Macromitrium* spp., *Porotrichodendron* spp., *Pylaisiella falcata* (also decaying wood).
Twig epiphytes Hepatics. *Aureolejeunea* spp., *Colura* subgen. *Oidocorys, Blepharolejeunea* spp., *Diplasiolejeunea papillionacea, Drepanolejeunea* spp., *Harpalejeunea grandis* (Colombia), *Pseudocephaloziella* (Venezuela). Mosses. *Daltonia* spp., *Entodon* spp., *Leptotheca boliviana*, *Orthotrichum* spp., *Streptopogon* spp., *Syntrichia* spp.

Decaying wood Hepatics. *Blepharostoma*, *Temnoma* (also upper montane).
Soil and rock; open subalpine Mosses. *Breutelia* spp., *Leptodontium* spp.

DRY FORESTS AND SAVANNAS

In regions with a dry season (or seasons) exceeding 3-4 months annually, rain forests are replaced by deciduous and sclerophyllous vegetation types, including low woodlands, scrubby vegetations, or grasslands (savannas). High forests have largely vanished in these regions due to human interference or to fire; small patches may remain along rivers (gallery forest) and on steep slopes in the mountains.

Dry forests and savannas are much poorer in bryophytes than rain forests, and are mostly inhabited by mosses (Pócs, 1982). Hepatics include a few drought-tolerant epiphytes and thalloid species of Marchantiales (e.g., *Riccia* spp.) and hornworts. The vegetations are often affected by fire and this further reduces the chances for development of a diversified bryophyte vegetation. However, in local moist pockets such as hill tops that receive morning mist, a somewhat more luxuriant bryophyte flora may be developed.

The largest tracts of dry forests in tropical America are in the Planalto region of Brazil, where various types of dry woodlands and scrubby vegetations ("cerrado," "caatinga") as well as savanna occur. The Chaco forest, a subset of the Planalto, is found in portions of eastern Bolivia, western Paraguay, and northeastern Argentina. Extensive savannas occur in the Guianas and on the leeward side of the Andes in Venezuela and northeastern Colombia, where they are called "llanos." Dry montane forests occur in Mexico, Central America, the Greater Antilles, and in the dry "interandean" vallies of the Andes, especially in the Central Andes.

Characteristic bryophytes of dry forests and savannas
Epiphytes Many drought-tolerant epiphytes may also occur in the outer canopy of rain forests, where relatively dry climatic conditions prevail. This has been called the "canopy-effect" (Cornelissen & Gradstein, 1990). Hepatics. *Frullania* spp. (e.g., *F. caulisequa*, *F. ericoides*, *F. gibbosa*, various members of *F.* subgen. *Trachycolea*), *Acanthocoleus, Acrolejeunea, Archilejeunea auberiana, Brachiolejeunea phyllorhiza, Caudalejeunea*, *Cheilolejeunea* subgen. *Euosmolejeunea*, *Chonecolea doellingeri*, *Diplasiolejeunea rudolphiana*, *Frullanoides*, *Lejeunea* spp. (especially *L. laetevirens*), *Lepidolejeunea* spec. nov., *Mastigolejeunea auriculata*, *Leucolejeunea*, *Pycnolejeunea*, *Schiffneriolejeunea polycarpa*. Mosses. *Aulacopilium glaucum*, *Erpodium* spp., *Felipponea montevidensis*, *Helicophyllum torquatum*, *Jonesiobryum* spp. (Brazilian planalto), *Rhachithecium perpusillum*, *Stereophyllaceae* (also logs).
Soil and rock Hepatics. Most indicator taxa of dry soil and rock are thalloid hepatics of the order Marchantiales. Often they grow in somewhat sheltered habitats under rocks and or in rock crevices. Characteristic indicators of dry regions are *Cronisia*, *Exormotheca fimbriata*, *Fossombronia*, *Notothylas*, and *Riccia* spp. In southern Brazil and in Mexico, near the northernmost and southernmost limits of the Neotropics, the genera *Corsinia*, *Oxymitra,* and *Sphaerocarpos* may be found. These genera have their largest expansion in subtropical and

mediterranean regions with a pronounced seasonal climate. Among leafy hepatics, indicators of dry soil or rock are scarce and include *Cylindrocolea* (Cephaloziellaceae) and some species of *Frullania* and *Lejeunea*.
In dry mountain regions of the Central Andes and of Mexico, thalloid genera of Aytoniaceae (*Cryptomitrium, Plagiochasma, Reboulia*), Cleveaceae (*Sauteria*), *Riccia,* and Targioniaceae (*Cyathodium*, *Targionia*) are characteristic on soil and rock.
Mosses. *Barbula* spp., *Didymodon* spp., *Pseudocrossidium.*

ALPINE HABITATS: PÁRAMO, PUNA, ZACATONAL

Alpine (or "tropic-alpine") regions are found in the Andes and Central America between the timber line at (3000-)3500-4000 m up to perennial snowline at 4800-5000 m. They include the dry "punas" of the central Andes, the dry "zacatonales" of northern Central America and Mexico, and the humid "páramos" of the northern Andes (northern Peru, Ecuador, Colombia, Venezuela) and Costa Rica. Much of the alpine regions are covered by grasslands and rocky ground, with low bushes occurring at lower elevations and in sheltered habitats. Swamps, lakes, and *Sphagnum* bogs may be found in depressions in the landscape, particularly in the humid páramos. The latter habitats are particularly rich in bryophytes.
The alpine habitats are mainly inhabited by terrestrial bryophytes and are made up of a mix of tropical and temperate families. Antheliaceae, Arnelliaceae, Gymnomitriaceae, and many Jungermanniaecae are almost exclusive to alpine regions. Because they are humid, páramos are rich in hepatics. About 290 species in 88 genera have been reported, more than 25% of them endemic to páramos (Gradstein, 1998, 1999). Moss diversity in páramos is also very high; 543 species (almost twice as many as the hepatics) in 1163 genera have been recorded (Churchill & Griffin, 1999). Significant numbers of páramo mosses are also found in open areas in the montane forest belt.

Characteristic bryophytes of alpine habitats

Soil and rock, including leaf litter and humus
Hepatics. *Anthelia*, Arnelliaceae (*Gongylanthus, Southbya*), Gymnomitriaceae (*Gymnomitrium, Marsupella, Paramomitrium, Stephaniella, Stephaniellidium*), Herbertaceae (*Herbertus, Triandrophyllum*), various Jungermanniaceae (*Anastrophyllum, Andrewsianthus*, *Barbilophozia, Cryptochila, Gymnocoleopsis*, *Jamesoniella* spp., *Lophozia* spp., etc.), *Isotachis* spp., *Jensenia*, *Lethocolea*, *Marchantia*, *Noteroclada*, *Ruizanthus, Triandrophyllum*.
Mosses. *Aloinella* spp., *Amphidium tortuosum*, *Andreaea* spp., *Breutelia* spp., *Conostomum* spp., *Distichium capillaceum*, *Encalypta* spp., *Erythrophyllastrum andinum*, *Grimmia* spp., *Hedwigidium integrifolium*, *Leptodontium* spp., *Notoligotrichum*, *Oreoweisia* spp., *Racomitrium* spp. (extending to open upper montane), *Schizymenium* spp.

Fens
Hepatics. *Austrofossombronia, Marchantia plicata.*
Mosses. *Pleurozium schreberi*, *Sanionia uncinata.*

Sphagnum bogs
Hepatics. *Anastrophyllum* spp., *Cephalozia* spp., *Jensenia florschuetzii*, *Kurzia verrucosa*, *Leptoscyphus cleefii*, *Pseudocephalozia, Riccardia* spp.
Mosses. *Calliergon* spp., *Drepanocladus* spp. *Sphagnum* spp.

Rivers

Hepatics. *Clasmatocolea*, *Gymnocoleopsis*, *Isotachis* spp., *Jungermannia ovato-trigona*, *Lophozia laxiflora*, *Noteroclada* (also montane), *Triandrophyllum*. Mosses. *Andreaea nitida*, *Dendrocryphaea latifolia* (Colombia), *Hygrodicranum* spp., *Platyhypnidium aquaticum* (also montane), *Racomitrium* spp. (e.g., R. *subfalcata*).
Lakes Hepatics. *Isotachis lacustris, I. obtusa*. Mosses. *Drepanocladus* spp., *Gradsteinia andicola*.

How to collect and process bryophytes

Specimens deposited in herbaria (plant libraries) are very important tools for the study of bryophytes or other plant groups. They are an invaluable scientific asset that represent a significant part of the history and floristic patrimony of a country. To maintain these scientific collections, it is essential that correct techniques for collecting, curating, processing, and maintenance of specimens are employed.

Before going into the field, one should seek contact with local bryologists, herbaria, or other competent authorities to obtain collecting permits. Also, it is recommended to gather information about collecting sites, i.e., location (coordinates); type of climate, soils and vegetation; and geological history if known. Needed tools in the field are: a 10(-20) x hand-lens, paper bags of different sizes, plastic bags (used for taking fresh samples to the laboratory or samples that need to be preserved or fixed in special reagents), a jack-knife or camper's knife, a chisel and a small mallet to gather saxicolous species, waterproof markers, a field notebook (preferably weatherproof type), altimeter, GPS for recording the precise coordinates of the collecting site, and a collecting knapsack. When field trips are long, it is recommended to bring a plant press with blotting cardboard and newspapers to press thalloid liverworts, epiphylls, hornworts, and voluminous samples. Vials with fixatives should be brought to the field if preservation of fresh material is needed for further morphological and cytological studies.

It may be useful to number and set the date on the bags before going into the field, to avoid errors. When collecting, it is very important to pack each species separately as much as possible, either in the field or directly after returning from the field, when the specimens are still fresh, unless the species are too small to allow separation in the field. This is the case with epiphylls, which should be collected on the whole leaves and sorted in the laboratory using a dissecting microscope. The substrate from which the sample was taken and all other relevant data on its habitat, including elevation, vegetation type, conservation status of the habitat (disturbed/undisturbed), etc. should carefully be recorded in the field, on the bag or on supplementary note paper. When an epiphyte is being collected, it is important to record the height on the trunk at which the sample was taken and, if known, the identity of the host tree. Characteristics of the living bryophyte, its color, growth form, fertility, etc. should also be noted. By using pre-printed labels with lists of habitat factors and other categories that can be selected or filled out, the process of data gathering in the field can be accelerated.

Upon returning from the field, all information gathered during collecting and any other data that may be of importance in evaluating the area must be written in the field notebook. In order to dry the samples, the filled collecting bags should be placed open on a table or floor in a dry place without strong air currents or, alternatively, loosely packed in a broad weave sack or bag and hung in a well-ventilated area. Thalloid hepatics and epiphylls should be pressed in the same fashion as vascular plants and the paper replaced daily. As hepatic capsules tend to open when drying, releasing their spores, it is recommended to place some specimens with capsules in a manila or newspaper envelope with the rest of the sample, to ensure that some unopened capsules are preserved. As to hepatics, it may also be important to keep some material alive for study of the oil bodies in the laboratory. For this purpose, a small portion of the sample may be kept in plastic, within the bag or separately. It is important that the living material is kept cool (but not frozen!) and examined under the microscope as soon as possible, within a few days, otherwise the oil bodies may have begun to degenerate and their morphology to change.

Upon returning to the laboratory, moss samples can be airdried with a weight on top of them or they can be dried in an electric or light bulb oven at low temperature (40-60° C), checking the samples every day. For leafy hepatics it is preferable to airdry them or, when

they are very humid, to place them in the oven to extract excess humidity and then have them air dried. By lightly pressing the leafy hepatics (e.g., *Herbertus, Bazzania, Plagiochila*) and peat mosses (*Sphagnum*), more manageable herbarium samples are obtained.

Once dried, samples can be stored in their original packet if they cannot be processed immediately, or preferably transferred to recycled paper envelopes, size 10 x 15 cm, with the specimen labels inside. Envelopes are made by folding a sheet of paper in which an index card has been placed in the center of it. The lower part of the sheet is folded downwards over the lower portion giving rise to an envelope (Fig. 12). Samples that are closely attached to the substrate, e.g., rock or bark, may be mounted on a white cardboard or blank index card. Very small samples should be placed in tiny paper envelopes and then placed in standard size herbarium envelopes, to avoid loss of the material.

Labels should be a little smaller than herbarium packets and should have as much information as possible about the sample (Fig. 13). It is useful to register all information in a computer database. This information will serve to derive data for floristic and ecological evaluations, to track samples for study, exchange, or re-collecting; and for printing of labels.

Processed material is placed in metal or wooden cabinets, or in cardboard boxes (shoebox size) when cabinets are not available. Within the cabinets or boxes, naphthalene can be placed in little bags, to prevent attack by insects. Avoid having the collection near very humid, dark, and poorly ventilated areas where insects and fungi may proliferate.

Finally, as a matter of policy, one should always leave one duplicate set of the collection at one of the herbaria of the host country.

Important herbaria in tropical America

The following address list of important herbaria in tropical America is based on Holmgren et al. (1990). National herbaria as well as herbaria with important bryophyte collections are included. For additional addresses contact BRIOLATINA, the newsletter of the *Sociedad Latino-Americana de Briología* (c/o Dr. N. Salazar A., Smithsonian Tropical Research Institute, Apartado 2072, Balboa, República de Panamá).

Argentina

Herbario, Fundación Miguel Lillo, Casilla de Correo 11, Miguel Lillo 251, 4000 San Miguel de Tucumán, Tucumán, Argentina

Belize

Herbarium, Forestry Department, Ministry of Agriculture, Forestry and Fisheries, Belmopán, Bélize

Bolivia

Herbario Nacional de Bolivia, Correo Central Cajón Postal 10077, La Paz, Bolivia

Brazil

Herbário, Departamento de Botânica, Instituto Nacional de Pesquisas da Amazônia, Caixa Postal 478, 69011-970 Manaus, Amazonas, Brazil.

Herbário, Departamento de Botânica, Museu Paraense Emílio Goeldi, Caixa Postal 399, 66630-040 Belém, Pará, Brazil

Herbário, Jardim Botânico do Rio de Janeiro, Rua Pacheco Leão 915, CEP 22460-030 Rio de Janeiro, RJ; Brasil

Herbário, Instituto de Botânica, Caixa Postal 4005, 01061-970 São Paulo, SP, Brasil

Herbário, Departamento de Botânica, Universidade Federal do Rio Grande do Sul, 90046-900 Porto Allegre, Rio Grande do Sul, Brasil

Colombia

Herbario, Centro de Investigaciones Ciencias Exactas y Naturales (CIENS), Universidad de Antioquia, Apartado Aéreo 1226, Medellín, Colombia

Herbario Nacional, Instituto de Ciencias Naturales, Universidad Nacional de Colombia, Apartado Aéreo 7495, Santafé de Bogotá, Colombia

Costa Rica

Herbario Nacional, Museo Nacional de Costa Rica, Apartado 749-1000, San José, Costa Rica

Herbario, Escuela de Biología, Ciudad Universitaria Rodrigo Facio, Universidad de Costa Rica, San José, Costa Rica

Cuba

Herbario Academia de Ciencias, Instituto de Ecología y Sistemática, Carretera de Varona Km 3 1/2, Capdevila, Boyeros, Apartado 8010, 10800 Habana 8, Cuba

Herbario, Centro Oriental de Biodiversidad y Ecosistemas (BIOECO), Ministerio de Ciencia, Tecnología y Medio Ambiente (CITMA), José Antonia Saco N° 601, Esq. Barnada, C.P. 90100, Santiago de Cuba, Cuba

Dominican Republic

Herbario, Jardin Botánico Nacional “Dr. Rafael M. Moscoso,” Ave. República de Colombia, Esq. Ave. de Los Próceres, Apartado Postal 21-9, Santo Domingo, República Dominicana

Ecuador

Herbario, Departamento de Biología, Pontificia Universidad Católica del Ecuador, Apartado 2184, Quito, Ecuador

Herbario, Museo Nacional de Ciencias Naturales, Apartado 67, Calle Tamayo, Quito, Ecuador

El Salvador

Herbario, Departamento de Biología, Facultad de Ciencias y Humanidades, Universdad de El Salvador, San Salvador, El Salvador

French Guiana

Herbarium, ORSTOM, B.P. 165, 97323 Cayenne Cédex, French Guiana

Guatemala

Herbario, Facultad de Agronomía, Universidad de San Carlos, Zona 12, Apartado Postal 1545, Guatemala City, Guatemala

Guyana

Guyana National Herbarium, Biology Department, University of Guyana, P.O. Box 101110 Georgetown, Guyana

Haiti

Herbier National E.L. Ekman, Faculté d’Agronomie et de Médecine Vétérinaire, Université d’Etat d’Haiti, Damien, Haiti

Honduras

Herbario, Departamento de Biología, Universidad Nacional Autónoma de Honduras, Tegucigalpa, Honduras

Jamaica

Herbarium, Natural History Division, Institute of Jamaica, 12-16 East Street, Kingston, Jamaica

Herbarium, Botany Department, University of the West Indies, Mona, Kingston, Jamaica

Mexico

Herbario Nacional, Departamento de Botánica, Instituto de Biología, Universidad Nacional Autónoma de México, Apartado Postal 70-367, 04510 Mexico City, D.F., Mexico

Nicaragua

Herbario Nacional de Nicaragua, Universidad Centroamericana, Apartado 69, Managua, Nicaragua

Panama

Herbario, Departamento de Botánica, Universidad de Panamá, Panamá City, Panama

Paraguay

Herbario, Sección Botánica, Faculdad de Ciencas Químicas, Universidad Nacional de Asunción, Casilla de Correo 1055, Asunción, Paraguay

Perú

Herbario, Museo de Historia Natural, Universidad Nacional Mayor de San Marcos, Casilla 14-0434, Lima 14, Peru

Herbario Vargas, Faculdad de Ciencia Biológicas, Universidad Nacional San Antonio Abad del Cuzco, Apartado 367, Cuzco, Peru

Puerto Rico

Herbarium, Department of Botany, University of Puerto Rico, P.O. Box 5000, Mayagüez, Puerto Rico 00681-5000

Suriname

National Herbarium, Faculty of Technology, University of Suriname, P.O. Box 9212, Paramaribo, Suriname

Trinidad and Tobago

National Herbarium of Trinidad and Tobago, Department of Plant Sciences and Biochemistry, University of the West Indies, St. Augustine, Trinidad

Venezuela

Herbario Nacional de Venezuela, Apartado 2156, Caracas 1010-A, Venezuela

Herbario, Centro Jardín Botánico de Mérida, Universidad de los Andes, Apartado Postal 717, Mérida 5101, Venezuela

Glossary

This Glossary is based on *Glossarium Polyglottum Bryologiae* (Magill, 1990) with modifications.

abaxial. The side of a leaf away from the stem; the lower side of the leaf (opposite of **adaxial**).
acidophytic. Growing in acid habitats.
acrocarpous. Producing the sporophyte at the apex of a stem or main branch (opposite of **pleurocarpous**).
acrogynous. Archegonia at the apex of a stem or branch (opposite of **anacrogynous**).
acroscopic. Directed toward the apex (opposite of **basiscopic**).
acumen. A slender, tapering point.
acuminate. Slenderly tapered to a sharp point, angle less than 45º (cf. **acute**) (Fig. 8B).
acute. Sharply pointed at an angle less than 90º but greater than 45° (cf. **acuminate**) (Fig. 8B).
adaxial. The side of a leaf toward the stem; the upper surface of the leaf (opposite of **abaxial**).
adnate. United, fused. Fusion of unlike parts.
air chamber. A cavity in the thallus of Marchantiales (Fig. 74A,F).
alar cells. Cells at basal margins (angles) of a leaf; these cells are often differentiated in size, shape or color from other leaf cells (Figs. 8F; 9M,N,Q-S).
alpine. Treeless upper vegetation belt on high mountains extending from the timberline up to the perennial snowline, between ca. 3500 - 5000 m in the Tropics. In the Neotropics the alpine belt is called “páramo,“ “puna,“ or “zacatonal.“
amphigastria (sing. **amphigastrium**). Underleaves in leafy liverworts; in a few mosses, smaller leaves on the upper or lower stem surface.
anacrogynous. Archegonia in a lateral position on stem, branch, or thallus, not at the apex (opposite of **acrogynous**).
analogous. With similar functions that do not have a common phylogenetic origin (opposite of **homologous**).
androecium (plur. **androecia**). Antheridia and surrounding bracts; the male gametoecium (Fig. 1A).
anisophyllous. Having stem and branch leaves morphologically dissimilar, or bearing two distinct types of leaves.
anisosporous. Producing spores of different sizes within the same capsule; the smaller spores may give rise to male gametophytes.
annual. Of one year's duration; completing life cycle in one year.
annular thickenings. Ring-like thickenings extending over both tangential and radial cell walls in liverwort capsules.
annulus. Zone of differentiated cells between the capsule urn and operculum, facilitating the opening of the capsule (Fig. 11T).
antheridiophore (= male **gametangiophore**). Stalked, antheridium-bearing receptacle on the thallus of the Marchantiaceae (Fig. 2F).
antheridium (plur. **antheridia**). Male sex organ or gametangium, producing antherozoids (=spermatozoids) (Fig. 1A).
antherozoid (= **spermatozoid**). Male gamete (Fig. 1A).
antical. The dorsal surface of a stem; the leaf margin oriented towards the shoot apex (opposite of **postical**).
anticlinal. Perpendicular to the surface.
aperture. An opening or hole.

apical. At the tip.
apical cell. A cell at the growing tip that divides repeatedly to form new cells.
apical lamina. In *Fissidens*, the part of the leaf above or distal to the vaginant and dorsal laminae.
apiculate. Abruptly ending in a short point (**mucronate** is shorter pointed; **cuspidate** is longer and stoutly pointed) (Figs. 8B; 11N).
apophysis. Neck at the base of the moss capsule.
appendicule. In mosses, short projections from horizontal wall pairs, often borne on endostomial cilia (= **trabeculae**). In liverworts, cilia, auricles, or other appendages at leaf bases.
appendiculate. With short projections or appendages.
appressed. Lying closely together, leaves lying close or flat against the stem (Fig. 7F).
aquatic. Of plants, growing permanently submerged, completing the life cycle in water (cf. **rheophytic**).
archegoniophore (= female **gametangiophore**). Stalked, archegonia-bearing receptacle on the thallus of many Marchantiales (Fig. 2E).
archegonium (plur. **archegonia**). Female sex organ or gametangium, containing an egg (Fig. 1A).
arcuate. Curved like a bow.
areolation. The cellular network of a leaf.
aristate. Ending in an awn (Fig. 8B).
arthrodontous. Having a peristome of one or two rings of teeth consisting essentially of periclinal cell-wall pairs (lamellae) (Fig. 11T-Y).
articulate. Jointed. In liverworts, seta with epidermal cells in even tiers (Fig. 4K).
ascending. Pointing obliquely upward, away from the substrate.
athecal. Without a sheath of tissue at the base; said of collarless branches (Fig. 3E-G).
attenuate. Slenderly tapering (Fig. 7Q).
auricle. A small, ear-like lobe, often present at leaf base (Figs. 8C; 81K).
auriculate. With **auricles** (Fig. 8C).
austral. Southern; of the Southern Hemisphere.
autoicous (= **autoecious**). With archegonia and antheridia on separate branches of the same plant. The ending "**-oecious**" applies to diploid sexuality and is therefore less applicable to bryophytes (Fig. 1B).
awn. Hair-point, usually formed by an excurrent costa (Fig. 177E).
axil. Angle between stem and leaf.
axillary. In the leaf axils.
axillary hair. Uniseriate hair found in the leaf axils, generally inconspicuous and well concealed by the leaf bases.
axis. The main stem.

basal. At the base or proximal end.
basal membrane. A short tube or cylinder supporting the endostome or the teeth of the haplolepidous peristome (Fig. 11U).
basiphytic. Growing on basic substrates, such as limestone, dolomite, sandstone, or chalk.
basiscopic. Directed toward the base, away from the apex (opposite of **acroscopic**).
beak (= **rostrum**). Elongated apex of an operculum, calyptra, or perianth (Fig. 5A).
bicostate. With two midribs (Fig. 9B).
bifid. Divided into two parts.
bipinnate. Twice pinnately branched (Fig. 7T).
bisbifid. Twice bifid with the subsequent parts more shallowly bifid (Fig. 57C-D).

biseriate. Made up of two rows of cells; e.g., a biseriate antheridial stalk.
bistratose. Composed of two cell layers; e.g., leaves that are two layers of cells thick.
bog. Wet, spongy ground consisting chiefly of decaying moss and other vegetable matter.
bordered. Having margins differentiated from the rest of the structure in shape, size, color, or thickness.
boreal. Northern, especially of the coniferous forests that occur in the Northern Hemisphere between the treeless tundra and the deciduous forest belt.
bracts. Specialized leaves surrounding reproductive organs (Figs. 2A; 5A).
bracteole. A modified underleaf associated with a gametangium (in liverworts).
brood body (= **propagule**). A vegetative reproductive structure.
bulbil. Bulb-like axillary propagule or rhizoidal gemma.

c-shaped papilla. Papilla (or mammilla) appearing crescent-shaped (occasionally circular) when viewed from above (Fig. 188D).
caducous (= **deciduous**). Detaching, falling off.
caespitose. Tufted, growing in cushions or sods.
calciphytic (= **basiphytic**). Growing on basic substrates.
calyptra. A membrane of haploid tissue over the developing sporophyte, derived largely from the archegonial venter. In mosses, the venter generally ruptures near the base and the calyptra is carried upward by the elongating seta. In liverworts, the venter ruptures near the apex and is not carried upwards by the seta (Figs. 1A; 5A; 11O).
campanulate. Bell-shaped (Fig. 11O).
canaliculate. Channeled (lengthwise).
cancellate. Lattice-like.
cancellinae (sing. **cancellina**). Areas of large, empty, and usually hyaline basal leaf cells (Fig. 9O,P).
capillary. Slender, hairlike.
capitulum. Head.
capsule (= **theca**). The sporangium or spore-bearing portion of the sporophyte (Figs. 1A; 4K; 11A-M).
catenulate. Chain-like.
caulonema (plur. **caulonemata**). The brown, bud-generating part of the filamentous moss protonema, consisting of long cells with oblique end walls (cf. **chloronema**).
central strand. A small group of narrowly elongated cells forming a central axis in stems or thalli (Fig. 6L).
cernuous. Nodding or drooping.
channelled. Hollowed out like a gutter and semicircular in cross-section.
chlorocyst. Green cell, containing chlorophyll (opposite of **hyalocyst**) (Fig. 9G,L).
chloronema (plur. **chloronemata**). The green, photosynthetic part of the filamentous moss protonema, consisting of short cells with perpendicular end walls (cf. **caulonema**).
chlorophyllose. Containing chlorophyll (=green pigment), generally green unless masked by some other pigments.
chloroplast. An organelle inside the cell containing chlorophyll (=green pigment) and carrying on photosynthesis.
cilia (sing. **cilium**). Hair-like or thread-like structures, mostly one cell wide and unbranched.
ciliate. With hair-like appendages.
circinate. Curved in a circle.
circumboreal. Widespread in the higher, boreal latitudes of the Northern Hemisphere (cf. **boreal**).
cladia (sing. **cladium**). Modified, small caducous branches for vegetative reproduction.

cladocarpous. Producing sporophytes terminally on short lateral branches.
clathrate. Latticed or pierced with apertures.
clavate. Larger and thickened towards the apex, club-shaped.
cleistocarpous. Indehiscent; capsule without a regular mechanism for opening.
coalesced. Fused together. Union of like parts.
coelocaule. A specialized shoot calyptra in certain leafy liverworts, characterized by extreme axial growth and complete penetration of the sporophyte into the shoot apex; frequently associated with the absence of a perianth; e.g., in *Trichocolea*.
collar. Sheath of tisse around the base of branches in leafy liverworts (Fig. 3A-D).
collenchymatous. With cell walls more heavily thickened at the angles (Fig. 31D,G).
columella. The central, sterile column of tissue in the capsule of mosses and hornworts.
comal tuft. A tuft of leaves at the tip of a stem or branch (Fig. 7E).
comose. With larger leaves forming tufts at the stem tips.
complanate. Flattened or compressed; e.g., leaves flattened into one plane (Fig. 7O).
complicate. Folded together.
complicate-bilobed. Having 2 leaf lobes folded against one another (Figs. 41G; 66H).
concolorous. Uniform in color.
conducting strands. The central group of leptoids or hydroids inside the stem.
conduplicate. Folded longitudinally along the middle.
confluent. Blending of two structures into one.
conical. Cone-shaped (Fig. 11N).
connate. Fused.
connivent. Directed or pointing together; e.g., tips of leaf segments converging towards one another (Fig. 19G).
constricted. Abruptly narrowed; e.g., urn below capsule mouth.
contorted (= tortuose). Irregularly curved or twisted (Fig. 191K).
contracted. Abruptly narrowed or shortened.
convolute. Rolled together.
cordate. Heart-shaped. Of leaves: with two large, rounded areas at base (Fig. 8C). Of trigones: with 2 convex sides and 1 concave side (Figs. 34A; 35H).
cortex. Stem tissue located between the central strand and epidermis (Fig. 6L,M), often used in liverworts to denote the differentiated outer ring or epidermal cell layer of the stem (Fig. 4E).
cortical. Referring to the outer part of a stem, or cortex.
corticolous. Growing on bark.
cosmopolitan. Occurring in all major floristic zones of the world.
costa (= **midrib, nerve**). Mid-vein of a leaf or thallus, always more than one cell thick (Figs. 2D; 8D-G; 9E,F).
costate. With a costa.
crenulate. With minute, rounded teeth (Fig. 54F-G).
crisped (= **crispate**). Strongly wavy; variously curled, twisted and contorted.
cristate. Crested; bearing a crest-like ridge.
cucullate. Hooded or hood-shaped; a calyptra split along one side only (Fig. 11O); also used to describe leaves strongly concave and erect or inflexed at the tips (Fig. 8B).
cultriform. Curved and asymmetric.
cuneate (= **cuneiform**). Wedge-shaped (Fig. 8C).
cupulate. Cup-shaped, rounded and swollen.
cushions. Growth form with stems $\pm$ erect, tightly clustered and somewhat radiating at edges (Fig. 6C).
cuspidate. Ending abruptly in a stout, rigid point (Fig. 8B).
cuticle. A cutinized layer on the outside surface of the epidermis.

cygneous. Curved like a swans neck.
cylindrical. Narrowly elongate, circular in transverse section (Fig. 11D).
cymbiform. Concave and broadly boat-shaped (Fig. 209H).

deciduous (= **caducous**). Detaching, falling off.
decolorate. Discolored, colorless.
decorticated. Lacking bark.
decumbent. With stem prostrate but with ascending tips.
decurrent. With leaf bases extending down the stem beyond the leaf insertion (Fig. 8C).
dehiscent. Having a distinct opening mechanism; e.g., capsule opening by means of an operculum or valves (opposite of **indehiscent**).
deltoid. Shaped like an equilateral triangle.
dendroid. Tree-like; with erect stems (cf. **frondose**) that are branched only in the upper part on all sides, the lower part forming the “trunk“ or **stipe**.
dentate. With sharp, coarse teeth (Fig. 10C).
denticulate. Finely toothed (Fig. 43F,J).
depauperate. Poorly developed.
dextrorse. Twisted to the right, or clockwise when seen from the apex; e.g., twist of seta (opposite of **sinistrorse**).
diaspore. An agent of dispersal; any structure that becomes detached from the parent plant and gives rise to a new individual.
dimorphic. Occurring in two forms; e.g., with two types of leaves.
dioicous (= dioecious). With archegonia and antheridia on separate plants (see note after **autoicous**) (Fig. 1B).
diploid. Having a double set of chromosomes (2n).
diplolepidous. Arthrodontous peristome with two concentric circles of teeth: an outer circle (**exostome**) and an inner circle (**endostome**). The exostome is generally more heavily thickened than the endostome; one of the two circles may be vestigial. In a strict sense diplolepidous refers to an arthrodontous peristome with teeth having two rows of cells on its dorsal plate (opposite of **haplolepidous**).
disciform. Flat and circular.
discoid. Flat and rounded, shaped like a disc.
distal. Away from the base or point of attachment; towards the apex of a leaf or stem; the outer, convex face of a spore (opposite of **proximal**).
distant. Well-spaced; e.g., leaves positioned with a space between adjacent leaves.
distichous. Leaves in two rows (Fig. 7A,P).
divergent. Turned in opposite directions.
divisural line (= **median line**). Longitudinal line on the surface of a peristome tooth, usually zigzag and sometimes recessed in a furrow (Fig. 11U).
dorsal. The upper surface, away from the substrate. In mosses, the abaxial surface of leaves (opposite of **ventral**).
dorsiventral. Flattened, with distinct upper and lower surfaces.
double peristome. Having both an endostome and an exostome (cf. **diplolepidous**)
doubly serrate. Serrate with teeth in pairs (Fig. 10C).

ecostate. Without a costa (Fig. 9A).
egg. The female gamete, produced in an archegonium (Fig. 1A).
edentate. Without teeth.
elaters. Long, slender, hygroscopic, 1-celled structures with spiral thickenings, found interspersed among the spores of liverworts and hornworts, derived by mitotic divisions (Fig. 4L).

elaterophore. A tuft or brush-like mass of cells to which elaters are attached, at the base or the apex of some liverwort capsules (e.g., in *Riccardia*, *Metzgeria*) (Fig. 2C).
elimbate. Lacking a border.
elliptical. Oblong with convex sides.
emarginate. Having a broad and shallow notch at the apex (cf. **retuse**) (Fig. 8B).
embryo. Young sporophyte, developing from a zygote (Fig. 1A).
emergent. Partially exposed, referring to capsules or perianths only partly projecting beyond the tips of perichaetial leaves or bracts.
endemic. Limited to a single country or floristic area.
endogenous. Originating from internal rather than superficial cells or tissues.
endosporic. Inside the spore wall.
endostome (= **inner peristome**). The inner circle of teeth of a double (diplolepidous) peristome (Fig. 11U).
ensiform. Sword-shaped.
entally. Towards the inner side, referring to the position of the hyaline papilla on the lobule of Lejeuneaceae.
entire. Without teeth (Fig. 10C).
ephemeral. Short-lived.
epidermis. The outer cell layer of a stem or thallus (Fig. 6L).
epilithic (= **saxicolous**). Growing on rock.
epiphragm. A circular membrane positioned over the capsule mouth of some mosses (Fig. 11P).
epiphyllous (= **foliicolous**). Growing on living leaves of other plants.
epiphyte. A plant growing on another living plant.
epiphytic. Growing on another living plant.
epistatic. In leafy liverworts, lobules of male bracts not overlapping ventrally (opposite of **hypostatic**) (Fig. 39A).
equidistant. Regularly separated or spaced.
equitant. Straddling; referring to conduplicate and strongly sheathing leaf bases; e.g., in *Fissidens*.
erect. With leaves directed toward stem apex; with leaf margins curved upward; with capsules straight, not curved (Figs. 7H; 11C-I).
erose. Irregularly notched or ragged.
excurrent. Extending beyond the apical margin; e.g., an awn formed by a protruding costa (Fig. 9C).
exosporic. Outside the spore wall.
exostome (= outer peristome). The outer circle of teeth of the diplolepidous peristome (Fig. 11U).
exothecium. The outermost layer of the capsule wall; the capsule epidermis (Fig. 11Q,T).
exserted. Protruding and largely exposed (cf. **emergent**) (Fig. 11A).
exsiccatae (sing. **exsiccata**). Dried plants; referring to widely distributed sets of herbarium specimens with printed labels, used as standards for comparison.

falcate. Curved like the blade of a sickle (Fig. 7N).
falcate-secund. Strongly curved and turned to one side (Fig. 7M).
fascicle. Cluster or bundle or branches.
fasciculate. In bundles or fascicles.
fenestrate. Pierced with openings or perforations.
fertile. In bryophytes, with gametangia or sporophytes (opposite of **sterile**).
fibril. Fine, fiber-like wall thickening.
filamentous. Thread-like.

filiform. Slender and elongate.
flaccid. Soft, limp.
flagelliform. Whip-like; branches with a gradual attenuation from ordinary leaves at the base to minute, scale-like leaves at the tip .
flagellum (plur. **flagella**). Whip-like structure; a branch with scale-like leaves (Fig. 58C).
flexuose. Slightly and irregularly bent or twisted.
foliicolous (= **epiphyllous**). Growing on leaves of other plants.
foliose. Leafy or leaf-like.
foot. Basal portion of the bryophyte sporophyte, embedded in the gametophyte and serving as an organ of absorption and attachment (Figs. 4K; 5A).
fovea. A depression or pit.
foveolate. Pitted.
fragmentation. Breaking up; a method of vegetative reproduction in which an organ (or plant) is separated into parts capable of producing a new organism.
fringed. With a ciliate margin.
frond. The erect, foliose stem (including branches) of a **frondose** bryophyte.
frondose. With erect stems that are branched only in the upper part in one plane (Fig. 6H) (cf. **dendroid**).
furcate. Forked.
furrowed. Grooved (Fig. 11F).
fusiform. Spindle-shaped; narrow (more than 3 times as long as wide) and tapered at both ends.

gametangiophore. Stalked receptacle bearing gametangia, arising from the thallus in Marchantiales (cf. **antheridiophore**, **archegoniophore**).
gametangium. Sex organ (cf. **archegonium, antheridium**).
gamete. Sexual reproductive cell (cf. **spermatozoid**, **egg**).
gametoecium. Gametangia and surrounding bracts (cf. **androecium**, **gynoecium**).
gametophyte. The haploid, sexual generation producing gametes (spermatozoids and eggs) in antheridia and archegonia. In bryophytes, the gametophyte is the actual plant (Fig. 1A).
gemmae (sing. **gemma**). Vegetative diaspores (Fig. 9J,K).
gemmae cup. Cup-shaped, gemmae-containing structure (Fig. 2E,F).
gibbous. Swollen on one side.
glabrous. Smooth.
glaucous. Whitish-blue.
globose. Spherical (Fig. 11H).
granular. Composed of small globules, referring to segmented oil bodies (Fig. 4C)
granulose. Roughened with minute, blunt projections.
gregarious. Growing together in loose tufts.
guard cells. Specialized cells bordering a stoma in the capsule wall (Fig. 11S).
guide cells. Large, thin-walled cells found in a median layer across the costa of many mosses, part of the conducting cells (Fig. 9F).
gymnostomous. Lacking a peristome.
gynoecium (plur. **gynoecia**). Archegonia and the surrounding bracts; the female gametoecium (Fig. 1A).

habit. The general appearance of a plant.
habitat. The local environment of a plant.
hair-point. Awn, usually formed by an excurrent costa (Figs. 132K; 177E).
haploid. Having a single set of chromosomes (n).

haplolepidous. Arthrodontous peristome with only one circle of teeth (homologous with the endostome of the diplolepidous peristome). In a strict sense referring to an arthrodontous peristome with teeth having a single row of cells on the outer plate (opposite of **diplolepidous**).
heliophilous. Growing in sunny places.
heteroicous (= **polyoicous**). Used for species that can be both monoicous and dioicous.
heterophyllous. Having leaves of different sizes or shapes.
hexagonal. With 6 angles, usually of cells (Fig. 10A).
hispid. With short, stiff hairs; bristly.
homologous. With a common phylogenetic or developmental origin (opposite of **analogous**).
homomallous. Pointing the same way (cf. **secund**) (Fig. 139A-B)
humus. Decomposing organic material.
hyaline. Colorless or transparent.
hyaline papilla. Tiny, thin-walled, secretory cell associated with leaf initial cells in liverworts and persisting in mature leaves, e.g., at the tip of the stylus in the Jubulaceae, at the base of the leaf lobe and at the base and the apex of the lobule in the Lejeuneaceae. The position of the papilla at the lobule apex can be proximal or distal (Fig. 4G,H).
hyalocyst (= **leucocyst**). Large, empty, water-storage cell without chlorophyll in leaves of *Sphagnum* and *Leucobryum* (Fig. 9G I,L).
hyalodermis. Stem epidermis of enlarged, hyaline cells (Figs. 4E; 6M).
hydroid. Tracheid-like conductive cell in the central strand and costa of some bryophytes, especially mosses.
hydrophilous. Growing in water.
hygrophytic. Growing in wet (= hygric) places.
hygroscopic. Moving in response to changes in humidity; e.g., peristome teeth, elaters.
hypostatic. In leafy liverworts, lobules of male bracts overlapping ventrally, imbricate (opposite of **epistatic**) (Figs. 35C; 49A).

imbricate. Overlapping, like shingles on a roof (Fig. 7G).
immersed. Submerged, completely below the surface (Fig. 11B).
inclined. Bent down (Fig. 11M).
incrassate. With thickened cell walls.
incubous. In liverworts, an oblique leaf insertion in which the antical leaf margins are oriented toward the dorsal side of the stem (when viewed from above, each leaf overlaps the one above) (opposite of **succubous**) (Fig. 3L,M).
incurved. Curved upward (adaxially) and inward .
indehiscent. Lacking a distinct opening mechanism (opposite of **dehiscent**).
inflexed. Bent abruptly upward (adaxially) at more than 90° and inwardly.
inflorescence = **gametoecium**.
inner peristome (= **endostome**). The inner circle of teeth of a diplolepidous peristome (Fig. 11U).
innovation. A branch formed at the base of a gynoecium (mosses) or at the base of the perianth (liverworts). In Lejeuneaceae, innovations can be lejeuneoid (Fig. 4J) or pycnolejeuneoid (Fig. 4I).
inrolled = **involute**.
insertion. The place or line of attachment of a structure.
intercalary. Intermediate in position, somewhere below the apex.

intercalary branch. Branch originating from the inside of stem, away from the apex, usually having a collar at the base; the associated leaves are not modified by branch formation (opposite of **terminal branch**) (Fig. 3A-D).
involucre. A structure, usually tubular or scale-like, surrounding the gametangia or the developing sporophyte; also, the bracts (and bracteoles) of the gynoecium (= **perichaetium**) (Fig. 2C).
involute. Rolled upward (adaxially) and tightly inward (opposite of **revolute**) (Fig. 10B).
isodiametric. About as broad as long (Fig. 10A).
isophyllous. Having stem and branch leaves similar.

julaceous. Smoothly cylindric, like a catkin (Fig. 7R).

keel. A fold (Fig. 4F).
keeled. Folded along the middle, like the keel of a boat (Fig. 10B).

lacerate. Appearing deeply and irregularly slashed or torn.
laciniae (sing. **lacinia**). Appendages coarser than cilia, more than one cell wide (Fig. 57B-C).
laciniate. Fringed with lacinia (Figs. 57C; 62K).
lamella. Ridge, plate, or filament-like outgrowth of the surface (Fig. 172N-O).
lamina. The thin, flattened portion of the leaf excluding the costa and the border (Fig. 8D,G); the thin wings on either side of the midrib of a thallose liverwort (Fig. 70G-I).
lanceolate. Lance-shaped, narrow and tapered from near the base (Fig. 8A).
lanuginose. Woolly, tomentose.
lax. Loosely.
leptoid. Conductive cell similar to sieve tube elements in form and function; found in the central strand and costa of some mosses; e.g., in Polytrichaceae.
leucocyst = **hyalocyst**.
lignicolous. Occurring on dead, decorticated wood.
ligulate. Strap-shaped; long and narrow with parallel sides (sometimes used to mean tongue-shaped or **lingulate**) (Fig. 206A-B).
limbidium. Differentiated leaf border.
limb. Leaf lamina above a differentiated leaf base (Fig. 8E).
linear. Very long and narrow, with parallel sides; narrower than lingulate (Figs. 8A; 10A).
lingulate. Tongue-shaped, oblong below, broader toward the apex (cf. **ligulate**) (Fig. 186G).
lobe. A major segment of a leaf, larger than a tooth (cf. **lobule**) (Fig. 4F).
lobule. A small lobe; e.g., the smaller segment of a complicate-bilobed leaf with unequal segments (Fig. 4F).
longitudinal. Lengthwise, parallel to the long axis; e.g., longitudinal leaf insertion.
lumen (plur. **lumina**). The cavity of a cell, enclosed by a wall.

macronemata (sing. **macronema**). Large, branched rhizoids produced around branch primordia and at the base of buds (opposite of **micronemata**).
mammilla (plur. **mammillae**). Hollow projection from the cell surface, with the cell lumen extending into the protuberance (opposite of **papilla**) (Fig. 10D).
mammillose. With **mammillae** (Fig. 10D).
marsupium. A modified shoot calyptra or coelocaule that penetrates downward into the substrate, in certain liverworts (Fig. 5D).
mat. Growth form with stems horizontal and densely interwoven.
median. Central, middle.

median line (= **divisural line**). Longitudinal line on the surface of a peristome tooth, usually zig-zag and sometimes recessed in a furrow (Fig. 11U).
medulla. Internal tissue of stem and seta (Fig. 4E).
meristem. A tissue composed of actively dividing (by mitosis), undifferentiated cells.
merophyte. A segment cut off from the apical cell and the tissues and organs derived from it. A mature merophyte consists of one leaf and associated stem tissue.
mesophytic. Growing in moist (= mesic) places.
micrometer (= **micron**). One thousandth of a millimeter (abbreviated µm).
micronemata (sing. **micronema**). Small, thin, sparsely branched rhizoids produced on stem between leaves (opposite of **macronemata**).
microphyllous. Small-leaved (cf. **flagelliform**).
mid-leaf. Middle of a leaf (Fig. 8D).
midrib = **costa**.
mitrate (= **mitriform**). Conical and undivided (similar to a bishop's mitre) or equally lobed at base (Fig. 11O).
monochasial. An arrangement of gynoecia in a row, formed by repeatedly innovating branches (Figs. 49G; 54D).
monoicous (= **monoecious**). Bisexual, with antheridia and archegonia on the same plant; including **autoicous**, **synoicous** and **paroicous** (see note after **autoicous**) (Fig. 1B).
monolete. In spores, having a single, linear scar on the proximal surface that marks the point of attachment in the tetrad (cf. **trilete**).
montane. Pertaining to mountains; altitudinal belt between lowlands and timberline.
mucro. A short, abrupt point.
mucronate. Ending in a short, abrupt point (**apiculate** is somewhat longer; **cuspidate** is even longer and stouter) (Fig. 8B).
multi-. Many.

n. The haploid (gametophytic) chromosome number of an organism.
neck. The sterile, basal portion of a capsule, sometimes considerably differentiated (**= apophysis**); also, the upper, narrow part of archegonium (Fig. 11L).
nematodontous. A peristome consisting of whole, dead cells with more or less evenly thickened walls (e.g., Polytrichaceae) (Fig. 11R).
nerve = **costa**.
nodulose. With minute, knob-like wall thickenings.
Non-articulate. Not in distinct, even tiers; e.g., the epidermal cells of the seta (opposite of **articulate**).

oblanceolate. Lance-shaped, narrow and tapered towards the base, broadest at apex (Fig. 8A).
oblate. Wider than long.
oblique. Slanted; e.g., an oblique leaf insertion is one that is between transverse and longitudinal.
oblong. Rectangular with rounded corners or ends (Fig. 8A).
obovate. Egg-shaped with apex broader than base (Fig. 8A).
obtuse. Blunt, broadly pointed, at an angle greater than 90º (Fig. 8B).
ocellus (plur. **ocelli**). A specialized cell in the leaves (and perianth) of some members of *Frullania* and Lejeuneaceae, having one large oil body and lacking chloroplasts.
oil body. A membrane-bound organelle containing terpenoids, characteristic of liverwort cells (Fig. 4A-D).
oil cell. Small, colorless cell in the thallus of the Marchantiales, containing a large oil body and no chloroplasts.

opaque. Not transparent.
operculum. Lid covering the mouth of the capsule, falling away when the spores are mature; in mosses and some thalloid liverworts (Marchantiales) (Figs. 1A; 11N).
orbicular. Nearly circular (Fig. 8A).
outer peristome = **exostome**.
oval. Widely elliptical (Fig. 10A).
ovate. Egg-shaped, broader at the base than at the apex (Fig. 8A).
ovoid. Egg-shaped, used in reference to a solid (cf. **ovate**: an egg-shaped plane) (Fig. 11I).
ovum. Egg.

paired. Associated in groups of two; e.g., hairs, teeth (Figs. 69F; 157M).
palmate. Lobed or branched in a radiating fashion, resembling fingers spreading from the palm of a hand (Fig. 65M).
papilla (plur. **papillae**). A solid projection from the cell surface (opposite of **mammilla**) (Fig. 10D).
papillose. Roughened by papillae (Fig. 10D).
paraphyllia (sing. **paraphyllium**). Small, green outgrowths of various shapes, i.e., filiform, lanceolate, scale- or leaf-like.
paraphyses (sing. **paraphysis**). Hairs associated with antheridia and archegonia.
paroicous (= **paroecious)**. With antheridia in the axils of bracts just below the perichaetium, on the same shoot (see note after **autoicous**) (Fig. 1B).
peat. Decomposed vegetable matter (including *Sphagnum*).
pegged rhizoids. Rhizoids with papilla-like projections on the inner wall surface.
pellucid. Clear, transparent.
pendent (= **pendulous**). Hanging downward (Figs. 6J; 11L).
percurrent. Extending to the apex (Fig. 9D).
perforate. Pierced through (Fig. 11W).
perianth. Organ of foliar origin enclosing the archegonia in most leafy liverworts (Figs. 2A; 5E-P).
perichaetium. Cluster of modified leaves (bracts, bracteoles) enclosing the archegonia.
periclinal. A plane of cell division parallel to the surface.
perigonium. Cluster of modified leaves (bracts, bracteoles) enclosing the antheridia.
perigynium. A somewhat fleshy, tubular structure surrounding and protecting the archegonia and the developing sporophyte, derived from axial cells; a perigynium may or may not be associated with a shoot calyptra (Fig. 5C).
peristome. A circular structure of teeth (i.e., 4, 8, 16, 32, or 64), arranged in a single or double row around the mouth of a capsule (Fig. 11P,T,U).
piliferous. With hair point (Fig. 177E).
pilose. With long hairs.
pinnate. Branched in a feather-like fashion, with numerous branches in a plane on opposite sides of the stem (Fig. 7S).
pitted. Having small depressions or holes in the cell wall (Fig. 10D).
plane. Flat (Fig. 10B).
pleurocarpous. Producing sporophytes laterally (from a very short branch) rather than at the stem tip (opposite of **acrocarpous**).
plica (plur. **plicae**). Longitudinal furrow.
plicate. With longitudinal furrows (Fig. 91G; 160A-B).
pluripapillose. Having several papillae on the cell surface (Fig. 10D).
plumose. Closely and regularly pinnate, feathery.
polymorphic. Of more than one form, variable.

pore. A small opening.
porose. Having pores.
postical. The vental surface of a stem; the leaf margin oriented towards the base of an obliquely inserted leaf (opposite of **antical**).
precocious. Developing early; e.g., spores germinating inside the capsule.
preperistome = prostome.
primary stem. Main stem; in some mosses a long creeping, rhizome-like stem from which secondary leafy shoots arise.
procumbent. Spreading, prostrate.
prolate. Longer than wide.
propagule. Reduced bud, branch, or leaf serving in vegetative reproduction (cf. **diaspore**).
prorate (= **scindulose**). Having papillae or mammillae borne at the tips of cells, or formed by projecting cell ends (Fig. 10D).
prostome (= **preperistome**). A rudimentary structure outside, and usually adhering to, the peristome teeth; e.g., Pterobryaceae.
prostrate. Laying flat on the ground; creeping.
protonema (plur. **protonemata**). A filamentous or thalloid structure resulting from spore germination and giving rise to one or more gametophores (Fig. 1A).
proximal. Near the base or the point of attachment; the internal face of a spore (opposite of **distal**).
pseudoelater. The unicellular or multicellular sterile cells in the hornwort capsule, lacking spirals (Fig. 79E; 80G,N).
pseudoparaphyllium. Small, filiform or foliose structure resembling paraphyllium, but restricted to the areas of the stem around branch primordia; found in pleurocarpous mosses.
pseudoperianth. The inner one of two involucres in some thalloid liverworts; usually a thin, tubular structure of thalline origin surrounding the archegonia, the calyptra, and the developing sporophyte, and enclosed by the outer involucre (Fig. 70A,M).
pseudopodium. An elongation of the gametophyte axis below the sporophyte in *Sphagnum* and *Andreaea*, serving as a seta.
pseudopores. Pore-like structures with a thin membrane (revealed only by staining).
punctate. Dotted.
pyrenoid. A proteinaceous structure involved in carbohydrate synthesis, found in the chloroplasts of hornworts (and most green algae).
pyriform. Pear-sheaped (Fig. 11E).

quadrate. Square or nearly so (Fig. 10A).
quadrifid. Divided into four lobes or segments.

radiculose. Covered with rhizoids.
ramenta. Strap-shaped, leaf-like paraphyses that develop after fertilization, e.g. in *Neckeropsis.*
ranked. In vertical rows.
receptacle. A disc or wart-like structure bearing antheridia or archegonia in thalloid liverworts; found on the thallus, inside the thallus, or elevated on a stalk-like branch (cf. **gametangiophore**).
rectangular. Longer than wide with straight angles (Fig. 10A).
recurved. Curved downward (abaxally) and inward.
reflexed. Bent abruptly down (abaxally) at more than 90° and inwardly.
regeneration. The development of a new plant from a dedifferentiated adult cell.
reniform. Kidney-shaped (Figs. 41E; 46H).

resorption. Disappearance or erosion of parts of cell walls.
resorption furrow. In *Sphagnum*, furrow along the leaf margin, produced by resorption of the outer wall of elongated leaf margin cells.
reticulate. Forming a network.
retort cells. In *Sphagnum*, flask-shaped hyalodermis cells terminating in a pore.
retrorse. Directed backward or downward (opposite of **antrorse**).
retuse. Having a narrow, shallow indentation or a small notch in a broad, rounded apex (cf. **emarginate**) (Fig. 8B).
revolute. Rolled downward (abaxally) and backward (opposite of **involute**) (Fig. 10B).
rheophytic. Growing in running water (rivers, creeks) but producing reproductive organs on emerged shoots (cf. **aquatic**).
rhizoid. A root-like hair that functions as anchorage; in liverworts and hornworts 1-celled, in mosses many-celled and with oblique end walls (Fig. 2A).
rhizoid disc. A cushion-like swelling at the base of an underleaf in leafy liverworts, from which rhizoids originate (cf. **secondary rhizoid disc**) (Fig. 51A).
rhizome. A slender, creeping, often subterranean stem with reduced leaves, giving rise to erect secondary stems or fronds.
rhombic. Diamond-shaped, oblong-hexagonal (Fig. 10A).
rhomboidal = **rhombic**.
rosette. In mosses, a compact cluster of leaves encircling the stem; in thalloid liverworts, a rounded, segmented thallus with segments radiating from a central point; in leafy liverworts (Jubulaceae, Lejeuneaceae), a small rounded area on the spore surface consisting of radially arranged spines (Fig. 4M).
rostrate. Beaked (Fig. 11N).
rostrum. Beak.
rugose. With transverse wrinkles or undulations (Figs. 159H; 184C).

saccate. Sac-like; abruptly and deeply concave.
saxicolous (= **epilithic**). Growing on rocks.
scabrose (**= scabrous**). Rough.
scale. A thin, membranous structure (Fig. 2G).
scleroderm. Cylinder of thick-walled cells inside the hyalodermis.
scindulose = **prorate**.
secondary rhizoid disc. Disc of fused rhizoids in epiphyllous bryophytes (Fig. 53E,H).
secund. Turned to one side (cf. **homomallous**) (Fig. 139A-B).
sensu. In the sense of, according to.
septum (plur. **septa**). A partition or wall.
seriate. A row, e.g., uni-, bi-, tri-, multiseriate; applied to adjacent rows of cells.
serrate. Saw-toothed; with marginal teeth pointing forward (towards apex) (Fig. 10C).
serrulate. Minutely serrate.
sessile. Without a stalk or seta.
seta (plur. **setae**). Stalk-like portion of the sporophyte, between capsule and foot (Figs. 1A; 2A; 4K).
setaceous. Bristle-like.
sheathing. Surrounding and clapsing the stem or base of seta (Fig. 8C,E).
shoot calyptra. A somewhat fleshy calyptra derived from the archegonial venter and from axial or thalline tissue peripheral to the archegonium (Fig. 5B).
shoulder. An area of abrupt narrowing; e.g., the area where the leaf base is abruptly narrowed into the lamina (Fig. 8E).
sigmoid. Doubly curved in opposite directions, S-shaped.

simple second stem. Unbranched secondary leafy shoot, usually arising from rhizome and upright (Fig. 6I).
sinistrorse. Twisted to the left, or counterclockwise when seen from apex; e.g., twist of seta (opposite of **dextrorse**).
sinuate (= **sinuose**). Wavy (Fig. 10D).
sinus. A depression separating two segments or lobes.
slime hair. A hair-like, mucilage-secreting outgrowth of the epidermis.
slime papilla. A clavate, mucilage-secreting cell.
spathulate. Tapering to the base from a broad, rounded apex (Figs. 209G; 210C).
spermatozoid (= **antherozoid**, **sperm**). The male gamete, produced in an antheridium.
spinose. With sharp, pointed teeth (Fig. 10C).
spore. In bryophytes, a reproductive unit produced in the capsule as a result of meiosis, upon germination giving rise to a protonema (Figs. 1A, 4M).
sporeling. Protonema and juvenile gametophore arising from a spore.
sporophyte. The diploid, asexual generation producing (meio)spores; in bryophytes consisting of a foot, seta, and capsule and attached to the gametophyte (Figs. 1A; 4K).
spreading. Forming an angle of 45º or more (Fig. 7J).
squarrose. Spreading at right angles (Fig. 7K).
stegocarpous. Referring to capsules dehiscing by an operculum (opposite of **cleistocarpous**).
stellate. Star-shaped.
stereids. Elongate, thick-walled cells found in groups (**stereid bands**) in the costa or stems of some mosses (Fig. 9F, I).
sterile. In bryophytes, without gametangia or sporophytes (opposite of **fertile**).
stipe. The unbranched basal part of an erect stem (cf. **dendroid**).
stipitate. Having a stipe or stalk-like base.
stoloniferous. With slender, leafless branches.
stolon. Slender branch or shoot without leaves.
stoma (plur. **stomata**). Pore bordered by two guard cells, occurring in the capsule wall of hornworts and mosses (Fig. 11S).
-stratose. In layers; e.g., uni-, bi-, multistratose (Fig. 10C).
striate. Marked with fine ridges or lines (Fig. 11V,Y).
striolate. Finely ridged.
struma. Cushion-like swelling at the base of the capsule (Fig. 11Js).
strumose. With a cushion-like swelling at the base of the capsule (Fig. 11J).
stylus (plur. **styli**). A minute, subulate to triangular structure usually crowned by a slime papilla, found between the lobule and the stem in some leafy liverworts (e.g., *Frullania*) (Fig. 27Bs; 28Fs).
subfloral innovation. A branch that arises just below the perianth (leafy liverworts) or a perichaetial leaf (mosses).
sub-. Under, below.
subula. A long, slender point.
subulate. Slender and long acuminate.
succubous. In liverworts, an oblique leaf insertion in which the antical leaf margins are oriented toward the ventral side of the stem (when viewed from above, each leaf overlaps the one next below) (opposite of **incubous**) (Fig. 3H,I).
sulcate. Strongly plicate, with deep longitudinal furrows or grooves.
synoicous (**= synoecious**). With antheridia and archegonia mixed in the same gametoecium (see note after **autoicous**) (Fig. 1B).

teniola (plur. **teniolae**). Intramarginal row (border) of differentiated cells in a leaf, generally more than one cell thick (Fig. 9P).
terete. Smooth-cylindrical, rounded in cross-section.
terminal. At the apex or distal end (opposite of **basal**).
terminal branch. A branch formed at the stem apex; the branch is often associated with a half-leaf or half-underleaf and has no collar at its base (opposite of **intercalary branch**) (Fig. 3E-G).
terrestrial (= **terricolous**). Growing on soil.
tetrad. Group of 4 spores produced by meiotic division of a spore mother cell, often tightly pressed together so that the inner (= proximal) face shows the mark of the other spores.
tetrahedral. Four-sided; e.g., apical cell of most leafy liverworts.
thallus (plur. **thalli**). A flattened plant body, not differentated into stems and leaves.
thalloid (= thallose). Thallus-like; flat and ribbon- or rosette-like.
theca (plur. **thecae**). See **capsule**.
thecal. With a sheath of tissue around the base; said of collared branches (Fig. 3A-D).
tomentose. Woolly.
tomentum. A felt-like covering of abundant rhizoids.
tooth (plur. **teeth**). Sharp, projecting cells on margin or face of leaf; divisions of a peristome (Fig. 11R,T-Y).
tortuose. Irregularly bent or twisted (Fig. 191G).
trabecula (plur. **trabeculae**). Projections from the horizontal walls on either face of arthrodontous peristome teeth.
transverse. Across, perpendicular to the axis; e.g., the cross-wise attachment of a leaf, as opposite of an oblique attachment (Fig. 3J,K).
trifid. Divided into three segments.
trigone. A 3-angled thickening at corners of cells (cf. **collenchymatous**) (Fig. 31D,G).
trigonous. Three-angled; applied to a 3-keeled perianth (Fig. 34F; 39A).
trilete. In spores, having a triradiate scar on the proximal surface that marks the point of attachment in the tetrad (cf. **monolete**).
tristichous. With leaves in 3 ranks (Fig. 7B).
truncate. Abruptly cut off at the apex (Fig. 8B).
tuber. Multicellular gemma borne on rhizoids (**= rhizoidal gemma**) or on the ventral side of the axis or thallus.
tuberculate. With small warts (coarser than papillae).
tubulose. Tube-like, referring to leaves or thalli with strongly incurved or overlapping margins (Fig. 10B).
tuft. Small cushion; growth form with stems erect but radiating at the edges.
turf. Growth form with stems erect, parallel and close together (Fig. 6A,B).

underleaves (= **amphigastria**). A third row of leaves found on the ventral surface of the stem in liverworts (Figs. 2A; 4F).
undulate. Wavy (Figs. 159H; 184C).
unipapillose. With one papilla per cell (Fig. 10D).
uniseriate. In one row.
unistratose. One layered, of a single cell layer.
urceolate. Urn-shaped (Fig. 11C).
urn. Spore-bearing portion of a capsule (Figs. 1A; 11P).
utricle. A bladder-shaped appendage, vesicle; the enlarged water-sac on branch leaves of *Ceratolejeunea*.

vaginant lamina. In *Fissidens*, the expanded lamina at the base of the leaf which clasps the stem and the base of the leaf above it.
vaginate. Sheathing.
vaginula. In mosses, a ring or sheath enveloping the base of the seta, derived from the base of the archegonium.
valve. One of the segments into which the capsule of liverworts, hornworts, and *Andreaea* separates upon dehiscence (Fig. 2A).
ventrad. Tilted to the ventral side of the stem, referring to leaves of liverworts.
ventral. The lower surface, next to the substrate. In mosses, the adaxial surface of leaves (opposite of **dorsal**).
vermicular. Narrowly cylindrical and curved, like a worm (Fig. 10A).
verrucose (= **papillose**). Roughened by small, wart-like elevations.
verticillate. Whorled.
vide. See.
vitta. In liverworts, the longitudinal band of elongated, often thicker-walled cells in a leaf, resembling a nerve but only one cell layer thick (Fig. 54I).

wart (= **papilla**). A small elevation or protuberance.
weft. A loosely interwoven, often ascending growth form.
wide spreading. Spreading at a wide angle, but less than 90º.
wing. A thin, flat membranous expansion or appendage.

xerophytic. Growing in dry (=xeric) places.

Abbreviations

aff. = *affinity*; related to
alt.= *altitude*; elevation
auct. = *auctoribus*; of certain authors
ca. = *circa*; approximately
cf. = *confer*; compare
c.fr. = *cum fructibus*; with sporophytes
c.sp. = *cum sporis*; with spores, with sporophytes
e.g. = *exempli gratia*; for example
et al. = *et alii*; and others
det. = *determinavit*; determined by
i.e. = *id est*; that is, in other words
incl. = including
in litt. = *in litteris*; in correspondence
leg. = *legit*; collected by
plur. = plural
p.p. = *pro parte*; partly
s.d. = *sine dato*; without date
sing. = singular
s.l. = *sensu lato*; in a broad sense
s.n. = *sine numero*; without number
spp. = species (plural)
s.str. = *sensu stricto*; in a narrow sense
viz. = *videlicet*; namely

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PART II. KEYS AND DESCRIPTIONS

Liverworts and hornworts

S. Robbert Gradstein

Liverworts
(Hepaticae)

Plants (= gametophyte) leafy or thalloid, growing by means of a 2-4-sided apical cell, meristem lacking. Leaves (in leafy liverworts) in 2-3 straight rows, the third row ventral, usually reduced in size or absent; leaves usually only one layer of cells thick, without midrib, undivided or divided into segments. Thallus (in thalloid liverworts) at least several cells thick in the middle, with or without midrib, inner tissue undifferentiated or with a specialized green, photosynthetic layer containing air chambers and pores. Cells with numerous chloroplasts and usually with oil bodies, pyrenoids lacking, cell walls often with trigones. Rhizoids unicellular (very rarely made up of several cells). Antheridia spherical, stalked, 1-several in axils of leaf-like bracts, in thallus cavities or on the thallus surface. Archegonia flask-shaped, 1-several surrounded by leaf-like bracts (leafy plants) or an involucre (thalloid plants). Sporophyte consisting of foot, seta, and capsule (= theca), enveloped until maturity in a calyptra and usually surrounded by additional protective structures: a perianth, perigynium, or marsupium in leafy plants; an involucre or pseudoperianth in thalloid plants. Seta colorless and rather fragile, elongating after spore maturation. Capsule spherical to cylindrical, wall without stomata, containing spores and elaters, columella absent; dehiscence of capsule usually by means of (1-)4 valves; peristome absent. Protonema very small, thalloid, normally giving rise to only one new gametophyte.

The class Hepaticae or liverworts contains about 5000 species worldwide, in 300 genera and 50 families. About one fourth of the species (ca. 1350) occur in tropical America, in 191 genera and 41 families. The Hepaticae are usually classified into six orders, Calobryales, Jungermanniales, Marchantiales, Metzgeriales, Monocleales, and Sphaerocarpales. The Jungermanniales and Calobryales are plants with leaves and are therefore called "leafy liverworts." The other groups lack leaves (a few members of the Metzgeriales excepted) and are the "thalloid liverworts."

All six orders of the Hepaticae are represented in the neotropical flora. The Jungermanniales (= leafy liverworts s.str.) are the largest group by far, containing about 1100 species or over 80% of the entire liverwort flora. The second largest group are the Metzgeriales (ca. 150 spp.), and the third largest the Marchantiales (ca. 100 spp.). The remaining orders Calobryales, Monocleales, and Sphaerocarpales are represented in the Neotropics by only a single species each.

In this treatment the families of the liverworts are arranged according to orders. The introductory key leads to the orders of the liverworts as well as to the class hornworts.

Introductory key to the liverworts and hornworts of tropical America

1. Plants with leaves 2
1. Plants without leaves 6
2. Leaves divided into segments ..... **Jungermanniales** (p. 86)
2. Leaves not divided into segments 3
3. Leaves in 3 equal rows, leaf insertion transverse ..... **Calobryales** (p. 88)
3. Leaves not in 3 equal rows (leaf insertion various) 4
4. Leaves incubous or transverse ..... **Jungermanniales** (p. 86)
4. Leaves succubous (or exactly longitudinal: thallus segments of *Symphyogyna*) 5
5. Leaf base several layers of cells thick. Rhizoids colorless, pale brown or purple. Cells thin-walled, without trigones, cuticle smooth. Sporophyte arising from dorsal surface of stem, away from apex ..... **Metzgeriales** (p. 184)

5. Leaf base only one layer of cells thick (except Lepidoziaceae: *Hygrolembidium, Pseudocephalozia*). Rhizoids colorless, pale brown or reddish, never purple. Cells thin-walled or thick-walled, often with trigones, cuticle smooth or papillose. Sporophyte from apex of stem or a short branch .... **Jungermanniales** (p. 86)
6. Plants consisting of a filamentous protonema or a tiny stem without leaves. Gametoecia on leafy branches ..... **Lepidoziacea**e
6. Plants thalloid, not consisting of a filamentous protonema or a tiny stem. Leafy branches absent 7
7. Dorsal surface of thallus covered by numerous obovate to cylindrical involucres, the involucres to 3 mm long (Fig. 72H). Thallus delicate, to 1 cm long. Subtropical regions .... **Sphaerocarpales** (p. 195)
7. Dorsal surface of thallus not covered by numerous involucres 8
8. Thallus unistratose throughout, without midrib ..... fern prothallium
8. Thallus more than one cell thick, or unistratose and with a midrib (midrib simple, not branched; when branched: Hymenophyllaceae!) 9
9. Epidermal cells with only 1 large chloroplast (2-4 in *Megaceros*). Capsules long-cylindrical to linear, green (turning ± black after dehiscence), without seta; usually numerous capsules projecting from the thallus surface. Thallus growing in rosettes ..... **Hornworts** (p. 209)
9. Epidermal cells with numerous small chloroplasts. Capsules globose to ellipsoidal, black, immersed in the thallus (then without seta), hanging down from stalked receptacles, or projecting upwards from the thallus on a long, colorless seta 10
10. Thallus with air chambers (cross section) and numerous small pores on the dorsal surface. Thallus underside with scales, at least near the tip. Antheridia and archegonia usually born in receptacles ..... **Marchantiales** (p. 195)
10. Thallus lacking air chambers and pores. Thallus underside with or without scales. Receptacles absent (except *Dumortiera*, couplet 13, which has stalked receptacles, and Monocleales, couplet 12, which have sessile male receptacles) 11
11. Plants growing in complete or incomplete rosettes (loosely forked in aquatic plants). Upper surface of the thallus with a median groove. Sporophytes embedded in the thallus .... **Marchantiales** (Ricciaceae, Oxymitraceae) (p. 195)
11. Plants not growing in rosettes. Upper surface of the thallus without median groove. Sporophytes not embedded in the thallus 12
12. Thallus surface in fresh material densely spotted with numerous small, whitish or darkish dots. Thallus without midrib, usually large (3-20 cm long), forked, with crispate-undulate margins. Capsules opening along a single, longitudinal fissure ..... **Monocleales** (p. 194)
12. Thallus surface not densely spotted in fresh material. Thallus with or without midrib. Capsules opening along 2-4 fissures or irregularly 13
13. Thallus large, 1-3 cm wide, forked, with a ventral midrib made of rhizoids. Rhizoids papillose (tuberculate). Archegonia and antheridia on stalked receptacles ..... **Dumortiera**
13. Thallus smaller, less than 1 cm wide, simple, forked or pinnate, without ventral midrib made of rhizoids. Rhizoids smooth. Stalked receptacles lacking 14
14. Thallus unbranched or with a few short, ventral-intercalary branches. Thallus margins, at least near the apex, with long, sausage-shaped slime papillae. Midrib present, narrow, on the ventral side with rhizoids in interrupted tufts. Sexual organs on leafy branches .... **Pteropsiella**
14. Thallus variously branched. Thallus margins without sausage-shaped slime papillae. Midrib present or absent, rhizoids when present not in interrupted tufts. Sexual organs on the thallus surface or under the surface in cavities, not on leafy branches ..... **Metzgeriales** (p. 184)

Order CALOBRYALES

Plants foliose, with erect leafy stems arising from a leafless rhizome. Branches lateral, *Fontinalis*-type, without collar, originating from the epidermis (similar to *Radula*-type but branch base not associated with a leaf). Leaves originating from only 1 initial cell, usually undivided, in three ± equal rows, underleaves similar to leaves or slightly smaller. Rhizoids lacking. Dioicous. Antheridia and archegonia borne in discs terminal on the stem, surrounded by bracts and bracteoles in one or a few series. Sporophyte surrounded by a fleshy calyptra; perianth lacking. Seta thick, of numerous cells (cross-section). Capsule cylindrical, opening by 1-4(-5) valves, wall only one cell-layer thick.

Contains only the genus *Haplomitrium* (family Haplomitriaceae), with an almost worldwide distribution.

Haplomitrium (Fig. 14) - One species in tropical America (7 worldwide): *H. blumii* (Nees) Schust. (= *H. andinum* (Spruce) Schust.), known from a few localities in the Lesser Antilles, Costa Rica, and the Andes.

HABITAT. *Haplomitrium blumii* usually grows on rotten wood, humus and wet rock surfaces in more or less undisturbed, lower montane rain forests, between 500 and 1500 m. In addition, there are two records from much higher, alpine elevations: one from the páramo of El Angel, northern Ecuador, where the species occurs in large moss cushions in a *Polylepis* woodland at ca. 4000 m, and the other from the puna of northern Bolivia, where the species grows submerged in swamp vegetation at almost 5000 m.

DESCRIPTION. **Plants** light green, 1.5-5 cm high, growing upright from a whitish leafless rhizome. **Stems** pale, without any trace of rhizoids. **Leaves** transverse, ovate-orbicular to broadly reniform, with very narrow insertion, margins ± entire, basal part of leaf more than 1 cell thick (2-4-stratose). **Cells** very large, ca. 50-100 µm long, quadrate to rectangular, arranged in rows, uniformly thin-walled, without trigones, cuticle smooth; oil bodies small, homogeneous, many per cell. **Underleaves** similar to leaves. **Reproductive structures** as for the order Calobryales.

DISCUSSION. The upright stems without rhizoids and with three ± equal rows of large, transversely inserted, undivided leaves are unmistakable. The leaves are more than 1 cell thick in the basal part and the leaf cells are large, very thin-walled, and ± arranged in rows. The capsule of *H. blumii* is unusual for its dehiscence by means of only two valves. The alpine populations of *H. blumii* are basically similar to the lower montane plants except for their somewhat larger size and broader, more reniform leaves.

Leaves with pluristratose bases are rare among neotropical hepatics and also occur in *Hygrolembidium* and *Noteroclada*, both of which have undivided leaves like *Haplomitrium*. In *Hygrolembidium* and *Noteroclada*, however, leaf insertion is clearly succubous and the underleaves are very small or absent.

LITERATURE. Bartholomew-Began, S. E. 1991. A morphogenetic re-evaluation of *Haplomitrium*. Bryophytorum Bibliotheca 41: 1-297, fig. 1-508 [key].

Order JUNGERMANNIALES

Plants foliose (rarely thallose: some Lepidoziaceae), with creeping, ascending, or erect leafy stems; rhizome present or absent. Branches lateral or ventral, originating from leaf-initial cells or from stem-cells, never of the *Fontinalis*-type. Leaves in 2-3 rows: 2 lateral rows and 0-1 ventral row (= underleaves), each leaf originating from 2 initial cells, undivided or divided. Leaf cells usually with trigones and oil bodies. Underleaves present or absent, when present usually smaller than the lateral leaves. Rhizoids usually present on the ventral side of the stem, always with smooth walls. Antheridia in leaf axils. Archegonia terminal on long or short shoots, surrounded by bracts and often by bracteoles. Sporophyte surrounded by a perianth or a fleshy perigynium, or both. Capsule globose to cylindrical, opening by four valves, wall 2-10-layered.

The largest order of the Hepaticae; about 1000 species in tropical America, in 153 genera and 25 families.

Key to the families and genera of Jungermanniales of tropical America

1. Leaves deeply dissected into hair-like segments which are not more than 1-2 cells wide at base 2

1. Leaves undivided or divided into segments which are more than 2 cells wide at base 5
2. Leaves divided to the base into 1-4 filaments (= uniseriate segments), margins entire. Plants very small, alga-like 3
2. Leaves divided into 4-9 segments, margins strongly ciliate. Plants larger, not alga-like 4
3. Underleaves ± as large as lateral leaves. Cuticle of leaf cells with narrowly elongated papillae ("striate-papillose"). Perianth at stem apex ..... **Pseudolepicoleaceae** (p.)
3. Underleaves smaller than lateral leaves or absent. Cuticle of leaf cells smooth or with small, rounded papillae ("verruculose"). Perianth on short ventral branch..... **Lepidoziaceae** (p.)
4. Leaves 4-9-lobed, the segments split into numerous ciliate parts, the plants strongly "hairy.“ Leaf cells with uniformly thickened walls, trigones lacking. Underleaves smaller than lateral leaves. Plants whitish-green or brown ..... **Trichocolea** (p.)
4. Leaves 4-lobed, the segments not split into numerous ciliate parts. Leaf cells with large trigones. Underleaves as large as lateral leaves. Plants gray- or bluish-green or brown .... **Lepicolea** (p.)
5. Leaves differentiated into lobe and lobule (lobule = small or large fold or sac appressed to the leaf, usually on the ventral side of leaf, sometimes on the dorsal side). Lobe and lobule connected by a well-defined keel or nearly free from each other ..... **Section 1**
5. Leaves not differentiated into lobe and lobule 6
6. Leaves modified into a swollen sac 7
6. Leaves plane to deeply concave but not modified into a sac (a small ventral sac present in *Nowellia*: p.) 8
7. Plants robust, to 1 cm wide. Sac open to the ventral side. Leaf margins with long cilia. Underleaves lacking ..... **Szweykowskia** (p.)
7. Plants smaller. Sac fully closed. Lleaf margins without cilia. Underleaves present .... **Colura** (p.)
8. Leaves with (1-)2 large, sausage-shaped slime papillae at the tips of the segments or on the rounded margins. Plants very small, less than 1 mm wide, whitish-green, the leaves almost longitudinally inserted on the stem. On decaying wood in rain forest .... **Zoopsidella** (p.)
8. Leaves without large slime papillae at the tips or on the margins 9
9. Leaves incubous ..... **Section 2**
9. Leaves succubous or transverse 10
10. Underleaves present ..... **Section 3**
10. Underleaves absent (or very small) ..... **Section 4**

Section 1. Leaves divided into lobe and lobule

1. Leaves transverse, sharply folded and keeled, at least in the upper half. Keel often winged. Stems at base with leafless stolons ..... **Lepidoziaceae** (p.)
1. Leaves incubous or succubous 2
2. Lobule present on the dorsal side of the leaf 3
2. Lobule present on the ventral side of the leaf 5
3. Underleaves present ..... **Balantiopsis** (p.)
3. Underleaves lacking 4
4. Leaves incubous, deeply concave, strongly clasping the stem. ..... **Pleurozia** (p.)
4. Leaves succubous, plane or slightly concave, not clasping the stem ..... **Scapaniaceae** (p.)
5. Underleaves present 6
5. Underleaves lacking 8
6. Lobule for most of its length attached to lobe along a keel; keel and lobule usually widely diverging from stem. Plants variously colored but never reddish or purple ..... **Lejeuneaceae** (p.)
6. Lobule almost free from the lobe, keel lacking or indistict; lobule oriented more or less parallel to the stem or weakly diverging 7
7. Underleaves undivided. Lobules plane, with rounded apex, margins of lobule often dentate to laciniate, at least near the base. Plants green to brown, robust ..... **Porella** (p.)
7. Underleaves divided (rarely undivided). Lobules usually inflated, sac-like (sometimes plane, then with acute apex), margins of lobule ± entire. Plants usually reddish or purple, sometimes green ..... **Jubulaceae** (p.)
8. Plants robust, more than 3 mm wide, turning reddish or purple. Leaves strongly concave, clasping the stem ..... **Pleurozia** (p.)
8. Plants smaller, less than 3 mm wide, green or brown, not turning reddish or purple 9
9. Plants usually very small, less than 1 mm wide. Lobules very narrowly attached to stem, by only 1-4 cells. Stems very thin, epidermis of only 5 rows of cells (except *Myriocoleopsis*). Rhizoids from

ventral surface of stem. Leaf cells with many (more than 2) small, colorless oil bodies .... **Lejeuneaceae** (p.)
9. Plants larger. Lobules broadly attached to stem. Stems rigid, epidermis of numerous thick-walled cells. Rhizoids in tufts from lobule. Leaf cells with 1-2(-5) large, brownish oil bodies. .... **Radula** (p.)

Section 2. Leaves incubous, lobule absent

1. Underleaves present 2
1. Underleaves absent 6
2. Underleaves and leaves of similar size, 2-3-parted ..... **Herbertaceae** (p.)
2. Underleaves smaller than leaves 3
3. Leaves with 3 or more segments or teeth ..... **Lepidoziaceae** (p.)
3. Leaves with 0-2 segments or teeth 4
4. A vestigial lobule (consisting of only a few cells) present at ventral base of leaf. Ventral branches lacking. Stems fragile, ventral stem surface only 2-4 cells wide, hyalodermis often present. Gynoecia at stem apex or on a lateral branch ..... **Lejeuneaceae** with reduced lobules (p.)
4. Lobule entirely lacking. Ventral branches usually present. Stems rigid, ventral stem surface more than 4 cells wide, hyalodermis absent. Gynoecia on a short ventral branch 5
5. Stems forked, flagelliform ventral branches present. Sporophyte enveloped in a perianth ....**Bazzania** (p.)
5. Stems simple or irregularly branched, flagelliform ventral branches lacking. Sporophyte in a marsupium ..... **Calypogeia** (p.)
6. Plants robust, more than 3 mm wide, turning reddish or purple. Perianths large, terete, without a beak ..... **Pleurozia** (p.)
6. Plants less than 2 mm wide, pale green, not turning reddish or purple. Perianths inflated-plicate or flattened, with a beak ..... **Lejeuneaceae** without underleaves and with reduced lobules (p.)

Section 3. Leaves succubous or transverse, underleaves present

1. Leaf margins toothed 2
1. Leaf margins entire 5
2. Leaves 4-lobed, underleaves as large as leaves ..... **Lepicolea** (p.)
2. Leaves not 4-lobed, underleaves smaller than leaves 3
3. Dorsal leaf base decurrent. Leaves asymmetrical, ventral margin arched, dorsal margin ± straight. Stems brown (or bluish), with thick-walled cortex ..... **Plagiochilaceae** (p.)
3. Dorsal leaf base not decurrent. Leaves ± symmetrical. Thick-walled cortex lacking 4
4. Leaves ± transversely inserted, deeply concave. Branches originating from the ventral side of the stem .....**Isotachis** (p.)
4. Leaves ± longitudinally inserted, not deeply concave. Branches originating from the lateral and ventral side of the stem ..... **Geocalycaceae** (p.)
5. Leaves undivided 6
5. Leaves divided into segments 8
6. Stem base with leafless stolons ..... **Lepidoziaceae** (p.)
6. Stolons lacking 7
7. Underleaves entire, oblong-lanceolate. Rhizoids scattered ..... *Nardia succulenta* (p.)
7. Underleaves divided or toothed, rarely entire. Rhizoids in tufts ..... **Geocalycaceae** (p.)
8. Leaves divided into 3-4 segments 9
8. Leaves divided into 2(-3) segments 13
9. Plants more than 2 mm wide 10
9. Plants less than 2 mm wide 11
10. Leaves transverse, densely crowded in a rosette. Leaf tips long-acuminate-piliferous. Leaf cells without trigones ..... **Ruizanthus** (p.)
10. Leaves succubous, not densely crowded in a rosette. Leaf tips shorter. Leaf cells with large trigones ..... **Barbilophozia** (p.)
11. Leaves succubous, leaf segments ± diverging 12
11. Leaves transverse, leaf segments not diverging ..... **Lepidoziaceae** (p.)
12. Plants ca. 1 mm wide. Perianth at stem apex inflated-urceolate, surface of perianth often with cilia ..... **Chaetocolea** (p.)
12. Plants smaller, less than 0.5 mm wide. Perianth on a short ventral branch, 3-keeled, surface of perianth smooth ..... **Kurzia** (p.)
13. Leaves in 3 equal rows, underleaves as large as leaves 14

13. Leaves not in 3 equal rows, underleaves smaller than leaves 19
14. Leaves distinctly elongate, (1.5-)2-7 times as long as wide. Leaf cells strongly elongate except near leaf margin, forming a broad vitta. Trigones very large ..... **Herbertus** (p.)
14. Leaves shorter. Vitta absent. Trigones small or lacking 15
15. Plants 1-5 mm wide, growing upright. Rhizoids in tufts 16
15. Plants smaller, less than 1 mm wide, creeping. Rhizoids scattered 17
16. Mid-leaf cells rectangular, 2-3 times as long as wide. Plants reddish, purple-brown or black....: .....*Isotachis* (p.)
16. Mid-leaf cells quadrate. Plants light green to brown .....**Triandrophyllum** (p.)
17 Leaves tightly appressed to the stem and densely imbricate. Leaf margins smooth. On soil in high-alpine environments (above 4000 m) ..... **Anthelia** (p.)
17. Leaves ± spreading, not densely imbricate. Leaf margins coarsely papillose 18
18. Plants pale green. Leaves distinctly wider than the stem, leaf tips acute. Twig epiphyte near forest line ..... **Pseudocephaloziella** (p.)
18. Plants brownish to whitish. Leaves scarcely wider than stem, leaf tips blunt. On soil in páramo (above 4000 m) ..... **Paramomitrion** (p.)
19. Leaves transverse, strongly concave. Sporophyte in a fleshy perigynium .... **Isotachis** (p.)
19. Leaves succubous. Sporophyte in a perianth 20
20. Leaves and underleaves divided to the middle into 2-3 segments. Rhizoids in tufts .... **Paracromastigum** (p.)
20. Leaves and underleaves always 2-lobed, never 3-lobed, usually less deeply divided. Rhizoids scattered or in tufts 21
21. Leaf insertion line not reaching dorsal midline of stem, dorsal side of stem "leaf-free". Rhizoids scattered ..... **Cephaloziaceae** (p.)
21. Leaf insertion line reaching dorsal midline. Rhizoids in tufts 22
22. Plants often reddish. Branching purely ventral. Leaf cells narrowly rectangular, cuticle with elongated papillae ("striate-papillose"). ..... **Neesioscyphus** (p.)
22. Plants never reddish. Branching lateral and ventral. Leaf cells usually shorter, cuticle smooth or with small, rounded papillae ("verruculose") ..... **Geocalycaceae** (p.)

Section 4. Leaves succubous or transverse, underleaves absent (or minute)

1. Plants producing caducous leaves 2
1. Plants not producing caducous leaves 3
2. Plants whitish-green or glaucous when fresh, with numerous leafless stolons at the base. Stems pale. Oil bodies brown, filling up cell-lumen. Sporophyte in a marsupium **Acrobolbaceae** (p.)
2. Plants green or brown. Stems brown, usually darker than leaves. Oil bodies colorless, not filling up cell-lumen. Sporophyte in a flattened perianth ..... **Plagiochilaceae** (p.)
3. Plants worm-like, small, less than 2 mm wide, with closely imbricate and appressed leaves. Leaves transverse, entire or bifid, often hyaline or whitish. Stolons present. Alpine .... **Gymnomitriaceae** (p.)
3. Plants not worm-like, leaves less imbricate; or plants larger 4
4. Plants minute, less than 0.5 mm wide. Leaf cells small, 8-25(-30) µm, without trigones .... **Cephaloziellaceae** (p.)
4. Plants larger. Cells with or without trigones 5
5. Dorsal margin of leaves deflexed, distinctly decurrent along stem. Leaf surface convex near dorsal margin and concave towards ventral margin. 6
5. Dorsal margin of leaves plane or inflexed, not or little decurrent. Leaf surface ± plane or concave 9
6. Plants with reddish or purple pigmentation. Leaves opposite (rarely alternate). Sporophyte in an inflated perianth ..... **Jungermanniaceae** (p.)
6. Plants lacking reddish or purple pigmentation. Leaves alternate (rarely opposite). Sporophyte in a flattened or trigonous perianth or in a marsupium 7
7. Stem with hyalodermis. Leaf insertion line not reaching dorsal midline of stem, dorsal side of stem leaf-free. Leaf cells huge, 70-150 µm long, thin-walled, without trigones. Guayana Highland .... **Haesselia** (p.)
7. Stem without hyalodermis. Leaf insertion usually reaching dorsal midline of stem. Leaf cells usually smaller, with or without trigones 8
8. Plants whitish-green or glaucous when fresh (gray or brown when dry). Leaf apex obliquely truncate-emarginate. Stems pale. Oil bodies brown, numerous, filling up cell-lumen. Sporophyte in a marsupium ..... **Acrobolbaceae** (p.)

8. Plants green or brown. Leaf apex various, but usually not obliquely truncate-emarginate. Stems brown, darker than leaves. Oil bodies colorless, not filling up cell-lumen. Sporophyte in a flattened perianth. ..... **Plagiochilaceae** (p.)
9. Leaves opposite, dorsal leaf bases united 10
9. Leaves alternate, dorsal leaf bases not united 10a
10. Cells 35-50 µm wide in middle of leaf, becoming longer and narrower towards ventral leaf margin. Leaves densely imbricate. (Sub)alpine, terrestrial ..... **Arnelliaceae** (p.)
10. Cells 20-35(-40) µm wide in middle of leaf, not elongated towards ventral margin. Leaves distant or subimbricate. Montane-alpine, epiphytic or terrestrial .....**Syzygiella** (p.)
10a. Leaf base several layers of cells thick ..... Order **Metzgeriales** (p.)
10a. Leaf base only one layer of cells thick 11
11. Leaves (2-)3-4-lobed 12
11. Leaves 2-lobed or undivided 14
12. Leaves divided to 1/2 into 2-4 subulate segments. Rhizoids in tufts. Guayana Highland .... **Odontoseries** (p.)
12. Leaves not divided into subulate segments. Rhizoids scattered 13
13. Leaves 3-lobed, segments very unequal, the dorsal segment much smaller. Plants with rust-red gemmae on leaf margins ..... **Tritomaria** (p.)
13. Leaves 2-4-lobed, segments equal. Gemmae lacking ..... **Acrobolbus** (p.)
14. Plants with stolons or arising from a rhizomatous base 15
14. Stolons or rhizome absent 21
15. Plants with upright flagelliform branches producing gemmae ..... **Cephaloziaceae** (p.)
15. Plants without such gemmiparous branches 16
16. Dorsal margin of leaves ± inflexed (towards stem). Leaves transverse. Stem rigid, with thick-walled cortex. Gametoecia at stem base on abbreviated branches. ..... **Adelanthus** (p.)
16. Dorsal margin of leaves plane or deflexed. Leaves succubous, rarely transverse 17
17. Leaf cells small, less than 25 µm, without trigones. Plant less than 1 mm wide..... .....**Cephaloziellaceae** (p.)
17. Leaf cells larger, with or without trigones. Plants usually wider than 1 mm (rarely less than 1 mm) 18
18. Leaf insertion line not reaching dorsal midline of stem, dorsal side of stem leaf-free .... **Cephaloziaceae** (p.)
18. Leaf insertion line reaching dorsal midline of stem, dorsal side of stem not leaf-free 19
19. Leaf cells papillose. Plants whitish-green to yellowish-green (sometimes brown when dry). Sporophyte in a marsupium ..... **Acrobolbaceae** (p.)
19. Leaf cells smooth. Plants green to reddish-brown to black. Sporophyte in a perianth 20
20. Leaves ovate-orbicular. Leaf cells without trigones. Perianth inflated .... **Cryptochila** (p.)
20. Leaves oblong. Leaf cells with distinct trigones. Perianth flattened .... **Leptoscyphopsis** (p.)
21. Leaves entire .....
22. Leaves 2-lobed 23
22. Ventral margin of leaves bordered by narrow cells. Sporophyte in a marsupium. Plants whitish-green to yellowish-green. Leaves tongue-shaped. ..... **Lethocolea** (p.)
22. Ventral margin of leaves not bordered by narrow cells. Sporophyte in a perianth .... **Jungermanniaceae** (p.)
23. Stem with hyalodermis ..... **Cephaloziaceae** (p.)
23. Stem without hyalodermis 24
24. Leaf cells with trigones. Gemmae often present ..... **Jungermanniaceae** (p.)
24. Leaf cells without trigones. Gemmae lacking 25
25. Leaf cells with uniformly thickened walls. Perianth entirely smooth, without keels or folds. Alpine ..... **Gymnocoleopsis** (p.)
25. Leaf cells completely thin-walled. Perianth with keels or folds, at least near apex. Not alpine 26
26. Leaves transverse, obcuneate, conspicuously narrowed to the base. Leaf tips rounded .... **Cephaloziopsis** (p.)
26. Leaves succubous, ovate, not conspicuously narrowed to the base. Leaf tips acute or obtuse 27
27. Leaf insertion extending to dorsal midline of stem. Plants pure green to purplish. Perianth broad, bell-shaped with a wide, truncate mouth ..... **Chonecoleaceae** (p.)
27. Leaf insertion not extending to dorsal midline of stem. Plants pale green to red or brown. Perianth narrow-cylindrical with a narrow mouth ..... **Cylindrocolea** (p.)

ACROBOLBACEAE

Plants usually glistening whitish-green to pale bluish-green, in the Neotropics without secondary pigmentation (rarely brown), creeping or upright, sometimes with a stoloniferous base. Stems with or without thick-walled cortex. Branches intercalary (lateral or ventral); stolons present or absent. Leaves succubous, undivided or 2-lobed (rarely 3-4-lobed). Cells usually with a papillose cuticle; oil bodies brown, finely granular. Underleaves ± lacking. Rhizoids scattered. Sporophyte in a fleshy, pendent marsupium; perianth lacking. Seta (cross-section) of numerous cells. Capsule with acute tip, wall very thick, 5-10-layered. Vegetative reproduction rare, by caducous leaves or gemmae.

DISCUSSION. A family of 6 genera, mostly in the Southern Hemisphere; 4 in tropical America. The succubous leaves, the lack of underleaves, the pale color of the plants, the brownish oil bodies, the presence of a marsupium instead of a perianth and, especially, the acute tip of the capsule are important characteristics of this family. The acute capsule tip may readily be observed by means of longitudinal sections of young marsupia, containing immature capsules (R. Grolle, pers. comm.). The neotropical Acrobolbaceae are still rather poorly known; keys to the species are lacking.

LITERATURE. Schuster, R. M. 1980. Acrobolbaceae. The Hepaticae and Anthocerotae of North America, Vol. IV: 539-554. .

1. Leaf apex rounded, entire. Leaf cells conspicuously elongated along ventral margin of leaf. Oil bodies 1-2 per cell. Usually alpine.....**Lethocolea**
1. Leaf apex truncate to 2-lobed (rarely a few apices rounded), dentate or entire. Cells not conspicuously elongated along ventral margin of leaf. Oil bodies numerous, 5-40 per cell. Montane (rarely lowlands) 2
2. Leaves symmetrically divided to 1/3-1/2 of their length into 2(-4) equal lobes. Leaf apices long-acuminate. Plants creeping, lacking stolons ..... **Acrobolbus**
2. Leaves with truncate apex or shallowly and asymmetrically divided (to less than 1/3) into 2 unequal segments. Leaf apices shorter, not acuminate. Plants ascending from a stoloniferous base ...3
3. Gynoecia terminal on elongated, leafy shoots. Leaf cells with trigones. Stems with a cortex of small, thick-walled cells in (1-)2-4 layers ..... **Tylimanthus**
3. Gynoecia on very short branches near stem base. Leaf cells thin-walled, ± without trigones. Stems without a cortex of small, thick-walled cells ..... **Marsupidium**

Acrobolbus (Fig. 14) - Probably 2 species in tropical America (10-12 worldwide): *A. antillanus* Schust. rather widespread in the Greater Antilles, Central America, and the northern Andes, and *A. laceratus* Schust. in the high Andes of Venezuela. The distribution and status of the species are incompletely known. Reports of the European *A. wilsonii* Taylor ex Nees from the Neotropics may refer to *A. antillanus* (see Schuster, 1980).

HABITAT. Epiphytic in montane rain forests and in subalpine scrub, in very moist environments. In the Cerro de la Muerte, Costa Rica, *Acrobolbus antillanus* is a rather common species of moss-covered trunks in the upper montane cloud forest, 2600-3200 m.

DESCRIPTION. **Plants** strongly glossy whitish-green, creeping, forming small mats; stolons lacking. **Stems** rather fragile, lacking a thick-walled cortex. **Leaves** succubous, ovate-oblong to quadrate, divided to 1/3-1/2 of their length into 2(-4) equal segments, with acuminate to long-piliferous tips and entire or sparingly toothed margins. **Cells** with small to medium-sized trigones, cuticle papillose; oil bodies numerous, 5-40 per cell, brown. **Underleaves** lacking. **Antheridia** only 1-2 per bract (4-10 per bract in *Tylimanthus*). **Archegonia** terminal on long shoots, surrounded by large, dentate-ciliate bracts which are often strongly spreading, forming a flower-like involucre. **Marsupium** short.

DISCUSSION. The glistening whitish-green plants with creeping stems (not ascending as in *Tylimanthus*) and rather deeply 2(-4)-lobed leaves with long and narrow tips are very characteristic. Female plants may be recognized immediately by the strongly spreading, ciliate-dentate bracts forming a flower-like involucre.

LITERATURE. Schuster, R. M. 1980 (see family ref.).

Lethocolea (Fig. 14) - A southern-temperate genus (ca. 5-6 spp.), with 1 species, *L. glossophylla* (Spruce) Grolle, common at high elevations in the Andes, Costa Rica, and southeastern Brazil.

HABITAT. *Lethocolea glossophylla* occurs on moist soil of shaded earth banks, along rivulets, etc., in subalpine and alpine vegetation, at 2500-4000 m in the Andes and at somewhat lower elevation (ca. 1800-2150 m) in southeastern Brazil. The species is especially common in páramos.

DESCRIPTION. **Plants** yellowish-green to bluish-green, creeping, often in dense mats, stem base with a few stolons . **Leaves** succubous, lingulate, with broadly rounded apex and entire margins. **Cells**

conspicuously elongated along the ventral margin of the leaf, thin-walled, with conspicuous trigones, cuticle papillose; oil bodies large, brown, only 1-2 per cell (5-40 in *Acrobolbus* and *Tylimanthus*). **Underleaves** lacking. **Marsupium** narrow-cylindrical.

DISCUSSION. *Lethocolea* may be confused with *Jungermannia* (especially *J. amplexifolia* (Hampe ex Lehm.) Grolle) but differs in the bluish-green to yellowish-green color, the papillose cuticle, and the large, brown oil bodies. The plants also resemble *Gongylanthus* but the latter has distinctly opposite leaves (alternate in *Lethocolea*). The marsupium in *Lethocolea* is much longer than in the other genera of the family and usually penetrates deeply into the substrate.

Marsupidium (Fig. 15) - A southern-temperate genus (ca. 12 spp.), with 2 species rare in tropical America: *M. gradsteinii* Grolle in Central Amazonia and the Guianas, and *M. latifolium* Schust. collected once in the Andes of Mérida, Venezuela.

HABITAT. The two neotropical *Marsupidium* species have quite different habitats. *Marsupidium gradsteinii* grows on bark and rock in rain forests at rather low elevations, below 1500 m, usually on periodically inundated banks of rivers and creeks. *Marsupidium latifolium* occurs in subpáramo vegetation (ca. 3150 m).

DESCRIPTION AND DISCUSSION. Rather similar to *Tylimanthus* but differing in the more flaccid stems with ± thin-walled cortex, thin-walled leaf cells ± without trigones, smooth cuticle (*M. gradsteinii*), and, especially, the gametoecia on very short branches, bearing only a few bracts and lacking vegetative leaves. The gametoecia are usually hidden among the stolons, at the base of the stems, and are rather inconspicuous.

LITERATURE. Grolle, R. 1989. *Marsupidium* in Guayana. Journal of the Hattori Botanical Laboratory 66: 337-342.

Tylimanthus (Fig. 15) - About 5 species in the mountains of tropical America (20-30 worldwide), including the widespread *T. approximatus* (Lindenb.) Besch. and *T. laxus* (Lindenb.) Spruce, and *T. ciliato-dentatus* Steph. at high elevations in the northern Andes.

HABITAT. Epiphytes of montane and subalpine rain forests, 500-3500 m. In dense forests, the species usually grow high up in the canopy. In more open situations (along trails, at forest margin, in gaps), they may occur lower down on bark and also on humic soil.

DESCRIPTION. **Plants** glossy whitish-green to bluish-green when fresh, sometimes brownish when dry, usually rather fleshy, growing upright from a stoloniferous base, forming dense tufts. **Stems** rather rigid, with a thick-walled cortex of (1-)2-4 cell-layers. **Leaves** succubous, ovate to oblong, with typically oblique and truncate to emarginate apex, leaf tips rounded to acute to ciliate, margins entire or finely toothed towards the apex. **Cells** with trigones, cuticle usually papillose; oil bodies numerous, 10-40 per cell, brown. **Underleaves** lacking. **Gametoecia** on elongated leafy shoots. **Antheridia** rather numerous, ca. 4-10 per bract.

DISCUSSION. *Tylimanthus* may be confused with *Plagiochila* but is easily recognized, when fresh, by the glossy whitish-green to bluish-green color of the plants and the pale stems. However, upon drying, the plants often turn brown. The obliquely truncate-emarginate leaf apex and the usually papillose cuticle of both stem and leaf cells (cuticle smooth in *T. approximatus*) are further characteristic features. Female plants are immediately recognized by the short, pendent marsupium at the shoot apex.

ADELANTHACEAE

A small family of 2-3 genera, mostly in the tropics and the temperate regions of the Southern Hemisphere; 1 genus in tropical America.

Adelanthus (Fig. 15) - About 8-9 species in the mountains of tropical America (15 worldwide), including *A. decipiens* (Hook.) Mitt. widespread in the region, and *A. lindenbergianus* (Lehm.) Mitt. and *A. pittieri* (Steph.) Grolle in the high Andes and the mountains of Central America. The other species are rare ones.

HABITAT. On bark in montane rain forests and on humic soil in páramo vegetation, 1000-4500 m. In dense forests, the species are usually restricted to well-illuminated sites and occur in the canopy or closer to the ground along trails, at forest margin and in gaps.

DESCRIPTION. **Plants** dark green to brown, growing upright from a stoloniferous base. **Stems** rigid, usually brown, with a thick-walled cortex. **Branches** exclusively ventral-intercalary. **Leaves** transversely inserted with conspicuously decurrent dorsal bases, undivided or shallowly bilobed with acute tips, margins entire or toothed, sometimes bordered; dorsal leaf margin plane or curved upwards (towards the stem). **Cells** ± quadrate, 12-35 µm, uniformly thick-walled or with trigones, cells

along the leaf margin often thicker-walled and forming a border, towards the leaf base sometimes elongated and forming a weak vitta, cuticle smooth; oil bodies finely granular. **Underleaves** lacking. **Rhizoids** scarce, usually restricted to the stolons. **Gametoecia** born on very short branches arising from the leafless stem bases or from the stolons. **Sporophyte** in a perianth or a fleshy calyptra. **Seta** of numerous cells (cross-section). **Capsule** elongate, wall rather thick (4-6-layered). **Vegetative reproduction** rare, by gemmae from leaf margins.

DISCUSSION. *Adelanthus* may be confused with *Plagiochila* but differs in the dorsal margin of the leaf which is plane or incurved (recurved in *Plagiochila*), the transverse leaf insertion (oblique in *Plagiochila*), and the ventral-intercalary branches (lateral-intercalary in *Plagiochila*). The occurrence of gametoecia on very short, leafless branches near the stem bases, is another characteristic feature of *Adelanthus*. In *Plagiochila*, gametoecia always arise terminally, on long, leafy shoots.

Following Grolle (1972), the species of *Adelanthus* may be divided into two groups: those producing perianths and those lacking them. The latter species are sometimes placed in the separate genus *Calyptrocolea* Schust. All neotropical species possess perianths, hence are typical members of the genus *Adelanthus*.

LITERATURE. Grolle, R. 1972. Zur Kenntnis von *Adelanthus*. Journal of the Hattori Botanical Laboratory 35: 325-370 [key to 6 neotropical spp.]. - Grolle, R. 1989. *Adelanthus* am Mt. Roraima. Journal of the Hattori Botanical Laboratory 67: 243-247.

ANTHELIACEAE

A monotypic family.

Anthelia (Fig. 16) - A widespread, arctic-alpine genus (2 spp.) with one species, *A. juratzkana* (Limpr.) Trevis., occurring at high elevations in tropical America. The species has been recorded from Mexico, Venezuela, Ecuador, and Bolivia.

HABITAT. On moist, bare soil in tropical alpine environments, above 4000 m.

DESCRIPTION. **Plants** very small (usually less than 1 cm long), pale green to brown, often becoming white due to the secretion of a whitish crystalline substance, creeping, simple or forked. **Stems** fragile, with relatively large, thin-walled epidermis cells (cross-section). **Branches** terminal, *Frullania*-type; stolons lacking. **Leaves** transverse, deeply 2-lobed, tips acute, margins entire. **Cells** uniformly thick-walled, cuticle smooth; oil bodies lacking. **Underleaves** similar to the leaves. **Rhizoids** scattered. **Sporophyte** surrounded by a perianth and a fleshy calyptra. **Seta** of numerous cells (cross-section). **Capsule** spherical. **Vegetative reproduction** unknown.

DISCUSSION. The very small, creeping plants with three equal rows of densely imbricate, 2-lobed leaves, are unmistakable. In habit, the plants somewhat resemble a tiny *Herbertus* but the leaf areolation is entirely different (walls uniformly thickened, trigones lacking; no vitta) and there are no oil bodies. In general appearance, *Anthelia* more resembles a moss than a liverwort.

LITERATURE. Schuster, R. M. 1974. Antheliaceae. The Hepaticae and Anthocerotae of North America, Vol. III: 621-641.

ARNELLIACEAE

Plants rather small, green to brown or purplish, sometimes whitish, creeping. Branches intercalary (lateral or ventral), stolons lacking. Leaves succubous, opposite with the dorsal bases united, orbicular to oblong, with rounded apex and entire margins. Cells thin-walled or with trigones, elongated to the ventral margin, cuticle smooth or papillose; oil bodies finely granular. Underleaves lacking or very small. Rhizoids scattered. Gametoecia on leading shoots. Sporophyte surrounded by a perigynium: a pendent marsupium or a perianth with a fleshy base. Seta of numerous cells (cross-section). Capsule elongate, wall 2-layered. Vegetative reproduction unknown.

DISCUSSION. A small family of 4 genera worldwide; 2 in tropical America. The opposite leaves with the dorsal bases united (ventrally free), the virtual absence of underleaves, and the presence of a perigynium are the main morphological characteristics of this family.

1. Leaves strongly concave to almost plane. Cuticle of leaf cells smooth. Leaf cells along the lower part of the ventral margin conspicuously elongated, 4-10 times as long as wide. Sporophyte produced in a marsupium ..... **Gongylanthus**
1. Leaves ± plane. Cuticle of leaf cells finely papillose. Leaf cells along ventral margin hardly elongated. Sporophyte produced in a perianth ..... **Southbya**

Gongylanthus (Fig. 16) - Four species at high elevations in tropical America (5-6 worldwide), including *G. liebmannianus* (Lindenb. & Gott.) Steph. widespread from Mexico to Bolivia and SE Brazil, and 3 further species with more restricted distributions.

HABITAT. On bare soil or rock in open, upper montane and alpine environments, along rivulets, on road banks, etc., 2500-4500 m.

DESCRIPTION. **Plants** glossy, green to whitish or purplish, attached to the substrate by numerous, long, pale rhizoids. **Leaves** succubous, opposite with the dorsal bases united, orbicular to oblong, strongly concave to almost plane, apex rounded, margins entire. **Cells** strongly elongated towards the ventral margin, to 150 µm long, about 4-10 times as long as wide, cuticle smooth in neotropical species; oil bodies finely granular, 3-8(-12) per cell. **Sporophyte** in a fleshy marsupium; perianth lacking. Further characteristics as for the family.

DISCUSSION. *Gongylanthus* is easily recognized by the opposite leaves and the presence of a marsupium. Opposite leaves are also found in *Syzygiella* (Jungermanniaceae) but the latter has smaller leaf cells and a perianth instead of a marsupium. Moreover, *Syzygiella* is primarily montane and usually grows as an epiphyte (sometimes terrestrial or saxicolous) whereas *Gongylanthus* is (sub)alpine and terrestrial or saxicolous, never epiphytic.

There is no key to the neotropical species. *Gongylanthus liebmaniannus* (Lindenb. & Gott.) Steph., the most common neotropical species, may be easily recognized by the strongly involuted leaf margins.

Southbya (Fig. 16) - A small genus with 4 species in Asia and Europe and 1 species, *S. organensis* Herzog, in the Serra dos Orgãos (Morro Assú), SE Brazil.

HABITAT. On soil, about 2000 m (?).

DESCRIPTION. **Plants** small, to 1 cm long, brownish, attached to the substrate by long rhizoids. **Leaves** succubous, opposite, dorsally united, ventrally free, orbicular, almost plane, apex rounded, margins entire. **Cells** thin-walled, hexagonal, large, ca. 40-100 µm, little elongated towards the ventral margin, cuticle finely papillose; oil bodies unknown. **Sporophyte** surrounded by a perianth with a fleshy base. Further characteristics as for the family.

DISCUSSION. Similar to *Gongylanthus* in general appearance but with a papillose cuticle, leaf cells little elongated towards the ventral margin, and a perianth instead of a marsupium.

LITERATURE. Herzog, T. 1950. Miscellanea bryologica. I. Neotropica. Memoranda Societatis pro Fauna et Flora Fennica 25: 43-72 [descr. of *S. organensis*].

BALANTIOPSIDACEAE
(Isotachidaceae)

Plants green, red, purple, brown or black (green in shade), creeping or erect. Stems usually with a thick-walled cortex. Branches ventral-intercalary, occasionally terminal, *Frullania*-type; stolons lacking. Leaves transverse to succubous or weakly incubous, 2(-4)-fid, margins entire or sharply toothed. Cells ± rectangular, thin-walled or slightly thickened, with or without trigones, cuticle smooth or striate-papillose; oil bodies finely granular, colorless, 2-3(-5) per cell. Underleaves well-developed, similar to the lateral leaves but smaller. Rhizoids in tufts from underleaf bases. Gametoecia on long shoots.Sporophyte surrounded by a perigynium, a marsupium, or a fleshy perianth. Seta of numerous cells (cross-section).. Capsule elongate, wall 3-4-layered, valves linear and strongly spirally twisted, rarely straight (*Ruizanthus*). Vegetative reproduction unknown.

DISCUSSION. A family of 7 genera, mostly in the Southern Hemisphere; 4 in tropical America. Important characteristics of the Balantiopsidaceae are 1) the capsule valves spirally twisted in the unopened capsule; 2) the tufted rhizoids; 3) the transverse to succubous; 2-lobed leaves; 4) the conspicuous underleaves; and 5) the rather fleshy structures surrounding the sporophyte (perianth, perigynium, marsupium).

The spirally twisted capsule valves are the most unusual feature of this family and are otherwise found only in the Calypogeiaceae. However, the latter family has incubous leaves which are mostly undivided and gametoecia on short ventral branches. The perianth in the Balantiopsidaceae is often reduced and replaced by an erect perigynium in *Isotachis* or a pendent marsupium in *Balantiopsis*.

1. Leaves complicate-bilobed with a small dorsal segment and a large ventral segment. Sporophyte produced in a marsupium. SE Brazil ..... **Balantiopsis**
1. Leaves divided into 2-3 segments, not complicate-bilobed. No marsupium 2
2. Leaves 4-5-lobed. Leaf apices long-acuminate-piliferous. Páramos of northern South America ..... **Ruizanthus**

2. Leaves 2(-3)-lobed. Leaf apices shorter..... 3
3. Leaves strongly concave. Leaf insertion ± transverse (at least dorsally). Plants growing erect or creeping. Underleaves small or large ..... **Isotachis**
3. Leaves flat or weakly concave. Leaf insertion very oblique, the leaves clearly succubous. Plants creeping. Underleaves always small, less than half the length of the leaves. Occurring at relatively low elevations, below 2000 m ..... **Neesioscyphus**

Balantiopsis (Fig. 16) **-** A southern-temperate genus (11 spp.), with 1 species, *B. brasiliensis* Steph., widespread in southeastern Brazil. A second species, *B. crocea* Herzog, has been recorded from Rio Grande do Sul.

HABITAT. On soil in shady, wooded habitats and along streams, 1150-2300 m.

DESCRIPTION. **Plants** light-green to rose-tinted, large, to 7 cm long. **Branches** primarily terminal, *Frullania*-type, ventral branches scarce. **Leaves** succubous, complicate-bilobed with a large ventral segment and a smaller dorsal segment, margins strongly toothed. **Cells** rectangular, 50-90 µm long, thin-walled, cuticle finely papillose to almost smooth; oil bodies as in the family. **Underleaves** slightly smaller than the leaves, flat, 2-lobed, with strongly toothed margins. **Sporophyte** in a short, pendent marsupium at the tip of the stem.

DISCUSSION. The large, light-green to rose-tinted plants with complicate-bilobed leaves (large ventral segment, small dorsal segment) and large underleaves are unmistakable. Similar leaves are found in *Scapania* which, however, lacks underleaves. The strongly toothed leaf margins and the marsupium are further characteristic features of *Balantiopsis*.

LITERATURE. Bueno, R. M. 1986. Gênero *Balantiopsis* Mitt. (Hepaticopsida) no Brasil. Rickia 13: 29-33. - Engel, J. J. 1968. A taxonomic monograph of the genus *Balantiopsis*. Nova Hedwigia 16: 83-130, tab. 27-59 [key].

Isotachis (Fig. 17) **-** A Southern-Hemisphere genus (ca. 15 spp.), with 7-8 species at higher elevations in tropical America.

HABITAT. On moist soil and on rock covered by a thin layer of earth, in rather open montane and alpine environments (rarely at sea level), along rivulets, on road banks, etc., (0-)500-4500 m. Sometimes submerged in streamlets or lakes (e.g., *Isotachis lacustris* Herzog).

DESCRIPTION. **Plants** green, red, brown or black, usually erect, sometimes creeping. **Branches** ventral-intercalary. **Leaves** transverse (sometimes slightly succubous or incubous), 2-lobed, about as long as wide, strongly concave, leaf tips rounded, acute or mucronate, margins entire or toothed. **Cells** as in the family. **Underleaves** similar to the leaves but smaller, about half the size (sometimes larger or smaller) and more flat. **Sporophyte** in a conical, fleshy perigynium at the tip of long shoots.

DISCUSSION. *Isotachis* may be recognized by its erect growth (prostrate in *I. lopezii* (Schust.) Gradst. and *I. multiceps* (Lindenb. & Gott.) Gott.), the ± transverse leaves which are 2-lobed and strongly concave, and the rather large, 2-lobed underleaves. The plants are often strongly pigmented and in the common *I. serrulata* (Sw.) Gott. they are usually deep red. The latter species is easily recognized by the sharply toothed leaf margins.

Isotachis multiceps has recently been placed in a separate genus *Hypoisotachis*, as *H. multiceps* (Lindenb. & Gott.) J. J. Engel & G. Merrill (Fieldiana, Botany N.S. 37: 56. 1997), because of the gametangia on short, ventral branches rather than on long shoots. Since gametangia are still unknown in many neotropical species of *Isotachis*, *I. multiceps* is kept in the genus *Isotachis* in this treatment, at least for the time being.

LITERATURE. Fulford, M. H. 1963. *Isotachis*. Manual of the leafy Hepaticae of Latin America, Part I. Memoirs of the New York Botanical Garden 11 (1): 63-79 [key to 11 neotropical spp.; some may be synonyms].

Neesioscyphus (Fig. 17) - A neotropical genus of 5 species, at rather low elevations. Most of the species are rare; *N. argillaceus* (Nees) Grolle is the most frequent species of the genus. The center of diversity of *Neesioscyphus* is in SE Brazil (4 spp.).

HABITAT. On moist earth and on thin soil over volcanic rock, below 2000 m.

DESCRIPTION. **Plants** pale green to reddish, creeping. **Branches** ventral-intercalary. **Leaves** distinctly succubous, 2-lobed with the segments usually unequal in size, about as long as wide, flat or weakly concave, leaf tips rounded or acute, margins entire or somewhat toothed. **Cells** as in the family. **Underleaves** rather small, about 1/3 the size of the leaves. **Sporophyte** produced in a perianth which is rather fleshy (2-3-stratose) in the lower half.

DISCUSSION. The prostrate habit, somewhat reddish color, rather flat and distinctly succubous leaves, and small, 2-lobed underleaves with tufted rhizoids at the base are characteristic of *Neesioscyphus*. Unlike *Isotachis*, the sporophyte is produced in a fleshy perianth with bracts at the base, not in a perigynium. When sterile, the genus may be confused with *Lophocolea*, but the reddish

color, the ventral instead of lateral branching, the usually very unequal leaf segments, and the narrow rectangular leaf cells with striate-papillose cuticle, may serve to distinguish *Neesioscyphus*.

LITERATURE. Grolle, R. 1966. Notulae hepaticologicae XIV. Zwei weitere *Neesioscyphus*-Arten. Revue Bryologique et Lichénologique 34: 182-186 [key]. - Reiner-Drehwald, M. E. & U. Drehwald. 1995. Zum Vorkommen von *Neesioscyphus homophyllus* (Hepaticae, Balantiopsaceae) in NO-Argentinien. Fragmenta Floristica et Geobotanica 40: 47-52 [figs.].

Ruizanthus (Fig. 17) - A monotypic, neotropical genus, with *R. venezuelanus* Schust. at high elevations in the Cordillera de Talamanca, Costa Rica, and in the Andes of Colombia (Sierra Nevada de Santa Marta) and Venezuela (Mérida).

HABITAT. On bare soil in páramo, 3000-4100 m.

DESCRIPTION. **Plants** greenish to somewhat rose-tinged, creeping to ascending, usually forming small and dense mats. **Branches** ventral-intercalary. **Leaves** transverse, 4-5-lobed, strongly concave, leaf tips short- or long-piliferous, margins entire except for a few short teeth at the base. **Cells** as in the family. **Underleaves** small, about 1/3 the size of the leaves, 2-lobed. **Sporophyte** produced in a perianth which is rather fleshy (2-4-stratose) in the lower half. **Capsule** ovoid, valves straight.

DISCUSSION. The small plants forming rosettes of densely imbricate, 4-lobed leaves with piliferous tips, are unmistakable. The straight instead of spiralled capsule valves are the most remarkable feature of this genus, separating it from all other members of the Balantiopsidaceae.

A second species described in *Ruizanthus*, *R. lopezii* Schust. from the northern Andes, has spiralled capsule valves and 2-lobed leaves and belongs in the genus *Isotachis*, as *Isotachis lopezii* (Schust.) Gradst.

LITERATURE. Schuster, R. M. 1986. Studies on Venezuelan Hepaticae III. Families Blepharostomataceae and Balantiopsidaceae. Nova Hedwigia 42: 49-79.

CALYPOGEIACEAE

Plants translucent whitish-green to deep-green to brownish, creeping. Branches exclusively ventral-intercalary, usually sparse; stolons lacking. Leaves incubous, undivided or very short-bifid, margins entire or finely crenulate, sometimes bordered. Cells thin-walled, cuticle smooth or finely papillose; oil bodies finely or coarsely granular, colorless, sometimes bluish or sepia (*C. peruviana*). Underleaves small, undivided or bifid. Rhizoids in tufts from underleaf bases. Gametoecia born on very short ventral branches. Sporophyte in a fleshy, subterrranean marsupium. Seta of numerous cells (cross-section). Capsule cylindrical, wall 2-layered, valves spirally twisted as in the Balantiopsidaceae. Vegetative reproduction by gemmae produced on flagelliform shoots or by caducous leaves.

DISCUSSION. A family of 4 genera worldwide; 2 in tropical America. The family Calypogeiaceae may be easily recognized by the incubous leaves with entire to very short-bifid apex, the absence of a lobule and the presence of underleaves. The long, subterranean marsupium, originating from a short ventral branch, and the twisted capsule valves are also very characteristic.

1. Underleaves undivided or retuse (rarely divided to1/5). Leaf apex undivided. Plants deep green to brown. Gemmae lacking ..... **Mnioloma**
1. Underleaves distinctly bifid. Leaf apex bilobed, rarely entire. Plants pale green, often producing gemmae ..... **Calypogeia**

Calypogeia (Fig. 18A) - About 15 species at low and high elevations in tropical America (ca. 35 worldwide): Ten species of *Calypogeia* treated by Fulford (1968) have been transferred to *Mnioloma*.

HABITAT. On moist earth, litter, rock, occasionally on bark, in lowland and montane forests, always in shaded, moist habitats, 0-3500 m. The species of *Calypogeia* are common in undisturbed as well as disturbed habitats. Most of the species occur below 2000 m; a few including the common *C. peruviana* Nees & Mont., are also found at higher elevations and may occur in páramos. *C. miquelii* Mont. (= *C. amazonica* (Spruce) Steph.) is a very common species on clay soil along trails in lowland and submontane rain forests.

DESCRIPTION. **Plants** pale-green. **Leaves** incubous, apex short bifid, rarely entire, leaf margins sometimes bordered by elongated cells. **Cells** thin-walled, trigones small to medium-sized, cuticle smooth, striate or papillose. **Oil bodies** pale-colored, bluish, or sepia (*C. peruviana*), coarsely granular (resembling a small grape-cluster). **Underleaves** variable in size and shape, bilobed to at least 1/4 of their length, border lacking. **Gametoecia** as in the family. born on very short ventral branches. **Vegetative reproduction** by gemmae produced on flagelliform shoots.

DISCUSSION. The genus *Calypogeia* as treated by Fulford (1968) has recently been split into two different genera, *Calypogeia* and *Mnioloma* (Schuster, 1995). The species of *Calypogeia* have bifid underleaves, coarsely granular oil bodies (resembling a small grape-cluster) and are pale green in color, those of *Mnioloma* have entire underleaves, are finely granular oil bodies, and are deep green to brown in color. Vegetative reproduction is by gemmae in *Calypogeia*, by caducous leaves in *Mnioloma*. The two groups also differ somewhat in ecology; species of *Mnioloma* often grow on bark of trees and are mostly found in undisturbed forest, those of *Calypogeia* are particurly common on soil and are frequently found in disturbed habitats, along trails, etc.

LITERATURE. Fulford, M. H. 1968. Calypogeiaceae. Manual of the leafy Hepaticae of Latin America, Part III. Memoirs of the New York Botanical Garden 11 (3): 279-310 [key].

Mnioloma (Fig. 18 B-F, as „*Calypogeia*“). A pantropical genus of 10 species, 9 of them restricted to the Neotropics and mostly occurring in the West Indies, Central America, and northern South America.

HABITAT. On damp soil, humus, tree trunks, rock, or hanging from twigs in the understory of lowland and montane rain forests, always in shaded, moist habitats, (0-)500-1500(-2000) m. The majority of the species grow in undisturbed submontane rain forests.

DESCRIPTION. **Plants** deep green to brown. **Leaves** incubous, apex undivided, rounded to apiculate, margin bordered or unbordered. **Cells** thin-walled, trigones small, cuticle rough. **Oil bodies** brownish, finely granular. **Underleaves** undivided or narrowly divided to 1/5 of their length, lobes obtuse, margin bordered; cells often elongated and hyaline. **Vegetative reproduction** by caducous leaves.

DISCUSSION. See under *Calypogeia*.

LITERATURE. Schuster, R. M. 1995. Phylogenetic and taxonomic studies of Jungermannidae, III. Calypogeiaceae. Fragmenta Floristica et Geobotanica 40: 825-888. 1995 [key to the spp.].

CEPHALOZIACEAE

(Alobiellaceae, Odontoschismataceae, Trabacellulaceae)

Plants pale green to brown, red or purplish, creeping to ascending. Stems often with a hyalodermis. Branches ventral-intercalary or lateral, *Frullania*-type; stolons or flagella sometimes present. Leaves succubous, rarely transverse, 2-lobed or undivided, inserted laterally on the stem, dorsal side of the stem leaf-free, margins usually entire. Cells usually large and pellucid, thin-walled, cuticle smooth or papillose; oil bodies present or absent. Underleaves lacking or small, rarely large. Rhizoids scattered. Gametoecia on leading shoots or on short ventral branches. Sporophyte surrounded by a perianth. Seta of 12 rows of cells: 8 outer rows and 4 inner rows. Capsule elongate, wall 2-layered. Vegetative reproduction by gemmae produced on ascending flagelliform shoots.

DISCUSSION. A family of about 15 genera worldwide, 9 in tropical America. The lateral insertion of the leaves, not extending to the dorsal midline of the stem, the scattered rhizoids, the usually large, thin-walled cells, and the very thin seta of only 12 rows of cells (8 outer rows), are important characteristic features of this family.

LITERATURE. Fulford, M. H. 1968. Cephaloziaceae, Alobiellaceae, Trabacellulaceae. Manual of the leafy Hepaticae of Latin America, Part III. Memoirs of the New York Botanical Garden 11 (3): 311-381 [keys].

1. Ventral side of the leaf forming an inflated sac ..... **Nowellia**
1. Ventral side of the leaf not forming a sac 2
2. Leaves undivided or shallowly retuse 3
2. Leaves distinctly 2-lobed 9
3. Underleaves large, 2-lobed. Leaves narrowly ovate-lanceolate ..... **Alobiella**
3. Underleaves lacking or very small. Leaves broader 4
4. Plants very small, less than 1 mm wide, whitish-green to reddish. Gemmae usually present ... 5
4. Plants larger. Gemmae present or absent 6
5. Cells in the middle of the leaf 40-100 µm long, with uniformly thickened walls, trigones lacking ..... **Alobiellopsis**
5. Cells in the middle of the leaf 15-30(-40) µm long, with trigones ..... **Odontoschisma**
6. Leaf cells very large, more than 40 µm wide. Gemmae lacking. Guayana Highland 7
6. Leaf cells smaller. Gemmae usually present 8
7. Plants 1.5-3 mm wide, brown. Leaves tilted to the ventral side of the stem, apex rounded and with a few teeth, or acuminate and entire. Cell surface without thickened bands, cuticle smooth ..... **Haesselia**

7. Plants smaller, ca. 1 mm wide, pale yellow-brown. Leaves horizontal, not tilted to the ventral side of the stem, apex ± rounded and without teeth. Cell surface covered by yellow-brown thickened bands, cuticle seemingly papillose ..... **Trabacellula**
8. Plants (2-)2.5-4 mm wide. Leaves oblong-rectangular, with undulate margins. Underleaves with numerous slime papillae; fresh plants sticky due to abundant secretion of mucus. Stem epidermal cells conspicuously smaller than the medullary cells ..... **Anomoclada**
8. Plants smaller, 1-2.5 mm wide. Leaves usually shorter, margins not undulate. Underleaves without or with very few slime papillae; plants not sticky. Stem epidermal cells not or hardly smaller than the medullary cells ..... **Odontoschisma**
9. Underleaves lacking. Stem with a distinct hyalodermis ..... **Cephalozia**
9. Underleaves present, sometimes small. Hyalodermis present or absent 10
10. Leaves short 2-lobed to less than 1/4 of leaf length. Leaves plane ..... **Alobiella**
10. Leaves more deeply 2-lobed to 1/3-1/2 of leaf length. Leaves concave..... **Iwatsukia**

Alobiella (Fig. 18) - A monotypic, neotropical genus, with *A. husnotii* (Gott.) Steph. at rather low elevations in the West Indies, on Mt. Roraima, in northern Peru, and in Central and SE Brazil. The Peruvian and Brazilian plants were described as *A. campanensis* Steph., which is a synonym of *A. husnotii* (see Gradstein & Florschütz-de Waard, 1989).

HABITAT. On steep, moist clay soil, on rock walls of cut road banks, along streams, in forests, etc., 500-1500 m. Often together with *Alobiellopsis dominicensis* and *Paracromastigum bifidum*.

DESCRIPTION. **Plants** medium-sized, 1-2 mm wide, pale to rather deep green, creeping to ascending. **Stems** fragile, with hyalodermis (cross-section). **Branches** purely ventral-intercalary, often stoloniform. **Leaves** succubous, wide-spreading, very flat, inserted almost longitudinally along the lateral side of the stem, narrowly ovate-lanceolate, apex acute or short-bifid. **Cells** long and narrow (60-100 µm long), becoming narrower toward the leaf margin to form a weak border, cuticle slightly papillose; oil bodies rather large and grayish, 1-2 per cell, finely granular. **Underleaves** large, deeply bifid, with narrowly acuminate segments. **Gemmae** not observed.

DISCUSSION. A very distinct genus, characterized by lanceolate leaves with acute or short-bifid apices, and large, bifid underleaves with narrowly acuminate segments. The very long and narrow leaf cells are another striking feature.

LITERATURE. Fulford, M. H. 1968 (see family ref., p. 378-381). - Giancotti, C. & D. M. Vital. 1990. The genus *Alobiella* (Spruce) Schiffner new to Brazil. Lindbergia 15: 103-105. - Gradstein, S. R. & J. Florschütz-de Waard. 1989. Results of a botanical expedition to Mount Roraima, Guyana. I. Bryophytes. Tropical Bryology 1: 25-54. - Schuster, R. M. 1969. Studies on Hepaticae XLVI-XLVII. On *Alobiella* (Spr.) Schiffn. and *Alobiellopsis* Schust. Bulletin of the National Science Museum, Tokyo 12: 659-683.

Alobiellopsis (Fig. 18) - A small pantropical genus with 2 species at low elevations in tropical America. *Alobiellopsis dominicensis* (Spruce) Fulford is the only widespread species, occurring in the West Indies, along the Pacific coast of Colombia and Costa Rica, and on the Galapagos Islands. A second species has been described from northern Peru.

HABITAT. On steep, compact clay soil of cut road banks, along trails, rivers, etc., below 1000 m.

DESCRIPTION. **Plants** very small, less than 1 mm wide, whitish-green to reddish, creeping except for the upright, gemmiparous shoots. **Stems** fragile, all cells similar in size, hyalodermis lacking. **Branches** purely ventral-intercalary, frequently stoloniform. **Leaves** succubous, inserted laterally on the stem, suborbicular with rounded, truncate or retuse apex. **Cells** relatively large, elongate (ca. 40-100 µm long), larger towards leaf base, walls uniformly thickened, without trigones, cuticle smooth; oil bodies large, finely granular, 1-4 per cell. **Underleaves** minute, of only a few cells, hidden between the long, colorless rhizoids; on gemmiparous and sexual shoots, however, they are large, lanceolate, with narrow undivided apex. **Gemmae** frequently produced at the tips of upright flagelliform shoots.

DISCUSSION. The rounded leaves inserted laterally on the stem (as usual in the family) and with a rounded to truncate-retuse apex, the large leaf cells with uniformly thickened walls, and the virtual lack of underleaves, are characteristic of *Alobiellopsis*. The plants resemble *Odontoschisma* but are smaller, more fragile, and leaf cells larger, with the walls uniformly thickened and lacking trigones.

LITERATURE. Fulford, M. H. 1968 (see family ref., p. 349-352). - Schuster, R. M. 1969. Studies on Hepaticae XLVI-XLVII. On *Alobiella* (Spr.) Schiffn. and *Alobiellopsis* Schust. Bulletin of the National Science Museum, Tokyo 12: 659-683.

Anomoclada (Fig. 19) - A monotypic, neotropical genus, with *A. portoricensis* (Hampe & Gott.) Váña (= *A. mucosa* Spruce) in the Greater Antilles (Cuba, Puerto Rico), the Guayana Highland (Venezuela, Guyana), and adjacent northern outliers of the Amazon Basin.There is an old, unconfirmed record from Rio de Janeiro (Fulford, 1968).

HABITAT. On rotten logs, roots, and trunk bases in the understory of submontane and lower montane rain forest and scrub, 500-2200 m. Also on moss-covered rock and boggy ground.

DESCRIPTION. **Plants** relatively large, 2-4 mm wide, glistening green, strongly sticky when fresh. **Stems** rigid, epidermal cells smaller and thicker-walled than the inner cells. **Branches** ventral-intercalary or dorsal-intercalary ("*Anomoclada*-type"). **Leaves** succubous, undivided, inserted laterally on the stem, more or less rectangular, with undulate margins. **Cells** with large, bulging trigones and stellate lumina, cuticle papillose; oil bodies unknown (probably as in *Odontoschisma*). **Underleaves** very small, covered with numerous slime papillae. **Gemmae** frequently produced at the tips of upright flagelliform shoots.

DISCUSSION. The rather large plants which are glistening green and very sticky when fresh, are unmistakable. The stickiness of the plants, due to the abundant secretion of mucus from slime papillae on the underleaves, is an excellent field characteristic. The plants resemble *Odontoschisma* but differ in the copious slime production, the presence of dorsal-intercalary branches ("*Anomoclada*-type"), the undulate leaf margins, small epidermal cells, and relatively large plant size (2-4 mm wide).

LITERATURE. Fulford, M. H. 1968 (see family ref., p. 346-347).

Cephalozia (Fig. 19) - Eight species in tropical America (24 worldwide), 6 in the subgenus *Cephalozia* and 2 in the subgenus *Macrocephalozia* (= *Fuscocephaloziopsis*). Subgen. *Cephalozia* is widespread in the region, subgen. *Macrocephalozia* is scattered in the West Indies and along the Pacific coast of Colombia.

HABITAT. The species of subgen. *Cephalozia* grow on earth banks, humus, peat, rotten wood, and on trunk bases in humid montane forests, scrub, and páramos, 1000-4000 m. The most common are *C. crossii* Spruce (= *C. dussii* Fulford), characteristic of *Sphagnum* bogs in páramo but also occurring lower down in montane habitats, and *C. crassifolia* (Lindenb. & Gott.) Fulford, which is restricted to the montane belt. The holarctic *C. pleniceps* (Austin) Lindb. and *C. bicuspidata* (L.) Dumort. have been found a few times in *Sphagnum* bogs in páramos. Another holarctic species, *C. catenulata* (Hüb.) Lindenb., occurs on decaying logs in montane conifer forests of Mexico, in a liverwort community together with *Nowellia curvifolia* and *Lophozia longiflora*.

The species of the subgen. *Macrocephalozia* occur at lower elevations (than those of subgen. *Cephalozia*) and grow on the bark of trees in more or less undisturbed, wet lowland and submontane rain forests, below 1000 m. *Cephalozia infuscata* Schust. (= *Fuscocephaloziopsis biloba* (Herzog) Fulford) is common in the rain forests of western Colombia.

DESCRIPTION. **Plants** small to medium-sized, 0.5-2 mm wide, whitish-green to reddish or brown, creeping. **Stems** fragile, with a distinct hyalodermis. **Branches** ventral-intercalary or terminal, *Frullania*-type; stolons or flagella sometimes present. **Leaves** succubous, 2-lobed, concave, inserted laterally on the stem, leaving the dorsal side of the stem leaf-free, orbicular to ovate, tips acute to narrow-acuminate, margins entire. **Cells** thin-walled, variable in size, cuticle smooth; oil bodies lacking. **Underleaves** lacking. **Gemmae** not observed.

DISCUSSION. *Cephalozia* may be recognized by the small, whitish-green (sometimes reddish or brown) plants with large, pellucid stem epidermal cells (hyalodermis present), by the concave, ovate-orbicular leaves which are 2-lobed with a rounded incision and very narrow tips, and by the absence of underleaves. The thin-walled leaf cells without oil bodies are also characteristic. The species of subgen. *Macrocephalozia* differ from the typical *Cephalozia* species in the less deeply bifid leaves and much larger cells (50-100 µm long).

Small, sterile plants of *Cephalozia* may be confused with *Cephaloziella*. For differences between these two genera see under the latter.

LITERATURE. Fulford, M. H. 1968 (see family ref., p. 311-326 [key to 8 spp.; for revised taxonomy see Váña 1984]). - Váña, J. 1984. *Cephalozia* (Dum.) Dum. in Africa, with notes on the genus. Beiheft zur Nova Hedwigia 90: 179-198.

Haesselia (Fig. 19) - Endemic to the Guayana Highland, with 2 species (*H. acuminata* Gradst., *H. roraimensis* Grolle & Gradst.) known only from the north slope of Mt. Roraima.

HABITAT. *Haesselia roraimensis* Grolle & Gradst. grows on rotten wood in humid, virgin lower montane rain forest (500-1600 m); *H. acuminata* Gradst. occurs on moist soil in montane scrub (ca. 2000 m).

DESCRIPTION. **Plants** relatively large, 1.5-3 mm wide, glossy brownish, creeping to ascending. **Stems** with a 1-3-layered hyalodermis. **Branches** intercalary (lateral or ventral); stolons lacking. **Leaves** succubous, undivided, densely imbricate, convex, "plagiochiloid" with the dorsal half ± horizontal and recurved and the ventral portion strongly "ventrad" (tilted to the ventral side of the stem), apex rounded to acuminate, margins entire or with a few teeth along the ventral margin, ventral leaf bases ampliate, sometimes forming a crest. **Cells** huge (70-150 µm), polygonal, thin-walled, cuticle smooth; oil bodies unknown. **Underleaves** lacking. **Gemmae** not observed.

DISCUSSION. The large, glossy brown plants with ventrad leaves and very large leaf cells, are unmistakable. In *H. roraimensis*, ventral leaf bases are strongly ampliate and turned downwards, away from the stem, forming a crest as found in many species of *Plagiochila*.

LITERATURE. Gradstein, S. R. & J. Florschütz-de Waard 1989. Results of a botanical expedition to Mount Roraima, Guyana. I. Bryophytes. Tropical Bryology 1: 25-54. - Grolle, R. & S. R. Gradstein 1989. *Haesselia*, a new genus of Cephaloziaceae from Mt. Roraima, Guyana. Journal of the Hattori Botanical Laboratory 64: 327-334.

Iwatsukia (= *Cladomastigum*) (Fig. 20) - A small pantropical genus (4 spp.), with 3 species in tropical America: *I. bifida* (Fulford) Schust. and *I. spinosa* (Fulford) Schust. in the Guayana Highland, and *I. jishbiae* (Steph.) Kitag. in Central America (also Old World).

HABITAT. On trunk bases and sandstone bluffs in humid, virgin montane forests, 1000-2500 m.

DESCRIPTION. **Plants** very small, less than 1 mm wide, pale green, creeping to ascending. **Stems** rigid, of thick-walled cells, hyalodermis lacking. **Branches** purely ventral-intercalary, often flagelliform. **Leaves** succubous, wide-spreading, 2-lobed to 1/3-1/2 of leaf length, concave and somewhat canaliculate, inserted almost to the dorsal midline of the stem, ovate to lanceolate. **Cells** rather small (20-30 µm long), uniformly thick-walled, cuticle slightly papillose; oil bodies unknown. **Underleaves** present, large or small, usually 2-lobed. **Gemmae** not observed.

DISCUSSION. Resembling *Alobiella*, but leaves conspicuously concave-canaliculate (not flat) and are more deeply 2-lobed. Moreover, the leaf cells are much smaller and thicker-walled, with a conspicuous primary middle lamella. The underleaves are variable in size and are smaller in *I. jishbiae* than in the other species.

LITERATURE. Schuster, R. M. 1968. Studies on Hepaticae XLV. On *Iwatsukia*. Bulletin of the National Science Museum, Tokyo 11: 309-317 [key]. - Schuster, R. M. 1990. Origins of neotropical leafy Hepaticae. Tropical Bryology 2: 239-264.

Nowellia (Fig. 20) - A tropical-holarctic genus (10 spp.), with 6 species in tropical America, primarily in the northern part of the region: Central America, the West Indies, and adjacent parts of northern South America.

HABITAT. Almost always on dead wood, especially on decorticated logs, in montane rain forest with little disturbance, 500-3000 m. A few records are from rocky substrates. The holarctic *Nowellia curvifolia* (Nees) Schiffn. is a characteristic species of a bryophyte community on decaying logs in Mexican conifer forests (Gradstein & Váña, 1994).

DESCRIPTION. **Plants** small, 0.5-1.5 mm wide, whitish-green to red, rose or purplish, creeping. **Stems** fragile, with a distinct hyalodermis. **Branches** ventral-intercalary or terminal, *Frullania*-type; stolons lacking. **Leaves** transverse, standing upwards away from the stem, 2-lobed (rarely undivided), deeply concave, saccate below due to inrolling of the ventral margin, leaf tips acute to long-acuminate-piliferous (rarely rounded), margins entire or toothed. **Cells** thin-walled, cuticle smooth; oil bodies lacking. **Underleaves** lacking. **Gemmae** not observed.

DISCUSSION. *Nowellia* is easily recognized by the peculiar leaves, which are saccate at the base due to the inrolling of the ventral margin. The plants are often reddish or purplish and the leaves are usually 2-lobed, with acuminate tips, except in *N. reedii* from Costa Rica which has ± undivided leaves.

LITERATURE. Fulford, M. H. 1968 (see family ref., p. 326-333). - Gradstein, S. R. & J. Vána. 1994. A boreal bryophyte community in a tropical montane forest of Mexico. Tropical Bryology 9: 31-34 [ecol.]. - Grolle, R. 1968. Monographie der Gattung *Nowellia*. Journal of the Hattori Botanical Laboratory 31: 20-49 [key to 5 spp.]. - Robinson, H. 1970. Notes on the genus *Nowellia*. The Bryologist 73: 150-152 [key to 6 spp.].

Odontoschisma (Fig. 20) - A tropical-holarctic genus (10-12 spp.), with about 5-6 species in tropical America.

HABITAT. On rotten wood, logs, and humus in rather open, humid environments, 0-4000 m. The species occur most frequently in montane forests, zacatonal, páramo, and puna and are very rare in lowland forests.

DESCRIPTION. **Plants** small to medium-sized, 0.5-2.5 mm wide, glossy green to red or yellowish-brown, little-branched, creeping or ascending from a stoloniform base. **Stems** rigid, of rather uniform thick-walled cells, hyalodermis lacking. **Branches** ventral-axillary, stolons present. **Leaves** succubous, undivided, inserted laterally on the stems as usual in the family (insertion line not reaching the dorsal stem-midline), flat to strongly concave, orbicular or ovate, with a broad, rounded apex, margins sometimes bordered by thicker-walled cells. **Cells** ± isodiametric, uniformly thin-walled or with large trigones and stellate lumina, cuticle smooth or papillose; oil bodies rather large, 2-5 per cell, finely

granular. **Underleaves** lacking or minute. **Gemmae** frequently produced at the tips of upright flagelliform shoots.

DISCUSSION. The green to reddish or yellowish-brown color of the plants, the rigid stems lacking a hyalodermis, the undivided, orbicular to ovate leaves, the lack of underleaves, and the ventral stolons are the most distinctive features of *Odontoschisma*. The genus may be confused with *Jungermannia* but in *Jungermannia* the leaf insertion extends to the dorsal midline of the stem (not so in *Odontoschisma*), and stolons and gemmae are lacking (always present in neotropical *Odontoschisma*).

The neotropical species of *Odontoschisma* are still poorly known and the treatment by Fulford (1968) is not very satisfactory. Size of the trigones, an important character for species identification in Fulford's key, is not always reliable.

LITERATURE. Fulford, M. H. 1968 (see family ref., p. 334-346 [key to 10 spp., some of these may be synonyms]).

Trabacellula (Fig. 21) - Endemic to the Guayana Highland and monotypic.

HABITAT. The only species, *T. tumidula* Fulford, grows on moist, shaded sandstone cliffs, bases of trunks, roots, and litter in the understory of humid montane rain forests and scrub, 500-2500 m.

DESCRIPTION. **Plants** rather small, ca. 1 mm wide, dull pale yellow-brown, little-branched, creeping. **Stems** rigid, with a distinct hyalodermis. **Branches** ventral-axillary, stolons lacking. **Leaves** succubous, undivided, inserted laterally on the stem, rather flat, ± quadrate with a broad, rounded to truncate apex. **Cells** ± isodiametric, large, 45-60 µm, uniformly thick-walled, trigones lacking, cuticle smooth or finely papillose; cell surface densely covered by yellow-brown thickened bands; oil bodies unknown. **Underleaves** lacking. **Gemmae** not observed.

DISCUSSION. Superficially resembling *Odontoschisma*, but differing in the presence of a distinct stem hyalodermis, lack of stolons, and larger leaf cells with uniformly thickened walls, without trigones. A unique feature of the genus are the numerous yellow-brown thickened bands covering the leaf cells.

LITERATURE. Fulford, M. H. 1968 (see family ref., p. 352-353).

CEPHALOZIELLACEAE

Plants very small, thread-like, usually less than 0.5 mm wide and less than 1 cm long, creeping or ascending, sometimes with a stoloniform base. Stems without hyalodermis. Branches variable, ventral- or lateral-intercalary and terminal, *Frullania*-type. Leaves transverse or succubous, 2-lobed or entire, insertion line extending to dorsal midline or not. Cells small, less than 20 µm (larger in *Cephaloziopsis*), with thin or uniformly thickened walls, trigones lacking, cuticle smooth or papillose; oil bodies finely granular. Underleaves very small or lacking. Rhizoids scattered. Gametoecia on leading shoots or very short branches. Sporophyte surrounded by a long-cylindrical perianth, mouth of the perianth often crenate and bordered by conspicuously elongate, thick-walled cells. Seta very thin, of only 8 rows of cells: 4 large outer rows and 4 small inner rows. Capsule elongate, wall 2-layered. Vegetative reproduction by gemmae in *Cephaloziella*.

DISCUSSION. A family of about 7-8 genera worldwide; 4 in tropical America. The very small size of the plants and the very thin seta of only 8 rows of cells, are the main features of this family.

LITERATURE. Fulford, M. H. 1976. Cephaloziellaceae. Manual of the leafy Hepaticae of Latin America, Part IV. Memoirs of the New York Botanical Garden 11 (4): 393-419 [keys].

1. Stems arising from a stoloniform base. Leaves undivided or short bifid (to ¼ or less)..... ..... **Kymatocalyx**
1. Stems without a stoloniform base. Leaves bifid to 1/3 or more 2
2. Leaves obcuneate, widest above the middle. Leaf segments rounded to obtuse .... **Cephaloziopsis**
2. Leaves not obcuneate, widest in the lower half or the middle. Leaf segments acute, rarely obtuse. 3
3. Leaves ± transverse. Leaf insertion reaching the dorsal midline of the stem. Cells in the middle of the leaf 8-15 µm, usually thick-walled ..... **Cephaloziella**
3. Leaves distinctly succubous. Leaf insertion not reaching the dorsal midline of the stem. Cells in the middle of the leaf 12-25 µm, thin-walled ..... **Cylindrocolea**

Cephaloziella (Fig. 21) - About 10 species in tropical America (ca. 50 (?) worldwide), in montane and alpine regions.

HABITAT. Usually on moist earth, in shaded and exposed environments, 500-3500 m. Occasionally on rotten wood or rock.

DESCRIPTION. **Plants** dull green to brown or red; stolons lacking. **Stems** rigid, without hyalodermis. **Leaves** almost transverse, inserted to the dorsal midline of the stem, 2-lobed, tips acute, margins entire or toothed. **Cells** very small (ca. 8-15 µm), usually thick-walled, without trigones, cuticle smooth or papillose; oil bodies as in the family. **Underleaves** lacking or very small. **Gemmae** sometimes produced on upright flagelliform shoots.

DISCUSSION. *Cephaloziella* can readily be distinguished from *Cephalozia* by the small stem epidermal cells (a hyalodermis is lacking in *Cephaloziella*) and the very small, often thick-walled leaf cells. Moreover, the leaves in *Cephaloziella* are smaller, hardly wider than the stem, and more transverse, and the cells have oil bodies (lacking in *Cephalozia*). Due to the small, thick-walled cells, *Cephaloziella* species are more rigid and dull-colored than *Cephalozia* species.

Paramomitrion (Gymnomitriaceae) from the upper páramo region of Venezuela (Mérida) is very similar to *Cephaloziella* but differs by the possession of large underleaves.

LITERATURE. Fulford, M. H. 1976 (see family ref., p. 402-419 [key to 9 spp., except *C. inaequalis* Schust., *C. grisea* Schust. and *C. stolonifera* Schust.]).

Cephaloziopsis (Fig. 21) - A monotypic, neotropical genus. The only species, *C. intertexta* (Gott.) Schust., occurs disjunctly in the West Indies and northern Central America, and again in the Central Andes (Peru, Bolivia) and southeastern Brazil.

HABITAT. On moist earth banks and wet rocks, along rivulets and streams, (100-)500-2500 m. Rarely on bases of trunks in humid montane forests.

DESCRIPTION. **Plants** light green, lacking secondary pigmentation; stolons lacking. **Branches** sparse, predominantly ventral-intercalary. **Leaves** almost transverse, inserted to the dorsal midline of the stem, 2-lobed to 1/3-1/2, obovate to obcuneate, tips rounded to obtuse, margins entire. **Cells** relatively large, ca. 20-35 µm, very thin-walled, without trigones, cuticle smooth. **Underleaves** lacking or very small. **Gemmae** lacking.

DISCUSSION. The obovate to obcuneate leaves with 2 rounded to broadly obtuse tips, are very characteristic of *Cephaloziopsis.* Moreover, the leaf cells are much larger than in other neotropical members of the Cephaloziellaceae. The genus may only be confused with *Chonecolea* (Chonecoleaceae). However, in the latter the leaves are more obliquely inserted, almost horizontally spreading, and broadest in the middle (not in the upper part). Moreover, the leaf tips in *Chonecolea* are narrower (obtuse to subacute) and branching is purely lateral, never ventral.

LITERATURE. Fulford, M. H. 1976 (see family ref., p. 396-398).

Cylindrocolea (Fig. 21) - A pantropical genus (ca. 12 spp.), with 5 species in tropical America, at rather low elevations. Like *Cephaloziopsis*, this genus mostly occurs in the outer, peripheral regions of the Neotropics and seems to be very scarce in equatorial regions.

HABITAT. On earth banks, bark of trees, rotten logs, and rock, 0-1500 m. The species of *Cylindrocolea* are more often epiphytic than other members of the family.

DESCRIPTION. **Plants** light green to brown or reddish; stolons lacking. **Leaves** succubous, inserted laterally on the stem, insertion not reaching the dorsal midline of the stem, 2-lobed, tips acute or somewhat obtuse, margins entire. **Cells** ca. 12-25 µm, thin-walled, cuticle smooth; oil bodies as in the family. **Underleaves** lacking. **Gemmae** not observed.

DISCUSSION. Closely related to *Cephaloziella* but with leaves succubous instead of transverse and inserted laterally on the stem, leaving a dorsal strip of 2 rows of stem cells "leaf-free" (as in Cephaloziaceae). Another difference from *Cephaloziella* are the larger, thin-walled leaf cells.

LITERATURE. Fulford, M. H. 1976 (see family ref., p. 398-402).

Kymatocalyx (= *Stenorrhipis*) (Fig. 22) - A pantropical genus (4 spp.), with 2 species in tropical America: *K. cubensis* Gott. ex Steph. (= *K. dominicensis* (Spruce) Váña) widespread in tropical America, and *K. rhizomatica* (Herzog) Gradst. & Váña (= *Stenorrhipis rhizomatica* Herzog) in Central America (Panama, Costa Rica) and Colombia. The latter species also occurs in Indonesia.

HABITAT. On moist earth and rock near running water, usually along rivers or creeks, in undisturbed lowland rain forests or in rather open, moist habitats, 150-2000 m.

DESCRIPTION. **Plants** pale green to dark green to brown, with a stoloniform base, forming small mats. **Branching** purely ventral-intercalary. **Leaves** succubous or almost transverse, inserted to the dorsal midline of the stem or not, orbicular to somewhat elongated, apex rounded, truncate, emarginate or short bifid (to ¼ or less), margins entire. **Cells** 12-22 µm long, walls slightly thickened, cuticle smooth. **Underleaves** lacking. **Gemmae** not observed.

DISCUSSION. The tiny plants with erect leafy shoots arising from creeping stolons, are unmistakable. The lower portions of the erect shoots are often leafless or have rudimentary leaves.

Kymatocalyx was recently revised by Gradstein and Váña (1999), who united *Kymatocalyx* with the palaeotropical genus *Stenorrhipis*. Two species occur in the Neotropics, *K. rhizomatica* and *K.*

cubensis. *Kymatocalyx rhizomatica* is pale green and has short bifid leaves, *K. cubensis* is dark green to brown and has undivided to shallowly emarginate leaves. The latter resembles a small *Jungermannia* but differs in the stoloniform stem base, the very small size (less than 1 mm wide), and the thin, cephalozielloid seta consisting of only 8 cell rows. In the past, the species of *Kymatocalyx* have sometimes been considered members of the family Jungermanniceae.

LITERATURE. Gradstein, S. R. & J. Váña. 1999. On the taxonomy of *Kymatocalyx* and *Stenorrhipis* (Cephaloziellaceae). Haussknechtia Beiheft 9: 155-170.

CHONECOLEACEAE

A monotypic, pantropical family, containing only the genus *Chonecolea.*

Chonecolea (Fig. 22) - An pantropical genus (3 spp.), with 2 species in tropical America: *C. doellingeri* (Nees) Grolle at low elevations and disjunct in Florida, southeastern Brazil and northern Argentina, and *C. andina* Grolle & Váña at high elevations in the Peruvian Andes. A third species, *C. acutiloba* (Schiffn.) Schust. from southeastern Brazil, does not belong in *Chonecolea* but is a member of the genus *Cylindrocolea* (*C. acutiloba* (Schiffn.) J. J. Engel).

HABITAT. *Chonecolea doellingeri,* the most widespread species of the genus, is a common, drought-tolerant epiphyte in open environments in SE Brazil: in cerrado vegetation, on roadside trees, in towns, in parks, etc., 0-900 m. The species even occurs in highly polluted areas such as São Paulo City. In Florida, the species is much less common and grows on bark in moist, inundated lowland forests ("hammock forests"). Recently, the species has been reported from Australia, where it is apparently introduced in urban areas.

Chonecolea andina has a very different ecology and occurs on earth and rock in the high Andes, between 2700 and 4300 m.

DESCRIPTION. **Plants** very small, ca. 0.5-0.8 mm wide, pure green to purplish, creeping. **Stems** very fragile, of thin-walled cells, hyalodermis lacking. **Branches** lateral-intercalary. **Leaves** succubous with insertion line reaching the dorsal midline of the stem, spreading almost horizontally, bilobed to ca. 1/3(-1/2), tips narrowly rounded to subacute, margins entire. **Cells** ca. 15-25 µm long, very thin-walled, lacking trigones, cuticle smooth; oil bodies minute, homogeneous, numerous per cell. **Underleaves** absent or small, subulate. **Rhizoids** scattered. **Gametoecia** on elongated shoots. **Sporophyte** in an inflated, bell-shaped perianth with a broad, truncate mouth and 3-4 plicae above. **Seta** of 12 cells, as in the Cephaloziaceae. **Capsule** spherical, wall 2-layered. **Vegetative reproduction** by caducous perianths.

DISCUSSION. Resembling *Cylindrocolea* (Cephaloziellaceae) but leaves extending to the dorsal midline of the stem, branching purely lateral-intercalary (mostly ventral-intercalary or *Frullania*-type in *Cylindrocolea*), and perianth usually shorter, bell-shaped. Moreover, the capsule in *Chonecolea* is spherical, not ellipsoidal.

LITERATURE. Schuster, R. M. 1980. Chonecoleaceae. The Hepaticae and Anthocerotae of North America, Vol. IV: 317-325 [key].

GEOCALYCACEAE
(Lophocoleaceae)

Plants green to brown or reddish-brown, creeping to ascending. Stems without hyalodermis, cortex usually not differentiated. Branches variable, *Frullania*-type and intercalary (lateral and ventral); stolons or flagella usually lacking. Leaves succubous, usually almost horizontal in position, insertion line usually reaching dorsal stem-midline, 2-lobed or undivided, leaf margins entire or toothed. Cells thin-walled, with or without trigones, cuticle usually smooth; oil bodies granular, rarely homogeneous. Underleaves present, small or large, usually 2-lobed and often toothed. Rhizoids usually in tufts from underleaf bases, rarely scattered. Gametoecia on leading shoots or on short branches. Sporophyte prduced in a perianth or a marsupium, perianth 0-3-keeled, inflated or laterally compressed. Seta of numerous cells (cross-section). Capsule wall 3-8-layered. Vegetative reproduction rare, by gemmae or caducous leaves.

DISCUSSION. A family of about 20 genera worldwide; 7 or 8 in tropical America. Characteristic features of the Geocalycaceae are 1) strongly succubous, almost horizontal leaves; 2) well-developed underleaves, often united on one or both sides with leaf bases; and 3) rhizoids in tufts at underleaf bases. The sporophyte is produced in a perianth (subfamily Lophocoleoideae) or a marsupium

(subfamily Geocalycoideae). The neotropical genera are members of the Lophocoleoideae with exception of *Saccogynidium*, which has a marsupium and belongs to the Geocalycoideae.

1. Leaf apex entire 2
1. Leaf 2-3-lobed or toothed 7
2. Lower portions of the stems almost leafless, stoloniform, with flagella ..... **Leptoscyphopsis**
2. Lower portions of the stems not stoloniform, flagella lacking 3
3. Leaves reniform, about twice as wide as long, stiffly appressed to each other, stem invisible from above ..... **Platycaulis**
3. Leaves ovate-orbicular to oblong, as wide as long or longer than wide, appressed or spreading, the stem usually visible 4
4. Underleaves 4-5 times as wide as the stem, with numerous teeth (usually more than 8). Leaves flat. Perianth without keels. Monoicous ..... **Heteroscyphus**
4. Underleaves smaller, with fewer teeth or entire Leaves convex or concave, rarely flat. Perianth with 0-2 keels. Dioicous 5
5. Plants pale green, small, less than 2 mm wide. Leaf cells thin-walled, trigones ± lacking, cuticle smooth. Underleaves small, usually narrower than the stem, entire or short-bifid, the margins without teeth. On moist soil and rock, usually near running water ..... **Clasmatocolea**
5. Plants usually brownish, rarely green, small or large. Leaf cells with trigones, cuticle smooth or rough. Underleaves small or large, bifid, the margins with or without teeth. On bark, rock, or soil 6
6. Cuticle of stem cells densely papillose. Leaves about 2 times as long as wide. Underleaves free from the leaf, deeply bifid, with entire margins. Sporophyte produced in a marsupium on a short lateral branch. Southeastern Brazil ..... **Saccogynidium**
6. Cuticle of stem cells smooth. Leaves less than 2 times as long as wide. Underleaves free or connate with leaves, shallowly or deeply bifid, margins entire or toothed. Sporophyte produced in a perianth[2].
Leptoscyphus
7. Leaves ± transverse, strongly caducous. Plants minute, yellowish green, ca. 0.5 mm wide. Tiny epiphyte in upper montane cloud forest and páramo .....**Campanocolea**
7. Leaves distinctly succubous. Plants larger 8
8. Leaf apex mostly entire, occasionally with a spinose tooth ..... **Leptoscyphus**
8. Leaf apex always toothed or bifid 9
9. Gametangia on short ventral branches hidden under the leaves. Perianth smooth, without sharp keels. Monoicous, usually fertile. Leaf apex truncate, with (1-)2-3-teeth or cilia **Heteroscyphus**
9. Gametangia on long branches, not hidden under the leaves. Perianth 3-keeled (rarely smooth). Monoicous or dioicous. Leaf apex various: truncate to bifid, with teeth or cilia .... **Lophocolea**

Campanocolea - A monotypic, neotropical genus, with *C. fragmentissima* (Schust.) Schust. (= *Lophocolea fragmentissima* Schust.) in the high Andes of northern South America, from northern Peru to Venezuela, and in the Cerro de la Muerte, Costa Rica.

HABITAT. On bark of mossy trunks and twigs in upper montane cloud forest, subalpine dwarf forest and in the lower páramo region, 3200-4000 m.

DESCRIPTION. **Plants** tiny, fragile, ca. 0.5 mm wide, yellowish green to pale brown, creeping, irregularly branched, the shoots partly denuded by caducous leaves. **Branches** *Frullania*-type. **Leaves** ± transverse, crowded at shoot tips, on lower parts of the shoots distant and easily falling away from the shoots, broader than long, obtrapezioidal, deeply 2-lobed, leaf lobes often widely divergent, obtuse to acute, leaf margins entire. **Cells** ± thin-walled, trigones small, cuticle smooth; oil bodies (Schuster, 1997) faintly granular. **Underleaves** free, about half the size of the leaves, 2-lobed. **Dioicous**. **Gametoecia** on elongated shoots. **Perianths** large, inflated, urn-like, with a wide mouth. **Vegetative reproduction** by caducous leaves.

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[2] Here would also key out *Heteroscyphus integrifolius* (Lehm. & Lindenb.) Fulf., a Patagonian species known from Bolivia and Peru, and *Lophocolea platensis* Mass. from southern Brazil and northern Argentina. *Heteroscyphus integrifolius* is a monoicous plant with large reniform underleaves, 3-5x stem width and very flat, almost opposite, ovate leaves. The leaf cells are thin-walled, with small trigones and an almost smooth cuticle, and the sexual branches are very short and hidden under the leaves. *Lophocolea platensis* is a dioicous plant with small underleaves, scarcely wider than the stem, and suborbicular leaves. The cells in the upper part of the leaf rather rather small, 15-25 µm in diameter, and thin-walled, ± without trigones, with a rough cuticle (for descriptions see Fulford, 1976; *L. platensis* is treated there as a synonym of *L. semiteres*).

DISCUSSION. *Campanocolea fragmentissima* is a tiny epihyte from scrubby vegetations near the forest line. The species is recognized in the field by the minute yellowsh-green shoots less than 1 mm wide that are partly denuded due to the production of numerous caducous leaves. The leaves are transversely inserted and deeply bifid with diverging lobes, and are usually not overlapping (except at the shoot tips). The perianths are large, inflated, bell-shaped, hence the name "*Campanocolea.*"

LITERATURE. Schuster, R. M. 1997. On *Campanocolea* Schust. and asexual reproduction in the Geocalycaceae. Journal of the Hattori Botanical Laboratory 82: 253-259.

Clasmatocolea (Fig. 23) - A southern-temperate genus (20 spp.), with 1 species, *C. vermicularis* (Nees) Grolle (= *Notoscyphus lindmannii* (Steph.) Schiffn.), in SE Brazil and at high elevations in the Andes, reaching northwards to Costa Rica.

HABITAT. On moist or wet earth and on rock along running water, in gulleys, and on steep, clayey roadsides, in the Andes at about 2000-4500 m, in SE Brazil at much lower elevations (100-2400 m).

DESCRIPTION. **Plants** small, 1-2 mm wide, to 2 cm long, pale green, creeping, sparingly branched. **Branches** as in the family. **Leaves** succubous, ± concave to almost flat, somewhat vertically oriented, ovate-subquadrate, apex rounded or truncate, margins entire. **Cells** thin-walled, trigones absent or very small in the neotropical species, cuticle smooth; oil bodies very finely granular, 2-3 per cell. **Underleaves** variable, ovate to lanceolate to subulate, undivided or short-bifid, margins entire. **Dioicous**. **Antheridia** on elongated shoots. **Perianths** rare, strongly inflated, with a wide, open mouth.

DISCUSSION. *Clasmatocolea vermicularis* is easily recognized by the small, pale green, creeping stems, somewhat vertically oriented leaves with ± truncate apex and thin-walled cells, and small underleaves, which are entire or short-bifid and may vary considerably in size and shape on a single stem. Rhizoids originate as short tufts from the bases of the underleaves.

A recent proposal by Hässel de Menendez (Nova Hedwigia 63: 493-516. 1996) to replace the name *Clasmatocolea* with *Chiloscyphus*, a small holarctic genus with only one species, is considered premature by lack of a critical monograph of *Lophocolea* and *Chiloscyphus* and is not accepted here.

LITERATURE. Engel, J. J. 1980. A monograph of *Clasmatocolea*. Fieldiana, Botany 3: 1-229 [key].

Heteroscyphus (Fig. 23) - About 10 species in montane regions of tropical America (ca. 30 (?) worldwide).

HABITAT. On rotten wood, bases of trunks, and moist rock in montane forests, (500-)1000- 3500 m. In dense forests usually growing in the understory.

DESCRIPTION. **Plants** medium-sized to large, 2-5 mm wide, green to brown, creeping, irregularly branched. **Branches** usually ventral-intercalary. **Leaves** succubous, ± flat, alternate to opposite, ovate-subrectangular, apex entire, short-bifid or with a few teeth, dorsal margin usually entire, ventral margin entire or toothed and often somewhat undulate. **Cells** thin-walled or with distinct trigones, cuticle smooth or weakly papillose; oil bodies unknown. **Underleaves** usually connected to the leaves, 2-lobed, often toothed. **Monoicous**, the androecia and gynoecia usually side by side. **Gametoecia** on very short ventral branches hidden behind the stem leaves. **Male branches** tiny, catkin-like. **Perianths** inflated, without keels, often immersed within the bracts, perianth mouth 3-lobed and ciliate.

DISCUSSION. *Heteroscyphus* is recognized by the very short sexual branches, originating from the axils of the underleaves and usually hidden behind the leaves, and the perianth without keels. The plants are frequently fertile and androecia and gynoecia usually occur side by side on the stem. Sterile material may be very difficult to distinguish from *Lophocolea*. The branches in *Heteroscyphus* originate almost exclusively from the ventral side of the stem; in *Lophocolea* they may be lateral or ventral. Furthermore, the ventral leaf margins are frequently toothed and somewhat undulate in *Heteroscyphus*; in *Lophocolea* they are more often plane and entire (toothed in *L. liebmanniana, L. muricata, L. polychaeta,* and *L. trapezoidea*). Finally, the underleaves in *Heteroscyphus* are always connate with the lateral leaves on both sides; in *Lophocolea* they may be free, connate on one side, or on both sides. When doubt remains, Fulford's descriptions of the neotropical species should be consulted.

LITERATURE. Fulford, M. H. 1976. *Heteroscyphus*. Manual of the leafy Hepaticae of Latin America, Part IV. Memoirs of the New York Botanical Garden 11 (4): 485-505 [key].

Leptoscyphopsis - A monotypic, neotropical genus, with *L. paradoxus* Schust. in the Andes of Venezuela (Mérida). The species is known only from the type collection.

HABITAT. Unknown.

DESCRIPTION. **Plants** creeping, black when dry, the stem bases ± stoloniform and with flagella. **Branches** ventral- and lateral-intercalary, no terminal branching. **Leaves** succubous, rather flat, oblong, apex truncate to bidentate, margins entire. **Cells** with rather large trigones, cuticle smooth; oil bodies smooth and ± homogeneous, 8-15 per cell, rather large, filling most of the cell-lumen.

Underleaves very small and inconspicuous, consisting of only 1-2 short cilia. **Perianths** 2-keeled, laterally flattened, the mouth toothed.

DISCUSSION. Similar to *Leptoscyphus* but differing in the stoloniform stem bases and the presence of flagelliform branches originating from the lower portions of the stems. *Leptoscyphopsis* is the only neotropical genus of Geocalycaceae with stolons and flagella. Other unusual features are the homogeneous oil bodies (granular in other neotropical Geocalycaceae) and the very small size of the underleaves.

LITERATURE. Schuster, R. M. 1978. Studies on Venezuelan Hepaticae I. Phytologia 39 (4): 247 [brief diagn.].

Leptoscyphus (Fig. 23) - An Afro-American genus (ca. 17 spp.), with 12 species in tropical America, usually in montane and alpine regions.

HABITAT. Common canopy epiphytes of montane forests and scrub, (100-)500-4000 m. Also on earth and rock, e g., on roadsides and in river valleys. The species usually occur in rather exposed habitats, except *L. amphibolius* (Nees) Grolle which prefers shaded environments, e.g., tree bases and humic soil in the understory of the forest.

Leptoscyphus porphyrius (Nees) Grolle has a very wide elevational range and has also been found in lowland rain forest (canopy). *Leptoscyphus cleefii* Fulford is a species of *Sphagnum* bogs in the páramos of the northern Andes.

DESCRIPTION. **Plants** small to large, 1-5 mm wide, greenish-brown to dark brown, black or reddish-brown, creeping, irregularly branched. **Branches** intercalary (ventral or lateral), rarely *Frullania*-type. **Leaves** succubous, strongly concave or almost flat, alternate to ± opposite, ovate-orbicular to oblong, undivided in neotropical species, apex rounded or truncate, rarely retuse, margins entire, occasionally with a few teeth or cilia near the ventral base (in *L. quadridentatus* (Spruce) Grolle with 3-4 long cilia at the apex!). **Cells** usually with large trigones (small in *L. amphibolius*), cuticle smooth or papillose; oil bodies finely granular. **Underleaves** connected to the leaves, 2-lobed (rarely undivided), often toothed. **Rhizoids** tufted or scattered. **Dioicous**. **Androecia** on elongated shoots or short ventral branches. **Perianths** 2-keeled, laterally flattened. **Vegetative reproduction** by caducous leaves.

DISCUSSION. The perianth in *Leptoscyphus*, being strongly inflated below, flattened above with 2 (instead of 3) keels, and located on long shoots, separates this genus from other neotropical members of the family (except *Leptoscyphopsis*). When sterile, *Leptoscyphus* is easily recognized by the brownish color, the undivided leaves with ± entire margins, the large trigones, and the conspicuous underleaves. An exception is *L. amphibolius,* which may often be pure green, without secondary pigmentation, and with very small trigones. The lack of pigmentation and cell-wall thickenings in this species correlate with its preference for shaded environments.

LITERATURE. Fulford, M. H. 1976. *Leptoscyphus*. Manual of the leafy Hepaticae of Latin America, Part IV. Memoirs of the New York Botanical Garden 11 (4): 505-535 [key]. - Grolle, R. 1962. Monographie der Lebermoosgattung *Leptoscyphus* Mitt. Nova Acta Leopoldina 25: 1-143 [key].

Lophocolea (Fig. 24) - About 20 species in tropical America (possibly more than 100 worldwide), very common in lowland and montane regions, rare above the tree line.

HABITAT. On bark and rotten wood in moist lowland and montane forests, and in the lower páramo, from sea level to about 4000 m. Sometimes on moist rock or earth; occasionally on living leaves. Most of the species are montane, a notable exception being *Lophocolea martiana* Nees, which is one of the common hepatics on rotten wood in the lowland rain forest.

DESCRIPTION. **Plants** small to large, 1-2 mm wide, (pale)green, rarely brown, creeping, irregularly branched. **Branches** *Frullania*-type or intercalary, lateral or ventral. **Leaves** succubous, alternate to ± opposite, ovate-orbicular to rectangular, apex truncate, 2-lobed or with a few teeth or cilia, in the Neotropics rarely rounded (*L. platensis*), margins entire or toothed to ciliate, leaf surface smooth or with teeth-like processes in *L. muricata*. **Cells** usually thin-walled, trigones lacking or small, rarely large (*L. trapezoidea*), cuticle smooth or papillose; oil bodies usually finely granular. **Underleaves** free or connected to the leaves, 2-lobed, often toothed. **Dioicous** or monoicous. **Gametoecia** on elongated shoots. **Perianths** 3-keeled, long-exserted beyond the bracts. **Gemmae** or caducous leaves sometimes produced.

DISCUSSION. The species of *Lophocolea* are mostly (pale) green with thin-walled cells except *L. trapezoidea*, which is usually brownish and may have large trigones. The characteristics of the latter species seem to reflect its occurrence in rather exposed habitats, e.g., forest canopies and forest margins. Other *Lophocolea* species grow in more sheltered habitats and are typical of the forest understory. The presence of long cilia on the leaf margins is another unusual feature of *L. trapezoidea*. They are also seen in *Lophocolea quadridentata* Spruce, a rare Andean species which has recently been transferred to *Leptoscyphus* (as *Leptoscyphus quadridentatus* (Spruce) Grolle) because of its

terete perianth. Vegetatively, the two species are very similar and may be distinguished only by the number of cilia on the leaves: 5-10 in *L. trapezoidea*, 3-4 in *L. quadridentata* (see Fulford 1976).

Lophocolea may be confused with *Heteroscyphus*; for differences see under the latter. A recent proposal to replace the name *Lophocolea* with *Chiloscyphus*, a small holarctic genus, is not accepted in this treatment.

LITERATURE. Fulford, M. H. 1976. *Lophocolea*. Manual of the leafy Hepaticae of Latin America, Part IV. Memoirs of the New York Botanical Garden 11 (4): 420-485 [key to spp., except *L. heterophylla* (Cuba and holarctic)].

Platycaulis - A monotypic, neotropical genus, with *P. renifolia* Schust. in the Andes of Venezuela (páramo de Tamá). The species is known only from the type collection.

HABITAT. Unknown.

DESCRIPTION. **Plants** robust, erect, brown, simple or sparingly branched. **Stems** with a thick-walled, brown, 1-layered cortex, all cells narrowly elongate. **Branches** *Frullania*-type and lateral-intercalary. **Leaves** vertically oriented and laterally appressed (obscuring the stem), insertion not reaching dorsal stem-midline, ca. 1.5 mm long, reniform, almost twice as wide as long, flat, undivided, margins entire. **Cells** with large trigones and papillose cuticle; oil bodies unknown. **Underleaves** small, ca. 1 mm long with cilia included, deeply bilobed, each segment with 2-3 cilia, underleaf base with rhizoids in a bundle. **Perianths** unknown.

DISCUSSION. The robust plants with undivided, reniform leaves that are laterally appressed to each other (like in *Jamesoniella rubricaulis*) and the stiff, blackish-brown stems with a thick-walled epidermis are striking features of *Platycaulis*. The plants are very similar to *Plagiochila dependula* Taylor (= *Jamesoniella dependula* (Taylor) Steph.) but stand out by the well-developed underleaves and the rhizoids in bundles.

LITERATURE. Schuster, R. M. 1995. Studies on Venezuelan Hepaticae VI. On *Platycaulis* Schust. Nova Hedwigia 61: 391-396.

Saccogynidium (Fig. 24) - A mainly Austral-Indomalesian genus (7 spp.), with 1 species, *S. caldense* (Ångstr.) Grolle, in southeastern and southern Brazil.

HABITAT. On bark and humic soil in montane forests, 750-1600 m.

DESCRIPTION. **Plants** medium-sized, to 6 cm long and 3-4 mm wide, green to brown, creeping, irregularly branched. **Branches** ventral-intercalary. **Stems** with densely papillose cuticle. **Leaves** succubous, ± convex, opposite, the bases free, ligulate-oblong, apex rounded-truncate, margins entire. **Cells** thin-walled, with rather small trigones, cuticle papillose; oil bodies unknown. **Underleaves** free from the leaves, deeply 2-lobed, margins entire. **Dioicous**. **Gametoecia** on very short ventral branches. **Male branches** tiny, catkin-like. **Perianths** lacking, sporophyte developing in a marsupium.

DISCUSSION. The opposite leaves, about twice as long as wide, with entire margins and a rounded-truncate apex, the densely papillose cuticle of both leaf and stem cells, and the gametoecia on very short ventral branches (as in *Heteroscyphus*) are important characteristics of *Saccogynidium caldense*. In fresh material, the stem is usually somewhat bluish-green in color. The species is separated from all other neotropical Geocalycaceae by the development of the sporophyte in a marsupium instead of a perianth. As in *Calypogeia*, this marsupium develops about halfway along or near the base of the stem instead of near the tip, out of a very short ventral branch.

LITERATURE. Grolle, R. 1960. Über *Saccogyna* Dum. und *Saccogynidium*, eine neue Lebermoosgattung. Journal of the Hattori Botanical Laboratory 23: 41-67.

GYMNOMITRIACEAE

Plants small, worm-like, 0.2-2 mm wide, green to brownish or purplish, sometimes silver-white, creeping to erect, usually forming small and very dense mats or cushions, little branched, stem bases with stolons. Stems with a thick-walled cortex. Branches lateral-intercalary. Leaves transverse, usually densely imbricate, 2-lobed or entire, insertion line extending beyond the dorsal midline of the stem (merophytes "interlocking"), leaf margins entire or crenulate. Cells usually small, ca. 12-25 µm in mid-leaf, with trigones, cuticle smooth or papillose; oil bodies usually 2-3 per cell, finely granular. Underleaves normally lacking. Rhizoids scattered. Gametoecia on leading shoots. Sporophyte surrounded by tubular bracts, a perianth lacking or rudimentary. Seta of numerous cells (cross-section). Capsule spherical, wall 2-layered. Vegetative reproduction unknown.

DISCUSSION. A family of at least 10 genera worldwide; 5-7 in tropical America. They are small, worm-like plants of cold, alpine regions (páramo, puna, zacatonal), with transverse, usually densely imbricate leaves and without underleaves (present in *Paramomitrion*). The species are always

terrestrial and the stems are usually attached to the substrate by stolons. The leaf cells may be entirely devoid of chlorophyll, giving the plants a characteristic grayish-green or whitish appearance.

LITERATURE. Schuster, R. M. 1974. Gymnomitriaceae. The Hepaticae and Anthocerotae of North America, Vol. III: 1-170. - Schuster, R. M. 1996. Studies on antipodal Hepaticae. XII. Gymnomitriaceae. Journal of the Hattori Botanical Laboratory 80: 1-147.

1. Leaves undivided, completely hyaline, the cells without chlorophyll. Stems on the dorsal side with numerous green paraphyllia 2
1. Leaves 2-lobed, not hyaline, the cells at least in part with chlorophyll. Stems without paraphyllia 3
2. Leaves plicate ..... **Stephaniellidium**
2. Leaves not plicate ..... **Stephaniella**
3. Leaf margins or entire leaf whitish, plants usually silver-white or gray. ..... **Gymnomitrion**
3. Leaf margins not whitish, plants green, brown, black, reddish, or purple 4
4. Underleaves present, large, about as long as leaves. Very tiny plants (less than 0.5 mm wide) of upper páramo region, above 4000 m ..... **Paramomitrion**
4. Underleaves lacking ..... **Marsupella**

Gymnomitrion (Fig. 25) - Seven species in tropical America (20 worldwide), in the páramo and puna regions of the Andes, Central America, and Mexico.

HABITAT. On exposed soil and rock, above 2700 m.

DESCRIPTION. **Plants** silver-whitish or gray, sometimes gray-green; stems ascending to erect, forming dense little cushions. **Leaves** transverse and densely imbricate, 2-lobed or emarginate, leaf tips rounded, acute or long-acuminate-piliferous, margins or almost entire leaf whitish, marginal cells without oil bodies. **Perianths** entirely lacking. Other characteristics as in the family.

DISCUSSION. The little silver-whitish or gray cushions are unmistakable.

Marsupella (Fig. 25) - About 10 species in tropical America (ca. 45 worldwide), distribution as for *Gymnomitrion.*

HABITAT. On exposed soil and rock, above 3000 m.

DESCRIPTION. **Plants** green, brown, black, reddish or purple, never whitish; stems erect, forming small mats. **Leaves** transverse, loosely to densely imbricate, erect-spreading, usually not tightly appressed to the stem, 2-lobed or emarginate, leaf tips rounded or acute, margins never decolorate-whitish, all leaf cells with oil bodies. **Perianths** present but very small (lacking in *M. revoluta*), hidden between the tubular bracts. Other characteristics as in the family.

DISCUSSION. Closely related to *Gymnomitrion* but leaf margins never whitish. The plants usually grow in flat mats, whereas *Gymnomitrion* tends to form small cushions.

Schuster (1996) recognizes 9 subgenera, 4 of which occur in the Neotropics: subgen. *Apomarsupella*, subgen. *Nanocaulon* and subgen. *Nanomarsupella* each with 1 species, and subgen. *Marsupella* with the remaining species. According to Schuster, *Apomarsupella* and *Nanomarsupella* may also be considered autonomous genera. *Apomarsupella*, containing *A. revoluta* (Nees) Schust. recorded from the páramo of Venezuela, is recognized by the possession of dorso-lateral branches and the total lack of a perianth. *Nanomarsupella*, containing the rare *N. xenophylla* (Schust.) Schust. from Venezuelan páramo, is a minute plant with flagelliform stems and strongly tuberculate leaf cells.

Paramomitrion - A monotypic, neotropical genus, with *P. paradoxum* Schust. in the high Andes of Venezuela (Mérida). The species is only known from the type collection.

HABITAT. On exposed soil irrigated by melting snow in páramo, 4160 m.

DESCRIPTION. **Plants** brown to reddish-purple, becoming whitish in older parts, very tiny, less than 0.5 mm wide; stems creeping, scarcely branched, flagelliform, very sparsely leaved. **Leaves** scale-like, transverse, distant, and spreading away from the stem, 2-lobed, leaf tips rounded to obtuse, margins never decolorate-whitish. **Cells** ± thin-walled, trigones lacking, cuticle coarsely papillose; oil bodies unknown. **Underleaves** large, about as long as the leaves, lanceolate to ligulate, at apex undivided or shallowly 2-lobed. **Androecia** forming small, swollen heads at stem tips. **Gynoecia** unknown.

DISCUSSION. Resembling *Cephaloziella* but differing by the presence of large underleaves. The position of this genus in the family Gymnomitriaceae is questionable (Schuster, 1996).

Stephaniella (Fig. 25) - An alpine, Afro-American genus of 4 species, all of them occurring in tropical America, from Mexico to northern Argentina. *Stephaniella paraphyllina* J. B. Jack is distributed throughout the neotropical range of the genus and, in addition, occurs in the Drakensberg area of South Africa. The other species are mostly restricted to the Andes.

HABITAT. On soil in open, exposed habitats, 2500-4500 m; once found at a very unusual, low elevation in Costa Rica: Guanacaste, at about 1000 m (leg. G. Dauphin). Plants withstanding strong desiccation and radiation.

DESCRIPTION. **Plants** gray or brownish; stems creeping, forming large, low mats, strongly attached by long ventral stolons. **Leaves** densely imbricate and somewhat laterally appressed to the stem, colorless, convex with smooth surface (not plicate), ovate to reniform, often wider than long, strongly asymmetrical with broad antical part and apex turned backwards, the apex blunt or acute to acuminate, sometimes cucullate, the margins incurved especially the postical margin. **Cells** mostly pale, without chlorophyll and lacking oil bodies except for a few green cells near the base. **Paraphyllia** numerous on the dorsal side of the stem, covered by leaves, linear or lanceolate-triangular, green, all cells with chlorophyll and oil bodies. **Perianths** present.

DISCUSSION. *Stephaniella* is one of the most specialized leafy hepatics, adapted to life under extreme alpine conditions. The leaves are very densely imbricate and almost without chlorophyll. They function as a protective shield for the green paraphyllia on the dorsal side of the stem, which take over the assimilatory function of the leaves. Long stolons serve to attach the plants firmly to the soil and prevent them from being blown away by the wind.

LITERATURE. Schmitt, U. & S. Winkler, 1968. Systematische Untersuchungen über die foliose Lebermoosgattung *Stephaniella.* Oesterreichische Botanische Zeitschrift 115: 120-133 [key].

Stephaniellidium (Fig. 25) - A monotypic, Andean genus. The only species, *S. sleumeri* (K. Müll.) S. Winkl., has been recorded from northern Argentina, Peru, and Colombia (Sierra Nevada de Santa Marta).

HABITAT. On exposed soil, above 3000 m.

DESCRIPTION and DISCUSSION. Similar to *Stephaniella* but leaves plicate, with several longitudinal folds. According to Winkler (1969), the sporophyte of *Stephaniellidium* is developed in a marsupium.

LITERATURE. Winkler, S. 1969. Systematisch-anatomische Untersuchungen über die marsupialen Lebermoose der Sierra Nevada de Santa Marta in Kolombien. Mitt. Inst. Colomb. Alemán Invest. 3: 59-76.

HERBERTACEAE

Plants medium to very robust, green to brown or reddish-brown, ascending to erect or pendent, often with a rhizome-like creeping base, irregularly branched, with three ± equal ranks of leaves. Stems rigid, usually with a brown cortex of small, thick-walled cells in 1-3 layers. Branches ventral-intercalary or *Frullania*-type, the ventral branches often flagelliform. Leaves transverse or incubous, 2-3-lobed, usually long and narrow and asymmetrical with the dorsal segment broader, margins entire or toothed. Cells without or with large trigones, vitta present or absent; oil bodies granular. Underleaves similar to the leaves but more symmetrical. Rhizoids absent or very scarce, in tufts from underleaf bases or occasionally from a leaf. Dioicous. Gametoecia on elongated shoots. Antheridia in the axils of both the bracts and the bracteoles. Sporophyte surrounded by a strongly plicate perianth and a fleshy calyptra. Seta of numerous cells (cross-section). Capsule spherical, wall 4-7-layered. Vegetative reproduction unknown.

DISCUSSION. A family of 3 genera worldwide; 2 in tropical America, in montane and alpine regions. They are moss-like plants, with leaves and underleaves ± similar to each other and densely imbricate. Important characteristics of the family are 1) leaves and underleaves 2-3-lobed, ± identical; 2) leaves transverse or incubous; 3) stems rigid, with well-developed cortex; 4) perianths deeply plicate, on long shoots; and 5) presence of antheridia in axils of leaves (bracts) and underleaves (bracteoles). The latter character is unique among neotropical Jungermanniales; in all other families antheridia are borne solely in the axils of bracts, never in the axils of bracteoles.

LITERATURE. Fulford, M. H. 1963. Herbertaceae. Manual of the leafy Hepaticae of Latin America, Part I. Memoirs of the New York Botanical Garden 11(1): 85-105 [keys].

1. Leaves 2-lobed. Mid-leaf cells strongly elongated, forming a vitta, cells with large trigones..... ..... **Herbertus**
1. Leaves 2-3-lobed. Mid-leaf cells quadrate-subrectangular, not forming a vitta, cells without or with small trigones. ..... **Triandrophyllum**

Herbertus (= *Herberta*) (Fig. 26) - Ten species in tropical America (ca. 25 worldwide), widespread in montane and alpine regions.

HABITAT. Robust epiphytes of montane cloud forests, often forming large mats or tufts on trunks and thick canopy branches; also on rock and soil in humid páramo, puna, and zacatonal; (0-)500-4500 m. In ever-wet rain forests of western Colombia (Chocó) occurring at sea level.

DESCRIPTION. **Plants** usually robust and very long, to 10-30 cm, sometimes smaller, green to brown, reddish-brown or purple, ascending to erect or pendent from a rhizome-like base. **Leaves** transverse, spreading or falcate, asymmetrical, 2-7 times longer than wide, deeply 2-lobed with narrow, lanceolate to linear segments (the dorsal segment broader), leaf tips acute to long-piliferous, sometimes ending in a whitish hairpoint, leaf margins entire or toothed. **Cells** short along the margins, elongated towards the middle and forming a broad vitta from leaf base to apex; cell walls with very large trigones and intermediate thickenings, cuticle papillose; oil bodies faintly granular, often numerous. **Underleaves** similar to leaves but more symmetrical.

DISCUSSION. In the field, this remarkable genus may at first be taken for a moss. However, the leaves divided into two segments indicate that a liverwort is at hand. The leaves are densely imbricate, spreading or distinctly falcate, and the underleaves are as large as the leaves. Leaves and underleaves can be readily distinguished from each other by the asymmetrical shape of the leaves, the dorsal segment being somewhat broader than the ventral one, especially near the leaf base. In the underleaves, the segments are quite equal in width. The presence of a vitta in the leaves is a striking feature of this genus.

LITERATURE. Fulford, M. H. 1963 (see family ref.; for revised key see Van Reenen, 1982). - Van Reenen, G. B. A. 1982. Studies on Colombian Cryptogams XII. High Andean species of *Herbertus*. Lindbergia 8: 110-120 [key to 8 spp.].

Triandrophyllum (Fig. 26) - A small southern-temperate genus (4 spp.), with 2 species in the Tropical America:*T. subtrifidum* (Hook. f. & Taylor) Fulford & Hatcher, common at high elevations in SE Brazil, the Andes, and Central America northwards to Mexico, and *T. eophylla* (Schust.) Gradst. in the superpáramo of Ecuador (above 4000 m).

HABITAT. On moist rock and soil in rather open places in upper montane and alpine regions, especially in páramo, 2000-4500 m. Often forming dark green mats on stones in rivulets and sometimes growing submerged. The species may also grow profusely on volcanic ash and rock outcrops above 4000 m.

DESCRIPTION. **Plants** medium-sized, to 6 cm long, green to brown, creeping or ascending, sometimes with stolons at the base, irregularly branched. **Leaves** incubous, erect to spreading and somewhat deflexed, ± asymmetrical with the dorsal leaf lobe slightly longer than the ventral one, shallowly trifid or bifid (to 1/10-1/2 of leaf length), dorsal leaf tip acute, ventral leaf tip acute or blunt, leaf margins entire or with a few small teeth. **Cells** small, quadrate to short rectangular, the walls thin or slightly thickened, with or without small trigones, vitta lacking, cuticle smooth or finely striate-papillose; oil bodies finely granular. **Underleaves** similar to leaves but more symmetrical.

DISCUSSION. Recognized by the 2-3-lobed leaves and underleaves (sometimes purely 2-lobed) and the cells without or with small trigones. Robust plants differ in habit from *Herbertus* by the rather dark green (to brown) color when fresh and the often procumbent rather than erect growth, with incubous instead of transverse leaves. Under the microscope, the two are immediately separated by the very different leaf areolation.

Plants from high elevations, above 4000 m, may produce 2-lobed leaves only. The genus *Olgantha*, described by Schuster (1996) from the superpáramo of Ecuador (4200-4300 m) and containing the single species *Olgantha eophylla* Schust., is such a bilobed high-elevation form of *Triandrophyllum*. The densely concave, imbricate leaves in three straight, equal ranks, the quadrate leaf cells without or with small trigones, the asymmetrical leaf tips, and the antheridia in the axils of leaves and underleaves are all as in *T. subtrifidum*. The only difference with the latter species seems to be the rather shallowly incised leaf apex (to ca. 0.1 of leaf length). The correct name for this species should be ***Triandrophyllum eophyllum*** (Schust.) Gradst. **comb**. **nov**. (*Olgantha eophylla* Schust., Nova Hedwigia 63: 535. 1996).

LITERATURE. Fulford, M. H. 1963 (see family ref.; for revised taxonomy see Solari 1973). - Schuster, R. M. 1996. On *Olgantha* Schust., gen. n. Nova Hedwigia 63: 529-543. - Solari, S. 1973. Miscelanea Briológica (Hepaticae) I. Boletín de la Sociedad Argentina de Botánica 15: 197-203.

JUBULACEAE
(Frullaniaceae)

Plants small or large, green to brown, reddish, or purple-blackish, creeping to ascending or pendent, ± pinnate. Stems rigid, without hyalodermis. Branches always lateral, usually *Frullania*-type, sometimes *Lejeunea*-type. Leaves incubous, divided into three portions: a large dorsal lobe, a small

ventral lobe (=lobule) hidden under the dorsal lobe, and a tiny stylus between the lobule and stem; lobe margins usually entire, rarely toothed. Lobules almost free from the dorsal lobe, inflated and transformed into a water-sac, rarely flat. Cells with trigones, cuticle smooth; oil bodies finely granular. Underleaves small or large, usually bifid. Rhizoids in tufts from underleaf bases. Gametoecia on leading shoots or on short branches. Sporophyte surrounded by a perianth; mouth of the perianth usually contracted into a short beak. Foot of the sporophyte not penetrating into the stem. Seta very short, thick (*Frullania*) or thin (*Jubula*). Capsule globose, wall 2-layered. Elaters attached to the capsule valves, arranged vertically inside the capsule. Spores large, multicellular, germination endosporic. Vegetative reproduction rare, by caducous or fragmenting leaves.

DISCUSSION. A family of 4 genera worldwide; 2 in tropical America including the large genus *Frullania*. The outstanding character of the Jubulaceae is the presence of a small ventral lobule, which is almost free from the dorsal portion of the leaf (= lobe) and is transformed into a water-sac. This water-sac is formed entirely from the lobule and is thus essentially different from the water-sac of the Lejeuneaceae, which is made up of lobule and lobe together.

Jubulaceae and Lejeuneaceae are important epiphytic families of the rain forest and are closely related (differences: see Lejeuneaceae). Important features shared by the the two families are the peculiar leaves, which are always divided into three parts: a large dorsal lobe, a small ventral lobule and a stylus. In the Lejeuneaceae, however, the stylus is usually reduced to a small slime papilla. Furthermore, the perianth in the two families is always beaked, the sporophyte develops entirely within the calyptra (the foot does not penetrate the tip of the stem as it usually does), the seta is very short, the elaters are vertically arranged and attached to the capsule wall by their tips, and the spores germinate precociously within the spore wall inside the unopened capsule The very short seta of the Jubulaceae and Lejeuneaceae may be interpreted as an adaptation to the epiphytic growth of the plants; their occurrence high up on the tree might have made the development of a long seta, lifting the capsule up into the air, unnecessary. The peculiar water-sac and the green spores which germinate inside the capsule, before dehiscence, may also be interpreted as adaptations to the epiphytic habitat.

Literature. Schuster, R. M. 1992. Jubulaceae. The Hepaticae and Anthocerotae of North America, Vol. V: 1-286.

1. Plants pure green, without any trace of reddish pigmentation. Leaf margins toothed. Lobule very small, attached to the ventral margin of the lobe at some distance from the stem ..... **Jubula**
1. Plants usually with reddish pigmentation, rarely pure green. Leaf margins entire, rarely toothed. Lobule usually very close to the stem (at some distance from the stem in subgen. *Diastaloba*: small reddish plants) ..... **Frullania**

Frullania (Fig. 27, 28) - About 75 species in tropical America (ca. 300 worldwide), very common from sea level to the alpine belt. The neotropical species are classified in 6 subgenera.

HABITAT. On bark and rock in rather open habitats, in evergreen or deciduous forests, scrubby vegetation, plantations, pastures, savannas, and on road banks; also on fine twigs and living leaves, 0-4000 m. In the dense forest they are typical canopy epiphytes and are lacking in the understory except in well-illuminated sites, e.g., in forest gaps, or when growing on branches fallen from the canopy. The subgenera each have a somewhat different ecology (see below).

DESCRIPTION. **Plants** usually reddish, reddish-brown, or purplish, sometimes dull green, creeping, ascending or pendent, regularly or irregularly 1-3-pinnately branched. **Branches** *Frullania*-type, on broken stems sometimes *Lejeunea*-type; innovations normally lacking. **Leaves** incubous with a very short, subtransverse insertion; leaf lobe usually ovate-orbicular, the apex rounded to acute to acuminate, the margins entire, rarely toothed; leaf lobule usually very close to the stem (at some distance from the stem in subgenus *Diastaloba*), globose to linear, sometimes ± flat; stylus (between lobule and stem) usually linear and minute, sometimes large. **Cells** usually with trigones and intermediate thickenings, the trigones often confluent with the walls irregularly sinuose; ocelli sometimes present in leaf lobes. **Underleaves** rather large, usually 2-lobed, rarely undivided. **Dioicous** or autoicous, rarely paroicous. **Androecia** usually on a very short, globose male branch. **Gynoecia** on short or elongated shoots, without innovations. **Perianths** flattened or inflated, with 0-12 keels, the mouth contracted into a beak. **Seta** massive, of numerous rows of cells.

DISCUSSION. *Frullania* is easily recognized by the usually reddish or purplish pigmentation of the plants, the pinnate branching, the incubous leaves with entire margins, and the lobules, which are usually involuted forming a sac („saccate“) and are not or only shortly connected with the leaf lobe. Sometimes the involution is incomplete so that the lobule is more or less flattened ("laminate"), for example in the common *F. ericoides* (Nees) Mont. The shape of the lobule varies considerably and is an important subgeneric characteristic.

The strong pigmentation of the plants is probably an adaptation to their growth in exposed sites, with strong radiation. Vegetative reproduction is rare in *Frullania* and is mostly by caducous leaves, e.g., in *F. schaefer-verwimpii* Yuzawa & Hattori from southeastern Brazil.

LITERATURE. Gradstein, S. R. 1989. A key to the Hepaticae and Anthocerotae of Puerto Rico and the Virgin Islands. The Bryologist 92: 329-348 [key to 10 spp.]. - Schuster, R. M. 1992 [see family ref.].

Key to the subgenera of *Frullania* of tropical America

1. Opening of the lobule turned toward the apex of the plant (lobule pendent) ....subgen. **Homotropantha**
1. Opening of the lobule turned toward the base of the plant (lobule erect or oblique, not pendent) 2
2. Lobules distant from the stem (separated from the stem by at least their own width), usually clearly visible beyond the underleaves ..... subgen. **Diastaloba**
2. Lobules very close to the stem (separated from the stem by less than their own width), often hidden behind the underleaves 3
3. All or at least some lobules saccate 4
3. Saccate lobules absent, all lobules laminate 7
4. Lobules with a narrow or broad flattened portion below ..... subgen. **Chonanthelia**
4. Lobules without narrow or broad flattened portion below, saccate along its entire length 5
5. Lobules as long as wide. Ventral surface of perianth rough by scattered tubercles or scale-like outgrowths .....subgen. **Trachycolea**
5. Lobules longer than wide (1.2-2.5 x). Ventral surface of perianth without tubercles or scale-like outgrowths 6
6. Leaves wrapped around the stem when moist. Leaf base with two large (dorsal and ventral) auricles, deeply cordate. Plants longly pendent, remotely branched. ..... subgen. **Meteoriopsis**
6. Leaves spreading when moist. Leaf base with only one (dorsal) auricle, not cordate. Plants creeping or ascending, rarely pendent, usually densely branched ..... subgen. **Frullania**
7. Leaves squarrose when moist ***F. ericoides*** (subgen. **Trachycolea**)
7. Leaves not squarrose when moist [perianths needed for identification] 8
8. Ventral surface of perianth rough by scattered tubercles or scale-like outgrowths .....subgen. **Trachycolea**
8. Ventral surface of perianth without tubercles or scale-like outgrowths 9
9. Ventral surface of perianth with 2 or more keels ..... subgen. **Chonanthelia**
9. Ventral surface of perianth with 0-1 keels ....., ... subgen. **Frullania**

1. **Frullania** subgen. **Chonanthelia** (Fig. 27A-C) - mainly neotropical, 29 species in tropical America; from sea level to 4000 m in the Andes but predominantly montane.
LITERATURE. Yuzawa, Y. 1991. A monograph of subgen. *Chonanthelia* of gen. *Frullania* of the world. Journal of the Hattori Botanical Laboratory 70: 181-291 [key].

2. **Frullania** subgen. **Diastaloba** (Fig. 27D-F) - less than 10 species in tropical America, at rather low elevations (below 2500 m). The two most common neotropical species of this subgenus are *F. caulisequa* (Nees) Nees with rounded leaf apex and sparse branching, and *F.apiculata* (Reinw. *et al*.) Nees with pointed leaf apices (at least in some leaves) and densely pinnate branching. A third species, *F. vitallii* Yuzawa & S. Hatt. from southeastern Brazil, stands out by the numerous ocelli in the leaf lobes.
LITERATURE. Schuster, R. M. 1992 (see family ref.).

3. **Frullania** subgen. **Frullania** (Fig. 27G-J) - the largest subgenus in tropical America, with over 30 species; from sea level to almost 4000 m in the Andes but predominantly montane.
LITERATURE. Stotler, R. E. 1969. The genus *Frullania* subgenus *Frullania* in Latin America. Nova Hedwigia 18: 397-555 [key]

4. **Frullania** subgen. **Homotropantha** (Fig. 28A-C) - mainly Asiatic, with only 1 species, the common pantropical *F. nodulosa* (Reinw. *et al.*) Nees, in tropical America. The species is a characteristic canopy epiphyte of rain forests, dry evergreen woodlands, scrubby vegetation, and savanna in lowland regions of northern South America (Amazonia, Guianas). In savanna, *F. nodulosa* may also grow terrestrially.

5. **Frullania** subgen. **Meteoriopsis** (Fig. 28G-J) - mainly neotropical and with few species, including the common neotropical *F. convoluta* Lindenb. & Hampe (leaf apex obtuse) and *F. peruviana* Gott. (leaf apex acute to short acuminate). The members of this subgenus are pendent epiphytes in montane cloud forests and páramo, usually above 1500 m but at lower elevations on islands.
LITERATURE. Kron, K. A. 1988. Taxonomic study of Venezuelan members of *Frullania* subg. *Meteoriopsis*. Journal of the Hattori Botanical Laboratory 64: 347-358 [key to 7 spp.]

6. **Frullania** subgen. **Trachycolea** (Fig. 28D-F) - less than 10 species in tropical America, at rather low elevations. The most common species are *F. ericoides* (Nees) Mont., an ubiquitous species of scrubby vegetation, plantations, isolated trees, and rock in rather dry environments, and *F. glomerata* (Lehm. & Lindenb.) Mont. The two are easily distinguished by the squarrose leaves of *F. ericoides* (not squarrose in *F. glomerata*).
Frullania ericoides often grows together with *F. gibbosa* Nees (subgen. *Chonanthelia*) and these two are among the most xerophytic species of leafy hepatics in the Neotropics.
LITERATURE. Schuster, R. M. 1992 (see family ref.).

Jubula (Fig. 29) - A small tropical-holarctic genus (4-5 spp.), with 1 species, *J. bogotensis* Steph. (= *J. pennsylvanica* subsp. *bogotensis* (Steph.) W. R. Guerke), in the northern part of tropical America. The species has been recorded from the Greater Antilles, Mexico, Costa Rica, and the northern Andes and seems to be nowhere common.

HABITAT. On bases of trunks and humic soil in the understory of lower montane forests, 1000-2500 m.

DESCRIPTION. **Plants** pure green, creeping, regularly pinnate. **Branches** *Frullania*-type or *Lejeunea*-type; innovations normally present. **Leaves** incubous with a long, J-shaped insertion; leaf lobe ovate, the apex mucronate to long-piliferous, the margins sharply toothed or ± entire; leaf lobule very small, attached to the ventral margin of the lobe at some distance from the stem, globose-saccate, sometimes ± flat ("explanate"). **Cells** thin-walled, with minute trigones. **Underleaves** 2-lobed, with long decurrent bases and deeply arched insertion. **Autoicous**. **Androecia** on tiny, elongated branches. **Gynoecia** on elongated shoots, with 1-2 innovations. **Perianths** flattened, with 3 keels (2 lateral, 1 ventral), the mouth contracted into a beak. **Seta** of only 20 rows of cells: 4 inner rows and 16 outer rows.

DISCUSSION. *Jubula* is distinguished from *Frullania* by 1) the regularly pinnate, pure green plants, without any trace of reddish pigmentation; 2) the acuminate, often toothed leaves; 3) the bifid underleaves with deeply arched insertions; and 4) the thin seta. The lobule is very small and attached to the ventral margin of the lobe at some distance from the stem. The total lack of red pigmentation in *Jubula* is a very notable feature of the genus and is correlated with its occurrence in shaded habitats in the forest understory.

LITERATURE. Guerke, W. R. 1978. A monograph of the genus *Jubula*. Bryophytorum Bibliotheca 17: 1-118 [key].

JUNGERMANNIACEAE
(Lophoziaceae)

Plants green to brown to red or purple, creeping or erect, rarely pendent, simple or irregularly branched. Stems without hyalodermis, cortex weakly differentiated. Branches variable, *Frullania*-type and intercalary (lateral, ventral, dorsal); stolons or flagella sometimes present. Leaves succubous, alternate, rarely opposite (*Syzygiella*), undivided or 2-4-lobed, leaf margins entire, rarely toothed, insertion line usually reaching dorsal stem-midline. Cells usually with trigones; oil bodies granular or homogeneous. Underleaves usually lacking or very small. Rhizoids scattered, sometimes reddish. Gametoecia on leading shoots. Sporophyte surrounded by a perianth, the perianth inflated, plicate or smooth. Seta of numerous cells (cross-section). Capsule wall 2-5-layered. Vegetative reproduction lacking or by gemmae, the gemmae usually angular-stellate.

DISCUSSION. A large family of about 35 genera worldwide; 14 in tropical America. The family is subdivided into several subfamilies. The most important characteristics of the family are 1) succubous leaves, which are inserted to the dorsal stem-midline (exception: *Vanaea*), 2) reduced underleaves, 3) lack of a hyalodermis, 4) scattered rhizoids, 5) often reddish pigmentation, 6) gametoecia on leading shoots, and 7) inflated-cylindrical perianth. The leaves are undivided or 2-4-lobed; genera with lobed leaves are sometimes placed in a separate family Lophoziaceae.

The members of the Jungermanniaceae grow in rather open environments and generally avoid the shaded understory of dense forest. Their frequently reddish pigmentation is probably an adaptation to growth in rather open habitats with strong radiation.

1. Leaves undivided to retuse 2
1. Leaves 2-4-lobed 8
2. Leaves distinctly opposite with the leaf bases united dorsally and ventrally (rarely free dorsally). Usually epiphytic ..... **Syzygiella**
2. Leaves not opposite, leaf bases free 3
3. Leaves narrowly oblong, more than twice as long as wide. Leaf apex narrowly truncate to bidentate. Endemic to the Guayana Highland ..... **Vanaea**
3. Leaves less than twice as long as wide. Leaf apex broadly rounded to retuse 4
4. Underleaves large, about half the length of the leaf or more, oblong to lanceolate ..... **Nardia**
4. Underleaves lacking or very small, subulate 5
5. Leaves, at least the upper ones, appressed face to face, leaf margins usually incurved. Stems usually long and rigid, (2-)4-8 cm long, with or without rhizoids. Plants sometimes orange-brown or black 6
5.Leaves spreading, the upper ones not appressed, leaf margins not incurved. Stems shorter and rather fragile, usually with numerous rhizoids. Plants never orange-brown or black 7
6. Leaf cells without trigones, cuticle smooth. Stem bases with stolons. *Frullania*-type branches lacking ..... **Cryptochila**
6. Leaf cells with trigones, cuticle papillose. Stolons lacking. *Frullania*-type branches sometimes present ..... **Jamesoniella**
7. Underleaves present (small, often hidden between the rhizoids). Rhizoids colorless ..... **Nardia**
7. Underleaves lacking. Rhizoids reddish, brown or colorless ..... **Jungermannia**
8. Plants minute, leafy shoots less than 0.5 mm wide. Underleaves very large, similar to leaves. Subalpine twig epiphyte ..... **Pseudocephaloziella**
8. Plants larger. Underleaves small or lacking 9
9. Stem-leaves 3-4-lobed, never 2-lobed 10
9. Stem-leaves 2(-3)-lobed 12
10. Leaves strongly laterally appressed to each other. Leaf margins ciliate. Plants turning reddish to purplish. Venezuelan Andes ..... **Rhodoplagiochila**
10. Leaves spreading, not laterally appressed. Leaf margins entire. Plants green or brown, not turning reddish or purplish 11
11. Leaf segments very unequal, the dorsal segment much smaller. Gemmae numerous, rust-red ..... **Tritomaria**
11. Leaf segments equal. Gemmae lacking or scarce, brown ..... **Barbilophozia**
12. Plants usually turning reddish-brown or purple. Perianth often with a white mouth. Trigones usually large. Leaves very concave, leaf insertion on the dorsal side of the stem transverse .... **Anastrophyllum**
12. Plants green or brown, not reddish or purple. Perianth without white mouth. Trigones small or lacking. Leaves not very concave, leaf insertion on the dorsal side of the stem oblique 13
13. Leaf segments rounded or obtuse 14
13. Leaf segments acute or acuminate 15
14. Leaf cells with uniformly thickened walls, trigones lacking. Perianth smooth **Gymnocoleopsis**
14. Leaf cells with trigones. Perianth plicate ..... **Lophozia**
15. Plants with flagelliform branches of the *Anomoclada*-type, originating from the dorsal end of the leaf axils. Autoicous ..... **Andrewsianthus**
15. *Anomoclada*-type branches lacking. Dioicous ..... **Lophozia**

Anastrophyllum (Fig. 29) - About 10 species at high elevations in tropical America (35-40 worldwide). *Anastrophyllum* is one of the most characteristic genera of the páramo.

HABITAT. Common on moist earth, boggy soil, and in rock crevices in páramos; occasionally epiphytic in montane forest (*A. piligerum* (Nees) Steph., *A. hellerianum* (Nees) Schust.); elevation 1000-4500 m. *Anastrophyllum auritum* (Lehm.) Steph. (= *A. leucocephalum* (Taylor) Steph., fide J. Váña, pers. comm.) is the most common neotropical species in the genus and is usually abundant in páramos; in addition, it occurs on humid road banks in the high Andes. Other common páramo species include *A. tubulosum* (Nees) Grolle, *A. crebrifolium* (Hook. f. & Taylor) Steph. (= *A. leucocephalum* (Taylor) Steph.) and *A. nigrescens* (Mitt.) Steph. The holarctic *A. hellerianum* is a characteristic species of decaying logs in montane conifer forests of Mexico.

DESCRIPTION. **Plants** small to medium-sized, 0.5-3 mm wide, dark reddish-brown or purple, sometimes brownish-green, creeping or ascending, little branched. **Branches** variable, terminal and

intercalary. **Stems** fragile to rigid. **Leaves** succubous, ± symmetrically 2-lobed, the dorsal segment transversely inserted and the ventral segment oblique, strongly concave to canaliculate with the tips often somewhat incurved, apices acute to acuminate, rarely obtuse, margins entire. **Cells** usually with large trigones, cuticle smooth or papillose; oil bodies finely granular. **Underleaves** lacking. **Rhizoids** scarce. **Dioicous** (usually). **Perianths** plicate, usually with a white mouth. **Capsule** wall (2-)3-5-layered. **Gemmae** present or absent, when present yellow-brown to wine-red to purplish, angular, produced on the apices of upper leaves, sometimes on upright flagelliform shoots.

DISCUSSION. *Anastrophyllum* is readily recognized by the dark reddish or purplish color of the plants, the deeply concave, bilobed leaves, the absence of underleaves and the white mouth of the perianth. The species are identified by leaf characters (see Vána, 1984): longly acuminate leaf tips are characteristic of *A. crebrifolium*, shallowly bifid, boat-shaped leaves of *A. nigrescens*, etc.

LITERATURE. Váña, J. 1984. *Anastrophyllum* in Latin America - preliminary information. Proceedings of the Third Meeting of the Bryologists from Central and East Europe, Praha (ed. J. Vána), p. 99-106.

Andrewsianthus (Fig. 29) - Mainly in the Asian tropics and the temperate regions of the Southern Hemisphere (ca. 30 spp.); 1 species, *A. jamesonii* (Mont.) Váña (= *A. achrous* (Spruce) Schust.), occurs in the high mountains of tropical America, from Mexico to Peru.

HABITAT. On steep earth banks and on rock in somewhat shaded habitats in the upper montane and alpine belts, along roads, in ravines, etc.; not occurring in forests; elevation 2500-4700 m.

DESCRIPTION. **Plants** rather small and fleshy, ca. 1-1.5 mm wide, pale green to yellowish-brown, creeping. **Branches** mostly intercalary, sometimes flagelliform and originating from the dorsal end of the leaf axils (*Anomoclada*-type branch). **Stems** fragile. **Leaves** succubous, often forming a crispate head, asymmetrically 2-lobed, the dorsal segment smaller than the ventral segment, apices sharply cuspidate, margins sharply toothed to subentire. **Cells** thin-walled with non-bulging trigones, cuticle smooth; oil bodies unknown. **Underleaves** lacking or very small, subulate. **Rhizoids** numerous. **Autoicous** (in Neotropics), often fertile. **Perianths** large, plicate. **Gemmae** common, pale green, 1-celled, angular, produced on the apices of upper leaves.

DISCUSSION. The pale green color of the living plants, the fleshy stems, the often crowded-crispate leaves at the shoot apex, the toothed leaves, the green gemmae, and, especially, the flagelliform, *Anomoclada*-type branches developing from leaf axils on the dorsal side of the stem, are characteristic of *Andrewsianthus jamesonii*. The species is autoicous - the only one in the genus, all other species of *Andrewsianthus* being dioicous - and the plants are frequently fertile.

Andrewsianthus jamesonii is similar to *Lophozia incisa*, which occurs in the same habitats, but the latter lacks *Anomoclada*-type branches, is dioicous and usually sterile. When sporophytes are available, the two are distinguished by the 2-layered capsule wall of *A. jamesonii* (3-5-layered in *L. incisa*).

LITERATURE. Gradstein, S. R., T. Pócs & J. Váña. 1983. Disjunct Hepaticae in tropical America and Africa. Acta Botanica Hungarica 29: 127-171. - Schuster, R. M. 1964. Studies on Hepaticae XIX-XX. *Cephaloziopsis* Schust. and *Andrewsianthus* Schust. Nova Hedwigia 8: 201-209.

Barbilophozia (Fig. 30) - A widespread holarctic genus of 11 species. Two species have been recorded from tropical America, *B. barbata* (Schmidel ex Schreb.) Loeske from Mexico and *B. floerkei* (Weber & D. Mohr) Loeske from Peru. The neotropical records are each based on only one collection.

HABITAT. On soil and in rock crevices at high elevations; *B. floerkei* was found at about 4600 m in the Andes of Peru.

DESCRIPTION. **Plants** medium-sized to large, 2-5 mm wide, green to brown, creeping or ascending, without stolons. **Leaves** succubous, (2-)3-4-lobed, apices obtuse or acute to acuminate, margins entire, ventral leaf bases often with cilia. **Cells** with or without large trigones, cuticle ± papillose; oil bodies finely granular. **Underleaves** present, 2-lobed. **Rhizoids** usually numerous, short. **Dioicous**, usually sterile. **Gemmae** rare, lacking in *B. barbata* and *B. floerkei*.

DISCUSSION. *Barbilophozia* is sometimes treated as a subgenus of *Lophozia,* but differs from the latter in the 3-4-lobed leaves and the frequent presence of underleaves. The plants are usually rather robust and cilia are often present at the ventral base of the leaf (lacking in *B. barbata*).

LITERATURE. Schuster, R. M. 1969. *Lophozia* subgen. *Barbilophozia* and subgen. *Orthocaulis*. The Hepaticae and Anthocerotae of North America, Vol. II: 261-360.

Cryptochila (Fig. 30) - A southern-temperate genus of 6 species. One species, *C. grandiflora* (Lindenb. & Gott.) Grolle, occurs at high elevations in the Andes, in SE Brazil (Serra de Itatiaia, Serra de Caparaó) and further north in Central America.

HABITAT. On moist earth and rock in the upper montane and alpine belts, in rather open but very humid environments, often along rivulets, at (1500)-2500-4500 m.

DESCRIPTION. **Plants** rather long and narrow, 2-8 cm long and 1-2 mm wide, green to dark reddish brown to black, ascending to erect, with numerous stoloniform branches at the stem base, otherwise unbranched. **Branches** ventral-intercalary. **Stems** rigid. **Leaves** ± transverse, laterally appressed to the stem, sometimes weakly spreading, often somewhat secund, weakly concave, undivided, ovate-orbicular, leaf apex broadly rounded, margins entire and usually somewhat incurved, bases decurrent. **Cells** rather small, ± quadrate, 20-25 µm in leaf middle, elongated at the base, cell walls slightly thickened, ± without trigones, cuticle smooth; oil bodies finely granular. **Underleaves** lacking. **Rhizoids** scarce, usually restricted to the stolons. **Dioicous**. **Perianths** plicate, the folds usually somewhat spirally twisted towards the mouth. **Capsule** wall 5-layered. **Gemmae** lacking.

DISCUSSION. In its upright shoots with recurved tips and the rounded, transverse leaves which are somewhat appressed to each other, this plant resembles *Jamesoniella*, especially *J. rubricaulis*. The dark color of *Cryptochila grandiflora* (never orange-brown), the stolons at the base of the stem, and, especially, the smooth, quadrate leaf cells without trigones serve to distinguish it from *Jamesoniella rubricaulis*.

LITERATURE. Grolle, R. 1971. *Jamesoniella* und Verwandte. Feddes Repertorium 82: 1-99 [key].

Gymnocoleopsis (Fig. 30) - A monotypic, alpine Afro-American genus. The only species, *G. multiflora* (Steph.) Schust., occurs in the high Andes from Bolivia to Venezuela, and in the mountains of East Africa (Zaire).

HABITAT. On moist, boggy ground among higher plants and on moist rock in páramos, often near running water, 3500-4400 m; most frequently occurring above 4000 m.

DESCRIPTION. **Plants** small, ca. 1 mm wide, pale green to dark brown, creeping, without stolons. **Branches** lateral-intercalary only. **Leaves** succubous, 2-lobed, apices obtuse, margins entire. **Cells** with uniformly thickened walls, trigones lacking, cuticle smooth; oil bodies finely granular. **Underleaves** lacking. **Rhizoids** sparse. **Autoicous**. **Perianths** smooth, without plicae. **Capsule** wall 2-3-layered. **Gemmae** lacking.

DISCUSSION. The obtuse to almost rounded leaf segments, the unformly thickened cell walls without trigones, and the smooth perianths without keels are characteristic of *Gymnocoleopsis multiflora.* The species resembles *Lophozia laxiflora* (Mont.) Grolle, which grows in the same habitats and also has obtuse leaf tips. The latter, however, has leaf cells with trigones, plicate perianths, and stolons.

LITERATURE. Gradstein, S. R., T. Pócs, T. & J. Váña. 1983. Disjunct Hepaticae in tropical America and Africa. Acta Botanica Hungarica 29: 127-171. - Schuster, R. M. 1967. A note on the genus *Gymnocolea*. The Bryologist 70: 111-112 [brief diagn.].

Jamesoniella (Fig. 30) - Three species at high elevations in tropical America (14 worldwide): *J. rubricaulis* (Nees) Grolle widespread in the region, *J. undata* (Mont.) Steph. endemic to the páramo, and *J.autumnalis* (DC.) Steph. in Mexico, Central America, and the northern Andes. The latter species is widespread in the temperate part of the Northern Hemisphere and seems to have recently migrated southwards into the neotropical region.

HABITAT. On moist soil, rock, rotten wood, peat, and in bark in shaded or rather open, but always very humid environments, on the continent usually occurring at 2000-4500 m, in islands and in SE Brazil at lower elevations, from 500 m upwards. *Jamesoniella rubricaulis* is very common in páramos. In addition, the species grows as a canopy epiphyte in upper montane cloud forests and subalpine scrub, and is a common invader of moist road banks. The holarctic *J. autumnalis* is a characteristic species of rotten logs in conifer forest of Mexico and Guatemala; in addition, it has been found a few times on rotten wood in montane forest and on peat in *Sphagnum* bogs in the northern Andes.

DESCRIPTION. **Plants** medium-sized to large, usually rather long, 2-8 cm long and 1-3 mm wide, yellowish-green to orange-brown to reddish brown or olive-brown, creeping to erect with decurved shoot apex, little branched, stolons lacking. **Branches** terminal, *Frullania*-type, and ventral-intercalary. **Stems** rigid. **Leaves** transverse to succubous, laterally appressed to the stem or ± spreading, weakly concave, undivided, ovate-orbicular, leaf apex broadly rounded, margins entire and usually somewhat incurved, bases decurrent. **Cells** 25-35 µm in leaf middle, elongated at the base, usually with large trigones (small in *J. autumnalis*), cuticle papillose; oil bodies finely granular. **Underleaves** very small, subulate. **Rhizoids** only on creeping shoots. **Dioicous**. **Perianths** plicate or smooth, when plicate the folds straight, not twisted. **Capsule** wall 4-5-layered. **Gemmae** lacking.

DISCUSSION.The common *Jamesoniella rubricaulis* is easily recognized by the light yellowish-green to orange-brown color of the plants, the long, erect shoots with decurved apex, the very regularly appressed, rounded leaves, and the ± absence of rhizoids. The huge trigones and strongly papillose cuticle are also very characteristic. The species may only be confused with *Cryptochila* (see under the

latter). In the closely related *J. undata*, a species endemic to páramos, the leaves are more strongly imbricate and longer-decurrent.

Jamesoniella autumnalis is a smaller, creeping plant and resembles *Jungermannia* or *Nardia*. The leaves are never as strongly concave as in the latter genera, however, and are occasionally somewhat appressed to the stem (but mostly spreading). The plants are yellow-brown to olive-brown, rarely wine-red in color, and grow on rotten wood or peat.

LITERATURE. Grolle, R. 1971. *Jamesoniella* und Verwandte. Feddes Repertorium 82: 1-99 [key].

Jungermannia (Fig. 31) - Eight species in montane and alpine environments in tropical America (ca. 125 worldwide).

HABITAT. On moist earth, humus, and soil-covered rock in open or sheltered habitats, on steep earth banks, on rock walls, along roads, etc.; not epiphytic and not occurring in forests; elevation 800-4200 m. The holarctic *J. sphaerocarpa* Hook. is the most common species in the upper montane and lower alpine belts, where it may grow abundantly as a pioneer on moist road banks. *Jungermannia ovato-trigona* (Steph.) Grolle is endemic to páramo and grows in dark green mats on rock in running water, above 3000 m. The remaining species are montane taxa, occurring mainly below 3000 m.

DESCRIPTION. **Plants** small to medium-sized, 0.6-4 mm wide, pale green to reddish or brown, creeping or ascending, little branched, stolons lacking. **Branches** usually lateral-intercalary. **Stems** fragile. **Leaves** succubous, usually somewhat spreading, concave and clasping the stem in the lower half, undivided, ovate-orbicular, rarely lingulate, leaf apex broadly rounded, margins entire, not incurved, bases not or short-decurrent. **Cells** with usually rather small trigones, cuticle smooth or papillose; oil bodies finely granular. **Underleaves** lacking. **Rhizoids** numerous, often reddish or brown. **Dioicous** or paroicous. **Perianths** plicate, long-exserted or short and hidden between the bracts, perianth base sometimes united with the bracts and forming a short perigynium (subgen. *Plectocolea*), perianth mouth sometimes narrowed into a short beak (subgen. *Solenostoma*). **Capsule** wall 2-layered. **Gemmae** lacking.

DISCUSSION. *Jungermannia* is recognized by the pale green to reddish color, and the undivided, ovate-orbicular leaves which are succubous and concave, somewhat clasping the stem. Several species have reddish or brownish rhizoids. Lingulate leaves are characteristic of *J. amplexifolia* (Hampe ex Lehm.) Grolle (= *J. linguifolia* Gott.). The perianth is free or, in the subgen. *Plectocolea* (*J. callithrix* Lindenb. & Gott., *J. decolor* Schiffn., *J. hyalina* Lyell ex Hook.), united with the bracts in the lower half, forming a short, fleshy perigynium.

LITERATURE. Váña, J. 1974. Studien über die *Jungermannioideae*. 4. *Jungermannia* subg. *Plectocolea* und subg. *Solenostoma*: allgemeines, süd- und mittelamerikanische Arten. Folia Geobotanica et Phytotaxonomica 9: 179-208 [key].

Lophozia (incl. *Leiocolea*, *Lophonardia*) (Fig. 31) - Eight species in tropical America (65-70 worldwide), at high elevations in the Andes and Central America. *Lophozia laxifolia* (Mont.) Grolle and the holarctic *L. incisa* (Schrad.) Dumort. are the only widespread species in the region, the others having very local distributions.

HABITAT. On steep, moist earth banks, rock, and rotten wood in páramo, puna, and zacatonal, and in upper montane areas, 2000-4500 m. *Lophozia incisa* typically grows on somewhat disturbed soil and may invade steep, cut road banks as a pioneer. Moist rocks in rivulets are the habitat of *L. laxifolia*. The holarctic *Lophozia longiflora* (Nees) Schiffn. is a characteristic species of decaying logs in Mexican conifer forests, in a bryophyte community with *Nowellia curvifolia, Cephalozia catenulifera,* and *Jamesoniella autumnalis* (Gradstein & Váña, 1994).

DESCRIPTION. **Plants** small to medium-sized, ca. 1-2 mm wide, pale green to brown, creeping or ascending, ventral stolons sometimes present. **Branches** variable, terminal and intercalary. **Stems** usually fragile. **Leaves** succubous, 2(-3)-lobed, apices acute to acuminate, sometimes obtuse, margins entire or toothed. **Cells** with small trigones, cuticle smooth or papillose; oil bodies finely granular or homogeneous. **Underleaves** lacking. **Rhizoids** usually numerous. **Dioicous** or monoicous. **Perianths** usually plicate. **Capsule** wall 3-5-layered. **Gemmae** often present, green, brown, or reddish, angular-stellate.

DISCUSSION. *Lophozia* is recognized by the rather small, creeping plants with 2-lobed leaves (sometimes 3-lobed), cells with small trigones, and the lack of underleaves. The same characters are found in *Anastrophyllum* but the latter is more reddish, has more transverse leaves, and a perianth with a conspicuously white mouth. The oil bodies in *Lophozia* are usually finely granular, but in *L. incisa* (subgen. *Schistochilopsis*) they are homogeneous. This species may be confused with *Andrewsianthus jamesonii* (see under the latter). Ventral stolons are characteristic of *Lophozia laxifolia* and *L. stolonifera* Schust. (subgen. *Hypolophozia*).

An unusual, sterile, *Lophozia*-like plant from the páramos of Venezuela, characterized by purely *Frullania*-type branching and thin-walled cells, was described as a new genus and species,

Lophonardia caespitosa Schust. (Schuster, 1978). According to J. Váña (pers. comm.), this taxon is a synonym of *Lophozia laxifolia*.

LITERATURE. Gradstein, S. R. & J. Váña. 1994. A boreal bryophyte community in a tropical montane forest of Mexico. Tropical Bryology 9: 31-34 [ecol.]. - Schäfer-Verwimp, A. 1996. New or interesting records of Brazilian bryophytes. V. Candollea 51: 283--302 [report of *L. bicrenata* (Schmidel ex Hoffm.] Dumort. and *L. patagonica* Herzog & Grolle]. - Schuster, R. M. 1969. *Lophozia*. The Hepaticae and Anthocerotae of North America, Vol. II: 252-638 [keys]. - Schuster, R. M. 1978. Studies on Venezuelan Hepaticae I. Phytologia 39 (4): 239-251 [descr. of *L. verruculosa* Schust., *L. stolonifera* Schust., and *Lophonardia caespitosa*]

Nardia (Fig. 31) - Two species in montane regions of tropical America (16 worldwide), *N. succulenta* (Rich. ex Lehm.) Spruce in the West Indies, Central America, and the northern Andes, and *N. nuda* (Lindenb. & Gott.) Váña endemic to Mexico.

HABITAT. On moist soil and rock in shaded or exposed habitats, (600-)1000-3500 m. In the Andes usually not occurring below 1500 m. *Nardia succulenta* is a characteristic species of seepage areas and springs, and may grow on the banks of hot sulphur springs and fumaroles, or on steep, dripping road banks where the water is rich in minerals. The species nearly always grows in extensive, and often pure carpets. The habitat of *N. nuda* is unknown.

DESCRIPTION. **Plants** small to medium-sized, 1-2.5 mm wide, green, gray-green, reddish-brown or purple, ascending to erect, little branched, stolons lacking. **Branches** terminal, *Frullania*-type, and ventral-intercalary. **Stems** fragile. **Leaves** succubous, usually somewhat spreading, concave and often clasping the stem in the lower half, undivided, ovate-orbicular, leaf apex broadly rounded to retuse, margins entire, flat or incurved, bases short-decurrent. **Cells** with small or medium-sized trigones, cuticle smooth; oil bodies finely granular in neotropical species. **Underleaves** present, small or large, sometimes almost as long as the leaves but narrow, lanceolate to oblong. **Rhizoids** numerous, long, colorless. **Dioicous** but often fertile. **Perianths** plicate, hidden between the bracts to long-exserted, the lower half sometimes fleshy and united with the bracts, forming a perigynium (*N. succulenta*). **Capsule** wall 2-layered. **Gemmae** lacking.

DISCUSSION. *Nardia* is similar to *Jungermannia* but differs in the presence of underleaves. They are small in *N. nuda* but quite large and conspicuous in *N. succulenta*. The occurrence of the latter species on hot, volcanic substrates is a rather unique ecological feature of the genus. *Telaranea nematodes* is the only other hepatic found by the author in such habitats in the Neotropics.

LITERATURE. Engel, J. 1988. The taxonomic position of *Apotomanthus*. Beihefte zur Nova Hedwigia 90: 203-221. - Váña, J. 1976. Studien über die *Jungermannioideae*. 10. *Nardia*. Folia Geobotanica et Phytotaxonomica: 11: 367-426 [key to spp.].

Pseudocephaloziella (Fig. 32) - A monotypic, neotropical genus, with *P. epiphytica* Schust. in the Andes of Venezuela (Páramo de Tamá). The species is known only from the type collection.

HABITAT. On twigs in low, scrubby vegetation transitional between the subalpine shrub region and the open páramo, 3100-3200 m.

DESCRIPTION. **Plants** very small, ca. 0.25-0.4 mm wide, light green, creeping, without stolons. **Branches** intercalary (ventral and lateral). **Leaves** transverse, 2-lobed for 1/3-1/2 of their length, apices acute, margins roughened by large papillae. **Cells** with thickened walls and small trigones, cuticle coarsely papillose; oil bodies unknown. **Underleaves** almost as large as the leaves and similar in shape, 2-lobed. **Rhizoids** few. **Dioicous**. **Perianths** plicate. **Gemmae** lacking.

DISCUSSION. A tiny, subalpine twig epiphyte, resembling *Cephaloziella*. The plants differ from all other members of the Jungermanniaceae in the large underleaves, which are similar to the lateral leaves, both in size and shape. The coarsely papillose cuticle of the leaf cells is a further characteristic of this peculiar species.

LITERATURE. Schuster, R. M. 1991. Studies on Venezuelan Hepaticae V. On *Pseudocephaloziella*. Nova Hedwigia 53: 331-339.

Rhodoplagiochila - A monotypic, neotropical genus, with *R. rosea* Schust. in the Andes of Venezuela (Mérida). The species is known only from the type collection.

HABITAT. Epiphytic in cloud forest near the forest line, ca. 3700 m.

DESCRIPTION. **Plants** reddish to purplish, erect with decurved shoot apices, strongly laterally compressed, irregularly branched. **Branches** lateral-intercalary, often stoloniform. **Leaves** succubous, strongly appressed to the stem, leaf insertion line extending beyond the dorsal midline of the stem (as in Gymnomitriaceae), 3-4-lobed, margins plane, with yellowish-brown cilia. **Underleaves** lacking.

DISCUSSION. The systematic position of *Rhodoplagiochila* is uncertain because perianths are unknown. Because of the lobed leaves, lack of underleaves and, especially, the reddish pigmentation, the genus was tentatively placed in the Jungermanniaceae by Inoue (1984).

LITERATURE. Inoue, H. 1984. The genus *Plagiochila* in Southeast Asia. Academic Scientific Book Inc., Tokyo [brief disc.]. - Schuster, R. M. 1978. Studies on Venezuelan Hepaticae I. Phytologia 39 (4): 239-251 [short diagn.].

Syzygiella (Fig. 32) - A tropical-montane genus (ca. 20 spp.), with 16 species in tropical America. The center of diversity of this genus is in the Neotropics.

HABITAT. Epiphytes on bark in montane cloud forests, scrubby vegetation and páramos, usually in rather open, exposed sites, (750-)1000-4000 m. Also on rock. In dense forests usually restricted to the canopy.

DESCRIPTION. **Plants** small to large, 1-6 mm wide, green to yellowish-brown to reddish-brown to purplish, nearly always with reddish or purplish pigmentation, creeping to erect. **Branches** variable, terminal and intercalary. **Stems** rigid. **Leaves** succubous or nearly transverse, opposite with the bases united both dorsally and ventrally, wide-spreading or appressed to the stem, ± undivided, apex rounded to truncate to shallowly bidentate, margins entire or with a few teeth, dorsal margin plane or recurved, dorsal base sometimes decurrent. **Cells** usually with large trigones, cuticle smooth or papillose; oil bodies finely granular. **Underleaves** lacking or rudimentary. **Rhizoids** usually scarce, scattered or in tufts. **Dioicous**. **Perianths** strongly inflated, plicate. **Capsule** wall 4-5-layered. **Gemmae** lacking.

DISCUSSION. *Syzygiella* is easily recognized by the opposite leaves, with the bases united both dorsally and ventrally (dorsally free in *S. liberata* Inoue), and the reddish or purplish coloration of the plants. The species are common canopy epiphytes and their pigmentation may be an adaptation to growth in habitats with strong radiation. Some species are similar to *Plagiochila*; the latter differs mainly in the lack of reddish pigmentation, the flattened perianth, and the leaves which are never united both dorsally and ventrally.

LITERATURE. Inoue, H. 1966. A monograph of the hepatic genus *Syzygiella*. Journal of the Hattori Botanical Laboratory 29: 171-213 [key].

Tritomaria (Fig. 32) - A small holarctic genus (8 spp.); 1 species, *T. exsecta* (Schrad.) Loeske, has been found in Mexico (rare).

HABITAT. On decaying logs and on rocks in upper montane (coniferous?) Mexican forest, 2000-3000 m.

DESCRIPTION. **Plants** small to medium-sized, 1-2 mm wide, pale green to brown, creeping or ascending. **Leaves** succubous, asymmetrically 3-lobed, the dorsal segment much smaller, the dorsal half of the leaf transversely inserted and the ventral half oblique, strongly concave, apices acute to acuminate, margins entire. **Cells** with trigones, these sometimes elongated and confluent, cuticle smooth or papillose; oil bodies finely granular. **Underleaves** lacking. **Rhizoids** numerous, short. **Dioicous**. **Perianths** plicate. **Capsule** wall 3-5-layered. **Gemmae** often present, brown to red, stellate-angular.

DISCUSSION. Closely related to *Lophozia* but differing in the asymmetrically 3-lobed leaves with a very small dorsal segment (resembling a tooth). The leaves are very concave and the dorsal portion of the leaf is inserted transversely instead of obliquely (as in *Anastrophyllum*). The masses of rust-red gemmae on the leaf tips in *T. exsecta* are also characteristic.

LITERATURE. Schuster, R. M. 1969. *Tritomaria*. The Hepaticae and Anthocerotae of North America, Vol. II: 638-704 [key].

Vanaea (Fig. 32) - A monotypic, neotropical genus, with *V. plagiochiloides* (Inoue & Gradst.) Inoue & Gradst. (= *Anastrophyllum plagiochiloides* Inoue & Gradst.) known only from the north slope of Mt. Roraima, Guyana.

HABITAT. A pendent epiphyte of very moist habitats, on branches of *Bonnetia* in open, boggy scrub and on canopy twigs in wet montane forest, 1400-2300 m.

DESCRIPTION. **Plants** long and slender, 3-8 cm long and 3-5 mm wide, reddish to purplish, pendent, almost unbranched. **Stems** rigid. **Leaves** succubous, laterally inserted on the stem, insertion line not continuing to the dorsal midline of the stem, wide-spreading, flat to somewhat convex, narrowly oblong, leaf apex narrowly truncate or shallowly bidentate with two unequal teeth, margins entire. **Cells** with huge, confluent trigones, cuticle smooth; oil bodies unknown. **Underleaves** and rhizoids lacking.

DISCUSSION. This peculiar Guyanan endemic is characterized by the wide-spreading, narrowly oblong leaves, which are laterally inserted on the stem, leaving a dorsal strip of the stem leaf-free (as in Cephaloziaceae), and also by the shallowly bidentate leaf apex with two unequal teeth, and by the huge trigones. The plants are rust-red, very much like *Anastrophyllum*, and grow pendent from branches in wet, open habitats (scrub, forest canopy).

LITERATURE. Gradstein, S. R. & J. Florschütz-de Waard. 1989. Results of a botanical expedition to Mount Roraima, Guyana. I. Bryophytes. Tropical Bryology 1: 25-54. - Inoue, H. & S. R. Gradstein. 1988. A remarkable new species of *Anastrophyllum* from Mt. Roraima, Guyana. Bulletin of the National Science Museum, Tokyo, Ser. B, 14: 87-91 [as *Anastrophyllum* subgen. *Vanaea*].

LEJEUNEACEAE

Plants green, yellowish, brown, black or whitish, never reddish; creeping to ascending or pendent, pinnate, forked or irregularly branched. Stems with or without hyalodermis. Branches usually *Lejeunea*-type, sometimes *Frullania*-type, rarely *Aphanolejeunea*-type (*Aphanolejeunea*); innovations of the *Radula*-type; stolons lacking. Leaves incubous, divided into a large dorsal lobe and a small ventral lobule, the lobule broadly attached to the dorsal lobe along a keel; stylus reduced. Cells with homogeneous or segmented oil bodies; ocelli sometimes present. Underleaves undivided or bifid, rarely lacking (Cololejeuneae). Rhizoids in tufts from underleaf bases. Gametoecia on leading shoots or on short branches. Androecia usually with 1-2 antheridia per bract, antheridium globose, on a long 1-seriate stalk. Gynoecia with only 1 archegonium. Sporophyte surrounded by a perianth; mouth of the perianth usually contracted into a short beak. Sporophyte with reduced foot, not penetrating the stem. Seta very short, thin, of 16 or 20 rows of cells, rarely thicker (*Bryopteris*, *Marchesinia*). Capsule globose, wall 2-layered. Elaters attached to the capsule valves, arranged vertically inside capsule, spirals well-developed or reduced. Spores large, germination endosporic. Vegetative reproduction by gemmae, caducous leaves, caducous branches or fragmentation.

DISCUSSION. A large tropical family with hundreds of species in about 90 genera; 70 genera are described in this treatment for tropical America. Most of the species are epiphytic and occur on trunks and branches, fine twigs, or living leaves in rain forest. Growth on living leaves is a special feature of many species of Lejeuneaceae; indeed, almost all epiphyllous bryophytes of the tropical rain forest are members of this family (Gradstein, 1997).

The family Lejeuneaceae is immediately recognized by the incubous leaves with a large dorsal lobe and a smaller ventral lobule longly attached to the lobe along a keel, and by the usual presence of underleaves (sometimes lacking in the tribe Cololejeuneae), with rhizoids in tufts from underleaf bases. The *Lejeunea*-type branches and the single archegonium per gynoecium are further important characteristics of the family.

The Lejeuneaceae are the sister group of the Jubulaceae and differ from the latter mainly in the lack of reddish pigmentation (exception: *Lepidolejeunea eluta*), in the attachment of the lobule to the lobe along a long keel (except when the lobule is reduced), and in the presence of only one archegonium in each gynoecium. Further differences are the presence of a stem hyalodermis in many genera of the Lejeuneaceae and the attachment of the underleaves to the stem by means of specialized U-shaped cells ("superior central cells"), features that seem to be absent in the Jubulaceae.

Lobules attached to the lobes along a long keel are also found in the Radulaceae, but in the latter family underleaves are lacking and the rhizoids originate from the lobules, not from the stem. Moreover, branching in the Radulaceae is of the *Radula*-type, there are numerous archegonia in each gynoecium, the foot of the sporophyte penetrates the tip of the stem, and the elaters are free, not attached to the valves.

The numerous genera of the Lejeuneaceae have been variously classified into subfamilies and tribes. In this treatment, they are arranged in 2 subfamilies and 4 tribes following Gradstein (1994) with the addition of the tribe Cololejeuneae.

Subfamily **PTYCHANTHOIDEAE**

Tribe **Ptychantheae:** *Acrolejeunea, Archilejeunea, Bryopteris, Caudalejeunea, Cephalantholejeunea, Frullanoides, Fulfordianthus, Lopholejeunea, Marchesinia, Mastigolejeunea, Schiffneriolejeunea, Spruceanthus, Thysananthus, Verdoornianthus*

Subfamily **LEJEUNEOIDEAE**

Tribe **Brachiolejeuneae:** *Acanthocoleus, Blepharolejeunea, Brachiolejeunea, Dicranolejeunea, Lindigianthus, Neurolejeunea, Odontolejeunea, Stictolejeunea, Symbiezidium*

Tribe **Lejeuneae:** *Amblyolejeunea, Amphilejeunea, Anoplolejeunea, Aureolejeunea, Bromeliophila, Ceratolejeunea, Cheilolejeunea, Crossotolejeunea, Cyclolejeunea, Cyrtolejeunea, Cystolejeunea, Dactylolejeunea, Drepanolejeunea, Echinocolea, Haplolejeunea, Harpalejeunea, Leiolejeunea, Lejeunea, Lepidolejeunea, Leptolejeunea, Leucolejeunea, Luteolejeunea, Macrolejeunea, Metalejeunea, Microlejeunea, Myriocolea, Omphalanthus, Oryzolejeunea, Otolejeunea, Physantholejeunea, Pictolejeunea, Pluvianthus, Potamolejeunea, Prionolejeunea, Pycnolejeunea,*

Rectolejeunea, Rhaphidolejeunea, Schusterolejeunea, Sphaerolejeunea, Taxilejeunea, Trachylejeunea, Vitalianthus

Tribe **Cololejeuneae:** *Aphanolejeunea, Cololejeunea, Colura, Diplasiolejeunea, Myriocoleopsis*.

The subfamilies and tribes may be distinguished by the following synoptic key (for identification of the genera use "Artificial key to the genera of Lejeunaceae of tropical America"!):

1. Capsule valves spreading after dehiscence, inner walls brownish, covered by a fenestrate thickening layer. Elaters usually 72 per capsule, with well-developed spiral bands, upper ends attached to valve surface and margins. Spores isodiametric. Seta with 16 or more outer rows of cells. Underleaves undivided. Ventral merophyte 4 or more cells wide. Ocelli absent (subfamily Ptychanthoideae) Tribe **Ptychantheae** (p.)

1. Capsule valves not spreading after dehiscence, remaining (sub)erect, walls pale, lacking a thickening layer. Elaters 4 or less per capsule, with rudimentary spiral bands, upper ends attached to valve margins only. Spores elongated-rectangular. Seta with 12 or 16 outer rows of cells. Underleaves bifid or undivided. Ventral merophyte 2-4 cells wide, rarely wider. Ocelli sometimes present (subfamily Lejeuneoideae) 2
2. Seta epidermis consisting of 16 longitudinal rows of cells. Underleaves undivided ..... Tribe **Brachiolejeuneae** (p.)
2. Seta epidermis consisting of only 12 longitudinal rows of cells. Underleaves bifid, undivided or lacking 3
3. Underleaves one per leaf pair ..... Tribe **Lejeuneae** (p.)
3. Underleaves one for each leaf or lacking ..... Tribe **Cololejeuneae** (p.)

LITERATURE. Gradstein, S. R. 1994. Lejeuneaceae: Ptychantheae, Brachiolejeuneae. Flora Neotropica Monograph 62: 1-216. - Schuster, R. M. 1980. Lejeuneaceae. The Hepaticae and Anthocerotae of North America, Vol. IV: 706-1314.

Artificial key to the genera of Lejeuneaceae of tropical America

1. Leaves highly specialized, upper part forming an inflated sac (= extension of the lobule); leaves usually erect, standing away from the substrate ..... **Colura** (p.)
1. Leaves less specialized, upper part not forming an inflated sac 2
2. Underleaves lacking 3
2. Underleaves present 5
3. Plants growing upright from a stoloniferous base, in or near running water. Stems rigid, made up of thick-walled cells, epidermis of 5-30 cell rows. Gynoecia numerous, in clustered cymes ..... **Myriocoleopsis**
3. Plants creeping, without stoloniferous base. Stems of thin-walled cells, epidermis of 5 cell rows. Gynoecia not in clustered cymes 4
4. Athecal branches (without collar at their base) present. Leaves on each plant usually of two types, with lobule and without lobule; rarely all leaves similar. Leaf margins without hyaline border of dead cells ..... **Aphanolejeunea** (p.)
4. Athecal branches lacking, all branches with a collar at their base. Leaves not usually of two types. Leaf margin with or without hyaline border of dead cells ..... **Cololejeunea** (p.)
5. Underleaves undivided to weakly emarginate ..... **Section 1. Holostipous Lejeuneaceae**
5. Underleaves divided ..... **Section 2. Schizostipous Lejeuneaceae** (p.)

Section 1. Holostipous Lejeuneaceae

1. Leaf margins toothed, at least near apex 2
1. Leaf margins entire 17
2. Ventral merophyte 4 or more cells wide 3
2. Ventral merophyte only 2(-3) cells wide 11

The width of the ventral merophyte must be carefully measured as the number of epidermal cells across the ventral stem surface in the area where the underleaves are attached, but not in the direct neighborhood of the underleaf base because there the number of epidermal cells is variable.

3. Leaf cells with evenly thickened walls, trigones lacking. Lobules with a very long (5-10 cells), curved tooth. Underleaves toothed, emarginate. Northwestern South America and Central America ..... **Fulfordianthus** (p.)

3. Leaf cells with trigones, walls not evenly thickened. Lobules with or without a short tooth (less than five cells long), or with several teeth. Underleaves entire or toothed 4
4. Median leaf cells elongate; trigones cordate 5
4. Median leaf cells isodiametric, trigones various, not cordate 8
5. Underleaves toothed 6
5. Underleaves entire 7
6. Plants pinnate or forked, branches predominantly *Frullania*-type. Innovations lacking ..... **Bryopteris** (p.)
6. Plants irregularly branched, branches *Lejeunea*-type. Innovations present ..... **Thysananthus** (p.)
7. Lobules with 7-9 teeth. Underleaf apex ± rounded, the bases auriculate. Perianths 8-10-keeled, with innovations. High Andes of Peru ..... **Frullanoides laciniatiflora** (p.)
7. Lobules with 1-3 teeth. Underleaf apex emarginate, the bases not auriculate. Perianths 3-keeled, without innovations. Throughout tropical America ..... **Caudalejeunea** (p.)
8. Underleaf insertion line ± straight. Plants 1.5-2 mm wide. Perianth with two ventral keels, innovations lacking ..... **Lopholejeunea nigricans** (p.)
8. Underleaf insertion line deeply arched. Plants usually more than 2 mm wide. Perianth without ventral keels, innovations present or absent 9
9. Apical portion of leaf broadly recurved. Ventral merophyte 4 cells wide, epidermal cells thin-walled. Plants glossy brown. Northern Andes, Costa Rica, above 2000 m ..... **Lindigianthus** (p.)
9. Leaf ± plane. Ventral merophyte more than 4 cells wide, epidermal cells thick-walled. Throughout tropical America 10
10. Lobules plane, with (1-)2-4 distinct teeth. Perianth terminal on main stem or elongated branches, with two innovations ..... **Marchesinia** (p.)
10. Lobules strongly inflated-rounded, very small and hidden behind the underleaves, without distinct teeth. Perianth on a very short branch, appearing lateral on the stem, with or without one short innovation. Pacific coast of northern South America and Costa Rica ..... **Symbiezidium dentatum** (p.)
11. Underleaves very large, 6-10x stem width, at apex short-bifid or notched. Perianth terete, smooth ..... **Taxilejeunea sulphurea** (p.)
11. Underleaves smaller, apex undivided (shallowly emarginate in **Harpalejeunea**, couplet 21). Perianth keeled 12
12. Lobules large, ca. half leaf length, truncate. Leaves strongly falcate. Plants small (up 1.2 mm wide), creeping, brown ..... **Blepharolejeunea** subgen**. Blepharolejeunea** (p.)
12. Lobules less than 2/5 leaf length, not truncate. Leaves not falcate 13
13. Leaves with ocelli: scattered, in a short row, or 1-2 near leaf base 14
13. Ocelli lacking 15
14. Plants pale green. Disciform gemmae usually produced on dorsal leaf margins. Perianth toothed. ..... **Cyclolejeunea convexistipa** (p.)
14. Plants brown. Disciform gemmae lacking. Perianth with four bulbiform extensions ..... **Ceratolejeunea** subgen. **Ceratophora** (p.)
15. Leaves with (5-)7-25 teeth. Underleaves toothed or entire. On living leaves or bark ..... **Odontolejeunea** (p.)
15. Leaves with 1-5 teeth. Underleaves entire. On bark or rock, not on living leaves 16
16. Branches predominantly *Frullania*-type. Epidermal cells strongly bulging (stem cross-section). Female bracteoles toothed ..... **Dicranolejeunea** (p.)
16. Branches predominantly *Lejeunea*-type. Epidermal cells not bulging. Female bracteoles entire ..... **Acanthocoleus** (p.)
17. Underleaves toothed 6
17. Underleaves entire 18
18. Leaves with ocelli: scattered, in a row, or 1-2 near leaf base 19
18. Leaves without ocelli 26
19. Ocelli in a row or 1-2 near leaf base 20
19. Ocelli scattered 22
20. Row of ocelli 7-22 cells long. Ventral merophyte 4-6 cells wide. Lobule tooth 3-5 cells long ..... **Neurolejeunea** sect. **Neurolejeunea** (p.)
20. Row of ocelli 1-6 cells long. Ventral merophyte 2(-3) cells wide. Lobule tooth 1 cell long 21
21. Lobule entirely and strongly inflated, bottle-shaped, with a long, falcate tooth. Perianth sharply 5-keeled, the keels smooth or toothed, never extending into horns. ..... **Harpalejeunea** (p.)

21. Lobule inflated in the lower half, flattened above, rectangular, with a short, blunt tooth. Perianth 4-keeled, the keels smooth and extended into inflated horns ....**Ceratolejeunea desciscens** (p.)
22. Ventral merophyte 4 or more cells wide 23
22. Ventral merophyte 2(-3) cells wide (see note in couplet 2) 24
23. Underleaf apex undivided. *Frullania*-type branches frequently present. Stem without hyalodermis. Leaf apex rounded ..... **Stictolejeunea** (p.)
23. Underleaf apex notched. *Frullania*-type branches lacking. Stem with a distinct hyalodermis. Leaf apex acute, rarely rounded..... **Lepidolejeunea eluta** (p.)
24. Plants tiny, less than 1 mm wide. Underleaves orbicular, 2-3x stem width. Leaf apex often with a whitish border of dead cells. West Indies ..... **Physantholejeunea** (p.)
24. Plants more than 1 mm wide. Underleaves reniform, 6-10x stem width. Leaf apex without whitish border 25
25. Leaf cells ± thick-walled, with large trigones. Ocelli conspicuous, usually larger than green leaf cells. Epidermal cells thick-walled. Lobules curved downward. Pacific coast of northern South America and Panama ..... **Luteolejeunea** (p.)
25. Leaf cells very thin-walled, with minute trigones. Ocelli rather inconspicuous, equal in size to or smaller than other leaf cells. Epidermal cells thin-walled. Lobules straight or somewhat curved upwards. Northern Andes, Cuba ..... **Lepidolejeunea spongia** (p.)
26. Ventral merophyte 4 or more cells wide 27
26. Ventral merophyte 2 cells wide (see note in couplet 2) 53
27. Leaf cells with cordate trigones. Median leaf cells ± elongated. Leaves mostly convolute when dry, occasionally plane 28
27. Trigones various but not cordate. Median leaf cells isodiametric, rarely elongated. Leaves spreading and plane, curved down or somewhat folded when dry 38
28. Underleaf apex distinctly emarginate 29
28. Underleaf apex rounded or truncate, not emarginate 30
29. Plants robust, (2-)2.5-3.5 mm wide, leaves when dry strongly convolute. Stems rigid, without hyalodermis, ventral merophyte 8 cells wide. Perianth with innovations. Plants usually growing pendent on branches..... **Thysananthus** (p.)
29. Plants smaller, 1.5-2.5 mm wide, leaves usually not convolute. Stems flaccid, with distinct hyalodermis, ventral merophyte 4 cells wide. Perianth without innovations. Plants growing in small tufts on leaves or twigs ..... **Caudalejeunea** (p.)
30. Lobules with 3-10 teeth (the teeth sometimes inflexed) 31
30. Lobules with 0-2 teeth 33
31. Plants blackish in older stem portions. Perianth with 5-10 keels, with innovations. Common throughout tropical America ..... **Frullanoides** (p.)
31. Plants becoming yellowish-brown, never blackish. Perianths with 3-10 keels, innovations present or absent. Throughout tropical America but very rare in the West Indies 32
32. Underleaf insertion line slightly curved, underleaf base plane. Perianth with 5-10 keels, innovations lacking. Flagelliform branches (producing caducous leaves) frequently present. Tropical America, lowlands (below 1000 m) ..... **Acrolejeunea** (p.)
32. Underleaf insertion line deeply arched, underleaf bases folded. Perianth with 3(-4) keels, innovations present. Flagelliform branches lacking. Tropical and southern temperate America, usually montane ..... **Brachiolejeunea** (p.)
33. Medulla cells thick-walled. Ventral epidermal cells not, or scarcely, larger than medulla cells (stem cross-section) 34
33. Medulla cells thin-walled. Ventral epidermal cells distinctly larger than medulla cells 36
34. Leaf apex acute. Female bracts and bracteole toothed ..... **Thysananthus** (p.)
34. Leaf apex rounded. Female bracts and bracteole without teeth 35
35. Plants turning olive- to reddish-brown with age. Innovations lacking. Female bract apices acute-acuminate. Leaves when dry strongly wrapped around the stem. Throughout tropical America but mainly on islands and in coastal areas, rare inland ..... **Schiffneriolejeunea** (p.)
35. Plants turning dark-brown to black with age. Innovations present. Female bract apices rounded. Leaves when dry rather flat-appressed to the stem, not wrapped around the stem. Common throughout tropical America ..... **Mastigolejeunea** (p.)
36. Leaf lobules mostly reduced ..... **Acanthocoleus** (p.)
36. Leaf lobules well-developed, never reduced, with two teeth 37
37. First lobule tooth short, incurved and blunt, second tooth long, pointing outwards, sharp. Lobules truncate. Leaves not squarrose. Tropical and southern temperate America, in tropical America above 2000 m ..... **Blepharolejeunea** subgen. **Oreolejeunea** (p.)

37. Lobule teeth equal or the first tooth larger than the second. Lobules oblique or truncate. Leaves squarrose when moist. Tropical and southern temperate America, lowland or montane .... **Brachiolejeunea** (p.)
38. Median leaf cells about 2 times longer than wide. Plants robust. Ventral merophyte more than 10 cells wide. Lobules often reduced. Perianth with 5-8 keels. Coastal lowland region of Ecuador, very rare ..... **Spruceanthus** (p.)
38. Median leaf cells isodiametrical or only slightly elongated 39
39. Lobules with 2-4 teeth 40
39. Lobules with only one tooth or teeth lacking 44
40. Leaf apex strongly and broadly recurved, acute. Epidermal cells thin-walled. Plants glossy brown. Northern Andes, Costa Rica, above 2000 m ..... **Lindigianthus** (p.)
40. Leaf apex ± plane, rounded or acute-acuminate. Epidermal cells thick-walled 41
41. Epidermal cells distinctly higher (1.5-2x) than medulla cells, medulla cells thin-walled 36
41. Epidermal cells not or hardly higher (less than 1.5x) than medulla cells, medulla cells thick-walled 42
42. Insertion line of underleaves deeply arched (more than 100 µm deep). Ventral merophyte 6-12 cells wide. Plants more than 2 mm wide, often black. Perianth without ventral keels. Predominantly montane, in higher latitudes also at sea-level ..... **Marchesinia** (p.)
42. Insertion of underleaves straight or shallowly curved. Ventral merophyte 4 cells wide. Plants smaller, never black. Perianth with two ventral keels. Lowland and submontane, below 1000 m 43
43. Plants whitish or gray . Second lobule tooth much larger than the first. Androecia on short-specialized branches, male bracteoles reduced ..... **Leucolejeunea unciloba** (p.)
43. Plants pale green to brown. Lobule teeth identical or the first tooth larger than the second. Androecia on elongated shoots, male bracteoles not reduced **Archilejeunea auberiana** (p.)
44. Branches predominantly *Frullania*-type 36
44. Branches predominantly *Lejeunea*-type 45
45. Underleaf insertion line straight or shallowly curved 46
45. Underleaf insertion line deeply arched, over 100 µm deep 51
46. Plants whitish, pale-yellowish, or grayish ..... **Leucolejeunea** (p.)
46. Plants darker: green, brown, or black 47
47. Robust, dark-brown rheophyte growing in or near running water, with very small underleaves, reduced lobules, and numerous short, often bisexual branches, each bisexual branch with a few male bracts and with gynoecia arising from the axils of the male bracts ....**Cephalantholejeunea** (p.)
47. Plants different, bisexual branches lacking 48
48. Median leaf cells small, 10-20 µm in diameter, with confluent trigones, the cell walls almost evenly thickened. Lobules flask-shaped, often darker than the lobe. Plants usually black .... **Neurolejeunea** subgen. **Aneurolejeunea** (p.)
48. Median leaf cells larger, trigones not confluent, the cell walls not evenly thickened. Lobules not flask-shaped, not darker than the lobe. Plants green, brown or black 49
49. Epidermal cells distinctly larger than medulla cells (stem cross-section). Perianth keels ciliate-laciniate, innovations lacking. Plants glossy black or dark-brown (rarely green in shade). Oil bodies homogeneous ..... **Lopholejeunea** (p.)
49. Epidermal cells not or little larger than medulla cells. Perianth keels smooth or denticulate, innovations present, rarely lacking. Plants green or brown (black: **Archilejeunea parviflora**, couplet 50). Oil bodies segmented 50
50. Innovations present. Free margin of lobule plane. Leaves when moist widely spreading, not squarrose. Throughout tropical America, common ..... **Archilejeunea** (p.)
50. Innovations lacking. Free margin involuted, at least near apex. Leaves when moist obliquely spreading, ± squarrose. Inner Amazonia and Guianas, rare ..... **Verdoornianthus** (p.)
51. Lobules small, less than 1/4 leaf length. Leaf cells with radiate trigones. Perianth on a very short branch (appearing lateral on the stem), keels ciliate-laciniate. Lowland and montane ....**Symbiezidium** (p.)
51. Lobules larger, 1/4-1/2x leaf length. Leaf cells usually with large bulging trigones. Perianth on an elongated shoot, keels smooth. Exclusively montane 52
52. Lobules subquadrate-trapezoid, to 1/3 lobe length. Plants green to yellowish-brown, growth usually pendent ..... **Omphalanthus** (p.)
52. Lobules ± rectangular, 2/5-1/2 lobe length. Plants usually dark brown or reddish-brown, creeping or ascending ..... **Aureolejeunea** (p.)
53. Lobules uniformly swollen and strongly involuted, the free margin inrolled 2-3 times .... **Anoplolejeunea** (p.)

53. Lobules not or only weakly involuted 54
54. *Frullania*-type branches present, sometimes few only. Lobules when well-developed with two teeth. Plants usually brown 16
54. *Frullania*-type branches entirely lacking. Lobules with one tooth only. Plants pale green, rarely brown 55
55. Lobules more than 1/3 lobe length 56
55. Lobules small, less than 1/3 lobe length 60
56. Underleaf apex emarginate with broad and obtuse diverging lobes ..... **Leiolejeunea** (p.)
56. Underleaf apex rounded or truncate, not emarginate 57
57. Underleaves more than 3x stem width. Plants (0.5-)1-2.5 mm wide, pale green (when brown: **Aureolejeunea,** couplet 52) ..... **Amphilejeunea** (p.)
57. Underleaves less than 3x stem width. Plants tiny, to 1 mm wide 58
58. Lobule with a long-linear, acuminate tooth, hyaline papilla distal. Free margin of the lobule inflexed, forming a straight line from the base to the junction with the ventral margin of the lobe, apex oblique. Leaves little spreading, suberect ..... **Cyrtolejeunea** (p.)
58. Lobule with a short, blunt tooth, hyaline papilla proximal or distal. Free margin of the lobule plane, not forming a straight line, apex truncate. Leaves wide-spreading 59
59. Apex of lobule with enlarged margin cells. Hyaline papilla proximal to the apical tooth. Perianth terete, without keels. Guadeloupe ..... **Amblyolejeunea** (p.)
59. Margin cells of lobule not enlarged. Hyaline papilla distal to the apical tooth. Perianth keeled. West Indies and northern South America ..... **Oryzolejeunea** (p.)
60. Leaf cells with large trigones. Hyaline papilla of the lobule distal to the apical tooth..... ..... **Cheilolejeunea** (p.)
60. Leaf cells with minute trigones. Hyaline papilla proximal of the apical tooth 61
61. Plants pale green. Underleaf apex rounded, recurved or plane. Ocelli lacking. Gynoecia on short branches..... **Amphilejeunea** (p.)
61. Plants brownish. Underleaf apex emarginate, plane. Ocelli present in leaves and underleaves, but often rather inconspicuous in herbarium material. Gynoecia terminal on the stems .... **Lepidolejeunea spongia** (p.)

Section 2. Schizostipous Lejeuneaceae

1. Leaves highly specialized, upper part forming an inflated sac (= extension of the lobule); leaves usually erect, standing away from substrate ..... **Colura** (p.)
1. Leaves less specialized, upper part not forming an inflated sac 2
2. Underleaf lobes widely diverging (Fig. 44F) 3
2. Underleaf lobes not widely diverging 9
3. One underleaf to each leaf, the underleaves usually densely overlapping. Leaf apex rounded ... . **Diplasiolejeunea** (p.)
3. One underleaf to every alternate leaf, the underleaves usually distant. Leaf apex acute-acuminate to rounded 4
4. Underleaf lobes subulate, 1-3 cells wide at base, acute at apex 5
4. Underleaf lobes broader, more than 3 cells wide at base, blunt at apex 7
5. Leaves ovate-lanceolate, widest near the base. Leaf apex acute-acuminate. Underleaf margins not bordered by large cells ..... **Drepanolejeunea** (p.)
5. Leaves elliptical to obovate, widest in the middle or in the upper part. Leaf apex rounded to acute. Underleaf margins sometimes bordered by large cells 6
6. Lobule tooth long, falcate. Underleaf margins not bordered by large cells ....**Rhaphidolejeunea** (p.)
6. Lobule tooth short, blunt. Underleaf margins bordered by large cells ..... **Leptolejeunea** (p.)
7. Leaves without ocelli ..... **Leiolejeunea** (p.)
7. Leaves with ocelli, at least near the base of the lobe 8
8. Leaves with 1-3 ocelli in an unbroken row at the base of the lobe. Innovations lejeuneoid .... **Harpalejeunea** (p.)
8. Leaves usually with 3-4(-10) ocelli in a broken row or scattered through the lobe, sometimes with only (1-)2 ocelli at the base. Innovations pycnolejeuneoid ..... **Drepanolejeunea** (p.)
9. Leaf margins with long, ciliate teeth, the teeth mostly more than 2 cells long. West Indies .... **Dactylolejeunea** (p.)
9. Leaf margins entire or with shorter teeth 10
10. Lobules very large, more than 1/2 of lobe length (some lobules may be reduced, however). Leaves suberect, almost parallel to the stem. Plants minute, less than 0.5 mm wide 11
10. Lobules smaller (maximally up to 1/2 of lobe length). Leaves spreading 12

11. Plants monoicous. Leaf base without ocelli. Innovations pycnolejeuneoid. (Plants usually yellowish, with very thick-walled leaf cells; lobule keels crenate) ..... **Metalejeunea** (p.)
11. Plants dioicous. Leaf base usually with 1 or more ocelli. Innovations lejeuneoid .... **Microlejeunea** (p.)
12. Ocelli scattered in leaves and underleaves 13
12. Ocelli lacking or in leaves only, never in underleaves 15
13. Ocelli reddish or brown ..... **Pictolejeunea** (p.)
13. Ocelli colorless, rarely gray-brown (*Lepidolejeunea eluta*) 14
14. Plants very small, 0.5-0.7 mm wide. Leaves obliquely spreading, obovate-spathulate. Leaf apex broadly rounded ..... **Haplolejeunea** (p.)
14. Plants larger. Leaves widely spreading, ovate-oblong. Leaf apex pointed or rounded .... **Lepidolejeunea** (p.)
15. Underleaves very large, at least 6 times stem width 16
15. Underleaves smaller 20
16. Leaf cells uniformly thick-walled or with conspicuous trigones. Plants dull green or brown (rarely whitish: **Pycnolejeunea**, couplet 18) 17
16. Leaf cells uniformly thin-walled or with very small trigones. Plants pale green, yellowish-green or whitish (stems often long and slender, pendent; perianths always on short lateral branches) .19
17. Cell walls ± pale brown, trigones radiate (or lacking). Leaf margins often somewhat toothed (sometimes entire). Perianth usually with horns ..... **Ceratolejeunea** (p.)
17. Cell walls colorless, trigones simple-triangular, sometimes swollen but not radiate. Leaf margins entire or crenulate. Perianth without horns 18
18. Ocelli present, 1-several at leaf base or scattered through the lobe. Lobule apex with hyaline papilla proximal to the tooth ..... **Pycnolejeunea** (p.)
18. Ocelli lacking. Hyaline papilla distal to the tooth ..... **Cheilolejeunea** (p.)
19. Perianth single on a very short lateral branch, without innovation (or occasionally with a short, sterile innovation) ..... **Macrolejeunea** (p.)
19. Perianths several in a row on a lateral branch, with fertile innovations .... **Taxilejeunea** (p.)
20. Underleaf lobes with rounded apex, the lobes separated from each other by a broad and shallow, lunulate sinus ..... 7 (or **Section 1. Holostipous Lejeuneaceae**)
20. Underleaf lobes obtuse to acute to acuminate, sinus narrower 21
21. Leaf margins, and sometimes the entire dorsal leaf surface, toothed by conically projecting cells with thick-walled tips (crowned by a small papilla). Ocelli lacking 22
21. Leaf margins entire or ± toothed, but not toothed by conically projecting papillose cells. Ocelli present or absent..... 23
22. Dorsal leaf surface (and leaf margins) ± spinose. Perianth inflated, with 5 keels. Innovations lejeuneoid ..... **Echinocolea** (p.)
22. Dorsal leaf surface smooth (rarely spinose-papillose), spines usually restricted to leaf margins. Perianth flattened, with 2 keels. Innovations pycnolejeuneoid or absent .... **Prionolejeuna** (p.)

(Cyclolejeunea accedens (Gott.) A. Evans is similar to *Prionolejeunea* but differs in disciform gemmae along leaf margins and papillae on leaf surface. *Pycnolejeunea* and *Trachylejeunea* may have crenulate leaf margins with projecting papillose cells; the leaves usually have ocelli).

23. Stems robust, ventral merophyte more than 4 cells wide. (Plants growing in or near running water, densely pinnate, with numerous short sexual branches) 24
23. Stems thinner, ventral merophyte 2(-4) cells wide 25
24. Leaves transversely inserted, insertion line very short. Plants growing upright from a rhizome-like base. Paroicous; antheridia in axils of female bracts ..... **Myriocolea** (p.)
24. Leaves longitudinally inserted, insertion line long. Plants creeping or pendent, without rhizome-like base. Autoicous; antheridia on separate branches ..... **Potamolejeunea** (p.)
25. Vegetative reproduction by means of caducous leaves 26
25. No vegetative reproduction by caducous leaves 29
26. Plants brownish. Lobules large, ca. ½ leaf length, bottle-shaped. Perianth with horns .... **Ceratolejeunea** subgen. **Caduciloba** (p.)
26. Plants (pale) green. Lobules shorter, not bottle-shaped. Perianth without horns 27
27. Caducous leaves conspicuously smaller than ordinary leaves, usually produced on flagelliform branches. Leaves with ocelli. Leaf cells less than 20 µm in diameter (the ocelli larger), trigones lacking ..... **Rectolejeunea** (p.)
27. Caducous leaves not smaller than ordinary leaves, not produced on flagelliform branches (exception: *Lejeunea phyllobola*). Leaves without ocelli. Leaf cells more than 20 µm in diameter, trigones present or absent 28

28. Lobule tooth long and sharp, hyaline papilla distal. Lobules never reduced. Margins of caducous leaves with rhizoids ..... **Cheilolejeunea adnata** (p.)
28. Lobule tooth short and blunt, hyaline papilla proximal. Lobules sometimes reduced, at least in some leaves. Margins of caducous leaves without rhizoids .... **Lejeunea** subgen. **Heterolejeunea** (p.)
29. Vegetative reproduction by means of disciform or reniform gemmae from leaf margins .... **Cyclolejeunea** (p.)
29. No vegetative reproduction by means of gemmae..... 30
30. Leaves with ocelli: scattered, in a row, or 1 to several at leaf base 31
30. Leaves without ocelli 37
31. Underleaf margins bordered by large cells. Underleaf lobes subulate, inserted at the outer edges of the underleaf ..... **Leptolejeunea** (p.)
31. Underleaf margins unbordered. Underleaf lobes wider, not inserted at outer edges of underleaf 32
32. Plants very small, 0.3-0.7 mm wide 33
32. Plants larger 34
33. Ocelli in a row 3-6 cells long. Leaf apex pointed. Atlantic coast of Brazil ... **Vitalianthus** (p.)
33. Ocelli scattered. Leaf apex rounded ..... **Haplolejeunea** (p.)
34. Plants brown or brownish-green. Walls of leaf cells ± pale brown, trigones radiate (or lacking). Branch bases sometimes with a huge, strongly inflated lobule ('utricle'). Perianth usually with horns ..... **Ceratolejeunea** (p.)
34. Plants green, whitish or brown. Walls of leaf cells colorless, trigones not radiate. Utricles lacking (except **Pluvianthus**, couplet 36). Perianth without horns 35
35. Leaf margins crenulate-denticulate. Underleaves distant, small. Perianth swollen, 4-5-keeled (when 2-keeled and expanded above into short auricles: *Cyclolejeunea*) **Trachylejeunea** (p.)
35. Leaf margins entire. Underleaves usually imbricate. 36
36. Leaf apex acute. Innovations lejeuneoid. Trigones lacking or very small. SE Brazil .... **Pluvianthus** (p.)
36. Leaf apex rounded. Innovations pycnolejeuneoid. Trigones usually well developed .... **Pycnolejeunea** (p.)
37. Leaves (1.2-)2-4 times longer than wide. Plants growing in rivers, in leaf axils of bromeliads, or epiphyllous 38
37. Leaves always less than 2 times longer than wide 40
38. Leaves with very short insertion, attached to the stem by only 2-3 cells. Plants rheophytic (growing in rivers) ..... **Schusterolejeunea** (p.)
38. Leaves with a longer insertion. Plants not rheophytic
39. Mid-leaf cells 35-70 µm long, 1.5-4x longer than wide. Perianth inflated, 5-keeled, the keels not expanded into auricles. Plants growing in leaf axils of bromeliads .....**Bromeliophila** (p.)
39. Mid-leaf cells 20-30 µm long, subisodiametrical. Perianth flattened, 2-keeled, the keels expanded into large auricles. Plants growing on living leaves, not in leaf axils of bromeliads ....**Otolejeunea** (p.)
40. Walls of leaf cells ± pale brown, trigones radiate (or lacking). Perianth usually with horns. Plants brownish or brownish-green. Branch bases sometimes with a huge, strongly inflated lobule ('utricle'). ..... **Ceratolejeunea** (p.)
40. Walls of leaf cells colorless, trigones not radiate. Perianth without horns. Plants green, whitish, or brown. Utricles lacking (when present: **Pluvianthus**, couplet 36) 41
41. Leaf apex pointed 42
41. Leaf apex rounded 45
42. Trigones usually well-developed, leaf cells smooth or papillose. Leaf apex reflexed, obtuse to acute. Hyaline papilla distal to the lobule tooth. Oil bodies very large (more than 1/2 the cell lumen in length), coarsely segmented ..... **Cheilolejeunea** subgen. **Strepsilejeunea** (p.)
42. Trigones lacking or very small. Leaf apex not reflexed, acute-acuminate. Hyaline papilla proximal to the lobule tooth. Oil bodies much smaller (less than 1/4 the cell lumen in length), finely segmented or homogeneous..... 43
43. Leaf and bract margins ± crenulate (to denticulate), underleaf margins often with a tooth. Perianth keels toothed to laciniate..... **Crossotolejeunea** (p.)
43. Leaf and bract margins entire, underleaf margins without teeth. Perianth keels smooth, papillose or with plate-like outgrowths 44

44. Perianths in rows of (2-)3-6 on lateral branches, the innovations (1 per gynoecium) repeatedly fertile. Stems in cross-section sometimes with more than 25 medullary cells .... **Taxilejeunea** (p.)
44. Perianths single or maximally 2 in a row on lateral branches. Stems in cross-section with less than 25 medullary cells..... **Lejeunea** (p.)
45. Lobules strongly swollen, globose, free margin conspicuously involuted. (Plants rather robust, ca. 2 mm wide, dull pale to brownish. Leaf cells papillose, with large, swollen trigones and no intermediate thickenings. Perianth flat, without beak) 46
45. Lobules swollen or not swollen but not globose, free margin plane or inflexed 47
46. Plants very small, less than 0.5 mm wide. Leaves suberect to obliquely spreading. Leaf cells plane, without papilla. Lobule tooth very long, ca. 6 x longer than wide. Perianth 5-keeled, with beak ..... **Cyrtolejeunea**
46. Plants larger. Leaves wide spreading. Leaf cells convex, usually bulging outwards as a large, lenticular papilla. Lobule tooth short. Perianth flat, without beak ..... **Cystolejeunea** (p.)
47. Leaves bordered by elongated, hyaline cells in 1-2 rows. Gynoecia on very short lateral branches, with or without very short, sterile innovations. (Lobules strongly inflated) .... **Sphaerolejeunea** (p.)
47. Leaves unbordered. Innovations well-developed 48
48. Lobule apex with 2 small, blunt, closely associated teeth. Innovations usually lacking. Ventral merophyte 2-6 cells wide ..... **Trachylejeunea** (p.)
48. Lobule apex with only 1, short or long tooth. Innovations present. Ventral merophyte 2 cells wide (rarely more than 2 cells wide) 49
49. Hyaline papilla distal to the lobule tooth. Trigones usually well developed. Lobules always strongly inflated, never reduced. Oil bodies very large (more than 1/2 the cell lumen in length), coarsely segmented ..... **Cheilolejeunea** (p.)
49. Hyaline papilla proximal to the lobule tooth. Trigones lacking or very small. Lobules less inflated, sometimes reduced. Oil bodies much smaller (less than 1/4 the cell lumen in length), finely segmented or smooth 44

LEJEUNEACEAE Tribe PTYCHANTHEAE

Plants deep green to brown or blackish. Stems relatively robust; ventral merophyte 4-20 cells wide. Vegetative branching *Lejeunea*-type and *Frullania*-type. Leaf insertion long, J-shaped. Lobule apex with hyaline papilla displaced towards the inner surface of the lobule. Ocelli lacking. Underleaves undivided. Androecia on long shoots, male bracteoles present throughout the spike, male bracts usually with large, hypostatic lobules (sometimes smaller and epistatic). Perianths with 0-5 ventral keels. Seta usually not articulate, of 16 or more outer rows of cells and 4 or more inner rows. Capsule valves wide-spreading after dehiscence, inner wall brownish, covered by a fenestrate sheath of thickening, outer wall colorless, with nodulose cell-wall thickenings. Elaters usually 72 per capsule, sometimes fewer, upper ends attached to valve surface and margins, spirals well-developed, brown. Spores ± isodiametric, with rosettes on each facet.

About 18-19 genera worldwide; 14 genera in tropical America. Most of the species are xerotolerant epiphytes of forest canopies or rather open, wooded vegetation, at low elevations.

Acrolejeunea (Fig. 33) **-** A pantropical genus (15 spp.), with 3 species: *A. emergens* (Mitt.) Steph., *A. heterophylla* (A. Evans) Grolle & Gradst., and *A. torulosa* (Lehm. & Lindenb.) Schiffn., in lowland areas of northern South America and Central America. The genus is virtually lacking in the West Indies and in SE Brazil.

HABITAT. On bark in plantations, pastures, savannas, scrubby vegetation, gallery woodlands, and in the high canopy of lowland rain forest, in rather dry and sunny situations, 0-1000 m. Occasionally on rock. The species of *Acrolejeunea* are among the most xerotolerant of neotropical Lejeuneaceae and avoid the shaded interior portions of the forest.

DESCRIPTION. **Plants** rather small, 1-2 mm wide, yellow-green to yellow-brown, creeping. **Branches** *Lejeunea*-type, occasionally *Frullania*-type. **Stems** with a hyalodermis; ventral merophyte 4-6 cells wide. **Leaf lobes** wide-spreading and often ± squarrose, when dry strongly convolute, apex rounded, margins entire. **Cells** slightly longer than wide, trigones cordate; oil bodies homogeneous. **Lobules** 2/5-1/2 leaf length, never reduced, with (2-)3-8 teeth. **Underleaves** undivided, margins entire, insertion line shallowly curved. **Male bracts** rather similar to leaves, with epistatic lobules. **Gynoecia** without innovations; female bract apices rounded to obtuse. **Perianths** with 5-10 smooth keels. **Vegetative reproduction** by tiny caducous leaves produced on upright flagelliform shoots.

DISCUSSION. The neotropical species of *Acrolejeunea* are easily recognized by 1) the glossy green to yellow-brown color of the plants; 2) the very densely imbricate leaves which are strongly convolute when dry, giving the plants an almost worm-like appearance; 3) the lobules with several small teeth along the free margin; 4) the cordate trigones; 5) the gynoecia with pluriplicate perianths and no innovations; and especially 6) by the vegetative reproduction by means of specialized caducous leaves. The caducous leaves in *Acrolejeunea* originate from the apex of tiny, upright flagelliform shoots and are very small, about 0.2-0.3 mm long. In *A. tortulosa*, they are highly modified, with the lobule about as large as the lobe and with a long, apical rhizoid. In the other species the caducous leaves possess rather small lobules and an apical rhizoid is absent. The flagelliform shoots are 1-5 mm long and devoid of leaves (except near the apex), and bear tiny, densily imbricate or squarrose underleaves.

LITERATURE. Gradstein, S. R. 1994 (see family ref.)

Archilejeunea (Fig. 33) - A pantropical genus (ca. 12 spp.), with 7 species at low elevations in tropical America, 4 in subgen. *Archilejeunea* and 3 in subgen. *Dibrachiella*.

HABITAT. On bark in lowland and submontane rain forests and in scrubby vegetation, in shaded or sunny locations, 0-1000(-1500) m. Occasionally on isolated trees in pasture lands; also on rock. *Archilejeunea parviflora* (Nees) Schiffn. (subgen. *Dibrachiella*) occurs only in the moist, shaded understory of the rain forest as well as on wet rock near streams; it is the most hygrophytic species of the genus and is widespread throughout the Neotropics. *Archilejeunea fuscescens* (Hampe) Fulford (subgen. *Archilejeunea*) is a very common epiphyte on tree trunks and canopy branches in Amazonian and Guianan lowland rain forests, in the understory as well as in the canopy of the forest.

DESCRIPTION. **Plants** small to large, 1-3.5 mm wide, dull to glossy green to brown or black, creeping or ascending. **Branches** *Lejeunea*-type, occasionally *Frullania*-type. **Stems** simple, without hyalodermis, all cell walls colorless, medulla cells thick-walled; ventral merophyte 4-6(-8) cells wide. **Leaf lobes** wide-spreading, when dry not appressed or convolute, apex rounded, margins entire. **Cells** (sub)isodiametric, trigones simple-triangular to radiate; oil bodies coarsely granular. **Lobules** 1/3-1/2 leaf length, sometimes reduced, with 1-2 teeth, free margin usually plane. **Underleaves** undivided, with entire margins and straight or weakly curved insertion line. **Gynoecia** with 1-2 lejeuneoid or pycnolejeuneoid innovations; female bract apices rounded to obtuse. **Perianths** with 4-5 keels, the keels smooth or slightly toothed above. **Vegetative reproduction** by regeneration from leaf cells.

DISCUSSION. *Archilejeunea* is distinguished from other holostipous Lejeuneaceae by 1) the rather uniform structure of the stems, lacking enlarged epidermal cells; 2) isodiametric leaf cells lacking blackish pigmentation in the walls; 3) coarsely granular oil bodies; and 4) gynoecia with 1-2 innovations and 4-5-keeled perianths with smooth or weakly toothed keels. Branching is primarily of the *Lejeunea*-type and innovation leaf sequence is lejeuneoid in subgen. *Dibrachiella*, pycnolejeuneoid in subgen. *Archilejeunea*.

LITERATURE. Gradstein, S. R. 1994 (see family ref.).

Bryopteris (Fig. 33) - A small, primarily neotropical genus with 2 species, *B. diffusa* (Sw.) Nees and *B. filicina* (Sw.) Nees, at rather low elevations throughout tropical America. A third species occurs in Madagascar. *Bryopteris filicina* is one of the most common neotropical species of Lejeuneaceae and, due to its large size, has been collected more frequently than any other hepatic in the region.

HABITAT. On bark or rock in moist primary and secondary submontane and lower montane rain forests, (0-)100-2500 m. The species are characteristic indicators of the frequent occurrence of clouds or mist and may form large festoons on the branches of trees and shrubs in these sites.

DESCRIPTION. **Plants** robust, to 25 cm long, 2-4 mm wide, dull dark green with glossy light green growing points, brown with age, dendroid, erect from a rhizome-like shoot, (bi)pinnate or forked. **Vegetative branches** usually *Frullania*-type, sexual branches *Lejeunea*-type. **Stems** with a dark-brown cortex of thick-walled cells in 3-5 layers surrounding a colorless, thin-walled medulla, epidermal cells larger than subepidermal cells; ventral merophyte more than 10 cells wide. **Leaf lobes** wide-spreading, when dry usually convolute, apex pointed, margins toothed or entire. **Cells** longer than wide, trigones cordate, intermediate thickenings 0-3 per wall; oil bodies homogeneous. **Lobules** small, to 1/4 leaf length, never reduced, with 0-4 teeth. **Underleaves** undivided, quadrate to spathulate, apex sharply toothed, insertion line straight. **Gametoecia** on very short branches. **Gynoecia** without innovations; female bract apices acute-acuminate. **Perianths** with 3 smooth keels. **Vegetative reproduction** by cladia.

DISCUSSION. *Bryopteris* is readily recognized by the large, feather-like or forked habit of the plants, the *Frullania*-type branches, the toothed leaves and underleaves (but leaves sometimes entire), the elongated leaf cells with well-defined cordate trigones, and by the gynoecia on short-specialized

branches, lacking innovations and with a sharply 3-keeled perianth. Growth of the plants is always dendroid, with a creeping rhizome and erect or pendent fronds.

Bryopteris may be confused with *Fulfordianthus*, which has a similar growth habit. The latter, however, has *Lejeunea*-type instead of *Frullania*-type branches, smaller leaf cells with uniformly thickened walls lacking trigones, and gynoecia on elongated shoots, with two innovations.

LITERATURE. Gradstein, S. R. 1994 (see family ref.).

Caudalejeunea (Fig. 34) - A pantropical genus (ca. 15 spp.), with 1 species, *C. lehmanniana* (Gott.) A. Evans, at low elevations in tropical America.

HABITAT. On living leaves, twigs and branches in scrubby vegetation, swamps and lowland rain forests, in rather open situations, 0-1000 m. *Caudalejeunea lehmanniana* is a xerotolerant species and in forests it grows in rather open sites, in the high canopy, at the forest margin, or in gaps.

DESCRIPTION. **Plants** small to medium-sized, 1.5-2.5 mm wide, green to brown, creeping to ascending. **Branches** *Lejeunea*-type. **Stems** with a hyalodermis; ventral merophyte 4 cells wide. **Leaf lobes** obliquely spreading and somewhat falcate, when dry spreading or appressed to stem, apex obtuse, margins entire (in the neotropical sp.). **Cells** longer than wide, trigones cordate, intermediate thickenings 1-2 per wall; oil bodies homogeneous. **Lobules** 1/3-2/5 leaf length, sometimes reduced, with (1-)2-3 teeth. **Underleaves** emarginate, margins entire, bases decurrent, insertion line curved. **Gynoecia** without innovations; female bract apices acute-acuminate. **Perianths** with 3 sharp keels (4-5 keels in palaeotropical spp.), keels smooth or dentate. **Vegetative reproduction** by disciform gemmae from dorsal surfaces of the leaves.

DISCUSSION. The distinguishing feature of *Caudalejeunea*, by which it differs from all other Ptychantheae, is the asexual reproduction by means of disciform gemmae. The gemmae are produced on the dorsal surfaces of the leaves, from the upper portions of ascending vegetative branches. Gemmae are not always present, however, and in *C. lehmanniana* they are only rarely produced. This species may be readily recognized by the falcate leaves with (1-)2-3-toothed lobules, the emarginate underleaves, the presence of a stem hyalodermis, and by the sharply 3-keeled perianth lacking innovations.

Caudalejeunea is the only genus of Ptychantheae that is frequently epiphyllous. Large, adhesive rhizoid discs, produced at the underleaf bases, serve as holdfasts for the epiphyllous plants. These discs are apparently an adaptation to growth on living leaves and are entirely lacking in corticolous plants.

LITERATURE. Gradstein, S. R. 1994 (see family ref.).

Cephalantholejeunea - A monotypic, neotropical genus, with *C. temnanthoides* Schust. in Amazonian Brazil. The genus is known only from two old records and one of them is without exact provenance. An intensive search in potentially suitable habitats should be undertaken to determine the current distribution of this unusual plant.

HABITAT. On periodically inundated substrates in or along streams, in Amazonian rain forest areas.

DESCRIPTION. **Plants** rather robust, pinnate, dark brown, loosely creeping or hanging. **Stems** without hyalodermis, cells ± thick-walled; ventral merophyte 4 or more cells wide. **Leaf lobes** wide-spreading, apex rounded, ± plane, margins entire. **Cells** plane, thin-walled; oil bodies unknown; ocelli lacking. **Lobules** reduced, hyaline papilla proximal. **Underleaves** small, undivided or emarginate, insertion line almost straight. **Gametoecia** numerous, on short branches arising from both sides of the stem, the branches with up to 6 series of male bracts and with very short female branches (consisting of one leaf and a perianth) arising from the axils of the male bracts, 1 gynoecial branch per male bract; innovations lacking. **Perianths** with 5 denticulate keels. **Vegetative reproduction** not observed.

DISCUSSION. *Cephalantholejeunea temnanthoides* is a robust rheophytic plant with stout, pinnately branched stems and very small, distant underleaves. The plants are similar to *Potamolejeunea* but differ from the latter genus in: 1) undivided underleaves; 2) peculiar, bisexual branch systems with very short female branches arising from the axils of male bracts; 3) denticulate perianth keels; and 4) the very different sporophytes. By its sporophyte, *Cephalantholejeunea* is a member of the subfamily Ptychanthoideae, not of subfam. Lejeuneoideae where is was previously placed (Reiner-Drehwald & Weis, submitted).

LITERATURE. Reiner-Drehwald, M. E. & G. Weis. On *Cephalantholejeunea* Schust. (Lejeuneaceae) from South America. Submitted to Systematic Botany. - Schuster, R. M. 1963. An annotated synopsis of the genera and subgenera of Lejeuneaceae. Beihefte zur Nova Hedwigia 9 [as *Potamolejeunea* subgen. *Cephalolejeunea,* p. 122-123].

Frullanoides (Fig. 34) - A primarily neotropical genus, with 7 species in tropical America; one of them, *F. tristis* (Steph.) van Slageren, also occurs in Africa and India.

HABITAT. On bark and rock in dry or moist lowland and montane forests, scrubby vegetation, savannas, plantations and pastures, from sea level to 3500 m in the Andes. The species are rather xerotolerant and in forests they are usually restricted to the canopy, gaps or forest margin. Most of the species occur below 1000 m except for the common *Frullanoides densifolia* Raddi (500-3500 m, also at sea level in SE Brazil) and the Peruvian endemic *F. laciniatiflora* (Loitles.) van Slag. (above 2000 m).

DESCRIPTION. **Plants** small to large, 1-10 cm long, 1-3 mm wide, green to black, creeping or ascending, rarely pendent, often forked. **Branches** *Frullania*-type and *Lejeunea*-type. **Stems** with a hyalodermis; medulla cells thick-walled, ventral merophyte 4-12 cells wide. **Leaf lobes** wide-spreading, when dry convolute, apex rounded to acute, margins entire or toothed. **Cells** slightly longer than wide, walls often with blackish pigmentation, trigones cordate; oil bodies homogeneous. **Lobules** 1/3-2/3 leaf length, never reduced, with 3-11 teeth. **Underleaves** undivided, margins entire, bases rounded or auriculate, insertion line straight to deeply arched. **Male bracts** with epistatic lobules. **Gynoecia** with 2 pycnolejeuneoid innovations; female bract apices rounded to apiculate. **Perianths** with 5-11 smooth keels. **Vegetative reproduction** not observed.

DISCUSSION. *Frullanoides* is the largest genus of the Ptychantheae in the Neotropics. The plants are recognized by their blackish-green pigmentation, the leaf cells with cordate trigones and numerous small, homogeneous oil bodies, the auriculate underleaves (except *F. corticalis* and *F. bahamensis*), the lobules with numerous teeth along the free margin, the presence of a stem hyalodermis, and the gynoecia with 2 innovations and pluriplicate perianths. When sterile, *Frullanoides* may be confused with *Mastigolejeunea,* which may also turn blackish-green. The lobules in *Mastigolejeunea* have only 1(-3) teeth, however, and the leaf cells contain large, granular oil bodies. Moreover, a stem hyalodermis is lacking in *Mastigolejeunea*.

LITERATURE. Gradstein, S. R. 1994 (see family ref.) - Van Slageren, M. W. 1985. A taxonomic monograph of the genera *Brachiolejeunea* and *Frullanoides*. Meded Bot. Mus. Herb. Utrecht 544: 1-309.

Fulfordianthus (Fig. 34) - A small neotropical genus, with 2 species, *F. pterobryoides* (Spruce) Gradst. and *F. evansii* (Fulford) Gradst., at low elevations in northwestern South America and Central America. *Fulfordianthus pterobryoides* is a Chocó species, largely restricted to the wet Pacific coast of northern South America, from northern Ecuador to southern Costa Rica. A few records are from across the Andes in eastern Amazonia. *Fulfordianthus evansii* is a rare species of the Caribbean coast of Central America.

HABITAT. On bark and leaves in the understory of virgin lowland and submontane rain forests, usually on small tree trunks, treelets, and lianas, 0-1500 m. Also occurring on rock.

DESCRIPTION. **Plants** usually large, 1-10 cm long, 1.5-4 mm wide, dull dark green with glossy light green growing points, brown with age, dendroid, erect from a rhizome-like shoot, usually densely pinnate. **Branches** *Lejeunea*-type only. **Stems** with a dark brown cortex of small, thick-walled cells in 4-5 layers surrounding a colorless, thin-walled medulla; ventral merophyte more than 10 cells wide. **Leaf lobes** wide-spreading, when dry not appressed or convolute, apex broad, margins toothed. **Cells** subisodiametric, very small, 10-15 µm long, walls uniformly thickened, trigones lacking; oil bodies absent. **Lobules** small, to 1/5 leaf length, never reduced, with 1 long, curved tooth. **Underleaves** deeply emarginate, obcuneate, margins toothed, insertion line straight. **Gynoecia** with 2 lejeuneoid innovations; female bract apices acute. **Perianths** with 3 smooth keels. **Vegetative reproduction** not observed.

DISCUSSION. *Fulfordianthus* is readily recognized by the erect, feather-like habit of the plants, the deeply emarginate underleaves, the crenulate to sharply toothed leaf margins, and the very small leaf cells with uniformly thickened walls without trigones and lacking oil bodies. The absence of oil bodies is a unique feature of *Fulfordianthus*; as far as is known all other genera of Lejeuneaceae produce oil bodies.

The plants are rather similar in habit to *Bryopteris*, but the latter genus differs in *Frullania*-type instead of *Lejeunea*-type branching, larger leaf cells with cordate trigones and oil bodies, rounded underleaf apices, and gynoecia without innovations. Moreover, in *Bryopteris* the cells of the stem epidermis are larger than those of the inner cortical layers; in *Fulfordianthus* the epidermal cells are not enlarged.

LITERATURE. Gradstein, S. R. 1994 (see family ref.).

Lopholejeunea (Fig. 35) - A large pantropical genus (ca. 40 spp.), with 4 species at rather low elevations in tropical America.

HABITAT. On bark and rock in lowland and lower montane rain forests and in plantations, usually in sunny locations or partial shade, 0-1800 m. The genus is typically xerotolerant and in forests usually restricted to the high canopy, gaps, or forest margins.

DESCRIPTION. **Plants** rather small, 1-2 mm wide, glossy green to black (or brown), usually creeping. **Branches** *Lejeunea*-type, occasionally *Frullania*-type. **Stems** with a hyalodermis; ventral merophyte 4 cells wide. **Leaf lobes** wide-spreading, when dry not appressed or convolute, apex rounded to apiculate, margins entire. **Cells** (sub)isodiametric, walls often with blackish pigmentation, trigones simple-triangular or radiate; oil bodies homogeneous. **Lobules** 1/4-1/2 leaf length, sometimes reduced, strongly inflated in the lower half, with 0-1 teeth. **Underleaves** undivided, margins entire, insertion line curved (not deeply arched). **Gynoecia** without true innovations. **Perianths** with 4-5 dentate-laciniate keels; female bract apices rounded to acute. **Vegetative reproduction** not observed.

DISCUSSION. The species of *Lopholejeunea* typically form black patches on bark or rock. Dark pigmentation of the cell walls is a characteristic feature of the genus although not all species exhibit this character. In *L. quelchii* Steph., a rare Caribbean species, the cell walls are barely pigmented and the plants are usually brown instead of black. Further characteristics of *Lopholejeunea* include the presence of a stem hyalodermis, the isodiametric leaf cells with ± radiate trigones and small, homogeneous oil bodies, the strongly inflated-gibbose lobules with 0-2 obscure teeth, the usual absence of innovations, and the perianth with 4-5 sharp, dentate-laciniate keels.

LITERATURE. Gradstein, S. R. 1994 (see family ref.).

Marchesinia (Fig. 35) - An Afro-American genus (5 spp.), with 2 species, *M. brachiata* (Sw.) Schiffn. and *M. robusta* (Spruce) Schiffn., at montane elevations in tropical America. *Marchesinia brachiata* is widespread in the Neotropics; it also occurs in tropical Africa; *M. robusta* occurs in the Andes and Costa Rica.

HABITAT. On bark and rock in submontane and montane rain forests, scrubby vegetation and plantations, from almost sea level to 3300 m in the Andes. The species of *Marchesinia* are rather xerotolerant and in forests they occur mainly in the canopy, in gaps, or at the forest margin, in partial shade.

DESCRIPTION. **Plants** often large, 2- 10 cm long, 2-4 mm wide, deep green to black or brown, ascending or pendent, often forked. **Branches** *Lejeunea*-type, occasionally *Frullania*-type. **Stems** with weakly enlarged epidermis, the epidermis usually brownish, medulla cells thick-walled; ventral merophyte 6-11 cells wide. **Leaf lobes** wide-spreading, when dry plane or deflexed (not convolute), ovate-oblong, apex rounded to acuminate, margins entire or toothed. **Cells** (sub)isodiametric, trigones usually triradiate; oil bodies homogeneous (in neotropical spp.) **Lobules** 1/5-1/3 leaf length, sometimes reduced, usually flat, with (1-)2-4 teeth, free margin usually plane. **Underleaves** undivided, margins entire or toothed, often recurved, bases decurrent, insertion line deeply arched. **Gynoecia** with 2 pycnolejeuneoid innovations; female bract apices rounded acute-apiculate. **Perianths** flat, margins entire. **Vegetative reproduction** by caducous or fragmenting leaves.

DISCUSSION. *Marchesinia* is readily recognized by 1) ovate-oblong leaves with ± isodiametric cells and radiate trigones; 2) small and rather flat lobules with 2-4 teeth; 3) large, strongly decurrent underleaves with deeply arched insertion line (depth of underleaf insertion equals underleaf length as measured from rhizoid disc to apex); and 4) a strongly flattened perianth subtended by a pair of innovations. The apical margin of the leaves often bears a few small irregular teeth. The underleaf margins are often revolute and are strongly toothed in *M. robusta*; in *M. brachiata* they are entire.

Marchesinia closely resembles *Symbiezidium* (Brachiolejeuneae) when sterile, but the latter has tiny, strongly inflated lobules with involute free margins and without discrete teeth. When fertile, *Marchesinia* is immediately recognized by the very flat and completely smooth perianths on long shoots, subtended by 2 innovations which are frequently fertile again. In *Symbiezidium*, the perianths are ciliate-laciniate and positioned on very short lateral branches, each with 1 short, sterile innovation.

Flat perianths with 2 innovations are also found in the Andean genus *Lindigianthus*, but the latter has broadly recurved leaf apices (± plane in *Marchesinia*) and fragile stems of thin-walled cells (thick-walled in *Marchesinia*). *Lindigianthus* is easily recognized in the field and in the herbarium by the glossy brown color of the plants (blackish in *Marchesinia*).

LITERATURE. Gradstein, S. R. 1994 (see family ref.).

Mastigolejeunea (Fig. 35) - A pantropical genus (ca. 15 spp.), with 3 species at low elevations in tropical America. Two species occur in Amazonia, *M. innovans* (Spruce) Steph. and *M. plicatiflora* (Spruce) Steph. The third, *M. auriculata* (Wilson) Schiffn., is widespread in the region except in the Amazon and Orinoco basins where it is virtually absent and replaced by the other two species.

HABITAT. On bark and rock in primary and disturbed lowland and lower montane rain forests, in scrubby vegetation and in plantations, usually in rather open and sunny locations, 0-1500 m. The species are xerotolerant and in forests are usually restricted to the canopy, gaps, or forest margins.

DESCRIPTION. **Plants** 1.5-2.5 mm wide, somewhat glossy deep green to dark green, becoming blackish or dark brown with age, creeping or ascending. **Branches** *Lejeunea*-type only. **Stems** with enlarged dorsal epidermis (ventral epidermis not enlarged), epidermis ± brown, medulla cells thick-

walled; ventral merophyte 5-10 cells wide. **Leaf lobes** wide-spreading, when dry appressed to the lateral side of the stem, apex rounded, margins entire. **Cells** slightly longer than wide, trigones cordate; oil bodies coarsely granular. **Lobules** 1/4-1/2 leaf length, never reduced, with 1(-3) teeth, free margin plane or inflexed. **Underleaves** undivided, with entire margins and straight or weakly curved insertion line. **Gynoecia** with 1(-2) lejeuneoid innovations; female bract apices rounded. **Perianths** with 3(-10) keels. **Vegetative reproduction** by regeneration from leaf cells.

DISCUSSION. Characteristic features of *Mastigolejeunea* are the blackish-green or dark brown plants with entire-margined leaves with rounded apices, elongated leaf cells with cordate trigones, lobules with 1(-3) teeth, and untoothed gynoecia with a 3(-7)-keeled perianth and 1(-2) innovations. The stem epidermis is strongly asymmetrical (cross-section), consisting of large dorsal cells and small ventral cells.

When dry, *Mastigolejeunea* may be readily recognized by the characteristic position of the leaves, being suberect and strongly appressed against the stem with the apical portion ± plane and clearly visible in dorsal view. A similar leaf position is found in the closely related genus *Thysananthus*; the latter, however, has stems without enlarged epidermal cells, and toothed gynoecia. The only neotropical species, *Thysananthus amazonicus* (Spruce) Schiffn., is readily distinguished from the neotropical species of *Mastigolejeunea* by the apiculate leaves.

Mastigolejeunea may also be confused with *Frullanoides* and *Schiffneriolejeunea*; for differences see under the latter genera.

LITERATURE. Gradstein, S. R. 1994 (see family ref.).

Schiffneriolejeunea (Fig. 36) - A pantropical genus (14 spp.), with 2 species, *S. polycarpa* (Nees) Gradst. and *S. amazonica* Gradst., at low elevations in tropical America. *Schiffneriolejeunea polycarpa* occurs mainly on the northern and southern edges of the Neotropics (Mexico, Greater Antilles, SE Brazil) whereas *S. amazonica* is endemic to the Amazon Basin.

HABITAT. On bark and rotten wood in rather mesic or dry evergreen lowland and submontane woodlands and scrub, at forest edges, in savannas, and in plantations, usually in rather open situations, 0-700(-1300) m. *Schiffneriolejeunea* is a xerotolerant genus and in forests occurs only in the high canopy, in gaps, or at the forest margin, in partial shade.

DESCRIPTION. **Plants** 1-2 mm wide, green to rather glossy brown, creeping or ascending. **Branches** *Lejeunea*-type, occasionally *Frullania*-type. **Stems** with enlarged dorsal epidermis (ventral epidermis not enlarged), epidermis brown, medulla cells thick-walled; ventral merophyte 4-8 cells wide. **Leaf lobes** wide-spreading, when dry convolute and wrapped around the stem, apex rounded, margins entire. **Cells** slightly longer than wide, trigones cordate; oil bodies coarsely granular. **Lobules** 1/3-1/2 leaf length, sometimes reduced, with 1-2 teeth, free margin not inflexed. **Underleaves** undivided, with entire margins and straight or weakly curved insertion line. **Gynoecia** without innovations; female bract apices acute-acuminate. **Perianths** with 4(-6) keels, the keels inflated-swollen or sharp. **Vegetative reproduction** by regeneration from leaf cells.

DISCUSSION. *Schiffneriolejeunea* is characterized by the glossy, brown color of the plants, the entire-margined leaves with rounded apex and 2-toothed lobules, the leaf cells with cordate trigones and coarsely granular oil bodies, the asymmetric epidermis with enlarged dorsal cells, the absence of innovations, and the 4-keeled perianths with 2 ventral keels in the upper half. The perianth keels vary somewhat in this genus. In *S. amazonica* and its African relative *S. occulta* (Steph.) Gradst., they are long and sharp, in *S. polycarpa* they are short and broadly rounded. In species of sect. *Pappeanae* (Africa), the ventral keels are reduced and the perianths have become terete-eplicate.

Schiffneriolejeunea is closely related to *Mastigolejeunea* but female plants of the latter are immediately separated by the presence of innovations. Plants without gynoecia can be separated by the different position of the leaves in the dry state (wrapped around the stem in *Schiffneriolejeunea*, not flattened) and the different color of the plants (glossy brown in *Schiffneriolejeunea*, blackish-green or dark brown in *Mastigolejeunea*).

LITERATURE. Gradstein, S. R. 1994 (see family ref.).

Spruceanthus (Fig. 36) - An Asiatic-Australasian genus (7 spp.), with 1 species in the Neotropics, *S. theobromae* (Spruce) Gradst. The species is known only from the foot of the Andes in the Prov. Los Ríos, coastal Ecuador, where it has been collected three times, lastly in 1997 (Gradstein, 1999a). The species has been listed as endangered in the World Red List of Bryophytes.

HABITAT. On bark of old cocoa trees near rivers, in plantations and gallery forest, at the foot of the mountains where clouds are frequent, 150-400 m.

DESCRIPTION. **Plants** robust, 3-4 mm wide, green to brownish, ascending or pendent, forked when fertile. **Branches** *Lejeunea*-type only. **Stems** with a brown cortex of small, thick-walled cells in 2-3 layers surrounding a colorless, thin-walled medulla; ventral merophyte ca. 16 cells wide. **Leaf lobes** wide-spreading, when dry not appressed or convolute, apex rounded, margins entire. **Cells** ca. 2 x

longer than wide (in the neotropical sp.), trigones radiate, intermediate thickenings 0-3 per wall; oil bodies homogeneous. **Lobules** very small, reduced to small fold, with 1 tooth. **Underleaves** undivided, with entire margins and straight insertion line. **Gynoecia** with 1-2 lejeuneoid innovations; female bract apices acute. **Perianths** with 5-8 keels. **Vegetative reproduction** not observed.

DISCUSSION. *Spruceanthus theobromae* is a very distinct species, easily recognized by the relatively large size, forked branching, and the numerous 5-8-plicate perianths which are often arranged in a monotropic series. In its gynoecia, *S. theobromae* somewhat resembles *Archilejeunea* (*A. auberiana*, *A. parviflora*), but the larger size of the plants, the more robust stems with a clearly differentiated epidermis and subepidermis, the flagelliform branches at stem bases, the elongated leaf cells with homogeneous oil bodies (segmented in *Archilejeunea*), and the ± pluriplicate perianths separate *Spruceanthus theobromae* from *Archilejeunea*.

LITERATURE. Gradstein, S. R. 1994 (see family ref.). - Gradstein, S. R. 1999. On the rediscovery of *Spruceanthus theobromae* (Spruce) Gradst. (Hepaticae), an endangered liverwort of cacao trees in western Ecuador. Bryobrothera 5: 81-86.

Thysananthus (Fig. 36) - A pantropical genus (ca. 10 spp.), with 1 species, *T. amazonicus* (Spruce) Schiffn., at low elevations in northern South America (Amazonia, Guianas), Costa Rica, and Cuba.

HABITAT. Pendent from branches and twigs in lowland and submontane rain forests and scrub, usually in rather mesic and somewhat open situations, 0-1000 m. *Thysananthus amazonicus* is particularly common in the dry evergreen woodlands on white sand of the northern part of the Amazon Basin and in Guyana, where it may form large festoons on treelets, lianas, and saplings.

DESCRIPTION. **Plants** rather robust, to 6 cm long, 2-4 mm wide, dull olive green to dark green to black or dark brown with age, ascending or pendent. **Branches** *Lejeunea*-type only. **Stems** without enlarged epidermis, the epidermis strongly thick-walled and brown, medulla cells thick-walled; ventral merophyte 6-10 cells wide. **Leaf lobes** wide-spreading, when dry convolute, apex acute, margins toothed or entire. **Cells** longer than wide, trigones cordate; oil bodies coarsely granular. **Lobules** small, to 1/4 leaf length, never reduced, with 1-2 teeth, free margin plane or inflexed. **Underleaves** undivided, spathulate and often squarrose, apex truncate to emarginate, margins toothed to entire, insertion line straight. **Gynoecia** with 1(-2) innovations; female bracts toothed, apices acute-apiculate. **Perianths** with 3 toothed keels. **Vegetative reproduction** not observed.

DISCUSSION. *Thysananthus* is closely related to *Mastigolejeunea* but differs in the lack of enlarged epidermal cells and in the dentate gynoecia. The single neotropical species of *Thysananthus*, *T. amazonicus*, is readily separated from the neotropical species of *Mastigolejeunea* in the pointed leaf apices (rounded in neotropical *Mastigolejeunea*).

LITERATURE. Gradstein, S. R. 1994 (see family ref.).

Verdoornianthus (Fig. 37) - A small neotropical genus with 2 species, *V. griffinii* Gradst. and *V. marsupiifolius* (Spruce) Gradst., at low elevations in the Amazon Basin and the Guianas. The species are known from only half a dozen collections and have probably been overlooked due to their occurrence in the forest canopy.

HABITAT. On twigs and branches, occasionally on leaves, in the canopy of dry and moist lowland rain forests, also in scrub (?), probably xerotolerant, 50-200 m.

DESCRIPTION. **Plants** 1-2 mm wide, dull olive green to dark brown when dry, loosely creeping. **Branches** *Lejeunea*-type only. **Stems** with enlarged dorsal epidermis (ventral epidermis not enlarged); ventral merophyte 4-8 cells wide. **Leaf lobes** obliquely spreading to falcate, when dry weakly convolute, apex rounded, margins entire. **Cells** (sub)isodiametric, trigones simple-triangular to radiate; oil bodies coarsely granular. **Lobules** 1/2 leaf length, never reduced, with 1 tooth, free margin often inflexed. **Underleaves** undivided, with entire margins and curved insertion line. **Gynoecia** without innovations; female bract apices rounded to obtuse. **Perianths** with 4-5 sharp keels, the keels slightly toothed above. **Vegetative reproduction** not observed.

DISCUSSION. The small genus *Verdoornianthus* is related to *Archilejeunea* but differs in the dull brownish color, the enlarged dorsal epidermis of the stem, the obliquely spreading leaves which are convolute when dry, the large swollen lobules with ± inflexed margins and, especially, in the lack of innovations. In dense forests, *Verdoornianthus* species seem to be exclusive to the canopy, whereas *Archilejeunea* spp. are common both in the forest understory and in the canopy.

LITERATURE. Gradstein, S. R. 1994 (see family ref.).

LEJEUNEACEAE Tribe BRACHIOLEJEUNEAE

Plants pale to deep green to brown or blackish. Stems thin or relatively robust; ventral merophyte 2-16 cells wide. Vegetative branching *Lejeunea*-type or *Frullania*-type. Leaf insertion long, J-shaped. Lobule apex with entally displaced hyaline papilla. Ocelli occasionally present. Underleaves undivided. Male bracteoles present throughout the spike or restricted to the base, male bract lobules large and hypostatic or small and epistatic. Gynoecia with pycnolejeuneoid innovations (in neotropical spp.). Perianths with 0-2 ventral keels. Seta articulate, of 16 outer rows of cells and 4 inner rows. Capsule valves remaining suberect after dehiscence, pale, inner and outer layers with ± nodulose cell-wall thickenings, brownish sheath of thickening lacking on inner valve. Elaters usually 34 per capsule, upper ends attached to valve margins only, pale, spiral rudimentary. Spores elongate-rectangular, with rudimentary rosettes.

Nine genera worldwide, all of them occurring in tropical America. The neotropical region is the center of diversity of this tribe. Most of the species grow in rather shaded, moist habitats.

Acanthocoleus (Fig. 37) - A pantropical genus (7-8 spp.), with 3 species at rather low elevations in tropical America: *A. aberrans* (Lindenb. & Gott.) Kruijt throughout the region, *A. juddii* Kruijt in the Greater Antilles and Mexico, and *A. trigonus* (Nees & Mont.) Gradst. in subtropical South America.

HABITAT. On bark and rock (rarely soil) in rather dry, semi-deciduous forests and scrub, or in the outer canopy of humid evergreen rain forests, at submontane and montane elevations, ca. 150-2600 m.

DESCRIPTION. **Plants** rather small, 1-4 cm long, 0.8-2 mm wide, dull green to brown, creeping. **Branches** *Lejeunea*-type, occasionally (robust vegetative shoots) *Frullania*-type. **Stems** with a hyalodermis; ventral merophyte 2(-3) cells wide. **Leaf lobes** wide-spreading, when dry ± convolute, apex rounded to acuminate, margins entire or toothed. **Cells** slightly longer than wide, trigones cordate; oil bodies finely granular. **Lobules** 1/4-2/3 leaf length, often reduced, with (1-)2 teeth, second tooth smaller. **Underleaves** undivided, margins entire, bases decurrent, insertion line shallowly curved to arched. **Male bracts** just below the gynoecium or on separate branches, with epistatic lobules. **Gynoecia** with (1-)2 pycnolejeuneoid innovations, female bracteoles entire. **Perianths** with (0-)3-5 keels, usually winged and ciliate-laciniate near apex, occasionally smooth. **Vegetative reproduction** not observed.

DISCUSSION. *Acanthocoleus* is closely related to *Dicranolejeunea*; the two genera differ in growth form, stem structure, and female involucre. *Dicranolejeunea* species are rather robust plants, with stems ascending from the substrate and often freely pendent; their branches are always of the *Frullania*-type. In contrast, species of *Acanthocoleus* are smaller, creeping plants which closely adhere to the surface. *Lejeunea*-type branches are more common in *Acanthocoleus* than *Frullania*-type branches.

Correlated with their different growth form is a difference in the anatomy of the stem of the two genera. In *Dicranolejeunea*, the epidermal cells of the stems are very large and bulge strongly outwards, and the walls of the outer medullary cells are conspicuously thickened, forming a rather distinct subepidermis; the walls of the inner cells are thin. In *Acanthocoleus*, the epidermal cells are smaller and never bulge outwards, and the outer medullary cells are scarcely thicker-walled than the inner medullary cells. The distinctly toothed female bracts and bracteoles of *Dicranolejeunea* also separate the genus from *Acanthocoleus*, which has a completely entire involucre or, occasionally, a few small teeth on the upper bract margins.

In spite of these differences, *Acanthocoleus* is similar to *Dicranolejeunea* in general appearance and some authors prefer to treat it as a mere subgenus of the latter.

LITERATURE. Gradstein, S. R. 1994 (see family ref.). - Kruijt, Ch. 1988. A monograph of the genera *Dicranolejeunea* and *Acanthocoleus*. Bryophytorum Bibliotheca 36: 1-135.

Blepharolejeunea (Fig. 37) - A New World genus (5 spp.), with 4 species at high elevations in tropical America and a fifth species in Tierra del Fuego. The neotropical species are classified in two different subgenera: subgen. *Blepharolejeunea* (1 sp., *B. saccata* (Steph.) Kruijt & Gradst.) scattered in the northern Andes, Central America, and the Greater Antilles, and subgen. *Oreolejeunea* (3 spp.) common in the high Andes and also occurring in the high mountains of Costa Rica and Mexico, the Guayana Highland, and in the Serra de Mantiqueira, SE Brazil.

HABITAT. On bark and rock in very moist and cloudy, but usually rather open environments, at the edges and in the canopy of montane cloud forests, in scrubby vegetation, and in páramos, 1200-4000 m. *Blepharolejeunea saccata* (subgen. *Blepharolejeunea*) is a lower montane species and occurs in more or less undisturbed cloud forests below 2000 m. The species of the subgenus *Oreolejeunea* are exclusively upper montane to alpine and occur above 2000 m.

DESCRIPTION. **Plants** rather small, 1-2 mm wide, glossy green to brown or blackish, creeping or ascending, often forked. **Branches** *Frullania*-type or *Lejeunea*-type. **Stems** with a weak hyalodermis; ventral merophyte 2-4 cells wide. **Leaf lobes** wide-spreading and often convex, when dry convolute,

apex rounded or apiculate, margins entire or toothed. **Cells** subisodiametric, trigones simple-triangular or cordate; oil bodies finely granular or homogeneous. **Lobules** ca. 1/2 leaf length, never reduced, truncate, with 2 teeth, second tooth larger than the first. **Underleaves** undivided, margins entire, insertion line straight or arched. **Male bracts** just below the gynoecium, with epistatic lobules. **Gynoecia** with 2 pycnolejeuneoid innovations. **Perianths** with 3(-5) keels, smooth or ciliate-laciniate near apex. **Vegetative reproduction** not observed.

DISCUSSION. *Blepharolejeunea* is closely related to *Brachiolejeunea* and *Dicranolejeunea* and is primarily separated from these by the peculiar truncate lobule with a short and blunt, often inconspicuous first tooth, and a long and sharp, clearly visible second tooth. The leaf margins are sharply toothed in *B. saccata* whereas the species of subgen. *Oreolejeunea* have entire leaf margins. The latter furthermore differ in their finely granular oil bodies (homogeneous in *B. saccata*).

LITERATURE. Gradstein, S. R. 1994 (see family ref.). - Van Slageren, M. W. & R. Ch. Kruijt. 1985. A review of the genus *Blepharolejeunea*. Beihefte zur Nova Hedwigia 80: 113-145.

Brachiolejeunea (Fig. 38) - A New World genus (6 spp.), with 4 species widespread in tropical America and 2 additional species in temperate southern South America. The neotropical species belong to two different sections: sect. *Brachiolejeunea* (2 spp., including the common *B. laxifolia* (Taylor) Schiffn.), and sect. *Phyllorhizae* (2 spp., including the common *B. phyllorhiza* (Nees) Kruijt & Gradst.).

HABITAT. On bark and rock in rather open situations, at the margin and in the high canopy of lowland and montane forests, in scrubby vegetation and (lower) páramo, in orchards, on roadside trees, etc., 0-3500 m. The species of sect. *Brachiolejeunea* are exclusively montane (above 1000 m), those of the section *Phyllorhizae* also occur at lower elevations. The species are generally drought-tolerant, particularly *Brachiolejeunea phyllorhiza*, which is a characteristic species of roadside trees and orchards in lower montane regions of the Neotropics.

DESCRIPTION. **Plants** medium-sized, 6 cm long, 1-3 mm wide, green or brown, creeping or ascending, often forked. **Branches** *Frullania*-type or *Lejeunea*-type. **Stems** with a hyalodermis; ventral merophyte 4-8 cells wide. **Leaf lobes** wide-spreading and often squarrose, when dry convolute, apex rounded to short-acuminate, margins entire. **Cells** slightly longer than wide, trigones cordate; oil bodies homogeneous. **Lobules** 1/3-1/2 leaf length, never reduced, with 2-4(-10) teeth. **Underleaves** undivided, margins entire, bases decurrent, insertion line deeply arched. **Male bracts** just below the gynoecium or on a separate branch, with epistatic lobules. **Gynoecia** with 1-2 pycnolejeuneoid innovations. **Perianths** with 3(-4) keels, smooth or ciliate-laciniate and ± winged near apex. **Vegetative reproduction** not observed.

DISCUSSION. *Brachiolejeunea* is primarily characterized by the predominantly *Frullania*-type branching, the somewhat squarrose leaves with 2-4(-10)-toothed lobules, the weakly elongated leaf cells with cordate trigones and homogeneous oil bodies, and the gynoecia with winged bracts and 3-keeled perianths subtended by (1-)2 innovations. The species of sect. *Brachiolejeunea* are paroicous and have smooth perianth keels, those of sect. *Phyllorhizae* (*B. phyllorhiza* and *B. conduplicata* (Steph.) Gradst.) are autoicous - with androecia on short-specialized branches near gynoecia - and the perianth keels are winged-ciliate.

LITERATURE. Gradstein, S. R. 1994 (see family ref.). - Van Slageren, M. W. 1985. A taxonomic monograph of the genera *Brachiolejeunea* and *Frullanoides*. Meded. Bot. Mus. Herb. Utrecht 544: 1-309.

Dicranolejeunea (Fig. 38) - A monotypic, neotropical genus. The only species, *D. axillaris* (Nees & Mont.) Schiffn., has a somewhat restricted, montane distribution. It is very common in the Andes and in the Galapagos Islands, is more scattered in Central America and in the West Indies, and seems to be completely absent from the mountains of southeastern Brazil.

HABITAT. On bark and rock in humid, montane environments, usually in rather open, scrubby secondary habitats, at forest margins, and in the high canopy of the dense forest, (500-)1000-3200 m. It is a common invader of disturbed habitats and may grow in great abundance on isolated shrubs and rocks, along roads and in pastures, at mid-montane elevations. On the summit cone of the volcano "La Soufrière" on Guadeloupe, I found *D. axillaris* growing profusely on low shrubs, in vegetation recovering from destruction by volcanic eruption.

DESCRIPTION. **Plants** rather long and narrow, to 7 cm long, 1-2 mm wide, glossy light green to yellow-brown, creeping, ascending or pendent, often forked. **Branches** *Frullania*-type, rarely *Lejeunea*-type. **Stems** with a hyalodermis, epidermal cells bulging strongly outwards; ventral merophyte only 2 cells wide. **Leaf lobes** obliquely spreading and convex, when dry convolute, apex acute-acuminate, margins entire or toothed. **Cells** slightly longer than wide, trigones cordate or rounded; oil bodies finely granular. **Lobules** ca. 1/4-1/3 leaf length, occasionally reduced, with 2 teeth, second tooth smaller. **Underleaves** undivided, margins entire, bases decurrent, insertion line arched.

Male bracts just below the gynoecium, with epistatic lobules. **Gynoecia** with (1-)2 pycnolejeuneoid innovations, female bracteoles toothed. **Perianths** 3-keeled with a low, broad ventral keel, ciliate-laciniate near apex. **Vegetative reproduction** not observed.

DISCUSSION. *Dicranolejeunea axillaris* is recognized by the brownish-green, laxly forked plants, obliquely spreading leaves with small lobules and ± toothed apex, widely spaced, orbicular underleaves, 2-celled ventral merophytes, and flattened ciliate-laciniate perianths with two long, repeatedly fertile innovations. The genus is closely related to *Acanthocoleus* but separated by the bulging stem epidermal cells, the toothed female bracteole, and the different growth form (see under *Acanthocoleus*).

LITERATURE. Gradstein, S. R. 1994 (see family ref.). - Kruijt, Ch. 1988. A monograph of the genera *Dicranolejeunea* and *Acanthocoleus*. Bryophytorum Bibliotheca 36: 1-135.

Lindigianthus (Fig. 38) - A monotypic, neotropical genus. The only species, *L. cipaconeus* (Gott.) Kruijt & Gradst., occurs at high elevations in the northern Andes and Costa Rica.

HABITAT. On bark, humic soil, litter, and on the rosette leaves of tree ferns (*Blechnum* sp.) in humid upper montane and subalpine scrub, at the edges of upper montane rain forests, and in *Sphagnum* bogs, always in very moist habitats, 2000-3500 m.

DESCRIPTION. **Plants** rather large, to 10 cm long, 1.5-3 mm wide, glossy brown, creeping, often forked. **Branches** *Lejeunea*-type or *Frullania*-type. **Stems** with a hyalodermis; ventral merophyte 4 cells wide. **Leaf lobes** wide-spreading with broadly recurved apex, when dry ± convolute, apex acute, margins entire or toothed. **Cells** subisodiametric, trigones radiate; oil bodies homogeneous. **Lobules** 1/3 leaf length, never reduced, with 2 teeth, second tooth smaller. **Underleaves** undivided, large, margins entire, recurved, insertion line deeply arched. **Male bracts** on a long branch (dioicous), with epistatic lobules. **Gynoecia** with 2 pycnolejeuneoid innovations. **Perianths** flat, smooth or toothed above. **Vegetative reproduction** not observed.

DISCUSSION. *Lindigianthus cipaconeus* is a robust, glossy brownish plant with strongly convex leaves having a broadly recurved, ± toothed apex and a large, 2-toothed lobule. The underleaves are very large, the underleaf margins are reflexed and entire, and the insertion line is deeply arched. The walls of stem- and leaf-cells are very thin (except for the radiate trigones and small intermediate thickenings) and colorless, without any trace of secondary pigmentation. The gynoecia have winged bracts and strongly flattened perianths (as in *Marchesinia*).The plants are unmistakable and cannot be confused with any other neotropical species of Lejeuneaceae.

LITERATURE. Gradstein, S. R. 1994 (see family ref.). - Kruijt, R. Ch. & S. R. Gradstein. 1985. A new genus of Lejeuneaceae from tropical America: *Lindigianthus* gen. nov. Beihefte zur Nova Hedwigia 80: 165-172.

Neurolejeunea (Fig. 39) - A neotropical genus of 4 species, mostly at low elevations. The species belong to two different sections: sect. *Neurolejeunea* (2 spp.) at rather low elevations in rain forest regions of northern South America, Central America, and the West Indies, and sect. *Aneurolejeunea* (2 spp., including the common *N. breutelii* (Gott.) A. Evans) widespread throughout the region.

HABITAT. On bark, leaves, rotten wood, and rock in lowland and montane rain forests and scrub, usually in rather open situations, e.g., at forest margin or in the canopy, 0-1500(-3000) m. The common *Neurolejeunea breutelii* is the only species occurring above 1500 m, ranging to 3000 m in the northern Andes.

DESCRIPTION. **Plants** small, 1-2 cm long, 0.7-1.5 mm wide, glossy olive-green to brown or black, creeping, often (bi)pinnate or forked. **Branches** *Lejeunea*-type. **Stems** simple, without enlarged epidermis; ventral merophyte 4-6 cells wide. **Leaf lobes** wide-spreading, when dry spreading or slightly convolute, sometimes with a row of ocelli, apex rounded, sometimes white-bordered, margins entire. **Cells** (sub)isodiametric, small, less than 20 µm long, walls with trigones or uniformly thickened, trigones obscure; oil bodies smooth to faintly granular. **Lobules** strongly inflated and flask-shaped, 1/5-1/2 leaf length, never reduced, with a long, curved tooth. **Underleaves** undivided, margins entire, insertion line straight to deeply arched. **Male bracteoles** limited to base of spike. **Gynoecia** with 2 pycnolejeuneoid innovations. **Perianths** with 2(-4) large auricles above. **Vegetative reproduction** not observed.

DISCUSSION. *Neurolejeunea* is readily recognized by the brown or blackish color of the plants, the lack of a stem hyalodermis, the bottle-shaped lobules which are often darker than the lobes and have a long and slender apical tooth, and the 3-keeled perianth with lateral keels expanded into auricles above. The hyaline papilla of the lobule is distal to the apical tooth, which technically represents the second tooth. The first tooth is lacking or rudimentary, except in *Neurolejeunea sastreana* Gradst. in which it is transformed into a large "papilla." A vitta composed of a row of ocelli characterizes the species of sect. *Neurolejeunea* (vitta lacking in sect. *Aneurolejeunea*).

Neurolejeunea is most closely related to *Stictolejeunea*, especially the *s*ubgen. *Leptostictolejeunea* (see there).

LITERATURE. Gradstein, S. R. 1994 (see family ref.).

Odontolejeunea (Fig. 39) - A small, primarily neotropical genus of 3 species, including *O. lunulata* (Weber) Schiffn., common and widely distributed throughout tropical America and also in East Africa, and *O. decemdentata* (Spruce) Steph. and *O. rhomalea* (Spruce) Steph., both with scattered distributions in rain forest areas of the Neotropics.

HABITAT. On living leaves and twigs in lowland and montane rain forests and in evergreen scrub, 0-2000(-3000) m. *Odontolejeunea decemdentata* and *O. rhomalea* are almost exclusively epiphyllous (or ramicolous) but *O. lunulata* may occasionally occur on bark, e.g., on the trunks and branches of trees.

DESCRIPTION. **Plants** small to medium-sized, 1-4 cm long, 0.8-3.5 mm wide, glossy green to brown, creeping. **Branches** *Lejeunea*-type, occasionally (robust vegetative shoots) *Frullania*-type. **Stems** with a hyalodermis; ventral merophyte only 2 cells wide. **Leaf lobes** wide-spreading, when dry irregularly crisped, ± convolute or revolute, apex rounded, margins sharply toothed. **Cells** (sub)isodiametric, trigones simple-triangular or cordate; oil bodies homogeneous or finely granular. **Lobules** 1/5-2/5 leaf length, occasionally reduced, with 1-6 teeth. **Underleaves** undivided, margins toothed or entire, bases decurrent and often folded, insertion line deeply arched. **Male bracts** on separate branches, with epistatic lobules. **Gynoecia** with or without 1(-2) pycnolejeuneoid innovations. **Perianths** 3-keeled with a low ventral keel, conspicuously winged and ciliate-laciniate above. **Vegetative reproduction** by cladia.

DISCUSSION. *Odontolejeunea* differs essentially from the other genera of Brachiolejeuneae in its asexual reproduction by means of "cladia." The morphology of the cladia varies among the 3 species of *Odontolejeunea* and provides a useful means of identification. Further characteristic features of the genus include the toothed leaves, the very large epidermal cells (to 5 times larger than the medullary cells), the 2-celled ventral merophytes, the dentate-ciliate perianths, and the predominant occurrence of the plants on living leaves and twigs. Large, adhesive rhizoid discs, characteristic of epiphyllous Lejeuneaceae, are frequently produced; they are an adaptation to growth on leaves and are lacking in plants growing on bark. A notable feature of *Odontolejeunea* is the occurrence within the genus of two types of oil bodies: homogeneous (*O. lunulata*) and segmented (*O. decemdentata*).

LITERATURE. Gradstein, S. R. 1994 (see family ref.).

Stictolejeunea (Fig. 39) - A small pantropical genus (3 spp.), with 2 species in tropical America, *S. squamata* (Willd. ex Weber) Schiffn. (subgen. *Stictolejeunea*) common and widespread in the region, and *S. balfourii* (Mitt.) E.W. Jones (subgen. *Leptostictolejeunea*) scattered in northern South America and Central America.

HABITAT. On bark, living leaves, and rock in the shaded understory of moist lowland and lower montane rain forests, 0-1500(-2400) m. *Stictolejeunea balfourii* is the most hygrophytic of the two neotropical species and occurs on rock or wood in creeks in very humid, ± primary lowland rain forest (0-500 m); it is a rather inconspicuous species and has been much overlooked. *Stictolejeunea squamata*, on the other hand, is a much more common and conspicuous plant that may be creeping or pendent, often forming large garlands on twigs and branches in the forest understory. Both species occur primarily in undisturbed rain forests.

DESCRIPTION. **Plants** small to large, 1-15 cm long, 1-3 mm wide, pale- to dark-green, brown or black with age, creeping, ascending or pendent, often (bi)pinnate. **Branches** *Frullania*-type or *Lejeunea*-type. **Stems** with or without a brown cortex of small, thick-walled cells in 1-3 layers surrounding a colorless medulla of thin-walled cells; ventral merophyte 4-18 cells wide. **Leaf lobes** wide-spreading, little altered when dry, with scattered ocelli, apex rounded, margins entire, often white-bordered. **Cells** (sub)isodiametric, walls uniformly thickened; oil bodies absent in green cells. **Ocelli** numerous, scattered in leaves, underleaves, bracts, bracteoles and perianths. **Lobules** small, to 1/4 leaf length, sometimes reduced, straight or curved backwards, with 0-4 teeth. **Underleaves** undivided, margins entire, sometimes white-bordered, insertion line straight to deeply arched. **Gametoecia** on very short branches. **Male bracteoles** limited to base of spike. **Gynoecia** without innovations or with one short, pycnolejeuneoid innovation. **Perianths** with 2 large auricles above, margins of the auricles sometimes white-bordered. **Vegetative reproduction** not observed.

DISCUSSION. *Stictolejeunea* is a very well-defined genus, with many diagnostic features. It is the only genus of the Brachiolejeuneae with scattered ocelli in leaves and underleaves. Scattered ocelli are more common in genera of the tribe Lejeuneae (*Physantholejeunea*, *Lepidolejeunea*, *Luteolejeunea*, *Pictolejeunea*) but these have stems with a distinct hyalodermis and a ventral merophyte of only 2 cells wide (4 cells wide in *Lepidolejeunea eluta*; this species has bifid

underleaves, however). In *Stictolejeunea*, enlarged epidermal cells are lacking and the ventral merophyte is at least 4 cells wide.

Further characteristic features of *Stictolejeunea* are the small, evenly thickened leaf cells, the frequent presence on leaves and perianths of whitish borders, consisting of dead cells, and the auricled perianths. Robust forms of *S. squamata* have a 2-layered subepidermis of very thick-walled cells, but in small, creeping plants the subepidermis is not produced. The presence of vegetative branches of the *Lejeunea*-type (instead of *Frullania*-type) and the orbicular (instead of reniform) underleaves separate subgen. *Leptostictolejeunea* from subgen. *Stictolejeunea*.

Stictolejeunea is most closely related to *Neurolejeunea*. The two differ in quite a number of features, however, including the presence of blackish pigmentation, the sharply toothed lobules, the elongated gynoecial shoots, the paired innovations, the presence of oil bodies in green cells, and the lack of scattered ocelli in *Neurolejeunea*.

LITERATURE. Gradstein, S. R. 1994 (see family ref.).

Symbiezidium (Fig. 40) - A small, primarily neotropical genus, with 3 species at rather low elevations in tropical America: the widespread *S. barbiflorum* (Gott.) A. Evans and *S. transversale* (Sw.) Trevis., and *S. dentatum* Herzog along the wet Pacific coast of northern South America and Central America. A fourth species, *S. madagascariensis* Steph., occurs in Madagascar and the Seychelles. The latter is morphologically very different from the neotropical species and has been placed in a separate subgenus, *Eosymbiezidium*.

HABITAT. On bark and living leaves in the understory and the canopy of lowland and montane rain forests, 0-1500(-2800) m. *Symbiezidium barbiflorum* has the largest distributional range and is the only species occurring above 1500 m, ranging to 2800 m in the Andes.

DESCRIPTION. **Plants** usually large, to 15 cm long, 2-5 mm wide, green to brown, creeping to pendent. **Branches** *Lejeunea*-type, sometimes *Frullania*-type. **Stems** with a hyalodermis, epidermal cells thick-walled; ventral merophyte 4-8 cells wide. **Leaf lobes** wide-spreading, little altered when dry, apex rounded to apiculate, margins entire, rarely toothed near apex. **Cells** isodiametric, trigones triradiate; oil bodies large, homogeneous. **Lobules** strongly inflated, ball-shaped, small, 1/10-1/4 leaf length, never reduced, with 0-1 tooth. **Underleaves** undivided, large, 4-10x stem width, margins entire, insertion line deeply arched. **Male bracteoles** limited to base of spike. **Gynoecia** on very short branches, without innovations or with 1 short, pycnolejeuneoid innovation. **Perianths** ± flat, ciliate-laciniate. **Vegetative reproduction** not observed.

DISCUSSION. The neotropical species of *Symbiezidium* are robust plants with elongated, oblong leaves, large underleaves (4-10x stem width) with deeply arched insertions, and small, strongly inflated lobules hidden behind the large underleaves. The genus closely resembles *Marchesinia* when sterile, but the latter has very different, rather flat and conspicuously toothed lobules; in *Symbiezidium* the lobules have no teeth or only an obscure one. Female plants of *Symbiezidium* are unmistakable in the ciliate-laciniate perianths, inserted on very short lateral branches and partially or entirely hidden behind the vegetative leaves. The leaf margins are usually entire, except in the rare, Pacific coastal *S. dentatum* which has toothed leaf apices.

LITERATURE. Gradstein, S. R. 1994 (see family ref.).

LEJEUNEACEAE Tribe LEJEUNEAE

Plants usually small and pale green, sometimes deep green or brown. Stems usually thin and fragile, with or without hyalodermis; ventral merophyte 2 cells wide, rarely broader. Branches ± exclusively *Lejeunea*-type; *Frullania*-type lacking. Leaf insertion long and J-shaped, occasionally very short. Cells usually (sub)isodiametric; ocelli present or absent. Lobule usually with only 1 tooth and with the hyaline papilla attached to a margin cell. Underleaves mostly bifid, sometimes undivided. Androecia on short-specialized branches, male bracteoles restricted to the base of the spike or (occasionally) present throughout, male bract lobules large, hypostatic. Perianths inflated or flattened, with 0-2 ventral keels. Seta articulate, of only 12 outer rows of cells and 4 inner rows. Capsule valves suberect after dehiscence, pale, outer layer with nodulose wall thickenings or ± thin-walled, inner layer with nodulose thickenings. Elaters few, 14-34 per capsule, upper ends attached to valve margins only, spiral rudimentary, pale. Spores elongate-rectangular, usually without rosettes.

DISCUSSION. The largest tribe of the Lejeuneaceae, containing about 65 genera worldwide; 42 are accepted here for tropical America. The neotropical reports of *Tuyamaella*, an Asiatic genera of the tribe Lejeuneae, is probably erroneous and is excluded here. The genus has been recorded from Peru (Revue Bryologique et Lichénologiqe 39: 235. 1974) based on an old specimen with an incomplete label, lacking locality and collector. Since there are no further collections of *Tuyamaella* from outside Asia, it is very likely that the label of the "Peruvian" specimen is erroneous.

The Lejeuneae are defined here in a broad sense, including genera with both long and short leaf insertions. The latter are sometimes placed in separate subfamilies (Myriocoleoideae resp. Tuyamaelloideae).

Amblyolejeunea (Fig. 40) - A monotypic, neotropical genus, with *A. fulfordiae* Jovet-Ast known only from Guadaloupe, West Indies.

HABITAT. On bark of trees and humus in partial shade, e.g., at forest margin, at low elevations, below 1000 m.

DESCRIPTION. **Plants** small, to 1 cm long, ca. 1-1.3 mm wide, light green to yellowish, creeping. **Stems** with hyalodermis; ventral merophyte 2 cells wide. **Leaf lobes** wide-spreading, convex, apex rounded, margins slightly crenulate due to swollen marginal cells. **Cells** with small trigones, cuticle smooth or finely verruculose; oil bodies unknown, ocelli lacking. **Lobules** 2/5 leaf length, never reduced, inflated below, flattened to apex, free margin plane, apex truncate, with a blunt, 1-celled tooth, apical margin of enlarged cells, hyaline papilla proximal. **Underleaves** undivided, orbicular, insertion line straight. **Gynoecia** on long shoots, with 1-2 lejeuneoid innovations. **Perianths** inflated-cylindrical, without keels, apex depressed, navel-like, without beak. **Vegetative reproduction** not observed.

DISCUSSION. *Amblyolejeunea fulfordiae* may be recognized by the undivided underleaves, the large, truncate lobule with a blunt apex and an apical margin of enlarged cells, and the completely smooth, cylindrical perianth, without keels and lacking a beak. It is similar to *Oryzolejeunea*, but the latter has a distal hyaline papilla and keeled perianths on short branches.

LITERATURE. Jovet-Ast, S. 1948. Hépatiques des Antilles françaises. Revue Bryologique et Lichénologique 17: 24-34.

Amphilejeunea (incl. *Cryptogynolejeunea*) (Fig. 40) - A neotropical genus of 5-6 species, including *A. reflexistipula* (Lehm. & Lindenb.) Gradst. widespread at rather low elevations in tropical South America, and 4 species of high elevations in the northern Andes and Costa Rica.

HABITAT. On twigs and branches in the high canopy and at the margins of lowland and montane rain forests, and in low, scrubby vegetation in montane regions and páramo, in rather exposed and usually very humid habitats, 100-4150 m. Most of the species occur above 1500 m, with the exception of *A. reflexistipula* (see above).

DESCRIPTION. **Plants** small to medium-sized, 0.5-4 cm long, (0.5-)1-2.5 mm wide, bright green to yellow, creeping, often forming small, dense cushions. **Stems** with hyalodermis; ventral merophyte 2 cells wide. **Leaf lobes** wide-spreading, convex, apex rounded, margins crenulate. **Cells** with small, concave-sided trigones and intermediate thickenings, cuticle smooth or minutely papillose; oil bodies very small and numerous, 12-40 per cell, homogeneous, sometimes with a few septa; ocelli lacking. **Lobules** 1/6-1/2 leaf length, sometimes reduced, conspicuously inflated along the keel, flattened towards the free margin, apex oblique, with 1(-2) obscure, blunt, 1-celled teeth, hyaline papilla proximal, marginal or somewhat entally displaced. **Underleaves** undivided, orbicular to reniform, margin plane or recurved, insertion line curved to deeply arched. **Gynoecia** on long shoots or on short branches, with 1-2 lejeuneoid innovations. **Perianths** 4-5-keeled, sometimes longly stipitate. **Vegetative reproduction** not observed.

DISCUSSION. *Amphilejeunea* is related to *Lejeunea* but the underleaves are undivided instead of bifid. They are typical twig epiphytes that may grow scattered among other hepatics or in pure, bright-green, somewhat spongy cushions. In some species, the perianths are on long shoots with 2 innovations, in others they are on short branches with only one innovation. The latter are sometimes placed in a separate genus, *Cryptogynolejeunea* (Schuster, 1994), which is included here in *Amphilejeunea*. The following new combination is therefore necessary: **Amphilejeunea reflexistipula** (Lehm. & Lindenb.) Gradst., **comb. nov.** (*Jungermannia reflexistipula* Lehm. & Lindenb., in Lehmann, Pugillus 5: 10. 1833; *Cryptogynolejeunea reflexistipula* (Lehm. & Lindenb.) Schust.). A second species, *Cryptogynolejeunea costaricensis* (Steph.) Schust. seems to be a robust, high-altitude form of *Amphilejeunea reflexistipula*.

LITERATURE. Schuster, R. M. 1987. Venezuelan Hepaticae IV. *Amphilejeunea* and *Aureolejeunea* Schust. Nova Hedwigia 44: 1-23. - Schuster, R. M. 1994. Studies on Lejeuneaceae, I. Preliminary studies on new genera of Lejeuneaceae. Journal of the Hattori Botanical Laboratory 75: 211-235 [*Cryptogynolejeunea*].

Anoplolejeunea (Fig. 41) - A monotypic, neotropical genus, with *A. conferta* (Meisn.) Schiffn. common and widespread at higher elevations in tropical America

HABITAT. A typical canopy epiphyte of trunks, branches, and fine twigs in montane forests and scrubby vegetation to the páramo, always in rather sunny but humid environments, (0-)600-3700 m. In

dense forests, the species occurs at the forest margin or in the high canopy and avoids the shaded interior.

DESCRIPTION. **Plants** small, to 1-2 cm long, 1-1.5 mm wide, pale whitish-green to pale brown, creeping. **Branches** often microphyllous. **Stems** with hyalodermis; ventral merophyte 2 cells wide. **Leaf lobes** wide-spreading, convex, apex rounded, margins entire. **Cells** with small, concave-sided trigones; oil bodies finely granular, ocelli occasionally present, 1-3 at leaf base. **Lobules** ca. 1/3-2/5 leaf length, highly inflated with strongly inrolled margin, occasionally reduced, tooth obscure, hyaline papilla distal. **Underleaves** undivided, broadly obovate-obcuneate, apex rounded to truncate, insertion line slightly curved. **Gynoecia** on elongated shoots or short branches, with 1(-2) pycnolejeuneoid innovations. **Perianths** sharply 5-keeled above. **Vegetative reproduction** not observed.

DISCUSSION. *Anoplolejeunea* is recognized by its highly inflated lobule with the free margin strongly rolled inwards into the sac. The inrolled margin inside the lobule can easily be observed under low magnification. The very pale whitish-green color of the plants, the undivided underleaves, and the frequent presence of microphyllous branches are also characteristic of the genus. Ocelli are normally absent but have been observed in material from Jamaica (Evans, 1908).

LITERATURE. Evans, A. W. 1908. Hepaticae of Puerto Rico IX. Bulletin of the Torrey Botanical Club 35: 155-179.

Aureolejeunea (Fig. 41) - A New World genus (5-6 spp.), with 4 species at high elevations in tropical America, primarily in the northern Andes, also in Mexico, Costa Rica, the Guayana Highland (Mt. Roraima), and southeastern Brazil. Additional species occur in southern Chile (*A. lumae* (Herzog) van Slageren) and on St. Helena (*A. rotalis* (Hook. f. & Taylor) Gradst. & Geissler).

HABITAT. On twigs and branches in scrubby páramo and in the high canopy and at the edges of upper montane cloud forests, always in very humid and rather exposed habitats, (2000-)2500-4200 m.

DESCRIPTION. **Plants** small to medium-sized, 1-5 cm long, 1-2.5 mm wide, usually glossy brown, sometimes orange-brown or reddish-brown, green in shade, creeping to ascending. **Stems** rigid, brown, of thick-walled cells, epidermis not enlarged; ventral merophyte 2-4 cells wide. **Leaf lobes** wide-spreading, convex, apex rounded to subacute, margins often crenulate. **Cells** often mammillose, strongly thick-walled with large, sometimes coalesced trigones, walls brownish, intermediate thickenings lacking; oil bodies large, 2-4 per cell, coarsely granular; ocelli lacking. **Lobules** rather large, 2/5-1/2 leaf length, rectangular, conspicuously inflated along the keel, flattened towards the free margin, apex blunt or with a 1-3-celled, obtuse tooth, hyaline papilla distal. **Underleaves** large, undivided, suborbicular to reniform, margins often recurved, insertion line deeply arched. **Gynoecia** on long shoots, with (1-)2 lejeuneoid innovations. **Perianths** with 3-10 keels, sometimes almost eplicate. **Vegetative reproduction** not observed.

DISCUSSION. The glossy brownish color of the plants, the large, rectangular lobules with a distal papilla, the cells with very large, swollen trigones and no trace of intermediate thickenings, and the perianths with paired lejeuneoid innovations, serve to distinguish this high-montane genus from other lejeuneoid genera with undivided underleaves. All the neotropical species are páramo plants with the exception of *A. fulva* Schust., which is a species of montane forests.

LITERATURE. Gradstein, S. R. 1990. A key to the New World species of holostipous Lejeuneaceae. Tropical Bryology 3: 45-57 [key to 4 spp.]. - Schuster, R. M. 1987. Venezuelan Hepaticae IV. *Amphilejeunea* and *Aureolejeunea* Schust. Nova Hedwigia 44: 1-23 [key to 4 spp.].

Bromeliophila (Fig. 41) - A neotropical genus of 2 species, *B. natans* (Steph.) Schust. along the atlantic coast of southeastern Brazil and *B. helenae* Gradst. in the Guayana Highland (Macizo del Chimantá) and the Lesser Antilles (Dominica).

HABITAT. *Bromeliophila* is unique among hepatics in its exclusive occurrence in the water-filled leaf axils ("tanks") of Bromeliaceae. Among mosses, only the rare genus *Philophyllum* (Leucomiaceae) has the same habitat. The two species of *Bromeliophila* are apparently restricted to terrestrial bromeliads growing in rather open environments. *Bromeliophila natans* is a lowland species (0-800 m) and has been found in the leaf axils of *Vriesea glutinosa*, *Aechmea nudicaulis*, and *Quesnelia arvensis*, growing in open habitats in rain forest areas on sandy soils. *Bromeliophila rotundata*, on the other hand, is a montane species (800-2200 m); in the Guayana Highland it was found growing in wet, swampy savanna in the leaf axils of *Brocchinia hechtioides*.

DESCRIPTION. **Plants** 1.5-2 mm wide, pale yellow-green, turning dark brownish to black when dry, creeping or floating in water. **Stems** with hyalodermis; ventral merophyte 2 cells wide. **Leaf lobes** laxly inserted and wide-spreading, with a long insertion line (11-16 cells long), narrowly oblong to linear-lanceolate in outline, sometimes shorter, broad-ovate, apex rounded or acuminate, plane or recurved, margins ± sinuate to crenulate. **Cells** in narrowly elongated leaves 50-70 x 15-40 µm, ca. 1.5-4 as long as wide, in broad-ovate leaves shorter, completely thin-walled, without trigones, cuticles smooth; oil bodies unknown; ocelli lacking. **Lobules** very short, with long insertion line (9-10 cells),

with (1-)2(-3) short, blunt teeth, hyaline papilla proximal to the first tooth. **Underleaves** rather small, bifid, tips rounded or obtuse. **Autoicous**, with numerous short male branches and some female branches side by side. **Male branches** linear, with 3-10(-20) pairs of bracts. **Female branches** short or long, with or without 1(-2) sterile lejeuneoid innovations. **Perianths** inflated, 5-keeled, the keels undulate and broadly 2-winged, perianth base stalked. **Vegetative reproduction** unknown.

DISCUSSION. *Bromeliophila* is easily recognized by the peculiar, long and narrow leaves, to 4 times as long as wide, with a very long insertion line of both lobe and lobule (to 3/4 the width of the leaf) and conspicuously elongated cells. Plants with shorter, ovate leaves and shorter cells occur as well, however, and these become very similar to *Lejeunea*. The plants are usually copiously fertile, with numerous slender male spikes and some female branches occurring side by side on the stem. The gametoecial arrangement and the long leaf-insertion are also characteristic of *Potamolejeunea* and other aquatic Lejeuneaceae, and may be adaptations to aquatic habitats.

LITERATURE. Gradstein, S. R. 1997. *Bromeliophila helenae*, a new species of Lejeuneaceae from the Neotropics. Cryptogamie, Bryologie et Lichénologie 18: 217-221. - Schuster, R. M. 1994. Studies on Lejeuneaceae, I. Preliminary studies on new genera of Lejeuneaceae. Journal of the Hattori Botanical Laboratory 75: 211-235.

Ceratolejeunea (Fig. 42) - A pantropical genus (ca. 30 spp.), with about 20 species at rather low elevations in tropical America. The genus is subdivided into 3 subgenera (see below).

HABITAT. On bark and living leaves in the understory and the canopy of lowland and montane rain forests, at forest margin and in scrubby vegetation, 0-2000(-3000) m. Also on rock. Most of the species occur below 1000 m but *C. spinosa* (Gott.) Steph. is often abundant in cloud forests. *Ceratolejeunea cornuta* (Lindenb.) Steph. is the most common species and thrives in the high canopy of the dense forest as well as in secondary forests, plantations, and on isolated trees and shrubs. .

DESCRIPTION. **Plants** small to medium-sized, 1-5 cm long, 0.5-2 mm wide, glossy greenish-brown to dark brown, creeping to ascending or pendent. **Stems** with hyalodermis; ventral merophyte 2 cells wide. **Leaf lobes** wide-spreading, apex rounded to acute, margins entire or toothed. **Cells** with elongated, triradiate trigones or uniformly thick-walled, the walls pale brown with darker brown middle lamellae, cuticle smooth, rarely bulging and tuberculate; oil bodies small, finely granular; ocelli present or absent, when present 1-10 at the base or in the lower half of the leaf, sometimes in a short row, rarely present in the underleaves. **Lobules** 1/6-1/3(-1/2) leaf length, sometimes reduced, inflated, ovate to globose (elongated, flask-shaped in *C. patentissima)*, at the base of branches sometimes much enlarged ("utricle"), apical tooth 1-celled, the cell short and obtuse or long and sharp, hyaline papilla proximal. **Underleaves** bifid or undivided (subgen. *Ceratophora*), small or large, insertion line shallowly curved to deeply arched. **Gynoecia** on long or short branches, with 1-2 pycnolejeuneoid innovations. **Perianths** normally with 4 keels which are extended above into narrow, horn-like or bulbous projections. **Vegetative reproduction** by caducous leaves in subgen. *Caduciloba*.

DISCUSSION. *Ceratolejeunea* is characterized by the glossy brown color of the plants, the pale brownish cell walls with a dark brown middle lamella and triradiate trigones or a continuous sheath of thickening, and by the striking, horn-like projections of the perianths. These projections may be narrow-tubular and very long (to almost as long as the perianth), or swollen and short-bulbous; in a very few species they are rudimentary, occurring as low crests. The huge lobules at the branch bases ("utriculi"), present in many species, are a further distinctive feature of the genus; they are otherwise known only in *Pluvianthus* and *Microlejeunea cystifera* Herzog. Ocelli are commonly present at leaf bases or in the lower half of the leaf (sometimes absent); in *C. grandiloba* J. B. Jack & Steph. they are even present in the underleaves (R. Grolle, pers. comm.). Many species have toothed leaf margins.

The taxonomy of *Ceratolejeunea* is poorly known and the keys referred to below may sometimes be confusing or contradictory. The genus is provisionally subdivided into 3 subgenera (Schuster, 1980): subgen. *Ceratolejeunea* (ca. 15 spp.) with bifid underleaves, subgen. *Ceratophora* (3-4 spp.) with undivided underleaves (Grolle, 1987), and subgen. *Caduciloba* (2 spp.) characterized by caducous leaf lobes, flask-shaped lobules, and bifid underleaves. A revision of the genus *Ceratolejeunea* in tropical America by G. Dauphin is in preparation.

LITERATURE. Fulford, M. H. 1945. Studies on American Hepaticae IV. *Ceratolejeunea*. Brittonia 5 (4): 368-403 [key to 19 spp.]. - Grolle, R. 1987. *Ceratolejeunea* subgen. *Ceratophora* Schust. In: W. Frey (ed.), Moosflora und -vegetation in Regenwäldern NO-Perus. Beihefte zur Nova Hedwigia 88: 91-92 [key to 4 spp.]. - Onraedt, M. 1989. Contribution à la flore bryologique de Guyane Française. IV. Cryptogamie, Bryologie et Lichénologie 10: 119-129 [key to 9 spp.]. - Schuster, R. M. 1980. *Ceratolejeunea*. The Hepaticae and Anthocerotae of North America, Vol. IV: 909-929. [key to subgenera and 3 spp.].

Cheilolejeunea (Fig. 42) - A large pantropical genus (ca. 60-70 spp.), with about 20 species in tropical America, in three subgenera: *Cheilolejeunea* (1-3 spp.), *Euosmolejeunea* (ca. 10 spp.), and

Strepsilejeunea (7-8 spp.). Some of the species are among the most common neotropical members of the Lejeuneaceae.

HABITAT. On bark in the canopy of lowland and montane forests, at forest margin, in scrubby vegetation, in plantations, and on isolated trees, usually in rather open, sunny environments, 0-4300 m. Also on rock and occasionally on soil.

Species of subgenera *Cheilolejeunea* (e.g., *C. adnata* (Kunze) Grolle) and *Euosmolejeunea* (e.g., *C. rigidula* (Mont.) Schust., *C. trifaria* (Reinw. *et al.*) Mizut.) are common at low elevations, those of subgen. *Strepsilejeunea* (e.g., *C. inflexa* (Hampe ex Lehm.) Grolle, *C. oncophylla* (Ångstr.) Grolle & E. Reiner) mostly occur in montane regions. Species of upper montane forests and páramos all belong to *Strepsilejeunea*.

Cheilolejeunea rigidula and *C. trifaria* are the most common species of *Cheilolejeunea* in tropical America and abound in undisturbed and disturbed lowland rain forests, in orchards, plantations, etc.; *C. inflexa* is a characteristic species of montane cloud forests.

DESCRIPTION. **Plants** small to medium-sized, 1-4 cm long, 0.5-2.5 mm wide, rather dull pale green to olive green to brown, creeping to ascending, rarely pendent. **Stems** usually with enlarged epidermis, cells ± thick-walled; ventral merophyte 2(-6) cells wide. **Leaf lobes** wide-spreading, apex rounded to acute, plane or recurved, margins entire or sinuate with mammillose or tuberculate cells. **Cells** plane, mammillose or bulging with a broad, lenticular papilla, trigones small to large, intermediate thickenings scarce; oil bodies very large, 1-3 per cell, sausage-shaped, coarsely granular; ocelli lacking. **Lobules** small, 1/10-1/3 leaf length, ovate, rather strongly inflated with inflexed free margin, constricted at the apex, keel sometimes with large papillae (*C. inflexa*), apical tooth 1-celled, the cell short and obtuse or long and sharp, hyaline papilla distal. **Underleaves** small or large, bifid, rarely undivided, margins entire, insertion line shallowly curved to arched. **Gynoecia** on long or short shoots, with (0-)1(-2) lejeuneoid (rarely pycnolejeuneoid) innovations. **Perianths** with 4-5 smooth keels. **Vegetative reproduction** rare, by caducous leaves in *C. adnata*.

DISCUSSION. The species of subgenus *Strepsilejeunea* are immediately recognized by the reflexed, acute or obtuse leaf apices. They are mostly robust plants of high elevations and the leaf cells often have very large trigones. In *C. inflexa,* the keel of the leaves is covered by huge papillae.

Plane, rounded leaf apices are characteristic of subgenera *Euosmolejeunea* and *Cheilolejeunea*. Members of subgen. *Cheilolejeunea* are small, delicate, deep green plants of low elevations, with thin-walled cells and a long, sharp lobule tooth. Those of subgen. *Euosmolejeunea* are more olive-green or brown, the cells usually have conspicuous trigones, and the lobule tooth is short and blunt. Members of these two subgenera may sometimes be confused with *Lejeunea* and other genera. Differences from *Lejeunea* include the duller color in *Cheilolejeunea*, the usually larger trigones (small in subgen. *Cheilolejeunea*), the much larger and more coarsely segmented oil bodies, the thick-walled stem cells without hyaloderm, and the strongly inflated lobules, which are never reduced and have a distal hyaline papilla. The distal papilla also separates *Cheilolejeunea* from other genera that may be similar, e.g., *Pycnolejeunea* and *Pluvianthus*. The papilla is positioned in a small sinus beyond the apex of the lobule and is very small; in dried material it is often collapsed. When the papilla is lacking, the presence or absence of a small sinus distal to the tooth may be helpful in ascertaining the characteristic distal position of the papilla.

The underleaf apex is normally bifid in *Cheilolejeunea* but in some undescribed South American species it is undivided. The latter plants are similar to *Leucolejeunea* but differ in the smaller lobule and the narrower ventral merophyte, which is 2 cells wide. The innovations in *Cheilolejeunea* are normally lejeuneoid but pycnolejeuneoid innovations have been observed in *C. acutangula* (Nees) Grolle and *C. discoidea* (Lehm. & Lindenb.) Kachroo & Schust. (= *C. myriantha* (Nees & Mont.) Schust.). The latter is the smallest neotropical species of the genus (plants ca. 0.5 mm wide) and somewhat resembles *Microlejeunea* and *Cyrtolejeunea*.

LITERATURE. Reiner-Drehwald, M.E. 1998. Las Lejeuneaceae (Hepaticae) de Misiones, Argentina. V. *Cheilolejeunea* y *Lepidolejeunea*. Tropical Bryology 14: 53-68 [key to 5 neotropical spp.]. - Schuster, R. M. 1980. *Cheilolejeunea*. The Hepaticae and Anthocerotae of North America, Vol. IV: 848-909 [key to 5 neotropical spp.].

Crossotolejeunea (Fig. 43) - A neotropical genus with 11 species (Reiner-Drehwald & Goda, in prep.) at low and mid elevations.

HABITAT. On bark, living leaves, rotten wood and on rock in undisturbed or disturbed lowland and montane rain forests and in scrubby vegetation, usually in humid environments, from sea level to about 3000 m.

DESCRIPTION. **Plants** rather small, 0.7-1.5 mm wide, pale yellowish green, usually glossy and pellucid, creeping. **Stems** with hyalodermis, ventral merophyte 2 cells wide. **Leaf lobes** spreading, apex apiculate or acute-acuminate, plane or recurved, margins ± crenulate to slightly toothed, rarely entire. **Cells** plane, usually with well-developed trigones, cuticle smooth or finely papillose; oil bodies

small or large, finely to rather coarsely granular, sometimes numerous in basal leaf cells; ocelli lacking. **Lobules** to 1/3 leaf length, sometimes reduced, ovate, apical tooth short and blunt, hyaline papilla proximal. **Underleaves** small, deeply bifid, lateral margins sometimes with a tooth, insertion line shallowly curved. **Gynoecia** on long or short shoots, with 1-2 lejeuneoid innovations. **Perianths** inflated, with 5 (crenulate-)dentate to laciniate keels. **Vegetative reproduction** not observed.

DISCUSSION. *Crossotolejeunea* is closely related to *Lejeunea* and is now considered a synonym of the latter (E. Reiner-Drehwald, pers. comm.). The somewhat pointed leaf tips and the toothed perianth keels are the main features that separate *Crossotolejeunea* from *Lejeunea*; in the latter genus the leaf tips are typically rounded (except in subgen. *Otigoniolejeunea*) and the perianths are untoothed. In *Crossotolejeunea* there is often a tendency for the margins of leaves and bracts to become crenulate to somewhat toothed. In the type species, *C. boryana* (Mont.) Schiffn., the underleaves are very deeply bifid (to 2/3-3/4) with a wide sinus and very narrow lanceolate lobes, and the outer margins of the underleaves bear a conspicuous tooth.

LITERATURE. Reiner-Drehwald, M. E. and A. Goda (in prep.). Revision of the genus *Crosstolejeunea*. - Schuster, R. M. 1980. *Crossotolejeunea*. The Hepaticae and Anthocerotae of North America, Vol. IV: 1102-1113 [descr. of 1 sp.]. - Schuster, R. M. 1992. The oil bodies of the Hepaticae. II. Lejeuneaceae. Journal of the Hattori Botanical Laboratory 72: 163-359 [*Crossotolejeunea* on p. 273-276]. - Spruce, R. M. 1884. *Lejeunea* subgenus *Crossotolejeunea*. Hepaticae Amazonicae et Andinae. Transactions and Proceedings of the Botanical Society of Edinburgh 15: 161-164 [descr. of 3 spp.].

Cyclolejeunea (Fig. 43) - A neotropical genus of 6-7 species at low elevations throughout the region.

HABITAT. Mostly epiphyllous but also on bark or rock, in the understory and lower canopy of lowland and lower montane rain forest, in rather moist and shaded environments, 0-2000 m. *Cyclolejeunea convexistipa* (Lehm. & Lindenb.) A. Evans and *C. peruviana* (Lehm. & Lindenb.) A. Evans are very common epiphyllous hepatics in the Neotropics.

DESCRIPTION. **Plants** small, 0.8-2 mm wide, pale green to brownish, creeping. **Stems** with hyalodermis, ventral merophyte 2 cells wide. **Leaf lobes** wide-spreading, apex rounded or apiculate, margins finely crenulate to denticulate, dorsal lobe surface smooth or, in *C. accedens* (Gott.) A. Evans, elevated by large papillae (one per cell). **Cells** convex, with trigones and intermediate thickenings, cuticle smooth or with a large papilla; oil bodies small, finely granular, usually 2-4 per cell; ocelli 1-3 at lobe base, side by side, rarely absent (*C. accedens*). **Lobules** ca. 1/3 leaf length, ovate-inflated, free margin involute, with a short, 1-celled tooth, hyaline papilla proximal. **Underleaves** bifid or undivided (*C. convexistipa*), margins entire or toothed, insertion line curved. **Androecial bracteoles** restricted to the base of the spike or throughout. **Gynoecia** on short or long branches, with 1 pycnolejeuneoid innovation. **Perianths** flattened-pyriform, somewhat inflated ventrally and with 2 broad lateral keels expanded above into short auricles. **Vegetative reproduction** by means of multicellular, disciform gemmae, the gemmae orbicular, occasionally reniform or elongated (*C. luteola* (Spruce) Grolle).

DISCUSSION. *Cyclolejeunea* is one of the most common neotropical hepatic genera inhabiting living leaves. The species are usually not obligate epiphylls, however, and may also grow on other substrates. Characteristic of *Cyclolejeunea* are the rather broad leaves with rounded or short apiculate apices, the finely serrulate to denticulate margins of leaves and underleaves, the usual presence of 1-2(-3) ocelli at the base of the leaves, the flattened perianth with lateral keels expanded above into low auricles, and, especially, the vegetative reproduction by means of large, usually disciform gemmae produced on the leaf margins. As shown by Lücking (1999), the species may be recognized by the morphology of the gemmae.

In its serrulate leaf margins and auriculate perianth *Cyclolejeunea* resembles *Prionolejeunea*, but the latter lacks true ocelli and has a different leaf shape (leaf lobes abruptly dilated beyond the keel, from a very narrow base). Moreover, disciform gemmae are not produced in *Prionolejeunea*.

The underleaves in *Cyclolejeunea* are usually bifid, except in *C. convexistipa* which has undivided to emarginate underleaves and is easily recognized by this character. The tuberculate leaf cells (each provided with a large papilla) and the absence of ocelli are diagnostic features of *C. accedens* (Gott.) A. Evans.

LITERATURE. Bernecker-Lücking, A. 1998. The genus *Cycolejeunea* A. Evans in Costa Rica. Phyton 38: 175-193. - Evans, A. W. 1904. Hepaticae of Puerto Rico IV. Bulletin of the Torrey Botanical Club 31: 183-226 [descr. of 4 spp.]. - Grolle, R. 1984. Zur Kenntnis der Lejeuneoideae in Cuba (1): *Cyclolejeunea*. Wissenschaftliche Zeitschrift der Friedrich-Schiller-Universität, Jena, Naturwissenschaftliche Reihe, 33 (6): 759-764 [key to 5 spp.].

Cyrtolejeunea (Fig. 43) - A small neotropical genus of 2 species, *C. holostipa* (Spruce) A. Evans throughout tropical America and a new species with short bifid underleaves in southeastern Brazil and Bolivia.

HABITAT. On bark and occasionally on living leaves, in the understory and the high canopy of lowland and lower montane rain forests and in open, scrubby vegetation, ca. 100-2500 m.

DESCRIPTION. **Plants** very small, to 1 cm long, ca. 0.4-0.7 mm wide, bright green to yellow-brown, creeping. **Stems** zig-zag, with hyalodermis; ventral merophyte 2 cells wide. **Leaf lobes** suberect to obliquely spreading, strongly convex, apex rounded, margins entire. **Cells** with small, concave-sided trigones; oil bodies finely granular, ocelli absent. **Lobules** large, ca. 1/2 leaf length, strongly inflated, ovoid, with strongly arched keel, free margin ± straight from base to apex and inflexed, with a long and sharp, 1-celled tooth, hyaline papilla distal. **Underleaves** undivided or with a short and narrow incision (1-4 cells deep), orbicular, margins entire, insertion line straight. **Gynoecia** on elongated shoots, with 1 short, sterile pycnolejeuneoid innovation. **Perianths** sharply 5-keeled above. **Vegetative reproduction** not observed.

DISCUSSION. In its very small size, zig-zag stems, and little spreading leaves with large lobules, *Cyrtolejeunea* somewhat resembles *Microlejeunea*, but the ± undivided underleaves and the very long and sharp lobule tooth, consisting of a strongly elongated cell, separate it from the latter. Moreover, the hyaline papilla in *Cyrtolejeunea* is distal to the apical tooth, whereas in *Microlejeunea* it is proximal. The genus is much more closely related to *Cheilolejeunea*, from which it differs mainly in the finely granular and smaller oil bodies (huge and very coarsely segemented in *Cheilolejeunea*).

Oryzolejeunea, sometimes considered a subgenus of *Cyrtolejeunea*, is treated as a separate genus because of the very different, truncate lobule with a short blunt tooth, homogeneous to septate (rarely finely granular) oil bodies, and lejeuneoid instead of pycnolejeuneoid innovations.

LITERATURE. Evans, A. W. 1903. Hepaticae of Puerto Rico III. Bulletin of the Torrey Botanical Club 30: 544-563.

Cystolejeunea (Fig. 44) - A monotypic, neotropical genus, with *C. lineata* (Lehm. & Lindenb.) A. Evans in the West Indies and adjacent mainland areas of Mexico, Costa Rica, Panama, the Chocó region of Colombia, and Guyana (Mt. Roraima). In addition, there is a record from SE Brazil (São Paulo State).

HABITAT. On bark, rarely on living leaves, in the understory and the canopy of wet submontane and lower montane rain forests and cloud forest, from sea level to about 1000 m.

DESCRIPTION. **Plants** rather robust, 1-5 cm long, ca. 1.5-2.5 mm wide, dull pale to somewhat brownish, creeping to ascending to pendent. **Stems** with epidermis hardly enlarged, all cells ± thick-walled; ventral merophyte 2 cells wide. **Leaf lobes** wide-spreading, convex, apex rounded or obtuse-apiculate, plane or recurved, margins sinuate. **Cells** convex, usually bulging outwards as large, lenticular papilla, trigones large, swollen, intermediate thickenings very scarce, present in basal cells; oil bodies very large, 2-3 per cell, sausage-shaped, coarsely granular; ocelli lacking. **Lobules** ca. 1/3 leaf length, somewhat elongated and strongly swollen with inflexed free margin, keel making a sharp angle with the ventral leaf margin, apical tooth short, hidden inside the lobule, hyaline papilla probably proximal. **Underleaves** bifid, small, only about 2x stem width, insertion line shallowly curved. **Dioicous**. **Gynoecia** on very short branches (with only one pair of leaves) or on elongated branches, innovations absent; bracts with reduced lobules. **Perianths** flattened (ventral surface often slightly inflated due to the bulging sporophyte), without beak. **Vegetative reproduction** not observed.

DISCUSSION. *Cystolejeunea* is easily recognized by its strongly swollen lobules with completely involute free margin, bulging leaf cells with large trigones and a broad papilla (papilla sometimes lacking), and flattened perianths without beak. The rather loose, somewhat pendent growth of the plants, their large size, and pale and rather dull color, are characteristic features by which the plants can be recognized in the field. The lobule in *Cystolejeunea lineata* is somewhat similar to that of *Anoplolejeunea*, but the convex leaf cells with large trigones, the flattened perianths, the lack of innovations, and the rather large size of the plants immediately separate *Cystolejeunea* from *Anoplolejeunea*.

LITERATURE. Evans, A. W. 1906. Hepaticae of Puerto Rico VI. Bulletin of the Torrey Botanical Club 33: 1-25.

Dactylolejeunea (Fig. 44) - A monotypic, neotropical genus, with *D. acanthifolia* Schust. known from Cuba and Dominica.

HABITAT. Usually epiphyllous on fern fronds (also on bark) in submontane rain forest, 400-550 m.

DESCRIPTION. **Plants** very small, less than 1 cm long, 0.5-0.7 mm wide, light green, creeping. **Stems** with 7 outer and 3 inner cell rows, cells thin-walled, epidermis hardly enlarged; ventral merophyte 2 cells wide. **Leaf lobes** turned upwards away from the substrate, obovate-obcuneate with conspicuously narrowed base and with 4-6 ciliate teeth along the broad, upper portion of the lobe,

uniseriate portion of teeth 2-4 cells long, base of teeth 2-4 cells wide. **Cells** with small, concave-sided trigones, cuticle smooth; oil bodies small or large, finely granular; ocelli lacking. **Lobules** 1/3 leaf length, never reduced, very strongly inflated with arched keel and involute free margin, constricted at apex, apical tooth 1-celled, rather short, hyaline papilla proximal. **Underleaves** small, bifid with rather broad, U-shaped sinus and erect, acute lobes, insertion line straight. **Autoicous**. **Gynoecia** on short branches, with 1 short, lejeuneoid innovation. **Perianths** inflated, sharply 5-keeled above, the keels with stiff, laciniate teeth and short horn-like projections. **Vegetative reproduction** not observed.

DISCUSSION. *Dactylolejeunea* is recognized by thhe obcuneate leaves with long-ciliate teeth along the margins. The leaves are strongly narrowed to the base and stand somewhat upwards, away from the substrate. In the narrow-based leaves, *Dactylolejeunea acanthifolia* resembles *Drepanolejeunea,* but differs from the latter by the lack of ocelli, the straight instead of diverging underleaf lobes, and the lejeuneoid instead of pycnolejeuneoid innovations. According to Reiner-Drehwald & Goda (in prep.), *Dactylolejeunea* is a synonym of *Lejeunea* (subgen. *Crossotolejeunea*).

LITERATURE. Reiner-Drehwald, M. E. and A. Goda (in prep.). Revision of the genus *Crosstolejeunea*. - Schuster, R. M. 1970. Studies on Hepaticae, XLIX-LIII. New Lejeuneaceae from Dominica and Jamaica. Bulletin of the Torrey Botanical Club 97: 336-352.

Drepanolejeunea (Fig. 44) - A large pantropical genus (ca. 100 spp.), with about 30 species, in 8 sections (Schuster, 1996), at montane elevations in tropical America. The ranges of the species are often quite limited and some seem to be truly endemic, e.g., *D. valiae* Jovet-Ast (Guadeloupe), *D. senticosa* Bischl. (Cuba), *D. aculeata* Bischl. (southeastern Brazil), *D. integribracteata* Bischl. (upper Rio Negro, Brazil), *D. ramentiflora* Steph. (Costa Rica), and *D. spinosa* Herzog (western Colombia). Most of these endemics are known only from undisturbed forests and are considered to be endangered (Gradstein, 1992).

HABITAT. On living leaves, fine twigs, bark and rock in montane rain forests, occasionally in lowland forests or entering the páramo, always in regions of high humidity, (0-)500-3000(-4200) m. *Drepanolejeunea* is particularly common and speciose in montane forests; in lowland forests the genus is poorly represented and often absent. The species normally occur below 3000 m, except *D. andina* Herzog, *D. araucariae* Steph., *D. aurita* Bischl., *D. navicularis* Steph., and possibly a few undescribed ones which grow on fine twigs in subalpine woodlands and páramo in the Andes between 3000 and 4200 m. Species occurring in lowland forests include *Drepanolejeunea palmifolia* (Nees) Steph., a common and characteristic element of Amazonian lowland forests, *D. integribracteata*, endemic to the upper Rio Negro, and *D. crucianella* (Taylor) A. Evans, *D. fragilis* Bischl., and *D. orthophylla* (Nees & Mont.) Bischl. The latter three are typically lower montane species; in lowland forest they occur in areas where rainfall is very high, e.g., in the Chocó region and in the eastern part of the Guianas.

DESCRIPTION. **Plants** very small, to 1.5 cm long, 0.3-1(-1.3) mm wide, light green to pale brown, creeping. **Stems** of 7 outer cells and 3 inner cells, epidermal cells not or slightly enlarged, no hyalodermis, all cells ± thick-walled; ventral merophyte 2 cells wide. **Leaf lobes** suberect to rather wide-spreading, asymmetrically ovate-triangular to lanceolate, usually falcate, with ocelli, apex acute-acuminate, plane or recurved, margins crenulate to dentate, or entire. **Cells** with trigones, cuticle smooth or coarsely papillose; oil bodies finely granular. **Ocelli** colorless, (1-)2-4(-10) in a broken or unbroken row (rarely lacking), the basal ocellus not conspicuously enlarged. **Lobules** 1/3-1/2(-3/4) leaf length, occasionally reduced, inflated, apical tooth 1(-2)-celled, long-falcate and sharp, a "pre-apical" tooth sometimes present at the junction between lobule and ventral leaf margin, hyaline papilla proximal. **Underleaves** small, remote, bifid with very slender, diverging lobes, the lobes 2-4(-6) cells long and 1-3 cells wide, lamina without border, insertion line straight; adhesive rhizoid discs well-developed in epiphyllous plants. **Gynoecia** on short branches, with 1 pycnolejeuneoid innovation. **Perianths** inflated, 5-keeled above, the keels extending into toothed, horn-like projections or auricles. **Vegetative reproduction** by cladia.

DISCUSSION. The species of *Drepanolejeunea* are tiny plants, usually less than a millimeter wide (less than 0.5 mm wide in species with suberect leaves), with asymmetrically elongated, ovate-lanceolate, acute-acuminate leaves that are spreading or suberect and almost parallel to the stem, and often strikingly falcate. Furthermore, the perianths are always irregularly toothed-winged, the underleaf lobes are very slender and always conspicuously diverging, and the lobule tooth is long and falcate. In many species there is a second, "pre-apical" tooth at the junction between the lobe and lobule, which is usually curved backwards and, when long, may cross the apical tooth, thus creating a circular opening to the interior of the lobule.

In its diverging underleaf lobes *Drepanolejeunea* closely resembles *Leptolejeunea* and *Rhaphidolejeunea*, but the latter genera have broader, elliptical to obovate leaves that are widest in the middle or in the upper part of the leaf (widest near leaf base in *Drepanolejeunea*) and are often rounded at the apex. Moreover, *Leptolejeunea* and *Rhaphidolejeunea* are typical lowland genera

whereas *Drepanolejeunea* is primarily montane. In *D. andina*, *D. aurita*, and *D. navicularis* from high altitudes in the northern Andes, the underleaves have rather broad and plump lobes (2-4 cells wide), similar to those of *Harpalejeunea.* The latter genus, however, has lejeuneoid instead of pycnolejeuneoid innovations.

LITERATURE. Bischler, H. 1964. Le genre *Drepanolejeunea* Steph. en Amérique Centrale et Méridionale. Revue Bryologique et Lichénologique 33: 15-179 [key]. - Bischler, H. 1967. Ibid., Part II. Revue Bryologique et Lichénologique 35: 95-134. - Bischler, H. 1967. Ibid., Compléments. Revue Bryologique et Lichénologique 35: 135-137. - Gradstein, S. R. 1992b. Threatened bryophytes of the neotropical rain forest: a status report. Tropical Bryology 6: 83-93. - Schuster, R. M. 1996. Studies on Lejeuneaceae, II. Neotropical taxa of *Drepanolejeunea* (Spr.) Schiffn. Nova Hedwigia 62: 1-46 [Bischler's treatment supplemented].

Echinocolea (Fig. 45) - A small neotropical genus (3-4 spp.), with *E. asperrima* (Spruce) Schust. in northern South America (Amazon Basin, Guianas), *E. dilatata* (A. Evans) Schust. in the Caribbean and Central America (Costa Rica, Panama, ? Venezuela), and an undescribed species from Mt. Roraima, Guyana. A fourth species has been recorded from Cuba.

HABITAT. On bark and living leaves in the understory and lower canopy of undisturbed lowland and lower montane rain forest, always in very humid and shaded environments, 50-1500(-2500) m.

DESCRIPTION. **Plants** small, 1-2 cm long, 0.4-1 mm wide, dull pale green to whitish-green, creeping. **Stems** with hyalodermis; ventral merophyte 2 cells wide. **Leaf lobes** suberect to wide-spreading, from a narrow base rather abruptly dilated beyond the keel, apex broadly rounded, margins and dorsal surface of the leaf crenate-denticulate by conically projecting, mammillose cells, the projecting cell walls usually thickened. **Cells** thin-walled, trigones lacking or minute, cuticle smooth; oil bodies finely granular, brownish, only one per cell; ocelli lacking. **Lobules** ca. 1/3-2/5 leaf length, inflated, free margin involute, with a 1-celled tooth, hyaline papilla proximal, keel usually strongly arched. **Underleaves** small, 1-2x stem width, bifid, margins entire or denticulate, insertion line straight. **Androecial bracteoles** restricted to the base of the spike. **Gynoecia** usually on long or short branches, with 1-2 lejeuneoid innovations. **Perianths** inflated, with 5 denticulate and sometimes winged keels. **Vegetative reproduction** rare, by means of caducous leaves, cladia, or linear, thalloid gemmae from leaf margins.

DISCUSSION. *Echinocolea* is rather similar to *Prionolejeunea*. In both genera the plants are small and delicate, the leaves are rather abruptly dilated beyond the keel, the leaf margins are crenate-denticulate, the lobules are swollen with inflexed free margins, strongly arched keels, and a short tooth with a proximal papilla, the underleaves are deeply bifid, the cells are thin-walled with only one finely granular oil body, etc. In *Echinocolea*, however, the dorsal leaf surface is ± rough with conical, spinose mammillae, the leaf apex is always broadly rounded, the perianth is inflated and 5-keeled (instead of flattened and 2-keeled), and the innovations are lejeuneoid (in *Prionolejeunea* pycnolejeuneoid or absent).

Echinocolea asperrima is the smallest species of the genus, with plants barely 0.5 mm wide and both lobes and lobules strongly roughened. *Echinocolea dilatata* is a larger plant, to 1 mm wide, with less roughened leaf lobes and smooth lobules.

LITERATURE. Schuster, R. M. 1992. The oil bodies of the Lejeuneaceae. II. Lejeuneaceae. Journal of the Hattori Botanical Laboratory 72: 163-359 [*Echinocolea* on p. 314-316].

Haplolejeunea (Fig. 45) - An Afro-American genus (2 spp.), with *H. cucullata* (Steph.) Grolle in southeastern Brazil and the Guianas (Guyana, Suriname).

HABITAT. A typical shade epiphyte on the buttresses of large trees, dead trunks, or rotten logs in humid and dry-evergreen lowland rain forest, always in the understory of the forest in shaded, permanently moist conditions, 0-400 m. The species seems to be restricted to undisturbed, primary forest.

DESCRIPTION. **Plants** small, to 1 cm long, 0.5-0.7 mm wide, glistening pale green, creeping. **Stems** with hyalodermis; ventral merophyte 2 cells wide. **Leaf lobes** obliquely spreading, asymmetrically obovate-spathulate with strongly constricted base, insertion line short J-shaped, apex broadly rounded, plane, margins finely crenulate. **Cells** rather small, 15-25 µm long in leaf middle, walls with small trigones to ± uniformly thickened, cuticle smooth; oil bodies 1(-3) per cell, finely granular. **Ocelli** similar in size to other leaf cells, colorless, 4-10 (or more) scattered in the lobe, also present in the underleaves, bracts, and perianth. **Lobules** 1/3 leaf length, narrowly attached to the stem by only 2-3 cells, very strongly inflated, almost spherical, free margin inflexed, tooth lacking, hyaline papilla in a small notch at the apex. **Underleaves** small, ca. 2x stem width, narrowly bifid to 1/2, base of the lobes with 1-2 ocelli, insertion line straight. **Gynoecia** on short branches, with 1 short, sterile pycnolejeuneoid innovation. **Perianths** flattened pyriform, somewhat inflated ventrally and with 2

broad lateral keels that are expanded above into short auricles. **Vegetative reproduction** not observed.

DISCUSSION. *Haplolejeunea* is recognized by the very small, glistening, bright green plants with obovate leaves, which are conspicuously narrowed at base and attached to the stem along a very short insertion line. The lobules are very conspicuously swollen, with an inflexed free margin, and lack a discrete tooth at the apex. The hyaline papilla is located in a small notch at the apex and is, by consequence, neither distal or proximal. The scattered ocelli in leaves, underleaves, bracts, and perianths, the small, somewhat elongated and bluntly bifid underleaves, and the flattened, subauriculate perianths similar to those found in *Prionolejeunea*, are further diagnostic features of this peculiar genus.

LITERATURE. Grolle, R. 1975. *Haplolejeunea* aus Madagascar - eine weitere neue Gattung der Tuyamaelloideae. Journal of the Hattori Botanical Laboratory 39: 203-210. - Grolle, R. 1979. Miscellanea hepaticologica 181-190. Journal of the Hattori Botanical Laboratory 45: 173-183.

Harpalejeunea (Fig. 45) - A pantropical genus (20-25 spp.), with about 10-15 species in tropical America (Grolle & Reiner-Drehwald, 1999).

HABITAT. On bark, living leaves, and rotten wood in lowland and montane rain forest, semi-deciduous forests, in scrubby vegetation, and on shrubs in the lower páramo, from sea level to about 3800 m. Occasionally on rock. The species prefer somewhat exposed environments, in partial shade; in dense forests, *Harpalejeunea* spp. are more common in the canopy and in gaps than in the understory.

DESCRIPTION. **Plants** small, to 1.5 cm long, usually less than 1 mm wide (rarely broader), yellow-green to olive-brown to dark brown, creeping. **Stems** of thick-walled cells, without hyalodermis; ventral merophyte 2 cells wide. **Leaf lobes** suberect to rather wide-spreading, with ocelli, asymmetrically ovate-falcate, apex rounded to acute to piliferous and ending in a hair, plane or recurved, margins entire, toothed, or with a few cilia, sometimes margins and dorsal surface of the leaf crenate-denticulate by conically projecting, mammillose cells. **Cells** rather small, 15-25 µm in leaf middle, with trigones, cuticle smooth; oil bodies finely granular. **Ocelli** colorless, 1-3 in an unbroken row near leaf base, forming a short vitta, the basal ocellus not conspicuously enlarged. **Lobules** 1/3-1/2 leaf length, never reduced, strongly inflated and somewhat flask-shaped, keel strongly arched, usually forming a sharp angle with the ventral leaf margin, apical tooth 1-celled, long-falcate and sharp, a "pre-apical" tooth sometimes present at the junction between lobule and ventral leaf margin (as in *Drepanolejeunea*), hyaline papilla proximal. **Underleaves** emarginate to shallowly bifid (rarely undivided) with broad and obtuse diverging lobes and a wide sinus, insertion line straight; adhesive rhizoid discs lacking or rudimentary. **Gynoecia** on short or long branches, with 1-2 lejeuneoid innovations. **Perianths** inflated, sharply 5-keeled, the keels smooth or denticulate, never extending into horns. **Vegetative reproduction** not observed.

DISCUSSION. The main diagnostic feature of *Harpalejeunea* are the emarginate to shallowly bifid underleaves with broad and blunt, diverging lobes (rarely are the underleaves completely undivided, holostipous).The peculiar shape of the underleaf is correlated with several other important characteristics, such as the ovate-falcate leaves with acute-acuminate apex (rarely obtuse), the strongly inflated lobule with a sharp, falcate tooth, the presence of 1-3 ocelli in an unbroken row at the leaf base, and the lejeuneoid innovations. The leaves are usually smooth; in an exceptional case the dorsal leaf surface is roughened by conically elevated mammillae as in *Echinocolea*.

The genus somewhat resembles *Drepanolejeunea*, but the latter has pycnolejeuneoid innovations, ocelli usually in a broken row (unbroken in *D. anoplantha* and related species), and narrower underleaf lobes (but sometimes broad; see under *Drepanolejeunea*). Epiphyllous plants of *Drepanolejeunea* invariably produce large, adhesive rhizoid discs but in *Harpalejeunea* rhizoid discs seem to be lacking or only rudimentary.

LITERATURE. Evans, A. W. 1903. Hepaticae of Puerto Rico III. Bulletin of the Torrey Botanical Club 30: 544-563 [descr. of 3 spp.]. - Grolle, R. & M. E. Reiner-Drehwald. 1999. A review of the genus *Harpalejeunea* (Lejeuneaceae) including the description of *H. grandis* sp. nov. from páramos of Colombia. Journal of Bryology 21: 31-45. - Spruce, R. 1884. *Lejeunea* subgenus *Harpalejeunea*. Hepaticae Amazonicae et Andinae. Transactions and Proceedings of the Botanical Society of Edinburgh 15: 165-178 [descr. of 18 spp.].

Leiolejeunea (Fig. 46) - A monotypic, neotropical genus, with *L. grandiflora* A. Evans recorded only from Blue Mountain Peak, Jamaica (Greater Antilles). The species is known from only three old collections.

HABITAT. On bark of trees in montane rain forest; altitude unknown (ca. 2000 m?).

DESCRIPTION. **Plants** very small, ca. 0.6 mm wide, dull yellow-green, creeping. **Stems** of thick-walled cells, without hyalodermis; ventral merophyte 2 cells wide. **Leaf lobes** rather wide-spreading

and squarrose, asymmetrically ovate-falcate, apex obtuse, plane, margins ± entire. **Cells** rather small, ca. 20 µm in leaf middle, with well-developed trigones and intermediate thickenings, cuticle smooth; oil bodies unknown; ocelli lacking. **Lobules** 1/2 leaf length, never reduced, strongly inflated, keel slightly arched, forming an almost continuous line with the ventral leaf margin, apical tooth 1-celled, falcate and sharp, a blunt "pre-apical" tooth sometimes present at the junction between the lobule and ventral margin of the leaf, hyaline papilla distal. **Underleaves** shallowly emarginate with broad and obtuse, diverging lobes; insertion line straight. **Dioicous**. **Gynoecia** on long branches, without true innovations, sometimes with 1-2 *Lejeunea*-type branches below the female bracts ("pseudo-innovations"). **Perianths** terete, smooth, without keels, beak short. **Vegetative reproduction** not observed.

DISCUSSION. *Leiolejeunea* is quite similar to *Harpalejeunea* in general habit and in the shape of the underleaves, but there are no ocelli, the keel of the lobule does not form a sharp angle with the ventral leaf margin, the hyaline papilla of the lobule is distal instead of proximal, and the perianth is terete, without keels (instead of 5-keeled). The genus is very little known and has not been recorded since it was originally described by Evans.

LITERATURE. Evans, A. W. 1908. New West Indian Lejeuneae. Bulletin of the Torrey Botanical Club 35: 371-389.

Lejeunea (Fig. 47) **-** A large pantropical and warm-temperate genus. As circumscribed here, there are about 40 species in tropical America, in 7 subgenera. When *Crossotolejeunea*, *Macrolejeunea*, *Microlejeunea*, and *Taxilejeunea* are also included in *Lejeunea*, the number of species becomes at least twice as high.

HABITAT. Very common on bark, living leaves, and rock in forests and open habitats, usually at rather low elevations, rarely occurring above 2000 m.

DESCRIPTION. **Plants** usually small, 0.5-1.5 mm wide, pale green to bright green, usually glossy, creeping. **Stems** with hyalodermis; ventral merophyte 2 cells wide. **Leaf lobes** spreading, apex rounded to obtuse, rarely subacute, plane, margins entire or somewhat crenulate, never toothed. **Cells** plane, usually thin-walled with small or minute trigones; oil bodies small, finely granular or homogeneous, cuticle usually smooth, sometimes rough (subgen. *Nanolejeunea*); ocelli lacking. **Lobules** usually less than 1/3 leaf length, sometimes reduced, ovate, apical tooth short and blunt, rarely very long (subgen. *Chaetolejeunea*); hyaline papilla proximal. **Underleaves** bifid, usually small with shallowly curved insertion, rarely large and cordate. **Gynoecia** on long or short shoots, with (0-)1-2 lejeuneoid (rarely pycnolejeuneoid) innovations that are usually sterile, rarely fertile. **Perianths** with 0-5 keels, the keels smooth or somewhat crenulate, rarely auriculate or with plate-like extensions (subgen. *Otigoniolejeunea*). **Vegetative reproduction** by caducous leaves (subgen. *Heterolejeunea*) or shoot fragmentation (subgen. *Nanolejeunea*) or lacking.

DISCUSSION. *Lejeunea* is one of the largest genera of Lejeuneaceae. The species are very poorly known, especially in the Neotropics. Moreover, the circumscription of the genus is unsettled. Important characteristics of the genus include 1) small, bifid underleaves with upright (not diverging) lobes; 2) thin stems with a hyalodermis and ventral merophyte 2 cells wide; 3) lobules with a proximal hyaline papilla; 4) cell walls without brownish pigmentation; 5) lack of ocelli; and 5) perianths with lejeuneoid innovations that are mostly sterile and do not develop into compound cymes.

Lejeunea is usually divided into subgenera, some of which are better defined than others. A synopsis of the subgenera currently recognized in the Neotropics is given below. *Crossotolejeunea*, *Macrolejeunea*, *Microlejeunea*, and *Taxilejeunea*, sometimes considered subgenera of *Lejeunea*, are kept as separate genera in this work, mostly for practical reasons. Although not always sharply different from *Lejeunea*, these groups can often be separated at a glance from typical *Lejeunea* spp. by their characteristic habit.

The synopsis of the subgenera presented here is a provisional one; the status of the subgenera and of the genera related to *Lejeunea* can only be ascertained by careful monographic study. A revision of the genus *Lejeunea* in the Neotropics by M. E. Reiner-Drehwald is in preparation (Reiner-Drehwald, M. E. 1999. Catalogue of the genus *Lejeunea* of Latin America. Bryophytorum Bibliotheca 54).

Key to the subgenera of *Lejeunea* in tropical America

1. Lobules vestigial, with a very long (5-15 cells), upright tooth ..... subgen. **Chaetolejeunea**
1. Lobule with a short tooth (1-2 cells) or tooth lacking 2
2. Plants with caducous leaves ..... subgen. **Heterolejeunea**
2. Plants without caducous leaves 3
3. Leaves obliquely spreading. Shoots very fragile, fragmenting. Cuticle rough. Plants very small, usually less than 0.5 mm wide ..... subgen. **Nanolejeunea**

3. Leaves wide-spreading. Shoots not fragmenting. Cuticle smooth 4
4. Leaf margins conspicuously crenulate. Perianths flattened, 4-keeled, without dorsal keel, the keels crenulate ..... subgen. **Prionocolea**
4. Leaf margins entire or weakly crenulate. Perianths inflated, 5-keeled or without keels 5
5. Perianth terete, without keels ..... subgen. **Inflatolejeunea**
5. Perianth 5-keeled 6
6. Perianth with lamellate or auricle-like extensions above ..... subgen. **Otigoniolejeunea**
6. Perianth without such extensions ..... subgen. **Lejeunea**

1. **Lejeunea** subgen. **Chaetolejeunea** (Fig. 47A-E) - A small pantropical group (4 spp.), with 2 species in tropical America, at low elevations (below 1000 m): the widespread *L. trinitensis* Lindenb. (= *L. pililoba* Spruce) with a uniseriate lobule tooth and *L. spiniloba* Lindenb. & Gott. (Mexico, Cuba) with a tooth 2-4 cells wide.
The very long lobule tooth (5-15 cells long) and the flattened perianths are characteristic of *Chaetolejeunea*. Because of its long lobule tooth, *Chaetolejeunea* has sometimes been considered a genus of its own, *Stylolejeunea* A. Evans. The flattened perianth, shared with the next subgenus, is also unusual in *Lejeunea* and has been a reason for Schuster (1980) to treat *Chaetolejeunea* as a subgenus of *Rectolejeunea*.
LITERATURE. Schuster, R. M. 1980. *Rectolejeunea* subgenus *Chaetolejeunea*. The Hepaticae and Anthocerotae of North America, Vol. IV: 1146-1156. [key].

2. **Lejeunea** subgen. **Heterolejeunea** (Fig. 47I-K) - An Afro-American group of about 5-6 species, very common at low elevations in tropical America. The African species are probably conspecific with the neotropical ones. The species are very common on fine twigs and branches of trees and shrubs, less frequent on tree trunks, and usually grow in open, well-illuminated environments.
Heterolejeunea is characterized by a flattened perianth and by the occurrence of caducous leaves. The subgenus is usually considered a subgenus of *Rectolejeunea*, but the latter genus differs in its ocellate leaves, pycnolejeuneoid innovations, and caducous leaves that are much smaller than ordinary leaves and produced on specialized, upright flagelliform shoots. In *Heterolejeunea*, the caducous leaves are similar to ordinary leaves and originate from ordinary stems or branches, rarely from specialized flagella (*L. phyllobola*).
LITERATURE. Schuster, R. M. 1980. *Rectolejeunea* subgenus *Heterolejeunea*. The Hepaticae and Anthocerotae of North America, Vol. IV: 1118-1146. .

3. **Lejeunea** subgen. **Inflatolejeunea** (Fig. 47L-N) - A small Afro-American group, with 2-3 species in tropical America, including *L. capensis* Gott., which also occurs in Africa.
The terete perianth, without keels, is the sole characteristic differentiating this group from subgenus *Lejeunea*.
LITERATURE. Giancotti, C. & D. M. Vital. 1989. *Lejeunea capensis* Gott. (Hepaticae: Lejeuneaceae) disjunct between South America and Africa. The Bryologist 92: 305-307. - Robinson, H. 1964. New taxa and new records of bryophytes from Mexico and Central America. The Bryologist 67: 446-458 [subgen. *Inflatolejeunea* on p. 455] - Schuster, R. M. 1992. The oil bodies of the Hepaticae. II. Lejeuneaceae. Journal of the Hattori Botanical Laboratory 72: 163-359 [subgen. *Inflatolejeunea* on p. 271-273].

4. **Lejeunea** subgen. **Lejeunea** (Fig. 47F-H) - About 15-20 species in tropical America, mostly at low elevations. The species are very poorly known and in serious need of study.
The "typical" *Lejeunea* spp. are characterized primarily by wide-spreading leaves with rounded tips and entire margins, small lobules with a short tooth and proximal papilla, small, bifid underleaves, and inflated, 5-keeled perianths with smooth keels.
LITERATURE. Schuster, R. M. 1980. *Lejeunea*. The Hepaticae and Anthocerotae of North America, Vol. IV: 929-1050 [key to 9 neotropical spp].

5. **Lejeunea** subgen. **Nanolejeunea** (Fig. 47O-Q) - A small pantropical group of 2-3 species at low elevations in tropical America, including the very common *L. laetevirens* Nees & Mont. This species grows on bark in the canopy and forest margin, scrubby vegetation, orchards, on roadside trees, etc., often in great abundance, and is one of the most xerotolerant species of Lejeuneaceae in the Neotropics.
The very small and brittle plants with somewhat obliquely spreading leaves and leafy shoots easily fragmenting into small pieces, are unmistakable. The finely papillose cuticle of the leaves is a very characteristic feature of the group.

LITERATURE. Schuster, R. M. 1980. *Lejeunea* subgenus *Nanolejeunea* The Hepaticae and Anthocerotae of North America, Vol. IV: 1092-1102.

6. **Lejeunea** subgen. **Otigoniolejeunea** - A neotropical group of about 5-6 species in northern South America and Central America. The species seem to be restricted to humid lowland rain forests, especially the dense, undisturbed ones, and have not been studied since their original description by Spruce (1884).
The principal characteristic of *Otigoniolejeunea* is the perianth keels which are more or less auriculate above or have lamellate extensions. The often pointed apices and armed perianths suggest a close relationship with *Crossotolejeunea*.
LITERATURE. Spruce, R. 1884. *Lejeunea* subgenus *Otigoniolejeunea*. Hepaticae Amazonicae et Andinae. Transactions and Proceedings of the Botanical Society of Edinburgh 15: 226-230 [descr. of 5 spp.].

7. **Lejeunea** subgen. **Prionocolea** - A small neotropical group with 2 species, one from Venezuela (2400 m) and the other one from the island of Gorgona, western Colombia. The precise ranges and habitats of the two species remain unknown.
Prionocolea is characterized by the leaves with crenulate margins and conspicuously narrowed dorsal bases, and by the flattened, pyriform perianths with toothed, subauriculate lateral keels. Following Grolle (1984), *Prionocolea* is treated here as a subgenus of *Lejeunea*. The subgenus is superficially similar to *Prionolejeunea*.
LITERATURE. Grolle, R. 1984. Zur Kenntnis der Lejeuneoideae in Cuba (1): *Cyclolejeunea*. Wissenschaftliche Zeitschrift der Friedrich-Schiller-Universität, Jena, Naturwissenschaftliche Reihe, 33 (6): 759-764. - Schuster, R. M. 1994. Studies on Lejeuneaceae, I. Preliminary studies on new genera of Lejeuneaceae. Journal of the Hattori Botanical Laboratory 75: 211-235.

Lepidolejeunea (Fig. 46) - A pantropical genus (12 spp.), with 6 species in tropical America. Three of them, *L. grossepapulosa* (Steph.) Piippo, *L. involuta* (Gott.) Grolle, and *L. ornata* (H. Rob.) Schust., are very common in the everwet Chocó region, which is the center of diversity of *Lepidolejeunea* in the Neotropics.

HABITAT. On bark, living leaves and rotten wood in the understory and canopy of humid lowland, submontane and montane rain forests, (50-)300-2500(-3500) m. The species usually occur below 2000 m, with the exception of *L. spongia* (Spruce) Thiers which inhabits upper montane rain forest canopies in the northern Andes, between 2500 and 3500 m (but occurring at lower elevations, 1300-1600 m, on Cuba). Most of the species grow in moist, shaded environments but *L. eluta* (Nees) Schust. grows in more open, dryer environments, in the forest canopy and at forest margins. An undescribed species occurs on shrubs in Amazonian savanna vegetation, in unusually dry, open habitats.

DESCRIPTION. **Plants** small to medium-sized, 1-4 cm long, 0.8-2 mm wide, yellowish-green to pale brown, dry material sometimes becoming reddish when moistened (*L. eluta*), loosely creeping to pendent. **Stems** of thin-walled cells, with hyalodermis; ventral merophyte 2 cells wide (4-10 cells wide in *L. eluta*). **Leaf lobes** wide-spreading, ovate-oblong, with scattered ocelli, apex rounded to acute-apiculate, often recurved, margins entire to crenulate to ± toothed. **Cells** plane, hexagonal, small, ca. 15-25(-30) µm long in lobe middle, walls thin, uniformly thickened or with small trigones, cuticle smooth or finely papillose; oil bodies lacking in green cells. **Ocelli** numerous, colorless, rarely gray-brown (*L. eluta*), scattered in leaves, underleaves, bracts, bracteoles and perianths, about as large as the green cells. **Lobules** ca. 1/5-1/3 leaf length, ovate, free margin usually incurved, apical tooth 1-celled, short-obtuse to somewhat elongated-acute, hyaline papilla proximal. **Underleaves** bifid or undivided (*L. spongia*), small or large, bases usually cordate, insertion line arched or almost straight. **Androecial bracteoles** present throughout the spike (in neotropical species). **Gynoecia** on elongated shoots, with 1-2 pycnolejeuneoid innovations. **Perianths** inflated, 5-keeled, the keels sometimes conspicuously swollen above. **Vegetative reproduction** occasionally, by caducous leaf lobes.

DISCUSSION. *Lepidolejeunea* is characterized by the soft-textured plants with fragile stems made up of thin-walled cells, the pointed (sometimes rounded) leaves with often conspicuously crenulate margins, by the rather small cells without oil bodies and, especially, by the numerous scattered ocelli in the leaves and underleaves. The underleaves of the neotropical species are bifid to emarginate, rarely undivided (*L. spongia*), and are often conspicuously cordate at the base.

The ventral merophyte in *Lepidolejeunea* is 2 cells wide except in *L. eluta,* which has a more robust stem with a ventral merophyte 4-10 cells wide. A unique feature of the latter species is that herbarium material, when soaked in water, turns rose-red, especially at the stem apices; this is not known from any other member of the Lejeuneaceae. The chemical basis of this color reaction is unknown.

LITERATURE. Piippo, S. 1986. A monograph of the genera *Lepidolejeunea* and *Luteolejeunea*. Acta Botanica Fennica 132: 1-69 [key].

Leptolejeunea (Fig. 46) - A pantropical genus (ca. 25 spp.), with 12 species at low elevations in tropical America. Most of the species are widely distributed but some have quite discontinuous ranges, e.g., *L. foraminulosa* Steph. disjunct in Mexico and the Guianas, and *L. serratifolia* Schiffn. and *L. diversilobulata* Bischl. known only from Cuba and Brazil. The disjunct ranges are biogeographically inexplicable and are probably due to inadequate collecting.

HABITAT. On living leaves (rarely on bark), especially on smooth, leathery leaves; in lowland rain forests, occasionally in submontane and lower montane rain forest, usually in very moist habitats and mostly in the dense understory and lower canopy of the forest, 0-800(-2000) m. The species occur mostly in lowland forests but the widespread *L. exocellata* (Spruce) A. Evans and *L. elliptica* (Lehm. & Lindenb.) Schiffn. extend to 1500(-2000) m and have also been found in lower montane rain forest. These are the only two species which do not grow exclusively on leaves but may also occur on bark. Moreover, they are not restricted to the dense forest but are also found in scrubby vegetation, orchards, coffee plantations, etc. in somewhat more mesic conditions (especially *L. elliptica*).

DESCRIPTION. **Plants** very small, to 1(-1.5) cm long, 0.3-1(-1.5) mm wide, green to pale brown to blackish, creeping, with a strong odor when fresh. **Stems** of 7 outer cells and 3 inner cells, epidermal cells weakly enlarged; ventral merophyte 2 cells wide. **Leaf lobes** obliquely spreading, often standing up when dry, elliptical or obovate from a narrow base, with ocelli, apex rounded or acute-apiculate, plane, margins entire or toothed above. **Cells** with small trigones, cuticle smooth; oil bodies small, few per cell, simple or composed of a few droplets. **Ocelli** colorless (rarely yellowish to reddish), usually in a broken, longitudinal line, becoming progressively smaller to the apex, the basal-most ocellus very large; a few scattered, small ocelli sometimes present in the upper third of the lamina. **Lobules** 1/3-1/2 leaf length, never reduced, inflated, apical tooth 1-celled, short and blunt, hyaline papilla proximal. **Underleaves** small, remote, often with a large, adhesive rhizoid disc, bifid with very slender, upright or diverging lobes, the lobes 2-4 cells long and 1(-2) cells wide, lamina with a conspicuous border of 6 large outer cells surrounding the smaller inner cells, insertion line almost straight. **Gynoecia** on short branches, without innovations. **Perianths** inflated, 5-keeled above, the keels extending into short, horn-like projections. **Vegetative reproduction** by cladia.

DISCUSSION. *Leptolejeunea* is distinguished by the tiny underleaves with 2 subulate, upright to diverging lobes and a lamina bordered by 6 large cells, and by the obliquely spreading, elliptical to obovate leaves with several ocelli (only one, basal ocellus in *L. exocellata* and *L. serratifolia*). The underleaf lobes are usually inserted at the outer edges of the underleaf. The ocelli are usually arranged in a broken, longitudinal line, the lowest ocellus being considerably larger than the others. The ocelli are conspicuously yellowish to reddish in *L. moniliata* Steph.; in the other species they are usually colorless.

A characteristic habit feature by which the genus can often be recognized at low magnification, is the tendency for the dry leaves to become elevated, almost perpendicular to the substrate. The plants produce monoterpenes that emit a strong fragrance when fresh. The odor may to some extent be characteristic for the species.

Leptolejeunea is one of the very few genera of hepatics that is almost exclusively epiphyllous. The underleaf lamina is normally covered by a large, adhesive rhizoid disc, a feature characteristic of epiphyllous Lejeuneaceae. The genus is closely related to *Drepanolejeunea* and *Rhaphidolejeunea*, which also have underleaves with diverging lobes and obliquely spreading, ocellate leaves. However, in the latter two genera the basal-most ocellus is not conspicuously larger than the others, the lobule tooth is long-falcate and sharp (short and blunt in *Leptolejeunea*), the underleaves are not conspicuously bordered, and the gynoecia always have innovations. In addition, *Drepanolejeunea* differs in the conspicuously asymmetrical, falcate leaves which are always widest near the base. In *Leptolejeunea* (and *Rhaphidolejeunea*), the leaves are always widest in the middle or in the upper part.

LITERATURE. Bischler, H. 1969. Le genre *Leptolejeunea* (Spruce) Steph. en Amérique. Nova Hedwigia 17: 255-350 [key].

Leucolejeunea (Fig. 48) - A pantropical genus (13 spp.), with 5-6 species in tropical America (Gradstein & Geissler, 1997).

HABITAT. As in *Anoplolejeunea*, these are typical canopy epiphytes of trunks, branches, and fine twigs in montane forests and scrubby vegetation, always in open and sunny but rather humid environments, from almost sea level to ca. 3500 m in the Andes. In dense forests, *Leucolejeunea* occurs at the forest margin or in the high canopy and avoids the shaded interior of the forest. The species usually occur below 2000 m with the exception of the widespread *L. xanthocarpa* (Lehm. & Lindenb.) A. Evans, which extends to the páramo.

DESCRIPTION. **Plants** small to medium-sized, 1-3 cm long, (0.7-)1-2.5 mm wide, dull whitish-, grayish- or yellowish-green, sometimes turning pale brown, creeping. **Stems** of thick-walled, pale cells, epidermis not or slightly enlarged; ventral merophyte 2-4 cells wide. **Leaf lobes** wide-spreading, convex, apex rounded, margins entire or crenulate, ventral margin sometimes inflexed. **Cells** (sub)isodiametric, sometimes mammillose, trigones small to medium-sized, intermediate thickenings scarce; oil bodies very large, only 1-3 per cell, sausage-shaped, coarsely granular; ocelli lacking. **Lobules** 1/3-1/2 leaf length, ovate to rectangular, truncate, inflated, apex with a short or long, 1-6-celled tooth, hyaline papilla distal. **Underleaves** undivided, wider than long, margins plane or recurved, insertion line curved to arched. **Gynoecia** on long or short shoots, with (0-)1(-2) pycnolejeuneoid innovations. **Perianths** with 4-5 smooth keels. **Vegetative reproduction** rare, by caducous leaves in *L. caducifolia* Gradst. & Schäf.-Verw.

DISCUSSION. The very pale and dull appearance of the plants, the rigid stems without hyalodermis, and the ventral merophyte 4 cells wide (sometimes only 2 cells), separate *Leucolejeunea* from other members of the Lejeuneae with undivided underleaves. The genus is perhaps closest to *Aureolejeunea*, but the latter is more brownish and usually has a more loose, less tightly prostrate growth. In the large, sausage-shaped oil bodies and various other features, the genus approaches *Cheilolejeunea* which is, however, nearly always schizostipous and has smaller lobules, at least in the neotropical species (see under *Cheilolejeunea*).

LITERATURE. Gradstein, S. R., R. Grolle & A. Schäfer-Verwimp. 1993. Two interesting species of Lejeuneaceae from Brazil. Journal of the Hattori Botanical Laboratory 74: 59-70 [*L. caducifolia* sp. nov.]. - Gradstein, S. R. & P. Geissler. 1997. Notes on the genus *Leucolejeunea* Evans. Cryptogamie, Bryologie et Lichénologie 18: 177-182. - Schuster, R. M. 1980. *Leucolejeunea*. The Hepaticae and Anthocerotae of North America, Vol. IV: 814-848 [key to 4 spp.].

Luteolejeunea (Fig. 48) - A monotypic, neotropical genus, with *L. herzogii* (Buchloh) Piippo endemic to the Pacific coast area of northern South America (Chocó region). The species has been recorded from northern Peru northwards to Costa Rica.

HABITAT. On large tree trunks in the understory of humid lowland and submontane rain forests, in primary as well as secondary forests, 50-800 m.

DESCRIPTION. **Plants** rather robust, to 4 cm long, 1.5-2 mm wide, pale yellowish-green to yellow-brown, loosely creeping. **Stems** rigid, of thick-walled cells, with enlarged epidermis; ventral merophyte 2 cells wide. **Leaf lobes** wide-spreading, with scattered ocelli as well as 1-2 at the base, apex rounded, usually recurved, margins crenulate to slightly toothed above. **Cells** 25-40 µm long in lobe middle, with swollen trigones; oil bodies present in all cells, 2-4 per cell, coarsely granular. **Ocelli** conspicuously larger than the green cells, occurring scattered in leaves, underleaves, bracts, bracteoles, and perianths. **Lobules** very small, ca. 1/10-1/7 leaf length, bottle-shaped, curved downward, free margin incurved, apical tooth inconspicuous, hyaline papilla proximal. **Underleaves** undivided, large, reniform, 6-10x stem width, insertion line deeply arched. **Androecial bracteoles** present throughout the spike. **Gynoecia** on short branches, with 1 pycnolejeuneoid innovation. **Perianths** inflated, 5-keeled, the keels horn-like swollen above. **Vegetative reproduction** not observed.

DISCUSSION. *Luteolejeunea* is easily recognized by the large, undivided underleaves, the tiny, downward-curved lobules hidden behind the underleaves, the rigid stems made up of thick-walled cells and with a 2-cells wide ventral merophyte, and the scattered ocelli in leaves and underleaves. The ocelli are very conspicuous, much larger than ordinary leaf cells, and may turn brown in dried plants.

The plants are relatively robust and bear the closest resemblance to *Pycnolejeunea.* The latter, however, does not have ocelli in the underleaves (usually only 1-2 at the leaf base) and has bifid, instead of undivided, underleaves.

LITERATURE. Piippo, S. 1986. A monograph of the genera *Lepidolejeunea* and *Luteolejeunea*. Acta Botanica Fennica 132: 1-69 [key].

Macrolejeunea (Fig. 48) - A small neotropical genus of 3-5 species in montane regions of tropical America.

HABITAT. Hanging loosely from trunks and branches of trees and twigs in montane rain forests and subalpine scrub, to the lower edge of the páramo, (100-)1000-3800 m. *Macrolejeunea pallescens* (Mitt.) Schiffn., the type species of the genus, is a common and characteristic species of upper montane cloud forests and scrub in the northern Andes, above 2500 m. The other species of the genus occur at lower elevations.

DESCRIPTION. **Plants** long and slender, to 10 cm long, 1.5-2 mm wide, pale green to yellowish-green, loosely creeping to laxly pendent. **Stems** with hyalodermis; ventral merophyte 2 cells wide. **Leaf lobes** spreading, apex narrow acuminate to broad rounded-apiculate, plane, margins entire or

weakly crenulate. **Cells** plane, with distinct trigones and intermediate thickenings; oil bodies small, finely granular; ocelli lacking. **Lobules** usually small, less than 1/3 leaf length, ovate, apical tooth short and blunt, hyaline papilla proximal. **Underleaves** bifid, large, 4-10x stem width, base often cordate, insertion line curved to deeply arched. **Dioicous**. **Female** branches very short, without innovations (rarely with 1 short lejeuneoid innovation). **Perianths** inflated, with 5 smooth keels or eplicate. **Vegetative reproduction** not observed.

DISCUSSION. *Macrolejeunea* is similar to *Taxilejeunea* in habit but the gynoecia are on highly abbreviated lateral branches, without innovations (rarely with a short sterile innovation). The genus is sometimes considered a mere subgenus of *Taxilejeunea* or *Lejeunea*.

LITERATURE. Grolle, R. 1987. Zur Kenntnis der Lejeuneoideae in Cuba (2): *Lejeunea* subg. *Macrolejeunea* Spruce. Wissenschaftliche Zeitschrift der Friedrich-Schiller Universität, Jena, Mathematisch-Naturwissenschaftliche Reihe 37: 169-176 [key]. - Spruce, R. 1884. *Lejeunea* subgenus *Macrolejeunea*. Hepaticae Amazonicae et Andinae. Transactions and Proceedings of the Botanical Society of Edinburgh 15: 224-226 [descr. of 2 spp.].

Metalejeunea (Fig. 49) - A monotypic, pantropical genus, with *M. cucullata* (Reinw. *et al.*) Grolle (= *Microlejeunea monoica* Bischler) at rather low elevations in the West Indies and northern South America (Guianas, Brazil). The species is quite common on Guadeloupe (Bischler *et al.*, 1963).

HABITAT. On living leaves and, more rarely, on bark in humid lowland and submontane rain forests, 0-800 m. In the West Indies, *M. cucullata* has been recorded from elevations between 500 and 800 m; in the Guianas, the species occurs almost at sea level.

DESCRIPTION. **Plants** very small, 0.2-0.3 mm wide, whitish-green to dull yellowish, creeping. **Stems** zig-zag, rather rigid, of thick-walled cells, in cross-section of 7 outer rows of cells and 3 smaller inner rows; ventral merophyte 2 cells wide. **Leaf lobes** distant, hardly spreading suberect, elongated, 1.5-2 x longer than wide, with very large lobules (more than 1/2 the size of the lobe), apex rounded, margins entire. **Cells** small, 12-17 µm long in middle of lobe, strongly and evenly thick-walled; oil bodies unknown; ocelli lacking. **Lobules** 0.5-0.8 leaf length, sometimes reduced, strongly swollen, keel crenate, apical tooth rather long and curved; hyaline papilla proximal. **Underleaves** bifid, small, 1.5-2.5x stem width. **Autoicous**. **Gynoecia** on long or short shoots, with 1 pycnolejeuneoid innovation, the innovation sterile or with androecia; bracts ± winged. **Perianths** inflated-pyriform, with 5 smooth keels. **Vegetative reproduction** not observed.

DISCUSSION. Similar to *Microlejeunea* in general habit, but differing in the autoicous inflorescence, the absence of ocelli at the lobe base, and, especially, in the pycnolejeuneoid instead of lejeuneoid innovation (Grolle, 1995). The elongated leaves (1.5-2 x longer than wide) with crenate keels and very thick-walled cells, are also characteristic of *M. cucullata*.

LITERATURE. Bischler, H., C. E. B. Bonner & H. A. Miller. 1963. Studies in Lejeuneaceae VI. The genus *Microlejeunea* Steph. in Central and South America. Nova Hedwigia 5: 359-411 [as *Microlejeunea monoica*]. - Grolle, R. 1995. An annotated catalogue of the Hepaticae and Anthocerotae of the East African Islands. Bryophytorum Bibliotheca 48: 1-178.

Microlejeunea (Fig. 49) - A pantropical and warm-temperate genus (ca. 20-30 spp.), with about 12 species in tropical America.

HABITAT. On bark, fine twigs, and living leaves in the understory and canopy of lowland and lower montane rain forest and in scrubby vegetation, occasionally in upper montane forest to the forest line, 0-2500(-3600) m. Occasionally on rock or soil. Most of the species occur below 2500 m but *M. bullata* (Taylor) A. Evans extends to the páramos.

DESCRIPTION. **Plants** very small, 0.2-0.4 mm wide, pale green to pure green, usually somewhat dull-colored, creeping. **Stems** zig-zag, very thin, of 7 outer rows of cells and 3 smaller inner rows; ventral merophyte 2 cells wide. **Leaf lobes** usually remote, not overlapping, hardly spreading, suberect, with very large lobules (more than 1/2 the size of the lobe), apex rounded to acute, margins entire or crenulate. **Cells** small, 15-25 µm long in middle of lobe, thin- or thick-walled; oil bodies small, finely granular; ocelli usually present, 1-3 at lobe base. **Lobules** 0.5-0.8 leaf length, sometimes reduced, strongly swollen, apical tooth rather long and curved, hyaline papilla proximal. **Underleaves** bifid, very small. **Dioicous**. **Gynoecia** on long or short shoots, with 1-2 lejeuneoid innovations; bracts ± winged. **Perianths** inflated-pyriform, with 0-5 smooth keels. **Vegetative reproduction** very rare, by cladia.

DISCUSSION. The very small plants with zig-zag stems and remote, hardly spreading leaves possessing very large lobules are unmistakable. Similar leaves may be found in *Cololejeunea* and *Aphanolejeunea*, but *Microlejeunea* has small, bifid underleaves whereas in the other two genera underleaves are always absent.

The species of *Microlejeunea* seem to be strictly dioicous. *Microlejeunea monoica* Bischler, the only monoicous species in tropical America, belongs in *Metalejeunea* (see there).

LITERATURE. Bischler, H., C. E. B. Bonner & H. A. Miller. 1963. Studies in Lejeuneaceae VI. The genus *Microlejeunea* Steph. in Central and South America. Nova Hedwigia 5: 359-411 [key]. - Schuster, R. M. 1980. *Lejeunea* subgen. *Microlejeunea*. The Hepaticae and Anthocerotae of North America, Vol. IV [key to some neotropical spp].

Myriocolea (Fig. 49) - A monotypic, neotropical genus, with *M. irrorata* Spruce known only from Ecuador, from the banks of the Río Topo (a tributary of the Río Pastasa) at the eastern foot of the Andes.

HABITAT. On twigs and small shrubs on rocky river margins, along a series of rapids moistened by the spray from the swiftly running water, periodically inundated, alt. ca. 1000 m. The species was collected in an area of undisturbed submontane rain forest.

DESCRIPTION. **Plants** robust, 1-1.3 mm wide, green, upright from a short, creeping, rhizome-like shoot, densely pinnate and extremely fertile, all branches with gametoecia. **Branches** without collar, *Radula*-type, one branch arising from below almost every leaf. **Stems** robust, of numerous thick-walled cells, epidermis not enlarged; ventral merophyte more than 4 cells wide. **Leaf lobes** (sub)erect, distant, transversely inserted with a very short insertion line, obovate apex rounded, plane, margins entire, undulate. **Cells** pellucid, thin-walled, without trigones; oil bodies unknown; ocelli lacking. **Lobules** reduced. **Underleaves** minute, narrower than the stem, subquadrate, bifid, lacking on branches. **Paroicous**. **Gynoecia** on lateral branches in complex heads of to 150 perianths, each gynoecium with one bract and 1-2 innovations which are again fertile, innovation-type unknown (due to lack of underleaves); antheridia 4-7 in the axils of the female bracts. **Perianths** inflated, with 5 smooth keels. **Vegetative reproduction** not observed.

DISCUSSION. The densely pinnate plants growing upright from a rhizome-like base, with stout stems and narrowly inserted, transverse leaves without lobules, are unmistakable. From below almost every leaf emerges a short branch carrying a globose head of numerous, clustered perianths. The vegetative branches are unique in being collarless, *Radula-type* branches, not known to occur in any other genus of Lejeuneaceae, except as innovations. Underleaves are present only on the main stems and are very small, bifid.

Myriocolea is a phylogenetically isolated genus and has been placed in a separate subfamily Myriocoleoideae. It cannot be confused with any other hepatic except, possibly, *Myriocoleopsis* (tribe Cololejeuneae). The androecia in *Myriocoleopsis* are on separate branches, however, and underleaves are completely absent.

Myriocolea has not been sighted since Richard Spruce discovered the genus in the middle of the 19th century. A recent field search in the type locality did not reveal any populations (B. Thiers, pers. comm.). Since deforestation and disturbance of water courses by human activities are severe in Ecuador, *Myriocolea* is considered a threatened taxon (Gradstein, 1992a, b)

LITERATURE. Spruce, R. 1884. *Myriocolea*. Hepaticae Amazonicae et Andinae. Transactions and Proceedings of the Botanical Society of Edinburgh 15: 305-307. - Thiers, B. 1983. Braching in Lejeuneaceae II. Nipponolejeunoideae, Tuyamaelloideae and Myriocoleoideae. Lindbergia 10: 4-18.

Omphalanthus (Fig. 49) - A neotropical genus of 4-5 species, in 2 subgenera, at high elevations throughout tropical America but apparently rare in the Guayana Highland.

HABITAT. Common on branches and twigs in montane cloud forests, in both the understory and the canopy, and in open, scrubby vegetation, 500-4000 m. Also on rock and occasionally on soil. *Omphalanthus filiformis* (Sw.) Nees is the most common species of the genus and is often abundant in cloud forests. The species is also a common invader of disturbed habitats and may grow in great abundance on isolated shrubs and on road banks at mid-montane elevations, always in humid environments.

DESCRIPTION. **Plants** long and slender, little branched, to 8 cm long, 1.5-2.5 mm wide, dull-colored, pale green to yellowish-brown, ascending or pendent. **Stems** rigid, of thick-walled cells, epidermis not enlarged; ventral merophyte 4-12 cells wide. **Leaf lobes** obliquely spreading, when dry convolute, convex, apex rounded to acuminate, margins entire. **Cells** (sub)isodiametric, with small or large, bulging trigones, intermediate thickenings present or absent; oil bodies large, rather coarsely granular; ocelli lacking. **Lobules** ca. 1/3 leaf length, ovate-trapezioid, truncate, rather flat, apex obtuse (tooth lacking), hyaline papilla distal. **Underleaves** very large, 4-10x stem width, undivided, rarely short-bifid (*O. jackii*), margins plane or recurved, bases rounded or long-decurrent, insertion line deeply arched. **Gynoecia** on long or short shoots, with 1 lejeuneoid innovation. **Perianths** with 0-5 smooth keels, with or without a long beak. **Vegetative reproduction** not observed.

DISCUSSION. The species of *Omphalanthus* are among the most robust members of the Lejeuneae. Due to their undivided underleaves and stout stems without enlarged epidermis, they are more similar to members of the Brachiolejeuneae and Ptychantheae. The loosely cespitose to pendent habit of the plants, the pale yellowish-brown color, the long and sparingly branched stems, the short, truncate

lobules, and the large underleaves, will at once separate it from other genera with undivided underleaves. The cells usually have large trigones but intermediate thickenings are often lacking.

The common *O. filiformis* (subgen. *Omphalanthus*) is at once recognized by the rounded leaf lobes and eplicate perianths. In *O. ovalis* (Lindenb. & Gott.) Gradst. and *O. jackii* (Steph.) Gradst., the leaf apex is acute to acuminate (sometimes obtuse in *O. ovalis*), and the perianth is 5-keeled, with a very long beak. These two species belong to the subgenus *Peltolejeunea*. *Omphalanthus jackii*, furthermore, stands out by its short-bifid underleaves, all other species being holostipous.

LITERATURE. Evans, A. W. 1908. Hepaticae of Puerto Rico VII. Bulletin of the Torrey Botanical Club 35: 1-34 [descr. of 1 sp.]. - Gradstein, S. R., R. Matsuda & Y. Asakawa. 1981. Studies on Colombian Cryptogams XIII. Journal of the Hattori Botanical Laboratory 50: 231-248 [key].

Oryzolejeunea (Fig. 50) - A small neotropical genus of 4 species, *O. grolleana* Bernecker-Lücking from Costa Rica, *O. saccatiloba* (Steph.) Gradst. (= O*. antillana* (Schust.) Schust.) in the West Indies, Central America, and Brazil, *O. venezuelana* (Schust.) Schust. in northern Venezuela, and a fourth, undescribed species in western Colombia.

HABITAT. On bark in montane forest areas, usually in rather open places, 500-2500 m.

DESCRIPTION. **Plants** small, to 1.5 cm long, ca. 1-1.3 mm wide, light green, creeping. **Stems** with hyalodermis; ventral merophyte 2 cells wide. **Leaf lobes** wide-spreading, convex, apex rounded, margins slightly crenulate due to swollen marginal cells. **Cells** (sub)isodiametric, trigones small; oil bodies homogeneous to septate, rarely finely granular (*O. grolleana*); ocelli lacking. **Lobules** 2/5-2/3 leaf length, never reduced, inflated below, flattened to apex, free margin plane, apex truncate, with a blunt, 1-celled tooth, hyaline papilla distal. **Underleaves** undivided or bifid with narrow incision, orbicular, margins entire, insertion line weakly curved. **Gynoecia** on short branches, with 1 sterile lejeuneoid innovation. **Perianths** 5-keeled above. **Vegetative reproduction** not observed.

DISCUSSION. *Oryzolejeunea* is recognized by its large, truncate lobules with a short, blunt apex and a distal hyaline papilla, and by the small, orbicular underleaves, which are undivided in *O. saccatiloba* and bifid in other species. *Oryzolejeunea saccatiloba* closely resembles *Amblyolejeunea fulfordiae* from Guadeloupe. The latter differs in the hyaline papilla being proximal in position rather than distal, and in the smooth, unkeeled perianths, which are situated on long instead of short branches.

LITERATURE. Lücking, A. 1995. Diversität und Mikrohabitatpräferenzen epiphyller Moose in einem tropischen Regenwald in Costa Rica. Dissertation, Ulm. - Schuster, R. M. 1992. The oil bodies of the Hepaticae. II. Lejeuneaceae. Journal of the Hattori Botanical Laboratory 72: 163-359 [*Oryzolejeunea* on p. 249-250].

Otolejeunea - A mainly paleotropical genus (10 spp.), with one species, *O. schnellii* (Tixier) Zhu & So (= *Allorgella schnellii* Tixier), in the Neotropics. The species is only known from the type specimen from Amazonia: Manaus (Brazil).

HABITAT. On living leaves, at low elevation.

DESCRIPTION. Plants small, creeping, 1-2 cm long, ca. 1-1.5 mm wide, yellowish green when dry. Stems with hyalodermis; ventral merophyte 2 cells wide. Leaf lobes obliquely to rather widely spreading, oblong, apex rounded, margins entire or slightly denticulate, plane, dorsal margin curved, ventral margin straight. Cells subisodiametrical, 20-30 µm long, thin-walled, trigones small, cuticle smooth; oil bodies unknown; ocelli lacking. Lobules reduced to a fold, 1/5 leaf length, narrow rectangular, tooth reduced, hyaline papilla on the tip of the toothdistal on the inner side of an apical margin cell distal to the tooth. Underleaves small, distant, 1.5-2.5 stem width, bifid, tips acute, margins entire or with a blunt tooth, insertion line straight. Autoicous. Androecial bracteoles restricted to the base of the spike. Gynoecia on a very short branch without innovations. Perianths ± flattened with 2 broad lateral keels expanded above into distinct auricles. Vegetative reproduction not observed.

DISCUSSION. *Otolejeunea* is a small epiphyllous plant with oblong leaves (ca. 2x longer than wide) and auriculate perianths. In its elongated leaves, *Otolejeunea schnellii* resembles *Bromeliophila* but in the latter the leaf cells are much longer (50-70 µm long), the underleaf tips are blunt, not acute, and the perianths are longly stalked and 5-keeled, without auricles. Moreover, *Bromeliophila* occurs exclusively in the leaf axils of bromeliads.

LITERATURE. Grolle, R. & M. E. Reiner-Drehwald (in press). *Otolejeunea* (Hepaticae, Lejeuneaceae) in the Neotropics. Journal of Bryology.

Physantholejeunea (Fig. 50) - A monotypic, neotropical genus, with *P. portoricensis* (Hampe & Gott.) Schust. scattered in the West Indies (Cuba, Puerto Rico, Dominica).

HABITAT. On twigs in virgin, lower montane cloud forests, 500-800 m.

DESCRIPTION. **Plants** small, 1-3 cm long, ca. 1-1.5 mm wide, yellowish-green to pale green, creeping to ascending to pendent. **Stems** with hyalodermis; ventral merophyte 2 cells wide. **Leaf**

lobes wide-spreading, with 10-20 scattered ocelli and a few ocelli in a row at leaf base, margins entire, apex rounded, the apex on creeping stems bordered by a group of elongated, finger-like hyaline cells (these cells lacking on leaves of ascending or pendent shoots). **Cells** small, 15-20 µm long, with ± uniformly thickened walls, the walls pale; oil bodies lacking in green cells. **Ocelli** numerous in leaves, underleaves, bracts, bracteoles and perianths, larger than green cells. **Lobules** 1/3-2/5 leaf length, ovoid, with a very long, acuminate-falcate, 1-celled apical tooth, hyaline papilla proximal; free margin bordered by elongated cells. **Underleaves** undivided, insertion line shallowly curved. **Dioicous**. **Gynoecia** on long or short branches, with 1 pycnolejeuneoid innovation. **Perianths** 4-keeled, the keels extended above into short, horn-like projections. **Vegetative reproduction** not observed.

DISCUSSION. *Physantholejeunea portoricensis* is recognized by the pale plants with undivided underleaves, small leaf cells with uniformly thickened walls, numerous scattered ocelli in leaves and underleaves, and the long, acuminate-falcate lobule tooth. It is a rare twig epiphyte of cloud forests in the West Indies and has a characteristic growth habit, with creeping primary shoots and ascending or pendent secondary ones. The leaves of the creeping shoots stand out by the presence of a hyaline border of finger-like cells at the leaf apex. A similar leaf border is found in *Cololejeunea cardiocarpa*. The perianths have short, horn-like extensions and somewhat resemble those of *Ceratolejeunea*.

LITERATURE. Evans, A. W. 1907. Hepaticae of Puerto Rico VII. Bulletin of the Torrey Botanical Club 35: 1-34 [as *Ceratolejeunea portoricensis*]. - Schuster, R. M. 1992. The oil bodies of the Hepaticae. II. Lejeuneaceae. Journal of the Hattori Botanical Laboratory 72: 163-359 [*Physantholejeunea* on p. 229-231].

Pictolejeunea (Fig. 50) - A small pantropical genus (3 spp.), with 2 species at low elevations in tropical America: *P. picta* (Gott. ex Steph.) Grolle in the Caribbean, Central America (Costa Rica, Panama), and northern South America (Amazon Basin, Chocó, Guianas), and the rare *P. sprucei* Grolle in Central Amazonia. A third species occurs in Indonesia.

HABITAT. *Pictolejeunea picta* occurs on rotten bark, roots, litter, and fern fronds in humid lowland and submontane rain forests, usually with little disturbance, at 50-1000 m. *Pictolejeunea sprucei* has been found only in Amazonian lowland rain forest, on rotten logs and moist sandstone bluffs.

DESCRIPTION. **Plants** small, creeping, 1-2 cm long, 0.7-1 mm wide, pale green to brown, often conspicuously dark-reddish spotted. **Stems** with hyalodermis; ventral merophyte 2 cells wide. **Leaf lobes** wide-spreading, with ocelli, apex rounded, often recurved, margins crenulate-papillose or entire. **Cells** with uniformly thickened walls, trigones lacking, cuticle smooth or with a large papilla; oil bodies unknown. **Ocelli** dark reddish to pale brown, scattered in leaves and underleaves, bracts and perianths. **Lobules** 1/3 leaf length, ovate-inflated, with a blunt, 1-celled tooth, hyaline papilla distal on the inner side of an apical margin cell distal to the tooth. **Underleaves** small, 1.5-2x stem width, bifid, margin entire or crenulate-toothed, insertion line curved. **Autoicous**. **Androecial bracteoles** restricted to the base of the spike. **Gynoecia** on a very short branch without innovations. **Perianths** ± flattened with 2 broad lateral keels expanded above into short auricles. **Vegetative reproduction** by means of linear gemmae, 2 cells wide, from the leaf margins.

DISCUSSION. The numerous, dark-reddish or brownish ocelli scattered in the leaves, underleaves, bracts, and perianths are unmistakable.

LITERATURE. Grolle, R. 1977. *Pictolejeunea* - eine neue Gattung der Lejeuneoideae aus der Neotropis und Borneo. Feddes Repertorium 88: 247-256 [key].

Pluvianthus (Fig. 51) **-** A monotypic, neotropical genus, with *P. squarrosus* (Steph.) Schust. & Schäf.-Verw. in montane regions (Serra do Mar, Serra de Mantiqueira) of southeastern Brazil.

HABITAT. On twigs and branches of shrubs in disturbed, open, cloudy environments, at forest edges and in pastures, ca. 500-2350 m.

DESCRIPTION. **Plants** small, ca. 1-1.2 mm wide, yellowish-green, creeping. **Stems** of only 7 outer rows of cells and 3 slightly smaller inner rows, no hyalodermis; ventral merophyte 2 cells wide. **Leaf lobes** wide-spreading, sometimes very squarrose, apex acute, often recurved, margins entire. **Cells** (sub)isodiametric, thin-walled, trigones very small, intermediate thickenings absent, cuticle smooth; oil bodies relatively small, 2-5 per cell, finely granular; ocelli present or absent in stem leaves (and perianths), variable in number, 2-4(-12) in a row, often forming a vitta. **Lobules** usually small, to 1/3 leaf length, ovate, apical tooth short and blunt, 1-celled, hyaline papilla proximal; lobules at the bases of branches and innovations sometimes greatly enlarged, forming a "utricle." **Underleaves** bifid, insertion line shallowly curved. **Gynoecia** on long shoots, with 1-2 lejeuneoid innovations, basal leaves of the innovations sometimes with large, utricle-like lobules; bracts with weakly developed wings. **Perianths** with 5 smooth keels. **Vegetative reproduction** not observed.

DISCUSSION. *Pluvianthus* is related to *Lejeunea* but differs in the squarrose, ocellate leaves, the *Ceratolejeunea*-like, swollen utricles at the bases of vegetative branches and innovations, and the lack of a hyalodermis.

The ocelli of *Pluvianthus* are quite variable in number and are much more numerous in plants from low elevations (500-1500 m) than from higher elevations (fide A. Schäfer-Verwimp, pers. comm.).

LITERATURE. Schuster, R. M. & A. Schäfer-Verwimp. 1995. On *Pluvianthus* (Lejeuneaceae: Lejeuneoideae). Nova Hedwigia 60: 59-72.

Potamolejeunea[3] - A small neotropical genus with 3 species, including *P. polyantha* (Mont.) E. Reiner & Goda (= *Neopotamolejeunea polyantha* [Mont.] E. Reiner) and *P. uleana* Steph. (= *N. uleana* (Steph.) E. Reiner) in Amazonia, and a third species in Jamaica (Reiner-Drehwald, in press). The records of *Potamolejeunea* are mostly based on old, 19th century specimens collected by Spruce and Ule along the upper Rio Negro and other tributaries of the Amazon river, and along the Orinoco. An intensive field search for *Potamolejeunea* in Amazonia is needed to determine the continued existence of the species.

HABITAT. Rheophytic plants, growing on periodically inundated tree trunks, roots, and rocks in or along the nutrient-poor "blackwater" streams of Amazonia, in areas of undisturbed lowland rain forest.

DESCRIPTION. **Plants** flaccid, 1-4 cm long, 1.5-3 mm wide, pinnate, yellowish to pale brown when dry, loosely creeping or hanging, often growing in large masses. **Stems** robust, of thick-walled cells (especially the inner cells thickened), hyalodermis lacking; ventral merophyte 4-10 cells wide. **Leaf lobes** wide-spreading, with very long insertion line, apex rounded to obtuse, plane, margins entire. **Cells** plane, thin-walled, without conspicuous trigones; oil bodies unknown; ocelli lacking. **Lobules** usually reduced, rather flat, with a short or long tooth, hyaline papilla apical or proximal. **Underleaves** bifid to ¼-½, insertion line arched or almost straight. **Gametoecia** on very short branches along both sides of the stem, usually copiously fertile (plants autoicous), gynoecia with 1(-2) lejeuneoid innovations. **Perianths** with 5 ± winged keels, the wings crenate above. **Vegetative reproduction** not observed.

DISCUSSION. The flaccid plants with regularly pinnate branching, stout stems with broad ventral merophytes and non-enlarged epidermis, large leaves with a very long insertion line, bifid underleaves, and numerous tiny gametoecia on short branches along both sides of the stem, are unmistakable. The robust stems and superfertility of the plants are characteristic of the rheophytic members of the Lejeuneaceae (*Cephalantholejeunea, Myriocolea, Myriocoleopsis, Potamolejeunea*) and are apparently adaptations to the rheophytic habitat. The very longly inserted leaves of *Potamolejeunea* may be another adaptive feature and is also found in the aquatic *Bromeliophila* and *Cephalantholejeunea*. For differences with *Cephalantholejeunea*, previously considered the sister genus of *Potamolejeunea* but now placed in the tribe Ptychantheae, see under the latter genus.

According to Reiner-Drehwald (in press), the name *Potamolejeunea* is a synonym of *Trachylejeunea* and should be replaced by *Neopotamolejeunea*.

LITERATURE. Reiner-Drehwald, M. E. 1999. On *Potamolejeunea polyantha* (Mont.) E.Reiner & Goda comb. nov. (Lejeuneaceae), a poorly known rheophytic liverwort from South America. Haussknechtia Beiheft 9: 299-306. - Reiner-Drehwald, M. E. (in press). On *Potamolejeunea* and *Neopotamolejeunea* gen. nov. Nova Hedwigia. - Spruce, R. 1884. *Lejeunea* subgenus *Potamolejeunea*. Hepaticae Amazonicae et Andinae. Transactions and Proceedings of the Botanical Society of Edinburgh 15: 249-251 [descr. of 3 spp.].

Prionolejeunea (Fig. 52) - A primarily neotropical genus of about 10-20 species, mostly at rather low elevations in tropical America. A few species occur in tropical Africa.

HABITAT. On bark, rotten wood, and leaves, occasionally on rock, in the understory of very humid lowland and lower montane rain forests, rarely extending to the upper montane rain forest, 0-2000(-3300) m. The species invariably grow in very moist environments and are normally restricted to the dense undergrowth of the forest. They mostly occur in primary and old-growth secondary forests, usually below 2000 m, with the exception of *Prionolejeunea schlimiana* (Gott.) Steph., which is a characteristic species of montane cloud forests in the northern Andes, to 3300 m.

DESCRIPTION. **Plants** very small to medium-sized, 1-2(-4) cm long, 0.5-1.5 mm wide, pale green to yellowish-brown, creeping, rarely pendent (*P. magnistipula* Herzog). **Stems** with hyalodermis; ventral merophyte 2 cells wide. **Leaf lobes** suberect to wide-spreading, from a narrow base rather abruptly dilated beyond the keel, apex acute-apiculate to rounded, margins crenulate-denticulate by conically projecting cells, the tips of the projecting cells often thickened by a papilla, lobe surface smooth, rarely spinose-papillose. **Cells** convex, with trigones and intermediate thickenings, cuticle smooth; oil bodies small, finely granular, mostly only one per cell; ocelli lacking, sometimes with “pseudo-ocelli“ (=

[3] The illustration of “*Potamolejeunea*“ (Fig. 51) is *Trachylejeunea polystachya* (Spruce) E. Reiner.

enlarged cells at leaf base resembling ocelli). **Lobules** ca. 1/3 leaf length, sometimes reduced, ovate-inflated, with a 1-celled tooth, hyaline papilla proximal, keel usually strongly arched. **Underleaves** small, 1-3x stem width, deeply bifid with a broad sinus, margins often with a few teeth, insertion line curved. **Autoicous**. **Androecial bracteoles** restricted to the base of the spike. **Gynoecia** usually on short branches, without innovations or with 1 short, pycnolejeuneoid (or lejeuneoid?) innovation, the innovation often with androecia. **Perianths** flattened-pyriform, somewhat inflated ventrally and with 2 broad lateral keels that are usually expanded above into short auricles. **Vegetative reproduction** rare, by means of caducous leaves, cladia, or linear, thalloid gemmae from the leaf margins.

DISCUSSION. *Prionolejeunea* may be recognized by the usually small, delicate plants with crenulate-denticulate leaf margins (leaf surface smooth), by the small, deeply bifid underleaves with a rather wide sinus, the flattened perianths with two low, entire to dentate-laciniate auricles (no auricles in *P. exauriculata* A. Evans), and the usual absence of innovations. The leaf denticulations are typically formed by conically projecting cells, which are usually somewhat thick-walled at the tips (crowned by a small papilla). They are normally restricted to the leaf margins; in *P. fendleri* Steph., *P. trachyodes* (Spruce) Steph., and some undescribed taxa from Colombia (Schuster, 1992) they are present all over the dorsal leaf surface, like in *Echinocolea*. Leaf shape in *Prionolejeunea* is also quite characteristic, the lobes broadening abruptly, and considerably beyond the lobule, from a very narrow base. As a consequence, the keel of the lobule stands at a sharp angle to the ventral margin of the lobe. Oil bodies in *Prionolejeunea* seem to be almost consistently 1 per cell (rarely more). Ocelli are completely lacking.

Prionolejeunea is closely related to *Cyclolejeunea* and *Echinocolea*; for a discussion of the differences see under the latter genera. The species of *Prionolejeunea* are very poorly known and apart from the treatment of the Puerto Rican species by Evans (1904) and Spruce's descriptions of selected Amazonian and Andean species, there is little means to identify them.

LITERATURE. Evans, A. W. 1904. Hepaticae of Puerto Rico IV. Bulletin of the Torrey Botanical Club 31: 183-226 [descr. of 5 spp.]. - Schuster, R. M. 1992. The oil bodies of the Hepaticae. II. Lejeuneaceae. Journal of the Hattori Botanical Laboratory 72: 163-359 [*Prionolejeunea* on p. 300-310]. - Spruce, R. 1884. *Lejeunea* subgenus *Prionolejeunea*. Hepaticae Amazonicae et Andinae. Transactions and Proceedings of the Botanical Society of Edinburgh 15: 152-161 [descr. of 10 spp.].

Pycnolejeunea (Fig. 52) - A pantropical genus (9 spp.), with 5 species at low to medium elevations in tropical America (He, 1999).

HABITAT. Typical canopy epiphytes of trunks, branches, and twigs in lowland and submontane rain forests, also in scrubby vegetation and on isolated trees, always in rather open and sunny environments, 0-1500(-2000) m. In dense forests, the species of *Pycnolejeunea* always occur at the forest margin, in gaps, or in the high canopy, and avoid the shaded interior.

DESCRIPTION. **Plants** small to rather robust, 1-4 cm long, 1-2.5 mm wide, dull and pale whitish to brownish, creeping. **Stems** of thick-walled cells, hyalodermis lacking; ventral merophyte 2(-4) cells wide. **Leaf lobes** wide-spreading, with ocelli, apex rounded, often recurved, margins usually entire. **Cells** convex, usually with large trigones, cuticle smooth; oil bodies large, coarsely granular. **Ocelli** large, scattered or restricted to the base of the lobe, lacking in underleaves. **Lobules** small or large, 1/6-1/2 leaf length, apical tooth 1-celled, short-obtuse to somewhat elongated-acute, hyaline papilla proximal. **Underleaves** usually large, narrowly bifid, orbicular to very broad-reniform, insertion line shallowly curved or arched. **Androecial bracteoles** restricted to the base of the spike. **Gynoecia** on elongated shoots, with 1-2 pycnolejeuneoid innovations. **Perianths** flattened, with 5 smooth keels. **Vegetative reproduction** not observed.

DISCUSSION. The presence of ocelli in the leaf lobes (not in the underleaves), the dull, whitish or brownish color of the plants, the rigid stems of thick-walled cells, the rounded leaf lobes with entire margins, the rather large trigones, the large, coarsely granular oil bodies, the usually broad underleaves, and the pycnolejeuneoid innovations are characteristic of *Pycnolejeunea*. The genus is most closely related to *Cheilolejeunea,* especially subgen. *Euosmolejeunea*, but the latter lacks ocelli and has a distal hyaline papilla.

LITERATURE. He, X.-L. 1999. A taxonomic monograph of the genus *Pycnolejeunea* (Lejeuneaceae, Hepaticae). Acta Botanica Fennica 163: 1-77.

Rectolejeunea (Fig. 52) - A small genus of probably no more than 3 species, *R. berteroana* (Gott.) A. Evans, *R. flagelliformis* A. Evans, and *R. emarginuliflora* (Gott. ex Schiffn.) A. Evans, at low elevations in the West Indies, Central America, northern South America, and SE Brazil. The genus is thus far only known from the Neotropics.

HABITAT. On twigs, bark, and living leaves in the canopy, in gaps, and at the margins of primary and secondary lowland and submontane rain forests, occasionally to the lower montane belt, in rather open but always humid environments, 0-1000(-1600) m. *Rectolejeunea emarginuliflora* and *R.*

flagelliformis seem to be exclusively lowland-submontane species. *Rectolejeunea berteroana* extends higher up and may also occur in the lower montane forest; it is a rather common species in SE Brazilian restinga vegetation.

DESCRIPTION. **Plants** small, 0.7-1 mm wide, dull pale green, creeping but often with a few tiny, stiffly upright flagelliform shoots. **Stems** with hyalodermis; ventral merophyte 2 cells wide. **Leaf lobes** wide-spreading, plane, apex rounded, margins entire, sometimes producing short rhizoids (on stems terminating in a flagelliform shoot), ventral margin forming a straight line with the keel. **Cells** plane, small, ca. 14-18 µm long in the middle of the lobe, walls thin or uniformly thickened, without trigones; oil bodies lacking in green cells or minute; ocelli present at the leaf base (usually forming a short row) and sometimes scattered through the lobe. **Lobules** small, ca. 1/4 leaf length, strongly inflated, ovoid, mouth truncate, apical tooth 1-celled, long and falcate-acuminate, hyaline papilla proximal. **Underleaves** bifid, small, without ocelli, obovate, margins angulate, insertion line almost straight. **Gynoecia** on long shoots, with 1-2 pycnolejeuneoid innovations. **Perianths** compressed, 3-keeled, with a broad 2-angled ventral keel. **Vegetative reproduction** by caducous leaves with marginal rhizoids, the caducous leaves usually small, without lobules and produced on upright flagelliform shoots, sometimes produced on ordinary leafy shoots (*R. emarginuliflora*).

DISCUSSION. The species of *Rectolejeunea* are typically twig-epiphytes that reproduce vegetatively by small caducous leaves with marginal rhizoids. In *R. flagelliformis* and *R. berteroana*, the caducous leaves are developed on specialized, upright flagelliform shoots but in *R. emarginuliflora* they are produced on ordinary leafy shoots. The ocellate leaves with small cells with ± uniformly thickened walls, the ovoid lobules with a long, sharp tooth, and the pycnolejeuneoid innovations are further characteristics of this genus.

Rectolejeunea is defined here in a narrow sense, following Grolle (1995). The species of subgen. *Heterolejeunea* (*R. phyllobola*, *R. brittoniae*, etc.) and subgen. *Chaetolejeunea* (*R. pililoba,* etc.) are referred to the genus *Lejeunea* (see there). They differ significantly from *Rectolejeunea* in the lack of ocelli, larger leaf cells, trigones instead of uniformly thickened cell walls, very different lobules, and lejeuneoid instead of pycnolejeuneoid innovations.

LITERATURE. Evans, A. W. 1906. Hepaticae of Puerto Rico VI. Bulletin of the Torrey Botanical Club 33: 1-25 [descr. of 3 spp.]. - Grolle, R. 1995. An annotated catalogue of the Hepaticae and Anthocerotae of the East African Islands. Bryophytorum Bibliotheca 48: 1-178 [note on the genus *Rectolejeunea* on p. 16]. - Schuster, R. M. 1980. The Hepaticae and Anthocerotae of North America, Vol. IV: 1156-1160. [descr. of 1 species].

Rhaphidolejeunea (Fig. 53) - A southeast Asian genus (9 species) with 1 species, *R. polyrhiza* (Nees) Bischl., at low elevations in northern South America (Amazonia, French Guiana). The genus apparently does not occur in Africa and is one of the few hepatic genera with a tropical Asiatic-American distribution (other examples: *Pictolejeunea*, *Spruceanthus*).

HABITAT. *Rhaphidolejeunea polyrhiza* is exclusively epiphyllous and grows on smooth, leathery leaves in the understory of virgin lowland rain forest, from sea level to 550 m. The Asian species of the genus are also typical epiphylls (with few exceptions).

DESCRIPTION. **Plants** very small, to 1.5 cm long, 0.4-0.5 mm wide, green to pale brown, creeping. **Stems** of 7 outer cells and 3 inner cells, epidermis slightly enlarged; ventral merophyte 2 cells wide. **Leaf lobes** obliquely spreading, short ovate-elliptical with a broad base, with ocelli, apex rounded, plane, margins entire or crenulate. **Cells** small, ca. 20 µm in leaf middle, with evenly thickened walls, trigones ± lacking, cuticle smooth; oil bodies unknown in the neotropical species. **Ocelli** colorless, 2-3 in a row in the lower half of the leaf, the basal-most ocellus not conspicuously enlarged. **Lobules** usually reduced, when well-developed 1/3-1/2 leaf length, inflated, apical tooth 1-celled, long-falcate and sharp, hyaline papilla proximal. **Underleaves** small, remote, often with a large, adhesive rhizoid disc, bifid with very slender, almost horizontally diverging lobes, the lobes 3 cells long and 1 cell wide, lamina with a weak border, insertion line straight. **Gynoecia** on short branches, with 1 pycnolejeuneoid innovation. **Perianths** inflated, 5-keeled above, the keels extending into short, horn-like projections. **Vegetative reproduction** by cladia.

DISCUSSION. In its elliptical leaves with a broad rounded apex and seriate ocelli, *Rhaphidolejeunea* is similar to *Leptolejeunea*. It differs from the latter, however, in the smaller, evenly thick-walled leaf cells, the long-falcate lobule tooth, the frequent occurrence of reduced lobules, the lack of a conspicuous border of large cells along the underleaf margins, and the presence of innovations (one per gynoecium). According to Grolle & Zhu (2000), *Rhaphidolejeunea* is a subgenus of *Drepanolejeunea*.

LITERATURE. Bischler, H. 1968. Monographie du genre *Rhaphidolejeunea* Herzog. Revue Bryologique et Lichénologique 36: 56-104 [key]. – Grolle, R. & R. L. Zhu. 2000. A study of *Drepanolejeunea* subg. *Rhaphidolejeunea* (Herzog) Grolle & R. L. Zhu, stat. nov. Nova Hedwigia 70: 373-396.

Schusterolejeunea (= *Cladocolea*) (Fig. 53) - A monotypic, neotropical genus, with *S. inundata* (Spruce) Grolle in the Guianas and in inner Amazonia (upper Río Negro, Río Uaupés, Amazonian Peru). The species has a characteristic, peri-Amazonian distribution, occurring only at the northern and westernmost limits of the Amazon Basin, towards the origins of the main tributaries of the Amazon River.

HABITAT. On branches of trees, roots, and rock in and along streams, in areas of undisturbed lowland rain forest, to 100 m. Rarely on living leaves.

DESCRIPTION. **Plants** small, 1-1.3 mm wide, pale green, creeping to loosely pendent. **Stems** of thick-walled cells, epidermis hardly enlarged, hyalodermis lacking; ventral merophyte 2 cells wide. **Leaf lobes** obliquely spreading, elliptical, 2(-3)x as long as wide, apex rounded, plane, margins entire, base of the lobe very narrow, insertion line only 2-3 cells long. **Cells** pellucid, thin-walled, without trigones; oil bodies unknown; ocelli lacking. **Lobules** small, with very narrow base, quite variable in shape, triangular with a short apex to narrowly ligulate with the apex longly and broadly expanded (beyond the keel), standing obliquely upwards, hyaline papilla terminal (proximal?) at the apex. **Underleaves** tiny, narrower than the stem, longer than wide, narrowly bifid with erect, lanceolate lobes. **Autoicous**. **Gametoecia** numerous, on very short branches (shorter than leaves) at both sides of the stem. **Gynoecia** 2-4 in a monochasial row, each gynoecium with 1 pycnolejeuneoid or lejeuneoid innovation which is again fertile (except the outermost one). **Perianths** inflated, with 5 smooth keels. **Vegetative reproduction** not observed.

DISCUSSION. *Schusterolejeunea* is a peculiar rheophytic member of the Lejeuneae. It is characterized by obliquely spreading, narrow-elliptical leaves with a very narrow, almost transverse insertion on the stem, thin stems with only 7 rows of epidermal cells (most rheophytes have much more robust stems), ligulate lobules, and very tiny, bifid underleaves, which are narrower than the stem and distinctly longer than wide. The male and female branches are very small, shorter than the leaves, and the perianths are in small clusters.

The peri-Amazonian distribution of the only species, *S. inundata*, is another distinctive feature of the genus.

LITERATURE. Grolle, R. 1980. *Schusterolejeunea* Grolle nom. nov. statt *Cladocolea* Schust. 1963, *non* van Tieghem 1895. Journal of Bryology 11: 105-106. - Kachroo, P. 1967. Three new genera of Lejeuneaceae. Philippine Journal of Science 96: 9-23 [as *Cladocolea*].

Sphaerolejeunea (Fig. 53) - A monotypic, neotropical genus, with *S. umbilicata* Herzog in the Western Cordillera of the Andes of Colombia (Dept. Cauca). The species is known only from the type collection (*Killlip s.n.*, 1922).

HABITAT. On living leaves, presumably in undisturbed, humid lower montane rain forest, 1400-1800 m.

DESCRIPTION. **Plants** epiphyllous, 2 mm wide, pale green, creeping. **Stems** with hyalodermis; ventral merophyte 2 cells wide. **Leaf lobes** spreading, plane, suborbicular, apex broadly rounded, margins entire, bordered by tangentially elongated, dead and hyaline cells in 1-2 rows. **Cells** very thin-walled, without trigones, hyaline; oil bodies unknown; ocelli lacking. **Lobules** small, 1/6 leaf length, subquadrate with truncate apex, strongly inflated-globose for the most part, flattened at apex and free margin, apical tooth blunt, 1-2 cells long, hyaline papilla proximal. **Underleaves** small, ca. 2x stem width, narrowly bifid, tips obtuse, bases cordate, with large adhesive rhizoid discs. **Autoicous**. **Gynoecia** on very short branches, with or without one short, sterile innovation. **Perianths** inflated and smooth, without keels, apex umbilicate, beak absent. **Vegetative reproduction** not observed.

DISCUSSION. In its sessile gynoecia mostly without innovations, *Sphaerolejeunea* resembles *Macrolejeunea*, but the small underleaves, strongly inflated lobules, and bordered leaves separate it from the latter.

In spite of intensive bryological collecting in the northern Andes in recent years, *Sphaerolejeunea umbilicata* has not been recorded since its discovery in 1922. Apparently, it is a rare species. In view of the massive deforestation of the area in which it has been found, the species is considered endangered.

LITERATURE. Herzog, T. 1938. *Sphaerolejeunea*, eine neue Gattung der Lejeuneaceae Schizostipae. Annales Bryologici 11: 86-89.

Taxilejeunea (including *Dicladolejeunea*) (Fig. 54) - A large, primarily neotropical genus of about 20-30 species, mostly at montane elevations.

HABITAT. Hanging from trunks and branches of trees and twigs in very humid lowland and montane rain forests and subalpine scrub, or creeping loosely over litter, living leaves, etc., always in very humid environments, (0-)1000-3000 m.

DESCRIPTION. **Plants** usually long and slender, 2-10 cm long, 1-2 mm wide, pale green to yellowish-green to whitish, loosely creeping to laxly pendent. **Stems** with hyalodermis, medulla in robust plants of more than 25 cell rows; ventral merophyte 2 cells wide. **Leaf lobes** spreading, apex acute-acuminate or apiculate, occasionally rounded, plane, margins entire or toothed. **Cells** plane, with or without small trigones and intermediate thickenings; oil bodies small, finely granular, occasionally homogeneous; ocelli lacking. **Lobules** usually very small, ovate, apical tooth short and blunt, hyaline papilla proximal. **Underleaves** bifid, large, (3-)4-10x stem width, base often cordate, insertion line curved to deeply arched. Usually autoicous. **Gynoecia** on short branches 2-6 in a cymose row, each gynoecium with a short lejeuneoid innovation which becomes fertile again; bracts small, with reduced lobules. **Perianths** small, inflated, eplicate or with 5 smooth or toothed keels. **Vegetative reproduction** not observed.

DISCUSSION. The species of *Taxilejeunea* are typically pale-colored, soft-textured, long and slender plants, with rather large, bifid underleaves having (deeply) cordate bases, rounded to pointed leaves made up of large, thin-walled cells, tiny lobules and, most importantly, gynoecia arranged in rows on lateral branches. Each gynoecium is subtended by a short innovation which quickly and repeatedly becomes fertile again, thus creating a sympodial branch system of 2-6 gynoecia arranged in a row.

The female branches are usually small and slender (sometimes falcate), with leaves much smaller than those of the main stems, and the perianths are often tiny and inconspicuous. The latter vary from completely smooth and eplicate in the common *Taxilejeunea sulphurea* (Lehm. & Lindenb.) Schiffn., to 5-keeled with the keels smooth or irregularly winged-dentate above in the common *T. pterigonia* (Lehm. & Lindenb.) Schiffn. and its allies.

The neotropical species of *Taxilejeunea* are very poorly known and the taxonomy of the genus is in a chaotic state. A revision of the species is urgently needed.

LITERATURE. Evans, A. W. 1921. *Taxilejeunea pterogonia* and certain allied species. Bulletin of the Torrey Botanical Club 48: 107-136 [descr. of 4 spp.]. - Spruce, R. 1884. *Lejeunea* subgenus *Taxilejeunea*. Hepaticae Amazonicae et Andinae. Transactions and Proceedings of the Botanical Society of Edinburgh 15: 212-224 [descr. of 15 spp].

Trachylejeunea (Fig. 54) - A neotropical genus with less than 10 species at low elevations in the West Indies, northern South America (Amazon Basin, Guianas), and southeastern Brazil.

HABITAT. On rotten logs in the understory of virgin lowland and lower montane rain forests, 0-2000 m. Occasionally on rock, soil, or the bark of living trunks. In the West Indies, the species seem to occur primarily in montane forests, in northern South America mostly in lowland rain forest.

DESCRIPTION. **Plants** small, 1-2 cm long, 0.8-1 mm wide, dull gray-green to brown, creeping. **Stems** of thin- or thick-walled cells, hyalodermis present or absent; ventral merophyte 2-4(-6) cells wide. **Leaf lobes** densely imbricate-convex, wide-spreading, with or without ocelli, apex usually rounded, rarely acuminate (*Trachylejeunea acanthina* (Spruce) Schiffn.), often recurved, margins crenulate to dentate, sometimes coarsely papillose. **Cells** convex, trigones small or large, cuticle smooth or with a large papilla; oil bodies large, coarsely granular. **Ocelli** 1-several at lobe base or lacking, sometimes forming a short vitta, lacking in underleaves. **Lobules** 1/3-1/2 leaf length, inflated, often with two closely associated short, blunt, 1-celled teeth, hyaline papilla proximal on the inner side of the lobule. **Underleaves** usually small and distant, 2-3x stem width, bifid, margins crenulate or coarsely toothed, suborbicular, insertion line curved. **Androecial bracteoles** restricted to the base of the spike. **Gynoecia** usually on short branches, with or without 1 short, pycnolejeuneoid innovation. **Perianths** flattened, with 5 crenulate-papillose or toothed keels. **Vegetative reproduction** not observed.

DISCUSSION. The genus *Trachylejeunea*, as currently circumscribed, is rather heterogenous and most of the species are poorly known (Schuster, 1992; Pócs, 1999). Many species have been erroneously included in this genus in the past. The most distinctive character of *Trachylejeunea*, seen in the type species *T. anaeogyna* (Spruce) Grolle, is probably the presence of two closely associated, 1-celled teeth at the lobule apex, with the hyaline papilla situated on the inner surface of the lobule, at the proximal side of the first tooth. *T. anaeogyna* usually lacks innovations and often has microphyllous branches.

The species of *Trachylejeunea* are mostly small, creeping plants with, typically, a rather dull grayish-green color, small, distant underleaves, and densely imbricate leaves with crenulate-denticulate margins. In some species there are several large ocelli near leaf base; additional smaller ocelli may occur scattered in the upper half of the leaf (in *T. pandurantha* (Spruce) Steph.). The underleaves are always devoid of ocelli.

A revision of the genus *Trachylejeunea* by X.-L. He is in preparation.

LITERATURE. Pócs, T. 1999. *Trachylejeunea grolleana*, a new representative of the Neotropical subgenus *Hygrolejeuneopsis* in Madagascar. Haussknechtia Beiheft 9: 283-290. -

Schuster, R. M. 1992. The oil bodies of the Hepaticae. II. Lejeuneaceae. Journal of the Hattori Botanical Laboratory 72: 163-359 [*Trachylejeunea* on p. 251-255]. - Spruce, R. 1884. *Lejeunea* subgenus *Trachylejeunea*. Hepaticae Amazonicae et Andinae. Transactions and Proceedings of the Botanical Society of Edinburgh 15: 180-186 [descr. of 6 spp.].

Vitalianthus (Fig. 54) - A monotypic, neotropical genus, with *V. bischlerianus* (Porto & Grolle) Schust. & Giancotti endemic to the Atlantic coast of Brazil, from Pernambuco to Paraná.

HABITAT. On bark in primary or secondary lowland and submontane rain forest, 0-800 m.

DESCRIPTION. **Plants** very small, 0.3-0.6 mm wide, yellow-green to olive-brown to dark brown, creeping. **Stems** of 7 outer cell rows and 3 smaller inner rows, cells thick-walled, hyalodermis lacking; ventral merophyte 2 cells wide. **Leaf lobes** rather wide-spreading, with ocelli, broadly ovate-falcate, apex acute to obtuse, plane or recurved, margins crenulate. **Cells** small, 15-20 µm in leaf middle, with small trigones, cuticle smooth; oil bodies finely granular. **Ocelli** colorless, 3-6 in an unbroken row near the leaf base, forming a short vitta, also present in female bracts and perianths. **Lobules** large, 2/5 leaf length, sometimes reduced, apical tooth 1-celled, long-falcate, a "pre-apical" tooth present at the junction between the lobule and ventral leaf margin, leaving a circular opening to the interior of the lobule, hyaline papilla proximal. **Underleaves** narrowly bifid to 1/2, lobes erect, very narrow, margins angular, insertion line straight. **Gynoecia** on short branches, with 1 pycnolejeuneoid innovation. **Perianths** somewhat flattened, bluntly 4-5-keeled, the keels smooth or crenulate, dorsal surface smooth or with a low keel. **Vegetative reproduction** by fragmentation.

DISCUSSION. The peculiar, Brazilian endemic *Vitalianthus bischlerianus* was originally described as a species of *Drepanolejeunea* because of the narrow-based, asymmetrically ovate-falcate leaves, 2-toothed lobule apex, presence of ocelli in leaves, very narrow underleaf lobes, and pycnolejeunoid innovations. However, the species differs from *Drepanolejeunea* in several important respects: 1) the underleaf lobes are upright instead of diverging, 2) the ocelli are in a continuous row rather than a broken one, 3) the perianth keels are ± smooth, without horn-like projections, and 4) vegetative reproduction is by fragmentation rather than by specialized caducous branches or cladia. Because of these differences, the species has been placed in a genus of its own.

LITERATURE. Pôrto, K. C. & R. Grolle. 1987. *Drepanolejeunea bischleriana* sp. nov. du Brésil. Cryptogamie, Bryologie et Lichénologie 8: 301-304. - Schuster, R. M. 1994. Studies on Lejeuneaceae, I. Preliminary studies on new genera of Lejeuneaceae. Journal of the Hattori Botanical Laboratory 75: 211-235.

LEJEUNEACEAE Tribe COLOLEJEUNEAE

Plants usually small and pale green, sometimes deep green, rarely brown. Stems very thin; ventral merophyte only 1-2 cells wide. Vegetative branching *Lejeunea*-type, rarely *Aphanolejeunea*-type; *Frullania*-type branches lacking. Leaf insertion very short. Lobule apex with hyaline papilla at the margin. Ocelli present or absent. Underleaves 1 per leaf and mostly bifid, or absent (then one rhizoid bundle per leaf). Androecia on short-specialized branches, male bracteoles restricted to the base of the spike, occasionally present throughout, male bracts with large, hypostatic lobules. Perianths with 0-2 ventral keels. Seta articulate, of only 12 outer rows of cells and 4 inner rows. Capsule valves suberect after dehiscence, pale, cells of outer layer thin-walled, cells of inner layer with small, nodulose wall thickenings. Elaters few, upper ends attached to valve margins only, spiral rudimentary, pale. Spores elongate-rectangular, without rosettes.

DISCUSSION. Eight genera worldwide; 5 in tropical America. The tribe Cololejeuneae is characterized by the "pendular" leaf segmentation: instead of developing one underleaf for each leaf pair, each leaf is associated with an underleaf (or with a rhizoid bundle, see below).

Two groups of genera may be recognized: those that produce underleaves (*Diplasiolejeunea*, *Colura*) and those that do not (*Cololejeunea, Aphanolejeunea, Myriocoleopsis*). In the second group, the pendular segmentation is apparent in the presence of a small bundle of rhizoids - always associated with underleaf bases in Lejeuneaceae - near the ventral base of each leaf.

Pendular segmentation is not restricted to the Cololejeuneae but commonly occurs in juvenile leafy hepatics, and is apparently a juvenile character in the order Jungermanniales (Fulford, 1957). The very thin stems of *Cololejeunea* and *Aphanolejeunea*, consisting of only 5 outer rows of cells and one inner row, are also characteristic of juvenile plants. The retention of these juvenile features in the adult phases of the Cololejeuneae is a case of paedomorphosis or neoteny and may be interpreted as an adaptation to their short-lived, epiphyllous or ramicolous habitat, enhancing rapid completion of the life cycle in ephemeral environments.

LITERATURE. Fulford, M. H. 1957. The young stages of the leafy Hepaticae: a resumé. Phytomorphology 6: 199-235. - Schuster, R. M. 1980. The Hepaticae and Anthocerotae of North America, Vol. IV: 1216-1314.

Aphanolejeunea (Fig. 55) - A pantropical genus (ca. 40 spp.), with 20-30 species at low elevations in tropical America.

HABITAT. On living leaves, less common on bark or rock, in the understory of primary and secondary, lowland and lower montane rain forests, always in moist and shaded environments, 0-2000 m.

DESCRIPTION. **Plants** minute, usually less than 0.5 mm wide, pale green, creeping. **Branches** purely *Aphanolejeunea*-type (without collar), or *Aphanolejeunea*-type and *Lejeunea*-type. **Stems** zig-zag, very thin, of 5 outer rows of cells and 1 inner row, with hyalodermis; ventral merophyte only 1 cell wide. **Leaves** distant, spreading, with a very short insertion, ovate-lanceolate, usually of two types, with or without a lobule, surface smooth or rough by conically elevated cells, apex rounded to acuminate, margins often crenulate-denticulate, hyaline border lacking. **Cells** thin-walled with small trigones, cuticle smooth or papillose-tuberculate; oil bodies finely granular; ocelli lacking. **Lobules** inflated when well-developed, with 1 tooth or with 2 teeth side by side, the teeth 1-2-celled and often curved, hyaline papilla distal (when 1 tooth) or ental (when 2 teeth). **Underleaves** absent; rhizoids in small bundles from the ventral side of the stem, near the base of each leaf. **Androecia** with very few pairs of bracts. **Gynoecia** on short or long branches, with 1-2 innovations. **Perianths** inflated, 5-keeled or without keels, smooth or papillose. **Vegetative reproduction** by multicellular, disciform gemmae from the leaf surfaces.

DISCUSSION. The species of *Aphanolejeunea* are among the smallest hepatics and are easily overlooked in the field. They are usually only visible with a good hand-lens. Although the species are common and widespread in the Neotropics, their taxonomy is still poorly understood and even less is known about their distribution. *Aphanolejeunea* is similar to *Cololejeunea* and has often been confused with the latter. Differences include the presence in *Aphanolejeunea* of athecal "*Aphanolejeunea*-type" branches (resembling *Lejeunea*-type branches but lacking a collar) and the usual presence of two types of leaves on a single stem, with and without lobules. Not all species of *Aphanolejeunea* have two types of leaves, but those possessing this character are immediately recognized as members of the genus. Branches in *Aphanolejeunea* are usually purely athecal, but in some species both thecal (*Lejeunea*-type) and athecal (*Aphanolejeunea*-type) branches are present.

A revision of the neotropical species of *Aphanolejeunea* by T. Pócs and A. Bernecker-Lücking is in preparation.

LITERATURE. Lücking, A. 1995. Diversität und Mikrohabitatpräferenzen epiphyller Moose in einem tropischen Regenwald in Costa Rica. Dissertation, Ulm [key to 10 spp.] - Pócs, T. 1984. Present knowledge on *Aphanolejeunea* Evans. Journal of the Hattori Botanical Laboratory 55: 307-313 [synopsis of the spp.]. - Schuster, R. M. 1980. *Aphanolejeunea*. The Hepaticae and Anthocerotae of North America, Vol. IV: 1284-1314. [key to 5 spp.].

Cololejeunea (= *Leptocolea*) (Fig. 55) - A large pantropical genus, with 30-40 species at rather low elevations in tropical America, in 4 subgenera.

HABITAT. Common pioneers on living leaves, less common on bark, rotten wood, or rock, in lowland, submontane and lower montane forests and scrub, usually below 1500 m (rarely higher). Most species grow in moist, shaded environments; a few, including the common *C. cardiocarpa* (Mont.) A. Evans and *C. minutissima* (Sm.) Schiffn., thrive in drier, semi-deciduous forest areas, savanna woodlands, and plantations.

DESCRIPTION. **Plants** very small, 0.2-0.8(-1.2) mm wide, pale green, creeping. **Branches** *Lejeunea*-type, never *Aphanolejeunea*-type. **Stems** usually zig-zag, very thin, with hyalodermis, normally cylindrical and of 5 outer rows of cells and 1 inner row, rarely flat and made up of 4 large cells in a row (*C. linopteroides* H. Rob.); ventral merophyte only 1 cell wide. **Leaf lobes** spreading, ovate-obovate to narrowly lanceolate, insertion very short (only a few cells), apex rounded to acute-acuminate, margins entire to denticulate, sometimes with a hyaline border of dead cells. **Cells** thin-walled with small trigones, sometimes sigmoid, cuticle smooth or papillose-tuberculate; oil bodies finely granular; ocelli lacking or present as a short vitta in subgen. *Taeniolejeunea*. **Lobules** small or large, usually inflated and with a long keel, sometimes reduced or flattened-erect with a short keel, apex with (0-)1-2 teeth, hyaline papilla proximal. **Underleaves** absent; rhizoids in small bundles from the ventral side of the stem, near the base of each leaf. **Androecia** in short spikes (4-10 pairs of bracts). **Gynoecia** on short or long branches, with 0-2 innovations. **Perianths** inflated 5-keeled or flattened 2-keeled, smooth or papillose. **Vegetative reproduction** by multicellular, disciform gemmae from the leaf surfaces.

DISCUSSION. The small plants with very thin stems without underleaves are unmistakable. *Cololejeunea* may only be confused with *Aphanolejeunea* (see there). The neotropical species may be classified in 4 subgenera (Tixier, 1991): *Pedinolejeunea* (ca. 20 spp.) characterized by hyaline-bordered leaves (at apex or all around) and flattened perianths, *Taeniolejeunea* (1-2 spp.) characterized by a row of ocelli in the leaf lobes, forming a vitta, and *Protocolea* (ca. 7 spp.) and *Cololejeunea* (6-7 spp.), both with unbordered leaves and inflated perianths. The limits of the last two

subgenera are not sharp but the majority of the species of subgen. *Cololejeunea* have papillose cells whereas members of *Protocolea* are always smooth-celled.

A revision of the neotropical species of *Cololejeunea* by T. Pócs and the late P. Tixier is in preparation.

LITERATURE. Schuster, R. M. 1980. *Cololejeunea*. The Hepaticae and Anthocerotae of North America, Vol. IV: 1230-1284. [key to 7 spp.]. - Tixier, P. 1991. Bryophyta exotica 9. Quelques Lejeuneaceae (Hépatiques) nouvelles pour l'Amérique du Sud. Candollea 46: 267-302 [key to 30 neotropical spp.].

Colura (Fig. 56) - A large pantropical genus (ca. 80 spp.), with 13 species in tropical America, in 5 sections: sect. *Lingua* (= genus *Macrocolura*) with 2(-3) spp., sect. *Oidocorys* with 3 spp., sect. *Colura* (= sect. *Macrorhamphus*) with 3 spp., sect. *Harmophyllum* (= sect. *Eucolura*) with 4 spp., and sect. *Gamolepis* with 1 species.

HABITAT. On fine twigs, living leaves, and trunks of trees in lowland and montane rain forests, also in scrubby vegetation, in plantations, and on isolated trees, always in well-illuminated sites, 0-3800 m. In high, dense forests *Colura* grows almost exclusively in the canopy, in gaps, or at forest margins, avoiding the shaded forest understory.

The altitudinal ranges of the different sections differ considerably. The species of sect. *Gamolepis* and sect. *Harmophyllum* are warm-tropical taxa of lowland and submontane regions, below 1000 m, those of sect. *Lingua* (*C. clavigera* (Gott.) Jovet-Ast, *C. lyrata* Steph.) are taxa of ± undisturbed cloud forests at mid-elevations and are very rare in lowland regions. Members of sect. *Oidocorys* have a very different distribution and are cool-temperate taxa, occurring in scrubby, subalpine vegetation and lower edges of páramos, between 3200 and 3800 m in the northern Andes (*C. naumannii* Steph., *C. ornithocephala* Herzog) and at about 2400 m on Serra de Itatiaia (*C. itatyana* Steph.). Finally, species of sect. *Colura* have a mostly lower-montane range in the Neotropics; the most common member, *C. tenuicornis* (A. Evans) Steph., usually occurs between 500-2500 m, but at somewhat lower elevations on islands. In the Galapagos archipelago, for example, it is a common epiphyllous species in coffee plantations between 200 and 400 m.

DESCRIPTION. **Plants** very small, usually less than 1 mm wide, pale green to yellow-green, becoming brownish when dry, creeping. **Stems** of ± thin-walled, pale cells, with hyalodermis; ventral merophyte 2 cells wide. **Leaves** usually upright (sometimes ascending only, e.g., in sect. *Lingua*), longer than wide, in the upper half with a closed sac formed by the lobule, margins entire or toothed. **Cells** of the lobe isodiametric-hexagonal to elongated, smooth or mammillose-papillose, usually with trigones; oil bodies homogeneous or granular; ocelli lacking. **Lobules** longer than the lobe, cylindrical, from a narrow base widening above into a closed sac, the sac rounded, conical, or cylindrical, sometimes with a long, linear beak (*C. tenuicornis*), the opening at the base closed by a valve. **Underleaves** 1 per lateral leaf, densely overlapping, bifid with diverging lobes, rarely merely emarginate, margins entire or with a tooth-like appendage (*C. clavigera, C. lyrata*), insertion line curved. **Gynoecia** on long or short shoots, with 1-2 innovations. **Perianths** with 3-5 smooth or horned keels. **Vegetative reproduction** by multicellular, disciform gemmae from the upper part of the sac.

DISCUSSION. The peculiar leaves, with an apical sac formed by a prolongation of the lobule, are a unique and unmistakable feature of *Colura*. In other respects (underleaves, gametoecia), the genus is rather similar to *Diplasiolejeunea*. The sac varies greatly in shape and size and has a complicated aperture mechanism like in Pleuroziaceae, made up of a valve and a hinge. The morphology of the valve varies considerably and has been a basis for subdividing the genus into sections (Jovet-Ast, 1953). One of them, sect. *Lingua*, has recently been raised to generic level (*Macrocolura* Schust.) based on the peculiar underleaf appendages and the presence of granular instead of homogeneous oil bodies (Schuster, 1994). Granular oil bodies, however, are not unique to this group and also occur in sect. *Oidocorys* and sect. *Gamolepis*.

The underleaves in *Colura* are normally bifid but in the rare *C. itatyana* (sect. *Oidocorys*) from Serra de Itatiaia they are merely emarginate, resembling those of "holostipous" Lejeuneaceae.

LITERATURE. Gradstein, S. R. 1986. The genus *Colura* (Hepaticae) in the Galapagos Islands. Hikobia 9: 353-356 [ecol.]. - Jovet-Ast, S. 1953. Le genre *Colura*. Revue Bryologique et Lichénologique 22: 206-312 [key]. - Schuster, R. M. 1994. Studies on Lejeuneaceae, I. Preliminary studies on new genera of Lejeuneaceae. Journal of the Hattori Botanical Laboratory 75: 211-235.

Diplasiolejeunea (Fig. 56) - A pantropical genus (ca. 40 spp.) with about 20 species in tropical America.

HABITAT. On living leaves, fine twigs, and smooth-barked trunks in lowland and montane rain forests, in scrubby vegetation, on isolated trees and in plantations, usually in well-illuminated sites, from sea level to 3500 m in the northern Andes. In forests, *Diplasiolejeunea* is mostly found in the canopy, at the margins, and in gaps, less commonly in the forest understory. Most of the species are

restricted to rain forest or cloud forest areas except for the common *D. cavifolia* Steph. and *D. rudolphiana* Steph., which are frequently found in more mesic woodlands or scrubby vegetation and may also thrive in plantations or orchards.

DESCRIPTION. **Plants** small to medium-sized, 1-3 cm long, 0.7-2 mm wide, pale green to pale brown, creeping, often closely appressed to the substrate. **Stems** of thick-walled, pale cells, epidermis not or slightly enlarged; ventral merophyte 2 cells wide. **Leaf lobes** wide-spreading, frequently with ocelli, convex, apex rounded, margins entire. **Cells** isodiametric-hexagonal, smooth, walls thin or uniformly thickened, occasionally with trigones; oil bodies small, usually coarsely granular-botryoidal. **Ocelli** scattered in leaf lobes in subgen. *Diplasiolejeunea*. **Lobules** usually large, 1/3-3/4 leaf length, inflated, apex with 2 short or long teeth, hyaline papilla at the inner base of the first tooth. **Underleaves** 1 per lateral leaf, often overlapping, deeply bifid with diverging lobes and a broad, V-shaped sinus, insertion line curved. **Gynoecia** on long or short shoots, with 1 innovation. **Perianths** with 5 sharp, smooth keels. **Vegetative reproduction** by multicellular, disciform gemmae from the leaf surfaces.

DISCUSSION. *Diplasiolejeunea* is easily recognized by the numerous, often densely overlapping underleaves (1 per leaf) with 2 widely diverging lobes. Similar underleaves are found in *Colura,* which differs sharply from *Diplasiolejeunea* (and other Lejeuneaceae) by its peculiar leaves. The underleaf lobes in *Diplasiolejeunea* vary considerably in shape, being very narrow and acute in some species and broad and rounded in others. The species typically grow very closely appressed to the substrate (leaves, twigs, smooth bark) and large rhizoid discs may be produced in epiphyllous plants.

The majority of the neotropical species have ocellate leaf lobes and belong in the subgen. *Diplasiolejeunea*. Hyaline-bordered leaves are characteristic of *Diplasiolejeunea pellucida* (Meisn. ex Spreng.) Schiffn., a very common epiphyllous species. Huge lobules, about 3/4 the length of the leaf lobes, occur in the rare, Central-American *D. involuta* Winkler.

LITERATURE. Evans, A. W. 1912. Hepaticae of Puerto Rico XI. *Diplasiolejeunea*. Bulletin of the Torrey Botanical Club 39: 209-225 [descr. of several spp.]. - Reyes, D. M. 1982. El género *Diplasiolejeunea* en Cuba. Acta Botanica Academiae Scientiarum Hungaricae 28: 145-180 [key to 13 spp.]. - Tixier, P. 1991. Bryophyta exotica 9. Quelques Lejeuneaceae (Hépatiques) nouvelles pour l'Amérique du Sud. Candollea 46: 267-302 [key to 9 neotropical spp.].

Myriocoleopsis (Fig. 56) - A small neotropical genus of 2 species at low elevations in tropical south America: *M. gymnocolea* (Spruce) E. Reiner & Gradst. (= *M. riparia* E. Reiner & Gradst.) in Amazonian Ecuador, southeastern Brazil (Minas Gerais to Santa Catarina) and northern Argentina (Misiones), and *M. fluviatilis* (Steph.) E. Reiner & Gradst. (= *M. puiggarii* Schiffn.) in the state of São Paulo and Santa Catarina.

HABITAT. On rocks in streams, moistened by the spray of the rushing water and periodically inundated, occasionally on small shrubs on the river banks, 100-1300 m.

DESCRIPTION. **Plants** small to medium-sized, 0.5-3 cm long, 0.8-1.2 mm wide, greenish to blackish, upright from a short, creeping, rhizome-like shoot, irregularly branched. **Branches** *Lejeunea*-type, rather long and usually fertile. **Stems** rigid, of thick-walled cells, epidermis not enlarged, in cross-section of 5-30 cells rows. **Leaf lobes** obliquely spreading, obovate, insertion very short, apex rounded, plane, margins entire or crenate. **Cells** thin-walled with small trigones; oil bodies finely granular; ocelli lacking. **Lobules** absent or reduced to a long, flat fold along the ventral margin of the lobe (to 2/3 of lobe length), with a hyaline papilla at the apex. **Underleaves** absent; rhizoids in small bundles from the ventral side of the stem, near the base of each leaf. **Autoicous**. **Androecia** in long spikes of (6-)10-22 pairs of bracts. **Gynoecia** in compound, cymose clusters, the lower gynoecia normally with 2 innovations and the upper ones with 1, the innovations repeatedly floriferous with to 6 perianths in a row. **Perianths** inflated, with 5 smooth keels, base often stalk-like elongated. **Vegetative reproduction** by multicellular, disciform gemmae from the leaf surfaces.

DISCUSSION. *Myriocoleopsis* is the only rheophytic member of the Cololejeuneae in tropical America. It closely resembles *Cololejeunea*, especially *C. minutissima* (subgen. *Protocolea*), but differs in 1) upright, instead of prostrate, growth; 2) possession of a rhizome-like base; 3) rigid stems without a hyalodermis; 4) long androecial spikes; and 5) gynoecia arranged in compound, cymose clusters (2 innovations below, 1 repeatedly fertile above). The plants are adapted to survive prolonged periods of inundation; gametoecia are developed when the plants grow emerged. This feature is characteristic of rheophytic bryophytes and is also seen in *Potamolejeunea*, *Myriocolea,* etc.

The two species of *Myriocoleopsis* are separated by their very different stems. Those of *M. gymnocolea* are like in *Cololejeunea*, consisting in cross section of 6 cells: 5 cortical cells and 1 medullary cell. The stem in *M. fluviatilis*, however, is much more robust and has a cortex of 20-30 cells, in 2-3 layers, surrounding the medullary cell.

LITERATURE. Reiner-Drehwald, M. E. & S. R. Gradstein. 1995. A. new species of *Myriocoleopsis* Schiffn. (Lejeuneaceae) from southeastern Brazil and northeastern Argentina. Journal

of Bryology 18: 479-484. - Reiner-Drehwald, M. E. & S. R. Gradstein. 1997. New combinations and synonyms in *Myriocoleopsis* Schiffn. (Lejeuneaceae). Journal of Bryology 19: 638-640.

LEPICOLEACEAE

A small family of 1-2 genera, 1 genus in tropical America.

Lepicolea (Fig. 57) - A mostly southern-temperate genus of about 8 species; 3 species in tropical America, at high elevations: *L. pruinosa* (Taylor) Spruce in the Andes and Central America (Bolivia to Costa Rica), *L. ramentifissa* Herzog in Bolivia, and *L. ochroleuca* (Spreng.) Spruce in Mexico and Central America. The latter species reoccurs further southwards in southern Brazil, Patagonia, and Tierra del Fuego.

HABITAT. Robust epiphytes of upper montane cloud forests and subalpine scrub, often forming large turfs on trunks and thick canopy branches; also on rock and soil in wet páramos; (1000-)2000-3800 m.

DESCRIPTION. **Plants** robust, to 10 cm long, light gray-green or bluish-green to brown, ascending to erect or pendent, regularly pinnate or 2-pinnate. **Branches** *Frullania*-type and often becoming flagelliform towards the tips, occasionally lateral-intercalary. **Stems** rigid, with a cortex of small, very thick-walled cells in 2-4 layers, the stem surface often with paraphyllia. **Leaves** transverse, deeply 4-lobed (bisbifid), slightly asymmetrical, segments lanceolate, margins densely ciliate-laciniate. **Cells** with thick walls and large trigones, cuticle papillose; oil bodies (in *L. pruinosa*, obs. B. Crandall-Stotler) very small, few per cell, faintly and finely segmented to almost homogeneous. **Underleaves** similar to the leaves but more symmetrical. **Rhizoids** in tufts on the flagelliform branches. **Dioicous**. **Gametoecia** on elongated shoots. **Sporophyte** surrounded by a fleshy perigynium ("coelocaule") densely covered by paraphyllia and scale-like leaves; perianth lacking. **Seta** of numerous cells (cross-section). **Capsule** wall 5-layered. **Vegetative reproduction** unknown.

DISCUSSION. *Lepicolea* is recognized by the large, bipinnate plants with deeply 4-lobed leaves and underleaves, all with ciliate-laciniate margins. The underleaves are as large as the leaves. The stems are covered with numerous paraphyllia in *Lepicolea pruinosa*; in *L. ochroleuca*, however, paraphyllia are lacking.

LITERATURE. Fulford, M. H. 1963. Lepicoleaceae. Manual of the leafy Hepaticae of Latin America, Part I. Memoirs of the New York Botanical Garden 11(1): 30-39 [key].

LEPIDOZIACEAE

(Cladomastigaceae, Paracromastigaceae, Phycolepidoziaceae, Regredicaulaceae, Zoopsidaceae)

Plants with leaves or thalloid, pale green to brown or reddish-brown, creeping to ascending, usually pinnate or forked, sometimes arising from a stoloniferous base. Stems with a weakly differentiated cortex, hyalodermis present or absent. Branches *Frullania*-type (sometimes *Microlepidozia*-type or *Acromastigum*-type) and ventral-intercalary, rarely lateral-intercalary; flagella frequently presentLeaves transverse, incubous or succubous, usually divided into several segments or teeth, rarely undivided, insertion extending to the dorsal midline of the stem or not, leaf margins usually entire. Cells variable, with or without oil bodies. Underleaves well-developed, rarely reduced. Rhizoids in tufts from underleaf bases. Gametoecia on short ventral branches, the androecia occasionally on long shoots. Sporophyte surrounded by a 3-keeled perianth. Seta of 8 or 16 outer rows of cells surrounding many (rarely only 4) small inner cells. Capsule elongate, wall 2-layered. Vegetative reproduction rare, by caducous leaves in *Bazzania*.

DISCUSSION. A family of about 28 genera worldwide, 16 in tropical America. The family is somewhat heterogeneous and is subdivided into several subfamilies. Important characteristics of the Lepidoziaceae are 1) rhizoids in tufts from underleaf bases; 2) gynoecia always on very short ventral branches; 3) seta rather thin, with an epidermis of a limited number of cells surrounding numerous (rarely only 4) small inner cells; 4) leaves usually divided into segments; and 5) underleaves often well-developed. The plants may be pinnately branched (e.g., *Lepidozia*), forked (*Bazzania*), or irregularly branched; in the latter case, the leafy shoots often arise from a branched rhizome system. Gemmae are completely lacking in this family.

LITERATURE. Fulford, M. H. 1963-68. Manual of the leafy Hepaticae of Latin America, Parts I-III. Memoirs of the New York Botanical Garden 11 (1-3).

1. Plants without leaves (except for the sexual branches), consisting of a small thallus, a minute shoot or a filamentous protonema 2
1. Plants with leaves 5
2. Plants consisting of a small thallus with a narrow midrib and unistratose wings .... **Pteropsiella**
2. Plants not thalloid 3
3. Plants consisting of protonematal filaments of 1 row of cells ..... **Protocephalozia**
3. Plants consisting of minute shoots of several rows of cells (2 dorsal rows) 4
4. Leaves rudimentary, consisting of one cell with a slime papilla on top. Stems flattened. Rhizoids arising in small tufts (or absent) ..... **Arachniopsis monodactyla**
4. Leaves entirely lacking, sometimes represented by small slime papillae. Stems cylindrical. Rhizoids scattered, arising singly (or absent) ..... **Phycolepidozia**
5. Leaves of 1-4 hair-like, uniseriate filaments, lamina lacking or very short 6
5. Leaves not made up of uniseriate filaments 7
6. Leaf filaments1-2, each filament 1 cell wide at base. Underleaves ± lacking, consisting of 2 small, adjacent cells each capped with slime papilla ..... **Arachniopsis**
6. Leaf filaments (2-)3-4, each filament 2 or more cells wide at base. Underleaves present, 1/4-1/2 the length of the leaves or more ..... **Telaranea**
7. Plants very small, less than 1 mm wide, whitish-green. Stems dorsally only 2 cells wide, flattened. Leaves very flat, attached to the lateral side of the stem and almost longitudinally inserted, apex rounded to short-bifid, with 1-2 large, sausage-shaped slime papillae (rarely lacking). On decaying wood ..... **Zoopsidella**
7. Plants larger, or leaves more obliquely inserted, variously lobed or undivided. Slime papillae lacking 8
8. Leaves incubous 9
8. Leaves succubous or transverse 10
9. Leaves divided into 4-6 segments. Branching (bi)pinnate. Plants 0.5-1.5 mm wide, whitish-green, rarely brown ..... **Lepidozia**
9. Leaves with 2-3 teeth at apex or undivided. Branching forked. Plants 1-6 mm wide, deep green or brown ..... **Bazzania**
10. Leaves folded and usually keeled, at least above, the keel often winged 11
10. Leaves not folded or keeled 12
11. Leaf apex bifid to 1/4. Underleaves absent ..... **Mytilopsis**
11. Leaf apex undivided or very short-bifid. Underleaves present, sometimes very small ....**Micropterygium**
12. Leaves undivided 13
12. Leaves 2-4-lobed 14
13. Leaves succubous, weakly to moderately concave, not clasping the stem. Cells in upper part of leaf ca. 25-35 µm, thin-walled. Plants green. In páramo ..... **Hygrolembidium**
13. Leaves transverse, deeply concave, clasping the stem. Cells in upper part of leaf 10-20 µm, thick-walled. Plants usually brownish. Montane, below 2500 m ..... **Micropterygium**
14. Underleaves ± lacking. Leaf insertion almost longitudinal, leaves divided into 2-4 subulate segments. Plants brown ..... **Odontoseries**
14. Underleaves present. Leaf insertion oblique to transverse 15
15. Leaves and underleaves shallowly divided (to 1/4 or less) into 3-4 triangular segments. Plants growing upright from a stoloniferous base ..... **Pseudocephalozia**
15. Leaves and underleaves more deeply divided. Plants creeping or ascending 16
16. Leaves 4-lobed ..... **Kurzia**
16. Leaves 2-3-lobed ..... **Paracromastigum**

Arachniopsis (= *Monodactylopsis*, *Regredicaulis* p.p.) (Fig. 57) - A small pantropical genus (5-6 spp.), with 3 species in warm regions of northern South America. *Arachniopsis diacantha* (Mont.) M. Howe (= *A. coactilis* Spruce) and *A. monodactyla* (Spruce) Schust. (*Regredicaulis monodactylus* (Spruce) Fulford) occur scattered in Amazonia, the Guianas, and along the Pacific coast of Colombia northwards to Costa Rica; *A. pecten* Spruce is a rare species of northern Amazonia (upper Rio Negro) and the Guianas.

HABITAT. On decaying wood (logs, stumps, bases of old trunks) in wet rain forests, especially in more or less undisturbed forests, and on moist sand in savanna, often associated with *Zoopsidella*. The species are restricted to lowland areas, with the exception of *A. diacantha*, which may also occur in montane rain forest, below 2000 m.

DESCRIPTION. **Plants** very small and fragile, filamentous, with hair-like leaves, less than 1 mm wide, whitish-green, creeping, irregularly branched. **Branches** purely ventral-intercalary. **Stems** flattened, very thin, with a hyalodermis. **Leaves** ± transverse, divided to the base into 1-2 uniseriate filaments,

the filaments only 1 cell wide from base to apex and 1-7 cells long. **Cells** longer than wide, thin-walled, cuticle smooth; oil bodies lacking (?). **Underleaves** lacking or very small, consisting of 2 small, adjacent cells, each topped with a slime papilla. **Dioicous** or monoicous. **Perianths** very long, cylindrical, mouth with long, bristle-like lacinia.

DISCUSSION. Members of *Arachniopsis* are very small, alga-like plants without underleaves (or with very small ones, consisting of only 2 cells), and with leaves consisting of 1-2 hair-like filaments: 2 in *A. diacantha*, 1 in *A. pecten*. They may be confused with *Telaranea nematodes*, but the latter has leaves usually consisting of 3 filaments, and well-developed underleaves. Moreover, branching in *Telaranea* is mostly lateral whereas *Arachniopsis* has only ventral branching.

Extreme reduction of leaves is seen in *Arachniopsis monodactyla*, having leaves of only one cell with a slime papilla on top. This microscopically small species, with a stem of only 4-5 rows of cells, is placed in a separate subgenus (or genus) *Monodactylopsis* Schust. It somewhat resembles *Phycolepidozia* (see under the latter).

LITERATURE. Fulford, M. H. 1963. *Regredicaulis, Arachniopsis*. Manual of the leafy Hepaticae of Latin America, Part III. Memoirs of the New York Botanical Garden 11(3): 358-364 [keys; *A. monodactyla* as *Regredicaulis monodactylus*].

Bazzania (Fig. 58) - A large genus with probably no more than 40 species in tropical America (over 100 worldwide), especially in montane regions.

HABITAT. Common on bark, rotten wood, humic soil, and rock covered with humus, in humid montane forests and scrub to the lower páramo, also in lowland rain forests but there usually scarce; 0-4000 m. *Bazzania* is one of the most conspicuous genera of the montane cloud forest, where the species may grow in large turfs on trunks and on thick, horizontal branches in the canopy. The turfs may capture large amounts of rain water and thus play an important role in the hydrology of the forest ecosystem. They also serve as a substrate for the establishment of other epiphytic plants, offer shelter to a great variety of invertebrates (insects, snails, earthworms) and micro-organisms, and provide nesting materials for birds.

DESCRIPTION. **Plants** small to large, 1-6 mm wide, typically bright green to olive-green, sometimes brown or reddish-brown, creeping, forked, with long ventral flagella. **Branches** *Frullania*-type and ventral-intercalary. **Leaves** incubous, wide-spreading, ovate-rectangular, apex truncate and divided into 2-3 large teeth, rarely rounded and without teeth, margins entire, rarely finely toothed. **Cells** with small or large trigones, cuticle smooth or papillose, a vitta sometimes present; oil bodies large, homogeneous or few-segmented. **Underleaves** large, undivided or shallowly lobed, margins entire or toothed, underleaf bases sometimes united with the leaves on one or both sides. **Dioicous**. **Gametoecia** as in the family. **Vegetative reproduction** by caducous leaves.

DISCUSSION. *Bazzania* is easily recognized by the forked branching, the incubous leaf arrangement, the 2-3-toothed leaf apex (rarely without teeth), and the large underleaves. The leaves are usually rectangular and wide-spreading. Another characteristic feature is the presence of long, flagelliform branches from the underside of the stem.

The neotropical species are still poorly known and identification is usually difficult.

LITERATURE. Fulford, M. H. 1963. *Bazzania*. Manual of the leafy Hepaticae of Latin America, Part I. Memoirs of the New York Botanical Garden 11(1): 106-172 [key].

Hygrolembidium (Fig. 58) - A southern-temperate genus (8 spp.), with 1 species, *H. andinum* (Herzog) Schust., in the Andes of Venezuela (one collection only) and in central Chile.

HABITAT. On marshy soil at lake margins in páramo, 3850 m.

DESCRIPTION. **Plants** turgid, small, to 1 mm wide, green, erect from a branched rhizome system, irregularly branched, lower part of leafy shoots usually with reduced leaves. **Branches** intercalary (lateral and ventral). **Stems** without hyalodermis. **Leaves** succubous, insertion line extending to the dorsal stem-midline, somewhat concave, ovate, undivided, margins entire, lamina in the lower half of the leaf 2-3 layers of cells thick. **Cells** thin-walled, ca. 22-35 µm long in upper part of leaf, longer towards the base, cuticle smooth to weakly papillose; oil bodies unknown in the neotropical species. **Underleaves** resembling leaves but much smaller. **Dioicous**. **Gametoecia** as in the family.

DISCUSSION. Resembling *Pseudocephalozia* but leaves and underleaves undivided instead of 3-4-lobed. Moreover, the leaves are succubous instead of transverse. The genus may also be confused with species of *Micropterygium* with unwinged leaves. *Micropterygium* is usually more brownish in color, the leaves are transverse (not succubous) and more deeply concave, and the leaf cells are much smaller and more thick-walled.

LITERATURE. Schuster, R. M. & J. J. Engel. 1987. Monograph of Lepidoziaceae subfam. Lembidioideae. Journal of the Hattori Botanical Laboratory 63: 247-350 [descr. of *H. andinum*].

Kurzia (= *Microlepidozia*) (Fig. 58) - About 3-4 species in tropical America (ca. 30 worldwide), including the widespread *K. capillaris* (Sw.) Grolle and *K. flagellifera* (Steph.) Grolle, and *K. brasiliensis* (Steph.) Grolle (? = *K. uleana* (Steph.) Grolle) in southeastern Brazil. The latter species is sometimes placed in a separate subgenus *Macrophylla* because of its broader, triangular leaf segments.

HABITAT. On moist humid soil, rock, peat, decaying wood, and bark in montane forests and páramo, (100-)1500-4000 m. In southeastern Brazil, *Kurzia capillaris* may descend almost to sea level. The species of *Kurzia* usually grow on acidic substrates and are particularly abundant at higher elevations, above 2000 m. In very humid upper montane cloud forest, *K. capillaris* and *K. flagellifera* may form large, compact brownish mats or cushions on tree trunks and on thick canopy branches. *Kurzia capillaris* is also a conspicuous species of *Sphagnum* bogs in páramos, from the forest line to about 4000 m. The páramo populations have sometimes been treated as a separate species, *K. verrucosa* (Steph.) Fulford, because of their strongly papillose cuticle.

DESCRIPTION. **Plants** very small, 0.5-2 cm long but only 0.3-0.4 mm wide, usually brown, creeping, 1-2-pinnate. **Branches** *Frullania*-type and *Kurzia*-type on alternate sides, often flagelliform towards the tip; ventral-intercalary branches also present, these sometimes stoloniform. **Leaves** minute, transverse, rarely succubous, deeply divided into 4 subulate (rarely narrow-triangular) segments, the segments straight or incurved, 2-3(-4) cells wide at the base, margins entire. **Cells** thick-walled, without trigones, cuticle verruculose-papillose; oil bodies finely granular. **Underleaves** about half the size of the leaves, deeply 2-4-lobed, the segments often unequal in length. **Dioicous**. **Gametoecia** as in the family.

DISCUSSION. *Kurzia* is closely related to *Lepidozia* but differs from the latter in several important respects: 1) the plants are smaller, less than 0.5 mm wide, and usually brown; 2) the leaves are transverse (rarely succubous), not incubous, more deeply divided and have narrower segments; and 3) the cuticle is conspicuously verruculose (with small, rounded papillae). A further peculiarity of *Kurzia* is the occurrence of *Frullania*-type branches on one side of the stem and *Kurzia*-type branches on the other.

LITERATURE. Fulford, M. H. 1966. *Microlepidozia*. Manual of the leafy Hepaticae of Latin America, Part II. Memoirs of the New York Botanical Garden 11(2): 224-234 [key].

Lepidozia (Fig. 59) - About 20 species in tropical America (ca. 75 worldwide), usually at high elevations. The species occur mainly in the Andes, in the mountains of Central America, and in SE Brazil, except for the widespread *L. cupressina* (Sw.) Lindenb., and *L. patens* Lindenb. occuring in the Caribbean, Central America, and the Western Cordillera of Colombia.

HABITAT. On bark, rotten wood and soil in humid montane forests, scrubby vegetation, and páramo, usually in rather open situations, 500-4000 m. In cloud forests, *Lepidozia* may form thick mats or cushions on horizontal branches in the tree crowns, or nearer to the ground where the forest canopy is rather open or low. In Caribbean cloud forests, *Lepidozia patens* is a very conspicuous species, hanging from tree trunks in large, fluffy, whitish-green garlands.

DESCRIPTION. **Plants** small to rather large but always narrow, 1-10 cm long but only 0.5-1.5 mm wide, typically pale green to whitish, sometimes greenish-brown, rarely dark, creeping, sometimes long pendent, 1-3-pinnate. **Branches** mostly *Frullania*-type, often ending in slender flagella; ventral-intercalary branches also present, these sometimes stoloniform. **Leaves** small, incubous, usually concave, divided into 4(-6) equal or very unequal segments, the segments triangular and usually incurved, margins entire or with a few teeth or cilia. **Cells** with uniformly thickened walls, trigones ± lacking, cuticle usually smooth; oil bodies finely granular. **Underleaves** about half the size of the leaves, divided into 4 equal segments. **Dioicous**, rarely monoicous. **Gametoecia** as in the family.

DISCUSSION. The very slender, whitish-green plants with regular 1-3-pinnate branching and small, concave leaves divided into 4-6 segments, are unmistakable. The branches become progressively narrower towards the tips and often end as a flagellum. The neotropical species are still poorly known and identification is difficult. Some of the species recognized by Fulford (1966) may be conspecific with the common and variable *L. cupressina*.

LITERATURE. Fulford, M. H. 1966. *Lepidozia*. Manual of the leafy Hepaticae of Latin America, Part II. Memoirs of the New York Botanical Garden 11(2):180-213 [key].

Micropterygium (Fig. 59) - A neotropical genus of about 18-19 species, in northern South America, Panama, Costa Rica, and the West Indies. Three species, *M. campanense* Reimers, *M. leiophyllum* Spruce, and *M. pterygophyllum* (Nees) Trevis., extend to SE Brazil. The center of diversity of *Micropterygium* is in the Guayana Highland, where about 10 endemic species occur.

HABITAT. On rotten bark of old trunks, decaying wood (logs), tree bases, twigs, moist sandstone rock, cliffs, and moist sand in lowland and montane rain forest and scrub, 0-2500 m. *Micropterygium leiophyllum* Spruce and *M. pterygophyllum* (Nees) Trevis. are characteristic species of Amazonian rain

forests (the latter also in the Chocó), *M. trachyphyllum* Reimers is abundant in the rain forests of the Guianas, and *M. carinatum* (Grev.) Reimers is common in the montane rain forests of the Caribbean. The remaining species are rarer and mostly restricted to the Guiana Shield.

DESCRIPTION. **Plants** small to medium-sized, 0.5-2 mm wide, light yellow-green to brown, ascending from a branched rhizome system, irregularly branched. **Branches** intercalary (lateral and ventral), often stoloniform. **Stems** with a thick-walled, brown, 1-2-layered cortex surrounding smaller, thin-walled medulla cells. **Leaves** transverse or succubous, insertion line extending to the dorsal stem-midline, orbicular to lanceolate, concave to complicate and keeled with a conspicuous wing in the upper half, the wing sometimes reduced, apex undivided or very short-bifid, margins entire or toothed. **Cells** small, 10-20 µm, usually thick-walled, the surface smooth or mammillose, cuticle smooth or papillose. **Underleaves** present, smaller to almost as large as the leaves. **Dioicous**. **Gametoecia** as in the family.

DISCUSSION. *Micropterygium* is easily recognized by the peculiar, folded leaves with keels, which is usually winged on the back. In some species, however, a wing is lacking; these species usually have very large underleaves. The rigid stems, usually little branched and leafless at the base, the small, ± thick-walled leaf cells, and the presence of underleaves are further characteristic features of this genus. The underleaves are quite variable in size and sometimes show a gradual decrease in size from the base of the stem to the apex.

LITERATURE. Fulford, M. H. 1966. *Micropterygium*. Manual of the leafy Hepaticae of Latin America, Part II. Memoirs of the New York Botanical Garden 11(2): 248-274 [key].

Mytilopsis (Fig. 59) - A monotypic, neotropical genus. The only species, *M. albifrons* Spruce, occurs in the Guayana Highland and surrounding areas, also in the foothills of the Andes (NE Peru, NW Colombia) and in Jamaica.

HABITAT. On trunks and branches of old trees, rotten wood, sandstone rock, and shaded soil in submontane and montane rain forest and scrub, 500-2200 m.

DESCRIPTION. **Plants** small, ca. 1 mm wide, whitish-green to brown, ascending from a branched rhizome system, irregularly branched. **Branches** ventral-intercalary, often stoloniform. **Stems** with a very strongly thick-walled, yellow brown, 1-layered cortex surrounding smaller, thin-walled medulla cells. **Leaves** transverse, with a long insertion line extending to the dorsal stem-midline and almost to the ventral midline, wide-spreading and boat-shaped, sharply keeled, the keel with or without a rudimentary wing, apex bifid to 1/4 of leaf length, margins crenulate-denticulate, bases broadly auriculate, clasping the stem. **Cells** small, 15-20 µm, thick-walled, mammillose, cuticle papillose. **Underleaves** lacking. **Dioicous**. **Gametoecia** as in the family.

DISCUSSION. *Mytilopsis albifrons* is closely related to *Micropterygium* but differs in the boat-shaped leaves with a distinctly bifid apex (to 1/4 of leaf length) and a reduced wing, and in the absence of underleaves. Other striking features of this genus are the broadly auriculate leaf bases, which conspicuously clasp the stem, and the cortex cells with exceedingly strongly thickened walls. The leaf margins are usually conspicuously crenulate-denticulate.

LITERATURE. Fulford, M. H. 1966. *Mytilopsis*. Manual of the leafy Hepaticae of Latin America, Part II. Memoirs of the New York Botanical Garden 11(2): 274-276.

Odontoseries (Fig. 60) - A monotypic, neotropical genus. The only species, *O. chimantana* Fulford, is known only from the Chimantá Massif in the State of Bolivar, Venezuela.

HABITAT. On damp rock-wall near waterfall, creeping over *Sphagnum*, 1900-2000 m.

DESCRIPTION. **Plants** small, about 1 mm wide, brown, creeping, little branched. **Branches** ventral-intercalary. **Stems** thin, dorsal side 2-3 cells wide, hyalodermis present. **Leaves** wide-spreading and very flat, succubous and almost horizontally inserted on the lateral side of the stem (dorsal side of the stem leaf-free), rectangular, narrowly 2-4-lobed to almost leaf middle, the segments subulate, mostly only 1 cell wide. **Cells** large, rectangular, 50-100 µm long in the leaf lamina, uniformly thickened, cuticle slightly papillose; oil bodies unknown. **Underleaves** reduced, made up of a few short ciliate segments. **Gametoecia** unknown.

DISCUSSION. The horizontally inserted leaves divided almost to the middle into 2-4 subulate segments, the large, rectangular leaf cells, the minute underleaves with rhizoids in tufts, and the brownish color of the plants are characteristic of this Guayanan endemic.

LITERATURE. Fulford, M. H. 1968. *Odontoseries*. Manual of the leafy Hepaticae of Latin America, Part III. Memoirs of the New York Botanical Garden 11(3): 364-366.

Paracromastigum (= *Bonneria*, *Leucosarmentum*) (Fig. 60) - A small southern-temperate and neotropical genus (ca. 5 spp.) with 2 species in tropical America: *P. pachyrhizum* (Nees) Fulford (= *P. bifidum* (Steph.) Schust.) throughout the Neotropics and *P. granatense* (Gott.) Schust. in the northern Andes.

HABITAT. On steep, moist soil banks and periodically flooded sandy soil, common on cut road banks and along rivers in montane rain forest regions, 400-3500 m. In the Andes above 1200 m.

DESCRIPTION. **Plants** small, 1-1.5 mm wide, pale green to yellow or greenish-brown, creeping, sometimes ascending from a stoloniform base, irregularly branched. **Branches** terminal (*Frullania*-type, *Acromastigum*-type, *Kurzia*-type) and ventral-intercalary, sometimes flagelliform. **Stems** with a weak hyalodermis. **Leaves** wide-spreading and somewhat concave, succubous, obliquely inserted on the lateral side of the stem (dorsal side of the stem leaf-free), ovate-elliptical or obcuneate, narrowed to the base, 2-3-lobed to leaf middle, the segments lanceolate. **Cells** with uniformly thickened walls, cuticle finely papillose; oil bodies finely granular. **Underleaves** similar to the leaves but smaller, about 1/2 the size. **Gametoecia** as in the family.

DISCUSSION. *Paracromastigum* superficially resembles *Cephalozia* due to its succubous leaves inserted laterally on the stem and its pale green color, but the leaves are 2-3-lobed instead of 2-lobed and there are large, 2-3-lobed underleaves (underleaves lacking in *Cephalozia*). The tufted rhizoids and the very short sexual branches indicate that a member of the Lepidoziaceae, rather than the Cephaloziaceae, is at hand.

LITERATURE. Fulford, M. H. 1966. *Bonneria*. Manual of the leafy Hepaticae of Latin America, Part II. Memoirs of the New York Botanical Garden 11(2): 178-180. - Fulford, M. H. 1968. *Leucosarmentum, Paracromastigum*. Manual of the leafy Hepaticae of Latin America, Part III. Memoirs of the New York Botanical Garden 11(3): 386-389.

Phycolepidozia (Fig. 60) - Endemic to tropical America. The only species, *P. exigua* Schust., is known only from the island of Dominica in the West Indies, where it has been collected once, in 1966.

HABITAT. On tree trunk in humid, submontane rain forest, ca. 500 m.

DESCRIPTION. **Plants** consisting of minute shoots to 5 mm long, without leaves and underleaves but with small, leafy sexual branches. **Stems** very thin, cylindrical, of 6 rows of cells (5 outer, 1 inner). **Branches** ventral-intercalary. **Leaves** and underleaves sometimes represented by small slime papillae. **Cells** with uniformly thickened walls; oil bodies finely granular. **Rhizoids** scarce, arising singly. **Gametoecia** as in the family. **Perianths** long-cylindrical, mouth deeply 6-lobed. **Seta** very thin, of 4 large outer rows and 4 small inner rows of cells.

DISCUSSION. An alga-like plant without leaves and with a very thin stem, of only 6 rows of cells. *Phycolepidozia* has been assigned to a separate family, Phycolepidoziaceae. In this treatment it is, tentatively, treated as a member of the Lepidoziaceae - perhaps in its own subfamily - because of the general similarity to *Arachniopsis* (subgen. *Monodactylopsis*) and *Protocephalozia*, both of which have reduced (but fertile) gametophytes. *Phycolepidozia* differs from the other members of the family in the rhizoids, which originate singly rather than in tufts, and in the cephalozielloid seta consisting of only 8 cell rows (4 outer, 4 inner). In view of the variation in seta structure found in the Lepidoziaceae, ranging from rather massive (*Bazzania, Lepidozia*) to 12-celled (*Zoopsidella, Pteropsiella, Arachniopsis* subg. *Monodactylopsis*), the 8-celled seta of *Phycolepidozia* might be interpreted as the culmination of seta reduction in the family.

LITERATURE. Fulford, M. H. 1966. *Phycolepidozia*. Manual of the leafy Hepaticae of Latin America, Part III. Memoirs of the New York Botanical Garden 11(3): 382-384. - Schuster, R. M. 1966. Studies on Hepaticae XXVIII. On *Phycolepidozia,* a new, highly reduced genus of Jungermanniales of questionable affinity. Bulletin of the Torrey Botanical Club 93: 437-449.

Protocephalozia (Fig. 60) - A monotypic, neotropical genus. The only species, *P. ephemeroides* (Spruce) Schiffn., occurs in northern Amazonia towards the foot of the Guayana Highland. Richard Spruce, the great explorer of the Amazon Basin, was the first to collect the species along the upper Río Negro near San Carlos, Venezuela, in the middle of the 19th century.

HABITAT. On soil and rock in lowland forest.

DESCRIPTION. **Plants** consisting of minute, light green protonematal filaments without leaves or underleaves but with small, leafy sexual branches. **Filaments** made up of a single row of short rectangular cells. **Cells** thin-walled, cuticle papillose. **Rhizoids** present on sexual branches, in small tufts. **Gametoecia** as in the family. **Perianths** long-cylindrical, mouth deeply 6-lobed. **Seta** very thin, of 8 large outer rows and 4 small inner rows of cells.

DISCUSSION. A minute, alga-like plant, consisting of a filamentous protonema from which short sexual branches arise, similar to those in other members of the Lepidoziaceae. The protonematal cells are short-rectangular, with a papillose cuticle. *Protocephalozia ephemeroides* has been very little collected and, due to its minute size, may have been overlooked.

LITERATURE. Fulford, M. H. 1968. *Protocephalozia*. Manual of the leafy Hepaticae of Latin America, Part III. Memoirs of the New York Botanical Garden 11(3): 333-334.

Pseudocephalozia (Fig. 61) - A southern-temperate genus (6 spp.), with 2 species in tropical America: *P. quadriloba* (Steph.) Schust. (= *Lembidium quadrilobum* (Steph.) Fulford) in Costa Rica and the northern Andes (Peru to Venezuela), and also in southern South America, and a second, undescribed species in the Serra de Itatiaia, SE Brazil.

HABITAT. Usually on peat in *Sphagnum* bogs in páramos, often in pure patches, 3200-4100 m. In Costa Rica, found in the summit region of volcán Poás (2600 m), on ash near the rim of the crater and on soil in ericaceous scrub forest.

DESCRIPTION. **Plants** small, 0.3-2 mm wide, light green to pale brown, ascending to erect from a branched rhizome system, irregularly branched. **Branches** mostly intercalary (lateral and ventral), rarely terminal (*Frullania*-type, *Microlepidozia*-type). **Stems** with a hyalodermis. **Leaves** transverse, insertion line extending to the dorsal stem-midline, concave, obtrapezoid, quite variable in size, shallowly (2-)3-4-lobed (to 1/4 of leaf length or less), segments triangular, margins entire, lamina in lower half of leaf 1-5 layers of cells thick. **Cells** ± thin-walled, cuticle smooth to weakly papillose; oil bodies coarsely granular, 2-3 per cell, or lacking. **Underleaves** similar to the leaves but usually smaller. **Dioicous. Gametoecia** as in the family.

DISCUSSION. The erect, leafy shoots arising from long, creeping stolons, and the very shallowly 3-4-lobed leaves and underleaves, are unmistakable. The leaves of *Pseudocephalozia* are transversely inserted, quite variable in size, and the underleaves are about as large as the leaves. *Pseudocephalozia quadriloba* is a somewhat turgid, pale-colored plant with rather fleshy leaves, being several layers of cells thick in the lower half.

LITERATURE. Fulford, M. H. 1966. *Lembidium*. Manual of the leafy Hepaticae of Latin America, Part II. Memoirs of the New York Botanical Garden 11(2): 245-248. - Schuster, R. M. & J. J. Engel. 1974. A monograph of the genus *Pseudocephalozia*. Journal of the Hattori Botanical Laboratory 38: 665-701 [key].

Pteropsiella (Fig.61) - A small neotropical genus of 2 closely related species, *P. frondiformis* Spruce and *P. serrulata* Spruce ex Steph., both occurring in northern Amazonia and Guyana.

HABITAT. On decaying wood and moist sand, on periodically flooded river banks and in moist savannas, 0-650 m. Also on termite mounds.

DESCRIPTION. **Plants** thalloid, with a midrib and unistratose wings, small, resembling a small *Symphyogyna* but with short, leafy sexual branches, 1-3 cm long, 3-5 mm wide, pale green, creeping. **Branches** ventral-intercalary. **Stems** retained as a narrow midrib, hyalodermis present. **Thallus** margin entire or toothed, sometimes bordered with thickened cells, with elongated slime papillae. **Cells** without trigones, cuticle weakly papillose. **Underleaves** reduced to a few cells, with rhizoids in tufts at the base. **Dioicous** or monoicous. **Perianths** long-cylindrical, mouth with long, bristle-like lacinia. **Seta** very thin, of only 8 outer rows of cells and 4 inner rows.

DISCUSSION. A very peculiar plant, related to *Zoopsidella* but thalloid (except for the sexual branches), possibly due to fusion and reduction of leaves on either side of the stem. The remnants of the leaves (= the leaf tips!) are marked by sausage-shaped slime papillae along the thallus margin, very much like those in *Zoopsidella*. The sporophytes are also similar to those of *Zoopsidella.*

LITERATURE. Fulford, M. H. 1968. *Pteropsiella*. Manual of the leafy Hepaticae of Latin America, Part III. Memoirs of the New York Botanical Garden 11(3): 372-376 [key].

Telaranea (Fig. 61) - A mostly southern-temperate genus (ca. 35 spp.), with 4-5 species in tropical America. *Telaranea nematodes* (Gott. ex Austin) M. Howe is the only common species in the Neotropics and occurs throughout the region; in addition, it is distributed in tropical Africa and western Europe. The other neotropical species are very rare taxa, three of them being known from only one collection each from the Venezuelan Andes (Schuster, 1978).

HABITAT. On bark and decaying wood in lowland and montane rain forests and scrub, often creeping among other bryophytes, from sea level (SE Brazil) to almost 4000 m. *Telaranea nematodes* has a remarkably wide elevational range and occurs in a great variety of forest types, but always in moist and shaded microhabitats.

DESCRIPTION. **Plants** very small, filamentous, less than 1 mm wide, pale green, 1-3-pinnate or irregularly branched. **Branches** mostly *Frullania*-type, sometimes *Microlepidozia*-type, often flagelliform towards the tip; a few ventral-intercalary branches also present. **Stems** with a hyalodermis. **Leaves** usually transverse (incubous in subgen. *Neolepidozia*), deeply divided into 2-3(-4) uniseriate filaments, an undivided lamina present or absent, the filaments only 1 cell wide except at the base, straight or incurved, margins entire. **Cells** usually large, longer than wide, the walls uniformly thin, cuticle smooth; oil bodies finely granular-papillose. **Underleaves** smaller than the leaves, usually 1/4-1/2 their length, deeply divided into 2-3 filaments. **Dioicous** or monoicous. **Gametoecia** as in the family.

DISCUSSION. *Telaranea* is recognized by the leaves, which are deeply divided into 3-4 hair-like filaments. In some species, the leaves have a short undivided lamina but in others, including the common *T. nematodes,* they are divided to the base. The base of the filaments is 2 or more cells wide. Underleaves are always present and resemble the leaves, but are shorter and with fewer filaments (2-3). Further characteristics include the large, thin-walled leaf cells that are much longer than wide, and the large, thin-walled stem epidermis (= hyalodermis).

Telaranea nematodes may be confused with *Arachniopsis* and with *Blepharostoma* (Pseudolepicoleaceae), both of which have leaves divided to the base into hair-like filaments. However, in *Arachniopsis* and *Blepharostoma* the base of the filaments is only 1 cell wide, in *Telaranea* usually 2 cells. *Arachniopsis* furthermore differs in the lack of underleaves, fewer (1-2) filaments per leaf, and purely ventral branching. *Blepharostoma* has larger underleaves, about as large as the leaves, no hyalodermis, and somewhat thick-walled cells with a finely striate-papillose cuticle (smooth in *Telaranea*). Due to the thickened cell walls, the leaves in *Blepharostoma* are usually rather stiff and dull in color while those of *Telaranea* are quite flexible and glistening.

LITERATURE. Fulford, M. H. 1966. *Telaranea*. Manual of the leafy Hepaticae of Latin America, Part II. Memoirs of the New York Botanical Garden 11(2): 234-245 [key to 2 neotropical spp.]. - Schuster, R. M. 1978. Studies on Venezuelan Hepaticae I. Phytologia 39 (4): 239-251 [descr. of 3 new spp.].

Zoopsidella (= *Regredicaulis* p.p., *Zoopsis* p.p.) (Fig. 62) - A genus of 6-7 species in tropical America, in warm regions of northern South America and the West Indies. Two further species occur in Asia and New Zealand (Schuster, 1993).

HABITAT. On decaying wood (logs, stumps, roots, bases of old trunks) and peaty humus in wet lowland and lower montane rain forest, often associated with *Arachniopsis*, 0-1600 m. The species mostly occur in undisturbed forests. Also recorded from rock walls and termite mounds.

DESCRIPTION. **Plants** small, usually less than 1 mm wide, whitish-green, creeping, irregularly branched. **Branches** ventral-intercalary, occasionally *Frullania*-type; ventral branches usually stoloniform. **Stems** thin, dorsal side 2 cells wide, hyalodermis present. **Leaves** very flat and wide-spreading, succubous and almost horizontally inserted on the lateral side of the stem (dorsal side of the stem leaf-free), quadrate to elongate, weakly 2-lobed or undivided, upper margins usually with 2 large, sausage-shaped slime papillae. **Cells** thin-walled, cuticle smooth; oil bodies small, finely segmented. **Underleaves** reduced. **Dioicous** or monoicous. **Perianths** long-cylindrical, mouth with long, bristle-like lacinia. **Seta** very thin, of only 8 outer rows of cells and 4 inner rows.

DISCUSSION. *Zoopsidella* is easily recognized by the very flat spreading leaves, attached to the lateral side of the stem, with 2 large, sausage-shaped slime papillae on the upper margins. The slime papillae mark the tips of the 2 leaf-segments potentially produced in this genus. In *Z. serra* (Spruce) Schust. (= *Regredicaulis serrus* (Spruce) Fulford), however, slime papillae are lacking.

LITERATURE. Fulford, M. H. 1968. *Regredicaulis, Zoopsis*. Manual of the leafy Hepaticae of Latin America, Part III. Memoirs of the New York Botanical Garden 11(3): 358-359, 368-372 [keys]. - Schuster, R. M. 1993. Studies on Hepaticae LXII-LXIV. Lepidoziaceae subf. Zoopsidoideae (1). Nova Hedwigia 56: 35-59 [descr. of *Zoopsidella dichotoma* Schust.]

PLAGIOCHILACEAE

Plants ± firm, green to brown, creeping to ascending or pendent, often with a rhizome-like creeping base. Stems usually with a brown cortex of thick-walled cells in several layers. Branches *Frullania*-type or lateral-intercalary, rarely ventral-intercalary (*Szweykowskia)*. Leaves succubous, alternate, rarely opposite (*Plagiochilion*), bases decurrent and dorsal margin usually recurved, insertion line reaching dorsal stemmidline, apex and margins (especially the ventral margin) toothed to ciliate, rarely entire. Cells variable; oil bodies usually granular. Underleaves normally lacking, when present very small. Rhizoids few, scattered, occasionally in tufts. Dioicous (in neotropical taxa). Gametoecia on elongated shoots. Androecia in long, terminal spikes. Sporophyte surrounded by a perianth, perianths laterally compressed, with a wide, truncate mouth, often with innovations. Seta of numerous cells (cross-section). Capsule wall thick, 4-9-layered. Spores sometimes with endosporous germination. Elaters with 1-2(-3) spirals. Vegetative reproduction by cladia, caducous leaves, or leaf fragmentation, rarely by gemmae.

DISCUSSION. A family of 8 genera; 4 in tropical America including the important genus *Plagiochila*. The family is characterized by 1) succubous, usually toothed leaves with recurved dorsal margins and decurrent bases; 2) ± absence of underleaves; 3) rigid, brown stems with a thick-walled cortex; 4) laterally compressed perianths with a wide, truncate mouth; and 5) very long male spikes.

Following Inoue (1984), *Rhodoplagiochila* is included in the Jungermanniaceae instead of Plagiochilaceae.

LITERATURE. Inoue, H. 1984. The genus *Plagiochila* in Southeast Asia. Academic Scientific Book Inc., Tokyo. - Schuster, R. M. 1980. Plagiochilaceae. The Hepaticae and Anthocerotae of North America, Vol. IV: 325-539.

1. Leaves strongly swollen and saccate with fully deflexed margins; leaf margins with numerous long cilia ..... **Szweykowskia**
1. Leaves not saccate 2
2. Shoot tips with light green clusters of flagella, producing tiny caducous leaves .... **Steereochila**
2. Clusters of flagella absent 3
3. Leaves opposite, leaf bases fully united both dorsally and ventrally ..... **Plagiochilion**
3. Leaves alternate or opposite, leaf bases never united both dorsally and ventrally ... **Plagiochila**

Plagiochila (Fig. 62) - The largest genus of hepatics with about 100 species in tropical America (ca. 400 worldwide), very common from lowland to alpine regions.

HABITAT. On bark and rotten wood in moist forests and páramos, from sea level to 4300 m; also on moist rock or earth, occasionally on living leaves. *Plagiochila* is one of the most abundant and conspicuous bryophyte genera of montane cloud forests, and most of the species are found there; fewer occur in lowland rain forests or in the alpine regions. Common species of lower elevations are *Plagiochila disticha* (Lehm. & Lindenb.) Mont. and the closely related *P. montagnei* Nees (= *P. hypnoides* Lindenb.), *P. gymnocalycina* (Lehm. & Lindenb.) Mont. (often misidentified as *P. rutilans* Lindenb.), *P. laetevirens* Nees & Mont., *P. patentissima* Lindenb., *P. raddiana* Lindenb. (= *P. guilleminiana* Nees & Mont. = *P. ludoviciana* Sull.), *P. simplex* (Sw.) Lindenb., and *P. subplana* Lindenb. Common in alpine regions (páramo, puna, zacatonal) are *P. ovata* Lindenb. & Gott. and *P. fuscolutea* Taylor. The latter - a large, conspicuous species characterized by almost untoothed leaves - is also abundant in the canopy of mossy, upper montane and subalpine cloud forests in Colombia, above 3000 m, where it may form huge turfs to 40 kg in fresh weight (Wolf, 1994).

DESCRIPTION. **Plants** small to very robust, (0.5-)1-10 mm wide, green to brown, creeping, ascending or pendent, on tree trunks, often dendroid with erect leafy shoots arising from a creeping rhizome-like stem, irregularly branched to regularly pinnate. **Branches** *Frullania*-type or lateral-intercalary. **Leaves** succubous, alternate, orbicular to ovate to oblong to almost linear, often asymmetrical, with reflexed dorsal margin and decurrent bases, apex undivided or 2-3-lobed, margins usually toothed to ciliate, especially along the apical and ventral margins, teeth at the apex often larger, margins rarely entire. **Cells** with conspicuous trigones or thin-walled, cuticle smooth or rough; oil bodies usually finely granular. **Underleaves** usually lacking, small when present. **Rhizoids** scattered, often lacking. **Gametoecia** as in the family. **Vegetative reproduction** common, by tiny leafy shoots developing from the leaf surfaces and by caducous or fragmenting leaves.

DISCUSSION. *Plagiochila* may be recognized by the rather firm, greenish or brownish plants with stiff stems - due to the presence of a thick-walled cortex - and somewhat asymmetrical, succubous leaves with reflexed dorsal margins and decurrent bases. Only in the tiny *P. exigua* Taylor (= *P. corniculata* auct.) and related species are leaf bases not decurrent. The leaf margins are normally toothed or ciliate, especially at the apex and along the ventral side, but occasionally they are completely entire (especially in species of the páramos). The ventral bases of the leaf are sometimes expanded into large auricles which tend to turn downwards and become united into a crest along the stem (e.g., in *P. disticha, P. raddiana*, *P. cristata* (Sw.) Lindenb., and *P. adiantoides* (Sw.) Lindenb. and its relatives).

The plants are always dioicous. Male plants are immediately recognized by the long and stiff, terminal androecial spikes, much narrower than the vegetative shoots and bearing numerous small, strongly imbricate bracts. Female plants have laterally flattened perianths with a wide, truncate mouth, fringed by numerous cilia or lacinia (rarely entire).

The neotropical species of *Plagiochila* have not yet been monographed and identification is very difficult. Some species are very widespread and may be identified with the keys cited below, but the majority seem to have rather restricted distributions and are not included in these keys. The classical monograph of the South American species by Spruce (1885) is very difficult for the beginner and, in part, outdated. The treatment by Carl (1931) provides a key to sections but lacks species descriptions. As a first tool to sort the neotropical species, the latter two publications are still very useful. A revision of the neotropical species of *Plagiochila* by S. R. Gradstein and J. Heinrichs for *Flora Neotropica* is in preparation (e.g., Heinrichs *et al.*, 1998, 1999; Heinrichs & Gradstein, 2000; Müller *et al.*, 2000).

LITERATURE. Carl, H. 1931. Die Arttypen und die systematische Gliederung der Gattung *Plagiochila*. Annales Bryologici Supplementary Volume 2: 1-170 [key to sections, in part outdated]. - Heinrichs, J., S. R. Gradstein & R. Grolle. 1998. A revision of the neotropical species of *Plagiochila* described by O. Swartz. Journal of the Hattori Botanical Laboratory 25: 1-32. - Heinrichs, J., H. Anton, S. R. Gradstein & R. Mues. 1999. Systematics of *Plagiochila* sect. *Glaucescentes* Carl (Hepaticae). Plant Systematics and Evolution 220: 115-138. - Heinrichs, J. & S. R. Gradstein. 2000. A revision of

Plagiochila sect. *Crispatae* and sect. *Hypnoides* (Hepaticae) in the Neotropics I. Nova Hedwigia 70: 161-184. - Inoue, H. 1989. *Plagiochila*. Pages 336-337 *in* S. R. Gradstein, A Key to the Hepaticae and Anthocerotae of Puerto Rico and the Virgin Islands. The Bryologist 92 [key to 23 spp.]. - Müller, J., J. Heinrichs & S. R. Gradstein 2000. A revision of *Plagiochila* sect. *Plagiochila* in the Neotropics. The Bryologist 102. - Schuster, R. M. 1980 (see family ref. [key to a few neotropical spp.]). - Spruce, R. 1885. *Plagiochila*. Hepaticae Amazonicae et Andinae. Transactions and Proceedings of the Botanical Society of Edinburgh 15: 449-499 [synoptic key to 69 spp., in part outdated]. - Wolf, J. H. D. 1994. Epiphyte communities of tropical montane rain forests in the northern Andes. Phytocoenologia 22: 1-103 [ecology].

Plagiochilion (Fig. 63) - A tropical Asian genus (12 spp.), with 2 species, *P. bryhnii* (Steph.) Inoue and *P. intermedium* Schust., in the Andes. The species have been collected only a few times and very little is known about their habitat.

HABITAT. Epiphytic in montane forests, 1950-2600 m.

DESCRIPTION. **Plants** rather small, ca. 2 mm wide, green to yellowish-brown, ascending from a creeping rhizome-like base. **Branches** intercalary (both lateral and ventral), the ventral-intercalary branches stoloniform. **Leaves** succubous, opposite, wide spreading and asymmetrically ovate-oblong, with reflexed dorsal margins and decurrent bases, apical and ventral margins toothed, the apical teeth sometimes larger. **Cells** with cordate trigones (two sides convex, one side concave) and intermediate thickenings, cuticle smooth; oil bodies unknown. **Underleaves** lacking. **Rhizoids** in tufts from near ventral bases of leaves.

DISCUSSION. Similar to *Plagiochila* but with completely opposite leaves, united at the bases both ventrally and dorsally. Opposite leaves are also found in *Syzygiella* (Jungermanniaceae), but the latter differs in the usually reddish pigmentation of the plants and the inflated perianth.

LITERATURE. Inoue, H. 1964. The genus *Plagiochilion*. Journal of the Hattori Botanical Laboratory 27: 51-72 [key].

Steereochila (Fig. 63) - A monotypic, neotropical genus, with *S. ecuadorica* Inoue in the Andes (Ecuador, Bolivia) and Costa Rica.

HABITAT. On bark of low trees and shrubs in upper montane cloud forests and bogs, usually in rather open places, 2600-3200 m. The species is quite common at the edges of mossy forest and in boggy places along the Panamerican Highway in the Cerro de la Muerte, Costa Rica.

DESCRIPTION. **Plants** rather robust, 6-7 mm wide, brown-green, in erect tufts arising from a creeping rhizome-like base, shoot apices with conspicuous yellowish-green clusters of flagella producing tiny caducous leaves. **Branches** mostly lateral-intercalary. **Leaves** succubous, subopposite, spreading, asymmetrically ovate-oblong, dorsal margins ± straight, reflexed, without teeth and with a long-decurrent base, ventral margins arched and usually toothed, ventral base ampliate. **Cells** 40-60 x 30-40 µm in the leaf middle, with elongated and almost confluent trigones, cuticle smooth; oil bodies rather finely granular. **Underleaves** lacking.

DISCUSSION. Identical to *Plagiochila* in general appearance but differing in the large clusters of flagelliform branches at the shoot apices, producing great quantities of minute, lanceolate caducous leaves. These apical clusters are conspicuously yellow-green and contrast sharply with the dull, olive-green leafy shoots. A further peculiarity of the genus is that the flagelliform branches arise from a terminal-type branch which originates from the ventral, instead of the lateral side, of the stem. The status of *Steereochila* as a genus separate from *Plagiochila* is questionable.

LITERATURE. Inoue, H. 1988. *Steereochila*, a new genus of the Plagiochilaceae from the Neotropics. Memoirs of the New York Botanical Garden 45: 279-282.

Szweykowskia (Fig. 63) - A monotypic, neotropical genus, with *S. cucullifolia* (J. B. Jack & Steph.) Gradst. & E. Reiner (= *Plagiochila cucullifolia* J. B. Jack & Steph.) in Ecuador (new, leg. M. Schwerdtfeger & G. Weis), in the Central and Western Cordillera of Colombia, and further northwards in the high mountains of Costa Rica and Panama.

HABITAT. On bark of trees and shrubs in very humid cloud forest areas and bogs, at the transition of lower montane to upper montane forest, 2200-2650 m. The species usually grows in rather open habitats, e.g., at forest margins and along road sides in somewhat disturbed environments.

DESCRIPTION. **Plants** robust, ca. 10 mm wide, green to brown, creeping to ascending from a short rhizomatous base, irregularly branched. **Branches** ventral-intercalary, the lower portions of the branches flagelliform. **Leaves** alternate, swollen and strongly saccate with fully deflexed margins, the margins with numerous long cilia. **Cells** very large,70-90 µm in the leaf middle, with trigones, cuticle smooth; oil bodies finely granular, 10-25 per cell. **Underleaves** lacking. **Spores** with endosporous germination, 55-70 µm in largest diameter. **Elaters** large, 400-700 µm long and 13-18 µm wide, with (2-)3 spirals.

DISCUSSION. A very striking plant with large, saccate leaves. The leaf margins are strongly deflexed and bear numerous long cilia. Other characteristics of this peculiar genus include the ventral-intercalary branches (instead of lateral-intercalary) and the large spores and elaters, the latter with mostly 3 spirals.

LITERATURE. Gradstein, S. R. & M. E. Reiner-Drehwald. 1995. *Szweykowskia*, a new genus of Plagiochilaceae from tropical America. Fragmenta Floristica et Geobotanica 40(1): 31-38.

PLEUROZIACEAE

A monotypic family.

Pleurozia (= *Eopleurozia*) (Fig. 64) - A mostly tropical genus (11 spp.), with 2 species in montane and subalpine regions of tropical America: *P. heterophylla* Steph. in the Guayana Highland (Mt. Roraima) and Central America, and *P. paradoxa* J. B. Jack (= *Eopleurozia paradoxa* (J. B. Jack) Schust.) in the northern Andes and the Guayana Highland (Gran Sabana). The latter species re-occurs at low elevations in southern Chile. A third species, *Pleurozia purpurea* Lindb., has been reported from Guadeloupe but this record is dubious and possibly based on an erroneous label.

HABITAT. On bark and moist rock in montane and subalpine scrub, in rather open and very humid environments, often near running water, 2000-3500 m.

DESCRIPTION. **Plants** robust, olive-green to deep wine-red to purplish, 2-10 cm long, 4-7 mm wide, creeping to ascending, loosely branched or in dense tufts. **Stems** rigid, usually brown, with a thick-walled cortex. **Branches** lateral-intercalary. **Leaves** incubous, deeply concave, and strongly enveloping the stem, undivided or divided into 2 segments, the dorsal segment usually smaller and saccate (sometimes explanate), opening of the sac controlled by a valve, leaf tips acute or short-bifid, margins entire or toothed, sometimes with a white border. **Cells** quadrate to rectangular, large, 40-100 µm long, with large trigones, cuticle smooth; oil bodies finely granular. **Underleaves** lacking. **Rhizoids** scarce, usually restricted to the stem bases, scattered. **Gametoecia** borne on short branches. **Perianths** large, cylindrical, of 2 types: fertile and plicate or sterile and completely smooth. **Seta** of numerous cells (cross-section). **Capsule** ovoid, wall thick (6-8-layered). **Vegetative reproduction** not observed.

DISCUSSION. Species of *Pleurozia* are conspicuous, often wine-red or purplish plants with deeply concave leaves, enveloping the stem in two ranks. In the field, they may at first sight be taken for a moss rather than a liverwort. The leaves are usually divided into a dorsal and a ventral segment, the dorsal one often being smaller and turned into a closed sac with a complicated aperture mechanism. However, in the neotropical *P. paradoxa* the leaves are simple, unlobed, and a sac is completely lacking. The latter species also stands out by the white leaf margins.

The distinction between dorsal and ventral in *Pleurozia* is difficult due to the absence of underleaves and the paucity of rhizoids, and may only be determined by observing the growth of the plants in the field, or by simply accepting that the sac is always dorsal. A unique feature of *Pleurozia* is the growth of the stem by means of a 2-sided apical cell; in other genera of the Jungermanniales it is always 3-sided. The occurrence of large, tubular perianths which are completely empty and sterile is another striking feature of this peculiar genus.

LITERATURE. Thiers, B. M. 1993. A monograph of *Pleurozia*. The Bryologist 96: 517-554 [key].

PORELLACEAE

A family of 3 genera,1 in tropical America. The family is closely related to the Jubulaceae and Lejeuneaceae but differs in 1) lobule normally flat, not turned into a water-sac; 2) archegonia numerous (to 30); 3) thicker capsule wall; and 4) elaters free, not attached to the capsule wall.

Porella (Fig. 64) - About 18 species, or less, in montane regions of tropical America (50-60 worldwide). *Porella brasiliensis* (Raddi) Schiffn., *P. crispata* (Hook.) Trevis. and *P. swartziana* (Weber) Trevis. are widespread in the region, the remaining species being restricted to Mexico, Central America, or the Andean countries.

HABITAT. On bark and rock in montane forests, ca. 1000-3500(-4000) m. Also at lower elevations in southeastern Brazil.

DESCRIPTION. **Plants** robust, 5-20 cm long and 3-7 mm wide, green to brown, creeping or pendent, (bi)pinnate. **Branches** *Frullania*-type. **Stems** brown, rigid, with a thick-walled cortex; paraphyllia sometimes present. **Leaves** incubous, divided into a large dorsal lobe and a small ventral lobe (=lobule), apex of the lobe rounded or mucronate, margins entire or toothed, bases sometimes ciliate-

laciniate. **Lobules** almost free from the dorsal lobe, flat and elongated, parallel to the stem or somewhat spreading, margins entire to toothed-ciliate or laciniate, apex broadly rounded. **Cells** with trigones and smooth cuticle; oil bodies small and homogeneous, numerous per cell. **Underleaves** large, longer than wide, undivided, apex broadly rounded. **Rhizoids** in tufts from underleaf bases. **Dioicous**. **Gametoecia** on short branches. **Sporophyte** surrounded by a bluntly 3-keeled perianth. **Seta** short and thick. **Capsule** wall 3-6-layered. **Elaters** free, not attached to the capsule valves. **Spores** large, multicellular, germination endosporous within the unopened capsule. **Vegetative reproduction** unknown.

DISCUSSION. *Porella* is easily recognized by the robust, pinnate plants with incubous leaves and, on the ventral side, a row of large, undivided underleaves and two rows of lingulate lobules, one on either side of the stem. The lobules are rather flat and usually arranged parallel to the stem or slightly spreading. The tips of lobules and underleaves are typically broad rounded.

The Latin American taxa of *Porella* were revised by Swails (1970) who recognized 23 species, including 18 in the tropical part of the region. His key is somewhat difficult to use, however, and it is likely that some species will fall into synonymy when a new study of the group is undertaken.

LITERATURE. Swails, L. F. 1970. The genus *Porella* in Latin America. Nova Hedwigia 19: 201- 291 [key].

PSEUDOLEPICOLEACEAE

(Blepharostomataceae, Chaetocoleaceae)

Plants pale green to brown, creeping to ascending, irregularly branched, stolons lacking. Stems with a weakly differentiated cortex of thick-walled cells. Branches *Frullania*-type, *Microlepidozia*-type and intercalary (ventral and lateral). Leaves transverse or succubous, deeply divided into 3-4(-5) uniseriate to lanceolate segments, margins entire or toothed. Cells normally with uniformly thickened walls and a striate-papillose cuticle; oil bodies granular. Underleaves similar to the leaves. Rhizoids in tufts from underleaf bases. Gametoecia on long shoots. Sporophyte surrounded by a plicate perianth, mouth of the perianth long-ciliate. Seta rather thin, with 8-20 outer rows of cells. Capsule ellipsoidal, wall 2-5-layered. Vegetative reproduction rare, by gemmae (*Blepharostoma*) or leaf fragmentation (*Chaetocolea*).

DISCUSSION. A family of 9 genera worldwide, 3 at high elevations in tropical America. The leaves and underleaves divided into (3-)4 narrow, often bristle-like segments and the cells which are uniformly thick-walled (except *Chaetocolea*) with striate-papillose cuticle, are characteristic. The underleaves are as large as the leaves or slightly smaller. The family shares many character with the Lepidoziaceae but the gametoecia are developed on leading shoots, not on short ventral branches, and the cuticle is typically striate-papillose (smooth or roughened by small, rounded papillae in Lepidoziaceae).

LITERATURE. Schuster, R. M. 1986. Studies on Venezuelan Hepaticae III. Families Blepharostomataceae and Balantiopsidaceae. Nova Hedwigia 42: 49-79.

1. Leaves succubous, divided to ca. 1/2 into narrow lanceolate segments. Segments 2-6 cells wide in the lower half, uniseriate above. Leaf cells with trigones ..... **Chaetocolea**
1. Leaves transverse, divided to at least 3/4 into subulate segments. Segments uniseriate throughout or the base of the segments 2-3 cells wide. Leaf cells with uniformly thickened walls, trigones lacking 2
2. Leaves divided to the base. Plants light green ..... **Blepharostoma**
2. Leaves not divided to the base, with a short lamina. Plants brown ..... **Temnoma**

Blepharostoma (Fig. 65) - A widespread holarctic genus of 3 species, including the common *Blepharostoma trichophyllum* (L.) Dumort., which extend southwards into the mountains of Central America and the Andes.

HABITAT. *Blepharostoma trichophyllum* occurs on litter, on peaty soil, under rocks, and on decaying wood in subalpine and alpine scrub and upper montane cloud forest, 2500-4000 m. The species usually grows in deep shade.

DESCRIPTION. **Plants** very small, to 1 cm long and less than 1 mm wide, pale green, little branched. **Branches** mostly *Frullania*-type. **Stems** without hyalodermis. **Leaves** transverse, divided to the base into 3-4(-5) stiff, uniseriate segments. **Cells** longer than wide, the walls uniformly thickened, cuticle finely striate-papillose; oil bodies granular, 3-7 per cell. **Underleaves** similar to the leaves but with 1 filament fewer, (2-)3-lobed. **Monoicous** or dioicous. **Perianth** surface smooth. **Vegetative reproduction** rare, by gemmae from upper leaf segments.

DISCUSSION. Recognized by the leaves divided to the base into 4 uniseriate, hair-like segments. Underleaves are like the leaves but usually with 1 segment fewer. *Blepharostoma* may be confused with *Telaranea* (Lepidoziaceae); for differences see under the latter.

LITERATURE. Schuster, R. M. 1986 (see family ref.).

Chaetocolea (Fig. 65) - A monotypic, neotropical genus, with *C. palmata* Spruce at high elevations in the northern Andes (Venezuela to Peru). The species is known only from about half a dozen collections.

HABITAT. On soil and over leaf litter in montane cloud forest areas, 2500-3300 m. In northern Peru the species grew in great abundance on a steep roadcut with scattered shrubs, bordering a meadow. In view of its occurrence on roadsides, it is surprising that the species has been so little collected.

DESCRIPTION. **Plants** small, to 5 cm long and 1 mm wide, greenish-brown to dark brown, irregularly branched. **Branches** terminal, *Frullania*-type, *Microlepidozia*-type and ventral-intercalary. **Stems** brown, without hyalodermis. **Leaves** succubous, cuneate to palmate with a narrow base, divided to ca. 1/2 into 3-4 narrow segments, the segments straight or conspicuously diverging, uniseriate above over a length of 4-6 cells, the lower part 2-6 cells wide. **Cells** with trigones, cuticle densely striate-papillose; oil bodies finely granular, 2-10 per cell. **Underleaves** large but shorter than leaves, deeply bifid with 2 lateral teeth (to 4-fid). **Monoicous**. **Perianths** inflated, urn-shaped, surface with scattered cilia.

DISCUSSION. The small, brownish plants with succubous leaves parted into 3-4 straight to conspicuously diverging segments, the large 2(-4)-fid underleaves, and the leaf cells with conspicuous trigones and very rough cuticle, are characteristic of *Chaetocolea*. The leaves are less deeply lobed than in *Temnoma* and *Blepharostoma* and the segments wider, 2-6 cells in the lower half. The occurrence of scattered cilia on the surface of the urn-shaped perianths is another striking feature of this neotropical endemic.

By the trigones and bifid underleaves that are smaller and quite different in shape from the leaves, *Chaetocolea* seems to be a deviating member of the family Pseudocoleaceae. The genus shares many characteristics with the Geocalycaceae and should possibly be referred to that family.

LITERATURE. Fulford, M. H. 1963. *Chaetocolea*. Manual of the leafy Hepaticae of Latin America, Part I. Memoirs of the New York Botanical Garden 11: 62-63. - Schuster, R. M. 1986 (see family ref.).

Temnoma (Fig. 65) - A southern-temperate genus (10 spp.), with 1 species, *T. chaetophylla* Schust., at high elevations in the northern Andes: near Mérida, Venezuela, and in the eastern Cordillera of Colombia (páramo de Pisba).

HABITAT. On decaying logs and peaty soil in upper montane cloud forest, in subalpine scrub, and on damp rock-walls, always in very humid and cool environments, 2500-3700 m.

DESCRIPTION. **Plants** very small, to 1 cm long and less than 1 mm wide, greenish-brown to golden-brown, little branched. **Branches** mostly terminal, *Frullania*-type and *Microlepidozia*-type. **Stems** brown, without hyalodermis. **Leaves** transverse, divided to ca. 3/4 into 3-4 stiff, subulate segments, the segments uniseriate except at the base where 2-3 cells wide, the lamina 4-5 cells high. **Cells** with uniformly thickened walls, cuticle of the lamina cells striate-papillose, of the lobe cells ± smooth; oil bodies very small, granular, 5-10 per cell. **Underleaves** similar to the leaves but somewhat smaller and with a lower lamina (2-3 cells high). **Dioicous**. **Perianth** surface smooth.

DISCUSSION. Resembling *Blepharostoma* but differing in the brown color of the plants and in the leaves not parted to the base, with a short lamina.

LITERATURE. Schuster, R. M. 1986 (see family ref.).

RADULACEAE

A monotypic family.

Radula (Fig. 64) - About 50 species in tropical America (ca. 150 worldwide).

HABITAT. On bark, twigs, rotten wood, living leaves, and rock in the understory and canopy of lowland and montane rain forests and woodlands, in scrub and in alpine vegetations, from sea level to over 4000 m. The majority of the species occur at rather low elevations, below 2500 m. *Radula voluta* Taylor (= *R. ramulina* Taylor) has the widest elevational range and occurs from 500 m on the Galapagos Islands to about 4200 m in the páramos of Colombia. Most species grow on bark but some, including *R. flaccida* Lindenb. & Gott., are primarily epiphyllous. The latter is one of the most common epiphyllous liverworts in neotropical lowland rain forests. A few epiphyllous species, including *R. aguirrei* Schust. (Chocó) and *R. yanoella* Schust. (Amazonia, Costa Rica), are neotenic and produce large, persistent, thalloid protonemata with reduced gametophytes (Schuster, 1991).

DESCRIPTION. **Plants** small to medium-sized, 1-10 cm long, ca. 1-3 mm wide, dull pale green to bright green, rarely brownish, creeping, sometimes pendent, (bi)pinnate. **Branches** *Radula*-type. **Stems** rigid, without hyalodermis. **Leaves** incubous, divided into a large dorsal lobe and a small ventral lobe (=lobule), apex of lobe rounded (occasionally acute), margins entire. **Lobules** broadly attached to the dorsal lobe by a keel and to the stem, quadrate to oblong, flat or somewhat inflated. **Cells** thin-walled or with small trigones, cuticle smooth; oil bodies very large, brown, 1-2 per cell, rarely more (3-5 in *R. stenocalyx*). **Underleaves** lacking. **Rhizoids** in tufts from the lobules. Usually dioicous. **Sporophyte** surrounded by a flattened, 2-keeled perianth. **Seta** short and thick. **Capsule** wall 2-3-layered. **Elaters** free, not attached to the capsule valves. **Spores** unicellular or multicellular, germination exosporous or endosporous. **Vegetative reproduction** by large, multicellular gemmae or caducous leaf segments. **Protonema** sometimes large, thalloid (epiphyllous species).

DISCUSSION. *Radula* is immediately recognized by the incubous leaves with a small ventral lobule which is long connected to the dorsal lobe and to the stem, and by the total lack of underleaves. The plants are usually pale, regularly pinnate with *Radula*-type branches, and the rhizoids are produced in tufts on the lobules instead of on the stem.

A revision of the neotropical species of *Radula* by K. Yamada is in preparation. For identification, the keys to selected species of northern Argentina, Cuba, Puerto Rico, northern Peru, and the Galapagos Islands (cited below) may be consulted. A comprehensive key to neotropical species will appear in Dr. Yamada's forthcoming monograph.

LITERATURE. Reiner-Drehwald, M. E. 1994. El género *Radula* Dum. en el Noreste de Argentina. Tropical Bryology 9: 5-22 [key to 8 spp.]. - Schuster, R. M. 1991. On neotenic species in *Radula*. Journal of the Hattori Botanical Laboratory 70: 51-62. - Yamada, K. 1987. *Radula.* In: W. Schultze-Motel & M. Menzel. Die Lebermoosflora im BRYOTROP-Transekt von Peru. Beihefte zur Nova Hedwigia 88: 77-81 [key to 20 spp.]. - Yamada, K. 1988. The genus *Radula* from Cuba. Journal of the Hattori Botanical Laboratory 65: 379-390 [key to 22 spp.]. - Yamada, K. 1989. *Radula*. Pages 337-338 *in* S. R. Gradstein, A Key to the Hepaticae and Anthocerotae of Puerto Rico and the Virgin Islands. The Bryologist 92 [key to 12 spp.]. - Yamada, K. & S. R. Gradstein. 1991. The genus *Radula* in the Galapagos Islands. Tropical Bryology 4: 63-68 [key to 7 spp.].

SCAPANIACEAE

Plants green to brown to red or purple, usually creeping, irregularly branched. Stems without hyalodermis, cortex weakly differentiated. Branches usually lateral-intercalary, sometimes *Frullania*-type; stolons lacking. Leaves complicate-bilobed with a small dorsal segment and a large ventral segment (sometimes the two segments subequal), the segments connected by a short or long keel, margins entire or toothed. Cells usually with trigones, cuticle smooth or papillose; oil bodies finely granular. Underleaves lacking. Rhizoids scattered. Gametoecia on leading shoots. Sporophyte surrounded by a dorsiventrally flattened perianth with a wide mouth. Seta of numerous cells (cross-section) Capsule wall 3-7-layered. Vegetative reproduction by small, green to brown or reddish gemmae (1-2-celled) from leaf margins.

DISCUSSION. A family of 6 genera, 2 in tropical America. The complicate-bilobed leaves with a small dorsal segment and a large ventral segment, the absence of underleaves, and the perianths which are usually dorsiventrally flattened, are the main characteristics of this family.

LITERATURE. Gradstein, S. R. & J. Váña 1987. On the occurrence of Laurasian liverworts in the tropics. Memoirs of the New York Botanical Garden 45: 388-425. - Schuster, R. M. 1974. Scapaniaceae. The Hepaticae and Anthocerotae of North America, Vol. III: 171-617.

1. Ventral leaf segment long, at least 2 times as long as wide. Perianth inflated, plicate .... **Diplophyllum**
1. Ventral leaf segment short, less than 2 times as long as wide. Perianth flat, smooth .... **Scapania**

Diplophyllum (Fig. 66) - Two species at high elevations in tropical America (ca. 20 worldwide), including *D. andinum* Schust. in the Andes of Mérida, Venezuela, and *D. obtusatum* (Schust.) Schust. in the northern Andes, Costa Rica, Jamaica, and also in North America and Asia.

HABITAT. *Diplophyllum obtusatum* grows on moist, loamy soil of steep roadcuts, always shaded, 2000-4200 m, in the Andes usually above 3000 m. In North America, the species occurs on natural rock outcrops. The occurrence of *D. obtusatum* in man-made environments in the Neotropics, as opposed to its more natural habitats in temperate regions, suggests that the species has been introduced into tropical America (Gradstein & Vána, 1987). *Diplophyllum andinum* is known only from high páramo vegetation at 4160 m.

DESCRIPTION. **Plants** small, 0.5-1.5 cm long and ca. 1-2 mm wide, pale green to reddish-brown, creeping. **Leaves** complicate-bilobed with rather long segments. **Ventral** segment wide-spreading, lingulate, 2-4 times as long as wide, apex usually rounded. **Dorsal** segment subparallel to the stem, about 1/2 the length of the ventral segment, apex rounded to long-acuminate. **Cells** small, uniformly thick-walled or with small trigones, a vitta sometimes present, cuticle papillose; oil bodies finely granular. **Perianths** inflated, plicate. **Gemmae** papillose-stellate. Other characteristics as in the family.

DISCUSSION. The small, terrestrial, creeping plants with complicate-bilobed leaves having a long ventral segment at once distinguish *Diplophyllum* from other leafy hepatics. The genus is uncommon in tropical America and most of the collections are of recent date. The two neotropical species are easily distinguished by the shape of the dorsal segment, which is ovate-oblong with a rounded to apiculate apex in *D. obtusatum* and lanceolate with a long-acuminate apex in *D. andinum*.

LITERATURE. Gradstein, S. R. & J. Váña. 1987 (see family ref.). - Schuster, R. M. 1974 (see family ref.).

Scapania (Fig. 66) - A large holarctic genus (ca. 75 spp.), with 1 species, *Scapania portoricensis* Gott., endemic to the Neotropics and widespread in mountainous regions. In addition, two holarctic species have been recorded from the Neotropics, each only once: *S. cuspiduligera* (Nees) K. Müll. from the Sierra Nevada de Sumapaz, Colombia, and *S. verrucosa* Heeg from Queretaro, central Mexico (Gradstein & Váña, 1987).

HABITAT. *Scapania portoricensis* is a characteristic epiphyte of ± virgin upper montane cloud forests, occurring between ca. 2000 and 3750 m in the Andes and at somewhat lower elevations, from 900 m upwards, in coastal areas and on the islands of the Caribbean. It also occurs on siliceous rocks. *Scapania cuspiduligera* and *S. verrucosa* are saxicolous species, the former occurring on limestone and the latter on siliceous rock. Both were found at high elevations, *S. cuspiduligera* at 4300 m and *S. verrucosa* at 2600 m.

DESCRIPTION. **Plants** small to very large, 0.5-20 cm long, 1-10 mm wide, pale green to reddish or brown, usually creeping, sometimes pendent. **Leaves** complicate-bilobed with rather short, ovate-obovate segments, dorsal segment shorter than ventral segment, apices rounded to apiculate, margins entire or toothed. **Cells** small or large, with trigones, cuticle smooth or papillose; oil bodies finely granular. **Perianths** dorsiventrally flattened, not plicate. **Gemmae** smooth or papillose-stellate. Other characteristics as in the family.

DISCUSSION. *Scapania* is easily recognized by the complicate-bilobed leaves with rather short, ovate-obovate leaves, the dorsal segment being smaller than the ventral. The common *S. portoricensis* is a robust plant with stems to 20 cm long and 1 cm wide. The plants usually turn deep wine-red with age. *Scapania cuspiduligera* and *S. verrucosa* are much smaller, greenish plants of high elevations.

LITERATURE. Gradstein, S. R. & J. Váña. 1987 (see family ref.). - Hong, W. S. 1988. Studies on *Scapania portoricensis* Hampe & Gott. in Latin America. Lindbergia 14: 69-72 - Müller, K. 1951-58. *Scapania*. Die Lebermoose Europas Part II: 914-1013. Rabenhorst Kryptogamenflora. - Schuster, R. M. 1974 (see family ref.).

TRICHOCOLEACEAE

A family of 2-3 genera, 1-2 in tropical America

Trichocolea (= *Leiomitra*) (Fig. 66) - A primarily tropical and southern-temperate genus (ca. 20 spp.), with about 10 species in tropical America.

HABITAT. On bark, decaying wood, and humic soil in montane cloud forests and subalpine scrub, to the lower edge of the páramo, ca. (50-)500-3500 m. *Trichocolea tomentosa* (Sw.) Gott., the most common neotropical species, may even occur at sea level in the everwet rain forests on the Pacific coast of Colombia.

DESCRIPTION. **Plants** small to large, whitish-green to pale brown, creeping, 1-3-pinnately branched, stolons lacking. **Branches** purely *Frullania*-type. **Stems** with a weakly differentiated cortex of thick-walled cells, sometimes with paraphyllia. **Leaves** succubous, densely hairy, deeply divided into 4-9 strongly ciliate segments. **Cells** narrowly elongate, with uniformly thickened walls, cuticle striate-papillose; oil bodies small, homogeneous. **Underleaves** similar to the leaves but slightly smaller. **Rhizoids** lacking or very scarce, in tufts from the bases of the underleaves. **Gametoecia** on long shoots or on short branches. **Sporophyte** surrounded by a fleshy perigynium (coelocaule) with or without a short perianth at the tip. **Seta** thick. **Capsule** ellipsoidal, wall 6-8-layered. **Vegetative reproduction** not observed.

DISCUSSION. The whitish-green, pinnate plants with densely hairy leaves are unmistakable. The leaves are deeply divided into ciliate segments and the lamina is usually very low, 5-6 cells high in *T. flaccida* (Spruce) J. B. Jack & Steph. and no more than 1-3 cells high in the widespread *T. tomentosa*. An unusually high lamina (8-14 cells) characterizes *T. brevifissa* Steph., a common species of SE Brazil. Paraphyllia are rare and occur in the robust, brownish *T. paraphyllina* (Spruce) Steph. (= *T. robusta* Steph.?).

In some species the gynoecia are produced terminal on long shoots, in others they are confined to short lateral branches. The latter species are sometimes placed in a separate genus, *Leiomitra*. Since gynoecia are often rare and still unknown in about half of the neotropical species, recognition of *Leiomitra* as a separate genus is not practical.

LITERATURE. Fulford, M. H. 1963. *Trichocolea*. Manual of the leafy Hepaticae of Latin America, Part I. Memoirs of the New York Botanical Garden 11(1): 40-53 [key].

Order METZGERIALES

Plants usually thalloid, occasionally foliose, prostrate, ascending or erect. Thallus with a thick, flattened central portion (= axis) and thinner, lateral wings, the axis often differentiated as a midrib, the lateral wings undivided, lobed, or deeply dissected into leaves. Thallus cross-section homogeneous, air chambers and pores lacking. Leaves (when present) undivided, originating from only 1 initial cell, longitudinally inserted or weakly succubous, always several layers of cells thick towards the base; underleaves lacking. Cells thin-walled, without trigones; oil bodies usually present. Ventral scales usually absent. Rhizoids all with smooth walls. Antheridia and archegonia within cavities, or on the surface of the axis and then surrounded by an involucre or scales, rarely naked. Sporophyte surrounded by a calyptra and, usually, by a pseudoperianth-like involucre. Seta well-developed, 1-10 cm long, thin to very thick. Capsule globose to cylindrical, opening by 2-4 valves or irregularly, wall 2-6-layered.

DISCUSSION. The Metzgeriales are the second largest order of the Hepaticae in tropical America, with about 150 species occurring in the region, in 6 families and 12 genera. A further genus, *Hymenophyton* (family Hymenophytaceae) from Chile and Australasia, resembling *Jensenia* but with gametoecia and sporophytes located on the ventral side of the thallus instead of dorsally, has been recorded from Colombia and Costa Rica. The Colombian specimen of *Hymenophyton*, without locality (leg. Weir), was studied by Evans (Bulletin of the Torrey Botanical Club 52: 491-506. 1925) and is presumably correctly identified; the Costa Rican specimen, however, is *Jensenia erythropus* (see Gradstein *et al.* 1994, Lindbergia 19: 82-83). It is possible that the Colombian specimen was erroneously labelled and originated from elsewhere. Pending the discovery of further material of *Hymenophyton* from the Neotropics, the genus is not treated in this Guide.

Members of the Metzgeriales are thalloid plants, except the Fossombroniaceae and *Noteroclada* (Pelliaceae) which have leaves. The leaves originate from only 1 initial cell, as in the Calobryales, and are always undivided. They differ essentially from the leaves of the Jungermanniales, which originate from 2 initial cells and are basically bilobed organs. Moreover, the leaves of the Metzgeriales are usually longitudinally inserted or weakly succubous, and are always several layers of cells thick at the base. Those of the Jungermanniales, however, are incubous, succubous or transverse, never longitudinal, and are usually unistratose to the base (rarely somewhat thickened).

A further fundamental difference between the two orders is the origin of the archegonia, which are "acrogynous" in the Jungermanniales but "anacrogynous" in the Metzgeriales. Thus, the archegonia of the Metzgeriales are developed from subapical cells of the main axis or branches, never from the apical cell, whereas in the Jungermanniales the apical cell is involved in archegonial formation. As a consequence, the archegonia and sporophytes in the Metzgeriales are always located on the dorsal (or ventral) surface of the plant, never at the apex. In the Jungermanniales they are restricted to the apex of stems or branches.

Key to the families of Metzgeriales of tropical America

1. Plants with leaves. Leafy shoots elongated or forming small rosettes 2
1. Plants thalloid, the thallus wings entire or deeply divided into segments; leaves absent 3
2. Rhizoids pale brown. Leaf margins not undulate, entire. Plants 4-10 mm wide, green to glaucous ..... **Pelliaceae**
2. Rhizoids purplish. Leaf margins undulate, usually sinuate or toothed. Plants smaller, 2-4(-6) mm wide, green to brownish, never glaucous ..... **Fossombroniaceae**

3. Thallus without midrib or midrib present only in branches. Thallus simple or ± pinnate. Gametoecia on short lateral branches ..... **Aneuraceae**
3. Thallus with a midrib throughout (but ill-defined in Allisoniaceae). Thallus simple or forked (rarely pinnate). Gametoecia on the midrib (dorsal or ventral side) 4
4. Thallus with dark cell walls. Underside of midrib with numerous archegonia and/or antheridia projecting from the surface ..... fern prothallium
4. Thallus not with dark cell walls. Underside of the midrib not with numerous archegonia and/or antheridia projecting from the surface 5
5. Midrib ill-defined, broad, gradually tapering into the thallus wings. Thallus wings strongly undulate to crisped. Thallus underside with small scales ..... **Allisoniaceae**
5. Midrib well-defined, sharply separated from the unistratose thallus wings. Thallus wings plane or undulate. Thallus underside without scales 6
6. Thallus 0.5-2(-3) mm wide, margins usually with hairs (lacking in *Steereella*). Midrib without central strand. Gametoecia on the ventral side of the midrib ..... **Metzgeriaceae**
6. Thallus broader, more than 3 mm wide, margins ± without hairs. Midrib with a narrow central strand. Gametoecia on the dorsal side of the midrib ..... **Pallaviciniaceae**

ALLISONIACEAE

A family of 3 genera, mostly in Asia and Australasia; 1 genus in tropical America.

Calycularia (Fig. 67) - A small, highly disjunct genus (2 spp.), of cool-temperate regions in the Northern Hemisphere and the tropics. One species, *C. crispula* Mitt., has been recorded from high elevations in Mexico and Costa Rica, and also from western North America, eastern Africa, and Asia. The genus is very rare in the Neotropics but an intensive field search in Central America, in potentially suitable habitats, might yield further localities of this interesting genus.

HABITAT. In Mexico found on shaded wet rock (limestone?) in humid, upper montane coniferous forest of *Abies religiosa*, in a gorge near Mexico City, ca. 3000 m. The habitat preferences of *Calycularia crispula* in the Neotropics remain incompletely known. In eastern Africa, the species has been found in mossy, upper montane rain forest and subalpine woodland, at 2000-3000 m, on the bases of trees, rotten logs, and shaded, wet rock (Jones, 1985). In Japan, the species grows mostly in limestone areas.

DESCRIPTION. **Plants** thalloid, pale green to dark green to somewhat purplish along the median portion of the thallus, 1-5 cm long, 4-7 mm wide, prostrate, forked, with a broad, ill-defined midrib which gradually tapers into the unistratose thallus wings; thallus wings undulate to crisped, margin entire. **Midrib** without central strand. **Oil bodies** very small and numerous, homogeneous. **Ventral scales** present, small, especially conspicuous at the apex of the thallus, hyaline or purplish, with a few slime papillae at the margins. **Dioicous**. **Gametoecia** on the dorsal surface of the midrib, with scales; antheridia in a long band on the midrib, hidden under laciniate scales; archegonia in small groups on the midrib, surrounded by scales. **Sporophyte** surrounded by a tubular, deeply laciniate pseudoperianth to 5 mm long. **Capsule** globose, opening irregularly. **Spores** small (ca. 30 µm), unicellular. **Elaters** with 2 spirals, free, not attached to capsule valves. **Vegetative reproduction** lacking.

DISCUSSION. The forked, rather pale-green thallus with strongly undulate wings, a broad, ill-defined midrib without a central strand, and small scales on the ventral surface near the thallus apex, are characteristic of *Calycularia*. The gametoecia develop on the dorsal surface of the midrib, protected by scales as in Pallaviciniaceae, and the capsule is spherical and opens irregularly, as in the Fossombroniaceae.

Calycularia may be confused with *Pallavicinia* and *Symphyogyna* which are very common throughout the Neotropics, but in the latter two genera the thalli have a more clearly defined midrib with a central strand of small, thick-walled cells. Moreover, the thallus wings in *Pallavicinia* and *Symphyogyna* are much less undulate and often bear teeth or papillae, and ventral scales are completely lacking.

Undulate thallus margins are otherwise found in *Monoclea* (Monocleales) which, however, has the thallus surface densely spotted by small, whitish or darkish dots, has no midrib, and is usually a larger plant.

LITERATURE. Davidson, P. G. & D. K. Smith. 1992. *Calycularia crispula* (Hepaticae) in the Aleutian Islands and Pacific Northwest of North America. The Bryologist 95: 266-269. - Grolle, R. 1980. Miscellanea Hepaticologica 201: *Calycularia* in Mexico. Journal of Bryology 11: 325. - Jones, E. W. 1985. African Hepatics XXXV. Some new or little-known species and some noteworthy records. Journal of Bryology 13: 497-508.

ANEURACEAE

Plants thalloid, pure green to blackish, rarely colorless (*Cryptothallus*), 1-10 cm long, 0.5-10 mm wide, prostrate to erect, unbranched or pinnate, without a midrib or with an ill-defined midrib in the branches, thallus apex with slime papillae. Central strand and ventral scales lacking. Oil bodies finely granular, sometimes absent. Monoicous or dioicous. Gametoecia embedded in cavities on short lateral branches or at the thallus margins, the antheridia in rows, the archegonia in small clusters. Sporophyte surrounded by a fleshy calyptra; pseudoperianth lacking. Capsule ellipsoidal, usually opening by 4 valves, wall 2-layered. Spores small, unicellular. Elaters with 1(-2) spirals, usually attached to the tips of the capsule valves. Vegetative reproduction occasionally by gemmae.

DISCUSSION. A family of 4-5 genera worldwide, 3 in tropical America. The principal characteristics of the Aneuraceae are 1) the pinnate (instead of forked) branching of the thallus, 2) the lack of a distinct midrib (but midrib sometimes present in thallus branches in *Riccardia*), 3) the gametoecia on short lateral branches, 4) the sporophyte surrounded by a fleshy calyptra (pseudoperianth lacking), and 5) the elongate capsules with elaters attached to the tips of the valves.

1. Plants growing subterraneous, almost colorless, cells ± lacking chloroplasts. Ventral and dorsal side of thallus with numerous rhizoids ..... **Cryptothallus**
1. Plants not growing subterraneous, green, cells with chloroplasts. Rhizoids, when present, originating from the ventral side of the thallus, dorsal side without rhizoids 2
1. Thallus prostrate, simple, or scarcely branched, 2-8 mm wide, margins undulate or crisped. Oil bodies more than 6 per cell. Male branches with antheridia in 2-6 rows ..... **Aneura**
1. Thallus prostrate or erect, irregularly or regularly pinnate, narrower, 0.5-2(-3) mm wide, margins plane or somewhat undulate. Oil bodies 0-5 per cell. Male branches with antheridia strictly in 2 rows ..... **Riccardia**

Aneura (Fig. 68) - About 3-4 species in tropical America (ca. 10 worldwide), including *A. latissima* Spruce in Amazonia, *A. sessilis* (Spreng.) Gott. *et al.* in the West Indies, and the subcosmopolitan *A. pinguis* (L.) Dumort. scattered throughout the region. A fourth species, *A. pseudopinguis* (Herzog) Pócs, has been described from the state of Santa Catarina, Brazil, and is widely recorded from tropical Africa (see Meenks & Pócs, 1985). The taxonomy of neotropical *Aneura* has not been studied critically and the distribution of the species within the region remains incompletely known.

HABITAT. On rotten and dead wood, humus, moist earth banks, and moist rock, in humid lowland and montane rain forests and in páramos, from sea level to about 4000 m in the Andes. In páramos often on boggy ground and wet soil.

DESCRIPTION. **Thallus** glistening pure green to dark green and somewhat fleshy, 1-5 cm long, 2-8 mm wide, prostrate, scarcely branched, without a midrib, thickened to near the margins, wings lacking or narrow, margins more or less lobed and usually undulate or crisped. **Oil bodies** usually numerous per cell, very small, finely granular. **Dioicous**. **Antheridia** in 2-6 rows on short branches. **Archegonia** in clusters in incisions of the thallus margin, hidden under small thallus wings. **Seta** thick, in cross-section 8-16 cells in diameter. **Vegetative reproduction** lacking.

DISCUSSION. *Aneura* is easily recognized by the rather fleshy, glossy pure green to dark green thalli, which are scarcely branched and usually somewhat undulate or crisped along the margins. A midrib is completely lacking. In the past the genus has been confused with *Riccardia* (see under the latter).

LITERATURE. Meenks, J. L. D. & T. Pócs. 1985. East African Bryophytes IX. Aneuraceae. Abstracta Botanica (Budapest) 9: 79-98 [key to *A. pinguis* and *A. pseudopinguis*]. - Meenks, J. L. D., B. J. van der Steen & E. Kliphuis. 1987. Studies on Colombian Cryptogams XXXIV. Chromosome studies in tropical Andean Aneuraceae. Abstracta Botanica (Budapest) 11: 71-80 [key to *A. latissima* and *A. pinguis*].

Cryptothallus - A genus of 2 species, *C. mirabilis* Malmb. in Europe and Greenland (Schuster, 1992) and *C. hirsutus* H. A. Crum in the Cerro de la Muerte, Costa Rica (Crum & Bruce, 1997).

HABITAT. In Costa Rica found growing embedded in damp humus just underground, at the edge of the páramo near the forest line, under bamboos (*Chusquea* sp.), 3100 m.

DESCRIPTION. **Thallus** colorless to pallid green, small, 1-4 mm wide, growing subterraneous in clusters (coralloid), forked or irregularly pinnate with short branches, without midrib; dorsal and ventral surfaces of thallus densely covered by rhizoids; thallus in transverse section more or less rounded, the inner cells of the ventral half of the thallus infested by numerous hyphae. **Cells** ± without chlorophyll. **Oil bodies** unknown. **Dioicous**, male plants smaller than female ones. **Antheridia** in 2 rows or

irregularly on short branches. **Archegonia** in clusters at the apex of short female branches. **Seta** thick, in cross section 12-16 in diameter. **Capsule** indehiscent (?), valves not observed. **Elaters** free, not attached to the apex of the capsule.

DISCUSSION. *Cryptothallus* is a unique, heterotrophic bryophyte without chlorophyll that grows underground and derives its organic nutrients from a fungus inside the thallus. The plants resemble *Aneura* but differ in the lack of chloroplasts and (in the neotropical species) by the occurrence of numerous rhizoids on both sides of the thallus.

The genus *Cryptothallus* was long considered endemic to Europe and monotypic, with *C. mirabilis* as its only species. A second species, *C. hirsutus*, was recently described from Costa Rica (Crum & Bruce, 1997). The neotropical species is unique in having capsules that are indehiscent, without discrete valves, and containing “free“ elaters. In *C. mirabilis* and all other species of the family Aneuraceae the capsules open by four valves (as usual in liverworts) and the elaters are attached to the apices of the valves. In view of its very different sporophyte, *C. hirsutus* should probably be placed in a separate (new) genus.

LITERATURE. Crum, H. & J. Bruce. 1997. A new species of *Cryptothallus* from Costa Rica. The Bryologist 99: 433-438. - Schuster, R. M. 1992. The Hepaticae and Anthocerotae of North America, Vol. V: 574-579.

Riccardia (Fig. 67) - About 40 species in tropical America (over 100 worldwide), throughout the region but especially at higher elevations. Thirty-six species have been recorded from the Andes which is the center of diversity for *Riccardia* in the Neotropics (Meenks, 1987).

HABITAT. On moist or wet soil, rock, boggy ground and on rotten wood and bark, in lowland and montane rain forests and in páramo, always in very humid environments, 0-4500 m.

Riccardia is one of the most abundant and speciose genera in neotropical páramos. The majority of the species occur above 1500 m in the Andes, elsewhere mostly above 500 m. Three species are characteristic of lowland rain forest (*R. amazonica* (Spruce) S. W. Arnell, *R. metzgeriiformis* (Steph.) Schust., and *R. sprucei* (Steph.) Meenks & De Jong); at least 10 species are exclusive to páramo (e.g., *R. aberrans* (Steph.) Gradst., *R. algoides* (Taylor) Meenks, *R. poeppigiana* (Lehm. & Lindenb.) Hässel, *R. wallisii* (Steph.) Gradst.); the remaining species are montane forest elements.

A group of particular ecological interest are the "dendroid" *Riccardia* spp., characterized by erect growth, opposite branching and nerved branches, sometimes placed in a separate genus *Acrostolia*. They are robust plants that grow in the shaded understory of high montane cloud forests and are apparently an adaptation to these cool and wet forest habitats. The dendroid *R. fucoidea* (Sw.) Schiffn. is widespread in the Neotropics, other species of this group are largely restricted to the Andes (*R. andina* (Spruce) Herzog, *R. ciliolata* (Spruce) Gradst., *R. plumaeformis* (Spruce) Meenks, *R. trichomanoides* (Spruce) Meenks, etc.) or to southeastern Brazil (*R. glaziovii* (Spruce) Meenks (= *R. alata* (Steph.) Hell)).

DESCRIPTION. **Thallus** green to blackish, 1-15 cm long, 0.5-2(-3) mm wide, prostrate, ascending or erect, sometimes with a short rhizome at the base, irregularly to regularly 1-4-pinnate, sometimes palmate with ± parallel branches, the axis and branches with or without a wing, the branches sometimes with a conspicuous midrib, margins of the branches entire or toothed. **Oil bodies** few, 0-5 per cell, large, finely to coarsely granular, in some species lacking or scarce. **Monoicous** or dioicous. **Gametoecia** in 2 rows on short branches. **Seta** thin, in cross-section 4 cells in diameter. **Vegetative reproduction** by gemmae from the surface of ascending thallus branches.

DISCUSSION. *Riccardia* is easily recognized by the pinnately (or palmately) branched thalli with gametoecia on short lateral branches. The plants grow either prostrate or more or less erect. In the older literature (e.g., Spruce, 1885), *Riccardia* is usually treated as a synonym of *Aneura*, but the narrower thallus (less than 3 mm wide), the pinnate branching, the less numerous oil bodies per cell (less than 6), and the thinner seta are reasons to consider it as a separate genus.

The neotropical species of *Riccardia* are still incompletely known and the keys cited below may not always work satisfactorily. Cross-sectioning of the thallus is usually necessary for identification of the species.

LITERATURE. Hell, K. G. 1967. Briófitas talosas dos arredores da cidade de São Paulo (Brasil). Boletim Botânica, São Paulo 25: 1-187 [key and descr. for 9 spp. of SE Brazil]. - Meenks, J. L. D. 1987. Studies on Colombian Cryptogams XXVIII. A guide to the tropical Andean species of *Riccardia*. Journal of the Hattori Botanical Laboratory 62: 161-182 [key to 36 spp. in the Andes]. - Meenks, J. L. D. in press. Aneuraceae of Cuba. Hepatic Flora of Cuba [key to 11 species in the Antilles]. - Meenks, J. L. D. & C. De Jong. 1985. Light microscope studies on the oil bodies of Andean Aneuraceae. Cryptogamie, Bryologie & Lichénologie 6: 1-24. - Spruce, R. 1885. *Aneura*. Hepaticae Amazonicae et Andinae: 540-551 [key to 14 spp.].

FOSSOMBRONIACEAE
(Codoniaceae)

Plants foliose (thalloid in some non-neotropical taxa), differentiated into stem and leaves, prostrate, simple or forked, often growing in rosettes. Leaves succubous, margins shallowly lobed and undulate. Central strand and ventral scales lacking. Oil bodies small and numerous, homogeneous. Rhizoids usually purplish. Gametoecia scattered on the dorsal surface of the axis, usually naked, without scales. Sporophyte surrounded by a bell-shaped pseudoperianth with a wide, open mouth. Seta rather short, thick. Capsule spherical to ovoid, opening irregularly. Spores large, thick-walled, surface ornamented by lamellae or spines. Elaters with 2-3 spirals, free inside the capsule. Vegetative reproduction occasionally by tubers (ventral) or by leafy buds sprouting from the dorsal side of the stem.

DISCUSSION. A family of 4 genera worldwide, 2 in tropical America. The outstanding features of the Fossombroniaceae are 1) the frequent presence of leaves; 2) the purplish rhizoids (rarely pale brown); 3) the occurrence of the gametoecia naked on the dorsal side of the stem; 4) the ± spherical capsule which opens irregularly; and 5) the large, thick-walled, richly ornamented spores.

1. Plants 5-6 mm wide, growing in alpine mires. Leaves deeply plicate ..... **Austrofossombronia**
1. Plants smaller, growing on open soil. Leaves not deeply plicate ..... **Fossombronia**

Austrofossombronia (Fig. 68) - A small Southern-Hemisphere genus (3 spp.), with 1 species, *A. peruviana* (Gott. & Hampe) Schust. ex Stotler *et al.* (= *Fossombronia ptychophylla* Spruce, see Buchloh, 1961) at high elevations in the Andes of Bolivia, Peru, Ecuador, Colombia, and Venezuela.

HABITAT. Submerged in alpine mires on gently sloping ground in páramo and humid puna, usually forming extensive, pure mats, 3600-4750 m. In Peru also collected once in moist rock crevices, at 4500 m (leg. Buchloh).

DESCRIPTION. **Plants** differentiated into stem and leaves, dark green to brown, becoming dark brown to black when dry, robust, to 5 cm long, 5-6 mm wide, leafy stem elongate and forked, not forming rosettes. **Leaves** densely imbricate, succubous, strongly plicate-undulate, margins irregularly toothed, sinuate to entire, base several cells thick. **Cells** large, thin-walled, with numerous minute, homogeneous oil bodies. **Rhizoids** short, purplish. **Dioicous**. **Seta** 16-20 cells in diameter. **Capsule** ovoid, wall 3-5-layered. Otherwise as in the family.

DISCUSSION. *Austrofossombronia peruviana* is a peculiar, little-known species from wet alpine habitats in the Andes. Related species occur in southern Australia and on subantarctic islands (Schuster, 1994). The plants are much more robust than *Fossombronia* species, more dark green to brown, the leaves are strongly plicate, the capsule wall and seta are thicker, and the habitat is completely different, *Fossombronia* species grow as pioneers on open soil, *Austrofossombronia* occur primarily submerged in mires.

When sterile, *Austrofossombronia* may be confused with *Noteroclada* which occurs in the same general habitat. However, the leaves in *Noteroclada* are plane (not plicate-undulate), the rhizoids are pale (not purplish) and the plants are usually glaucous, not dark green or brown. Material with mature sporophytes is immediately separated by the much longer seta of *Noteroclada*.

LITERATURE. Buchloh, G. 1961. Einige Species novae und Neufunde von Moosen aus den Anden von Peru. Nova Hedwigia 3: 507-516. - Crandall-Stotler, B., R. E. Stotler & A. V. Freyre. 1999. On the status of *Austrofossombronia peruviana* (Gottsche & Hampe) Schust. ex Stotler, Stotl.-Crand. & A. V. Freyre. Haussknechtia Beiheft 9: 67-78. - Schuster, R. M. 1994. Studies on Metzgeriales. III. The classification of the Fossombroniaceae and on *Austrofossombronia* Schust., gen. nov. Hikobia 11: 439-449. -

Fossombronia (Fig. 68) - About 10 (?) species in tropical America (ca. 30 worldwide), scattered throughout the region.

HABITAT. Pioneers on moist, exposed earth and stony soil along roads, trails, and rivers, often in somewhat disturbed environments, from sea level to 4250 m in the Andes, at low elevations in the West Indies (mostly below 1000 m).

DESCRIPTION. **Plants** differentiated into stem and leaves, pale green, small, 0.5-1(-2) cm long, 2-3 mm wide, often growing in rosettes. **Leaves** succubous, margins rounded to truncate to irregularly dentate, undulate to crispate, base several cells thick. **Cells** large, thin-walled, with numerous minute, homogeneous oil bodies. **Rhizoids** purplish, rarely pale brown. **Capsule** spherical, wall 2-layered. Otherwise as in the family.

DISCUSSION. The small, pale-green rosettes on bare soil, with densely imbricate, undulate to crispate leaves and purplish rhizoids, are unmistakable. Plants with elongate stems and less imbricate

leaves may also occur, however. The small, spherical capsules arising on short setae from the center of the rosettes and opening irregularly, are also highly characteristic of *Fossombronia*. A further conspicuous feature are the antheridia. They develop as small, orange-yellow bodies that are lying naked on the dorsal surface of the stem, unprotected among the leaves, and may be observed with the naked eye.

Fossombronia species are typically short-lived plants that may develop rapidly on seasonally wet earth. The thick-walled spores are very resistant to drought and may remain viable in the soil for many years. Mature spores are necessary for identification of the species. Since mature capsules dehisce easily and shed their spores when dried, it is advisable to carefully separate a few capsules when collecting the specimen and keep these in a separate, small envelope together with the rest of the collection.

Fossombronia may be confused with *Noteroclada*, especially in SE Brazil where the two genera sometimes occur together on road sides. In these localities, *Fossombronia* may be distinguished from *Noteroclada* by the purplish rhizoids, the homogeneous oil bodies, the naked antheridia (immersed in the stem in *Noteroclada*), and the very different sporophyte.

Unfortunately, the neotropical species of *Fossombronia* have received very little attention and except for Spruce's (1885) treatment of selected species of the Amazon basin and the Andes, there are no keys to species. A revision of the genus *Fossombronia* in tropical America by A. V. Freyre is in preparation.

LITERATURE. Schuster, R. M. 1992. *Fossombronia*. The Hepaticae and Anthocerotae of North America, Vol. V: 365-372. - Spruce, R. 1885. *Fossombronia*. Hepaticae Amazonicae et Andinae: 526-529 [key to 4 spp.].

METZGERIACEAE

Plants thalloid, narrow, to 2(-3) mm wide, with a narrow midrib and a unistratose lamina, prostrate or erect or pendent, forked, rarely pinnate, sometimes with ventral branches. Hairs usually present on thallus margins, on the underside of the midrib, and sometimes on the thallus surface. Midrib with large epidermal cells, without central strand. Oil bodies absent or very small, homogeneous. Ventral scales lacking. Monoicous or dioicous. Gametoecia on highly abbreviated branchlets scattered along the ventral side of the midrib, the antheridia inside a globose sac (= inrolled male branchlet), the archegonia hidden under a thallus flap (= female branchlet or "involucre"). Sporophyte surrounded by a fleshy calyptra; pseudoperianth lacking. Capsule spherical to ovoid, opening by 4 valves, wall 1-2-layered. Spores small, unicellular. Elaters with 0-1 spirals, attached to valve apices. Vegetative reproduction by gemmae or caducous branches.

DISCUSSION. A family of 2-4 genera worldwide, 2 in tropical America: the subcosmopolitan genus *Metzgeria* and the Antillean endemic *Steereella*. In addition, there is a 19th century record of *Apometzgeria pubescens* from Peru (Menzel, M., 1984. Willdenowia 14: 498). Since *Apometzgeria pubescens* is bipolar in distribution and occurs in North America as well as in southern South America, its occurrence in the Neotropics can reasonably be expected. Indeed, several other bipolar species occur in the high Andes, e.g., *Cephalozia pleniceps* (see Gradstein, S. R. & J. Vána. 1987. Memoirs of the New York Botanical Garden 45: 388-425). The occurrence of *Apometzgeria* in the Neotropics remains unconfirmed, however.

Important features of the Metzgeriaceae are 1) the thin, furcate thallus with a narrow midrib; 2) the numerous hairs along the thallus margins; 3) the midrib with large epidermal cells and without a central strand; 4) the scarcity of oil bodies; 5) the ventral position of the gametoecia, on the underside of the midrib; 6) the presence of a fleshy calyptra surrounding the sporophyte (pseudoperianth lacking); and 7) the elaters attached to the tips of the capsule valves. The last two characteristics are shared with the Aneuraceae.

The Metzgeriaceae are also ecologically well-defined. It is the only family of the Metzgeriales which is primarily epiphytic; most of the species grow on bark in montane rain forest. The other members of the Metzgeriales are mainly terrestrial or occur on rotten wood.

LITERATURE. Costa, D. 1999. Metzgeriaceae (Metzgeriales, Hepatophyta) no Brasil. Tese de Doutorado, Universidade de São Paulo, Instituto de Biociências, São Paulo, 261 p. [key to the spp. of Brazil] - Kuwahara, Y. 1986. The Metzgeriaceae of the Neotropics. Bryophytorum Bibliotheca 28: 1-254 [keys to 62 spp.].

1. Thallus margin with a border of very long and narrow cells, hairs lacking ..... **Steereella**
1. Thallus margin not bordered by very long and narrow cells, hairs present ..... **Metzgeria**

Metzgeria (Fig. 69) - About 50 species in tropical America (over 100 worldwide), most of them at montane elevations.

HABITAT. On bark, living leaves, dead wood, and moist rock in lowland and montane rain forests, in scrub, and in humid alpine vegetation (páramo, puna), from sea level to 4350 m in the Andes.

The majority of the species of *Metzgeria*, including the common, pendent *M. leptoneura* Spruce, grow in montane rain forests and occur above 500 m; the genus is very scarce in lowland forest. A group of particular ecological interest are the members of subgenus *Biforma*, characterized by attenuate thallus segments producing gemmae. They are usually tiny plants that mostly grow on fine twigs and small branches of shrubs in the páramo and at forest margins in the upper montane belt. Large numbers of gemmae are often produced on the narrowly tapering ends of ascending thallus segments. Some of the species have a very characteristic yellowish color when fresh; others become deep blue when dry.

Seven species of *Metzgeria* are known only from páramos, at elevations above 3200 m (*M. atramentaria* Kuwah., *M. bischleriae* Kuwah., *M. cleefii* Kuwah., *M. dorsipara* (Herzog) Kuwah., *M. metaensis* Kuwah., *M. neotropica* Kuwah., and *M. parviinvolucrata* Kuwah.).

DESCRIPTION. **Thallus** thin, with a narrow midrib, pale green to yellowish, sometimes blue when dry, 0.5-15 cm long, 0.3-2(-3) mm wide, prostrate to erect or pendent, forked, rarely irregularly pinnate, with numerous hairs along the margins, on the underside of the midrib, and, sometimes, on the ventral surface of the thallus; hairs unicellular, arising singly or in pairs, sometimes in groups of 3-5. **Thallus surface** plane to deeply concave with inflexed margins. **Midrib** 2-8(-12) cells wide, epidermal cells smooth or papillose, larger than the inner cells; central strand absent. **Thallus wings** unbordered. **Elaters** with 1 spiral. Otherwise see family description.

DISCUSSION. *Metzgeria* is easily recognized by the thin, furcate thalli with a narrow midrib, and by the presence of numerous hairs along the thallus margins and on the ventral surface of the midrib (and sometimes on the lamina as well). The epiphytic habitat of most of the species is a further unique feature of the genus and separates it from other thalloid hepatics, which are primarily terrestrial or saxicolous.

The peculiar, thalloid genus *Pteropsiella* (Lepidoziaceae) from Amazonia has sometimes been confused with *Metzgeria*.The lack of hairs, the very different thallus cells, and the occurrence of large slime papilla at the thallus margins (especially near the apex of the thallus) in *Pteropsiella* readily separate the two genera when sterile.

For identification of the neotropical species the treatment by Kuwahara (1986) may be consulted. The species are very variable, however, and in some cases identification is difficult using Kuwahara's keys. Also, the distribution and ecology of the species in tropical America remain very poorly known. It is obvious that further work on this important genus is necessary to arrive at a better understanding of the neotropical species and their habitats.

LITERATURE. Costa, D. 1999 (see family ref.) - Kuwahara, Y. 1986 (see family ref.).

Steereella (Fig. 69) - A small neotropical genus with 2 species, *S. lilliana* (Steph.) Kuwah. and *S. linearis* (Sw.) Kuwah., known only from the Greater Antilles (Cuba, Jamaica, Dominican Republic).

HABITAT. On bark of trees and shrubs in lower montane rain forest and in coffee plantations, probably at rather low elevations.

DESCRIPTION. **Thallus** thin, with a narrow midrib, pale green to yellowish, often blue at apices when dry, small, 1-3 cm long, 0.4-1 mm wide, prostrate, forked, margins toothed, without hairs. **Thallus surface** plane to slightly convex. **Midrib** 4-8 cells wide, epidermal cells smooth or papillose, scarcely larger than the inner cells; central strand absent. **Thallus wings** bordered by narrow cells, border 1-3 cells thick. **Elaters** without spirals. Otherwise see family description.

DISCUSSION. *Steereella* is a rather small *Metzgeria*-like plant with thalli only 1-3 cm long and usually less than 1 mm wide. The genus is readily separated from *Metzgeria* by the presence of a conspicuous thallus border, consisting of narrow cells, and by the absence of hairs; instead, there are scattered short spines along the margins of the thallus. Another notable difference from *Metzgeria* is the lack of spirals in the elaters.

The two species of *Steereella* are distinguished by the presence of a 2-3-stratose thallus border in *S. linearis* (border unistratose in *S. lilliana*) and the bluish coloration of the thallus apices and gemmae of *S. lilliana* when dry (pale olive-green in *S. linearis*).

LITERATURE. Kuwahara, Y. 1986 (see family ref.; *Steereella* on p. 178-188].

PALLAVICINIACEAE

Plants thalloid, 3-9 mm wide, with a distinct, swollen midrib and a unistratose lamina, prostrate or erect, simple or forked, sometimes with ventral branches. Midrib with 1(-3) central strands. Oil bodies

finely granular. Ventral scales lacking. Dioicous. Gametoecia on the dorsal surface of the midrib, with scales; antheridia in a long band on the midrib, hidden under laciniate scales; archegonia in small groups on the midrib, surrounded by a scale-like or closed-tubular involucre. Sporophyte surrounded by a deeply laciniate pseudoperianth or a fleshy calyptra. Capsule ellipsoidal to narrow-cylindrical, opening into (1-)2(-4) valves. Spores small, unicellular. Elaters with 2-3 spirals, free, not attached to capsule valves. Vegetative reproduction absent in neotropical genera.

DISCUSSION. A rather large family of about 8 genera, mostly in the Southern Hemisphere; there are 3 genera in tropical America. Important features of the Pallaviciniaceae are 1) midrib with a central strand, 2) elongate capsules usually opening by only 2 valves (sometimes 4 imperfect ones, occasionally only one), and 3) elaters free inside the capsule, not attached to the valves.

1. Thallus wings divided into segments ..... **Symphyogyna**
1. Thallus wings not divided into segments 2
2. Thallus erect from a prostrate rhizome 3
2. Thallus prostrate or slightly ascending, not erect 4
3. Archegonia surrounded by a ring of scales forming a cup-like involucre. After fertilization, a tubular pseudoperianth several times longer than the involucre develops from within the involucre .... **Jensenia**
3. Archegonia merely with a small scale inserted behind them (=side directed to the base of the thallus), cup-like involucre and pseudoperianth lacking ..... **Symphyogyna**
4. Thallus margins with scattered slime hairs 2-4 cells long. Midrib with 1 central strand. Archegonia surrounded by a ring of scales forming a cup-like involucre. After fertilization, a tubular pseudoperianth several times longer than the involucre developing from within the involucre .... **Pallavicinia**
4. Thallus margins without slime hairs. Midrib with 1-3 central strands. Archegonia merely with a small scale inserted behind them (=side directed to the base of the thallus), cup-like involucre and pseudoperianth lacking ..... **Symphyogyna**

Jensenia (Fig. 70) - A tropical and southern-temperate genus (ca. 10 spp.), with 3 species in tropical America: 1) *J. difformis* (Nees) Grolle scattered at mid elevations; 2) *J. erythropus* (Gott.) Grolle in the páramos of Costa Rica, the high Andes from Bolivia to Venezuela, and in the Serra de Itatiaia; and 3) *J. florschuetzii* Gronde in the páramos of Colombia and northern Ecuador.

HABITAT. Always terrestrial on moist earth and peaty soil in partial shade, in montane and alpine environments, 1600-4200 m. *Jensenia* seems to be a primarily alpine genus in the Neotropics; below the forest line the genus occurs almost exclusively in artificial habitats such as on steep, cut earth banks and along trails.

Jensenia erythropus is the most wide-ranging species of the genus in the Neotropics and is common in the upper montane belt and in páramos, between 2200 and 4000 m. The other two species have more restricted ecologies: *J. difformis* occurs along trails in lower montane cloud forests (ca. 1500-2500 m) and *J. florschuetzii* is a rare species of wet, peaty soils in the upper páramo belt, above 4000 m.

DESCRIPTION. **Thallus** pale green to reddish, to 5 cm long, 3-9 mm wide, dendroid, consisting of erect thalli ("fronds") arising from a prostrate rhizome, the erect thallus narrow and stalk-like below, broad, 2-4 times furcate above, the furcate part plane or deeply concave. **Midrib** very broad and thick, to 1/2 thallus width, with 1 central strand of narrow, thick-walled cells. **Thallus margins** entire or toothed. **Archegonia** in clusters at the lower furcations of the thallus, enclosed in a cup-like involucre with a fringed mouth. **Sporophyte** surrounded by a pseudoperianth. **Spore** surface cristate, with numerous irregular ridges.

DISCUSSION. By its peculiar dendroid habit, *Jensenia* is easily separated from other neotropical thalloid hepatics, with the exception of the dendroid members of *Symphyogyna (S. podophylla*, *S. bogotensis*). When fertile, *Jensenia* is readily distinguished from the latter by the presence of a cup-shaped involucre enveloping the archegonia; in *Symphyogyna* the archegonia are merely protected by a small scale. The separation of sterile material of the two dendroid groups is problematical, however, and needs to be studied.

Jensenia is most closely related to *Pallavicinia* and is sometimes considered a mere subgenus of the latter (*Pallavicinia* subgen. *Mittenia*). However, the two differ in several important respects, e.g., in growth form (see Key*)*, in the position of the gametoecia, and in spore morphology. The two groups may therefore be considered good genera (Grolle & Piippo, 1986). In tropical America, the two also differ in ecology, *Jensenia* occurring primarily terrestrially in open, upper montane and alpine environments while *Pallavicinia* grows in lower montane rain forests, usually as an epiphyte.

Of the three neotropical species of *Jensenia*, *J. difformis* stands out by its entire thallus margins; the other two, *J. erythropus* and *J. florschuetzii,* have dentate thallus margins.

LITERATURE. Grolle, R. & S. Piippo. 1986. Bryophyte flora of the Huon Peninsula, Papua New Guinea. XVI. Pallaviciniaceae (Hepaticae). Acta Botanica Fennica 133:59-79. - Gronde, K. van der 1980. Studies on Colombian Cryptogams. VIII. The genus *Jensenia*. Proceedings of the Koninklijke Nederlandse Akademie van Wetenschappen, Ser. C, 83: 271-278 [key]. - Hässel de Menéndez, G. G. 1961. Las especies sudamericanas del género *Pallavicinia*. Boletín de la Sociedad Argentina de Botánica 9: 261-282.

Pallavicinia (Fig. 70) - One species in tropical America (ca. 10 worldwide), *P. lyellii* (Hook.) Carruth., scattered throughout the Neotropics at lower montane elevations. The species is also widely distributed in the palaeotropics and in temperate, oceanic regions of eastern North America and Europe. Other species of *Pallavicinia* are subantarctic or Asiatic in distribution.

HABITAT. On rotten wood, tree bases, litter, humus, and thin soil over vertical rock, in the understory of ± undisturbed, wet submontane and lower montane rain forests, ca. 100-2200 m; mostly below 1000 m in the West Indies.

DESCRIPTION. **Thallus** green, about 2-6 cm long, 3-6 mm wide, prostrate, simple or forked, sometimes with ventral branches. **Midrib** ca. 1/8-1/6 of the thallus width, with 1 central strand of narrow, thick-walled cells. **Thallus wings** undivided, slightly bordered by somewhat narrower cells in 1-2 rows, the margins with 2-4-celled slime hairs, otherwise entire or with a few short teeth. **Archegonia** in clusters scattered on the midrib, enclosed in a cup-like involucre with a fringed mouth. **Sporophyte** surrounded by a pseudoperianth. **Spore** surface reticulate or punctate.

DISCUSSION. Female plants of *Pallavicinia lyellii* are immediately recognized by the cup-like involucre enveloping the archegonia. When gynoecia are lacking, the species is confusingly similar to *Symphyogyna*, especially the common *S. brasiliensis* Nees & Mont. The two can be separated, however, by the occurrence of slime hairs along the thallus margins in *P. lyellii*, especially near the thallus apex. These slime hairs consist of a slime papilla on a stalk 1-4 cells long. They are rather fragile organs that may break away easily; along older portions of the thallus margin rudiments of these slime hairs may be present as short teeth. In *Symphyogyna*, such slime hairs along the thallus margins are lacking (but Evans has reported the occurrence of slime papillae on a unicellular stalk in *Symphyogyna trivittata* Spruce, a species distributed in the West Indies. The latter can be distinguished easily from *P. lyellii* by the presence of 2-3 (instead of 1) central strands in the midrib).

When sterile, *Pallavicinia* may also be confused with *Pteropsiella* (see under *Symphyogyna*).

In view of the wide distribution of *Pallavicinia lyellii* in temperate regions of the Northern Hemisphere, it is surprising that the species is restricted to rather low, warm elevations in the tropics (in Africa the species has been recorded from about 500-2300 m and in tropical Asia from as low as 100 m). Moreover, the habitat of the species in tropical America is quite different from that in temperate areas. In the Neotropics, it is a forest plant whereas in temperate areas it occurs mostly in bogs, marshlands, and on river banks (see Schuster, 1992: p. 500). Possibly, the tropical plants are genetically different from the north-temperate ones; this remains to be investigated.

LITERATURE. Hässel de Menéndez, G. G. 1961. Las especies sudamericanas del género *Pallavicinia*. Boletín de la Sociedad Argentina de Botánica 9: 261-282. - Schuster, R. M. 1992. *Pallavicinia*. The Hepaticae and Anthocerotae of North America, Vol. V: 495-502.

Symphyogyna (Fig. 71) - An important tropical and southern-temperate genus (ca. 25 spp.), with about 15 species at higher elevations in tropical America, in three groups (see below).

HABITAT. On humic or peaty soil, on rotten wood and on moist rock, in montane rain forest environments and in the lower páramo, in undisturbed and disturbed habitats but always in humid, shaded environments, ca. (100-)500-4000 m (in SE Brazil down to almost sea level). In páramos, species of *Symphyogyna* occur on steep earth banks, along rivulets, in scrubby vegetation, etc. In the montane belt, the genus may occur inside the forest or on steep earth banks along trails.

The most common neotropical members of the genus are *S. brasiliensis* Nees & Mont. (thallus unlobed, entire) and *S. brongniartii* Mont. (thallus lobed, toothed). Both occur throughout the altitudinal range of the genus, from the submontane rain forest to the lower páramo belt, and grow in a wide variety of habitats, but always in shaded and permanently humid places. The dendroid *S. podophylla* (Thunb.) Mont. & Nees is a common species on road banks in the submontane and lower montane rain forests of southeastern Brazil.

DESCRIPTION. **Thallus** green, about 2-6 cm long, 3-6 mm wide, mostly prostrate, occasionally erect-dendroid from a prostrate rhizome, simple or forked, sometimes with ventral branches. **Midrib** to 1/6 of the thallus width, with 1(-3) central strands of narrow, thick-walled cells. **Thallus wings** undivided or lobed, sometimes bordered by narrow cells, the margins entire or toothed, without slime hairs. **Archegonia** in clusters scattered on the midrib, each cluster protected by a tiny scale, a closed involucre lacking. **Sporophyte** surrounded by a fleshy calyptra; pseudoperianth lacking. **Spore** surface variously ornamented.

DISCUSSION. *Symphyogyna* is recognized by the prostrate or (occasionally) erect thallus with a thick midrib with 1(-3) central strands, the undivided or sometimes deeply lobed thallus wings, and, especially, the presence of a small scale protecting the archegonia. In the other two neotropical genera of the Pallaviciniaceae (*Pallavicinia*, *Jensenia*), the archegonia are always enclosed in a cup-like involucre.

A further major difference is the lack of a pseudoperianth in *Symphyogyna*. Instead, the young sporophyte is protected only by a calyptra. The calyptra of *Symphyogyna*, however, is a much thicker and more rigid organ than in the other neotropical Pallaviciniaceae and is well suited for the protection of the developing sporophyte.

The neotropical species of *Symphyogyna* fall into three groups:

1. Dendroid species: *S. bogotensis* (Gott.) Steph., *S. podophylla* (Uribe-M., 1999). These are similar in habit to *Jensenia* and may be confused with the latter (see under that genus).

2. Prostrate species with the thallus wings deeply divided into segments: *S. aspera* Steph., *S. brongniartii*, *S. sinuata* (Sw.) Nees & Mont.

3. Prostrate species with undivided thallus wings. This group contains the bulk of the neotropical species, including the common *S. brasiliensis* characterized by entire-margined thalli. The latter may be confused with *Pallavicinia lyellii* (Hook.) Carruth. (for differences see under the latter).

Pteropsiella, a peculiar thalloid member of the family Lepidoziaceae (Jungermanniales) which occurs in lowland rain forest areas of northern Amazonia and the Guianas, somewhat resembles a small *Symphyogyna* or *Pallavicinia* when sterile. It is distinguished from the latter mainly by the peculiar elongate, sausage-shaped slime papillae along the thallus margins, the interrupted tufts of rhizoids on the ventral side of the midrib, and the lack of a central strand in the midrib. Fertile material of *Pteropsiella* is immediately recognized by the small, leafy sexual branches and the large perianth with a long-fringed mouth.

LITERATURE. Evans, A. W. 1925. The lobate species of *Symphyogyna*. Transactions of the Connecticut Academy of Arts and Sciences 27: 1-50 [key]. - Evans, A. W. 1927. A further study of the American species of *Symphyogyna*. Transactions of the Connecticut Academy of Arts and Sciences 28: 295-353 [key]. - Hell, K. G. 1967. Briófitas talosas dos arredores da cidade de Sao Pãulo (Brasil). Boletim Botânica, São Paulo, 25: 1-187 [key to 5 spp. of SE Brazil]. - Uribe-M., J. 1999. - Nuevo registro del género *Symphyogyna* (Hepaticae: Pallaviciniaceae) para Colombia. Revista de la Academia Colombiana de Ciencias Exactas, Fisica y Naturales 23 (Supplemento especial): 119-121 [key to 11 spp.]. - Uribe, J. & J. Aguirre. Las especies Colombianas del género *Symphyogyna*. Caldasia 17: 429-458 [key to 10 spp.].

PELLIACEAE

A small family of 2 genera: *Noteroclada* in Latin America and Africa and *Pellia* in the temperate regions of the Northern Hemisphere.

Noteroclada (Fig. 71) - A small Afro-American genus with 1(-2) species in tropical America, including *N. confluens* Taylor ex Hook. & Wilson in SE Brazil and the high mountains of Central and South America, from Mexico to Tierra del Fuego. A further species occurs in South Africa (Schuster, 1992).

HABITAT. On steep, moist earth banks and rock, often along rivulets close to the running water and sometimes submerged, also near waterfalls and in alpine bogs or mires, in the Andes in subalpine and alpine environments (3000-5000 m), in SE Brazil at much lower elevations (600 m and upwards). The ecology of *Noteroclada* is similar to that of *Pellia*, the other member of the family Pelliaceae, in North America and Europe.

DESCRIPTION. **Plants** foliose, green to glaucous, rather large, 4-10 cm long, 0.5-1 cm wide, very flat, prostrate, simple or forked. **Stems** fleshy, conspicuously flattened dorsally. **Leaves** succubous, almost longitudinally inserted, attached to the lateral side of the axis, ovate, plane to deeply concave, margins entire, lower half of the leaf 2-3 celllayers thick, otherwise leaf unistratose; central strand and ventral scales lacking. **Cells** large, completely thin-walled, each cell with 5-20 small, homogeneous or finely segmented oil bodies. **Rhizoids** pale brown. **Monoicous** or, occasionally, dioicous. **Gametoecia** on the dorsal surface of the stem, the antheridia scattered in small cavities, the archegonia in clusters. **Sporophyte** surrounded at the base by a short tubular pseudoperianth with a wide, open mouth. **Seta** long, 2-10 cm or more, thick. **Capsule** spherical, opening by 4 valves. **Spores** green, very large, to 100 µm in diameter, multicellular, germination endosporous. **Elaters** with 2-4 spirals, attached to the base of the capsule. **Vegetative reproduction** unknown.

DISCUSSION. *Noteroclada* is easily recognized by the robust, green to glaucous plants with colorless rhizoids and with large, undivided, horizontally spreading, succubous leaves which are attached to the

lateral side of the stem, leaving the dorsal surface leaf-free, and are several layers of cells thick near the base. The stems are usually firmly attached to the substrate and there is no trace of underleaves. A further characteristic feature of *Noteroclada* is the spherical capsule which contains very large, green spores and is elevated upon maturity on a long seta, to 10 cm or more in length in Andean populations.

Noteroclada has sometimes been confused with *Fossombronia* and *Austrofossombronia* (Fossombroniaceae); for differences see under the latter.

The southeast Brazilian populations of *N. confluens* are somewhat different from the Andean ones. The descend to much lower elevations (600 m in the Serra dos Orgãos), are green, never glaucous, the seta is somewhat shorter and thinner, and the oil bodies are finely segmented, those in *N. confluens* being typically homogeneous (see Gradstein *et al.*, 1994. Lindbergia 19: 83). If they prove to be different species, the correct name of the Brazilian plants is *N. confluens* and of the Andean plants *N. leucorrhiza* Spruce.

LITERATURE. Schuster, R. M. 1992. Pelliaceae. The Hepaticae and Anthocerotae of North America, Vol. V: 432-435. - Spruce, R. 1885. *Noteroclada*. Hepaticae Amazonicae et Andinae: 529-531 [as *N. leucorhiza* Spruce].

Order MONOCLEALES

A monotypic order, containing only the genus *Monoclea* (family Monocleaceae)

Monoclea (Fig. 72) - One species, *M. gottschei* Lindb., common and widespread in the mountains of tropical America, extending southwards to central Chile and Argentina (Gradstein *et al.*, 1992). A second species, *M. forsteri* Hook., occurs in New Zealand.

HABITAT. On moist earth, leaf-litter, rotten wood, trunk bases, and thin, wet soil over rock in undisturbed and disturbed montane rain forests and in river valleys, in shaded places, (0-)500-3500 m. The species is common along streams and on the wet forest floor, and usually grows near running water, frequently together with *Dumortiera hirsuta*. In southeastern Brazil the species occurs also at sea level.

DESCRIPTION. **Plants** thalloid, green, small to very large, 1-10(-20) cm long, 0.5-3 cm wide, prostrate, forked. **Thallus** without a midrib, in cross-section homogeneous, without differentiation of air chambers, the upper surface densely spotted by whitish or darkish dots in fresh material, margins usually crisped-undulate. **Oil bodies** large, colorless or brown, occurring singly and scattered in inner cells of the thallus, especially in the upper and lower subepidermis. **Ventral scales** lacking. **Rhizoids** pale, usually with smooth walls. **Dioicous**. **Gametoecia** within dorsal cavities. **Antheridia** in swollen receptacles along the median portion of the thallus, the receptacles rounded to linear or furcate. **Archegonia** beneath an elongate swelling (= involucre) along the median portion of the thallus, near the apex. **Sporophytes** arising 1-3 per involucre, the sporophyte when young surrounded by a thin calyptra; pseudoperianth absent. **Seta** long and thick, to 5 cm. **Capsule** cylindrical, opening by only 1 valve, wall 1-layered, with two sets of anastomosing thickening bands in the radial cell walls. **Spores** small, 15-20 µm in diameter. **Elaters** very long, with 2-3 spirals.

DISCUSSION. *Monoclea* is easily recognized by the large, little branched, bright green to dark green thallus without a midrib, with undulate to crisped margins, and with the surface densely spotted by minute whitish or darkish dots (fresh material). The dots are not pores, as in Marchantiales, but are oil bodies and crystal druses. The sporophyte arises near the thallus apex, from beneath an elongate swelling of the thallus, and has a long, thick seta. A unique feature is the opening of the capsule by means of only one longitudinal slit (hence the name "*Monoclea*"). The sporophytes frequently develop in pairs, or even triplets, from one involucre.

The antheridia develop in thickened receptacles on the thallus surface, which are quite variable in shape. In the neotropical plants, they are suborbicular to linear, sometimes furcate or horseshoe-shaped. In plants from warm-temperate regions of Chile and Argentina the receptacles are larger and orbicular, never elongate. Based on the different sizes and shapes of the male receptacles, *Monoclea gottschei* is divided into two subspecies, subsp. *elongata* Gradst. & Mues in tropical America (extending southwards to Tucumán, northern Argentina) and subsp. *gottschei* in temperate regions of Argentina (Neuquén) and Chile, occurring in a relatively small region between 38° and 44° S. Subspecies *gottschei* also occurs on the Juan Fernandez Islands (Gradstein *et al.*, 1992).

Monoclea often grows together with *Dumortiera* (Marchantiales) and fertile thalli of the two are immediately separated by the stalked receptacles of *Dumortiera*. Sterile thalli, however, may be difficult to separate. The thallus of *Dumortiera* is usually more glossy and evenly deep green than that of *Monoclea*, with almost plane margins, never crispate. In fresh material, the absence of dots on the thallus surface immediately separates *Dumortiera* from *Monoclea*. This character cannot be observed

in herbarium material, however. Probably the best character to separate sterile herbarium material of the two is the presence of a “midrib“ on the underside of the thallus in *Dumortiera*, consisting of closely associated rhizoids. This ventral midrib, which is usually clearly visible on the dorsal side, is completely lacking in *Monoclea*.

LITERATURE. Gradstein, S. R., R. Klein, L. Kraut, R. Mues, J. Spörle & H. Becker. 1992. Phytochemical and morphological support for the existence of two species in *Monoclea*. Plant Systematics and Evolution 180: 115-135. - Gradstein, S. R. (submitted). Monocleales. Flora Neotropica Monograph.

Order SPHAEROCARPALES

Plants thalloid, usually small, prostrate or erect. Thallus simple, without air chambers and pores, differentiated into a thickened median portion ("midrib") and 1-layered wings. Oil bodies lacking. Rhizoids all with smooth walls. Antheridia and archegonia on the thallus surface in involucres, each involucre containing only one gametangium. Sporophyte protected by the involucre, seta reduced. Capsule spherical, cleistocarpous, opening through decay of the capsule wall, the wall 1-layered. Spores large. Elaters lacking. Vegetative reproduction rare, by gemmae.

DISCUSSION. A small order with 3 genera (in 2 different families); 1 genus in tropical America: *Sphaerocarpos* (family Sphaerocarpaceae). They are plants of subtropical and Mediterranean regions with dry, hot summers and wet, rather cool winters. The principal characteristics of the order are 1) simple thalli, without internal differentiation; 2) antheridia and archegonia surrounded singly by a conspicuous, ± pear-shaped involucre; 3) sporophyte with a reduced seta and a cleistocarpous capsule; and 4) lack of elaters.

Sphaerocarpos (Fig. 72) - A subtropical-Mediterranean genus (ca. 12 spp. worldwide) with one species, *S. muccilloi* Vianna, in Rio Grande do Sul, southern Brazil. Further species have been recorded from Uruguay and Chile and the southern U.S.A. The genus has not been found in tropical regions, but should be looked for in Mexico.

HABITAT. On temporarily moist, compact soils in lightly shaded places at low elevations, in warm, subtropical regions with a pronounced seasonal climate.

DESCRIPTION. **Thallus** small and delicate, pale green, less than 1 cm long, thickened in the middle, unistratose towards the margins, the margins sinuose-lobed, the median thallus surface covered by numerous small, swollen involucres. **Dioicous**, female and male thalli quite different in size and shape. **Female thallus** suborbicular, 5-8 mm long, involucres 1-2 mm long, obovate to cylindrical, with a very narrow mouth. **Male thallus** smaller, 1-3 mm long, elongate and forked-lobed, involucres tiny, less than 1 mm long, flask-shaped. **Spores** in tetrads, yellow-brown, tetrads 100-180 µm in diameter, surface of individual spores covered by a fine network of areoles, the areoles 6-12 µm in diameter.

DISCUSSION. The small, prostrate thalli densely covered by numerous small, swollen involucres are unmistakable.

LITERATURE. Vianna, E. C. 1981. *Sphaerocarpos muccilloi*, a new hepatic from Brazil. Lindbergia 7: 58-60.

Order MARCHANTIALES

Plants thalloid, small to very large, prostrate, simple or forked, ventral or apical innovations sometimes present. Thallus with or without a midrib, dorsal surface usually with numerous small pores and often with a reticulate pattern. Thallus cross-section consisting of epidermis and inner tissue in 2 layers: a green upper layer composed of air chambers and photosynthetic tissue, and a compact, colorless to red or brown ventral layer. Thallus with scattered "oil cells" (containing 1 large oil body and lacking chlorophyll); green cells without oil bodies. Ventral scales usually present. Rhizoids of two types: with smooth walls and with tuberculate walls. Antheridia and archegonia in dorsal cavities, in cushions or on stalked receptacles, archegonia often surrounded by an involucre. Sporophyte on a stalked receptacle or ± immersed in the thallus, sometimes surrounded by a pseudoperianth. Seta short or lacking. Capsule spherical to ellipsoidal, often opening irregularly, sometimes with an operculum, wall 1-layered. Spores usually large (small in *Lunularia* and *Marchantia*) and usually with a conspicuously ornamented surface. Elaters usually with 2 or more spirals, sometimes elaters lacking.

DISCUSSION. About 100 species in tropical America, in 9 families and 18 genera. Characteristic features of the Marchantiales are 1) the complex thallus, internally differentiated into a green dorsal

part with air chambers, photosynthetic tissue and pores, and a colorless (or brown to red) ventral part consisting of compact tissue; 2) the presence of scales on the underside of the thallus; 3) two types of rhizoids: smooth and tuberculate ones; 4) lack of oil bodies in the green cells (but thallus often with specialized "oil cells" without chlorophyll); 5) gametoecia often produced on a stalked receptacle; 6) seta very short or absent; and 7) capsule with a thin, 1-layered wall, usually opening irregularly, sometimes with an operculum at the top.

Members of the Marchantiales are terrestrial or saxicolous (never epiphytic) and often rather xerophytic, growing in harsh environments with high illumination and great fluctuations in temperature and humidity. Most taxa can withstand prolonged periods of drought and may resume growth after months or even years of desiccation. They are typically plants of seasonal climates and are much more common in drier parts of the Neotropics than in the wet, equatorial regions. Thus, the greatest diversity is found towards the northern and southern limits of the Neotropics, in Mexico, the Central Andes (Peru to northern Argentina), and southern Brazil. They are also well represented on the Galapagos Islands which, although situated on the Equator, have a pronounced seasonal climate. The fleshy thallus of many Marchantiales may be interpreted as a xeromorphic adaptation.

A revision of the neotropical Marchantiales by H. Bischler and others for *Flora Neotropica* is in preparation.

LITERATURE. Bischler, H. 1998. Systematics and evolution of the genera of the Marchantiales. Bryophytorum Bibliotheca 51: 1-201. - Hässel de Menéndez, G. G. 1963. Estudio de las Anthocerotales y Marchantiales de la Argentina. Opera Lilloana 7: 1-297. - Schuster, R. M. 1992. The Hepaticae and Anthocerotae of North America, Vol. VI. - Vianna, E. C. 1985. Marchantiales. Boletim do Instituto de Biociências, Universidade Federal do Rio Grande do Sul. Porto Alegre 37: 1-213.

Key to the families of Marchantiales of tropical America

1. Upper surface of the thallus with pores, appearing as numerous tiny, colorless or whitish dots. Air chambers present (cross-section) 2
1. Thallus lacking pores. Air chambers absent or very inconspicuous 14
2. Gemma receptacles present on dorsal surface of thallus 3
2. Gemma receptacles absent 4
3. Gemma receptacles cup-shaped ..... Marchantiaceae: **Marchantia**
3. Gemma receptacles a lunate "scale" ..... **Lunulariaceae**
4. Thallus surface roughened by numerous conical swellings (=elevated roofs of air chambers), each swelling with a small central pore. Thallus small, less than 5 mm wide, without any tinge of purple ..... **Exormothecaceae**
4. Thallus surface not roughened by conical swellings 5
5. Thallus with a sharp median groove, often growing in (partial) rosettes, sometimes floating on water. Sporophyte in the groove or embedded in the thallus 6
5. Thallus lacking median groove, usually not in rosettes. Sporophyte not embedded in the thallus 7
6. Pores conspicuously star-shaped (due to strong thickening of the radial walls of the surrounding cells). Sporophyte in the median groove of the thallus, enclosed in ovoid involucres. Terrestrial, in subtropical regions (Mexico, S Brazil, N Argentina) ..... **Oxymitraceae**
6. Pores not star-shaped (surrounding cells thin-walled). Sporophyte sunken in the thallus, involucres lacking. Terrestrial or aquatic, widespread ..... **Ricciaceae**
7. Ventral scales lacking (except at thallus apex). Thallus translucent, very thin, 2-layered. Sporophyte embedded in a notch at the thallus apex ..... Targioniaceae: **Cyathodium**
7. Ventral scales present throughout. Thallus thicker, differentiated into midrib and wings. Sporophyte various, but not in a notch at the thallus apex 8
8. Pores star-shaped due to strong thickening of the radial walls of the surrounding cells. (Air chambers without photosynthetic filaments; sporophyte on stalked receptacle; plants of high elevations) ..... **Cleveaceae**
8. Pores not star-shaped, surrounding cells thin-walled 9
9. Air chambers in several layers (at least in median portion of the thallus), without photosynthetic filaments. Sporophytes produced on stalked receptacles 10
9. Air chambers in one layer, usually with photosynthetic filaments. Stalked receptacles present or absent 11
10. Ventral scales in several ill-defined rows. Air pores surrounded by only 1 ring of differentiated cells .....**Cleveaceae**
10. Ventral scales in 2 rows. Air pores surrounded by 1-several rings of differentiated cells .... **Aytoniaceae**

11. Pores compound, barrel-shaped, formed of several superimposed rings of cells (cross-section). Male and female receptacles stalked and variously lobed. Stalk of the female receptacle with 1-2 green strips (*Marchantia*) or without ..... **Marchantiaceae**
11. Pores simple. Receptacles sessile or only female receptacles stalked. Stalk of the female receptacle without green strips 12
12. Thallus 2-4 mm wide, completely black when dry, margins and underside dark purplish-black. Sporophyte in a dark, swollen, mussel-like involucre below the thallus apex. Plants of higher elevations (above 1000 m) ..... Targioniaceae*:* **Targionia**
12. Thallus 2-10 mm wide, not black when dry, margins and underside green or tinged with purple. Sporophyte on thallus surface or on a stalked receptacle. Low or high elevations 13
13. Ventral scales lanceolate, longer than wide. Pores surrounded by 1 ring of differentiated cells. Sporophyte on thallus surface, embedded in a calyptra and protected by a scale-like involucre. Gemmae lacking. Plants of dry lowland areas (below 1000 m) ..... **Corsiniaceae**
13. Ventral scales very broad, much wider than long. Pores surrounded by 3-5 rings of differentiated cells. Sporophyte (very rare) on stalked receptacle. Plants usually with gemmae produced on thallus surface. Plants of higher elevations (usually above 1000 m) ..... **Lunulariaceae**
14. Plants small, thallus segments less than 0.5 cm wide, often in (partial) rosettes. Thallus surface with median groove ..... Ricciaceae: **Riccia**
14. Plants large, thallus segments 1-3 cm wide, not in rosettes. Thallus surface without median groove .....Marchantiaceae: **Dumortiera**

AYTONIACEAE
(Rebouliaceae)

Thallus medium-sized, with simple pores, the pores rarely star-shaped, surrounded by 1-several rings of differentiated cells. Air chambers in 2 or more layers, the walls green, forming a network, filaments lacking. Ventral scales large, in 2 rows. Antheridia in irregular groups embedded in the dorsal surface of the thallus or in discrete, sessile receptacles; archegonia in receptacles. Female receptacles stalked after fertilization, stalk with or without a furrow, receptacle ± lobed, each segment with 1(-several) archegonia in a cavity surrounded by a 2-lipped or entire involucre. Fertilized archegonium and sporophyte sometimes surrounded by a pseudoperianth (*Asterella*). Sporophyte with a very short seta. Capsule opening by an operculum. Spores usually large. Vegetative reproduction lacking.

DISCUSSION. A family of 5 genera worldwide, all of which occur in tropical America. The principal characteristics of the family are 1) thallus with simple pores, but female receptacle with compound pores; 2) air chambers in 2 or more layers (instead of 1 layer), without filaments; and 3) capsule opening by an operculum.

1. Archegoniophore arising from the thallus surface (along the midline), on a very short, 1-5 mm long stalk without furrow. Involucre large, globose, scarcely covered by the receptacle, opening to the side. Thallus green to blue-green ..... **Plagiochasma**
1. Archegoniophore arising from a notch at the thallus apex, stalk usually longer, with furrow. Involucre smaller, borne underneath the deeply lobed receptacle, opening downwards. Thallus green to reddish, never blue-green 2
2. Sporophyte surrounded by a large, conical, whitish or purplish pseudoperianth which hangs down beneath the receptacle and is split above into 8-16 narrow segments ..... **Asterella**
2. Sporophyte surrounded only by an involucre, pseudoperianth lacking 3
3. Receptacle deeply lobed ..... **Reboulia**
3. Receptacle not deeply lobed 4
4. Female receptacle thin, flat, upper surface smooth. Involucre 2-valved, opening by a narrow slit. Epidermal cells of thallus thin-walled, without trigones ..... **Cryptomitrium**
4. Female receptacle thick, swollen, upper surface usually papillose. Involucre cup-shaped, with a wide opening. Epidermal cells with or without trigones ..... **Mannia**

Asterella (Fig. 72) - About 9 species at high elevations in tropical and subtropical America (ca. 80 worldwide). Three species have rather wide distributions in tropical America, *A. macropoda* (Spruce) A. Evans in the northern Andes and Costa Rica, *A. elegans* (Spreng.) Trevis. in the Greater Antilles, and *A. dominicensis* S. W. Arnell in Mexico, Central America and the Greater Antilles (Grolle, 1989). A further species, *A. venosa* (Lehm. & Lindenb.) A. Evans, occurs at the northern and southern limits of the Neotropics, in northern Mexico, southern Brazil, and northern Argentina (the record of *A. venosa* from Suriname - see Grolle, 1989 - is geographically aberrant and may be a label error). The

remaining neotropical species of *Asterella* are rare, little-known taxa that have been recorded mostly from Mexico.

HABITAT. On moist earth and thin soil over rock, usually in dry and moist montane and lower alpine regions, (0-)1500-3700 m. *Asterella venosa* occurs down to sea level in southern Brazil. The species characteristically grow outside the forest or at forest edges, along rivulets, on steep earth banks, roadsides, etc.

DESCRIPTION. **Thallus** green to reddish-purple, medium-sized, 1.5-8 mm wide; dorsal surface of thallus reticulate and with simple pores; epidermal cells with or without trigones; thallus underside usually reddish-purple, with large scales in 2 rows, each scale with 1-4 appendages. **Air chambers** in several layers, without filaments. **Monoicous** or dioicous. **Antheridia** in irregular dorsal groups or cushions. **Female receptacles** arising from thallus apex on a stalk with 1 furrow; receptacle strongly papillose above and 2-5-lobed, segments with a small group of archegonia underneath, surrounded by a cup-shaped involucre; each fertilized archegonium (and sporophyte) surrounded by a large pseudoperianth, splitting above into 8-16 narrow segments. **Sporophyte** as in the family.

DISCUSSION. *Asterella* is recognized by the female receptacles which have a conspicuously papillose dorsal surface and long, whitish to purplish pseudoperianths that hang down from the underside. The pseudoperianths are somewhat conical with acute tips. When mature, they split above into numerous narrow segments. The segments usually remain connected at the tip and are not ruptured by the capsule that opens within the pseudoperianth.

LITERATURE. Evans, A. W. 1919. Three South American species of *Asterella*. Bulletin of the Torrey Botanical Club 46: 469-480. - Evans, A. W. 1920. The North American species of *Asterella*. Contributions of the United States National Herbarium 20: 247-312. - Grolle, R. 1989. Über *Asterella* subgen. *Brachyblepharis* in Lateinamerika. Wissenschaftliche Zeitschrift der Friedrich-Schiller-Universität, Jena, Naturwissenschaftliche Reihe 38: 231-239 [key to 3 spp.].

Cryptomitrium (Fig. 73) - A small "tricentric" genus (3 spp. worldwide) with 1 species, *C. tenerum* (Hook.) Austin, disjunct in mostly subtropical regions of northern and southern America. Further species occur in South Africa, India, China, and Nepal. The northern part of the range of *C. tenerum* includes California, Mexico, Guatemala, and Costa Rica, the southern part northern Argentina (Salta) and Valparaíso, Chile. The species is very rare in the inner tropics. The records from Guatemala and Costa Rica are the only genuine tropical localities known thus far.

HABITAT. On rock in mountains in rather mesic, seasonal climates, 1500-2500 m (?).

DESCRIPTION. **Thallus** usually green, sometimes purplish below, medium-sized, 3-12 mm wide; dorsal surface of thallus reticulate, with simple pores; epidermal cells thin-walled, without trigones; thallus underside with large scales in 2 rows, each scale with 1-3 filiform appendages. **Air chambers** in several layers, without filaments. **Monoicous**. **Antheridia** in irregular dorsal groups behind the archegoniophore. **Female receptacles** arising from the thallus apex on a long stalk with 1 furrow; receptacle with sinuate margins, scarcely lobed, thin and convex, ± smooth above, with archegonia in 2-5 groups in cavities underneath, each group surrounded by a 2-valved involucre. **Pseudoperianth** lacking. **Sporophyte** as in the family.

DISCUSSION. *Cryptomitrium* is closely related to *Mannia*. In both genera, the female receptacles are scarcely lobed and originate from the thallus apex, on a stalk with one furrow; the pseudoperianth characteristic of *Asterella* is lacking. The female receptacles of *Cryptomitrium*, however, are rather thin and smooth above, and have 2-valved involucres underneath, which open by a narrow slit. In *Mannia*, the receptacles are much more swollen-convex, ± papillose above, and the involucres are cup-shaped with a wide, circular opening.

Bi-valved involucres as in *Cryptomitrium* are also found in *Reboulia,* but in *Reboulia* the female receptacles are deeply lobed, the thallus surface is not or scarcely reticulate, and the epidermal cells have large trigones.

LITERATURE. Hässel de Menéndez, G. G. 1963 (see order ref.).

Mannia - An arctic-alpine genus (15 spp. worldwide), with 1 species, *Mannia* cf. *triandra* (Scop.) Grolle, collected in the Andes of NW Peru (Dept. La Libertad) by E. Hegewald in 1977.

HABITAT. On soil over rock (limestone?), in rather dry, high mountain regions, 2300-3100 m.

DESCRIPTION. **Thallus** green to somewhat purplish, small, 2-4 mm wide, often forming a partial rosette; dorsal surface of thallus coarsely reticulate, with simple pores, in older parts sometimes ruptured and with openings; epidermal cells with or without trigones; thallus underside with large scales in 2 rows, each scale with 1-3 narrow appendages. **Air chambers** large, in several layers, without filaments. **Monoicous** or dioicous. **Antheridia** in irregular dorsal groups or cushions. **Female receptacles** arising from the thallus apex on a stalk with 1 furrow; receptacle thick and swollen, scarcely lobed, ± papillose above, underneath with archegonia in small groups in cavities, each group surrounded by a cup-shaped involucre. **Pseudoperianth** lacking. **Sporophyte** as in the family.

DISCUSSION. *Mannia* is similar to *Asterella* in many respects and sterile material can often be difficult to separate. The principal difference between the two genera is the lack of a pseudoperianth in *Mannia*. Since the genus is monoicous, the plants are very often fertile. The identity of the Peruvian plants is not yet clear. They seem to be rather similar to *Mannia triandra*, a species occurring in limestone mountains of North America and Europe. The tendency of the thallus surface to become ruptured with age, leaving holes in the surface through which the large underlying air chambers are visible, is characteristic of *M. triandra.*

LITERATURE. Schuster, R. M. 1992 (see order ref.).

Plagiochasma (Fig. 73) - 8 species in tropical America (16 worldwide) in relatively dry, montane regions. Mexico is the center of diversity of this genus in the Neotropics. The neotropical species are classified in two subgenera, subgen. *Plagiochasma* (7 spp.) and subgen. *Micropylum* containing only the widespread *P. rupestre* (Forst.) Steph.

The species of subgen. *Plagiochasma* are mostly found in Mexico; a few extend southwards to Central America or the Greater Antilles, or northwards to the desert region of the U.S.A. *Plagiochasma rupestre* (subgen. *Micropylum*) has a much wider distribution and occurs widely throughout montane regions of the Neotropics. It has a preference for rather arid mountain regions, however, and is much more common in Mexico and the Central Andes than elsewhere. It seems to be lacking in the Guayana Highland.

HABITAT. On rock in dry, montane regions with a distinctly seasonal climate, usually above 1000 m, to 4000 m. On islands, *Plagiochasma* may occur at lower elevations than in mainland areas. On the Galapagos Islands, for example, *Plagiochasma rupestre* is a rather common species in volcanic rock fissures from 350 m upwards.

DESCRIPTION. **Thallus** green or blue-green, often tinged with purple, small to medium-sized, usually 3-5 mm wide; dorsal surface of thallus not reticulate, with simple pores; epidermal cells with or without trigones; thallus underside with small or large scales in 2 rows, each scale with 1-3 appendages. **Air chambers** in several layers, without filaments. **Monoicous**. **Antheridia** in sessile receptacles. **Female receptacles** arising from the middle of the thallus surface, away from the apex on a very short stalk (to 5 mm long), without a furrow; divided into 1-4 shallow segments, each segment with a strongly swollen, globose involucre which is larger than the segment and opens sideways by 2 valves, holding unfertilized archegonia and a sporophyte. **Pseudoperianth** lacking. **Sporophyte** as in the family.

DISCUSSION. The female receptacles arising from the thallus surface, away from the apex, and the large, fleshy, almost globose involucres which project to the side, beyond the margin of the receptacle, are very characteristic of *Plagiochasma*. One to four involucres are produced per receptacle, each of which may hold one sporophyte. The involucres open sideways along a long, median slit. The mature capsules may be seen clearly from above because the large involucres are hardly covered by the receptacle.

The two subgenera of *Plagiochasma* differ in the morphology of the pores. In subgen. *Plagiochasma* the pores are conspicuous, often somewhat elevated above the thallus surface, and are surrounded by several rings of cells. In subgen. *Micropylum* (*P. rupestre*), however, the pores are rather inconspicuous, not elevated, and are surrounded by only one ring of small cells. Sometimes the cells surrounding the pores of *P. rupestre* have somewhat thickened walls and become ± star-shaped, as in Cleveaceae.

LITERATURE. Bischler, H. 1979. *Plagiochasma* Lehm. et Lindenb. IV. Les taxa américains. Revue Bryologique et Lichénologique 45: 255-333 [key].

Reboulia (Fig. 73) - A genus with only one species, *R. hemisphaerica* (L.) Raddi, widespread in subtropical and warm-temperate regions of the Northern and Southern Hemispheres. The species is very rare in the Neotropics and restricted to the outer, northern and southern limits of the region. There are records from the Greater Antilles (Jamaica, Puerto Rico), Mexico, and southern Brazil (Rio Grande do Sul).

HABITAT. On thin soil over rock, often in crevices, in seasonally dry mountain regions, elevation unknown, presumably above 500 m.

DESCRIPTION. **Thallus** usually dull green, sometimes purplish below, medium-sized, 3-12 mm wide, forked; dorsal surface of thallus not reticulate, with simple pores; epidermal cells with distinct trigones; thallus underside with large scales in 2 rows, each scale with 2-4 filiform appendages. **Air chambers** in several layers, without filaments. **Monoicous**. **Antheridia** often in sessile receptacles, near the base of the female receptacles. **Female receptacles** arising from the thallus apex on a stalk with 1 furrow; receptacle distinctly 4-7-lobed, weakly papillose above, with archegonia in small groups in cavities underneath, each group surrounded by a large, 2-valved involucre. **Pseudoperianth** lacking. **Sporophyte** as in the family.

DISCUSSION. Characteristic features of *Reboulia* are 1) the dull light green thalli lacking a reticulate pattern; 2) the epidermal cells with coarse trigones; 3) the ventral scales with very tiny, filiform appendages which may break away easily; and 4) the female receptacles arising from the thallus apex, deeply 4-7-lobed, with swollen involucres opening along a narrow slit underneath; no pseudoperianth.

Reboulia is similar to *Plagiochasma*, especially subgen. *Plagiochasma*. Fertile material is immediately separated by the very different archegoniophores: in *Reboulia* they arise from the thallus apex on a long stalk (over 1 cm long), with involucres underneath the receptacle; in *Plagiochasma* they arise from the thallus surface away from the apex, on a very short stalk (to 5 mm long), with large involucres to the side, not covered by the receptacle. Sterile material can be separated by the very different appendages of the ventral scales.

LITERATURE. Hässel de Menéndez, G. G. 1963 (see order ref.). - Schuster, R. M. 1992 (see order ref.). - Vianna, E. C. 1985 (see order ref.).

CLEVEACEAE

Thallus small to medium-sized, with simple pores, the pores surrounded by only 1 ring of differentiated cells and often star-shaped due to the strong thickening of the radial walls of the surrounding cells. Air chambers in 1(-2) layers, filaments lacking. Ventral scales in several rows. Antheridia in irregular or regular groups embedded in the dorsal surface of the thallus, archegonia in receptacles. Female receptacles stalked after fertilization, stalk short, with or without furrow, receptacle deeply lobed, dorsally with simple pores, each segment with archegonia surrounded by a 2-valved or tubular involucre. Pseudoperianth lacking. Sporophyte with a very short seta. Capsule opening by several irregular valves, operculum lacking. Spores large. Vegetative reproduction lacking.

DISCUSSION. A small family of 3 or more genera, mostly in arctic and alpine-temperate regions; 2 genera have been recorded from high elevations in tropical America. The family is related to the Aytoniaceae but the capsules open by irregular valves instead of by an operculum and the thallus has usually only 1 layer of air chambers. The epidermal pores in the Cleveaceae are often conspicuously star-shaped, due to the strong thickening of the radial walls of the ring of cells directly surrounding the opening of the pore.

1. Ventral scales without oil cells, apex of ventral scales broader, acuminate. Pores usually not star-shaped. Archegoniophores arising 1 or several in a row from the thallus surface along the thallus midline. Involucre and sporophyte standing up obliquely from the side of the receptacle **Athalamia**

1. Ventral scales of thallus with oil cells, apex of ventral scales narrowly filiform. Pores star-shaped. Archegoniophores arising from a notch at the thallus apex. Involucre and sporophyte hanging down from beneath the receptacle ..... **Sauteria**

Athalamia (= *Clevea*) (Fig. 74) - Two species in tropical America (12 worldwide), *A. andina* (Spruce) S. Hatt., recorded from the Andes of Ecuador, Peru, and northern Argentina, and a second species in Mexico (A. Whittemore, pers. comm.). The species seem to be generally rare.

HABITAT. On wet clay soil at the foot of steep, dripping rocks in river valleys and canyons, in montane rain forest regions, with *Dumortiera*, *Noteroclada*, *Megaceros*, etc., elevation ca. 2000-2800 m.

DESCRIPTION. **Thallus** bright green, tinged with purple, small, ca. 1-1.5 cm long, ca. 5 mm wide, forked; dorsal surface of thallus finely reticulate, with simple pores, the pores usually not star-shaped (in the neotropical species); thallus underside with long, purplish, lanceolate scales in several irregular rows, scales without oil cells, apex tapering-acuminate. **Air chambers** in 1(-2) layers, without filaments. **Monoicous**. **Female receptacles** arising singly or several in a row along the midline of the thallus surface, stalk very short, to 5 mm long, without a furrow, receptacle with 2-3 large, tubular, outwardly projecting involucres, each involucre 2-valved, opening by a long median slit, with one sporophyte. **Sporophyte** as in the family.

DISCUSSION. The female receptacles of *Athalamia* are similar to those of *Plagiochasma* but the distinctly reticulate dorsal surface of the thallus and the long-acuminate scales separate *Athalamia* from *Plagiochasma*. Most species of *Athalamia* have star-shaped pores but in *A. andina* the walls of the cells surrounding the pores seem to be usually thin-walled, hence the pores are not normally star-shaped.

LITERATURE. Bryan, G. S. 1929. Field observations on Peruvian Hepaticae. Botanical Gazette 88: 332-342. - Hässel de Menéndez, G. G. 1963 (see order ref., as *Clevea*).

Sauteria (Fig. 74) - A small genus (3 spp. worldwide) with one species, *S. chilensis* (Lindenb. ex Mont.) Grolle (= *S. berteroana* Mont. ex Gott. *et al.*) at rather dry, high elevations in the Andes of Peru, northern Argentina and Chile, and on the Galapagos Islands.

HABITAT. On bare soil among grassy vegetation or under bushes in rather dry and cool, high mountain environments, in the Andes above 3000 m, at lower elevations on islands. On the Galapagos Islands, the species occurs on gravelly, volcanic soil in the cool pampa region of volcán Cerro Azul, ca. 1200 m, together with *Targionia stellaris* and *Plagiochasma rupestris* (Gradstein & Weber, 1982). In Peru, *S. chilensis* was found at an elevation of ca. 3500 m on soil in rocky puna vegetation of grasses and scattered shrubs.

DESCRIPTION. **Thallus** dark green, small, to 1.2 cm long and 2.5 mm wide, forked; dorsal surface of thallus finely reticulate, with small, star-shaped pores; thallus underside with reddish-black scales in 2 irregular rows, reaching to the margin of the thallus, apex of scales with a cillate appendage. **Air chambers** narrow-rectangular, in 1(-2) layers, without filaments. **Monoicous**. **Female receptacles** arising from the thallus apex, on a very short stalk (to 5 mm long) with one furrow, the receptacle 3-5-lobed, convex above, each segment with a 2-valved involucre underneath. **Sporophyte** as in the family.

DISCUSSION. *Sauteria chilensis* is recognized by 1) the distinctly star-shaped pores; 2) the small scales terminating in a ciliate appendage; and 3) the female receptacles originating from a notch at the thallus apex, 3-5-lobed, with swollen, 2-valved involucres hidden beneath the segments.

LITERATURE. Gradstein, S. R. & W. A. Weber. 1982. Bryogeography of the Galapagos Islands. Journal of the Hattori Botanical Laboratory 52: 127-152. - Grolle, R. 1985. Miscellanea hepaticologica 240. *Sauteria chilensis*. Journal of the Hattori Botanical Laboratory 58: 200-201. - Hässel de Menéndez, G. G. 1963 (see order ref., as *Sauteria berteroana*).

CORSINIACEAE

Thallus medium-sized, with simple pores, the pores surrounded by only 1 ring of differentiated cells. Air chambers in 1(-2) layers, with or without filaments. Ventral scales scattered or in 2 rows. Stalked receptacles lacking. Antheridia in linear receptacles along the median line of the thallus. Archegonia in shallow depressions along the median line of the thallus, often covered by a scale- or hood-like involucre attached behind the archegonia. Pseudoperianth lacking. Sporophyte with a very short seta, enclosed in a calyptra. Capsule cleistocarpous. Spores large. Elaters reduced or short. Vegetative reproduction lacking.

DISCUSSION. A small family with 2 monotypic genera; one genus occurs in the Neotropics, the other in subtropical regions of South America (and elsewhere). They are plants of warm, rather arid climates and occur principally in tropical, subtropical and Mediterranean regions. Important features of the Corsiniaceae are 1) the lack of stalked receptacles; 2) the cleistocarpous capsules which develop in depressions on the thallus surface, are embedded in a calyptra, and are protected by a scale- or hood-like involucre; and 3) reduction of elaters. The elaters in the Corsiniaceae are short (*Cronisia*) or reduced to thin-walled cells without thickening bands *(Corsinia*).

1. Thallus underside light green, without any trace of purple. Ventral scales with 1 filiform appendage. Calyptra and sporophyte scarcely covered by the involucre. Outer surface of the calyptra strongly papillose or spinose. Southern Brazil and northern Argentina ..... **Corsinia**
1. Thallus underside purplish. Ventral scales with 1-6 filiform appendages, one usually longer than the others. Calyptra and sporophyte almost entirely covered by the involucre. Outer surface of the calyptra smooth. Scattered throughout dry regions of the Neotropics ..... **Cronisia**

Corsinia (Fig. 74) - A monotypic, Mediterranean-subtropical genus, with *C. coriandrina* (Spreng.) Lindb. common in southern Europe and North Africa but rare in the New World, with records from Texas, southern Brazil (Paraná, Rio Grande do Sul), and northern Argentina. *Corsinia* is lacking in truly tropical regions where it is replaced by the genus *Cronisia*. It should be looked for in Mexico.

HABITAT. On compact, periodically moist soil or rocky ground, in open areas with a seasonal, Mediterranean to subtropical climate, at low elevations. The species is quite drought-tolerant and can only be found during the rainy season. During the dry season the thallus dies back except for the growing tip.

DESCRIPTION. **Thallus** light green, without any trace of purplish pigmentation, to 2 cm long, (3-)4-6 mm wide, forked. **Dorsal** surface of thallus finely reticulate and with very small pores, epidermal cells thin-walled, often partly decaying. **Thallus** underside with scales in diffuse rows, each scale with a filiform appendage. **Air chambers** large, in 1 layer, with or without filaments. **Monoicous** or dioicous. **Sporophytes** in groups of 1-2 in depressions on the thallus surface scarcely covered by the scale-like

involucre, each sporophyte surrounded by a strongly papillose or spinose calyptra. **Capsule** wall without thickening bands. **Spores** ca. 100-150 µm in diameter. **Elaters** lacking.

DISCUSSION. *Corsinia* is recognized by the pale green, often somewhat glossy, reticulate thallus without any trace of purple, very flat above and swollen below; by the tiny pores, the colorless scales, and by the strongly papillose or spinose calyptrae on the thallus surface, which hold the sporophyte. When fresh, the plants emit a strong odor of coriander (hence the name "*coriandrina*").

LITERATURE. Hässel de Menéndez, G. G. 1963 (see order ref.). - Schuster, R. M. 1992 (see order ref.) - Vianna, E. C. 1985 (see order ref.).

Cronisia (Fig. 74) - A small, neotropical genus, with *C. mexicana* Hicks in Central Mexico and *C. weddellii* (Mont.) Grolle in the seasonally dry cerrado region of central and eastern Brazil (see Vital, 1974), the llanos of western Colombia (Dept. Meta), the island of Curaçao, and southern Veracruz (Lago Catemaco), Mexico. The species has a preference for regions with a pronounced seasonal climate.

HABITAT. On periodically moist soil, especially on river banks, in deciduous seasonal woodland areas, usually in open, well-illuminated environments, also found under exposed rock, from sea level to about 800 m (*C. weddelii*) and 2300 m (*C. mexicana*).

DESCRIPTION. **Thallus** light green, underside purplish or purplish-brown, to 3 cm long, 2-6 mm wide, forked; dorsal surface of thallus finely reticulate, with small pores, epidermal cells thin-walled, often partly decaying; thallus underside with scales in 2 rows, each scale with 1-6 filiform appendages, one appendage usually longer than the others when several. **Air chambers** large, in 1 layer, with or without filaments. **Monoicous** or dioicous. **Sporophytes** in groups of 1-3 in depressions on the thallus surface entirely covered by the scale-like involucre. **Capsule** wall with thickening bands. **Spores** ca. 60-90 µm in diameter. **Elaters** present.

DISCUSSION. *Cronisia* differs sharply from *Corsinia* by the characteristics given in the key and also by several striking features of the capsule: the presence of thickening bands in the capsule wall (lacking in *Corsinia)*, the presence of true elaters (reduced in *Corsinia*) and the smaller spores. In view of the striking differences between the two genera, *Cronisia* has been placed in a separate subfamily Cronisioideae by Schuster (1992).

LITERATURE. Hicks, M. 1993. A new species of *Cronisia* Berkeley (Corsiniaceae) from Mexico. Tropical Bryology 7: 1-6. - Jovet-Ast, S. 1964. Essai sur le genre *Cronisia* Berkeley. Revue Bryologique et Lichénologique 33: 180-184. - Schuster, R. M. 1992 (see order ref.). - Vital, D. M. 1974. On the identity of *Funicularia weddellii* (Mont.) Trevisan, *Funicularia bischleriana* Jovet-Ast and *Cronisia paradoxa* (Wils. et Hook.) Berkeley. Revue Bryologique et Lichénologique 40: 271-276.

EXORMOTHECACEAE

A small family of 3 genera; 1 genus in tropical America.

Exormotheca (Fig. 75) - A genus of about 7 species in seasonally dry, tropical to Mediterranean regions. One species is native to tropical America, *E. fimbriata* (Nees) Lindb. & S. W. Arnell in northern Argentina (Salta) and eastern Brazil (Pernambuco to Minas Gerais). A second species, *E. pustulosa* Mitt. from tropical Africa and southern Europe, occurs in the Botanical Garden of Mexico City, where it has been introduced.

HABITAT. On periodically moist earth and thin soil over rocks, in seasonally dry regions.

DESCRIPTION. **Thallus** clear green to glaucous-green to silver-white, lacking purplish or reddish pigmentation, small, 1.5-4 cm long, 1-4 mm wide; dorsal surface of thallus rough due to numerous small, volcano-like swellings, each swelling with a central pore; pores simple, surrounded by 1 ring of hardly differentiated cells, epidermal cells thin-walled; thallus underside green, with large colorless scales in 2 rows, the scales usually with long filiform appendages, the appendages sometimes branched. **Air chambers** in 1 layer, low or high, with numerous green filaments, the roof of the air chambers raised, volcano-like. **Monoicous** (usually). **Antheridia** embedded in a groove along the thallus midline. **Archegonia** in receptacles at the thallus apex. **Female receptacles** elevated on a very short stalk with 1 furrow, receptacle 2-lobed, each segment with a long, tubular, sideways pointing involucre enveloping the archegonia and 1-2 sporophytes. **Pseudoperianth** lacking. **Sporophyte** with a short seta. **Capsule** opening by an operculum and 4-5 irregular valves. **Spores** 50-150 µm in diameter. **Vegetative reproduction** by tubers.

DISCUSSION. *Exormotheca* is easily recognized by the coarsely "papillose" upper surface of the thallus, with numerous conical or volcano-like swellings. The swellings represent the elevated roofs of the air chambers. Each swelling has a small, central pore which gives access to the underlying air chamber. The thalli of *Exormotheca* are greenish to silver-colored without any trace of purplish or

reddish pigmentation, and the female receptacles arise on a very short stalk from an incision at the thallus apex.

Exormotheca fimbriata, the only species native to the New World and known only from sterile material (?), is characterized by the branched appendages of the ventral scales. In *E. pustulosa*, the appendages are simple or lacking.

LITERATURE. Bischler, H. 1976. *Exormotheca pustulosa* Mitten. Revue Bryologique et Lichénologique 42: 769-783. - Hässel de Menéndez, G. G. 1963 (see order ref.).

LUNULARIACEAE

A monotypic family.

Lunularia (Fig. 75) - A genus with only one species, *L. cruciata* (L.) Dumort., widespread in subtropical and warm-temperate regions of the Northern and Southern Hemispheres. The range of the species has been extended considerably by humans, by the introduction of gemmae in soil of garden plants, and is at least partly artificial. The species has been recorded a few times from tropical America (SE Brazil, Bolivia, Peru, Colombia, Jamaica). The localities from Bolivia (Dept. Tarija, leg. Gradstein) are natural ones (see below) but the others may be introduced occurrences. Even though the species is uncommon in the tropics, the statement by Schuster (1992) that "the species is absent from the entire tropical belt" is incorrect.

HABITAT. On loamy soil, mostly in man-made habitats with much human disturbance, above 1000 m (in southern Brazil sometimes lower). Often occurring in greenhouses and gardens or near springs. In southern Bolivia (Dept. Tarija), *Lunularia cruciata* grows naturally along rivers and in ravines in *Podocarpus-Alnus* woodlands and in cloud forest remnants, at 1600-2200 m elevation. In East Africa, the species occurs in natural habitats in tropical montane forests (Pócs, pers. comm.).

DESCRIPTION. **Thallus** clear green, medium-sized, 1.5-4 cm long, 0.5-1 cm wide; dorsal surface of thallus finely reticulate and with simple pores, the pores surrounded by 3-5 rings of differentiated cells; epidermal cells fully thin-walled (e.g., in greenhouse plants) or with trigones; thallus underside green, rarely purplish, with colorless scales in 2 rows, the scales very broad, with a rounded appendage. **Air chambers** in a single, very narrow layer bordering the epidermis, with numerous green filaments. **Dioicous**, mostly sterile and with gemmae. **Antheridia** and archegonia in receptacles. **Male receptacles** elliptical, at the thallus apex or on branches. **Female receptacles** 4-lobed, each segment with a long, tubular involucre enveloping the archegonia and sporophytes, receptacle becoming stalked only at spore maturity, stalk hairy and very fragile, without a furrow. **Pseudoperianth** lacking. **Sporophyte** with a rather long seta. **Capsule** opening by an operculum and 4 irregular valves. **Spores** very small, ca. 20 µm in diameter or less. **Vegetative reproduction** by discoid gemmae borne on the thallus surface, on the inner side of lunate, scale-like receptacles with entire margins.

DISCUSSION. *Lunularia cruciata* is easily recognized by the gemmae borne in lunate receptacles on the thallus surface. The gemmae-producing lunate receptacles are completely different from the cup-shaped receptacles of *Marchantia*. Gemmae are virtually always present in *Lunularia cruciata*, but sexual reproduction is absent or rare in most parts of the range of the species.

Further characteristics of *Lunularia cruciata* are the very clear green color of the plants, usually without purplish pigmentation (pigmentation present in *L. cruciata* fo. *thaxteri* from Chile and Argentina, see Hässel de Menéndez, 1963), the very narrow and broad scales in 2 rows, each scale with a rounded appendage, and the low air chambers in one very narrow layer, filled with numerous short, green filaments.

LITERATURE. Hässel de Menéndez, G. G. 1963 (see order ref.). - Schuster, R. M. 1992 (see order ref.).

MARCHANTIACEAE

Thallus usually large, dorsal surface with or without pores, pores compound when present, barrel-shaped (cross-section), surrounded by 1-several rings of differentiated cells. Air chambers in 1 layer or reduced, with or without green filaments. Ventral scales in 2-10 rows. Antheridia and archegonia developed on stalked receptacles (antheridiophore, archegoniophore) arising from the thallus tip, the stalk with 2(-4) furrows. Archegonia in rows on the ventral side of the receptacle, each row surrounded by an involucre. Each fertilized archegonium and young sporophyte sometimes surrounded by a pseudoperianth. Sporophyte with a short seta. Capsule opening by irregular valves. Spores small or large, unicellular. Vegetative reproduction sometimes by gemmae produced in cup-shaped receptacles on the thallus surface, or lacking.

DISCUSSION. A family of 5 genera worldwide, 2 in tropical America: *Marchantia* and *Dumortiera*. The latter genus has sometimes been placed in the family Wiesnerellaceae but is placed here in the Marchantiaceae at the advice of H. Bischler. A third genus, **Preissia***,* has been recorded from Mexico and Bolivia, but as shown by Grolle (1980) and Bischler (1984), these specimens were misidentified and are *Marchantia chenopoda* L. The possibility that *Preissia* occurs in the Neotropics should not be ruled out, however, since the genus occurs in Arizona, U.S.A., near the Mexican border. The genus has only one species, *P. quadrata* (Scop.) Nees and should be looked for in the mountains of Mexico, especially in limestone areas.

Principal characteristics of the family Marchantiaceae are the compound, barrel-shaped pores of the thalli and the stalked male receptacles (in other families male receptacles are sessile, not stalked). The important genus *Marchantia* stands out by its gemmae which develop in cup-like receptacles. In the Neotropics, these receptacles are unique to *Marchantia*; they are otherwise found only in the southern temperate genus *Neohodgsonia* (New Zealand, Tristan da Cunha).

LITERATURE. Bischler, H. 1984. *Marchantia* L. The New World species. Bryophytorum Bibliotheca 26: 1-228. - Grolle, R. 1980. Miscellanea hepaticologica 201-210. Journal of Bryology 11: 325-334.

1. Gemma-cups present on dorsal surface of thallus ..... **Marchantia**
1. Gemma-cups absent 2
2. Thallus surface without pores, uniformly deep green. Margins of male and female receptacles with numerous stiff hairs ..... **Dumortiera**
2. Thallus surface with numerous pores. Stiff hairs lacking 3
3. Ventral scales hyaline to violet, in 4-10 rows, the larger scales with a broad, rounded to reniform appendage. Male and female receptacles variously lobed or undivided. Very common throughout tropical America ..... **Marchantia**
3. Ventral scales deep reddish-purple, in 2 rows, each scale with a small, triangular appendage. Male receptacle circular, unlobed, female receptacle shallowly 4-lobed. Occurrence in tropical America possible (unproven) ..... **Preissia**

Dumortiera (Fig. 75) - A widespread tropical and warm-temperate genus, with one species, *D. hirsuta* (Sw.) Nees, throughout tropical America.

HABITAT. On moist soil, rock and rotten wood in shaded environments, in disturbed and undisturbed montane rain forests, often near running water and usually together with *Monoclea gottschei*, 0-3500 m.

DESCRIPTION. **Thallus** uniformly deep green, large, 5-20 cm long, 1-3 cm wide, forked, with a narrow midrib (cross-section); dorsal surface of thallus not reticulate, without pores and without epidermis, sometimes with papilliform cells in groups on the surface; thallus margins often with hairs. **Thallus** underside green, with small, colorless scales in 2 rows and rhizoids forming a narrow midrib, often radiating to the thallus margins. **Air chambers** lacking or vestigial. **Monoicous**. **Male receptacles** almost sessile, on a very short stalk, circular and ± unlobed, margins with stiff, bristle-like hairs. **Female receptacles** on an elongate, 3-6 cm long stalk, becoming 8-10-lobed after fertilization, margins with stiff, bristle-like hairs. **Archegonia** in groups on the ventral side of the segments, each group surrounded by a tubular involucre. **Pseudoperianth** lacking. **Spores** small, 20-35 µm in diameter. **Sporophyte** otherwise as in the family. **Vegetative reproduction** lacking.

DISCUSSION. *Dumortiera hirsuta* is recognized by the large and rather flat, uniformly deep green thalli without pores and without air chambers (epidermis lacking!). The absence of an epidermis and the reduction of the air chambers are unique features of *Dumortiera* and sharply separate it from the other members of the family. Fertile plants are immediately recognized by the numerous bristle-like hairs along the margins of the male and female receptacles. Another typical feature are the long, rhizoids on the ventral surface of the thallus, which are closely very associated along the thallus midline forming a rhizoidal strand, which resembles a ”midrib.“The rhizoidal strand is usually clearly visible on the dorsal side and has been interpreted as a true midrib by many authors.

When sterile, *Dumortiera* can be confused with *Monoclea* with which it often grows associated. However, *Monoclea* is immediately recognized by the lack of a midrib.

Dumortiera hirsuta occurs in two forms: one with crowded, papilliform cells on the dorsal surface of the thallus and one without such papilliform cells. The papilliform cells are the remnants of the filaments of the reduced air chambers and, when present, give a velvety appearance to the thallus. The form with papilliform cells is sometimes treated as a different species, *D. nepalensis* (Taylor) Nees but most authors nowadays consider *D. nepalensis* a synonym of *D. hirsuta*, or a mere subspecies or variety of the latter. It has also been suggested that the two differ in chromosome number, *D. hirsuta* being mostly haploid (n=9) and *D. nepalensis* diploid (n=18), but this remains unproven. In addition, triploid forms (n=27) have been reported. The relationship between morphology and karyology in *Dumortiera* needs further study.

LITERATURE. Evans, A. W. 1918. A taxonomic study of *Dumortiera*. Bulletin of the Torrey Botanical Club 46: 167-182. - Schuster, R. M. 1992 (see order ref.).

Marchantia (Fig. 76) - 9 species in tropical America (36 worldwide), mostly in montane regions. The species are classified in two subgenera: subgen. *Marchantia (M. polymorpha* L., *M. plicata* Nees & Mont., *M. berteroana* Lehm. & Lindenb.) and subgen. *Chlamidium* (6 spp.).

HABITAT.Common on moist soil and rock, occasionally on rotten wood or submerged in water, in montane and alpine regions, occasionally in lowland areas especially in wet, coastal regions, (0-)150-4500 m. The species often grow in disturbed, man-made habitats and are particularly common on earth banks, steep roadcuts, etc., always in permanently moist environments. They are found in open situations in regions with a more or less constantly humid climate. In areas characterized by drier climatic conditions, the plants occur only in the shade, under phanerogamic cover or in rock crevices (Bischler, 1984). *Marchantia* spp. avoid the shaded interior of the forest but are common at forest edges and along roads inside the forest.

In the Neotropics the two subgenera of *Marchantia* have significantly different altitudinal and regional preferences. Members of the subgenus *Chlamidium,* including the very common *M. chenopoda* L., occur mainly in submontane and lower montane regions, below 2500 m. They are the principal representatives of the family in the West Indies. *Marchantia berteroana*, *M. plicata,* and *M. polymorpha* (subgen. *Marchantia*), however, occur mostly above 2000 m, in upper montane and alpine regions (sometimes at lower elevations on islands). They are very common in páramos and *M. plicata* is a characteristic species of alpine mires; in addition, this species is a common colonizer of road banks in the high Andes. *Marchantia polymorpha* stands out among all members of the genus by its commonness in ruderal habitats. The species is often found near human settlements and is a common intruder in gardens, greenhouses, and plantations. It is in fact the only hepatic known to have a preference for substrates rich in nitrates.

DESCRIPTION. **Thallus** light green to rather dark green to glaucous, underside often purplish, plants medium to large, 3-20(-30) cm long, 0.3-2 cm wide, forked, with or without midrib (cross-section); dorsal surface of thallus finely reticulate, with pores and with epidermis, the pores compound, barrel-shaped, in cross-section consisting of 4-7 layers of cells, each pore connected with a small air chamber; thallus margins without hairs, sometimes with small scales protruding beyond the margin; thallus underside green or purple, with large hyaline to violet scales in 4-10 rows, median scales with an appendage. **Air chambers** (cross-section) present in one, narrow layer, with green filaments. **Dioicous**. **Male and female receptacles** on long stalks, shallowly or deeply lobed, the segments flat or terete (= "rays"), margins of the receptacles without hairs. **Archegonia** in rows on the ventral side of the female receptacles, each row surrounded by an involucre; each fertilized archegonium (and young sporophyte) protected by a pseudoperianth. **Spores** small, 10-35 µm in diameter. **Sporophyte** otherwise as in the family. **Vegetative reproduction** by discoid gemmae born in rounded, cup-shaped receptacles on the dorsal surface of the thallus; the margins of the receptacles usually strongly fringed (almost entire in *M. papillata*).

DISCUSSION. *Marchantia* is immediately recognized by the cup-shaped receptacles on the thallus surface, containing large, discoid, light-green gemmae. When gemma-cups are lacking, the genus can be recognized by the compound pores, which are barrel-shaped in cross-section. Compound pores otherwise occur only in *Preissia*, a monotypic genus containing *P. quadrata* (Scop.) Nees, widespread in the temperate regions of the Northern Hemisphere and to be looked for in Mexico (see discussion under the family Marchantiaceae). *Preissia* and *Marchantia* are distinguished by the presence of only 2 rows of large scales in *Preissia* (4-10 rows in *Marchantia*; see also key).

The two subgenera of *Marchantia* found in the Neotropics are primarily distinguished by the morphology of the female receptacles. In subgen. *Marchantia*, the female receptacles are deeply dissected into 9-11 narrow, terete segments ("rays"). In subgen. *Chlamidium*, however, the receptacles are less deeply dissected (sometimes they are only very shallowly lobed) and the segments are flat, not terete. Further differences are found in the thallus margins, which are somewhat crisped or lobulate in subgen. *Marchantia* but nearly plane in subgen. *Chlamidium*, in the outer surface of the gemma-cups, which is papillose in subgen. *Marchantia* but smooth in subgen. *Chlamidium* (except *M. paleacea* Bert.), and in the spores which are only 10-16 µm in diameter in subgen. *Marchantia*, but 20-36 µm in subgen. *Chlamidium*.

LITERATURE. Bischler, H. 1984 (see fam. ref.).

OXYMITRACEAE

A monotypic family.

Oxymitra (Fig. 77) - A small Mediterranean-subtropical genus (2-3 spp.), with *O. incrassata* (Brot.) Sérgio & Sim-Sim (=*O. paleacea* Bischl.) in the southern U.S.A., central and northern Mexico, and disjunct in subtropical South America (southern Brazil, Paraguay, northern Argentina); also in southern Europe and North Africa. The distribution of *O. incrassata* is similar to that of *Corsinia coriandrina*. A second species of *Oxymitra* occurs in southern Africa.

HABITAT. On periodically moist, bare, siliceous soils in relatively dry, open environments, often over granite rock, at rather low elevations. *Oxymitra incrassata* is strongly drought-tolerant and can only be found during the rainy season. It occurs on somewhat less compact and better drained soils than *Corsinia coriandrina* (Schuster, 1992).

DESCRIPTION. **Thallus** grayish-green, margins and underside reddish-purple, usually small, segments 3-6 mm wide, deeply forked with narrow oblong segments, sometimes forming partial rosettes; dorsal surface of thallus with a median groove, finely reticulate, with strongly star-shaped pores, each pore surrounded by 1 ring of differentiated cells with strongly thickened radial walls; thallus margins acute, with long, acuminate scales projecting far beyond the margin, the flanks of the thallus very steep-sloping. **Ventral scales** large, white or somewhat purplish, in 2 rows, apex long-acuminate to filiform, projecting beyond the thallus margin. **Air chambers** in 1 layer occupying 1/3-1/2 the height of the thallus, the chambers very narrow and high. **Monoicous** or dioicous. **Gametoecia** in groups in the median groove of the thallus, antheridia in elongate, swollen receptacles, archegonia hidden singly in ovoid involucres with a short beak. **Pseudoperianth** lacking. **Sporophyte** 1 per involucre, partially embedded in the thallus, consisting merely of a globose capsule, lacking foot and seta. **Capsule** cleistocarpous, wall disintegrated at the time of spore maturation. **Spores** large, ca. 100-175 µm in diameter, outer surface areolate. **Elaters** lacking. **Vegetative reproduction** lacking.

DISCUSSION. The small, swollen, gray-green thalli with a sharp median groove are characteristic of *Oxymitra*. The thalli tend to grow in rosettes or partial rosettes and resemble *Riccia* but differ in the presence of conspicuously star-shaped pores in the epidermis, with the radial cell walls adjacent to the opening of the pore strongly thickened. Stellate pores are otherwise found only in *Sauteria* and *Athalamia*, and occasionally in *Plagiochasma*.

Further characteristic features of *Oxymitra* are 1) the large, long-acuminate scales projecting far beyond the thallus margins, towards the dorsal surface of the thallus; 2) the very high and narrow air chambers in one layer; and 3) the occurrence of the gametoecia and sporophytes in the median groove of the thallus, the antheridia in swollen receptacles and the archegonia and sporophytes enclosed singly in ovoid involucres with a short beak. In *Riccia*, the gametoecia and sporophytes are sunken in the thallus, and receptacles and involucres are lacking.

LITERATURE. Hässel de Menéndez, G. G. 1963 (see order ref.). - Schuster, R. M. 1992 (see order ref.). - Vianna, E. C. 1985 (see order ref.).

RICCIACEAE

Thallus forming rosettes or gregarious patches, forked. Dorsal surface of thallus with a median groove (groove lacking in *Riccia* subgen. *Leptoriccia*) , pores present or absent, when present simple, surrounded by 1 ring of differentiated cells. Air chambers present or ± lacking, in 1-several layers, without filaments. Ventral scales scattered or in 1-2 rows, or absent. Gametoecia sunken in the thallus with only the necks projecting beyond the surface; receptacles lacking. Involucre and pseudoperianth lacking. Sporophyte embedded in the thallus, consisting merely of a globose capsule, lacking foot and seta. Capsule cleistocarpous, wall disintegrated at the time of spore maturation. Spores large, 50-200 µm in diameter, outer surface variously ornamented. Elaters lacking. Vegetative reproduction usually lacking, occasionally by tubers.

DISCUSSION. A family of 2 genera, the large genus *Riccia* and the monotypic *Ricciocarpos*. Both occur in tropical America. The species are mostly pioneers of open or disturbed soils and often grow in areas where occasional flooding occurs. The principal characteristics of the family are: 1) thalli usually with a dorsal groove and forming rosettes; 2) gametoecia and sporophyte embedded in the thallus, receptacles lacking; 3) sporophyte highly reduced, without foot and seta, and lacking elaters; and 4) capsule cleistocarpous, wall disintegrating at the time of spore maturation.

1. Plants terrestrial, rarely in water (*Riccia stenophylla*). Ventral scales large or small (or lacking), when present in 1-2 rows, without oil cells ..... **Riccia**
1. Plants floating on water, occasionally occurring on wet soil. Ventral scales large, scattered on ventral surface of thallus, with oil cells .....**Ricciocarpos**

Riccia (Fig. 77) - 54 species in tropical America (ca. 150 worldwide), throughout the region but particularly common in seasonally dry areas. The majority of the species occur near the northern and

southern limits of the Neotropics where seasonal climates prevail. Southern Brazil is the center of diversity in the Neotropics, with 22 species. Other areas rich in species are Mexico (13 spp.) and the central Andes, from Peru to northern Argentina (12 spp.). The wetter, equatorial regions are less suitable areas for *Riccia*: only 5 species are found in the northern Andes, 3 in Amazonia, while none have been reported from the Guayana Highland (see Jovet-Ast, 1991, 1993). Central America and the West Indies have 8 species each.

The neotropical species belong to four different subgenera: subgen. *Riccia* (38 spp.), subgen. *Ricciella* (14 spp.), subgen. *Leptoriccia* (1 sp., *R. membranacea* Gott. & Lindenb.) and subgen. *Thallocarpus* (1 sp., *R. curtisii* (James ex Austin) Austin). For morphological differences see discussion below. The subgenera *Riccia*, *Ricciella,* and *Leptoriccia* are widespread in the Neotropics but subgen. *Thallocarpus* is mainly confined to southern Brazil and northern Argentina; in addition, there is a single record from Costa Rica.

HABITAT. Pioneers on open and often somewhat disturbed, periodically moist soil and on rock covered by thin soil, rarely aquatic, in exposed or somewhat shaded environments, from sea level to over 4500 m in the Andes. The species are usually adapted to survive prolonged periods of drought and are often found in anthropogenic habitats such as gardens, cultivated land, ditches, river banks, trails etc., always on rather compact, and often somewhat stony soil. They may also grow at forest margins but are never found inside the forest. A good environment for *Riccia* are old botanical gardens; Jovet-Ast was able to report 6 species from the Botanical Garden of Mexico City.

In high alpine environments, above 4000 m, where disturbance by man is minimal, species of *Riccia* may grow on periodically moistened soil under shrubs, along rivulets, and in rock crevices.

DESCRIPTION. **Thallus** green, grayish-green or glaucous, often tinged with red or purple, usually small, thallus segments 0.5-4 mm wide, forked, often forming rosettes; dorsal surface of thallus usually with a median groove, usually not clearly reticulate, pores lacking or very small, dorsal epidermis without oil cells, sometimes decaying and then thallus surface with openings; thallus margins acute or obtuse, sometimes with cilia or with scales projecting beyond the margin, the flanks of the thallus usually steep-sloping. **Ventral scales** small or large, when large sometimes projecting beyond the thallus margin, variously colored, in 1-2 rows, without oil cells. **Air chambers** in 1-3 layers or ± lacking, when lacking the upper tissue of the thallus forming dense vertical rows. **Monoicous** or dioicous. **Gametoecia** and sporophyte as in the family.

DISCUSSION. *Riccia* is usually recognized by the small, forked thalli with a dorsal groove (groove lacking in *R. membranacea*), growing in rosettes, partial rosettes, or gregarious patches on open soil. In the majority of the species, the dorsal surface of the thallus lacks a reticulate pattern, with pores being absent or minute. In *R. membranacea* (subgen. *Leptoriccia*) the dorsal surface may have irregular openings due to decay of the epidermis.

The species of the subgen. *Riccia* are characterized by the lack of distinct air chambers; in all other groups these are well-developed. Subgen. *Leptoriccia* (*R. membranacea*) stands out by the very thin thallus (only 3-4 cell layers thick), the lack of a dorsal groove, and the irregular openings in the dorsal epidermis, and subgen. *Thallocarpus* (*R. curtisii*) is distinguished by the spores being released from the capsule in tetrads. The latter feature is a rare phenomenon in hepatics and is otherwise known to occur only in *Sphaerocarpos*.

LITERATURE. Jovet-Ast, S. 1991. *Riccia* L. (Hépatiques, Marchantiales) d'Amérique Latine. Taxons du sous-genre *Riccia*. Cryptogamie, Bryologie Lichénologie 12: 189-370. - Jovet-Ast, S. 1993. *Riccia* L. (Hepaticae, Marchantiales) from South America. Subgen. *Thallocarpus, Leptoriccia, Ricciella*. Cryptogamie, Bryologie Lichénologie 14: 219-301.

Ricciocarpos (Fig. 78) - A monotypic genus, with *R. natans* (L.) Corda widespread in temperate regions of the Northern and Southern Hemispheres. In tropical America, *R. natans* has been recorded from Mexico, Cuba, Panama, Colombia (?), Bolivia (fide A. Whittemore, pers. comm.), and Brazil (Amazonia, southeastern Brazil from Bahia to Rio Grande do Sul).

HABITAT. Floating on stagnant water or, occasionally, terrestrial on muddy banks of ponds and lakes that have dried up. In lowland and montane regions, from sea level to 2500 m.

DESCRIPTION. **Thallus** yellow-green to dark green, often with purple margins, medium-sized, to 1 cm long, the segments 3-6 mm wide, usually forming rosettes floating on water; dorsal surface of thallus with a median groove, finely reticulate and with small pores, dorsal epidermis with scattered oil cells. **Ventral scales** large, ligulate, purplish, in several diffuse rows, with oil cells. **Air chambers** large, in several layers (almost the entire thallus composed of air chambers). **Monoicous**. **Gametoecia** and sporophyte as in the family.

DISCUSSION. *Ricciocarpos natans* is usually aquatic and is easily recognized by the rather coarse rosettes (segments 3-6 mm wide) floating on water, with long, ligulate scales hanging down from the lower surface. Terrestrial plants, growing on the muddy shores of ponds and lakes that have dried up, have smaller scales and may be confused with *Riccia*. The presence of oil cells in the scales and

epidermis, and the large air chambers, occupying almost the entire thallus, may separate these land forms of *Ricciocarpos* from *Riccia*.

LITERATURE. Hässel de Menéndez, G. G. 1963 (see order ref.). - Schuster, R. M. 1992 (see order ref.). - Vianna, E. C. 1985 (see order ref.).

TARGIONIACEAE

Thallus medium-sized, with simple pores surrounded by 1-3 rings of differentiated cells. Air chambers in 1 layer, with or without filaments. Ventral scales in 2 rows. Stalked receptacles lacking. Antheridia sunken in the thallus surface or in small receptacles on short branches. Archegonia in a cluster at the thallus apex, after fertilization surrounded by a 2-valved involucre becoming displaced below the apex. Pseudoperianth lacking. Sporophytes 1-4 per involucre, with a very short seta. Capsule opening by an operculum. Spores large. Vegetative reproduction sometimes by gemmae from the thallus margins and by tubers produced on the ventral side of the thallus (*Cyathodium*).

DISCUSSION. A small family of 2 genera, both occurring in tropical America. The main feature of the family Targioniaceae is the large, 2-valved involucre below the apex of the thallus, enveloping the sporophyte.

1. Thallus margins and underside green. Thallus delicate, translucent, differentiated into midrib and thin wings. Ventral scales reduced ..... **Cyathodium**
1. Thallus margins and underside purplish. Thallus firm, leathery, not differentiated into midrib and thin wings. Ventral scales well-developed ..... **Targionia**

Cyathodium (Fig. 78) - A pantropical genus (ca. 14 spp.), with 3-4 species in tropical America, at rather low elevations. *Cyathodium africanum* Mitt. is widely distributed in the dry seasonal cerrado region of Brazil (Mato Grosso, Goias, Minas Gerais). Other species have been collected in Cuba, Mexico, Panama, and Peru.

HABITAT. Pioneer on moist soil in shaded places, on steep earth banks, on river banks and sometimes under rock overhangs, in seasonal and evergreen montane forest regions, from sea level to 1500 m. In Panama, also found on cement walls of flower buckets (obs. N. Salazar Allen).

DESCRIPTION. **Thallus** delicate, translucent, pale green to yellowish-green to glaucous-green, not tinged with purple, to 1.5 cm long, 1-4 mm wide, often forming partial rosettes, thin, 2-layered, sometimes slightly thicker in the middle, thallus margins often irregularly lobed; dorsal surface of thallus reticulate, with pores, epidermal cells thin-walled. **Ventral scales** usually reduced, in 2 rows near the thallus apex, scales with slime papillae at the margins and apex, and sometimes with a small appendage. **Air chambers** in 1 layer, without filaments. **Monoicous** or dioicous. **Sporophytes** 1-4 in a notch at the apex of the thallus, surrounded by a 2-valved involucre. **Vegetative reproduction** sometimes by gemmae from thallus margins and by tubers. Otherwise as in the family.

DISCUSSION. *Cyathodium* is characterized by the delicate, translucent thalli without purplish pigmentation and with archegonia and sporophytes developing in a notch at the thallus apex. The dorsal surface of the thallus is reticulate and has pores. Ventral scales are lacking or reduced in *Cyathodium* and may be seen only at the thallus apex. The cell layers of the thallus wings form, respectively, the roof and the floor of the air chambers, which are in a single layer and lack filaments.

The neotropical species are being studied by N. Salazar Allen.

LITERATURE. Proskauer, J. 1951. Notes on Hepaticae II. The Bryologist 54: 243-257. - Schiffner, V. 1938-39. Monographie der Gattung *Cyathodium*. Annales Bryologici 11: 131-140; 12: 123-142. - Vital, D. M. 1974. The occurrence of *Cyathodium* Kunze and *Targionia* L. (Hepaticae) in Brazil. Revue Bryologique et Lichénologique 40: 139-145.

Targionia (Fig. 78) - A small subtropical-Mediterranean genus (3 spp.), with 2 species in tropical America, usually at high elevations: the widespread *T. hypophylla* L. in Mexico, the Andes from Ecuador to northern Argentina, and central and southern Brazil, and *T. stellaris* (K. Müll.) Hässel in northern Argentina, Peru (?), and on the Galapagos Islands. The latter is endemic to South America.

HABITAT. On periodically moist, compact soil and over rocks, usually in partial shade, in mountain regions with a seasonally dry climate, at 1000-4000 m, usually above 3000 m in the Andes and Mexico.

DESCRIPTION. **Thallus** leathery, linear, deep green, margins and ventral surface black or blackish-purple, dry thalli narrowly linear and entirely black, thalli to 4 cm long, 2-4 mm wide; dorsal surface of thallus finely reticulate, with small whitish pores, the pores sometimes star-shaped, epidermal walls smooth or papillose, with bulging trigones. **Ventral scales** dark purple, in 2 rows, scales with oil cells and marginal slime papillae, each scale with a lanceolate appendage. **Air chambers** in 1 layer, with

filaments. **Rhizoids** smooth and tuberculate. **Monoicous** or dioicous. **Sporophytes** 1-3 in a large, purplish, mussel-like involucre, projecting forward from beneath the apex of the thallus. Otherwise as in the family.

DISCUSSION. The linear thallus with upcurved purplish-black margins, large purplish ventral scales and, when fertile, with a large, purplish, mussel-like involucre below the apex, is unmistakable. When dry, the thallus curls inwards, becomes narrowly linear and turns entirely black due to the dark underside being turned upwards. The large, bulging trigones in the epidermal cell walls are also characteristic of *Targionia*.

The neotropical ranges of *Targionia hypophylla* and *T. stellaris* are incompletely known and need to be studied. Both species have been recorded from scattered localities in the Andes. It may well be that the two have been confused. The principal differences between the two seem to be the form of the cells surrounding the pores (isodiametric in *T. stellaris*, elongate in *T. hypophylla*) and the position of the androecia, occurring on the main thallus in *T. stellaris* and on short branches in *T. hypophylla* (fide A. Whittemore, pers. comm.).

LITERATURE. Hässel de Menéndez, G. G. 1963 (see order ref.). - Schuster, R. M. 1992 (see order ref.). - Vianna, E. C. 1985 (see order ref.).

Hornworts
(Anthocerotae)

Plants thalloid, often in rosettes, growing by a wedge-shaped, 4-sided apical cell, sporophyte growing by a basal meristem. Thallus at least several cells thick in the middle, with or without a midrib, inner tissue ± undifferentiated, sometimes with large cavities. *Nostoc* colonies usually present inside the thallus, visible as dark dots. Epidermal cells with or without trigones, with 1(-4) large, plate-like chloroplasts, each containing a pyrenoid; oil bodies absent. Rhizoids unicellular, smooth. Gametoecia immersed in the thallus, each originating from an inner thallus cell; antheridia 1-several in cavities, ± spherical, stalked; archegonia borne singly, flask-shaped. Sporophytes projecting from the thallus surface, green, turning black after dehiscence, consisting of foot and capsule, seta lacking. Capsule narrow-cylindrical to long-filiform, surrounded at the base (to the apex in *Notothylas*) by a tubular involucre, wall with or without stomata, containing spores, (pseudo)elaters, and a columella (absent in *Notothylas*); dehiscence of capsule gradual, from apex downwards, by means of 2 valves; spore maturation asynchronous; peristome absent. Protonema very small, thalloid, normally giving rise to only one gametophyte.

DISCUSSION. The class Anthocerotae or hornworts contains less than 100 species worldwide, in 8-9 genera. About 30 species occur in the Neotropics (G.G. Hässel de Menéndez, pers. comm.).

Although superficially resembling thalloid liverworts, hornworts are easily recognized, even when sterile, by the single large chloroplast in each epidermal cell (exceptionally 2-4, in *Megaceros*) and the usual presence of *Nostoc* colonies in the thallus, visible as black dots. The sporophytes are very characteristic and consist of a long-cylindrical, hornlike capsule (hence the name "hornworts") and a foot which is embedded in the thallus (a seta is lacking). The capsule has a columella and epidermal stomata (usually), and opens by means of two valves. In fertile material, sporophytes normally project in great numbers from the thallus surface.

The most remarkable features of the hornworts, separating them from all other bryophytes, are the development of the gametoecia from inner cells of the thallus (instead of external cells), growth of the sporophyte by means of a basal meristem (instead of an apical cell), and the gradual, asynchronous ripening of the spores, those at the tip of the capsule ripening first, those at the base last. Spore maturation in the hornworts is essentially different from that in mosses and liverworts which always have synchronous spore maturation, with the spores being shed all at once. Spore maturation in the hornworts is not always asynchronous, however; in *Notothylas* it is synchronous (as in the mosses and hepatics).

The Anthocerotae are traditionally classified in a single family Anthocerotaceae, with the recognition of one or more subfamilies (Schuster, 1992). Recently, however, several families and even orders have been described (Hasegawa, 1994; Hässel de Menéndez, 1988; Hyvönen & Piippo, 1993). In tropical America, at least three different families may be recognized: Anthocerotaceae (*Anthoceros*, *Folioceros*, *Leiosporoceros* and *Phaeoceros*), Dendrocerotaceae (*Dendroceros* and *Megaceros*), and Notothyladaceae (*Notothylas*). Anthocerotaceae and Dendrocerotaceae are rather closely related; they are separated by the lack of stomata in the capsule walls and elaters with spiral thickening bands in the Dendrocerotaceae. The Notothyladaceae are a very different group with the sporophytes lying almost horizontally on the thallus instead of being erect, almost indehiscent capsules which are

enclosed in the involucre for most of their length, synchronous spore production, 1-celled elaters resembling spores, and the absence of columella and stomata. The large number of features unique to the Notothyladaceae lends support to the recent view that the group should be treated as a separate order (Hyvönen & Piippo, 1993).

Because knowledge of the neotropical hornworts is still poor and the number of genera rather limited, families or orders are not described in this treatment.

Most hornworts grow terrestrially and occur on open, disturbed soils which periodically dry up. Members of the Dendrocerotaceae (*Dendroceros*, *Megaceros*) have a very different habitat and occur as epiphytes in montane rain forests. For the identification of the genera and species of hornworts, mature sporophytes are usually required.

LITERATURE. Hasegawa, J. 1994. New classification of Anthocerotae. Journal of the Hattori Botanical Laboratory 76: 21-34. - Hässel de Menéndez, G. G. 1988. A proposal for a new classification of the genera within the Anthocerotophyta. Journal of the Hattori Botanical Laboratory 64: 71-86. - Hyvönen, J. & S. Piippo. 1993. Cladistic analysis of the hornworts (Anthocerotophyta). Journal of the Hattori Botanical Laboratory 74: 105-119. - Schuster, R. M. 1992. Anthocerotae. The Hepaticae and Anthocerotae of North America, Vol. VI: 710-858.

Key to the genera of hornworts of tropical America

1. Thallus with a distinct midrib and unistratose wings, light green. Thallus wings strongly crispate. On bark or living leaves ..... **Dendroceros**
1. Thallus lacking midrib and unistratose wings, light green to dark green. On soil, rock, or rotten wood 2
2. Thallus dark green, large (to 5-10 cm long), elongate, not in rosettes. Margins finely and densely fringed-crisped, ± colorless. Spores green. Elaters with a distinct spiral band. In montane forests on rotten wood, rock, or humic soil ..... **Megaceros**
2. Thallus light green to deep green (when alive), smaller, usually in ± orbicular rosettes. Margins plane to crispate, not finely fringed-crisped, green. Spores yellow, dark brown, or black. Elaters without a spiral band. In open environments on soil or rock, not in forests 3
3. Sporophytes present 4
3. Sporophytes lacking (identification not always possible) 8
4. Sporophytes small (less than 0.5 cm long), lying nearly horizontally on the thallus, almost entirely covered by the involucre ..... **Notothylas**
4. Sporophytes larger, erect, projecting far beyond the involucre at maturity 5
5. Spores dark brown to black. Thallus with internal cavities. Antheridial jacket composed of 4 tiers of cells 6
5. Spores yellow. Thallus solid, without cavities. Antheridial jacket composed of irregularly arranged cells 7
6. Elaters very thick-walled (cell lumina only visible as narrow lines in the center of the cells). Spores with long spines (4-6 µm long) ..... **Folioceros**
6. Elaters thin-walled, with irregular bands of thickenings. Spores with or without short spines (less than 4 µm long) ..... **Anthoceros**
7. Spores ovoid-oblong, completely smooth, without trilete mark ..... **Leiosporoceros**
7. Spores rounded-tetrahedral, roughly ornamented, with distinct trilete mark ..... **Phaeoceros**
8. Thallus with internal cavities. Dorsal surface of thallus usually reticulate ..... **Anthoceros** or **Folioceros**
8. Thallus solid, without cavities. Dorsal surface of thallus not reticulate 9
9. Lowland plants (below 1000 m). Thallus very flat, margins usually dissected ..... **Notothylas**
9. Montane plants (rarely in lowlands). Thallus entire or shallowly lobed 10
10. Dorsal surface of thallus velvety due to projecting epidermal cells. Margins plane or undulate, not crispate ..... **Leiosporoceros**
10. Dorsal surface of thallus not velvety, epidermal cells not projecting. Margins plane to crispate ..... **Phaeoceros**

Anthoceros (= *Aspiromitus*) (Fig. 79) - A widespread genus, with 8 species in tropical America (Hässel de Menéndez, 1989), primarily in the drier regions of the Neotropics, in areas with a pronounced seasonal climate.

HABITAT. On periodically moist, compact soil at rather low elevations, 0-2000 m. The species seem to occur mainly in disturbed, man-made habitats.

DESCRIPTION. **Thallus** light green, becoming blackish in the herbarium, usually forming rosettes to 1.5 cm in diameter, without a midrib, with large, mucilaginous cavities and *Nostoc* colonies (visible as

black dots); thallus margins irregularly dissected into small, often somewhat crispate segments, dorsal surface usually with a reticulate pattern, smooth or covered with crisped or toothed lamellae. **Antheridia** more than 4 in each antheridial chamber, antheridial jacket of 4 tiers of cells, opening at the apex. **Sporophytes** when mature erect, 1-5 cm long, linear, with epidermal stomata and a well-developed columella. **Spores** dark brown to black, rounded-tetrahedral, unicellular, usually with distinct trilete marks. **Elaters** (1-)2-4-celled, pale blackish-brown, flaccid, walls thin and with irregular bands of thickenings, never spirally thickened.

DISCUSSION. Characteristic features of *Anthoceros* are 1) the delicate, light green thalli with dissected margins and a ± reticulate dorsal surface; numerous crisped lamellae may sometimes cover the thallus; 2) the presence of cavities inside the thallus; 3) the blackish spores; and 4) the antheridial jacket composed of 4 even tiers of cells. The genus is most closely related to *Folioceros* and *Phaeoceros*; for differences see under the latter.

Some authors, including Schuster (1992, Hep. Anth. N. Am., Vol. VI), use the name *Aspiromitus* and apply the name *Anthoceros* to *Phaeoceros*. However, as shown by Grolle (1983), this is nomenclaturally untenable and must be rejected.

Anthoceros granulatus Gott. from Mexico and Colombia has spores with reduced trilete marks and was therefore placed in the separate genus *Sphaerosporoceros* Hässel (as *S. granulatus* (Gott.) Hässel).

LITERATURE. Grolle, R. 1983. Nomina generica Hepaticarum: references, types and synonymies. Acta Botanica Fennica 121: 1-62 [nomenclature, p. 5]. - Hässel de Menéndez, G. G. 1989. Las especies de *Anthoceros* y *Folioceros* (Anthocerotophyta) de América del Norte, Sud y Central; la ornamentación de sus esporas y taxonomía. Candollea 45: 201-220 [key based on spore characters].

Dendroceros (Fig. 79) - A pantropical genus, with 1 common, variable species in tropical America, *D. crispus* (Sw.) Dumort. (? = *D. crispatus* (Hook.) Nees). Several additional species have been described from the Neotropics but their status is unclear.

HABITAT. On bark of small trunks, lianas, twigs, and on leaves, in undisturbed and disturbed submontane and lower montane rain forests and in scrubby vegetation, rarely in lowland forest, (100-)300-2500 m.

DESCRIPTION. **Thallus** small, yellowish-green, 2-5 mm wide, ± pinnate or forked, with a midrib and unistratose wings, the midrib solid or with cavities (subgen. *Apoceros*), *Nostoc* colonies usually present (visible as black dots), the thallus wings conspicuously undulate-crispate; epidermal cells with trigones. **Antheridia** 1(-4) in each antheridial chamber. **Sporophytes** when mature erect, 1-5 cm long, linear, without epidermal stomata, columella present. **Spores** green, large, ca. 40-80 µm long, rounded, multicellular, germinating inside the capsule, outer spore surface papillose. **Elaters** long and narrow (to ca. 300 µm long), with a distinct spiral band.

DISCUSSION. *Dendroceros* is easily recognized by the delicate, yellowish-green thalli with a midrib and strongly crispate wings. The species typically grow on bark and living leaves in mossy cloud forests and are thus very different in their habitat from other hornworts (except *Megaceros*). The presence of trigones in the epidermal cell walls is another unique character of *Dendroceros*, all other hornworts having quite thin-walled cells.

The sporophytes of *Dendroceros* contain large, green, multicellular spores and elaters with distinct spiral bands, and the capsule walls are devoid of stomata. The latter two characters are shared with the otherwise very different genus *Megaceros*.

LITERATURE. Spruce, R. 1885. *Dendroceros*. Hepaticae Amazonicae et Andinae: 573-574 [key to 2 spp., including *D. crispatus*].

Folioceros - An Asiatic genus, with 1 species recorded from tropical America, *F. apiahynus* (Steph.) Hässel. The species is known only from the type specimen from SE Brazil (Sâo Paulo, Apiahy, leg. Puiggari).

HABITAT. Unknown.

DESCRIPTION and DISCUSSION. Similar to *Anthoceros* but elaters rigid, with strongly and evenly thickened walls, and spores with an indistinct trilete mark. A striking feature of *Folioceros apiahynus* are the long spines (4-6 µm) on the outer surfaces of the spores. In neotropical *Anthoceros* species, the spores have shorter spines (1-4 µm) or none at all.

LITERATURE. Hässel de Menéndez, G. G. 1989. Las especies de *Anthoceros* y *Folioceros* (Anthocerotophyta) de América del Norte, Sud y Central; la ornamentación de sus esporas y taxonomía. Candollea 45: 201-220.

Leiosporoceros (Fig. 80) - A monotypic, neotropical genus, with *L. dussii* (Steph.) Hässel ocurring rather widely through tropical America, at montane elevations. The species has thus far been recorded from Mexico, the West Indies (Jamaica, Guadeloupe, Martinique), and Ecuador.

HABITAT. On exposed, compact, moist soil and rock in montane rain forest areas, particularly on roadbanks and along rivers, 500-3000 m.

DESCRIPTION. **Thallus** deep green, fleshy, biconvex in section, forming elongated rosettes to 2 cm in diameter, without a midrib, solid, without mucilaginous cavities, with scattered *Nostoc* colonies (visible as black dots); thallus margins flat or somewhat undulate, not dissected, dorsal surface finely roughened by projecting epidermal cells, not reticulate. **Antheridia** unknown. **Sporophytes** when mature erect, to 4 cm long, linear, with epidermal stomata and a well-developed columella. **Spores** transparent, pale yellowish, small, ca. 20 µm long, ovoid-oblong, unicellular, surface quite smooth, without any trace of trilete marks. **Elaters** very long and narrow, to 280 µm long, 1-celled, yellowish-brown, walls considerably thickened, without spiral bands.

DISCUSSION. The small, transparent, ovoid-oblong spores of *Leiosporoceros* with completely smooth outer surfaces and lacking any trace of a trilete mark, are unmistakable. In habit, the genus resembles *Phaeoceros*, but the thalli are more fleshy and the dorsal surface of the thallus is somewhat velvety in appearance due to the projecting epidermal cells. The elaters are thick-walled like in *Folioceros*, but in the latter genus they are blackish-brown (not yellowish) and composed of 3-4 cells.

LITERATURE. Hasegawa, J. 1986. *Anthoceros dussii* Steph. (Anthocerotae) and its isobilateral spore tetrads. Hikobia 9: 357-360. - Hässel de Menéndez, G. G. 1986. *Leiosporoceros* Hässel n. gen. and *Leiosporocerotaceae* Hässel n. fam. of *Anthocerotopsida*. Journal of Bryology 14: 255-259.

Megaceros (Fig. 80) - A widespread, tropical and southern-temperate genus with one species common throughout tropical America, *M. vincentianus* (Lehm. & Lindenb.) Campb. Several other species have been described from the Neotropics but their status is unclear.

HABITAT. On rotten wood, moist rock, and humic soil in montane rain forests, ca. 500-3500 m.

DESCRIPTION. **Thallus** large, glistening dark green, to 5(-10) cm long and ca. 5-10 mm wide, ± forked, without a midrib, thallus solid, without cavities, *Nostoc* colonies present (visible as black dots) or lacking; thallus margins conspicuously and finely fringed-crisped, ± colorless; epidermal cells without trigones, usually with 2-4 chloroplasts. **Antheridia** solitary. **Sporophytes** when mature erect, very long, to 10 cm, linear, without epidermal stomata, columella present. **Spores** green, unicellular, rounded, outer surface papillose. **Elaters** long and narrow (to 450 µm long), with a distinct spiral band.

DISCUSSION. The large, dark green thalli with finely fringed-crisped margins and the very long capsules are unmistakable. The presence of more than one chloroplast in the thallus cells is also characteristic of *Megaceros.* In its occurrence in montane forests, the genus differs essentially from all other neotropical hornworts except *Dendroceros*. The latter, however, usually occurs on living bark and leaves, whereas *Megaceros* grows primarily on rotten wood and rock.

Notothylas (Fig. 80) - A pantropical genus, with at least 5 species at low elevations in tropical America: the widespread *N. breutelii* (Gott.) Gott. (= *N. amazonica* Spruce), *N. vitalii* Udar & Singh in SE Brazil, *N. galapagensis* M. Howe endemic to the Galapagos Islands, *N. dissecta* Steph. in Guatemala, and the holarctic *N. orbicularis* (Schwein.) Sull. in Brazil and (?) Mexico.

HABITAT. On periodically moist, compact soil and on thin soil over volcanic rock in warm lowland areas, in exposed sites, from sea level to about 1000 m. The species frequently occur on disturbed, compacted soil in man-made environments, and have been collected in gardens and plantations, on the sides of old ditches, and near buildings.

DESCRIPTION. **Thallus** light green to deep green, nearly flat, usually forming rosettes about 1-3 cm in diameter, without a midrib, irregularly dissected, solid, without mucilaginous cavities, with or without *Nostoc* colonies (visible as black dots); thallus margins entire to crenulate to lobulate, dorsal surface smooth or with a few lamellae, not reticulate; epidermal cells with 1(-2) chloroplasts. **Antheridia** 1-6 in each antheridial chamber, antheridial jacket of irregularly arranged cells. **Sporophytes** when mature short, to 4 mm long, lying almost horizontally on the thallus and largely enclosed in the involucre, cylindrical or banana-shaped, without epidermal stomata and columella reduced or absent, dehiscing imperfectly by 2 valves or rupturing irregularly. **Spores** dark brown or yellowish, ca. 40-60 µm in diameter, rounded-tetrahedral, unicellular, the surface ornamented and with distinct trilete marks. **Elaters** unicellular, ± rounded, pale brown, walls with irregular thickenings; sometimes elaters lacking (*N. vitalii*).

DISCUSSION. *Notothylas* is easily recognized by the small sporophytes lying almost horizontally on the thallus, being enveloped in the involucre for almost their entire length.

When sterile, the genus may be difficult to distinguish from *Phaeoceros.* However, *Phaeoceros* is mostly montane in the Neotropics, whereas *Notothylas* is a lowland genus. Moreover, the thalli of *Notothylas* are usually delicate and very flat whereas those of *Phaeoceros* are often rather fleshy, with the margins somewhat ascending.

LITERATURE. Cavalcanti Pôrto, K. & O. Yano. 1985. Novas occorrências de briófitas em Pernambuco. Rickia 12: 9-14. - Hässel de Menéndez, G. G. 1976. Taxonomic problems and progress

in the study of the Hepaticae. Journal of the Hattori Botanical Laboratory 41: 19-39 [*Notothylas*: p. 22-27]. - Schuster, R. M. 1992. *Notothylas*. The Hepaticae and Anthocerotae of North America, Vol. VI: 854-858.

Phaeoceros (Fig. 80) - A widespread genus, with about 9 species in tropical America (Hässel de Menéndez, 1989).

HABITAT. On compact, damp soil and on rock in moist or rather mesic environments, in exposed sites or in partial shade, from sea level to the forest line, to about 3500 m. In the Andes, *Phaeoceros* is common on cut roadbanks in montane forest regions.

DESCRIPTION. **Thallus** deep to dark green, rather fleshy, usually forming rosettes to 2-3 cm in diameter, without a midrib, solid, without mucilaginous cavities, usually with scattered *Nostoc* colonies (visible as black dots); thallus margins entire or crenate, flat or somewhat crispate, dorsal surface smooth, not reticulate. **Antheridia** 2-4 in each antheridial chamber, antheridial jacket made up of irregularly arranged cells, opening irregularly. **Sporophytes** when mature erect, 1-4(-9) cm long, linear, with epidermal stomata and a well-developed columella. **Spores** yellow, rounded-tetrahedral, unicellular, the surface ornamented and always with distinct trilete marks. **Elaters** (1-)2-4-celled, pale brown, walls thin and with irregular thickenings, never spirally thickened.

DISCUSSION. The yellow spores and the rather fleshy, solid thalli lacking internal cavities, with entire or crenate margins and smooth upper surfaces, are characteristic of *Phaeoceros*. The genus has in the past been confused with *Anthoceros*, which, however, is very different in the more delicate thallus with large internal cavities and strongly dissected, often crisped margins, black spores, and antheridia with a wall of 4 tiers of cells.

Some authors use the name *Anthoceros* instead of *Phaeoceros*; however, this is erroneous (see under *Anthoceros*).

LITERATURE. Hässel de Menéndez, G. G. 1989. Las especies de *Phaeoceros* (Anthocerotophyta) de América del Norte, Sud y Central; la ornamentación de sus esporas y taxonomía. Candollea 44: 715-739 [key based on spore characters].

Mosses

by

Steven P. Churchill and Noris Salazar Allen

MOSSES
(Musci)

Plants (=gametophyte) foliose, growing from a single tetrahedral (although a bifacial cell can be found in few forms, e.g., *Fissidens*) apical cell. Stem prostrate or erect, outer surface, with or without a cuticle, in few forms, with paraphyllia (*Cyrtohypnum*, *Thuidium*), pseudoparaphyllia present (many pleurocarps) or absent, in cross section with (Polytrichales) or without (most mosses) internal conducting tissues, hyalodermis present or absent. Leaves entire, never dissected, spirally arranged on the stem (sometimes in two rows, distichous), with or without a definite arrangement on the stem, mostly isophyllous but some taxa with anisophylly (one or two rows of leaves different in size and arrangement on the stem), leaves mostly unistratose (all cells chlorophyllous or with chlorophyllous and hyaline cells in different areas of the leaf) or multistratose (with various layers of cells, all chlorophyllous or with a central chlorophyllous layer surrounded by 1-(more) layers of hyaline cells), with or without midrib; midrib one or two (rarely more), sometimes the number varying within the same gametophyte. Leaf cells chlorophyllous, with discoid chloroplasts or hyaline (devoid of protoplast and usually porate), smooth or papillose; cell walls thin or thick, smooth or pitted, without trigones. Rhizoids multicellular, branched, hyaline or colored, cell walls thin or thick, smooth or papillose. Antheridia on the main shoot, on short shoots or on lateral branches, oval to $\pm$ spherical, pedicelate, surrounded by paraphyses, perigonial bracts differentiated or not from vegetative leaves; archegonia apical (acrocarpous mosses) or on lateral branches (pleurocarpous mosses), vessel shaped with a venter and a narrow neck, surrounded by paraphyses, perichaetial leaves differentiated or not from vegetative leaves. Sporophyte mostly exerted or inmersed, capsule spherical to oval or elliptical, with urn and operculum or without an operculum; operculum apiculate to conic or long rostrate united to the urn by a ring of cells, the annulus; urn multistratose, with or without stomata, outer cells smooth, papillose, mamillose or spinose, neck differentiated or not, columella present, its distal part in some taxa (Polytrichales) expanded into a membrane that closes the mouth of the urn (the epiphragm); mouth of the urn surrounded by one (single) or two (double) rows of teeth, the peristome or peristome absent. Capsule dehiscent by vertical slits, an operculum or indehiscent (cleistocarpous). Calyptra mitrate or cuculate, smooth or pleated, naked or hairy. Seta short or long, yellowish-green to green when young, straw-yellow to red-brown when mature, smooth, papillose, sometimes spiculose to spinose or with multicellular filaments (*Calyptrochaeta*), with or without a central strand. Protonema long persistent, filamentous and ramified or less frequent thallose, usually producing more than one foliose gametophyte.

Worldwide, the mosses (Musci) are estimated to include 12,800 species (a more realistic figure would be 8,000 species), in 900 genera. The diversity in the Neotropics is estimated at 76 families, 401 genera and 2,600 (2,300–2,950) species. For those desiring a taxonomic sequence of families, the following list is provided. This reflects some of the current ideas about the general patterns of evolutionary history with regards to mosses. It must be noted, however, that this is not necessarily a phylogenetic sequence. The monophyly of most families (or higher levels) has not been demonstrated, rather it is a traditional-based classification founded on *a priori* assumptions resulting in polythetic groups. Currently there is a healthy debate with regard to the definition of family limits and relationships within and between families. For that reason, the families of the mosses are treated here in a single alphabetical sequence and are not subdivided into orders as in the treatment of the Hepaticae. Since this manuscript was completed (ca. 1997) a substantial number of phylogenetic studies have appeared (at least in abstracts), both morphological and molecular, very few combining both; one can anticipate major changes in our understanding of relationships and resulting classifications at all levels.

Keys to the subclasses and families of mosses of tropical America

The following keys are intended to assist in the identification of mosses from the Neotropics. The keys are designed to stress gametophytic features whenever possible. Sporophytes are often not present in collected material, and, in some cases, not known in the Neotropics or elsewhere. For this reason, and because a number of families exhibit considerable variation, families are often keyed out in more than one place. The keys often emphasize salient features of families with primary emphasis on gametophytic characters, secondarily on sporophytic characters, and lastly on habitat or geography. In using the keys, one normally follows the lead that best fits the two alternative choices given. When one reaches a point in the keys in which neither lead appears appropriate, one then should follow both, hopefully ending with two alternative families. Both should then be compared carefully with the descriptions, keys to genera, and illustrations. If neither alternative appears appropriate, then one must back-track in the keys to find where the problem of interpreting a particular character exists. In any case, one should read carefully the family description, keeping in mind the variation exhibited by that family (this applies equally to genera).

Key to the subclasses

1. Plants typical of boggy or marshy sites, whitish; branches spirally arranged in fascicles; laminal cells of stem and branch leaves alternating between leucocyst (hyaline cells) and chlorocyst (green) cells; capsules globose, supported by a pseudopodium ..... **Sphagnopsida** (Sphagnaceae)
1. Plants mostly of drier sites, mostly green, yellow or brown; laminal cells uniformly similar with chlorophyll, or chlorophyll cells layered between hyaline cells above and below; not alternating between hyaline and green cells; capsules variously shaped, supported by a pseudopodium or seta 2
2. Plants small, dark red or blackish, largely restricted to open high elevations, in páramo and puna; capsules supported by a pseudopodium, opening by 4 (division throughout) or 8 (distal tip) slits or valves ..... **Andreaeopsida** (Andreaeaceae)
2. Plants small to medium sized or robust, present in all environments; capsules stegocarpic, supported by a seta, generally with a peristome and operculum 3
3. Leaves bearing rows of lamellae on distal upper surface; capsules with a single series of peristome teeth, teeth 16, 32, or 64, distally attached to a circular membrane (epiphragm) ..... **Polytrichopsida** (Polytrichaceae)
3. Leaves lacking rows of lamellae, or very rarely present (see Grimmiaceae, Pottiaceae); capsules either with a peristome in a single series with 16 teeth, or a double series with the outer series of 16 teeth (exostome), and inner series with a basal membrane bearing 16 segments and cilia (endostome), in a number of cases the peristome is reduced ..... **Bryopsida**

General key to the families

1. Plants whitish, laminal cells alternating or layered between leucocyst and chlorocyst cells ..... **Section 1**
1. Plants variously green, yellow to golden, or brown to blackish; laminal cells uniform, neither layered or alternating between leucocyst and chlorocyst cell walls 2
2. Upper distal surface of leaf with discontinuous or continuous rows of lamellae ..... **Section 2**
2. Upper distal surface lacking lamellae 3
3. Plants acrocarpous; stems erect or occasionally spreading, solitary or in short to long tufts or cushions; sporophytes terminal on stems or branched innovations; peristome single (a single series of 16 teeth or divided into 32 narrow segments) or double (two series, outer series of 16 teeth, inner series often with 16 segments and often cilia atop a short to tall membrane) 4
3. Plants pleurocarpous, stems creeping, spreading, or pendent, frondose or dendroid from conspicuous or inconspicuous creeping primary stems; sporophytes lateral on stems; peristome double or variously reduced 6
4. Leaves arranged in 2 ranks (distichous) or 4 ranks (but appearing 2-ranked) ..... **Section 3**
4. Leaves arranged in 3 or more rows 5
5. Laminal cells papillose or mammillose ..... **Section 4**
5. Laminal cells smooth ..... **Section 5**
6. Leaf costa absent, short and forked, or elongate and double 7
6. Leaf costa single 9
7. Leaves distinctly 2-ranked, usually strongly folded ..... **Section 6**

7. Leaves in 3 or more ranks, when complanate often with lateral asymmetric leaves (occasionally partially folded on one side) and median symmetric leaves 8
8. Leaves ecostate (most leaves lacking a costa, a few leaves may have a very weak costa) ..... **Section 7**
8. Leaves with costa, short and forked or elongate and double ..... **Section 8**
9. Leaves strongly dimorphic, upper or lower leaves on stems smaller and differing in shape than larger lateral leaves ..... **Section 9**
9. Leaves monomorphic, usually differing if at all between smaller branch leaves, or lateral leaves asymmetric and median leaves symmetric 10
10. Laminal cells mammillose or papillose ..... **Section 10**
10. Laminal cells smooth ..... **Section 11**

Section 1. Plants whitish, laminal cells alternating or layered between leucocyst and chlorocyst cells.

Plants whitish, occasionally reddish or purplish tinged; laminal cells differentiated, alternating or layered between hyaline cells (leucocysts) and green cells (chlorocysts).

1. Plants typically of boggy or seepy sites; forming a compact head of clustered short branches (capitulum), below capitulum, stems with short to elongate fasciculate branches; leaves of stem and branch dimorphic; in cross-section lamina unistratose, cells alternating between chlorocysts and leucocysts ..... **Sphagnaceae**
1. Plants of moist to semi-dry sites, often lignicolous or epiphytic; stem and branch leaves monomorphic, mostly evenly distributed along stems; in cross-section lamina bi- to multistratose, chlorocysts layered between 1 or more layers of leucocysts above and below 2
2. Leaves faintly singly costate, chlorocyst cells clustered near center on abaxial side (back) of leaf ..... **Leucophanaceae**
2. Leaves appearing ecostate; chlorocyst cells evenly distributed in a single row between leucocyst cells, not forming a cluster of cells toward the center ..... **Leucobryaceae**

Section 2. Upper distal surface of leaves with rows of lamellae or short filaments.

1. Lamellae in long continuous rows, occasionally rows few or discontinuous; peristome teeth 16, 32, or 64, entire, usually with tips of teeth attached to an epiphragm ..... **Polytrichaceae**
1. Lamellae forming short rows or occurring as short filaments scattered over surface; peristome of 16 teeth, often perforate or divided 2
2. Distal upper surface covered by filaments, often papillose, if with lamellae then leaves ovate with margins plane; calyptra cucullate ..... **Pottiaceae** p.p.
2. Distal upper surface covered by rows of lamellae, with leaf margins erect to incurved; calyptra campanulate, lobed at base ..... **Grimmiaceae** p.p.

PLANTS ACROCARPOUS

Plants acrocarpous, stems mostly erect or occasionally spreading, solitary or in short to tall loose or dense tufts; sporophytes terminal on stems or branched innovations; peristome single or double, rarely absent.

Section 3. Plants acrocarpous. Leaves arranged in 2 ranks (distichous) or in 4 ranks but appearing 2-ranked.

1. Leaf costa long excurrent, 2–3 times longer than lamina length; lower and basal cells linear-rectangular; confined to páramo and puna ..... **Ditrichaceae** p.p.
1. Leaf costa subpercurrent to short excurrent (rarely long excurrent), lower and basal cells quadrate to rectangular; lowland to high montane, rarely in páramo/puna 2
2. Leaves exhibiting an extended dorsal and ventral lamina from a sheath-like leaf base (vaginant laminae) 3
2. Leaves lacking an extended dorsal and ventral lamina from a sheath-like base 4
3. Plants solitary or forming tufts, erect to suberect; marginal border cells of leaf linear or oblong-linear, usually thick-walled; capsules long exserted ..... **Fissidentaceae**

3. Plants forming mats, procumbent (pleurocarpous); marginal border cells very large, subrectangular, thin-walled; capsules immersed ..... **Sorapillaceae**
4. Leaves strongly asymmetric; costa closer to one side of lamina; gemmae commonly clustered on denuded stem tips; wet lowlands ..... **Phyllodrepaniaceae**
4. Leaves ± symmetric or weakly asymmetric; costa longitudinally centered on leaf; gemmae if present in leaf axils; mostly montane or subalpine 5
5. Leaves folded, conduplicate 6
5. Leaves flat, not folded; laminal cells smooth 7
6. Laminal cells pluripapillose; leaves short oblong-ovate, less than 1 mm long ..... **Eustichiaceae**
6. Laminal cells smooth; leaves oblong-lanceolate, mostly 2–3 mm long ..... **Bryoxiphiaceae**
7. Stems spreading or creeping; leaves elliptical, bordered ..... **Mniaceae** p.p.
7. Stems erect; leaves ovate, lacking border ..... **Rhizogoniaceae** p.p.

Section 4. Plants acrocarpous. Leaves in 3 or more rows. Laminal cells papillose or mammillose (cells often isodiametric or shortly elongate).

1. Basal portion of leaf exhibiting a cancellinae (enlarged clear cells), strongly differentiated from basal margin and distal cells; marginal or intramarginal border often present; laminal cells above isodiametric, gemmae nearly always present on leaves, particularly leaf tips; plants mostly epiphytic ..... **Calymperaceae**
1. Basal portion of leaf lacking a cancellinae (see *Kingiobryum* etc. in páramo), cells either similar to distal cells or gradually differentiated toward base, if differentiated then leaf border lacking; gemmae absent from leaves 2
2. Leaves ecostate; mostly on rocks 3
2. Leaves costate; on various substrates including rocks 4
3. Leaf margins plane; laminal cells unipapillose on back; plants small, dark red or blackish, in páramo and puna; capsules opening by 4 (division throughout) or 8 (distal tip) slits or valves ..... **Andreaeaceae** p.p.
3. Leaf margins recurved; laminal cells 1-several papillose, papillae in a row; plants medium sized, dark green to brown or grayish; mid-montane to páramo or puna; capsules operculate, lacking a peristome ..... **Hedwigiaceae**
4. Leaves completely to partially bistratose distally 5
4. Leaves unistratose or only partially bistratose, particularly restricted to margins 8
5. Peristome of 16 teeth in 8 pairs; leaves spathulate, apex acute to apiculate ..... **Rhachitheciaceae** p.p.
5. Peristome of 16 unpaired teeth; leaves mostly ovate-lanceolate to lanceolate, if spathulate then costa excurrent 6
6. Laminal cells subquadrate to short rectangular, appearing bipapillose ..... **Ditrichaceae** p. p.
6. Laminal cells rounded, mammillose 7
7. Leaf margins uni-, bi- or tristratose; perichaetial leaf costa long excurrent with distal lamina erose or fimbriate; sporophytes immersed; seta short; capsules strongly asymmetric, obliquely and broadly ovoid below, narrow toward mouth; peristome double; plants usually found on soil ..... **Diphysciaceae**
7. Leaf margins bistratose, sometimes incomplete below; perichaetial leaf costae subpercurrent; sporophytes exserted; seta elongate; capsules symmetric; peristome single; plants exclusively found on rocks ..... **Grimmiaceae** p.p.
8. Laminal cells stellate, unipapillose, papillae over cell lumen; basal cells inflated; leaf margins recurved nearly throughout; distal stems naked with a few highly reduced leaves; plants of marshes and bogs at high elevations ..... **Aulacomniaceae**
8. Laminal cells not stellate, uni- to pluripapillose; basal cells not conspicuously inflated; lacking specialized distal branches or stems (sometimes with deciduous leaves); plants mostly of semi-wet or dry sites 9
9. Laminal cells narrowly to somewhat broadly rectangular with projecting papillae at cell ends (rarely single over cell lumen); leaf margins often coarsely toothed, teeth single or more often double; capsules subglobose, inclined or if erect then immersed ..... **Bartramiaceae**
9. Laminal cells mostly isodiametric or short rectangular; papillae mostly over cell lumina or cells mammillose; leaf margins entire, crenulate or a few teeth at apex; capsules ovoid to cylindrical ..... 10.
10. Laminal cells often bipapillose; capsules immersed to shortly exserted; peristome double or reduced; calyptra campanulate, plicate or not, hairy or naked; epiphytic or rarely on rocks .... **Orthotrichaceae** p.p.

10. Laminal cells uni- or pluripapillose, or mammillose; capsules mostly long, rarely short exserted; calyptra cucullate or if campanulate then long cylindrical, smooth; mostly terrestrial, occasionally epiphytic 11
11. Leaves bordered by few to several rows of hyaline cells, border extending from base to 1/3 leaf length, or to near apex; laminal cells uni-, bi- or pluripapillose; alar cells well differentiated .... **Dicranaceae** p. p.
11. Leaves lacking a border; cells variously ornamented; alar cell undifferentiated 12
12. Leaves differentiated, base clasping, limb spreading; plants of wet or moist sites 13
12. Leaves undifferentiated, or if so, then base not clasping stem or if clasping upper laminal cells pluripapillose 14
13. Laminal cells subquadrate, mammillose; costa percurrent ..... **Ditrichaceae** p.p.
13. Laminal cells short-rectangular, rounded, papillae projecting at cell ends; costa short excurrent ..... **Dicranaceae** p.p.
14. Leaf costa in cross-section little differentiated, well developed stereid band lacking 15
14. Leaf costa in cross-section usually well developed, stereid band present, only below guide cells or both above and below 17
15. Laminal cells mammillose or weakly unipapillose, cells crowded, little space between cell lumens ..... **Dicranaceae** p. p.
15. Laminal cells pluripapillose, cells widely spaced, or if crowded, papillae extending between cell lumens 16
16. Leaves spathulate or if narrowly oblong-lanceolate then hyaline basal cells extending upward along margin a short distance; peristome single, 16 teeth in 8 pairs .... **Rhachitheciaceae** p.p.
16. Leaves narrowly lanceolate to oblong- or ovate-lanceolate, basal cells uniform across; peristome double or variously reduced, 16 teeth, separated or in 8 pairs ..... **Orthotrichaceae** p.p.
17. Calyptrae long cylindrical-campanulate; leaves oblong-elliptical to -obovate, laminal cells coarsely pluripapillose, papillae usually branched; restricted to very high elevations (zacatonal, páramo or puna) ..... **Encalyptaceae**
17. Calyptra cucullate; leaves of various shapes; laminal cells uni- to pluripapillose, simple or branched; plants found in all zones ..... **Pottiaceae** p.p.

Section 5. Plants acrocarpous. Leaves in 3 or more rows, ranked or not. Laminal cells smooth.

1. Plants minute, ephemeral or not; leaves costate or ecostate, capsules cleistocarpous or gymnostomous, mostly immersed 2
1. Plants conspicuous, mostly medium sized to large, not ephemeral; leaves costate; capsules stegocarpous or rarely gymnostomous, mostly long exserted 7
2. Laminal cell walls firm, mostly rectangular to subquadrate 3
2. Laminal cell walls lax, short- to long-rhomboidal or hexagonal-rhomboidal..... 6
3. Leaves oblong to obovate or orbicular, margins entire; annulus well developed ..... **Rhachitheciaceae** p.p.
3. Leaves mostly lanceolate, if obovate then distal leaf margins usually crenulate or weakly serrulate; annulus absent or well developed 4
4. Spores very large, few ..... **Archidiaceae**
4. Spores small, numerous 5
5. Capsules with an elongate neck, often half or more the length of capsule, stomata often numerous in neck region ..... **Bruchiaceae** p.p.
5. Capsules with an inconspicuous neck or neck lacking, stomata few or absent .... **Ditrichaceae** p.p.
6. Stems fleshy, partially subterranean; capsules wrinkled or warty, if smooth then exserted and leaves ecostate ..... **Gigaspermaceae**
6. Stems from a persistent protonema, not subterranean; capsules smooth or weakly bulging-mammillose, immersed ..... **Ephemeraceae**
7. Laminal cells narrowly rectangular and strongly sinuose throughout except at basal margin; plants found exclusively on rocks ..... **Grimmiaceae** p.p.
7. Laminal cells not sinuose throughout, walls entire, or if sinuose not strongly so and restricted in distribution, not throughout; plants found on various substrates including rocks 8
8. Leaf margins bordered, border extending to apex or ending somewhat below, adjacent inner laminal cells large, often hexagonal-elongate to broadly fusiform or rhomboidal 9
8. Leaf margins lacking a border, or if bordered then confined to leaf base; marginal cells similar to or only slightly differentiated from inner laminal cells 12
9. Laminal cells subquadrate and rounded to oblong-oval, distally obliquely arranged

..... **Mniaceae** p.p.
9. Laminal cells rhombic to elongate-hexagonal, not obliquely arranged 10
10. Leaf border consisting of long linear cells; capsules often inclined to pendulous **Bryaceae** p.p.
10. Leaf border consisting of large, rectangular to fusiform cells; capsules erect, if inclined or subpendulous then seta hygroscopic 11
11. Capsules with a conspicuously modified, enlarged neck, often inflated or larger than urn; peristome single, 16 teeth united in pairs, or 8 teeth, often recurved when dry; plants usually epiphytic, on dung or decaying plant material ..... **Splachnaceae** p.p.
11. Capsules with an inconspicuous or narrowed neck; peristome absent, or single and represented by an exostome of 16 teeth, or double, teeth incurved when wet; plants mostly on soil .... **Funariaceae**
12. Alar cells differentiated, quadrate to oblong or oval, often dark colored, yellow to red 13
12. Alar cells undifferentiated 14
13. Alar cells dark red; low, somewhat irregular membrane formed around and external to peristome; plants on rocks associated with streams, mostly at high elevations .... **Seligeriaceae** p.p.
13. Alar cells often reddish-brown or golden; low, external membrane lacking; plants on various substrates and at low to high elevations ..... **Dicranaceae** p.p.
14. Leaves appearing 3-ranked; seta conspicuously elongate (to 10 cm long or more); exostome reduced, endostome well developed; plants of mid to high elevations in boggy sites .... **Meesiaceae**
14. Leaves spirally arranged, or more than 3-ranked; seta usually shorter; peristome various; plants either of drier sites or aquatic, rarely of boggy sites 15
15. Laminal cells distally linear-oblong or -fusiform and flexuose or not; capsules inclined to more often pendulous; peristome double, endostomial cilia often present, or represented by only a hyaline endostome with a low membrane ..... **Bryaceae** p.p.
15. Laminal cells isodiametric to short or long rectangular; capsules mostly erect to inclined; peristome single or double (Rhizogoniaceae) 16
16. Laminal cells above base isodiametric, small, thick-walled; plants often dark green, reddish-brown, or blackish 17
16. Laminal cells often short to long rectangular, or distally grading into subquadrate cells, walls thin- to rather thick-walled; plant mostly light to dark green 19
17. Costa in cross-section generally well developed, stereids above and below guide cells or only below, upper and lower epidermal cells differentiated or not; capsules often long exserted; peristome teeth often divided into 32 filaments; plants on soil or rocks, dry or wet sites, at all elevations ..... **Pottiaceae** p.p.
17. Costa in cross-section little or not differentiated; capsules short exserted or immersed, 4-valved or with peristome teeth perforate or divided only distally; plants confined to rocks and at very high elevations (páramo or puna) 18
18. Capsules 4-valved (peristome and operculum lacking); leaves strongly subulate from an ovate base or ovate with a very broad, diffuse costa to ca. 1/2 lamina length .... **Andreaeaceae** p. p.
18. Capsules with peristome, teeth often perforate or divided above; leaves percurrent to excurrent as a hyaline awn ..... **Grimmiaceae** p.p.
19. Leaves elliptical, obovate spathulate, obtuse to rounded; peristome either with 16 teeth in 8 pairs or exostome extremely reduced 20
19. Leaves mostly ovate-lanceolate to narrowly lanceolate; margins entire to serrate; peristome with teeth, when present not paired, nor with exostome extremely reduced 22
20. Leaves mostly 2 mm long or more; capsules with a modified, enlarged neck, often inflated or larger/longer than urn ..... **Splachnaceae** p.p.
20. Leaves mostly 1.2 mm long or less; capsules lacking a modified neck 21
21. Leaves obovate to elliptical, leaf apices not apiculate; perichaetial leaves similar to stem leaves, not long sheathing; capsules smooth ..... **Splachnobryaceae**
21. Leaves obovate to spathulate, leaf apices apiculate (most leaves); perichaetial leaves strongly differentiaed from stem leaves, long sheathing; capsules 8-ribbed ..... **Rhachitheciaceae** p.p.
22. Capsule neck elongate, 1.5–3 times longer than urn, stomata numerous in neck region; peristome absent or single (vertically striate below); costa subpercurrent; plants of disturbed sites, rather uncommon ..... **Bruchiaceae**

22. Capsule neck distinctly shorter than urn, or absent; peristome double or single (and often divided above); costa subpercurrent to excurrent; plants of various habitats 23
23. Perichaetia at mid-stem or base; leaf margins bistratose and doubly toothed, if singly toothed then distal stem tips with cylindrical, papillose gemmae; plants epiphytic or terrestrial ..... **Rhizogoniaceae** p.p.
23. Perichaetia terminal on stems; lacking the above combinations of characters; plants on soil or rocks 24
24. Capsules ribbed; annulus compound, exceeding or nearly so the length of the peristome; leaves setaceous from an ovate base; plants rare ..... **Seligeriaceae** p.p.
24. Plants lacking the above combination of characteristics 25
25. Peristome teeth terete, often divided to near base, into 32 filaments ..... **Ditrichaceae** p.p.
25. Peristome teeth flat below, entire or divided above ..... **Dicranaceae** p.p.

PLANTS PLEUROCARPOUS

Plants pleurocarpous; stems creeping, spreading, forming mats, or pendent, frondose or dendroid, often forming tufts, from a creeping primary stem; sporophytes lateral on stems; peristome double or variously reduced, rarely absent.

Section 6. Plants pleurocarpous. Leaves 2-ranked, strongly folded throughout or with sheath-like base.

1. Leaves exhibiting an extended dorsal and ventral lamina from a sheath-like leaf base (vaginant laminae); margins bordered, cells very large, subrectangular, thin-walled; capsules immersed . ..... **Sorapillaceae**
1. Leaves strongly folded, conduplicate, lacking a dorsal and ventral lamina; marginal border lacking; capsules shortly to fully exserted 2
2. Leaves to 1.5 mm long; apex mostly mucronate and reflexed; laminal cells entire, not porose ..... **Catagoniaceae**
2. Leaves 3 mm or more long; apices truncate or erect apiculate; laminal cells porose .... **Phyllogoniaceae**

Section 7. Plants pleurocarpous. Leaves ecostate.

1. Plants aquatic, attached to rocks in streams or epiphytic in inundated lowlands; capsules immersed ..... 2.
1. Plants terrestrial, on soil, rocks, and logs, or epiphytic, if aquatic then alar cells inflated; capsules mostly exserted 3
2. Leaves mostly distant, crowded only at stem or branch tips, oblanceolate to obovate or elliptical; plants confined to lowlands ..... **Hydropogonaceae**
2. Leaves mostly crowded, lanceolate; plants confined to montane habitats or páramo ..... **Fontinalaceae**
3. Leaves broadly ovate, acute to piliferous, narrowly bordered, border differentiated in color, often dark red; laminal cells appearing finely pluripapillose, papillae minute and numerous over and between cells ..... **Rhacocarpaceae**
3. Leaves variously shaped, acuminate, acute, or obtuse rounded; laminal cells smooth or if papillose, papillae single or few over cell lumina 4
4. Alar cells inflated, oval to oblong, mostly thick-walled, porose or not, often dark yellow or golden-red; laminal cells smooth or papillose, papillae over cell lumina ..... **Sematophyllaceae** p. p.
4. Alar cells absent or if present, then not inflated or oval, mostly subquadrate or oblate and quadrate-rounded to short oblong-rounded 5
5. Leaf apex narrowly long acuminate ..... **Leucomiaceae**
5. Leaf apex broadly acute or if acuminate then laminal cells rhomboidal to fusiform-rounded and thick-walled 6
6. Leaves short ovate-lanceolate, to 0.7 mm long; laminal cells on back projecting at distal angles; alar cells equally distributed on either side of leaf base, mostly quadrate; plants forming mats ..... **Myriniaceae** p.p.
6. Leaves variously shaped, ovate-lanceolate, ovate to oblong, mostly greater than 1 mm long; laminal cells smooth, or occasionally on back projecting at distal angles; alar cells lacking or equally or unequally distributed on either side of leaf base, quadrate to oblong; plants forming mats, dendroid or pendent 7

7. Stems complanate foliate, lateral leaves slightly asymmetric or not 8
7. Stems terete foliate 10
8. Leaf margins finely bifid toothed; gemmae clustered beneath stems or on specialized terminal branches; epiphytic or epiphyllous ..... **Pilotrichaceae** p.p.
8. Leaf margins entire to subentire; gemmae absent or if present, on leaf tips; epiphytic on base of trunks of trees, logs, or soil 9
9. Alar cells well differentiated, unequally distributed with cells on one side more numerous; upper laminal cells linear; gemmae absent; moist to wet lowlands ..... **Stereophyllaceae** p.p.
9. Alar cells undifferentiated; upper laminal cells large, elongate-hexagonal; gemmae few on leaf tips and distal margins; montane forests ..... **Hookeriaceae**
10. Leaf margins plane distally; laminal cells obliquely arranged above, transversely toward base or not; median and upper cells rhomboidal to fusiform-rounded, porose or not 11
10. Leaf margins strongly incurved distally; laminal cells longitudinally arranged, linear, mostly porose 12
11. Leaves broadly lanceolate and plicate, or ovate and smooth, short acuminate; capsules exserted ..... **Leucodontaceae**
11. Leaves broadly ovate to suborbiculate, smooth, broadly acute, or if acuminate then tip hyaline; capsules immersed ..... **Erpodiaceae**
12. Plants dendroid, or subpendent and rather stiff; gemmae commonly present in leaf axils .... **Pteryobryaceae** p.p.
12. Plants pendent or forming loose, spreading mats; gemmae absent ..... **Meteoriaceae** p.p.

Section 8. Plants pleurocarpous. Leaves costate; costae short and forked or double and elongate (often 1/2 or more of lamina length).

1. Leaves strongly cordate-auriculate; paraphyllia present, several branched .... **Hylocomiaceae** p.p.
1. Leaves not cordate-auriculate, if auriculate only weakly so; paraphyllia absent or if present then linear, unbranched 2
2. Leaf costa double and elongate, often 1/2 or more the lamina length ..... **Pilotrichaceae** p.p.
2. Leaf costa mostly short and forked, mostly less than 1/2 the lamina length 3
3. Leaves complanate 4
3. Leaves teretely foliate, falcate-secund or not 9
4. Leaf margins bordered by few to several rows of narrow cells, inner cells large, rhomboidal to hexagonal; costa often indistinct or distally forked from a short single costa; seta papillose and ciliate distally ..... **Daltoniaceae** p.p.
4. Leaf margins lacking a border, occasionally cells of lamina progressively narrowed toward margin ..... 5.
5. Leaves ovate-oblong to oblong-lingulate, often undulate; apices mostly broadly acute to obtuse; capsules immersed to shortly exserted ..... **Neckeraceae** p.p.
5. Leaves mostly ovate to ovate-lanceolate, smooth; apices mostly acute to long acuminate; capsules exserted 6
6. Alar cells numerous, extending along leaf margin to 1/5-1/3 length 7
6. Alar cells few to several, rarely extending more than a few cells along margin; capsules erect to horizontal 8
7. Laminal cells smooth; capsules erect ..... **Entodontaceae** p.p.
7. Laminal cells papillose at cell angles; capsules inclined ..... **Pterigynandraceae**
8. Distal branches flagellate and readily deciduous; seta distally roughened to papillose; urn spinose ..... **Symphodontaceae**
8. Distal branches not flagellate, if so not readily deciduous; seta smooth; capsules lacking ornamentation 9
9. Leaves weakly serrulate to subentire distally, short to long decurrent; capsules suberect to horizontal, cylindrical ..... **Plagiotheciaceae**
9. Leaves often serrulate to serrate throughout, not or weakly decurrent; capsules ovoid and horizontal to subpendent or cylindrical and erect ..... **Hypnaceae** p.p.
10. Leaves falcate-secund or branches and stems distally curved or curled 11
10. Leaves mostly erect to spreading, not falcate-secund, branches and stems not curved 12
11. Alar cells quadrate to short rectangular, moderately thick-walled, concolorous or yellow to golden, or cells inflated and hyaline, thin-walled; exothecial cell walls of urn mostly evenly thickened; operculum conic-apiculate to conic-short rostrate ..... **Hypnaceae** p.p.

11. Alar cells inflated, thick-walled, often golden-red, supra-alar cells often present, subquadrate; costa weakly short and forked or absent; exothecial cell walls often collenchymatous; operculum long rostrate ..... **Sematophyllaceae** p.p.
12. Stems either dark red with leaves concave and ovate with alar cells subquadrate and thick-walled (often dark red), or stems wiry with leaves concave and ovate, weakly plicate, costa separated at base; alar cells enlarged and thin-walled ..... **Hylocomiaceae** p.p.
12. Plants lacking the combination of characteristics given above 13
13. Stems spreading to subascending, evenly foliate; leaves mostly crowded, ovate-short lanceolate to ovate (and concave); capsules long exserted; confined to montane sites or high elevations .... **Amblystegiaceae** p.p.
13. Stems often pendent or lax and elongate; leaves often distant, often conspicuously so, except at branch and stem tips; leaves obovate to oblanceolate or elliptical, not concave or weakly so; capsules immersed; confined to lowlands ..... **Hydropogonaceae** p.p.

Section 9. Plants pleurocarpous. Leaves costate; costa single. Leaves strongly dimorphic, upper or lower leaves on stem smaller and differing in shape from larger lateral leaves.

1. Leaves on upper side of stem smaller; leaf margins lacking a border; costa of lateral leaves stoutly short excurrent ..... **Racopilaceae**
1. Leaves on lower side of stem smaller; leaf margins bordered or at least differentiated; costa of lateral leaves ending well below apex or weakly short excurrent 2
2. Plants procumbent; laminal cells unipapillose; apex of upper larger leaves obtuse-rounded to broadly acute; margins partially recurved; sporophytes immersed; semi-dry sites ..... **Helicophyllaceae**
2. Plants stipate-frondose; laminal cells smooth; apex of upper larger leaves rather sharply acute to short acuminate; margins plane; sporophytes exserted; moist montane sites..... ..... **Hypopterygiaceae**

[Sections 10–11. Plants pleurocarpous. Leaves monomorphic, usually differing only in that branch leaves are somewhat smaller, differing in shape or not; or lateral leaves asymmetric and median leaves symmetric, or primary and secondary stem leaves differentiated; costa single.]

Section 10. Plants pleurocarpous. Leaves costate; costa single; laminal cells mammillose or papillose.

1. Laminal cells pluripapillose (cells with a single papillae mixed with some cells occasionally 2–3-papillose keyed out here also) 2
1. Laminal cells uniformly unipapillose or mammillose 7
2. Papillae rather numerous, over cell lumen and side walls 3
2. Papillae few, confined to cell lumen 4
3. Leaves smooth, not plicate, erect-appressed or wide-spreading; apices either acute to short acuminate or narrowly long acuminate ..... **Meteoriaceae** p.p.
3. Leaves plicate, loosely erect to spreading; apices broadly long acuminate ....**Trachypodaceae** p.p.
4. Paraphyllia present on stems; leaves of stem and branch differentiated, the former ovate or triangular and acuminate, the latter ovate and acute or obtuse-rounded; stems regularly 1–3 pinnately branched; leaf apices ending in one or more papillae ..... **Thuidiaceae** p.p.
4. Paraphyllia absent; leaves of secondary stems and branches differing mostly in size; stems irregularly branched; leaf apices not papillose 5
5. Upper laminal cells isodiametric, mostly obscurely hexagonal ..... **Anomodontaceae** p.p.
5. Upper laminal cells elongate, linear to oblong-linear 6
6. Secondary stems rather rigidly erect, solitary or few branched; leaf margins strongly recurved ..... **Pterobryaceae** p.p.
6. Secondary stem soft or rigid, not erect, several to numerously branched; leaf margins not recurved, or if so only weakly, at base ..... **Meteoriaceae** p.p.
7. Stems differentiated between creeping primary stems and erect, subpendent or frondose/dendroid secondary stems 8
7. Stems not differentiated between primary and secondary stems, plants mostly forming mats or dense tufts 13

8. Creeping stems densely tomentose, leaves mostly obscurely hidden among tomentum; elongate branches (appearing as secondary stems) erect and often numerous; seta elongate, on terminal branches; calyptra mitrate-campanulate, often deeply lobed and plicate ..... **Macromitriaceae**
8. Creeping stems radiculose beneath, or naked; secondary stems erect to suberect, pendent or frondose to irregularly branched; seta lateral on stems 9
9. Upper laminal cells with papillae projecting at distal angles 10
9. Upper laminal cells with papillae over cell lumen 11
10. Plants not stipate, mostly irregularly branched; gemmae absent; seta very short, capsules immersed, sporophytes often several to rather numerous along one side of stems ..... **Cryphaeaceae** p.p.
10. Plants mostly stipate, often frondose; gemmae often present; seta elongate, capsules exserted ..... **Pteryobryaceae** p.p.
11. Leaf margins forming a border of somewhat elongate, smooth cells ..... **Trachypodaceae** p.p.
11. Leaf margins lacking a border, cells similar to intralaminal cells 12
12. Plants small, frondose; leaves ovate, smooth; upper laminal cells rhombic, walls entire ..... **Thamnobryaceae** p.p.
12. Plants medium sized to large, irregularly branched to subdendroid; leaves ovate-lanceolate, plicate; upper laminal cells rhomboidal to linear-rhomboidal, stellate ..... **Prionodontaceae**
13. Stem leaf margins strongly ciliate; laminal cell papillae strongly curved ..... **Anomodontaceae** p.p.
13. Stem leaf margins serrulate to serrate, not ciliate; laminal cell papillae erect or projecting .. 14
14. Plants forming tufts; leaves falcate-secund; some cells with papillae strongly projecting at distal angles on back of leaf ..... **Hylocomiaceae** p.p.
14. Plants forming mats; leaves not falcate-secund; papillae over cell lumen 15
15. Leaves loosely complanate, lateral leaves somewhat asymmetric, oblong acute-rounded; alar cells unequally distributed, more numerous on one side of costa ..... **Stereophyllaceae** p.p.
15. Leaves not complanate, ovate acuminate; alar cells equally distributed on either side of costa **Leskeaceae** p. p.

Section 11. Plants pleurocarpous. Leaves costate; costa single; laminal cells smooth.

1. Laminal cells elongate, mostly 8 or more times longer than wide 2
1. Laminal cells isodiametric to short oval or rhomboidal, mostly 5 or less times longer than wide 7
2. Secondary stems erect, arising from densely tomentose short creeping primary stems; leaves oblong-lanceolate, to 5 mm long, ending in a long capillary tip, finely plicate; laminal cells linear and porose; epiphytic in high montane to zacatonal, páramo, and puna .... **Lepyrodontaceae**
2. Stems and branches creeping or subascending, not densely tomentose below; leaves variously shaped, mostly ovate- to oblong-lanceolate, apex acute to long acuminate, not ending in a capillary tip, if plicate then rather coarsely so; laminal cells weakly porose or not; various substrates and elevations 3
3. Plants pendent, dendroid, or frondose, from a creeping primary stem (occasionally forming loose mats on banks or logs); stem and branch leaves often dimorphic or polymorphic in repeated series ..... 4.
3. Plants spreading or creeping, stems not differentiated between primary and secondary; stem and branch leaves differing only by degree of size and often by width 5
4. Plants mostly erect and frondose or dendroid, if pendent then leaves in 5-spiral rows; numerous filamentous pseudoparaphyllia present ..... **Pteryobryaceae** p.p.
4. Plants pendent or occasionally forming loose spreading mats; leaves not arranged in 5-spiral rows; filamentous pseudoparaphyllia absent ..... **Meteoriaceae** p.p.
5. Leaf alar cells asymmetrically distributed, more numerous on one side of costa ..... **Stereophyllaceae** p.p.
5. Leaf alar cells, if present, equally distributed on either side of costa 6
6. Plants mostly of wet habitats; leaves smooth; alar cells usually present, either thin-walled, enlarged and rounded or if quadrate to short rectangular then cells small and few; capsules horizontal, strongly asymmetric and curved ..... **Amblystegiaceae** p.p.
6. Plants of moist or semi-dry habitats, if aquatic then leaves broadly ovate, leaf margins serrulate throughout, upper laminal cells twice as long as wide; leaves plicate or smooth; alar cells quadrate to short rectangular, often rather numerous; capsules inclined to erect, weakly asymmetric .... **Brachytheciaceae** p.p.

7. Stems differentiated between creeping primary stems and erect to suberect secondary stems 8
7. Stems creeping or spreading, occasionally subascending, not differentiated between primary and secondary stems 15
8. Secondary stems distinctly stipate, subdendroid to frondose; attenuate flagellate branches often present 9
8. Secondary stems not stipitate or weakly so, rigidly erect; tips short attenuate or not, flagellate branches absent, microphyllous branches present or not 11
9. Secondary stem and branch leaves loosely to strongly complanate; secondary stem leaves ovate to more commonly oblong or oblong-ligulate, apex mostly acute to acute-rounded, often coarsely toothed at apex ..... **Thamnobryaceae** p.p.
9. Secondary stem and branch leaves mostly teretely foliate; leaves ovate to ovate-short or ovate-long acuminate 10
10. Secondary stem leaves abruptly long acuminate from a broad ovate base; margins serrulate to near base ..... **Rigodiaceae**
10. Secondary stem leaves gradually short acuminate; margins entire to serrulate at apex .... **Leptodontaceae** p.p.
11. Leaves bordered with narrowly linear cells and conspicuously differentiated from inner laminal cells; calyptra mitrate or campanulate and fringed with ciliate hairs ..... **Daltoniaceae** p.p.
11. Leaves lacking a border, marginal cells not differing greatly from inner laminal cells; calyptra mitrate or cucullate, base lacking hairs 12
12. Secondary stem leaves loosely to strongly complanate 13
12. Secondary stem leaves terete foliate 14
13. Leaves broadly ligulate, apex truncate; costa ca. 3/4 leaf length; attenuate branches uncommon; gemmae absent ..... **Neckeraceae** p.p.
13. Leaves broadly elliptical, apex acute; costa percurrent; stem and branch tips short attenuate with gemmae in axil of reduced leaves ..... **Adelotheciaceae**
14. Microphyllous branches present; median laminal cells fusiform to fusiform-rhomboidal; leaf margins plane; seta elongate, capsules exserted ..... **Leptodontaceae** p.p.
14. Microphyllous branches absent; median laminal cells oval to oblong-oval; leaf margins recurved or plane; sporophytes several to many along one side of stem, seta very short, capsules immersed ..... **Cryphaeaceae** p.p.
15. Leaf costa ca. 1/2 leaf length or less; laminal cells thin-walled; plants rather delicate, stems readily breaking when removing leaves 16
15. Leaf costa mostly 2/3 leaf length or longer; laminal cells rather thick-walled; stems resilient 17
16. Leaf margins denticulate, ciliate or entire; peristome present or absent; plants common ..... **Fabroniaceae** p.p.
16. Leaf margins serrulate above alar region; peristome absent; plants rare ..... **Myriniaceae** p.p.
17. Upper laminal cells subquadrate; costa strongly flexuose distally ..... **Anomodontaceae** p.p.
17. Upper laminal cells rhombic to short rhomboidal or oval; costa straight or weakly flexuose ..18
18. Branches ascending; leaf margins entire; costa often spurred below; exostome teeth ca. 1/2 the length of the endostome ..... **Regmatodonaceae**
18. Branches spreading or creeping; leaf margins dentate or serrulate; costa entire, not spurred; exostome subequal to or larger than endostome 19
19. Leaf apex relatively broad, acute; seta roughened or scabrous; capsule ovoid, to 1.1 mm long ..... **Myriniaceae** p.p.
19. Leaf apex relatively abruptly short to somewhat long acuminate; seta smooth; capsules cylindrical, mostly greater than 2 mm long ..... **Leskeaceae** p.p.

ADELOTHECIACEAE

A monotypic family, a member of the Hookeriales.

Adelothecium (Fig. 81) - A monotypic genus, with *A. bogotense* (Hampe) Mitt. rather widespread in the montane regions of the Neotropics (Mexico, Central America, Greater Antilles, tropical Andes, Guayana Highlands and southeastern Brazil) and East Africa.

HABITAT. Epiphytic, commonly on branches or trunks of shrubs and treelets; primary or slightly disturbed secondary montane forests, at elevations from 1140–3300 m.

DESCRIPTION. **Plants** somewhat large, forming tufts, olive green to golden-brown. **Primary stems** short, creeping, radiculose beneath. **Secondary stems** and branches erect-spreading, often perpendicular to substrate. **Stem leaves** complanate, 8-ranked, lateral leaves somewhat asymmetric and undulate, obovate, 3–4 mm long, apex rounded and apiculate, base asymmetric, slightly decurrent; margins plane, crenulate-dentate; costa single, strong, subpercurrent to percurrent; apical cells linear-fusiform, porose; median cells stellate, smooth to bulging; basal cells fusiform to irregularly rectangular and porose, golden brown; marginal cells narrow and smaller; dorsal and ventral leaves similar, symmetrical, oval to obovate. **Branch leaves** smaller, gradually attenuated distally, leaves reduced in size. **Gemmae** present at distal branch tips in axil of highly reduced leaves, gemmae short-cylindrical to clavate on axillary stalks. **Dioicous**. **Sporophytes** lateral; perichaetial leaves elongate, ovate-lanceolate or -subulate. **Seta** erect, short, ca. 2 mm long, smooth to weakly papillose. **Capsule** erect, urn ovoid. **Operculum** rostrate. **Peristome** double, exostome teeth 16, cross-striate, appearing furrowed with a hyaline border; endostome basal membrane low, segments 16, keeled and perforate, cilia absent. **Calyptra** mitrate, base weakly lobed, densely covered by long capillary hairs, plicate. **Spores** spherical, papillose-granulose.

DISCUSSION. The complanate leaves that are obovate, single costate with stellate laminal cells, combined with the gemmiferous branch and stem tips, should separate this taxon from other montane epiphytes. Sporophytes are exceedingly rare, and the principle mode of reproduction is asexual via gemmae. The relationship of this taxon within the Hookeriales is currently debated by several workers. The genus was previously placed in the Hookeriaceae; see comments under the Pilotrichaceae.

LITERATURE. Ochyra, R., H. Bednarek-Ochyra, T. Pócs & M. R. Crosby. 1992. The moss *Adelothecium bogotense* in continental Africa, with a review of its world range. The Bryologist 95: 287–295.

AMBLYSTEGIACEAE

Plants small to somewhat large, forming loose to dense mats or ascending tufts. **Stems** creeping, decumbent, or ascending, irregular to subpinnately branched; central strand usually present; paraphyllia only present in *Cratoneuron*; pseudoparaphyllia filamentous or foliose; rhizoids sparse. **Leaves** imbricate to somewhat distant, often subjulaceous or falcate-secund, appressed to spreading, short to long ovate-lanceolate, ovate or oblong, smooth, rarely plicate, concave or not, apex obtuse, acute or short to long acuminate, base often short to rather long decurrent; margins mostly plane, entire to weakly serrulate, usually elimbate (limbate and bi- or multistratose in *Limbella*); costa single and percurrent, or short and forked, or absent; laminal cells smooth, median cells rhombic to fusiform, or linear, thin-walled to occasionally ± thick-walled, entire; alar region often differentiated, cells either inflated and oblong with thin walls or cells few, quadrate, ± thick-walled. **Asexual structures** not observed. **Autoicous** or dioicous. **Perichaetia** lateral, leaves differentiated, elongate. **Seta** elongate, usually slender and wiry, smooth. **Capsule** exserted, mostly horizontal, urn cylindrical, asymmetric, weakly to strongly curved, smooth; exothecial cells quadrate to rectangular, often rounded, thin-walled to moderately thick-walled; annulus differentiated, 1–3 rows. **Operculum** conic. **Peristome** double, exostome teeth 16, cross-striate below, papillose distally; endostome basal membrane high, segments 16, cilia present. **Calyptra** cucullate, naked and smooth. **Spores** spherical, smooth to mostly finely papillose.

DISCUSSION. The Amblystegiaceae contain 30–40 genera and about 180 species mainly associated with the Northern Hemisphere; in the Neotropics 13 genera and ca. 45 species. Frequent in wet sites in the Neotropics, often in bogs and seeps at mostly high elevations. Many members of this family found in the Neotropics are common and widespread throughout the Northern Hemisphere. The distinction between the Amblystegiaceae and Brachytheciaceae is often not clear or impressive. Generalizations often made with regard to the Amblystegiaceae include wet habitats, such as marshes and bogs, leaf texture mostly smooth (rarely plicate), costa variable in a single plant (single, forked, or absent), alar cells undifferentiated, or if differentiated, then enlarged and oblong, or if quadrate, then cells few and small, capsules typically horizontal, strongly asymmetric and curved, exostome teeth yellow-brown. The Brachytheciaceae are typically associated with drier habitats, the leaves often plicate, alar cells often numerous, quadrate or slightly enlarged, and capsules suberect, the exostome teeth red-brown.

LITERATURE. Buck, W. R. 1988. Taxonomic and nomenclatural notes on West Indian Amblystegiaceae and Brachytheciaceae. Beiheft zur Nova Hedwigia 90: 337–343. - Hedenäs, L. 1992. Taxonomic studies on pleurocarpous mosses, with special reference to the *Calliergon-Scorpidium-Drepanocladus* complex in northern Europe. University of Stockholm. - Hedenäs, L. 1993. A generic revision of the *Warnstorfia-Calliergon* group. Journal of Bryology 17: 447–479. -

Kanda, H. 1975. A revision of the family Amblystegiaceae of Japan I. Journal of Science of the Hiroshima University, Series B, (Botany) 15: 201–276. - Kanda, H. 1976. A revision of the family Amblystegiaceae of Japan II. Journal of Science of the Hiroshima University, Series B, (Botany) 16: 47–119. - Karczmarz, K. 1971. A monograph of the genus *Calliergon* (Sull.) Kindb. Monographiae Botanicae 34. Warszawa [keys, illustrations, maps; includes *Calliergonella*].

1. Costa short and forked (occasionally absent) or variable, forked and single or multiple forked and elongate 2
1. Costa single and usually well-developed (to leaf middle or beyond) 6
2 Leaves spreading, slightly clasping and erect at base, apices narrowly acuminate . **Campylium**
2. Leaves erect or imbricate to secund, occasionally erect-spreading, apices broadly acuminate or acute to obtuse 3
3. Costa multiply forked, 4–5 or more segmented forks, to 3/4 lamina length; leaf apex often fimbrate; Colombian páramo ..... **Gradsteinia**
3. Costa short and forked, or variable, forked mixed with a few leaves with single costate 4
4. Costa well-developed, double, forked, or sometimes single (variable); stem leaves ovate- or triangular-lanceolate, weakly concave or not, apex broadly acuminate or acute **Hygrohypnum**
4. Costa short and double or lacking; leaves ovate, concave, apex acute to rounded-obtuse and often apiculate 5
5. Alar cells inflated in large, conspicuous auricles; stem hyalodermis present .....**Calliergonella**
5. Alar cells not differentiated or somewhat inflated in very small and inconspicuous groups; stem hyalodermis absent .....**Scorpidium**
6. Leaf margins bi- or multistratose bordered; laminal cells very thick-walled ..... **Limbella**
6. Leaf margins unbordered or weakly bordered but unistratose, laminal cells thin- to ± thick-walled ..... 7.
7. Costa broad, at base 3/4–4/5 leaf width; paraphyllia few and scattered along stem, filiform; Bolivia at 4800 m elevation ..... **Koponenia**
7. Costa narrower, at base less than 1/2 leaf width; paraphyllia absent or if present then lanceolate; generally widespread at mid to high montane or páramo/puna 8
8. Costa long excurrent; marginal cells longer than inner laminal cells, forming a weak border; weakly papillose on back of lamina, papillae projecting; alar region undifferentiated; submerged (Ecuador, Peru, SE Brazil ..... **Drepanocladus** p.p.
8. Costa ending well below apex to percurrent, rarely short excurrent; marginal cells mostly similar to inner laminal cells; laminal cells smooth or weakly papillose by projecting cell angles (see *Cratoneuron*); alar region usually well differentiated 9
9. Alar cells inconspicuous, few, subquadrate, thin-walled, not inflated; leaves erect, symmetric, not falcate-secund ..... **Amblystegium**
9. Alar cells conspicuous, inflated or differentiated as short rectangular or quadrate thick-walled cells; leaves often falcate-secund, at least at ends of stems and branches (except *Calliergon*) 10
10. Upper median leaf cells shortly oblong-rhombic; paraphyllia usually present ..... **Cratoneuron**
10. Upper median leaf cells linear; paraphyllia absent 11
11. Leaves rather abruptly long acuminate from an expanded ovate base, costa ca. 1/2 lamina length ..... **Campyliadelphus**
11. Leaves mostly long lanceolate, costa ca. 2/3 or more lamina length 12
12. Leaves ovate-oblong to elliptic; apices cucullate, apiculate or rounded ..... **Calliergon**
12. Leaves ovate-lanceolate to long lanceolate, narrowly long acuminate 13
13. Leaves smooth, not plicate; plants typically aquatic, in bogs or lakes ..... **Drepanocladus** p.p.
13. Leaves strongly plicate; plants often in marshes or semi-wet areas ..... **Sanionia**

Amblystegium (Fig. 81) - About eight species recorded for the Neotropics (Mexico, Central America, Greater Antilles, tropical Andes, Planalto and southeastern Brazil); a genus, including the poorly defined segregates *Hygroamblystegium* and *Leptodictyun* among others, stated to contain 43 species, primarily of the Northern Hemisphere.

HABITAT. On moist or wet soil or soil covered rocks; open or disturbed montane sites, rarely extending to alpine, (900–)2000–3900 m.

DESCRIPTION. **Plants** small to rather large, forming loose, soft mats, yellowish-green to pale green. **Stems** creeping to subascending, radiculose below, central strand present; pseudoparaphyllia foliose. **Leaves** mostly erect-spreading, lanceolate to ovate-lanceolate, 0.5–3 mm or more long, apex gradually long acuminate; margins plane, occasionally somewhat plicate at base, serrulate; costa single, 1/2–2/3 lamina length to percurrent or short excurrent; median cells narrowly hexagonal, rhomboidal, to linear-rhomboidal or oblong-rhombic, thin- to thick-walled; alar region not well

developed, cells subquadrate to oblong, firm- to thin-walled. **Autoicous**. **Seta** to 30 mm long, slender. **Capsule** inclined, urn cylindrical, to 2.5 mm long, ± asymmetric, weakly to strongly curved. **Operculum** conic-apiculate. **Peristome** with exostome teeth cross-striate below, distally papillose, with a median zig-zag line; endostome finely papillose, segments keeled, cilia 1–3, nodose. **Spores** finely papillose.

DISCUSSION. The genus is heterogeneous, however the various segregate genera are often ill defined and difficult to justify due to intermediate morphologies or combinations of characters expressed in various taxa. Characteristics of the genus, when broadly defined, include the erect-spreading, ovate-lanceolate to lanceolate leaves, plane, weakly serrulate margins, often flexuose, single costa, linear-rhomboidal or oblong-rhombic median cells, longer, oblong basal cells, alar cells weakly differentiated or not, capsules inclined, curved.

Calliergon (Fig. 81) - Four species in the Neotropics (tropical Andes and Hispaniola); about 10 species associated with cold temperate regions.

HABITAT. In wet boggy or marshy sites; páramo and puna, 3800–4600 m.

DESCRIPTION. Plants medium sized to robust, forming loose to dense tufts, glossy yellow, brown, or golden. **Stems** ascending, few to several branched, branch tips often cuspidate; in cross-section hyalodermis absent, outer 1–2 rows of cells small, rather thick-walled, inner cells larger, thin-walled, central strand weak; pseudoparaphyllia foliose. **Leaves** erect, imbricate, ovate or ovate-oblong to elliptical, 1.2–2.5 mm long, deeply concave, apex broadly rounded to short apiculate, cucullate or not, base slightly decurrent; margins plane or incurved to erect distally, entire; costa single, ca. 1/2–2/3 lamina length; laminal cells smooth, thin- to somewhat thick-walled, apical cells short, rhomboidal to short fusiform; median cells fusiform to linear or subrectangular; insertion cells long subrectangular, smooth to weakly porose; alar cells differentiated, oval to oblong to subrectangular, hyaline, mostly thin-walled. **Dioicous**. **Perichaetial** leaves differentiated, oblong-lanceolate, acuminate. **Seta** to 35 mm long or more, wiry. **Capsule** inclined to horizontal, urn ovoid-oblong, 2–3 mm long, when dry subcylindrical, curved and asymmetric. **Operculum** conic-apiculate. **Peristome** with exostome teeth cross-striate below, distal tips papillose, bordered and trabeculate; endostome segments keeled and often perforate, cilia 2–4, nodose. **Spores** lightly papillose.

DISCUSSION. Characteristics of the genus include the high elevation, boggy habitat, the tufted habit, small, thick-walled epidermal stem cells, the imbricate and erect, deeply concave elliptical leaves, rounded or apiculate apex, single costa, mostly elongate median laminal cells, and the hyaline, thin-walled alar cells. Two of the local species found in the Neotropics have been transferred recently to two separate genera by Hedenäs (1993). For the present time a traditional concept of *Calliergon* is maintained — *Calliergon sarmentosum* (Wahlenb.) Kindb. (*Warnstorfia sarmentosa* (Wahlenb.) Hedenäs) is known from Colombia, Peru, and Bolivia; *Calliergon stramineum* (Dicks.) Kindb. (*Straminergon stramineum* (Brid.) Hedenäs) is known from Guatemala, Colombia, Peru, and Bolivia.

LITERATURE. Hedenäs, L. 1992, 1993 (see family ref.). – Kanda, H. 1976 (see family ref.). – Karczmarz, K. 1971 (see family ref.).

Calliergonella (Fig. 82) - A single species in the Neotropics, *C. cuspidata* (Hedw.) Loeske, known from Jamaica, Colombia to Peru, and southeastern Brazil; a genus containing two species of mostly north temperate affinities. It is present also in the south temperate region.

HABITAT. Marshy or boggy sites; páramo and puna, 3000–4500 m.

DESCRIPTION. **Plants** medium sized to somewhat robust, forming loose to dense tufts, glossy green to yellow or golden-brown. **Stems** erect or ascending, few to several branched, branches short, often cuspidate at tips; in cross-section hyalodermis present, central strand weak; pseudoparaphyllia foliose. **Leaves** erect, imbricate, broadly ovate to ovate-oblong, ca. 2–2.5 mm long, to 2 mm wide, deeply concave, apex cucullate, obtuse to rounded, base auriculate; margins plane, entire; costae absent or occasional short and double (rarely to 5-forked); apical cells short; median cells linear; insertion cells elongate, strongly porose, golden to golden-red or -brown; alar region ± excavate, cells differentiated, oval to oblong, outer rows hyaline, thin-walled, inner rows golden-yellow. **Dioicous**. **Perichaetial** leaves differentiated, oblong-lanceolate, acuminate. **Seta** to 40 mm long or more, wiry. **Capsule** inclined to horizontal, urn oblong-ovoid, 3–4 mm long, when dry subcylindrical, curved and asymmetric. **Operculum** conic-apiculate. **Peristome** with exostome teeth cross-striate below, tips papillose, bordered and trabeculate, endostome segments keeled and often perforate, cilia 2–4, nodose. **Spores** lightly papillose.

DISCUSSION. The genus is characterized by the tufted habit, presence of a hyalodermis, deeply concave, ecostate, ovate to oblong-ovate leaves, cucullate, obtuse to rounded apex, auriculate base, linear median cells, and enlarged, thin-walled alar cells. This species may be confused with *Pleurozium schreberi*, but that species is differentiated by the red stems, epidermal cells small and

thick-walled, similar to outer cortical cells, and alar cells quadrate; *Scorpidium* is also rather similar, but lacks a hyalodermis, the leaves are not auriculate and alar cells only weakly differentiated if at all. This species is placed in *Calliergon* by some authors.

LITERATURE. Hedenäs, L. 1992 (see family ref.). – Kanda, H. 1976 (see family ref.). – Karczmarz, K. 1971 (see family ref.).

Campyliadelphus (Fig. 82) - Three species in the Neotropics all of which are rather widespread, *C. chrysophyllus* (Brid.) Kanda (Mexico, Central America, Greater Antilles, northern Andes, possibly southeastern Brazil), *C. polygamus* (Bruch, Schimp. & W. Gümbel) Kanda (Mexico, tropical Andes), and *C. stellatum* (Hedw.) Kanda (Mexico, Central America, Greater Antilles, possibly tropical Andes); a genus primarily of the Northern Hemisphere with 15 or more species.

HABITAT. On moist or wet soil, soil-covered rocks, often associated with marshes; open submontane to montane, extending into zacatonal, páramo and puna, (200–)1500–4100 m.

DESCRIPTION. **Plants** mostly medium sized to somewhat large, forming rather coarse mats, green, yellowish-green to golden-brown. **Stems** creeping to ascending, rigid, usually many branched; in cross-section central strand present; pseudoparaphyllia polymorphous, both filamentous and foliose. **Leaves** crowded to somewhat distant, erect- to wide-spreading with tips squarrose, ovate-lanceolate or triangular-subulate, 1.2–4 mm long, often channeled distally, ± concave, apex narrowly long acuminate, base suberect, often subdecurrent; margins plane or erect distally on one or both sides, recurved at base, serrulate throughout, or dentate at base; costa variable, single, or single and short to rather long forked; laminal cells smooth, upper and median cells linear to linear-fusiform, thick-walled; lower and basal cells shorter, oblong or rectangular-rounded, often porose; alar region usually differentiated, cells thick-walled and quadrate or short rectangular, often yellowish or golden or cells ± thin-walled and oblong, ± inflated and hyaline. **Autoicous**, synoicous or dioicous. **Perichaetial** leaves differentiated, enlarged, outer series ovate-subulate, inner leaves oblong- to lanceolate-subulate, sheathing. **Seta** to ca. 35 mm long, slender, often twisted. **Capsule** inclined to horizontal, urn short cylindrical, to 3 mm long, weakly to strongly curved and asymmetric, often constricted below mouth when dry; exothecial cells rectangular to oblong-hexagonal, thick-walled; annulus present, in 2–3 rows. **Operculum** conic-apiculate, oblique or not. **Peristome** with exostome teeth cross-striate, distally faintly to coarsely papillose, bordered and trabeculate; endostome segments keeled and perforate, lightly papillose, cilia 2–4, nodose. **Spores** lightly to coarsely papillose.

DISCUSSION. *Campyliadelphus* is distinguished from *Campylium* by larger and somewhat rigid plants, three or more layers of small, thick-walled stem cells, often erect- to wide-spreading leaves, and often single costa. The pseudoparaphyllia are said to be polymorphic in the former, and either foliose or filamentous in the latter.

LITERATURE. Hedenäs, L. 1997 (see ref. under *Campylium*). - Kanda, H. 1975 (see family ref.).

Campylium (Fig. 82) - Possibly four species in the Neotropics (Mexico, Central America, Greater Antilles, tropical Andes); a genus containing about 5–8 species associated with cool temperate regions.

HABITAT. On moist or wet soil, rocks and logs, often in disturbed sites; open montane, 1200–3000 m.

DESCRIPTION. **Plants** small, rather slender, forming rather soft mats, green, yellowish-green to -brown. **Stems** creeping to subascending, usually many branched; in cross-section outer 1–2 rows of cells small, thick-walled, inner cells large, thin-walled, central strand weak; pseudoparaphyllia mostly foliose. **Leaves** crowded to somewhat distant, squarrose to wide-spreading, triangular-subulate to narrowly ovate-long lanceolate, to ca. 0.8 mm long, concave below, channeled distally, apex abruptly acuminate, base suberect, subdecurrent or not; margins plane or erect distally on one or both sides, recurved at base, serrulate throughout, or dentate at base; ecostate or costae short and double (forked), occasionally absent or single and short; laminal cells smooth, upper and median cells linear to linear-fusiform, thick-walled; lower and basal cells shorter, oblong or rectangular-rounded; alar region usually differentiated, excavate, cells thick-walled and quadrate or short rectangular, often yellowish or golden. **Autoicous**. **Perichaetial** leaves differentiated, enlarged, outer series ovate-subulate, inner leaves oblong- to lanceolate-subulate, sheathing. **Seta** to ca. 15 mm long, slender, often twisted. **Capsule** suberect to horizontal, urn short cylindrical, to 2.5 mm long, ± curved and asymmetric, often constricted below mouth when dry; exothecial cells oblong-rectangular or -hexagonal, ± thin-walled; annulus present, in 2 rows. **Operculum** conic-apiculate. **Peristome** with exostome teeth cross-striate, tips finely to coarsely papillose, bordered and trabeculate; endostome segments keeled and perforate, finely papillose, cilia 1–2(3), nodose. **Spores** finely papillose.

DISCUSSION. The genus is characterized by the small habit, 1–2 layers of small, thick-walled outer stem cells, small (less than 0.8 mm), wide-spreading to squarrose leaves, short and forked costae (at

least in local species), serrulate margins, and 1–2(3) endostomial cilia. Kanda (1975) has separated *Campylium* into three genera, *Campyliadelphus* (see discussion above), *Campylophyllum* (*C. halleri* (Hedw.) Lindb.), and *Campylium* which includes at least four species recorded for the Neotropics: *C. hispidulum* (Brid.) Mitt. (Mexico, widespread in Northern Hemisphere) and related taxa — *C. quisqueyanum* W. R. Buck (Hispaniola), and two mostly Andean, *C. praegracile* (Mitt.) Broth. and *C. trichocladum* (Taylor) Broth. A recent alternative view of *Campylium* and related taxa has been presented by Hedenäs (1997).

LITERATURE. Buck, W. R. 1988 (see family ref.). - Hedenäs, L. 1997. A partial generic revision of *Campylium* (Musci). The Bryologist 100: 65–88. - Kanda, H. 1975 (see family ref.).

Cratoneuron (Fig. 83) - Apparently a single species in the Neotropics, *C. filicinum* (Hedw.) Spruce (Mexico, Guatemala, Andes, southeastern Brazil); a genus of about 6 species primarily distributed in temperate regions.

HABITAT. Marshy or boggy sites; subpáramo to full páramo and puna, 2700–4450 m.

DESCRIPTION. **Plants** medium sized to somewhat large, forming tufts or dense mats, green or yellowish-green or -brown. **Stems** mostly subascending to erect, branches short, irregularly pinnately branched; in cross-section central strand present; paraphyllia scattered and foliose, or absent. **Stem leaves** broadly ovate-lanceolate, 1.2–1.6 mm long, to 0.7 mm wide, erect to weakly falcate-secund, apex narrowly acuminate, often ± abruptly so, base decurrent; margins plane or weakly recurved at base, serrulate throughout; costa single, strong, subpercurrent, ending in acumen; upper and median cells rhomboidal to rhomboidal-fusiform, cell angles often blunt or rounded, occasionally tapered distally, thick-walled; alar region strongly differentiated, extending to costa, cells enlarged, oblong-rectangular, thick-walled, often golden red or yellowish. **Branch leaves** smaller, narrowly ovate to ovate-lanceolate, to 0.7 mm long. **Dioicous**. **Perichaetial** leaves narrowly lanceolate. **Seta** to 35 mm long. **Capsule** inclined to horizontal, urn short-cylindrical, to 2.5 mm long, curved, asymmetric, smooth, neck distinct. **Operculum** conic-apiculate to conic-rostrate. **Peristome** with exostome teeth cross-striate below, distally papillose; endostome finely papillose, basal membrane high, segments keeled, perforate, cilia 3, nodose. **Spores** finely papillose.

DISCUSSION. The genus is characterized by the distal portion of stems erect or ascending; erect to weakly falcate, broadly ovate, short lanceolate leaves; decurrent leaf base; serrulate margins; strong subpercurrent costa; relatively short, thick-walled upper and median cells; and strongly differentiated alar region with reddish-orange, enlarged, thick-walled cells. Two previously described species of *Cratoneuron*, both from Bolivia, are synonyms *fide* Ochyra (1989): *C. punae* Müll. Hal. = C. *filicinum*, and *C. submersum* Herzog = *Drepanocladus longifolius* (Wilson ex Mitt.) Broth.

LITERATURE. Ochyra, R. 1989. Animadversions on the moss genus *Cratoneuron* (Sull.) Spruce. Journal of the Hattori Botanical Laboratory 67: 203–242.

Drepanocladus (Fig. 83) - About 6–8 species in the Neotropics (Mexico, Central America, Greater Antilles, tropical Andes and southeastern Brazil); a genus, including several segregate genera not recognized here, containing nearly 40 species primarily from cool north temperate regions.

HABITAT. Mostly associated with boggy sites, also slow flowing mountain streams; in high montane-subpáramo transition to zacatonal, páramo, and puna, 2250–4550 m.

DESCRIPTION. **Plants** medium sized to somewhat large, forming dense mats of tufts, somewhat glossy, green or golden-brown. **Stems** short to long creeping, to more commonly ascending, irregularly to regularly pinnately branched; in cross-section central strand weak; pseudoparaphyllia foliose. **Leaves** mostly crowded, usually falcate-secund, ovate-lanceolate to long lanceolate, ca. 2–5 mm long, smooth, apex long acuminate, base decurrent or not; costa single, slender to somewhat strong, 2/3 lamina length to excurrent; median cells linear, somewhat vermicular; alar region differentiated, cells several, enlarged and ± inflated, oval to oblong, thin-walled. **Autoicous** or dioicous. **Perichaetial** leaves erect. **Seta** 25–50 mm long or more. **Capsule** inclined, urn short cylindrical or ovoid, 2–3 mm long, asymmetric, curved or not; annulus differentiated or not. **Operculum** conic apiculate to short rostrate. **Peristome** with exostome teeth cross-striate below, distally papillose; endostome finely papillose, segments keeled, perforate or not, cilia 1–3, nodose. **Spores** finely papillose.

DISCUSSION. This bog and lake inhabiting genus is distinguished by its often falcate, narrowly lanceolate to ovate-lanceolate leaves, gradually long acuminate apex, the slender, single costa not exceeding 3/4 the lamina length, linear median and upper laminal cells, and enlarged, thin-walled alar cells. The treatment presented here includes, in part, the genera *Hamatocaulis*, *Limprichtia* and *Warnstorfia*. *Richardsiopsis lacustris* (Herzog & P. W. Richards in P. W. Richards) Ochyra, described from Lake Titicaca, Peru (and known from Ecuador and southeastern Brazil), is treated by Hedenäs (1997) as a synonym of *Drepanocladus perplicatus* (Dusén) Roth.

LITERATURE. Hedenäs, L. 1997. The *Drepanocladus* s. str. species with excurrent costae (Amblystegiaceae). Nova Hedwigia 64: 535–547. - Janssens, J. A. 1983. Past and extant distribution of *Drepanocladus* in North America, with notes on the differentiation of fossil fragments. Journal of the Hattori Botanical Laboratory 54: 251–298. - Ochyra, R. 1986. On the taxonomic position of *Sciaromium lacustre* Herz. & Rich. in Rich. Journal of Bryology 14: 109–115 (described *Richardsiopsis*). - Wynne, F. F. 1944. Studies in *Drepanocladus* IV. Taxonomy. The Bryologist 47: 147–189.

Gradsteinia (Fig. 83) - A monotypic genus, with *G. andicola* Ochyra known only from the original collection from the Cordillera Oriental of Colombia.

HABITAT. On rocks in streams; páramo; at 3650 m elevation.

DESCRIPTION. **Plants** medium sized, forming dense tufts, distally yellowish-green or brown, below blackish-brown. **Stems** erect-ascending to spreading, somewhat stiff and wiry, irregularly branched, some appearing rather attenuate; in cross-section outer 2–3 rows of cells small, thick-walled, inner cells larger, rather thin-walled, central strand absent. **Leaves** loosely erect, somewhat distant, oblong to oblong-ovate, to 2 mm long, to 0.8 mm wide (older, lower leaves often eroded and fimbrate; branch leaves smaller), concave, apex rounded-acute, cucullate with apiculate and somewhat recurved tip; margins plane below, distally erect or inflexed, entire or distally weakly serrulate; costae appearing multiple, 3–5 or more irregular segments, to 3/4 lamina length, in cross-section often multistratose, cells undifferentiated; laminal cells thick-walled, weakly to rather strongly porose, apical cells short rhomboidal or oblong; median cells irregularly oblong-rhomboidal to -linear; basal cells short, strongly porose; alar cells undifferentiated. **Sexual** state and sporophytes unknown.

DISCUSSION. The genus is not likely to be confused with any other genus, the frimbrate, deeply concave oblong to oblong-ovate leaves with a diffuse multiple costae (3–5 segments) are distinctive. Ochyra described this as one of several monotypic aquatic taxa. He suggested placement of this taxon in the family Donrichardsiaceae, segregate of dubious value. The generic name honors the Dutch hepaticologist Stephan Robbert Gradstein (1943–), foremost specialist today on neotropical hepatics.

LITERATURE. Ochyra, R. 1990. *Gradsteinia andicola*, a remarkable aquatic moss from South America. Tropical Bryology 3: 19–28 [illustration].

Hygrohypnum (Fig. 84) - About 10 species presently recognized for the Neotropics (Mexico, Central America, tropical Andes, Planalto and southeastern Brazil); a genus mostly of the Northern Hemisphere with 33 species.

HABITAT. On rocks associated with streams; mostly lower montane to upper montane sites, 1700–4000 m.

DESCRIPTION. **Plants** small to somewhat medium sized, forming mats, rather dull to glossy, light to dark green or yellowish green. **Stems** creeping, decumbent or subascending, irregularly pinnately branched; in cross-section central strand absent or weak. **Leaves** falcate-secund or not, imbricate to erect-spreading, ovate, elliptical, oblong- to ovate-lanceolate, 0.5–2 mm long, concave, apex narrowly to broadly acute to short, rather bluntly acuminate, cucullate or not; margins plane to reflexed below or erect to incurved distally, entire to weakly denticulate or sharply serrulate distally; costae short to somewhat elongate, variable, single or ± long forked, often short, single and forked exhibited on the same plant; apical cells rhomboidal; median cells linear to linear-rhomboidal; lower and basal cells narrowly oblong-rectangular; alar region little differentiated, few cells short, rhomboidal to subquadrate, rarely inflated. **Dioicous**? **Perichaetial** leaves often striate, costae short, single or forked. **Seta** to 15 mm long. **Capsule** suberect to inclined, urn ovoid to obovoid, to ca. 1 mm long, slightly asymmetric; stomata on neck, superficial; annulus weakly defined, in 2 rows. **Operculum** conic to short rostrate. **Peristome** exostome teeth cross-striate below, papillose distally, trabeculate; endostome segments finely papillose, keeled and perforate, cilia 1–2.

DISCUSSION. The genus is noted for its gametophytic variability and association with aquatic habitats, primarily with streams; characteristics include the ovate, broadly elliptical or ovate-short lanceolate, imbricate leaves, broadly to somewhat narrowly acute apex, variable costae, single and forked (mixed), and few differentiated alar cells. *Hygrohypnum* is a rather ill defined taxon outside the north temperate region, and has served as a depository for miscellaneous taxa exhibiting some of the features of the Amblystegiaceae but which can not be placed elsewhere. This trend continues today. Sporophytes apparently are rare or have not been observed in the Neotropics. Synonyms of the rather widespread *H. reduncum* (Mitt.) N. Nishim. include *H. robinsonii* H. A. Crum, *H. tequendamense* Herzog, and the form described as var. *subfalcatum* Herzog; it may also include *H. pelichucense* R. S. Williams.

Koponenia (Fig. 84) - A monotypic neotropical genus, with *K. holoneuron* (Herzog) Ochyra only known from Bolivia.

HABITAT. Apparently aquatic, possibly on rocks; puna, at 4600 m.

DESCRIPTION. **Plants** rather small, forming mats. **Stems** stiff, irregularly short branched; central strand present; paraphyllia few and scattered, filiform. **Leaves** stiffly spreading, short lanceolate to triangular, to ca. 1.2 mm long, straight or somewhat falcate, apices acute or acute-rounded; margins plane, subentire to bluntly serrulate; costa single, very broad, filling distal half of acumen, ca. 3/4–4/5 lamina width, in cross-section undifferentiated with lamina bistratose at base; laminal cells thick-walled, elongate- to oblong-rhomboidal, smooth to weakly papillose by projecting distal angles; basal cells yellowish-brown; alar region undifferentiated. **Sporophytes** unknown.

DISCUSSION. The genus is characterized by the aquatic habitat, stiff, short branched stems, filiform paraphyllia, stiff spreading, triangular or short lanceolate leaves, very broad single costa (to 4/5 the width of leaf base), bistratose base, thick-walled upper laminal cells, and undifferentiated alar region. A genus of dubious merit assigned to a family of similar value, the Hypnobartlettiaceae. The generic name honors the Finnish bryologist Timo Juhani Koponen (1939–), an authority on the Mniaceae.

LITERATURE. Ochyra, R. 1985. *Koponenia*, a new pleurocarpous moss genus from Bolivia. Journal of Bryology 13: 479–486 [illustrations].

Limbella (Fig. 85) - A small genus, *L. bartlettii* (H. A. Crum & Steere) W. R. Buck is endemic to Hispaniola (Haiti), and *L. pachyloma* (Mont.) Müll. Hal. is distributed from Colombia to Tierra del Fuego, southeastern Brazil, and South Africa.

HABITAT. On rocks, in streams and waterfalls, high open montane and probably páramo, at elevations from 2650–4000 m.

DESCRIPTION. **Plants** medium sized to rather large, forming rather coarse mats, dull green to yellowish-brown or black. **Stems** and branches spreading to ascending, coarse and stiff, wiry, irregularly several branched; in cross-section outer 2–5 rows of cells small, thick-walled, inner cells large, thin- to firm-walled, central strand weak; pseudoparaphyllia foliose. **Leaves** stiffly spreading, ovate-lanceolate, 1.5–3.5 mm long, to 1 mm wide, apex bluntly acuminate; margins plane, entire, strongly bordered (as strong and wide as costa) and merging at apex; costa single, very strong, percurrent; laminal cells thick-walled, often rather obscure, median cells oblong-rectangular to linear-flexuose, in cross-section border multistratose in 3–10 or more rows and 2–9 layers, lamina unistratose to 2–3-stratose. **Dioicous**. **Perichaetial** leaves erect, lanceolate, long acuminate, lamina unistratose. **Seta** 18–30 mm long, flexuose. **Capsule** suberect to horizontal, urn short to rather long cylindrical, 1.5–2.5 mm long; annulus in a single row. **Operculum** conic-apiculate. **Peristome** with exostome teeth cross-striate below, papillose distally, narrowly bordered, trabeculate on back; endostome basal membrane ± high, segments keeled and perforate or divided distally, papillose, cilia 1–2, nodose. **Spores** papillose.

DISCUSSION. The aquatic habitat, the coarse and wiry gametophytes with ovate-lanceolate leaves with bi- or multistratose margins merging at the apex with the strong costa, the partial to fully bi- to tristratose lamina, and firm- to thick-walled laminal cells are distinctive features of the genus. The two neotropical species can be differentiated as follows: *L. bartlettii* with marginal border of 3–5 rows of cells that are 2-(3)stratose, upper laminal cells oblong-linear or linear flexuose (ca. 7–13:1) and *L. pachyloma* with marginal border of 10 or more rows of cells that are (3–)4-8-stratose, upper laminal cells oblong-hexagonal to -rhomboidal (ca. 3–5:1).

Ochyra (1986, 1987), in his typical ornithological approach to aquatic mosses, placed the two neotropical species in separate genera and families — *L. bartlettii* as *Sciaromiella bartletii* (H. A. Crum & Steere) Ochyra), Donrichardsiaceae, and *L. pachyloma* as *Vittia pachyloma* (Mont.) Ochyra), Vittiaceae.

LITERATURE. Ochyra, R. 1986. *Sciaromiadelphus* A. Abr. & I. Abr. — The relationship between extant and fossil moss specimens. Journal of the Hattori Botanical Laboratory 61: 309–332 [description & illustration of *L. bartlettii*]. - Ochyra, R. 1987. A revision of the moss genus *Sciaromium* II. The section *Limbidium* Dusén, with a description of *Vittia* gen. nov. (Vittiaceae fam. nov.). Journal of the Hattori Botanical Laboratory 62: 387–415 [illustrations & map of *L. pachyloma*].

Sanionia (Fig. 85) - A single, rather widely distributed temperate species, *S. uncinata* (Hedw.) Loeske is present in the Neotropics (Mexico, tropical Andes); a genus of three species mostly associated with the Northern Hemisphere.

HABITAT. Wet to semi-wet sites, on rock or soil among herbs; high open montane to páramo, 2800–4100 m.

DESCRIPTION. **Plants** medium sized, forming mats or tufts, pale green to yellow or golden. **Stems** spreading to suberect, branches subpinnate to rather irregular pinnate; in cross-section hyalodermis

present, central strand weak; pseudoparaphyllia foliose. **Leaves** crowded, strongly falcate-secund to circinate, long-lanceolate from a somewhat ovate base, to 4 mm long, to 0.8 mm wide, strongly plicate, apex long acuminate, base weakly decurrent; margins plane or appearing reflexed due to plications, distally serrulate; costa single, slender distally, extending into acumen but often obscured by plications; upper and median cells linear, smooth; basal cells weakly porose; alar region differentiated, cells ± lax, 3–5 rows at base, subquadrate-rounded to short rectangular-rounded. **Autoicous**. **Perichaetial** leaves long lanceolate, to 7 mm long, plicate, costate. **Seta** to 3.5 cm long, twisted. **Capsule** erect to inclined, urn short cylindrical, to 2.5 mm long; exothecial cells irregularly subquadrate to short rectangular-rounded, thick-walled; annulus large, in 3 rows. **Operculum** conic-apiculate. **Peristome** with exostome teeth lanceolate and ± constricted distally, finely cross-striate below, distal 1/3 hyaline, papillose; endostome segments hyaline, keeled and papillose, cilia short, nodose, 1–3. **Spores** finely papillose.

DISCUSSION. The genus is similar to *Drepanocladus* (from which it has been segregated), with falcate, long lanceolate leaves, gradually long acuminate apex, slender single costa, linear median and upper laminal cells and well differentiated alar cells. *Sanionia* differs from that genus by the rather numerous pseudoparaphyllia, and strongly plicate leaves. Some recent authors continue to treat this genus as a synonym of *Drepanocladus*.

LITERATURE. Hedenäs, L. 1989. The genus *Sanionia* (Musci) in northwest Europe, a taxonomic revision. Annales Botanici Fennici 26: 399–419. - Hedenäs, L. 1992 (see family ref.). - Kanda, H. 1976 (see family ref.).

Scorpidium (Fig. 84) - About four species in the Neotropics; about nine species, largely from the cold north temperate region.

HABITAT. Marshy or boggy sites; zacatonal, páramo and puna, (2400–)3500–4550 m.

DESCRIPTION. **Plants** large to somewhat robust, forming loose or dense mats or tufts, yellowish-brown or golden. **Stems** erect to procumbent, julaceous, irregularly to subpinnately branched, distal stem and branch tips secund; in cross-section central strand weak or absent; pseudoparaphyllia absent. **Stem leaves** imbricate, distally somewhat secund or not, broadly ovate, ovate-oblong or elliptical, 2.5–3 mm long, to 1.4 mm wide, deeply concave, distally cucullate, apex obtuse-rounded or broadly acute; margins plane, entire; costae variable, weak and short, forked, or absent; median laminal cells linear, somewhat vermicular, weakly porose; basal cells oblong-linear, lower 3–4 rows rusty red and strongly porose; alar region little differentiated, few cells enlarged to rather small, oblong-rounded to subquadrate, lax or firm-walled, hyaline or not. **Branch leaves** narrower, to 1.4 mm long. **Dioicous**. **Perichaetial** leaves lanceolate. **Seta** slender. **Capsule** inclined to horizontal, urn ovoid-cylindrical, curved and asymmetric; annulus present. **Operculum** conic. **Peristome** with exostome teeth cross-striate below, distally papillose, bordered and trabeculate; endostome segments keeled, cilia 2–3. **Spores** finely papillose.

DISCUSSION. The yellowish-brown to golden, turgid, large plants with strongly imbricate, deeply concave, ovate to oblong-ovate leaves, mostly short and forked costae, weakly porose, linear and vermicular median cells, firm-walled, strongly porose basal cells, and alar cells not or only a few differentiated, assist in the recognition of the genus.

ANDREAEACEAE

A monotypic family as presented here. Placed in its own class, the Andreaeopsida.

Andreaea (Fig. 86). - About 30 species, possibly 10–15, recorded for the Neotropics (Mexico, Central America, Hispaniola, tropical Andes, southeastern Brazil); stated to contain some 95 species widely distributed, a more realistic number is about 50.

HABITAT. On rocks, in open exposed sites or in streams; mostly associated with zacatonal, páramo and puna, 2800–5100 m.

DESCRIPTION. **Plants** mostly small to medium sized, forming tufts or mats, dark brown, reddish-brown or black, stem and branch tips green or yellowish green. **Stems** erect to somewhat spreading, few to several branched; in cross-section cells thick-walled, outer 2–4 rows of cells small, inner cells larger, central strand absent. **Leaves** loosely erect to appressed, occasionally contorted when dry, erect-spreading when wet, ovate- or oblong-lanceolate to -subulate, or broadly oblong-ovate to panduriform, to 3 mm long, concave, slightly clasping stem, often channeled above, apex narrowly to broadly acute or acuminate, base subauriculate or not; margins plane, erect to incurved or reflexed to recurved, entire or crenulate by bulging cell walls; ecostate or costate, if costa present then single, either short and broad (1/2 or more leaf width at base) or filling acumen; laminal cells thick-walled,

often sinuose and porose, upper and median cells quadrate to short rectangular, smooth to papillose; lower and basal cells short to long rectangular. **Autoicous** or dioicous. **Perichaetia** terminal, leaves differentiated, large, 2 or more times longer than stem leaves, often sheathing the pseudopodium. **Pseudopodium** (seta-like structure) ± short to elongate, to 5 mm long. **Capsule** erect, ovoid to cylindrical, 0.5–2 mm long, splitting by slits or valves, 8 divisions at distal tip or 4 divisions nearly the full length of capsule; true peristome and opercula absent. **Calyptra** mitrate-campanulate. **Spores** spherical, papillose.

DISCUSSION. *Andreaea*, a characteristic component of the tropical alpine life zone, is recognized by its black to reddish-black gametophytes, with costate or ecostate leaves exhibiting laminal cells thick-walled and often sinuose, and frequently papillose on the distal abaxial surface; when fertile the pseudopodium and 4 or 8 valved capsule are diagnostic. *Acroschisma wilsonii* (Hook. f. & Wilson) A. Jaeger is recognized as a segregate from *Andreaea* by some authors (cf. Churchill & Linares C., 1995, see general ref.). It is distinguished by the well exserted, long cylindrical capsule, opening by 8 divisions at the apex of the capsule; the species is distributed from Colombia to Tierra del Fuego. *Andreaea* requires a critical revision for the Neotropics where numerous species have been described. Presently, B. Murray is preparing a worldwide revision of this monogeneric family.

LITERATURE. Murray, B. M. 1988a. The genus *Andreaea* in Britain and Ireland. Journal of Bryology 15: 17–82. - Murray, B. M. 1988b. Systematics of the Andreaeopsida (Bryophyta): Two orders with links to *Takakia*. Beiheft zur Nova Hedwigia 90: 289–336. - Schultze-Motel, W. 1970. Monographie der Laubmoosgattung *Andreaea*. 1. Die costaten Arten. Willdenowia 6: 25–110 [keys].

ANOMODONTACEAE

Plants medium sized, rarely small, forming mats, often coarsely so, dark green to yellowish-brown. **Stems** undifferentiated and foliate, or primary stems creeping, leaves reduced and scale-like, with secondary stems spreading to erect, mostly short, terete; flagellate branches occasional. **Leaves** crowded, erect to appressed when dry, erect to wide-spreading, complanate or terete when wet, broadly ovate, ovate-lanceolate, ovate-ligulate or -oblong, apex obtuse-rounded to narrowly or broadly acute-apiculate with apiculus hyaline or acuminate and ending in a hyaline hair tip, tips fragile or not, base broadly decurrent or not; margins plane to recurved, crenulate to coarsely toothed or spinose-ciliate; costa single, strong below, mostly 2/3 lamina length to ending below leaf acumen; laminal cells subquadrate to rhombic or hexagonal, thin- to thick-walled, smooth to unipapillose, papilla over cell lumen or weakly projecting at cell angles, or pluripapillose; basal cells adjoining costa oblong, smooth, thick-walled. **Dioicous**. **Perichaetia** lateral, leaves differentiated. **Seta** elongate. **Capsule** erect, urn cylindrical to ovoid or ovoid-cylindrical, smooth to faintly wrinkled when dry; annulus absent or well developed in 1–2 rows, deciduous in fragments. **Operculum** conic-rostrate. **Peristome** double, exostome teeth 16, short or well developed, papillose or cross-striate to smooth below; endostome finely papillose, represented only by a low membrane, segments somewhat to notably rudimentary and adhering to exostome, or narrow, keeled, perforate or not, cilia absent or rudimentary. **Calyptra** cucullate, smooth and naked or with a few erect hairs. **Spores** spherical, appearing smooth to finely papillose.

DISCUSSION. The Anomodontaceae contain five genera and about 40 or more species; in the Neotropics three genera and nine species. Members of this family have previously been aligned with the Thuidiaceae, and still are treated as such by some authors.

LITERATURE. Granzow-de la Cerda, I. 1992. Análisis cladístico de la familia Anomodontaceae. Tropical Bryology 6: 95–104. - Granzow-de la Cerda, I. 1997. Revision and phylogeny of *Anomodon* and *Herpetineuron* (Anomodontaceae, Musci). Contributions from the University of Michigan Herbarium 21: 205–275 [keys, illustrations, maps].

1. Stem leaves as broad as long, margins ciliate; laminal cells strongly unipapillose ..... **Thelia**
1. Stem leaves mostly two times longer than wide; margins entire to serrate; laminal cells smooth or pluripapillose 2
2. Leaves entire to crenulate by projected papillose cell walls; laminal cells pluripapillose .... **Anomodon**
2. Leaves irregularly serrate; laminal cells smooth ..... **Herpetineuron**

Anomodon (Fig. 87) - Six species in the Neotropics (Mexico, Central America, Bolivia, Brazil, and Greater Antilles); a genus of 18 species mostly associated with the north temperate regions.

HABITAT. On soil, rocks, base and trunk of trees; montane forests, often associated with calcareous sites, 600–3140 m.

DESCRIPTION. **Plants** mostly medium sized to small, forming loose to dense mats, often coarsely so, dark green to yellowish-brown. **Primary stems** creeping, leaves reduced and scale-like. **Secondary stems** spreading to erect-ascending, mostly short, terete; flagellate branches occasional. **Leaves** crowded, erect-appressed to loosely erect or somewhat contorted when dry, erect to wide-spreading, complanate or terete when wet, ovate-lanceolate, ovate-lingulate or -oblong, apex obtuse-rounded to acute-apiculate with apiculus hyaline or acuminate and ending in a hyaline hair tip, tips fragile or not, base broadly decurrent or not; margins plane to revolute, crenulate; costa strong below, mostly 2/3 lamina length to ending below leaf acumen; laminal cells hexagonal, thin-walled, pluripapillose, papillae few to several over cell lumen; basal cells adjoining costa oblong, smooth, thick-walled. **Perichaetial** leaves differentiated, elongate, sheathing at base, cells elongate, smooth. **Seta** to 27 mm long. **Capsule** with urn cylindrical to ovoid or ovoid-cylindrical, to 3 mm long, smooth to faintly wrinkled when dry; annulus absent or well developed in 1–2 rows, deciduous in fragments. **Operculum** conic-rostrate, oblique. **Peristome** with exostome teeth short or well developed, papillose or cross-striate to smooth below; endostome finely papillose, represented only by a low basal membrane, segments somewhat rudimentary and adhering to exostome, or narrow, keeled, perforate or not, cilia absent or rudimentary. **Calyptra** smooth and naked or with a few erect hairs. **Spores** appearing smooth to finely papillose.

DISCUSSION. Characteristics of the genus include the spreading to ascending secondary stems, absence of paraphyllia, leaves often oblong or lingulate to gradually acuminate from an expanded base, entire or crenulate margins, laminal cells pluripapillose, isodiametric. Granzow-de la Cerda (1992, 1997) has demonstrated that *Haplohymenium* is derived within *Anomodon*, and treated it as a section within that genus. The only species previously assigned to *Haplohymenium* from the Neotropics is *A. triste* (Ces.) Sull. & Lesq., known from Mexico, Costa Rica, and Bolivia.

LITERATURE. Granzow-de la Cerda, I. 1992, 1997 (see family ref.).

Herpetineuron (Fig. 87) - Two species in the Neotropics, *H. acumifolium* (Mitt.) Granzow from Mexico (also Asia) and *H. toccoae* (Sull. & Lesq.) Cardot from Mexico, Central America (Guatemala, Honduras, Nicaragua), and Dominican Republic (also the southeastern United States and Old World subtropics); a genus of two species, rather widespread, at high elevations in the tropics.

HABITAT. On soil, rocks, logs, and tree trunks; open montane forests, at elevations from 800–2900 m.

DESCRIPTION. **Plants** medium sized. **Primary stems** creeping, leaves scale-like. **Secondary stems** erect, irregularly branched, attenuated branches present; in cross-section outer 2–3 rows of cells thick-walled, inner cells larger, firm-walled, central strand present. **Leaves** erect when dry, erect-spreading when moist, oblong-ovate to ovate short-lanceolate, to 2.5 mm long, concave to weakly keeled, indistinctly biplicate or not, apex narrowly acute, margins plane or recurved at base, distal 1/3 coarsely serrate; costa strong below, flexuose or straight distally; laminal cells rather thick-walled, subquadrate, smooth. **Perichaetial** leaves erect, subulate from a sheathing base. **Seta** to 15 mm long. **Capsule** with urn ovoid-cylindrical, to 3 mm long; stomata at urn base, superficial; annulus well developed. **Operculum** conic, rostrate. **Peristome** double, exostome teeth densely papillose, perforate; endostome basal membrane high, segments stoutly linear. **Calyptra** smooth and naked. **Spores** finely papillose.

DISCUSSION. The genus is characterized by erect secondary stems, leaves with a narrowly acute apex and irregularly serrate margins, a distally flexuose costa, and smooth laminal cells. Sporophytes have not been observed in the Americas. Reproduction is likely by the flagellate-attenuate branches. The two species can be differentiated as follows: *H. acumifolium* — leaves ovate short-lanceolate, distal portion of costa straight; and *H. toccoae* — leaves oblong-ovate, distal portion of costa strongly flexuose.

LITERATURE. Granzow-de la Cerda, I. 1992, 1997 (see family ref.).

Thelia - A single species in the Neotropics, *T. hirtella* (Hedw.) Sull., known from Dominican Republic (Sierra de Baoruco) and Mexico (Nuevo León, Tamaulipas), also eastern United States; a genus of three species of eastern North America.

HABITAT. On logs, base of trees, limestone rocks; dry-mesic forests including pines, acacias, and junipers, at elevations from 800–960 m.

DESCRIPTION. **Plants** medium sized, golden brown, forming dense, rather coarse mats. **Stem** creeping, regularly 1-pinnately branched, branches stiffly erect, terete to julaceous, radiculose or tomentose below; in cross-section outer 1–3 rows of cells small, thick-walled, inner cells large, thin-walled, central strand present; paraphyllia polymorphic, margins laciniate, cells smooth to weakly unipapillose. **Stem leaves** erect when dry, erect-spreading when moist, broadly ovate to ovate-deltoid, to 1.3 mm long (lamina to 0.3 mm long, to 0.3 mm wide), concave, apex acuminate-piliferous,

margins plane, spinose-ciliate; costa single, spurred or not, 1/3–2/3 leaf length or forked; laminal cells thick-walled, rhombic, unipapillose, papillae long and curved forward; basal cells elongate, mostly smooth; alar cells mostly quadrate and smooth. **Branch leaves** smaller, cilia few or none. **Perichaetial** leaves erect, subulate from a oblong sheathing base, upper margins long ciliate; upper cells unipapillose, basal cells rectangular, smooth. **Seta** to 12 mm long, distally twisted. **Capsule** with urn ovoid-cylindrical, to 2.5 mm long; exothecial cells irregularly rectangular, rather thin-walled; stomata at urn base, superficial; annulus none or in 2 weakly differentiated rows. **Operculum** conic, short rostrate, slightly oblique. **Peristome** double, exostome teeth densely papillose, perforate; endostome basal membrane high, segments rudimentary or none. **Calyptra** smooth and naked. **Spores** finely papillose.

DISCUSSION. The genus is distinguished by the polymorphic paraphyllia, broadly ovate or ovate-deltoid stem leaves with ciliate margins and long piliferous point, costa single and often spurred or forked, laminal cells with elongate curved papillae, and endostome reduced. Illustrations of this species can be found in Buck (1998: Plate 67; see general ref.).

LITERATURE. Buck, W. R. 1989. Miscellaneous notes on Antillean mosses, 1. *Thelia* (Anomodontaceae) and *Acaulon* (Pottiaceae) new to the West Indies. Moscosa 5: 186–188. - Buck, W. R. 1998 (see general ref.). - Crum, H. 1966. A taxonomic account of the genus *Thelia*. Bulletin of the National Museum of Canada 216: 123–127.

ARCHIDIACEAE

A monotypic family. Placed in a separate order, Archidiales, and by some authors in a separate subclass, Archidiidae. Gametophytically, this taxon exhibits features associated with the Dicranaceae and Ditrichaceae.

Archidium (Fig. 87) - Four or five species, mostly from the northern Neotropics (Mexico, the West Indies, and southeastern Brazil); a genus of 34 species rather widely distributed.

HABITAT. On sandy loam soil in exposed sites or open woodland; a single species from the Mexican zacatonal, the remaining species recorded from moist lowland areas, including savannas.

DESCRIPTION. **Plants** mostly small, forming tufts or cushions, occasionally gregarious, green to yellowish-green. **Stems** usually erect, simple to few branched, or multi-branched, fertile stems developing by innovations. **Leaves** erect-spreading to spreading, ovate-lanceolate to lanceolate, rarely oblong-ovate, to 1.7 mm long, acuminate to subulate or obtuse-rounded, base clasping; margins entire to weakly serrulate distally; costa single, strong, subpercurrent to excurrent; laminal cells thin- to thick-walled, smooth, median cells rhomboidal; basal cells rectangular; alar region differentiated, few rows of quadrate cells; marginal cells along base short rectangular. **Autoicous**. **Perichaetia** lateral, subsessile to sessile in axil of stem leaves, occasionally terminal; leaves often differentiated, smaller or larger than stem leaves, often distally serrulate, median cells linear-rhomboidal, basal cells firm to lax, thin-walled. **Seta** absent. **Capsule** immersed, sessile, globose, to ca. 0.5 mm in diameter, walls rupturing at maturity; stomata and annulus absent. **Opercula** and peristome absent. **Calyptra** only slightly differentiated as a thin membrane attached to the vaginula. **Spores** ca. 8–12 (ranging from 4–40), large, 110–310 µm in diameter, smooth to granulose or densely papillose.

DISCUSSION. These species are primarily perennial, not ephemeral. Sterile plants would be at best difficult to name even to genus; in the field *Archidium* may be mistaken for sterile *Bryum*. They would likely to be confused with various genera in the Ditrichaceae; however, the presence of sessile sporophytes with few, but exceedingly large, spores is diagnostic.

LITERATURE. Snider, J. A. 1975. A revision of the genus *Archidium* (Musci). Journal of the Hattori Botanical Laboratory 39: 105–201 [keys, illustrations].

AULACOMNIACEAE

A monotypic family, as defined here. The family is a member of the order Bryales.

Aulacomnium (Fig. 88) - Only *A. palustre* (Hedw.) Schwägr. known from the Neotropics (Mexico, Greater Antilles, Andes, southeastern Brazil); a mostly north temperate genus of five species.

HABITAT. Boggy or marshy sites associated with peaty soils; open montane to páramo and puna, 2150–4750 m.

DESCRIPTION. **Plants** medium sized to somewhat large, forming loose to dense tufts, yellowish-green or -brown. **Stems** erect, few branched, densely tomentose; in cross-section central strand

present. **Leaves** contorted and twisted when dry, erect-spreading when wet, oblong-lanceolate, 4–5.2 mm long, to 1 mm wide, apex short acuminate or acute, base weakly decurrent; margins recurved 2/3 leaf length, crenulate, distally serrulate; costa single, strong, subpercurrent, flexuose; median cells ± stellate and collenchymatous, unipapillose, papillae over cell lumen; basal cells inflated, thick-walled, reddish-brown. **Propagula** often present, clustered terminally on nearly naked elongate stems with a few scale-like leaves. **Dioicous**. [**Sporophytes** terminal. **Seta** elongate, 25–40 mm long, smooth. **Capsule** inclined to horizontal, urn oblong or ovoid-cylindrical, 2.5–4 mm long, asymmetric and curved, plicate and constricted below urn mouth when dry; annulus revoluble. **Operculum** conic to short-rostrate and oblique. **Peristome** double, exostome teeth 16, papillose, endostome basal membrane high, segments 16, keeled and perforate, cilia 2–4 . **Calyptra** cucullate, naked and smooth. **Spores** spherical, smooth.]

DISCUSSION. This species is characterized by the recurved leaf margins, stellate unipapillose laminal cells, reddish-brown, thick-walled, enlarged basal cells, and often defoliate distal portion of stems (the scale-like leaves readily deciduous and serving as propagule in asexual reproduction).

BARTRAMIACEAE

Plants commonly medium sized or large and robust, rarely small, forming loose to dense tufts. **Stems** erect (rarely pendent — in a few species of *Breutelia*), few to several branched by innovations, branches often forming a distal whorl of short subfloral innovations, radiculose; often densely tomentose; in cross-section hyalodermis present or absent, central strand present; axillary hairs with terminal cell elongate or rounded. **Leaves** commonly spirally arranged, rarely strongly 5-ranked (*Conostomum*), linear- to ovate-lanceolate, occasionally differentiated with a narrow linear to lanceolate limb and an oblong or oblong-obovate sheathing base, apex acute to acuminate, rarely obtuse, base occasionally subdecurrent; margins plane or reflexed to recurved below, dentate to more commonly bluntly or sharply serrate, singly or doubly toothed, elimbate; costa single, strong, subpercurrent to short or long excurrent, often papillose or toothed on back distally; upper and median cells subquadrate to more often short to long rectangular, often narrowly so, mostly papillose, papillae over cell lumen or projecting at angles, rarely smooth; lower and basal cells larger, mostly short to long rectangular, lax or firm; alar region occasionally differentiated with cells enlarged, inflated. **Asexual reproduction** uncommon, usually in the form of fragile leaf tips or deciduous limbs, rarely with swollen leaf tips. **Autoicous**, synoicous or dioicous. **Perichaetia** terminal but often appearing lateral by innovations, leaves often differentiated. **Seta** short to elongate, smooth. **Capsule** immersed to more commonly exserted, suberect to inclined, urn subglobose to globose, asymmetric, usually furrowed when dry, mouth small; annulus absent. **Operculum** plane to conic or shortly beaked. **Peristome** double or reduced to a single series, occasionally absent, exostome teeth 16, smooth or papillose, trabeculate; endostome often reduced, basal membrane ± high, segments often divided distally, cilia 1–3 or absent. **Calyptra** cucullate, naked and smooth. **Spores** mostly papillose or coarsely warty.

DISCUSSION. The Bartramiaceae contain 10 genera and nearly 400 species; in the Neotropics eight genera and about 90 species. In general, the Bartramiaceae are a typical and important element of the open montane, zacatonal, páramo, and puna. Relatively few taxa are epiphytic (*Leiomela* p.p.) or terrestrial in montane forests. The family is a member of the order Bryales.

Axillary hairs have been used in the subfamily classification by Griffin and Buck (1989). The Bartramiaceae is the only family in which this character have been employed in the treatment of neotropical families. Axillary hairs are best found at the leafy tip, in the axil of developing leaves. Careful removal of several leaves near the tip of the stem or branch will often reveal a few of the attached axillary hairs.

LITERATURE. Griffin, III, D. & W. R. Buck. 1989. Taxonomic and phylogenetic studies on the Bartramiaceae. The Bryologist 92: 368–380.

1. Leaves strongly 5-ranked; leaf cells mammillose; rhizoids smooth; operculum short rostrate ..... **Conostomum**
1. Leaves not 5-ranked; leaf cells papillose or smooth; rhizoids papillose; operculum conic to umbonate 2
2. Plants mostly with subfloral innovations; axillary hairs with terminal cell rounded, short, more or less globose; spores often warty or tuberculate 3
2. Plants mostly without subfloral innovations; axillary hairs with terminal cell elongate, not inflated; spores usually only papillose 5
3. Plants usually robust; leaves strongly plicate, with differentiated alar cells ..... **Breutelia**
3. Plants smaller; leaves not or weakly plicate, with undifferentiated alar cells 4
4. Leaves 3–4 mm long; stems without hyalodermis; seta short, mostly 2–7 mm long .. **Anacolia**

4. Leaves mostly 2 mm or less long; stems with hyalodermis; seta elongate, mostly 10 mm or more long ..... **Philonotis**
5. Leaves 3-ranked; leaf cells finely verruculose-striolate; axillary hairs with terminal cell thickened at the apex .....**Plagiopus**
5. Leaves not ranked; leaf cells papillose; axillary hairs with terminal cell not thickened at the apex 6.
6. Leaf cells papillose over lumen; axillary hairs with brown basal cells but otherwise hyaline .... **Flowersia**
6. Leaf cells papillose from projecting cell ends; axillary hairs with walls between cells brown but cells themselves hyaline 7
7. Capsules exserted, rarely immersed; seta elongate, rarely equal to capsule length; stems with hyalodermis; plants terrestrial ..... **Bartramia**
7. Capsules immersed; seta shorter than capsule length; stems without hyalodermis; plants epiphytic or terrestrial ..... **Leiomela**

Anacolia (Fig. 88) - A single species in the Neotropics, *A. laevisphaera* (Taylor) Flowers (Mexico, Central America, Greater Antilles, tropical Andes, southeastern Brazil; also North America, Africa, and India); a genus of seven rather widely distributed species.

HABITAT. On soil and soil covered rocks; lower to high montane regions, usually associated with open sites, including disturbed areas that are often somewhat dry, 1700–4300 m.

DESCRIPTION. **Plants** medium sized, forming loose tufts, dark green to yellowish-green, brown below. **Stems** erect, mostly 20–40 mm tall, few to several branched, subfloral innovations often not conspicuous, radiculose below; in cross-section epidermal cells small and thick-walled, central strand well developed; axillary hairs with terminal cell rounded, short, more or less globose. **Leaves** spirally arranged, loosely erect, tips often spreading, narrowly ovate-lanceolate, ca. 3–5 mm long, to 0.5 mm wide, apex narrowly acuminate to subulate; margins reflexed below, recurved above, sharply serrate distally, teeth double, becoming dentate below, entire at base; costa strong, short to rather long excurrent, toothed on back distally; upper and median cells short rectangular, papillose, papillae at one or both cell ends, occasionally appearing smooth; inner basal cells mostly long rectangular; alar region undifferentiated, or basal marginal cells quadrate. **Dioicous**. **Perichaetial** leaves little differentiated. **Seta** often short, 2–7 mm long, smooth. **Capsule** immersed, erect, urn globose, 2–3 mm in diameter, mouth small. **Operculum** low conic. **Peristome** absent. **Spores** spherical to somewhat ovoid, coarsely papillose.

DISCUSSION. A genus characterized by stems lacking a hyalodermis, narrowly lanceolate leaves with base little differentiated, median cells subquadrate with papillae weakly projecting at cell ends, and gymnostomous capsules rugose, not furrowed.

LITERATURE. Flowers, S. 1952. Monograph of the genus *Anacolia*. Bulletin of the Torrey Botanical Club 79: 161–183 [keys, illustrations].

Bartramia (Fig. 88) - About 15 species in the Neotropics (diverse in Mexico, Central America, and tropical Andes, few species in the Greater Antilles and southeastern Brazil); a genus of cool or cold temperate regions of the world with 71 species.

HABITAT. On humus, soil and rocks; common in montane forests, zacatonal, páramo and puna, (1300–) 2000–5300 m.

DESCRIPTION. **Plants** rather small to large, forming loose to dense tufts, light to dark green or yellowish-brown, occasionally glaucous. **Stems** erect, simple to few branched, radiculose below to densely tomentose; in cross-section hyalodermis present, rarely absent, central strand present; axillary hairs with terminal cell elongate, not thickened at the apex. **Leaves** spirally arranged, not ranked, crowded, erect-appressed to spreading, linear to narrowly lanceolate from an oblong to oblong-obovate sheathing base, 3–10 mm long, sheathing base concave, apex acuminate or tips broken or swollen; margins of limb plane to reflexed, singly or double serrate; costa strong, short to long excurrent, usually toothed on back; laminal cells of limb quadrate to short or long rectangular, thick-walled, papillose, papillae projecting sharply at distal ends, in cross-section lamina bistratose; sheath cells long rectangular, thin-walled, smooth, hyaline or colored; alar region undifferentiated. **Synoicous**, dioicous or autoicous. **Perichaetial** leaves differentiated or not. **Seta** 1–2, short to elongate, 2–9 mm long, erect or curved, stout, smooth. **Capsule** exserted or occasionally immersed, inclined to horizontal, urn ovoid to subglobose, 1.5–2.5 mm long, irregularly furrowed or wrinkled, mouth small. **Operculum** low conic-rounded to convex. **Peristome** double or variously reduced, exostome not united at base, finely papillose or smooth, strongly trabeculate on inner surface; endostome often rudimentary, basal membrane ± high, segments often shorter than exostome. **Spores** spherical to reniform, papillose or warty.

DISCUSSION. A genus recognized by the lack of subfloral innovations, presence of a stem hyalodermis, usually a well differentiated narrow limb and distinct oblong or obovate base, and laminal cells strongly papillose by projected cell ends. The generic name honors John Bartram (1699–1777), an 18th-century United States naturalist.

LITERATURE. Fransén, S. 1996[1995–1996]. A taxonomic revision of neotropical *Bartramia* section *Vaginella* C. Müll. Lindbergia 20: 147–179 [keys, illustrations, maps].

Breutelia (Fig. 89) - About 40 species in the Neotropics, possibly only 30 (in mountainous regions throughout tropical America); a genus containing 93 species, primarily from the Southern Hemisphere.

HABITAT. On soil, humus, logs, occasionally epiphytic or on rocks; open montane to zacatonal, páramo and puna, not uncommon in secondary vegetation, (50–) 1500–4600 m.

DESCRIPTION. **Plants** medium sized to typically large and often robust, forming loose to dense tufts, mostly dark green to golden-yellow or yellowish-brown. **Stems** erect to ascending, occasionally pendent, irregularly to regularly pinnately branched, mostly densely tomentose, rhizoids papillose; in cross-section central strand present; axillary hairs with terminal cell rounded, short, more or less globose. **Leaves** spirally arranged, erect- or wide-spreading, to squarrose-recurved, narrowly to broadly lanceolate from an ovate or obovate-triangular base, 2–8 mm long, plicate, sulcate with differentiated cells or not, base spreading or sheathing at insertion, apex short to long acuminate, rarely acute; margins plane to commonly revolute, serrulate to serrate above shoulder, often sharply serrate at apex; costa strong below, percurrent to commonly short or long excurrent; upper and median cells narrowly rectangular to linear, papillose by projecting distal angles; inner basal cells rectangular-rounded, often porose; alar region differentiated, cells enlarged, in one or more rows, short rectangular to quadrate, smooth, thick-walled. **Dioicous**. **Perichaetia** terminal, subfloral innovations present. **Seta** 6–22 mm long, stout, smooth. **Capsule** inclined to pendulous, urn ovoid to subglobose, 2–4 mm long, smooth to more often furrowed when dry. **Operculum** low conic to convex. **Peristome** double, exostome teeth papillose to papillose-granulose; endostome segments papillose or smooth below, cilia rudimentary or absent. **Spores** coarsely papillose or tuberculate, often areolate.

DISCUSSION. The genus is characterized by the robust habit, strongly plicate leaves, alar cells usually differentiated and short rectangular to quadrate, and subfloral whorls of branches. The northern Andean region is exceptionally rich in *Breutelia* species, and possibly one of the most diverse regions in the world. Dana Griffin is currently revising the neotropical members of this genus.

LITERATURE. Allen, B. & D. Griffin III. 1999. A new species of *Breutelia* (Bartramiaceae) from Central America, with a key to the species of *Breutelia* in Central America. Novon 9: 1–4 [key to 14 species]. - Griffin III, D. 1984a. Studies on Colombian cryptogams XXII. The *Breutelia subarcuata* complex in Colombia and neighboring areas. Acta Botanica Neerlandica 3: 375–282. - Griffin III, D. 1984b. *Breutelia* in Brazil with notes on the occurrence of the genus in the New World. Journal of the Hattori Botanical Laboratory 57: 83–95. - Griffin III, D. 1988. New World species of *Breutelia* with erect-appressed leaf bases. Beiheft zur Nova Hedwigia 90: 357–382 [keys, illustrations].

Conostomum (Fig. 89) - Three species in the Neotropics; *C. tetragonum* (Hedw.) Lindb. (syn. *C. pentastichum* (Brid.) Lindb.) is the most common species, known from the highlands of Mexico, Central America, Andes, high latitudes of north and south temperate region; the two remaining neotropical species are both known from Bolivia, *C. cleistocarpum* Herzog and *C. macrotheca* Herzog. A genus of seven species from cool temperate and tropical highland regions.

HABITAT. On soil, commonly among tufts of bryophytes and lichens; mostly zacatonal, páramo, and puna, 2700–4650 m.

DESCRIPTION. **Plants** rather small, forming dense tufts or cushions, dark reddish-brown below, distally olive green. **Stems** erect, ca. 15 mm tall, distally fasciculate with short branches, somewhat densely tomentose, rhizoids smooth; in cross-section central strand present. **Leaves** distinctly 5-ranked, erect, narrowly lanceolate to oblong-lanceolate, 2.4–3 mm long, to 0.4 mm wide, apex acuminate; margins plane below, distal 1/2 reflexed and rather sharply serrate; costa strong and broad, short to long excurrent as a hyaline awn, somewhat flexuose, smooth or with a few teeth, in cross-section lamina bistratose from costa to about midway to margin; upper and median cells oblong-linear, thick-walled, mammillose with distal ends rather sharply projecting on back; basal cells oblong-rectangular, smooth; alar region undifferentiated or with a single row of quadrate or rectangular cells along margin. **Asexual structures** absent. **Autoicous**. **Perichaetia** terminal, or appearing lateral by innovations, leaves similar to or larger than stem leaves. **Seta** elongate, to 15 mm long or more, rather stout. **Capsule** erect to horizontal, cleistocarpic or stegocarpic, urn elliptical to ovoid, apiculate or not, 2.2–3 mm long, striate or wrinkled when dry. **Operculum** absent or when present short

rostrate, ca. 0.8 mm long, oblique. **Peristome** absent or single, exostome teeth narrow, reduced, readily deciduous, smooth to faintly papillose. **Spores** warty.

DISCUSSION. A genus characterized by the five spirally arranged rows of leaves, and very broad and strong costa.

LITERATURE. Frahm, J.-P., H. Börner, N. Streiber, B. Wallau & S. Weitkus. 1996. Revision der Gattung *Conostomum* (Musci, Bartramiaceae). Tropical Bryology 12: 97–114.

Flowersia (Fig. 89) - Two species present in the Neotropics, *F. campylopus* (Schimp. ex Müll. Hal.) D. G. Griffin & W. R. Buck (Mexico, Guatemala, tropical Andes), and *F. setifolia* (Hook. & Arn.) D. G. Griffin & W. R. Buck (Ecuador to Bolivia); a rather widespread genus of at least four species.

HABITAT. On soil or soil covered rocks, rarely epiphytic; open upper montane forests to páramo and puna, 3000–4450 m.

DESCRIPTION. **Plants** forming tufts or mats, yellowish-green to reddish-brown. **Stems** suberect, to 8 cm tall, branched by innovations, tomentose; in cross-section hyalodermis absent, outer 3–4 rows of cells small, thick-walled, inner cells larger, thin-walled, central strand present; axillary hairs with terminal cell elongate, not thickened at the apex. **Leaves** spirally arranged, crowded, erect-appressed when dry, spreading when wet, to 4.5 mm long, ovate- to triangular-lanceolate, apices acuminate; margins revolute distally, occasionally to base, doubly serrate in distal 1/2; costa short to long excurrent; cells above base oblong to subquadrate, unipapillose, papillae centered over cell lumen; basal cells oblong, smooth. **Dioicous**. **Perichaetia** terminal or appearing lateral by innovations; leaves slightly longer than or twice as long as stem leaves. **Seta** short, 1.5–8 mm long, curved. **Capsule** suberect, urn subglobose, 3–4 mm long, wrinkled. **Operculum** plano-convex. **Peristome** absent. **Spores** coarsely papillose.

DISCUSSION. The absence of a hyalodermis, single papillae centered over the subquadrate cell lumen, wrinkled, not furrowed capsule and absence of a peristome characterize the genus. Previously treated as species of *Anacolia* by Flowers (1952), and recently as *Bartramidula* by Fransén (1988). *Flowersia campylopus* exhibits perichaetial leaves similar to or slightly longer than stem leaves, and *F. setifolia* exhibits perichaetial leaves twice as long as stem leaves. The generic name honors the United States bryologist Seville Flowers (1900–1968).

LITERATURE. Flowers, S. 1952. Monograph of the genus *Anacolia*. Bulletin of the Torrey Botanical Club 79: 161–183 [keys, illustrations]. - Fransén, S. 1988. On the status of *Bartramia campylopus* Schimp in C. Müll. and *Gymnostomum setifolium* Hook. et Arnott. Lindbergia 14: 30–32. – Griffin, III, D. & W. R. Buck, 1989 (see family ref.).

Leiomela (Fig. 90) - About 10 species recorded for the Neotropics; a genus of 13 species confined primarily to tropical America and Africa.

HABITAT. On soil in exposed sites, or epiphytic, on trunks and branches of trees; montane forests to páramo and puna, 900–4250 m.

DESCRIPTION. **Plants** somewhat small to medium sized, forming dense tufts, yellowish-green to dark green. **Stems** erect, few to several branched, densely tomentose, rhizoids papillose; in cross-section epidermal cells small and thick-walled, central strand present; axillary hairs with terminal cell elongate, not thickened at the apex. **Leaves** spirally arranged, loosely erect to erect-spreading, oblong-narrowly lanceolate or subulate, 3–8 mm long, apex acute to broadly or narrowly acuminate; margins plane to reflexed, serrate to near base; costa subpercurrent to long excurrent, often toothed on back; upper and median cells (above base) oblong-short to -long rectangular, papillose, papillae projecting at distal cell angles, thick-walled; basal cells linear-rectangular or oblong-long rectangular, usually smooth, somewhat porose; alar region undifferentiated. **Asexual reproduction** frequent, via deciduous leaf tips, limb, or whole leaves. **Synoicous** or dioicous. **Perichaetial** leaves longer than stem leaves, long-lanceolate, occasionally very long subulate. **Seta** very short, 1–3 mm long, smooth. **Capsule** immersed, erect to somewhat inclined, urn subglobose, 2–5 mm long, when dry somewhat globose-pyriform, smooth, not furrowed, mouth small. **Operculum** plano-convex. **Peristome** absent or present and fragile, exostome teeth inserted below mouth; endostome mostly rudimentary. **Spores** often coarsely papillose.

DISCUSSION. The genus is characterized by the narrowly long lanceolate or linear leaves, little differentiated leaf base, upper laminal cells papillose on one or both ends, capsules immersed, and smooth. *Leiomela* is the only genus in the family in which some of the species are epiphytic.

LITERATURE. Griffin, D. 1977. *Leiomela lopezii*, sp. nov., con observaciones sobre unas especies gimnóstomas del género. Revue Bryologie et Lichénologie 43: 383–387.

Philonotis (Fig. 90) - Forty-eight species recorded for the Neotropics, possibly only 30 or less; a widespread genus of wet habitats with fewer than the 169 species ascribed to it.

HABITAT. On soil or rocks, usually associated with wet sites such as stream banks or seeps; open lowland to zacatonal, páramo and puna, from near sea level to 4700 m.

DESCRIPTION. **Plants** mostly small, solitary to more often forming short dense tufts, pale to dark green or blackish. **Stems** erect to suberect, single or few branched, often with terminal short fasciculate branches; rhizoids usually conspicuous, often tomentose; axillary hairs with terminal cell rounded, short, more or less globose. **Leaves** spirally arranged, rarely ranked, somewhat distant to crowded, ovate- to oblong-lanceolate or lanceolate, 0.5–2.3 mm, apex acuminate, acute to obtuse; margins plane above, often recurved below, denticulate, bluntly to sharply serrate; costa strong, often toothed on back, subpercurrent to long excurrent; upper and median cells oblong-linear to rhombic, usually papillose at upper or lower ends, occasionally centered over lumen, papillae often large, on one or both surfaces; basal cells somewhat to distinctly larger, rectangular and firm-walled, to oblong and ± lax, smooth or papillose; alar region undifferentiated, occasionally marginal cells differentiated. **Autoicous** or more commonly dioicous. **Seta** ca. 10–30 mm long, smooth, erect to variously curved. **Capsule** suberect to inclined, urn subglobose, 1–3 mm long, striate when dry. **Operculum** conic. **Peristome** double, rarely single or absent, endostome membrane high, cilia present. **Spores** papillose.

DISCUSSION. The genus is recognized, in part, by the habitat, usually in seepy or permanently wet sites. The plants are generally small, stems lack a hyalodermis, subfloral innovations are present, leaves mostly 2 mm long or less, alar cells undifferentiated, seta elongate, and capsules furrowed when dry, peristome well developed and usually persistent. *Philonotis* is much in need of revision in the Neotropics. The treatment by Dismier (1910), although very much outdated, is still useful; the keys are partially functional. The present concept of *Philonotis* includes the genus *Bartramidula*.

LITERATURE. Allen, B. 1999. The genus *Philonotis* (Bartramiaceae) in Central America. Haussknechtia Beiheft 9: 19–36 [key to 9 species, illustrations]. - Crum, H. & D. Griffin, III. 1981. *Philonotis corticata*, new from Mexico [key to Mexican species]. The Bryologist 84: 399–401. - Dismier, M. G. 1910. Revision des *Philonotis* de l´Amérique. Mémoires Société Botanique de France 17: 1–37 [important ref. but dated]. - Zales, W. M. 1973. A taxonomic revision of the genus *Philonotis* for North America, north of Mexico. Ph. D. dissertation, University of British Columbia, Vancouver.

Plagiopus - A montypic genus, *P. oederiana* (Brid.) Limpr., is known from Central America and Bolivia; distributed primarily in temperate regions of the Northern Hemisphere.

HABITAT. On soil or rocks; apparently in seasonally moist forests, 3500 m.

DESCRIPTION. **Plants** medium sized, forming loose to dense tufts, green to yellowish-brown. **Stems** erect, 2–8 cm tall, several branched by innovations; in cross-section triangular, hyalodermis present, central strand absent; axillary hairs with terminal cell elongate, thickened at the apex. **Leaves** 3-ranked, somewhat contorted when dry, loosely erect to erect-spreading when wet, lanceolate, to 3.5 mm long, concave below, keeled distally, apex acuminate; margins revolute, distally doubly toothed, bistratose; costa percurrent to short excurrent, distally toothed on back; apical cells smooth; median cells quadrate to short rectangular, finely verruculose-striolate, thick-walled; basal cells elongate, larger and broader. **Synoicous**. **Perichaetial** leaves similar to stem leaves. **Seta** to 15 mm long, erect to slightly flexuose, smooth. **Capsule** inclined to horizontal, urn globose, to 2 mm long, furrowed when dry; annulus absent. **Operculum** conic. **Peristome** double, slightly inserted below the mouth, exostome teeth smooth to finely papillose; endostome basal membrane high, segments shorter than exostome teeth, cilia rudimentary or absent. **Spores** ellipsoid, coarsely papillose.

DISCUSSION. The finely verruculose-striolate but pluripapillose appearing cells are distinctive and in combination with the triangular stems with a hyalodermis and the absence of a central strand separate this genus from most other acrocarpous mosses.

BRACHYTHECIACEAE

Plants mostly medium sized to somewhat large, forming loose to dense mats or wefts. **Stems** creeping, distally stems spreading to subascending, loosely complanate or not, irregularly pinnately branched, radiculose; central strand often present; paraphyllia absent; pseudoparaphyllia foliose. **Leaves** crowded to somewhat distant, broadly to rather narrowly ovate, ovate- to oblong-lanceolate, often plicate at or near base or extending beyond median region, apex acute to short or long acuminate, base often short to long decurrent; margins plane or reflexed, serrulate or serrate, often to near base; costa single, to midleaf or percurrent, rarely short excurrent; upper and median cells smooth, elongate, mostly fusiform to linear, occasionally vermicular, walls ± firm, elimbate; alar region differentiated though not strongly so, cells subquadrate to oblong-rectangular. **Asexual structures** apparently absent. **Dioicous**, autoicous or rarely synoicous. **Perichaetia** lateral, leaves

differentiated, usually elongate. **Seta** elongate, rather stout, smooth or variously papillose throughout or distally. **Capsule** exserted, inclined to horizontal, occasionally erect, urn ovoid to ovoid-cylindrical, asymmetric; stomata usually at base of urn, superficial; annulus usually not well differentiated. **Operculum** conic to conic-short or long rostrate, oblique or not. **Peristome** double, exostome teeth 16, striate below, distally papillose; endostome basal membrane high, segments 16, keeled and perforate, rarely reduced or absent, cilia 1–4. **Calyptra** cucullate, naked and smooth, rarely roughened. **Spores** spherical, usually papillose.

DISCUSSION. There are some 30-40 genera ascribed to this family with estimates of about 550 species; in the Neotropics about 10 genera and 44 species. The traditional generic relationships within the Brachytheciaceae are poorly defined and would certainly profit from a rigorous phylogenetic analysis. *Eurhynchium* and *Rhynchostegium*, and their various segregates, are in need of regional and worldwide revision; see also comments under Amblystegiaceae. Four genera reported from the Neotropics, *Bryhnia*, *Camptothecium*, *Cirriphyllum* and *Homalothecium*, are questionable with regard to their presence in the area. *Bryhnia* is reported from Bolivia (*B. pflanzii* Broth., at an elevation of 4400 m) but seems unlikely; the genus is similar to *Brachythecium* but the distal cell angles exhibit distinct projecting papillae. *Camptothecium* reported from Colombia (*C. pseudolutescens* (Hampe) A. Jaeger) is likely a member of *Brachythecium*. *Cirriphyllum* is recorded with two species from Bolivia (*C. andinum* Herzog, and *C. laevifolium* Herzog) which may likewise represent *Brachythecium*; *Cirriphyllum* is often characterized by its subjulaceous stems and branched with piliferous leaf tips. The status of *Homalothecium* reported from Ecuador (*H. aequatoriense* Thér.) is unknown. Thériot was not overly meticulous in either his descriptions of new neotropical species or their generic placement.

LITERATURE. Buck, W. R. 1981. The taxonomy of *Eriodon* and notes on other South American genera of Brachytheciaceae with erect capsules. Brittonia 33: 556–563. - Buck, W. R. 1988. Taxonomic and nomenclatural notes on West Indian Amblystegiaceae and Brachytheciaceae. Beiheft zur Nova Hedwigia 90: 337–343. - Robinson, H. 1962. Generic revisions of North American Brachytheciaceae. The Bryologist 65: 73–146.

1. Leaf margins distinctly bordered, in cross-section bi- or multistratose; laminal cells very thick-walled ..... **Limbella** (see Amblystegiaceae)
1. Leaf margins unbordered, in cross-section unistratose 2
2. Leaves plicate, with plications extending well up the leaf 3
2. Leaves not plicate or plicate only at base 5
3. Stem leaves lanceolate and short-acuminate or elongate-triangular, with many ± quadrate cells at the base extending up the margins; leaves more acute toward branch tips; margins revolute throughout ..... **Rozea**
3. Stem leaves broader, ovate-lanceolate, acuminate; alar cells ± quadrate in well-defined groups not extending upward in marginal rows; leaves not more acute toward branch tips 4
4. Stem leaves entire to serrulate above base; median cells mostly longer than 50 µm; capsules inclined to horizontal ..... **Brachythecium**
4. Stem leaves serrulate at base, serrate above; median cells mostly shorter than 50 µm; capsules erect ..... **Palamocladium**
5. Costa short, ca. 1/3–1/2 leaf length; plants typically epiphytic .....**Aerolindigia**
5. Costa ± long, at least 1/2–3/4 leaf length; plants typically on rock or soil 6
6. Leaves ovate to oblong-ovate, obtuse, apex apiculate, or short-acute 7
6. Leaves lanceolate to ovate-lanceolate and acute to ± long-acuminate or elongate-triangular .. 9
7. Stems and branches julaceous; leaves deeply concave; leaf apex obtuse apiculate and reflexed; Jamaica, SE Brazil ..... **Pseudoscleropodium**
7. Stems and branches complanate or terete but not julaceous; leaves not or weakly concave; leaf apex acuminate to acute-rounded, not reflexed 8
8. Plants terrestrial, not associated with aquatic habitats, apices short-acute or apiculate .....**Eurhynchium**
8. Plants aquatic, commonly on rocks in or along streams; leaf apices obtuse and often bluntly acute ..... **Platyhypnidium**
9. Stem and branch leaves strongly differentiated; stem leaves broadly ovate-cordate, abruptly ± acuminate with recurved tips; branch leaves smaller, lanceolate to ovate-lanceolate, acuminate with straight tips ..... **Eurhynchium**
9. Stem and branch leaves of much the same shape and size (branch leaves progressively smaller) 10
10. Distal stems and branches suberect to appearing dendroid; flagellate branches present; stem leaves 1 mm or less long; Bolivia ..... **Flabellidium**

10. Distal stems and branches creeping, spreading or subascending; flagellate branches absent or infrequent; stem leaves mostly longer than 1 mm 11
11. Stems and branches terete; costa vanishing at its apex or occasionally projecting at back as an inconspicuous spine; alar cells ± quadrate, not differentiated at the margins; operculum conic or conic-apiculate .....**Brachythecium**
11. Stems and branches terete- to complanate-foliate, ± shiny; costa generally ending as a dorsal spine; alar cells generally short-rectangular or occasionally quadrate, generally bordered by longer, narrower cells; operculum long-rostrate from a conic base 12
12. Capsules inclined to horizontal; peristome well developed; common ..... **Rhynchostegium**
12. Capsules erect; peristome variously modified, endostome cilia rudimentary or absent; Ecuador to Bolivia 13
13. Capsules cylindrical, to 2.2 mm long; exostome narrow and much elongate (to 800 µm), distally smooth; endostomial cilia absent; leaves to 1.5 mm long; Ecuador and Peru ..... **Stenocarpidiopsis**
13. Capsules short ovoid, to 1.4 mm long; exostome broader, distally papillose; endostomial cilia rudimentary; leaves ca. 1 mm long; Bolivia ..... **Mandoniella**

Aerolindigia (Fig. 91) - A monotypic genus, with *A. capillacea* (Hornsch.) M. Menzel found in Central America, West Indies, tropical Andes and southeastern Brazil, also Africa and Madagascar.

HABITAT. Epiphytic, commonly on branches of trees and shrubs; submontane to upper montane forests, 750–3700 m.

DESCRIPTION. **Plants** small and rather slender, forming loose mats, mostly light green to yellowish-green. **Stems** creeping, distally spreading, branches few, short, irregularly pinnate; in cross-section outer 2–3 rows small and thick-walled, inner cells larger, thin-walled, central strand well developed; pseudoparaphyllia foliose. **Stem leaves** loosely erect-spreading, ovate-lanceolate, 1.9–2.1 mm long, to 0.9 mm wide, apex acuminate, often twisted, base slightly decurrent; margins mostly plane, reflexed at base, serrulate throughout or entire at base; costa ca. 1/2 leaf length or less; cells smooth, median cells fusiform to oblong-fusiform, rather thick-walled; basal cells occasionally weakly porose; inner marginal cells at base ± differentiated, oblong short to long rectangular. **Branch leaves** smaller, narrowly lanceolate, to 1.7 mm long. **Autoicous**. **Perichaetial** leaves lanceolate-subulate, to 2.2 mm long. **Seta** 3.5–4.5 mm long, ± flexuose, papillose throughout. **Capsule** suberect to inclined, urn ovoid-cylindrical, to 1.4 mm long, constricted below mouth when deoperculate; annulus present. **Operculum** conic-long rostrate, oblique. **Peristome** with exostome teeth densely cross-striate below, distally coarsely papillose, endostome basal membrane low, segments keeled and perforate, cilia absent. **Calyptra** naked, smooth below, distally roughened. **Spores** spherical, papillose.

DISCUSSION. The genus is recognized by the epiphytic habit, relatively short costa (1/3–1/2 lamina length) and papillose seta. Both Menzel (1991) and Visnadi and Allen (1991) agreed to the placement of this species in the Brachytheciaceae, the latter authors, however, placed this species in *Rhynchostegiella*, a mostly north temperate genus. The previously used name, *Lindigia aciculata* (Taylor) Hampe, is a synonym.

LITERATURE. Menzel, M. 1991. A taxonomic review of the genera *Lindigia* Hampe (Meteoriaceae, Leucodontales) and *Aerolindigia* gen. nov. (Brachytheciaceae, Hypnales), Bryopsida. Nova Hedwigia 52: 319–335. - Visnadi, S. R. & B. Allen. 1991. A revision of the genus *Lindigia* (Musci: Meteoriaceae) in the Neotropics. The Bryologist 94: 5–15.

Brachythecium (Fig. 91) - About 15 neotropical species; stated to contain 178 species, largely confined to cool temperate regions of the world.

HABITAT. On soil, humus and leaf litter, logs, rocks and occasionally at base of trees or shrubs; mostly in open mid to high montane, zacatonal, páramo and puna, 600–4600 m.

DESCRIPTION. **Plants** medium sized to large and robust, forming mats or tufts, glossy green, pale yellow to golden-brown. **Stems** and branches spreading to ascending, terete to weakly complanate distally, irregularly to regularly pinnately branched, radiculose; central strand present; paraphyllia absent; pseudoparaphyllia foliose. **Stem leaves** loosely erect to erect-spreading, ovate to more commonly ovate-triangular or -lanceolate, 1–2.7 mm long, generally plicate, plications weak to strong, concave, apex gradually to abruptly short to long acuminate, often half or fully twisted, base rounded to subcordate, usually decurrent; margins plane to reflexed or recurved toward base, entire to serrate or serrulate distally, rarely to near base; costa 1/2–2/3 leaf length, often ending in an indistinct tooth on back; laminal cells smooth, thin- to ± thick-walled, apical cells usually linear; median cells linear-vermicular to fusiform; basal cells irregularly rectangular to subhexagonal, usually porose; alar region differentiated, cells quadrate to rectangular, firm to ± lax. **Branch leaves** similar but smaller and often narrower. **Autoicous**, synoicous or dioicous, occasionally polygamous. **Perichaetial** leaves

differentiated, sheathing, abruptly long acuminate, acumen erect to spreading or flexuose. **Seta** 12–27 mm long, smooth to papillose. **Capsule** suberect to horizontal, urn oblong-ovoid to cylindrical, to 1–3 mm long, slightly curved, asymmetric; annulus differentiated or not. **Operculum** conic or conic-apiculate. **Peristome** with exostome teeth striate below, mostly papillose distally; endostome basal membrane high, cilia 1–3(–4). **Calyptra** naked and smooth. **Spores** spherical, nearly smooth to more commonly lightly papillose.

DISCUSSION. The genus is rather variable and necessarily defined by a series of characters. In general, stems and branches are terete-foliate, leaves of stem and branch little differentiated, the latter smaller, narrower, plicate or not, margins entire or serrulate, median and upper cells mostly greater than 50 µm, alar cells often quadrate, somewhat well differentiated, seta smooth to papillose throughout or distally, capsules curved or inclined, and operculum conic to conic-apiculate. McFarland (1988) recognized 28 species for Latin America out of an estimated 116 previously accepted species. If this trend continued, and when the paleotropical species are revised, *Brachythecium* would probably be reduced to something less than 100 species.

LITERATURE. McFarland, K. D. 1988. Revision of *Brachythecium* (Musci) for Mexico, Central America, South America, Antarctica, and Circum–Subantarctic Islands. Ph.D. Dissertation, University of Tennessee.

Eurhynchium (Fig. 91) - About 10 species in the Neotropics (*E. praelongum* (Hedw.) Bruch, Schimp. & W. Gümbel is the more common species); a genus reported to contain some 60 or more species, associated with temperate regions of the world.

HABITAT. On soil, rock, and logs, exposed, moist sites; montane open forests, 1800–4270 m.

DESCRIPTION. **Plants** forming rather coarse mats, dull dark green to occasionally golden- or yellowish-green. **Stems** spreading, distal stems and branches spreading to ascending, pinnately to irregularly branched; central strand present; pseudoparaphyllia foliose. **Leaves** of stems and branches differentiated, occasionally strongly dimorphic, not complanate. **Stem leaves** ovate to broadly ovate- or cordate-lanceolate, to 1.7 mm long, occasionally plicate, apex abruptly short to long acuminate, often strongly so, base short to long decurrent; margins plane or often reflexed at base, serrate to serrulate throughout, often entire at base; costa 1/2–4/5 leaf length (occasionally shorter), strong; apical cells mostly shorter and broader; median cells oblong to oblong-linear, thick-walled; basal cells thick- or thin-walled; alar cells not well differentiated. **Branch leaves** ovate-oblong or -short lanceolate, to 1.3 mm long, apex mostly bluntly acute; margins serrate throughout; costa 3/4–4/5 lamina length, usually ending in a tooth; apical cells distinctly shorter and broader than median cells, median cells oblong-linear. **Dioicous** or autoicous. **Seta** to 28 mm long, smooth to roughened or scabrous. **Capsule** inclined to horizontal, rarely subpendulous, urn ovoid-cylindrical, to 2.5 mm long. **Operculum** conic-long rostrate. **Peristome** with exostome teeth finely cross-striate; endostome basal membrane high, segments keeled and perforate, cilia present. **Calyptra** smooth and naked. **Spores** spherical, smooth.

DISCUSSION. The genus is generally characterized by broadly oblong-ovate or ovate leaves, at least with reference to branch leaves; the acute to acute-round apices; apical cells shorter than those of the mid-lamina; alar cells, if differentiated, oblong-rectangular; and the conic long-rostrate operculum. The present treatment includes both *Oxyrrhynchium* (Bruch, Schimp. & W. Gümbel) Warnst. and *Kindbergia* Ochyra (*Stokesiella* (Kindb.) H. Rob.); see Buck (1988) for a brief discussion of the problems associated with these genera. Some authors combine *Eurhynchium* with *Rhynchostegium*.

LITERATURE. Buck, W. R. 1988 (see family ref.). - Zomlefer, W. B. & W. R. Buck. 1990. A reassessment of four *Rigodium* types. The Bryologist 93: 303–308.

Flabellidium (Fig. 92) - A monotypic genus, with *F. spinosum* Herzog known from a single locality in Bolivia.

HABITAT. On exposed roots of trees; submontane forests, at ca. 1400 m elevation.

DESCRIPTION. **Plants** small, forming loose tufts, dull green to yellowish-green. **Stems** creeping with distal stems suberect, to 1 cm tall, appearing ± frondose, irregularly pinnately branched with flagellate branches; in cross-section outer 2–4 rows of cells small, thick-walled, central strand present; pseudoparaphyllia absent. **Leaves** crowded, creeping stem leaves ovate-acute to -acuminate, to 0.4 mm long, ascending stem leaves erect-spreading, ovate, to 0.7 mm long, apex acute, rather blunt, base subcordate, not decurrent; margins plane, distal 3/4 serrate, rather strongly so at apex, base serrulate; costa ca. 3/4 lamina length, rather strong, weakly spurred or not, distally toothed on back, tip projecting on back as a blunt spine; laminal cells moderately thick-walled, apical cells rhombic to hexagonal, shorter than cells below; median and upper cells rhomboidal to oblong-rhomboidal or -hexagonal, smooth or a few cells projecting at distal angles; alar region differentiated, cells quadrate to

transversely short rectangular. **Branch leaves** smaller, narrower, elliptic-lanceolate, distal margins slightly reflexed. **Dioicous**. **Perichaetial** inner leaves oblong-subulate, margins distally erose-serrulate, costa slender. **Seta** smooth (juvenile state). **Capsule** and other features unknown.

DISCUSSION. The genus is characterized by its small stature, frondose habit, secondary stem leaves differentiated from creeping primary stem leaves, laminal cells firm, median and upper with some cells projecting at distal angles, and alar cells quadrate or short rectangular. The status of *Flabellidium* has recently been reviewed by Enroth (1995) who concluded that it is a member of the Brachytheciaceae.

LITERATURE. Enroth, J. 1995. Commentary on the moss genus *Flabellidium* (Brachytheciaceae). Fragmenta Floristica et Geobotanica 40: 743–747.

Mandoniella (Fig. 92) - A monotypic genus, with *M. spicatinervia* (R. S. Williams) Herzog, apparently rare. It is only known from Bolivia.

HABITAT. Epiphytic, on trees; high montane or possibly puna, at 3350 m.

DESCRIPTION. **Plants** rather small, forming loose mats, yellowish-green. **Stems** spreading, irregularly branched, subterete; in cross-section outer 1–2 rows small, rather thick-walled, inner cells larger, central strand present; pseudoparaphyllia foliose, ovate. **Leaves** ovate-short lanceolate, 1.2 mm long or less, apex acute to short acuminate, usually twisted; margins plane above, reflexed at base, serrulate above base; costa ca. 2/3 leaf length, strong, ending as a spine on back; laminal cells firm, ± thin-walled, apical cells shorter than median cells; median cells oblong-fusiform or -linear; alar region distinct, cells subquadrate to short rectangular. **Autoicous**. **Perichaetial** leaves lanceolate, to 1.6 mm long, long acuminate. **Seta** to 9 mm long, smooth, slightly twisted. **Capsule** erect, urn ovoid, to 1.4 mm long; stomata few at urn base, annulus present, 1–2 rows. **Operculum** conic-long rostrate. **Peristome** double, exostome teeth finely cross-striate below, papillose distally; endostome nearly smooth, narrowly long perforate, cilia rudimentary.

DISCUSSION. *Mandoniella* is likely to be confused with *Rhynchostegium*. Both have similar leaves that are smooth, not plicate, a costa ending in a spine, and an often twisted apex. The former is distinguishing by the subterete branches, and the erect capsules, the latter by the somewhat complanate branches and inclined capsules. This species was originally described by R. S. Williams as *Helicodontium spicatinervum*.

LITERATURE. Buck, W. R. 1981 (see family ref.).

Palamocladium (Fig. 92) - A single species represented in the Neotropics, *P. leskeoides* (Hook.) E. Britton, distributed in southeastern United States, Mexico, highlands of the Neotropics including southeastern Brazil, eastern Africa, central and eastern Asia, and New Zealand; a genus of three species; of the two remaining species, one occurs in south-central Europe and the other in Hawaii.

HABITAT. Partly shaded to fully exposed sites on soil, tree trunks, logs, and rocks; lower to upper montane forests, also in secondary forests, 1100–3600 m.

DESCRIPTION. **Plants** medium sized, forming rather soft mats or tufts, glossy green to golden-green. **Stems** initially creeping, becoming suberect with few to several short branches or some long attenuate, to 4 cm long; central strand present. **Leaves** spreading, triangular-lanceolate, 1.5–3 mm long, to 1 mm wide, plicate, plications from base to 1/2–3/4 lamina length, apex broadly to ± narrowly acuminate, base slightly decurrent; margins serrate in distal 1/2, serrulate below; costa 2/3–3/4 lamina length; laminal cells smooth, thick-walled, apical cells shorter, broader than median; median cells linear-vermicular; lower and basal cells shorter and broader, porose; alar region differentiated, cells quadrate to short rectangular. **Dioicous**. **Perichaetial** leaves oblong- to broadly lanceolate-subulate, to 4 mm long. **Seta** 12–22 mm long, smooth, twisted distally or not. **Capsule** erect, urn ovoid-cylindrical, 2–3 mm long; exothecial cells oblong-rectangular, rather thick-walled; stomata rather numerous at base urn, appearing immersed; annulus present. **Operculum** long rostrate, 1.3 mm long. **Peristome** double, rather fragile, exostome teeth striate below; endostome basal membrane high, segments papillose, keeled, cilia absent. **Calyptra** to 3.4 mm long, smooth and naked. **Spores** spherical, lightly papillose.

DISCUSSION. The genus is characterized by the rather strongly plicate, triangular-lanceolate leaves, short median cells (less than 50 µm long), firm-walled, quadrate alar cells, smooth seta, erect capsules, and long rostrate operculum. Previous placed in *Homalothecium* and *Pleuropus* (as *P. bonplandii* (Hook.) Broth.).

LITERATURE. Hofmann, H. 1997. A monograph of the genus *Palamocladium* (Brachytheciaceae, Musci). Lindbergia 22: 3–20.

Platyhypnidium (Fig. 93) - Possibly 1–2 species in the Neotropics; 11 species rather widely distributed.

HABITAT. Submerged on rocks in streams; open montane to páramo and puna, 1300–4200 m.

DESCRIPTION. **Plants** medium sized to somewhat large, forming mats or tufts, dark green to blackish-green or -brown. **Stems** and branches spreading; central strand weak; pseudoparaphyllia foliose. **Leaves** of stem and branch similar, the latter smaller, erect-spreading to spreading, crowded, not complanate, broadly ovate to oval, 2–3 mm long, 1.5–2 mm wide, nearly as broad as long, concave below, appearing to sheath stem, apex broadly acute to obtuse; margins plane, serrate to serrulate to near base; costa 3/4–4/5 lamina length, tapering distally; laminal cells thick-walled, apical cells short, rhomboidal; median cells oblong-linear, angles tapered, smooth; basal and lower cells irregularly oblong-short rectangular; alar region undifferentiated. **Autoicous**. **Perichaetial** leaves oblong-subulate. **Seta** slender, to 24 mm long, twisted, smooth. **Capsule** suberect to horizontal, urn cylindrical, 1.8–2.2 mm long, asymmetric, curved. **Operculum** long rostrate, oblique. **Peristome** with exostome striate below, distally papillose; endostome basal membrane high, segments keeled and perforate, cilia 2. **Spores** smooth to lightly papillose.

DISCUSSION. *Platyhypnidium* is distinguished from other members of the family by the aquatic habitat and by the dark green to blackish-green color, the broadly ovate, acute leaves with apical cells shorter than median. The only features separating *Platyhypnidium* from *Eurhynchium* are the autoicous sexual condition and the typically aquatic habitat; additional characters include stem and branch leaves similar and costa smooth on back. Although retained here as a separate genus, it should probably be placed in *Eurhynchium* or possibly *Rhynchostegium*. *Platyhypnidium aquaticum* (A. Jaeger) M. Fleisch., one of the more common neotropical aquatic mosses, appears to tolerate rather well moderately polluted streams and rivers. The name *Platyhypnidium riparioides* (Hedw.) Dixon has been applied to collections from the Neotropics, but the local plants appear to be distinct from those of the Northern Hemisphere.

LITERATURE. Buck, W. R. 1988 (see family ref.).

Pseudoscleropodium (Fig. 93) - A monotypic genus, *P. purum* (Hedw.) M. Fleisch., know from Jamaica and southeastern Brazil in the Neotropics and probably introduced there; widespread though localized in mostly temperate regions.

HABITAT. On soil and rocks; in exposed, often disturbed sites (pasture clearings and trails), infrequent in montane forests, at elevations from 1450–1580 m.

DESCRIPTION. **Plants** large and rather robust, form dense mats, glossy light green to yellowish-brown or golden. **Stems** creeping, pinnately branched; in cross-section outer 2–3 rows of cells small, thick-walled, inner cells large, firm-walled, central strand weak; pseudoparaphyllia foliose. **Stems leaves** spreading to ascending, to 10 cm or more long, julaceous, subpinnately branched; in cross-section outer 2–4 rows of cells small, thick-walled, inner cells large, thin-walled, central strand present; pseudoparaphyllia foliose. **Leaves** crowded or imbricate, loosely erect, broadly ovate to oblong-ovate, to 2.4 mm long, deeply concave, apex obtuse-rounded, abruptly apiculate and reflexed; margins incurved distally, reflexed at base, finely serrulate distally; costa slender, ca. 2/3–3/4 lamina length, occasionally weakly spurred; apical cells linear-fusiform; median cells linear-vermicular, smooth or weakly projecting at cell angles; basal cells somewhat larger, oblong, porose; alar region weakly differentiated, few cells subquadrate. **Branch leaves** similar but smaller, more distinctly serrulate, to near base. **Perichaetial** leaves elongate, subulate. **Seta** to 40 mm or more long, smooth. **Capsule** inclined to pendent, ovoid-cylindrical, to 2.5 mm long, slightly asymmetric; stomata at urn base, superficial. **Operculum** conic-short rostrate. **Peristome** with exostome teeth finely cross-striate below, distally papillose, trabeculate on back; endostome basal membrane high, segments finely papillose, keeled, perforate, cilia 2–3, appendiculate. **Calyptra** smooth and naked. **Spores** spherical, smooth to faintly papillose.

DISCUSSION. The genus is characterized by the julaceous stems, deeply concave, ovate to oblong-ovate, smooth leaves, abruptly recurved, apiculate apex, and alar cells only weakly differentiated. *Pseudoscleropodium* is apparently indigenous to western Europe and adventive elsewhere in scattered localities throughout the world (Allen & Crosby, 1987). Given the spread to localities outside Europe is believed to be attributed to the use of this species as packing material for the distribution of horticultural plants to various localities during the previous century. The aggressive nature of this species in suitable habitats, and the rarity of this species in the region, an anthropogenic origin for this moss in the Neotropics is not impossible. Sporophytes are apparently unknown in the New World.

LITERATURE. Allen, B. H. & M. R. Crosby. 1987. *Pseudoscleropodium purum* re-established in South America. Journal of Bryology 14: 523–525.

Rhynchostegium (Fig. 93) - About 30 species recorded for the Neotropics, possibly only 5–10 are valid; a genus containing less than 100 species of primarily temperate regions.

HABITAT. On soil, logs and rocks, rarely epiphytic; submontane to upper montane forests, 450–4000 m.

DESCRIPTION. **Plants** somewhat small to rather large, more commonly medium sized, forming ± soft loose mats, often glossy, light to somewhat dark green, yellowish-green or golden. **Stems** spreading; central strand present. **Leaves** of stem and branch leaves mostly similar, erect-spreading to wide-spreading, often complanate, narrowly to broadly lanceolate to ovate-lanceolate, 1–2.3 mm long, smooth, not plicate, apex short to long acuminate, often twisted, base not or weakly decurrent; margins plane or reflexed at base, serrulate to serrate throughout or entire at base; costa usually weak, 1/2–3/4 lamina length; apical cells similar to median cells; median cells linear, ± thin-walled; alar region not well differentiated. **Autoicous**. **Perichaetial** leaves sheathing, long acuminate. **Seta** 9–24 mm long, smooth, often twisted. **Capsule** inclined to horizontal, urn ovoid-cylindrical, 1–2.2 mm long, curved. **Operculum** conic-long rostrate, oblique. **Peristome** with exostome teeth finely cross-striate; endostome basal membrane high, segments keeled and perforate, cilia present. **Calyptra** smooth and naked. **Spores** spherical, mostly smooth.

DISCUSSION. The genus is characterized by the weakly to rather strongly complanate leaves that are smooth, not plicate, similar apical and median cells, alar cells little differentiated, smooth seta and operculum obliquely long-rostrate. The neotropical members of this genus are poorly understood and in need of revision. Robinson (1987) has placed two of the most commonly encountered species (*Rhynchostegium scariosum* (Taylor) A. Jaeger and *R. serrulatum* (Hedw.) A. Jaeger) in a new genus, *Steerecleus*.

LITERATURE. Robinson, H. 1987. Notes on generic concepts in the Brachytheciaceae and the new genus *Steerecleus*. Memoirs of the New York Botanical Garden 45: 678–681.

Rozea (Fig. 94) - Two neotropical species, *R. andrieuxii* (Müll. Hal.) Besch. and *R. subjulacea* Besch. (both recorded from Mexico, Guatemala, Venezuela, Colombia); five species distributed in the northern Neotropics and Himalayan mountains of central Asia.

HABITAT. On tree bases, branches, and trunks, also on rock (calcareous); open or forested montane to shrubby subpáramo, 350–3670 m.

DESCRIPTION. **Plants** medium sized, forming rather dense mats, reddish-yellow or golden. **Stems** short spreading, distal stems and branches subascending, slightly curved, subjulaceous; in cross-section hyalodermis weak, outer 1–2 rows of cells small, thick-walled, inner cells larger, thin-walled, central strand absent. **Leaves** erect, erect-spreading when wet, ovate to oblong-ovate, 0.7–1.5 mm long, to 0.6 mm wide, plicate, biplicate, or with single longitudinal plication, concave, slightly asymmetric, apex acute to short acuminate, slightly flexed; margins recurved to near apex, on one, or more commonly, on both sides, distal 1/3 serrate; costa often with 1 or more spurs, rarely forked from base, (1/3–)1/2(–2/3) lamina length; apical cells short, some cells appearing unipapillose, papillae over lumen; median cells fusiform to linear-fusiform, smooth, rather thick-walled; basal cells short to ± long rectangular-rounded, golden; alar region differentiated, cells quadrate to short rectangular, thick-walled. **Dioicous**. **Perichaetial** leaves oblong-lanceolate, subulate. **Seta** 12–20 mm long, smooth. **Capsule** erect, ovoid-cylindrical, to 3.5 mm long; annulus absent. **Operculum** rostrate, oblique. **Peristome** with exostome teeth cross-striate below, distally papillose to smooth; endostome basal membrane high. **Calyptra** naked and smooth. **Spores** spherical, lightly papillose.

DISCUSSION. The genus is characterized by plants forming mats that are often golden to reddish-brown, the subjulaceous, ascending and often curved branches, biplicate leaves with margins revolute, the strong, single or occasionally forked costa, subquadrate cells at leaf insertion, and the erect capsules. The two neotropical species can be differentiated by the following: *R. andrieuxii* — leaves lanceolate, costa usually single, ending above midleaf, alar cells in 3 rows, and *R. subjulacea* — leaves oblong-ovate, costae usually forked, ca. 1/2 lamina length, alar cells in 3–5 rows. *Rozea* has been previously placed in the Entodontaceae.

LITERATURE. Buck, W. R. & H. Crum. 1976. Revision of the genus *Rozea* (Musci). The Bryologist 79: 406–421 [keys, illustrations].

Stenocarpidiopsis (Fig. 94) - A monotypic genus, with *S. salicicola* (Mitt.) M. Fleisch. known from Ecuador and Peru.

HABITAT. Epiphytic; apparently rare, in montane sites at 2000–2150 m.

DESCRIPTION. **Plants** medium sized, forming loose mats, somewhat glossy, light yellowish-green. **Stems** spreading, irregularly pinnately branched; in cross-section outer 2–3 rows of cells small, thick-walled, inner cells large, thin-walled, central strand weak. **Leaves** subcomplanate or not, loosely erect when dry, erect-spreading when wet, ovate-short lanceolate, to ca. 1.5 mm long, apex rather abruptly

short acuminate, often with 1/2 twist, base short decurrent; margins plane above, erect at base, serrulate to near base, distally somewhat coarsely serrate; costa ca. 2/3–3/4 lamina length, strong below, slender above, projecting as a spine at apex on back; laminal cells smooth, apical cells similar or only slightly smaller than median cells; median cells oblong-linear; alar region little differentiated, few cells short rectangular. **Perichaetial** leaves oblong-lanceolate, narrowly long acuminate, costate. **Seta** to 15 mm long, twisted, smooth. **Capsule** erect to suberect, urn cylindrical, to 2.2 mm long, slightly constricted below mouth; annulus in 1 row; stomata at urn base, superficial. **Operculum** stoutly long rostrate, oblique. **Peristome** with exostome teeth narrow, cross-striate below, 1–2 cells vertically striate, smooth above; endostome basal membrane rather low, segments sublinear, finely papillose, weakly keeled, perforate, cilia absent. **Calyptra** smooth and naked. **Spores** spherical, coarsely papillose.

DISCUSSION. This genus can possibly be confused with *Brachythecium* or, more likely, *Rhynchostegium*; the erect or suberect, symmetric capsules with conspicuously long peristome (to ca. 800 µm), narrow exostome teeth and slender endostome segments are distinctive. *Stenocarpidiopsis* is a rare Andean endemic. Little is known about the ecology of this genus.

LITERATURE. Buck, W. R. 1981 (see family ref.).

BRUCHIACEAE

Plants very small to somewhat medium sized, solitary or forming short tufts. **Stems** short, simple or few branched by innovations. **Leaves** mostly progressively larger distally, lanceolate to narrowly lanceolate or subulate from an oblong or oblong-ovate base; margins plane or recurved, entire or distal tips serrulate; costa single, subpercurrent to short excurrent; laminal cells smooth. **Asexual structures** absent. **Autoicous**. **Sporophytes** terminal; perichaetial leaves often larger and longer. **Seta** short to elongate, erect or curved to flexuose, smooth. **Capsule** immersed to exserted, urn obloid to pyriform with a neck distinctly elongate, occasionally as long as or much longer than the urn; stomata numerous in neck region, superficial; annulus often well developed. **Operculum** absent or present and rostrate. **Peristome** absent or single with 16 teeth. **Calyptra** cucullate or mitrate. **Spores** variously ornamented.

DISCUSSION. The present concept of the Bruchiaceae follows Buck (1979) in which there are four constituent genera - *Bruchia*, *Pringleella*, *Eobruchia*, and *Trematodon*. The family may contain 100 or more species; in the Neotropics there are four genera and about 17 species. Some past and present authors have placed this family under the Dicranaceae. Snider (*in* Sharp et al., 1994; see general ref.) places *Pringleella* in the Ditrichaceae and suggests that *Eobruchia* exhibits peristome features similar to those of *Ptychomitrium*. The conspicuous, elongate neck with numerous stomata is a distinctive feature of the family.

LITERATURE. Britton, E. G. 1913. Bruchiaceae. North American Flora 15(1): 47–54. - Buck, W. R. 1979. A re-evaluation of the Bruchiaceae with the description of a new genus. Brittonia 31: 469–473. - Delgadillo M., C. & Cárdenas S., A. 1991. Notes on ephemeral mosses from Mexico, including *Bruchia paricutinensis* sp. nov. The Bryologist 94: 294–297.

1. Capsule apiculate; neck 1/2 or less total capsule length; operculum, annulus, and peristome absent ..... **Bruchia**
1. Capsule with operculum long rostrate; neck equal to or longer than urn; operculum and annulus present, peristome absent or present 2
2. Capsule mostly exserted, short to long cylindrical; neck often longer than urn length; peristome absent or when present teeth vertically striate; calyptra cucullate ..... **Trematodon**
2. Capsule immersed, emergent or slightly exserted, ovoid to short cylindrical; neck nearly equal to urn length; peristome absent or when present smooth at base, papillose distally; calyptra mitrate 3
3. Seta elongate, curved or flexuose, longer than the urn; peristome present (teeth smooth at base, papillose distally); annulus revoluble; Brazil and Ecuador ..... **Eobruchia**
3. Seta short, erect, slightly shorter or equal to urn length; peristome absent; annulus persistent; Mexico ..... **Pringleella**

Bruchia (Fig. 94) - Four species in the Neotropics; 20 species, primarily distributed in North America.

HABITAT. On exposed soil and volcanic ash (Mexico), often disturbed sites; low (Brazil) to high (Mexico) elevations, from near sea level to 2300 m.

DESCRIPTION. **Plants** very small, solitary or forming low tufts. **Stems** short, to 4 mm tall, simple or few branched by innovation. **Leaves** distally longer and larger, suberect to spreading, somewhat

broadly lanceolate to subulate from an ovate or oblong base, to 3 mm long, acute to acuminate; margins plane, entire; costa subpercurrent to short excurrent, rather weak; distal laminal cells oblong-linear to short or rather long oblong-rectangular, thick-walled; basal cells longer, oblong-rectangular, rather lax. **Perichaetial** leaves larger than stem leaves. **Seta** short, 0.5–2.4 mm long. **Capsule** immersed to exserted, urn pyriform, 0.7–1.5 mm long, with short beak, neck distinct, 1/4–1/3 urn length, stomata numerous in neck region, superficial. **Operculum** and peristome absent. **Calyptra** mitrate, smooth, base lobed. **Spores** large, spinose to spinose-reticulate.

DISCUSSION. Plants of this genus are characterized by small size, cleistocarpous apiculate capsule (lacking an operculum and peristome), an elongate neck with numerous stomata, and spinose spores.

LITERATURE. Delgadillo M., C. & Cárdenas S., A. 1991 (see family ref.). - Rushing, A. E. 1985. Spore morphology in the genus *Bruchia* Schwaegr. (Musci). American Journal of Botany 72: 75–85. - Rushing, A. E. 1986. A revision of the genus *Bruchia* Schwaegr. (Musci). Journal of the Hattori Botanical Laboratory 60: 35–83 [keys, illustrations].

Eobruchia (Fig. 95) - Two species confined to the Neotropics: *E. bruchioides* (Müll. Hal.) W. R. Buck is found in montane southeastern Brazil, and *E. ecuatoriana* Steere from the páramos of Ecuador.

HABITAT. On exposed moist soil and stream banks; open montane to páramo, at elevations from 2000 to 4200 m.

DESCRIPTION. **Plants** small, 2–5 mm tall, solitary or forming loose, low tufts, yellow to brown. **Stems** short, erect, simple or few branched by innovations; in cross-section central strand weak. **Leaves** few, rather crowded, progressively larger and longer distally, short to long stout subula from an ovate- to oblong base, 1.5–3 mm long; margins entire; costa short to long excurrent, stout, rather weak at base, apices bluntly toothed; distal laminal cells rhomboidal to short oblong-fusiform, firm-walled, smooth; basal cells longer, oblong-rectangular; distal marginal cells quadrate. **Perigonia** at base of stems. **Perichaetial** leaves similar to but conspicuously longer than stem leaves. **Seta** elongate, 2–5 mm long, curved or flexuose, often rather stout, smooth. **Capsule** slightly exserted beyond perichaetial leaves, erect, urn somewhat ovoid, ca. 1 mm long, neck nearly equal to urn length; stomata numerous in neck region, superficial; annulus present, revoluble. **Operculum** long rostrate, straight. **Peristome** single, teeth short, smooth at base, distally papillose. **Calyptra** mitrate, smooth, base lobed. **Spores** coarsely papillose or papillose-spiculose.

DISCUSSION. The genus is characterized by curved or flexuose elongate seta, length of neck equal to urn, revolute annulus, and peristome teeth smooth at base and distally papillose.

LITERATURE. Buck, W. R. 1979 (see family ref.). - Steere, W. C. 1982. Four new species of Musci from the Andes of Ecuador and Colombia. Brittonia 34: 435–411.

Pringleella (Fig. 95) - A genus of three species, with *P. pleuridioides* Cardot endemic to central Mexico.

HABITAT. On exposed soil; open montane, at elevations from 2200–2700 m.

DESCRIPTION. **Plants** small, forming loose tufts, yellow to yellowish-brown. **Stems** erect, to 2.5 mm tall, radiculose below. **Leaves** small below, progressively crowded and larger above, erect-spreading, lanceolate to oblong-lanceolate, to 2 mm long, somewhat channeled above, apex long acuminate; margins plane, entire to serrate at tip; costa strong, percurrent to short excurrent; laminal cells above base mostly short to long rectangular, thick-walled; basal cells longer, thin-walled, somewhat lax. **Perichaetial** leaves longer, to 3.5 mm long, otherwise similar. **Seta** erect, short, to ca. 1 mm long, smooth. **Capsule** immersed to slightly emergent, erect, urn ovoid from a distinct neck, ca. 1 mm long; stomata somewhat numerous on neck, superficial; annulus conspicuous, persistent to deciduous in parts. **Operculum** long rostrate. **Peristome** absent. **Calyptra** mitrate-campanulate, base lobed, smooth and naked. **Spores** large, subreniform, spinose.

DISCUSSION. The genus is characterized by an erect seta and a capsule equal in length to the seta and with a distinct but short neck, the absence of a peristome, and a lobed mitrate-campanulate calyptra.

Trematodon (Fig. 95) - Eighteen species recorded for the Neotropics of which probably only about 10 are justified. Only *T. longicollis* Michx. appears to be common in Neotropics; a mostly tropical and subtropical genus with an overstated 83 species.

HABITAT. On exposed soil, rather weedy and usually associated with disturbed sites; locally widespread in open lowland to mid montane, from near sea level to 2200 m.

DESCRIPTION. **Plants** somewhat small, gregarious or forming low, loose tufts, green to yellowish-green. **Stems** short and erect, radiculose; in cross-section central strand present. **Leaves** crispate or

contorted when dry, erect to erect-spreading when wet, lanceolate to broadly subulate from an ovate or oblong sheathing base, 1.5–5 mm long, apex acute to subobtuse; margins recurved, entire or apices serrulate or dentate; costa subpercurrent; median laminal cells subquadrate; lower and basal cells rectangular. **Perichaetial** leaves convolute, longer than stem leaves. **Seta** elongate, 3–35 mm long, slender, smooth. **Capsule** erect to inclined, urn ovoid (obloid), 1.2–3 mm long, with a distinct neck equal to or much longer than urn, 1–5 mm long; exothecial cells elongate, thick-walled; annulus revoluble or adhering to urn and operculum. **Operculum** long rostrate, oblique. **Peristome** absent or present and single, teeth slightly set below urn mouth, vertical-striate, perforate, basal membrane distinct. **Calyptra** cucullate, naked. **Spores** coarsely papillose.

DISCUSSION. The genus is characterized by the elongate seta, well exserted capsules, peristome when present vertically striate, and the cucullate calyptra. *Trematodon* is in need of revision. Probably more than half of the species names attributed to the genus represent synonyms.

BRYACEAE

Plants small to large and robust, mostly forming dense tufts. **Stems** erect, solitary or few branched by innovations or stems connected by stolons (*Rhodobryum*), radiculose, occasionally densely tomentose; in cross-section central strand present. **Leaves** spirally arranged (subcomplanate and dimorphic in *Epipterygium*), usually small and distant below, equally spaced or distally crowded (comose) and occasionally forming a rosette, variously shaped, linear- to broadly lanceolate, ovate, oblong, or obovate, apex broadly acute to acuminate, occasionally decurrent; margins plane to recurved or reflexed, entire to serrate distally, often sharply so, limbate or elimbate; costa single, subpercurrent to excurrent; laminal cells smooth, median cells oblong-linear or short to long hexagonal or rhomboidal, walls ± firm, porose or not; basal cells short to long rectangular, lax- or firm-walled; alar region usually undifferentiated; marginal cells similar or of long linear cells if forming a border. **Asexual** structures occasionally present, as rhizoidal tubers or as a bulbil or cylindrical gemmae in leaf axils. **Autoicous** or dioicous, occasionally synoicous. **Perigonia** bud-like. **Perichaetia** terminal or appearing lateral, leaves usually little differentiated, or smaller or larger than stem leaves. **Seta** elongate, single or several (usually only in synoicous taxa), smooth. **Capsule** exserted, mostly pendulous, occasionally erect or suberect, urn ovoid to obloid, or more often pyriform, with a distinct short or long neck; exothecial cells mostly elongate, firm and thick-walled, stomata at base of urn, superficial; annulus often large and revoluble, or absent. **Operculum** conic or conic-apiculate. **Peristome** mostly double or variously reduced or single, typically exostome teeth 16, papillose and trabeculate; endostome basal membrane present, segments 16, keeled, hyaline or yellowish, cilia 1–3. **Calyptra** cucullate, naked and smooth. **Spores** spherical, often lightly papillose.

DISCUSSION. The Bryaceae, a large and diverse family, contain about 20 genera and about 1000 species; in the Neotropics there are 15 genera and about 175 species. The family is notoriously difficult. While many of the species are distinct and readily recognizable given some experience, features of the peristome are critical in the identification of many taxa in this family. Thus, sterile collections are at best difficult to name. Ochi (1980, 1981) has provided a synoptical treatment that covers many of the neotropical Bryoideae (*Acidodontium*, *Brachymenium*, and *Bryum* - including both *Anomobryum* and *Rhodobryum* which were recognized as subgenera by Ochi, but are returned to generic rank in our treatment).

Study guide. Stem leaves provide most of the essential features needed for identifying species of this family; however, as noted above, peristomial features are often necessary, for separating *Acidodontium* and *Brachymenium* and various of the species that they contain. Intact peristomes are mandatory for the identification of *Mielichhoferia* and *Schizymenium* species; sterile material of these two genera should not be collected.

LITERATURE. Ochi, H. 1980. A revision of the neotropical Bryoideae, Musci (First part). Journal of the Faculty of Education, Tottori University, Natural Science 29: 49–154 [keys, illustrations].- Ochi, H. 1992. A revised infrageneric classification of the genus *Bryum* and related genera (Bryaceae, Musci). Bryobrothera 1: 231–244. - Shaw, J. 1985. The correlation between taxonomy and peristome structure in the Bryaceae. Journal of the Hattori Botanical Laboratory 59: 79–100. - Shaw, J. 1987. Systematic studies on the Bryaceae. Memoirs of the New York Botanical Garden 45: 682–690.

1. Leaves dimorphic, upper (lateral) leaves ovate, lower (beneath) leaves smaller, narrowly lanceolate ..... **Epipterygium**
1. Leaves monomorphic 2
2. Leaves linear to oblong-lanceolate, rarely shortly ovate-lanceolate (see *Leptobryum*), not distinctly bordered; cells narrow, relatively long, 5:1 or longer 3

2. Leaves ± broad, elliptic to ovate or ovate-lanceolate, usually distinctly bordered; cells rather broad, generally less than 4:1 10
3. Capsules inclined or if erect then shiny pyriform; peristome double, well developed 4
3. Capsules erect or slightly inclined; peristome single (endostome lacking) or double but exostome and/or endostome variously reduced 6
4. Leaves setaceous or shortly ovate-lanceolate; capsules markedly pyriform (pear-shaped) and shiny, pendulous or erect; gemmae absent .....**Leptobryum**
4. Leaves lanceolate to linear-lanceolate; capsules usually with a sizable neck but less notably pear-shaped, rather dull, not shiny, pendulous or inclined; gemmae present or absent 5
5. Leaves ovate, apex apiculate; costa often short excurrent; margins entire ..... **Bryum** p.p.
5. Leaves broadly lanceolate to ovate-lanceolate, apex not apiculate; costa subpercurrent to percurrent; margins mostly serrate to serrulate distally .....**Pohlia**
6. Exostome teeth united in pairs from base to ca. 1/2 exostome length, papillose, reddish-brown; gemmae present (Mexico, Guatemala) ..... **Pseudopohlia**
6. Exostome teeth when present not united in pairs, variously ornamented; gemmae absent 7
7. Perichaetia and sporophytes distinctly terminal; peristome double, endostome basal membrane very low ..... **Orthodontium**
7. Perichaetia and sporophytes appearing lateral (by innovations); peristome usually single, rarely double, endostome basal membrane when present either low or high 8
8. Plants paroicous, autoicous, rarely synoicous; peristome usually single and endostomial, rarely absent or double; exostome when present smooth ..... **Schizymenium**
8. Plants dioicous; peristome single and exostomial or double with long exostome and an endostomial membrane not differentiated into segments and cilia; exostome teeth reticulate, papillose or striate 9
9. Endostome rudimentary or absent; exostome papillose or striate ..... **Mielichhoferia**
9. Endostome extending 1/2–2/3 the length of the exostome teeth and adherent to them (Central America); exostome finely cross-striate below, smooth above ..... **Synthetodontium**
10. Plants often epiphytic; capsules ± erect to subpendent, symmetric; cilia absent or rudimentary 11
10. Plants terrestrial, occasionally found on trunk base of trees; capsules inclined and asymmetric; cilia usually well developed 12
11. Endostome segments rudimentary; plants on trees, logs, humus, soil, rocks . **Brachymenium**
11. Endostome segments well developed; plants on trees ..... **Acidodontium**
12. Stems julaceous throughout; leaves small with rounded or subacuminate apex 13
12. Stems not julaceous or if so then plants whitish; leaves small to large, usually crowded and gradually or abruptly larger distally on stem, usually acuminate 15
13. Laminal cells lax, thin-walled; capsules clavate; exostome shorter than endostome; Guatemala .....**Plagiobryum**
13. Laminal cells firm-walled, not lax; capsules not clavate; peristome well developed or exostome short and adnate to basal membrane with segments and cilia absent 14
14. Peristome well developed; innovation leaves similar to stem leaves ..... **Anomobryum**
14. Peristome reduced, exostome teeth very short and truncate, endostomial membrane adhering to exostome; innovation leaves and stem leaves differentiated; central Mexico ..... **Anomobryopsis**
15. Leaves usually less than 5 mm long, ± evenly distributed, usually not rosulate-foliate; costal stereids well-developed; stolons absent; sporophytes solitary ..... **Bryum** p.p.
15. Leaves usually greater than 7 mm long, often rosulate-foliate; costal stereids absent or reduced; stolons often present; sporophytes often clustered ..... **Rhodobryum**

Acidodontium (Fig. 96) - A neotropical genus of 14 species, primarily Andean with two or three species extending to Central America and the West Indies.

HABITAT. Epiphytic, on trees and shrubs; mostly montane forests, extending to higher elevations in shrubby forests, (50–) 500–4300 m.

DESCRIPTION. **Plants** medium sized to rather large, forming dense tufts, dark green or reddish-brown, often glossy. **Stems** erect, few to several branched; central strand present. **Leaves** mostly erect, flexuose to crispate when dry, erect-spreading when wet, oblong-lanceolate, lanceolate or oblong-obovate, apex short to long acuminate; margins plane, reflexed to recurved below, serrulate or serrate distally, rarely entire, limbate; costa ca. 4/5 to long excurrent, mostly weak; median cells rhomboidal to narrowly hexagonal-rhomboidal, weakly to strongly porose; basal cells quadrate to short rectangular; marginal cells linear in 1–3(–4) rows, ± thick-walled. **Dioicous**. **Perichaetia** terminal, leaves usually differentiated, larger and more narrow. **Seta** to 4(–5) cm long. **Capsule** erect to suberect or horizontal, urn cylindrical-obloid or -pyriform, neck narrowly short or long. **Operculum**

convex-apiculate or conic-plano. **Peristome** double, exostome broad and joined at base, distal 1/4–1/3 abruptly narrowed; endostome basal membrane rather high, segments forked distally, cilia reduced or absent. **Spores** lightly to densely papillose.

DISCUSSION. One of only two common epiphytic bryaceous genera, *Acidodontium* exhibits a well developed double peristome, and an operculum that is commonly conic-apiculate or conic-plano. The other genus, although not exclusively epiphytic, is *Brachymenium*, which exhibits an endostome that is rudimentary or lacking, and a high or low conic or rostrate operculum.

LITERATURE. Ochi, H. 1980 (see family ref.).

Anomobryopsis (Fig. 96) - A monotypic genus, *A. tereticaulis* Cardot is only known from central Mexico.

HABITAT. On soil, elevation unknown.

DESCRIPTION. **Plants** small, forming tufts, yellowish brown. **Stems** erect, to 7 mm tall, simple (when sterile) to few branched. **Leaves** differentiated between stem and innovations; stem leaves crowded, rosulate, erect to erect-spreading, ovate to lingulate, to 1.3 mm long, apex rounded to bluntly acute; margins plane, mostly distally serrulate; costa ending several cells below apex. Innovation leaves evenly distributed, not rosulate, broadly short-ovate to lingulate, to 0.7 mm long, apex rounded; margins serrulate at apex; apical cells nearly isodiametric; median cells somewhat irregularly rhombic, rather thick-walled; basal cells short rectangular. **Dioicous**. **Perichaetia** terminal, with several subfloral innovations; leaves broadly short lanceolate, acute; apical cells rhombic to linear-rhomboidal, thick-walled. **Seta** erect, to 14 mm long, rather stout. **Capsule** horizontal to pendent, urn pyriform, neck distinct, nearly equal to urn length; annulus in 2 rows. **Operculum** conic to short rostrate and somewhat oblique. **Peristome** reduced, exostome of short truncate teeth, slightly exceeding the annulus cells, finely papillose; endostome of a short basal membrane adhering to exostome teeth. **Calyptra** not observed. **Spores** spherical, smooth, or nearly so.

DISCUSSION. *Anomobryopsis* is closely related to, and likely to be confused with, *Anomobryum*. Both genera exhibit similar gametophytic features including imbricate leaves, leaf shape and areolation; however, *Anomobryopsis* is distinguished by the subfloral innovations and the reduced peristome consisting solely of 16 short, truncate teeth with adhering short endostomial basal membrane. Shaw (1994) suggested that this taxon could readily be placed in *Anomobryum* which also contains members that exhibit rudimentary peristomes.

LITERATURE. Ochi, H. 1981. Taxonomic position of *Anomobryopsis*. Hikobia (Supplement) 1: 55–57. - Shaw, J. 1994. In Sharp et al. (see gen. ref.).

Anomobryum (Fig. 96) - Eleven species in the Neotropics; worldwide there are 47 species, many widely distributed.

HABITAT. On soil, often in wet seepy sites; mostly from open montane, zacatonal, páramo, and puna, 50–4600 m.

DESCRIPTION. **Plants** small and slender, gregarious or forming short tufts, lustrous light green or yellowish, to golden-brown. **Stems** erect, simple or few branched, julaceous; in cross-section central strand present. **Leaves** appressed, ovate, obovate, ovate-oblong to -short lanceolate, ca. 1.2–2 mm long, concave, apex broadly acute, obtuse to rounded, base slightly decurrent; margins plane, occasionally reflexed below, entire to finely serrulate; costa usually strong, subpercurrent to short excurrent; apical cells often short, rhomboidal; median cells linear to rhomboidal, often vermicular, usually thick-walled; lower and basal cells enlarged, rectangular, thin-walled and lax; marginal cells usually differentiated as a border of narrow elongate cells. **Dioicous**. **Perichaetia** terminal. **Seta** to 30 mm long, usually slender. **Capsule** inclined to pendulous, urn pyriform-cylindrical, neck short. **Operculum** conic, blunt to apiculate. **Peristome** double, rarely reduced, exostome teeth joined at base; endostome basal membrane high, segments keeled and perforate, cilia appendiculate. **Spores** spherical, finely papillose.

DISCUSSION. The julaceous stems and branches and appressed leaves are diagnostic for the genus. *Anomobryopsis* exhibits similar gametophytic features to *Anomobryum* but differs by its reduced peristome; see comments under the former genus. Ochi (1980) placed *Anomobryum* as a subgenus in *Bryum*. The treatment by Ochi (1980) is adequate, but given that the Neotropics is one of the more diverse regions in the world for *Anomobryum*, a detailed revision would be most informative.

LITERATURE. Ochi, H. 1980 (see family ref.). - Shaw, J. & A. J. Fife. 1984. The evolutionary and taxonomic significance of peristome morphology in *Anomobryum* (Bryaceae, Musci). Journal of the Hattori Botanical Laboratory 57: 285–298.

Brachymenium (Fig. 97) - At least 22 species recorded for the Neotropics; a genus containing ca. 100 species distributed in the tropics and extending into subtemperate regions worldwide.

HABITAT. Epiphytic on trees and shrubs, also on logs, humus, soil, and rocks; mostly submontane to upper montane forests, extending to zacatonal, páramo, and puna, from sea level to more commonly 1000–4000 (–4800) m.

DESCRIPTION. **Plants** medium sized to large, forming dense tufts, dark green, often lustrous. **Stems** erect, simple to few branched, radiculose, occasionally tomentose; in cross-section central strand present. **Leaves** equally distant or crowded distally, crispate to ± flexuose and erect to erect-spreading when dry, erect-spreading to spreading when wet, lanceolate, oblong-lanceolate, obovate-oblong, apex short to long acuminate, base slightly decurrent or not; margins limbate, plane above, often reflexed to recurved in lower 1/2, entire to more commonly serrulate or serrate; costa usually strong, short to long excurrent, rarely subpercurrent, awn smooth or toothed; median cells mostly thin-walled, broadly hexagonal or short to long rhomboidal-hexagonal, rhomboidal toward margin and apex; lower and basal cells short rectangular; marginal border cells linear and thick-walled, 1–4 rows. **Propagula** often present, as axillary bulbous gemmae in some species. **Dioicous**. **Perichaetia** terminal, leaves often larger. **Seta** 10–40 mm long, erect to weakly flexuose, slender to stout. **Capsule** suberect to commonly erect, urn obloid-cylindrical, rarely subglobose, slightly asymmetric, neck usually distinct. **Operculum** short to long conic, rarely rostrate. **Peristome** double, exostome teeth joined at base, distally papillose (fragile), trabeculae well developed; endostome basal membrane low, segments rudimentary, narrowly perforate, cilia absent or reduced. **Spores** spherical, lightly papillose.

DISCUSSION. A number of the species are epiphytic and likely to be confused with *Acidodontium* (see comments under that genus).

Robinson (1967, see general ref.) recognized *Osculatia columbica* De Not. as a distinct genus based primarily on the unique peristome arrangement for the family; the exostome teeth and endostome segments are opposite, not alternate, to each other. Robinson included as synonyms *Brachymenium columbicum* (De Not.) Broth., *B. globosum* A. Jaeger, *B. grubbii* E. B. Bartram, and *Neobryum costatum* R. S. Williams. No corroboration or resolution was provided in the treatment by Ochi (1980) other than to recognize the taxon as a member of *Brachymenium*.

LITERATURE. Allen, B. 1998. Two new species of *Brachymenium* (Bryaceae) from Central America, with a key to the species of *Brachymenium* in Central America. Novon 8: 107–112 [key to 16 species]. - Ochi, H. 1980 (see family ref.).

Bryum (Fig. 97) - About 50 species are reported for the Neotropics in this, the largest genus of the family. It is estimated that *Bryum* comprises 445 species distributed worldwide.

HABITAT. Commonly on soil, humus and rocks, rarely epiphytic or on logs; mostly from open submontane to upper montane forests, páramo and puna, rare in the lowlands, from near sea level to more commonly 1000–4500 m.

DESCRIPTION. **Plants** small to large and robust, forming loose to dense tufts, pale to dark green, reddish-brown or -yellow to golden. **Stems** erect, few to several branched by innovations, radiculose, occasionally densely tomentose; in cross-section central strand present. **Leaves** distant to more commonly crowded, plane to contorted or crispate, erect-appressed to erect, often erect-spreading when wet, ovate, lanceolate, ovate- to oblong-lanceolate, or elliptical, 0.5–6.5 mm long, apex acute to acuminate, base occasionally decurrent; margins usually reflexed to recurved, less often plane, entire to more commonly serrulate or serrate at midleaf or above; costa subpercurrent to ± long excurrent; upper and median laminal cells rhomboidal-hexagonal or hexagonal; lower and basal cells short to long oblong or rectangular, thin to ± thick-walled, occasionally lax; marginal cells usually forming a distinct border of long linear cells. **Dioicous**, autoicous or synoicous. **Perigonia** usually bud-like. **Perichaetia** terminal, leaves differentiated or not. **Seta** 8–50 mm long. **Capsule** suberect to more commonly inclined or pendulous, urn short to long oblong or cylindrical-pyriform, 1–5 mm long; stomata at urn base, superficial; neck short or long; annulus compound, revoluble. **Operculum** convex-conic or conic-apiculate. **Peristome** double, exostome teeth joined at base, mostly papillose, distally smooth, trabeculate; endostome lightly papillose, basal membrane ± high, segments keeled and perforate, cilia appendiculate or nodose, occasionally rudimentary or absent. **Spores** spherical, smooth to papillose.

DISCUSSION. A highly variable genus, both gametophytically and sporophytically; plants are typically terrestrial, leaves variable, ovate, oblong, obovate to lanceolate, margins weakly to strongly bordered, laminal cells broad, hexagonal, very rarely oblong-linear, and with a peristome well developed. Admittedly one of the most difficult genera of mosses, a worldwide revision would likely result in only half of the number of species presently recognized.

LITERATURE. Mohamed, M. R. 1979. A taxonomic study of *Bryum billardieri* Schwaegr. and related species. Journal of Bryology 10: 401–465 [keys, illustrations]. – Ochi, H. 1980 (see family ref.).

Epipterygium (Fig. 97) - Three species in the Neotropics; 12 species, pantropical in distribution but extending into the north temperate region.

HABITAT. On moist or wet soil, often in shade on bank slopes; submontane to upper montane forests, 320–3660 m.

DESCRIPTION. **Plants** small to somewhat medium sized, rather delicate and lax, whitish- to reddish-pale green. **Stems** suberect to procumbent, sparingly radiculose; in cross-section outer 1–2 rows of cells somewhat small, slightly thick-walled, inner cells larger, thin-walled, central strand present. **Leaves** weakly to rather strongly complanate, lateral leaves elliptical to oblong-obovate, ca. 1.4–3.8 mm long, ca. 0.7 mm wide; dorsal leaves smaller in ca. 2 rows, apex apiculate; base short decurrent; margins plane, entire to weakly serrulate toward apex; costa 1/2–3/4 lamina length, strong; laminal cells thin-walled, median cells large, rhombic to rhomboidal; basal cells ± larger, lax; marginal cells long linear, forming a border. **Dioicous**. **Perichaetia** terminal. **Seta** 6–15 mm long, smooth. **Capsule** inclined, urn short cylindrical to cylindrical-pyriform, 1–1.5 mm long; exothecial cells collenchymatous; neck short; annulus compound, 2–3 rows. **Operculum** conic, ± apiculate. **Peristome** double, exostome teeth papillose on outer surface, trabeculate and bordered; endostome basal membrane high, segments keeled and perforate, cilia 1–3, nodose. **Spores** lightly papillose.

DISCUSSION. The genus is readily recognized by the differentiated larger lateral and smaller dorsal leaves.

LITERATURE. Shaw, J. 1984. Quantitative taxonomic study of morphology in *Epipterygium*. The Bryologist 87: 132–142 [keys, illustrations].

Leptobryum (Fig. 98) - Three species in the Neotropics, *L. pyriforme* (Hedw.) Wilson is the most common species encountered; the remaining two species, previously recognized as *Wollnya* — *L. stellatum* (Herzog) Broth. and *L. wilsonii* (Mitt.) Broth. — are distributed from Ecuador to Bolivia; a small genus of some eight species distributed in temperate regions.

HABITAT. On moist or wet soil or over rock; mostly open montane to páramo or puna, 1300–4100 m.

DESCRIPTION. **Plants** rather small and slender, forming loose to dense tufts, pale green to yellowish-green. **Stems** erect and simple, to ca. 2 cm tall, radiculose at base; in cross-section outer 1–2 rows of cells small, thick-walled, inner cells large, thin-walled, central strand present. **Leaves** either distally larger and crowded, small and distant below, erect-spreading to spreading, ± flexuose, long subulate from a short ovate-oblong base, 1.3–3 mm long, 0.15 mm wide at base; or leaves uniform, not crowded, erect when dry, erect-spreading when wet, short ovate-lanceolate, to ca. 0.5 mm long, margins entire, occasionally dentate along distal margin; costa strong or weak, short excurrent to subpercurrent, upper cells linear to linear-rectangular or oblong-rectangular; lower and basal cells larger, long rectangular, or little differentiated. **Synoicous**. **Seta** to 20 mm or more long, slender and wiry, smooth. **Capsule** inclined to pendulous or erect, urn pyriform, 0.7–0.8 mm long, shiny smooth or somewhat irregularly furrowed when deoperculate, neck elongate (nearly equal to urn length); exothecial cells rectangular to subquadrate, ± thin-walled, stomata rather numerous at juncture of urn and neck, superficial; annulus revoluble, in 2 rows of elongate large cells. **Operculum** conic-mammillate, ca. 0.2 mm long. **Peristome** double, exostome teeth pale yellow, densely papillose and trabeculate; endostome white, basal membrane high, segments slightly shorter than exostome, finely papillose, keeled and perforate, cilia 3, appendiculate. **Spores** spherical, smooth to lightly papillose.

DISCUSSION. The genus is characterized by the flexuose long-subulate leaves from an oblong-ovate base or erect short ovate-lanceolate leaves, the conspicuously elongate and slender seta, shiny, erect to pendulous, pyriform, small mouthed capsules, and well developed double peristome.

Mielichhoferia (Fig. 98) - About 5–7 species in the Neotropics; a mostly temperate genus with far fewer than the 90 species presently recognized.

HABITAT On soil in exposed sites; open montane to zacatonal, páramo, and puna, 2200–4570 m.

Plants small, forming short tufts. **Stems** erect, to 5 mm tall, few branched, radiculose below. **Leaves** imbricate, erect to ± appressed, ovate-short lanceolate, to 0.8 mm long, apex acute; margins plane or slightly reflexed below, weakly serrulate near apex; costa ± strong, subpercurrent to percurrent; median cells narrowly long hexagonal to fusiform-hexagonal, smooth, thin-walled; lower and basal cells oblong-short rectangular, lax; marginal cells linear. **Dioicous**. **Perichaetia** appearing lateral by innovation. **Seta** to 10 mm long, smooth, usually flexuose. **Capsule** erect to suberect, urn pyriform, to 2 mm long (including neck), neck distinct, equal to or shorter than urn; annulus revoluble, in 3–4 rows. **Operculum** apiculate or conic-convex. **Peristome** single or double, exostome teeth 16, usually 8-paired, hyaline or yellowish at base, papillose; endostome lacking or rudimentary. **Spores** spherical, papillose.

DISCUSSION. The genus is gametophytically similar to *Schizymenium*; however, the peristome has a well developed exostome, with the teeth often paired, and endostome lacking or rudimentary. The earlier concept of *Mielichhoferia* is restricted to accommodate species previously placed in *Haplodontium*, with the majority of *Mielichhoferia* are now placed in *Schizymenium*. The taxonomy of *Mielichhoferia sensu lato* is currently under investigation by Jon Shaw. See comments under *Schizymenium*.

LITERATURE. Shaw, J. 1985. Nomenclatural changes in the Bryaceae, subfamily Mielichhoferioideae. The Bryologist 88: 28–30. - Shaw, J. & H. Crum. 1982. Comments on the Mielichhoferioideae of Central America, with the description of a new species of *Synthetodontium*. Contributions from the University of Michigan Herbarium 15: 209–217.

Orthodontium (Fig. 98) - Four species in the Neotropics, *O. pellucens* (Hook.) Bruch, Schimp. & W. Gümbel is most common; a small genus of some 14 species rather widely distributed in both tropic and temperate regions.

HABITAT. Epiphytic or on logs and soil (sand and clay); lower to upper montane open or marginal forests and subpáramo, 900–3700 m.

DESCRIPTION. **Plants** rather small, to 1 cm tall, forming lax and soft tufts, shiny green or golden-yellow or -brown. **Stems** short, erect, rusty-red, radiculose, occasionally densely tomentose; in cross-section central strand absent or weak. **Leaves** mostly erect-spreading to spreading and flexuose, narrowly lanceolate to linear-lanceolate, 2–4 mm or more long, usually folded, apex broadly acute to narrowly acuminate, concave toward base; margins plane, entire or often sparsely serrate at apex; costa subpercurrent to short excurrent; upper and median cells linear-oblong, ± vermicular, rather thick-walled; basal cells oblong-rectangular, thin-walled and somewhat lax, usually rusty-red. **Autoicous**. **Perigonia** usually numerous, bud-like, short stalked. **Perichaetia** terminal, leaves little differentiated. **Seta** to ca. 12 mm long, erect or slightly flexuose. **Capsule** erect to slightly inclined, urn ovoid-cylindrical, 1–2 mm long, slightly constricted below mouth, neck short. **Operculum** long rostrate, oblique. **Peristome** double, rather reduced, exostome teeth smooth to faintly papillose; endostome basal membrane low to absent, segments somewhat to much longer than exostome teeth, narrow, perforate. **Spores** rather coarsely papillose.

DISCUSSION. The genus is recognized by the narrowly lanceolate or linear-lanceolate leaves, linear upper laminal cells, erect capsules, smooth to finely papillose exostome teeth, endostomial segments somewhat to distinctly longer than exostomal teeth, and the basal membrane low and indistinct or absent.

LITERATURE. Meijer, W. 1951. The genus *Orthodontium*. North-Holland Publishing Company, Amsterdam [keys, illustrations].

Plagiobryum (Fig. 99) - A single species, *P. zieri* (Hedw.) Lindb. is widespread but rare in the Northern Hemisphere, and in the Neotropics is only known from Guatemala; nine species, seven in the Northern and two in the Southern Hemisphere.

HABITAT. On soil-covered limestone rocks, in *Juniperus standleyi* forest, 3500m.

DESCRIPTION. **Plants** small, forming dense soft tufts or mats, red- or silver-tinged. **Stems** erect, several branched by innovations, branches julaceous. **Leaves** imbricate, erect, lanceolate to oblong- or ovate-lanceolate, innovation leaves ovate, to 2 mm long; margins plane or slightly reflexed, entire to weakly toothed distally; costa subpercurrent to short excurrent, somewhat flexuose; laminal cells thin-walled, lax, upper and median cells rhomboidal-hexagonal; basal cells shorter; marginal cells oblong-linear. **Dioicous**. **Perichaetia** terminal. **Seta** rather short, 3–5 mm long, curved distally, smooth. **Capsule** horizontal to subpendulous, pyriform-curved, asymmetric, mouth oblique, narrowed, neck elongate, striate; stomata superficial; annulus revoluble. **Operculum** conic. **Peristome** double, exostome teeth rather short, exostome shorter than endostome, weakly papillose or cross-striate below, distally smooth; endostome adhering somewhat to exostome, basal membrane rather high, segments irregular, narrowly keeled, perforate above, cilia rudimentary. **Spores** rather large, ellipsoidal, forming tetrads until maturity, coarsely papillose.

DISCUSSION. Small plants whitish or silver colored, rather similar to *Bryum argentum* Hedw. In aspect; lax, rhomboidal-hexagonal upper laminal cells; distally curved, short seta; asymmetric curved-pyriform capsule with an obliquely oriented mouth; weakly ornamented short exostome teeth (less than 250 µm); and endostome length exceeding that of the exostome, are features that distinguishing this genus.

LITERATURE. Shaw, A. J. 1982. *Plagiobryum zieri* (Hedw.) Lindb. disjunct in Guatemala, with phytogeographic notes. The Bryologist 85: 243–250.

Pohlia (Fig. 99) - Presently 22 species recorded for the Neotropics, possibly 10–15 are valid; a genus with 127 species widely distributed. In the tropics *Pohlia* is mostly confined to mountainous regions.

HABITAT. On soil and rocks; mostly in open moist montane to páramo or puna, (300–)1500–4570 m.

DESCRIPTION. **Plants** small to somewhat medium-sized, mostly forming loose tufts, dull green. **Stems** erect, few branched by innovations; in cross-section central strand present. **Leaves** usually crowded distally, erect to ± erect-appressed when dry, erect-spreading when wet, lanceolate, occasionally ovate- to oblong-lanceolate, 0.6–2.5 mm long, acute to short acuminate; margins plane to reflexed below or to near apex, entire to more commonly serrulate or serrate at apex, elimbate; costa subpercurrent; upper and median cells oblong-hexagonal or -linear to rhomboidal; lower and basal cells ± larger. **Gemmae** present or not, in leaf axils, elongate to subglobose with several distal peg-like short appendages. **Dioicous**, autoicous, or paroicous. **Perigonia** bulbiform. **Perichaetia** terminal, leaves often differentiated, larger and elongate. **Seta** 15–35 mm long, smooth. **Capsule** inclined, urn oblong to short or long cylindrical-pyriform, 2–6.5 mm long, narrowed at mouth or not; exothecial cells elongate-rectangular or isodiametric; stomata at base of neck, superficial or slightly immersed; annulus compound, revoluble. **Operculum** conic to conic-apiculate. **Peristome** double, exostome papillose distally or throughout, trabeculate; endostome usually lightly papillose, basal membrane usually high, segments keeled and narrowly perforate, cilia rudimentary or absent to elongate and nodose. **Spores** spherical, lightly papillose.

DISCUSSION. The genus is characterized by the elimbate margins, usually serrate apex, percurrent or subpercurrent costa, elongate and narrow median and upper cells, and a well developed double peristome. The generic concept adopted here includes *Mniobryum* and *Webera*. The neotropical species are in need of revision.

LITERATURE. Shaw, J. 1982a. *Pohlia* Hedw. (Musci) in North and Central America and the West Indies. Contributions from the University of Michigan Herbarium 15: 219–295. - Shaw, J. 1982b. Character analysis, phylogeny, and classification of the moss genus *Pohlia*. Canadian Journal of Botany 62: 219–229.

Pseudopohlia (Fig. 99) - A single species in the Neotropics, with *P. didymodontia* (Mitt.) A. L. Andrews known from Mexico and Guatemala; a small, little known genus of two species, with the remaining species known from Africa, China, and the Philippines.

HABITAT. On soil bank; associated vegetation unknown, at elevations of 1500 m or more.

DESCRIPTION. **Plants** medium sized, forming loose tufts, dull green. **Stems** erect, to 12 mm high, simple or few branched, radiculose at base; in cross-section central strand well developed. **Leaves** crowded, imbricate, lanceolate, to 1.5 mm long, apex acute to short acuminate; margins plane, serrate distally; costa rather strong below, ending several cells below apex; upper and median cells linear; basal cells quadrate to short rectangular; marginal cells similar, not forming a border. **Gemmae** in distal leaf axils, 2-several per axil, obloid with several projecting concolorous leaf primordia at apex. **Dioicous**. **Perichaetia** terminal or appearing below on innovation terminal branches; leaves linear-lanceolate, recurved. **Seta** elongate, slender. **Capsule** erect to subinclined, urn cylindrical; neck short; stomata at urn base, superficial. **Operculum** low convex. **Peristome** double, exostome teeth united in pairs to ca. 1/2 length, papillose, inner surface papillose below, distally papillose or striate; endostome basal membrane low, segments irregular, perforate, not keeled, cilia usually 2, broad. **Calyptra** not observed. **Spores** coarsely papillose.

DISCUSSION. Closely related to and likely to be confused with *Pohlia*, particularly the neotropical species that exhibit gemmae; however, in *Pohlia* the gemmae are either linear-vermicular or the projecting primordia are green. The rather short, blunt peristome teeth that are united to ca. 1/2 their length are diagnostic. The preceding treatment adapted from Shaw (1994).

LITERATURE. Shaw, J. 1994 (see Sharp, A. J. et al. in general ref.).

Rhodobryum (Fig. 100) - Ten species in the Neotropics; a genus containing 34 species widely distributed in cool temperate regions, in the tropics largely confined to the highlands.

HABITAT. On soil or humus; mostly submontane to montane forests, occasionally extending along gallery forests in páramo and puna; (200)900–4000 m.

DESCRIPTION. **Plants** large to more often robust, to 6 cm tall, forming loose to dense tufts, dark green to reddish-brown. **Stems** erect, often connected by underground stolons, few to several branched by innovations, radiculose, often densely tomentose. **Leaves** distally or interruptedly in crowded rosettes, or ± equally spaced, mostly erect to erect-spreading and ± crispate when dry, erect-spreading to wide-spreading when wet, oblong-obovate to oblong, mostly 7–12 mm long, to 5 mm wide, apex obtuse-acute and often apiculate, rarely acuminate, base usually short decurrent; margins

distally plane, reflexed or recurved below, occasionally undulate, limbate, serrate, often sharply so, or serrulate; costa strong below and usually weak distally, short excurrent, in cross-section stereids usually poorly developed; upper and median cells rhomboidal to hexagonal, thin- to ± thick-walled, often weakly to strongly porose; basal cells long-rectangular; marginal border cells linear to linear-rhomboidal, 2–6 rows, ± thick-walled. **Dioicous**. **Perichaetia** lateral. **Seta** 1–2, elongate, 2–8 cm long, rather stout. **Capsule** horizontal to pendulous, urn long cylindrical or cylindrical-pyriform, curved, 4–6 mm long, neck short. **Operculum** conic-apiculate. **Peristome** double, exostome teeth lightly papillose, trabeculate; endostome basal membrane low to high, segments perforate and keeled, cilia well developed, appendiculate. **Spores** lightly papillose.

DISCUSSION. The genus is recognized by the large stature of the plants. Leaves are often 7-10 mm long or more, and usually with weakly to strongly bordered margins. Ochi (1981), among other authors, treats *Rhodobryum* as a subgenus of *Bryum*.

LITERATURE. Ochi, H. 1981. A revision of the neotropical Bryoideae, Musci (Second Part). Journal of the Faculty of Education Tottori University Natural Science 30: 21–55.

Schizymenium (Fig. 100) - About 30–40 species in the Neotropics; estimated to contain about 50 species. The genus is widely distributed, reaching its greatest diversity in the Andes.

HABITAT. On soil and soil-covered rocks; mid to high open montane to zacatonal, páramo, and puna, 2200–5100 m.

DESCRIPTION. **Plants** commonly small to occasionally medium sized, forming dense soft tufts, commonly glossy to dull light green. **Stems** erect, several to many branched by innovations; in cross-section central strand present. **Leaves** erect to erect-spreading, crowded, oblong-lanceolate to lanceolate, 0.7–1.5 mm long, apex acute to acuminate; margins plane, serrulate to serrate distally; costa mostly subpercurrent, rarely excurrent; upper and median cells linear-fusiform or -rhomboidal, mostly thin-walled; basal cells rectangular. **Paroicous**, less often synoicous or dioicous. **Perichaetia** terminal on stems, but appearing lateral by innovations ("pseudolateral"), leaves often smaller than stem leaves. **Seta** 4–22 mm long, rather short to elongate, often flexuose, smooth. **Capsule** erect to more commonly inclined to subpendent, urn pyriform or cylindrical-pyriform, 1.5–4 mm long, symmetric or asymmetric and curved, neck short to long (to as long as urn); annulus usually well developed. **Operculum** conic, conic-apiculate. **Peristome** single with endostome basal membrane short to high with segments smooth or papillose, cilia absent or reduced, or peristome rarely double, exostome teeth often reduced, smooth or papillose, with an endostome well developed. **Spores** spherical, lightly to densely papillose.

DISCUSSION. Features characterizing the genus include the light green, soft tufted plants with lanceolate to oblong-lanceolate elimbate leaves with mostly subpercurrent costa, plane margins and linear-fusiform upper laminal cells, lateral-appearing perichaetia and a single peristome represented by an endostome, or double peristome with exostome reduced and endostome well developed. Species of *Schizymenium* were previously placed in *Mielichhoferia*. Much of the distinction between species is based on peristomial features. There is no profit presently in collecting sterile collections, a situation that will persist until a revision is completed.

LITERATURE. Shaw, J. 1985. Nomenclatural changes in the Bryaceae, subfamily Mielichhoferioideae. The Bryologist 88: 28–30. - Shaw, J. & H. Crum. 1982. Comments on the Mielichhoferioideae of Central America, with the description of a new species of *Synthetodontium*. Contributions from the University of Michigan Herbarium 15: 209–217.

Synthetodontium (Fig. 100) - A neotropical genus of two species, *Synthetodontium costaricense* A. J. Shaw & H. A. Crum known from Costa Rica, and *S. pringlei* Cardot from Mexico.

HABITAT. On soil; (open?) montane forests, 3080 m.

DESCRIPTION. **Plants** small, forming soft tufts, pale green. **Stems** to 9 mm high, primarily subjulaceous, with subfloral innovations. **Leaves** (subfloral) crowded, appressed, ovate to oblong-ovate, 0.5–1.2 mm long, concave, apex broadly acute to obtuse, abruptly apiculate; margins plane, entire, elimbate; costa subpercurrent to percurrent; laminal cells laxly long-rhomboidal. **Dioicous**. **Perichaetia** appearing lateral by more distal stem innovations. **Seta** to 12 mm long, slender, flexuose. **Capsule** erect to suberect, urn pyriform, to 3.1 mm long, symmetric; neck elongate, 1/3 or more the length of the urn; stomata superficial, numerous. **Operculum** low conic-apiculate. **Peristome** double, inserted below mouth, exostome teeth finely cross-striate below to finely papillose, smooth above; endostome basal membrane ca. 1/3 the exostome length, segments shorter, adhering to exostome, or partially separated. **Spores** smooth to finely papillose.

DISCUSSION. Gametophytic features of *Synthetodontium* are similar to *Schizymenium*. The distinguishing feature of *Synthetodontium* is the short endostome segments fused to the exostome teeth.

LITERATURE. Shaw, J. 1994 (see Sharp, A. J. et al. in general ref.). – Shaw, J. & H. Crum. 1982 (see ref. under *Schizymenium*).

BRYOXIPHIACEAE

A monotypic family, placed in its own order, the Bryoxiphiales.

Bryoxiphium (Fig. 101) - Two species in the Neotropics, *B. mexicanum* Besch. endemic to central Mexico (1000–4100 m), and *B. norvegicum* (Brid.) Mitt. known from the Dominican Republic (2150–2500 m); a genus of 2–3 species distributed in the temperate regions of the Northern Hemisphere, widespread, but locally infrequent.

HABITAT. On vertical cliffs, often in moist, shaded sites; montane to zacatonal, at elevations from 1000–4100 m.

DESCRIPTION. **Plants** medium sized to somewhat large, forming loose tufts, glossy light green to golden-brown. **Stems** often perpendicular to substrate, stiffly erect to subpendent, 3–5 cm long, simple or few branched. **Leaves** gradually and progressively larger and longer distally, ca. 2–3 mm long, strongly 2-ranked (distichous), crowded, oblong-lanceolate, strongly conduplicate-keeled, apex of lower leaves bluntly rounded, distally apiculate; margins plane, entire; costa single, subpercurrent to percurrent; lamina unistratose; laminal cells smooth, firm-walled, upper cells linear; median cells oblong or rhomboidal to subquadrate; basal cells oblong-short rectangular to subquadrate; marginal cells elongate and forming a border toward the base, or similar to median laminal cells. **Dioicous**. **Perichaetia** terminal; leaves larger, to 10 mm long or longer, costa long excurrent. **Seta** short, erect or slightly curved, smooth. **Capsule** immersed, urn subglobose. **Operculum** short rostrate, somewhat oblique, remaining attached to columella for short period. **Peristome** absent. **Calyptra** cucullate, smooth and naked. **Spores** spherical.

DISCUSSION. *Bryoxiphium* is characterized by the growth habit, with stems perpendicular or subpendent from a vertical or inclined substrate, leaves 2-ranked and strongly keeled, and perichaetial leaves distinctly elongate with the costa long excurrent. Distal portion of stems with leaves exhibiting lamellae of several rows of cells on the back of the costa near the leaf tips. *Bryoxiphium mexicanum* differs from *B. norvegicum* by its larger size and laminal cells that are little differentiated at the margin; *B. norvegicum* exhibits a rather distinct border, particularly toward the base. The former taxon is recognized as a variety of the latter by some authors.

LITERATURE. Löve, A. & D. Löve. 1953. Studies in *Bryoxiphium*. The Bryologist 52: 73–94, 183–203.

CALYMPERACEAE

Plants very small to large, forming tufts or cushions, pale to dark green, glossy or dull. **Stems** mostly erect, simple to few branched; in cross-section central strand absent. **Leaves** often crispate, usually sheathing at base, base often expanded, ovate to oblong, limb distally lingulate or narrowly lanceolate, apex acute to acuminate; margins entire or more commonly serrate or ciliate (esp. on shoulders), teeth single, double or more; costae single, mostly percurrent; distal laminal cells smooth to more often papillose, uniform and ± thick-walled; basal cells strongly differentiated, region adjacent to costa of enlarged, clear cells (cancellinae), outer cells beyond the cancellinae often with a differentiated intramarginal band of linear cells (teniolae) usually separated by isodiametric cells or margins bordered by linear cells. **Gemmae** often present on the upper lamina or highly modified apices (often narrowed and club-shaped). **Dioicous**, rarely autoicous. **Perichaetia** terminal. **Seta** short to elongate, smooth. **Capsule** immersed to exserted, erect, urn cylindrical. **Operculum** rostrate. **Peristome** absent or present and single, teeth 16, papillose. **Calyptra** cucullate and deciduous, or campanulate and persistent (clasping at base) with few to several longitudinal slits. **Spores** spherical, smooth to finely papillose or granulate.

DISCUSSION. The Calymperaceae contain three genera and 150 species and varieties according to Reese (1993), with a pantropical distribution; in the Neotropics two genera and 46 species. Characteristics of the family (Reese, 1993) include the combination of the following features: stem central strand absent, basal cancellinae (enlarged, hyaline, prose cells), often thickened and toothed leaf margins, reduced or absent peristome, and uniseriate gemmae on leaves (on leaf tips or along costa). Ellis (1985) presented a broader concept of the family that included several additional genera (including *Octoblepharum* and *Leucophanes*) but which is not adopted here. The inclusion of *Leucophanes* in the Calymperaceae was based primarily on peristome features (cf. Ellis, 1985). It has been placed in its own family by some authors and as treated here (cf. Salazar Allen, 1993a, b; see

references under *Leucophanes*). The family is placed in the order Pottiales. The following keys are adopted from Reese (1993) for the Calymperaceae.

Study guide. Leaves provide all that is necessary for the identification of genera and species; however, care must be given to plants bearing normal stem leaves and gemmiferous leaves which can often be highly modified. Both should be examined. Attention must also be given to carefully removing leaves so that the basal portion is maintained intact (in some species the cancellinae are small and fragile and remain attached to the stem). A cross-section is often useful to observe ornamentation of laminal cells and costal cells. The cross-section should be made near or just above midleaf, or if the leaf is differentiated between sheathing base and limb, then midway on limb.

LITERATURE. Ellis, L. T. (1985). A taxonomic revision of *Exodictyon* Card. (Musci: Calymperaceae). Lindbergia 11: 9–37. - Reese, W. D. 1983. American *Calymperes* and *Syrrhopodon*: Identification key and summary of recent nomenclatural changes. The Bryologist 86: 23–30. - Reese, W. D. 1993. Calymperaceae. Flora Neotropica Monograph 58: 1–102 [keys, illustrations, maps]. Reese, W. D. 1997. Asexual reproduction in Calymperaceae (Musci), with special reference to functional morphology. Journal of the Hattori Botanical Laboratory 82: 227–244.

1. Sporophytes present 2
1. Sporophytes lacking 3
2. Calyptra clasping seta below capsule, persistent; peristome lacking ..... **Calymperes**
2. Calyptra cucullate, deciduous; peristome present or lacking ..... **Syrrhopodon**
3. Lamina above shoulders tristratose, upper and lower layers composed of leucocysts, mid layer of green cells (chlorocysts) ..... **Leucophanes** (see Leucophanaceae)
3. Lamina above shoulders unistratose, cells ± uniform 4
4. Margins of upper lamina with border of elongate hyaline cells (border sometimes incomplete to nearly lacking) ..... **Syrrhopodon**
4. Margins of upper lamina lacking border of elongate hyaline marginal cells, variously bordered otherwise or undifferentiated 5
5. Teniolae present (at least in some leaves) ..... **Calymperes**
5. Teniolae lacking 6
6. Margins of upper lamina not differentiated, unistratose; Amazonas ..... **Calymperes**
6. Margins of upper lamina clearly differentiated, bistratose or thicker; variously distributed 7
7. Upper lamina long and narrowly linear, its cells mostly transversely elongate; costa in section with 2 or more rows of guide cells ..... **Calymperes**
7. Upper lamina variously lanceolate to ovate or broadly linear, its cells mostly isodiametric to vertically elongate; costa in section mostly with a single row of guide cells 8
8. Lower laminal golden-brown to reddish; cancellinae mostly fragile and eroded ... **Syrrhopodon**
8. Lower lamina hyaline, mostly not colored as above (but sometimes yellowish in *S. incompletus*); cancellinae intact and persistent (sometimes eroded in *Syrrhopodon*) 9
9. Margins of upper lamina coarsely serrate-toothed in rows, teeth forming 3 or more irregular wings from shoulder to apex; cells of cancellinae with faint transverse bands ..... **Syrrhopodon**
9. Margins of upper lamina entire or bearing at most 2 rows of teeth; cells of cancellinae lacking bands 10
10. Margins of lower lamina bearing stout, sharp, spreading to recurved spinose teeth; rhizoids dark-red ..... **Syrrhopodon**
10. Margins of lower lamina entire to serrate or dentate, but lacking spinose-recurved teeth; rhizoids brown to reddish 11
11. Margins of lower lamina clearly bordered by several to many rows of elongate thick-walled cells ..... **Calymperes**
11. Margins of lower lamina lacking well-defined border of elongate, thick-walled cells 12
12. Cells of upper lamina papillose on back; margins of upper lamina entire or finely serrate above ..... **Calymperes**
12. Cells of upper lamina smooth to slightly bulging on back; margins of upper lamina doubly-toothed above ..... **Syrrhopodon**

Calymperes (Fig. 102) - Sixteen species and varieties are present in the Neotropics; about 50 species distributed throughout the tropics.

HABITAT. Epiphytic, occasionally on logs and rocks, rarely on soil; confined to wet or semi-dry lowland forests, from sea level to about 1000 m, rarely above that elevation.

DESCRIPTION. **Plants** medium sized to rather large, forming loose to dense tufts or occasionally solitary, glossy to dull green. **Stems** erect, mostly simple, occasionally branched. **Leaves** often crispate, contorted or coiled when dry, base differentiated or not from limb, obovate to oblong at base, sheathing, distal limb lanceolate to linear, or ligulate to lingulate, 2–14(–25) mm long, apex mostly

acute; margins along shoulder crenulate or serrulate, limb margin often thickened (multistratose), entire or serrate, occasionally coarsely toothed, teeth in 1 row; costa strong, subpercurrent, in cross-section guide cells in 1–2 or more rows; distal laminal cells isodiametric, irregularly quadrate-rounded to transversely elongate, upper and lower surface often differently ornamented, smooth, papillose or mammillose, cancellinae large, adjoining region with cells similar to those of distal lamina, distal cancellinae truncate, acute or rounded, with or without an intramarginal band of hyaline, linear cells (teniolae). **Gemmiferous leaves** often strongly differentiated. **Seta** 3–10 mm long, erect. **Capsule** exserted, erect, urn cylindrical, 1.5–3 mm long. **Peristome** absent. **Calyptra** persistent and enveloping capsule, campanulate, plicate, usually twisted at base, at maturity persisting with longitudinal slits. **Spores** smooth to more commonly finely papillose.

DISCUSSION. The features distinguishing the genus include the presence of teniolae (not in all species), absence of a peristome, and a persistent and enveloping calyptra. The genus is likely paraphyletic.

Calymperes is one of some 12 taxa that have been discovered in Dominican amber with an estimated age of 25-45 million years (Frahm & Reese, 1998; see also cited ref.); widespread and familiar species include: *Adelothecium bogotense*, *Calymperes palisotii*, *Octoblepharum* cf. *pulvinatum*, *Syrrhopodon africanus* subsp. *graminicola*, and *S. incompletus* var. *incompletus*.

LITERATURE. Frahm, J.-P. & W. D. Reese. 1998. *Calymperes palisotii* (Musci; Calymperaceae) found in Dominican amber. The Bryologist 101: 131-132. - Reese, W. D. 1961. The genus *Calymperes* in the Americas. The Bryologist 64: 89–140 [keys, illustrations]. - Reese, W. D. 1987. *Calymperes* (Musci: Calymperaceae): World ranges, implications for patterns of historical dispersion and speciation, and comments on phylogeny. Brittonia 39: 225–237.

Syrrhopodon (= *Calymperopsis*) (Fig. 103) - In the Neotropics 31 species and several varieties; a pantropical genus containing some 90 taxa.

HABITAT. Mostly epiphytic, on tree bases, trunks, and branches, lianas, also on logs and rocks, occasionally on soil or epiphyllous; common in wet and semi-dry lowland forest, decreasing in diversity to upper montane forests, at elevations from sea level to 3000 m.

DESCRIPTION. **Plants** small to large, occasionally rather robust, forming tufts, rarely solitary, dull to glossy, pale to dark green, black or reddish. **Stems** mostly erect, simple to few or several branched. **Leaves** crispate, flexuose, helically coiled or unaltered when dry, mostly sheathing from an oblong, obovate base, rarely narrower than limb, limb short to long lingulate, lanceolate or linear, 1–10(–20) mm long, apex often blunt, acuminate or acute to rounded; margins of sheathing base serrulate, serrate, ciliate, spinose or entire, limb entire to serrate, teeth in 1–2 or more rows; costa strong, in cross-section guide cells in 1 row; border of linear, generally hyaline, cells present (limbate) or absent (elimbate), in cross-section lamina unistratose or multistratose near margin, distal laminal cells mostly isodiametric, quadrate-rounded, rarely elongate, thick-walled, smooth to more often papillose (uni- to pluripapillose) or papillose-mammillose on both or one surface; cancellinae persistent or fragile and eroded, large and extending to shoulder, or reduced and inconspicuous. **Gemmiferous leaves** usually little differentiated, upper leaf tips bearing gemmae. **Seta** 0.7–20 mm long, erect. **Capsule** immersed to exserted, erect, urn cylindrical, rarely urceolate, 1–2.5 mm long. **Operculum** rostrate. **Peristome** single, papillose, often reduced or absent. **Calyptra** cucullate, rarely mitrate-campanulate, deciduous. **Spores** papillose to granulate, rarely smooth.

DISCUSSION. The genus is characterized by the emergent to exserted capsule, presence of a peristome in some of the species, and a deciduous, cucullate, rarely campanulate, calyptra. Gametophytic features are variable, but teniolae are never present, and at least half of the species exhibit a hyaline border.

LITERATURE. Orbán, S. & W. D. Reese. 1990. *Syrrhopodon prolifer* (Musci: Calymperaceae): A world view. The Bryologist 93: 438–444 [keys, illustrations]. - Reese, W. D. 1977. The genus *Syrrhopodon* in the Americas I. The elimbate species. The Bryologist 80: 1–31 [keys, illustrations]. - Reese, W. D. 1978. The genus *Syrrhopodon* in the Americas II. The limbate species. The Bryologist 81: 189–225 [keys, illustrations]. - Reese, W. D. 1987. World ranges, implications for patterns of historical dispersal and speciation, and comments on phylogeny of *Syrrhopodon* (Calymperaceae). Memoirs of the New York Botanical Garden 45: 426–445. - Reese, W. D. 1999. *Syrrhopodon* subgenus *Pseudocalymperes* in the Neotropics. The Bryologist 102: 76–79. - Reese, W. D. & S. P. Churchill. 1998. *Syrrhopodon perangustifolius* (Musci, Calymperaceae) *comb. et stat. nov.*, and new to the flora of Colombia. The Bryologist 101: 153–155.

CATAGONIACEAE

A monotypic family placed in the Leucodontales.

Catagonium (Fig. 103) - Two species in the Neotropics, *C. brevicaudatum* Müll. Hal. recorded from Mexico to Costa Rica, tropical Andes, southeastern Brazil, and *C. emarginatum* Lin from Bolivia and southeastern Brazil. A genus of four species with a circum-Antarctic distribution, extending into the mountainous tropics.

HABITAT. Epiphytic on shrubs and small trees, over humus or leaf-litter covered soil banks or over rock; mostly from upper montane forests to páramo, 2600–4700 m.

DESCRIPTION. **Plants** small to somewhat medium sized, forming loose to dense soft mats, occasionally pendent, yellowish-green to golden. **Primary stems** short, creeping, secondary stems spreading or pendent, 3–12 cm long, irregularly branched. **Leaves** complanate, appearing 2-ranked, ovate-oblong, conduplicate or deeply concave, 1.2–2 mm long, apex obtuse-rounded and short piliferous to mucronate or emarginate, tips often reflexed, base slightly auriculate; margins plane, entire; costae variable, absent or short, either forked or rarely single; median cells linear-vermicular, rather thick-walled, smooth; alar region undifferentiated. **Dioicous**. **Perichaetia** lateral. **Seta** elongate, to 9.5 mm long, smooth. **Capsule** erect to inclined, urn oblong-cylindrical, 1.6–1.7 mm long, ± asymmetric. **Operculum** short-rostrate. **Peristome** double, exostome teeth 16, cross-striate below, papillose distally; endostome lightly papillose, basal membrane high, segments 16, keeled and perforate, cilia 1–3. **Calyptra** cucullate, smooth and naked. **Spores** spherical, finely papillose.

DISCUSSION. *Catagonium* is characterized by the soft glossy mats, leaves strongly complanate, 2-ranked and oblong-ovate with short piliferous to mucronate or emarginate apices, subauriculate leaf bases and short, mostly forked or occasionally single costae. Sporophytes are extremely rare. Given the rather fragile nature of the stems and leaves, reproduction is likely asexual via propagula. The two neotropical species can be differentiated by the following: *C. brevicaudatum* — leaf apices piliferous-recurved, and *C. emarginatum* — leaf apices mucronate or emarginate.

LITERATURE. Buck, W. R & R. R. Ireland. 1985. A reclassification of the Plagiotheciaceae. Nova Hedwigia 41: 89–125. - Lin, S.-H. 1984. A taxonomic revision of Phyllogoniaceae (Bryopsida). Part II. Journal of the Taiwan Museum 37(2): 1–54 [keys, illustrations, maps].

CRYPHAEACEAE

Plants medium sized, forming loose to dense tufts or pendulous strands. **Primary stems** mostly short, creeping, leaves scale-like, often eroded and absent; radiculose. **Secondary stems** stiffly erect to loosely pendent, irregularly to regularly pinnately branched. **Leaves** appressed to imbricate when dry, erect to erect-spreading when wet, ovate, ovate- to narrowly-lanceolate, apex acute to acuminate; margins reflexed to recurved, entire to distally serrulate or serrate; costa single, strong, 1/2 to fully excurrent; apical cells oval to oblong, median cells oval to oblong or rhomboidal, smooth to slightly bulging unipapillose, thick-walled; alar region differentiated, cells numerous, quadrate to short rectangular and oblate. **Gemmae** absent. **Autoicous**. **Perichaetia** lateral, leaves differentiated, usually conspicuously longer than stem leaves, sheathing capsules, oblong to obovate and awned. **Seta** very short, erect, smooth. **Capsule** immersed, erect, ovoid-cylindrical to broadly ovoid or subglobose, symmetric to asymmetric. **Operculum** conic-mammillate or -rostrate. **Peristome** double or single, exostome teeth 16, papillose, rarely smooth below or throughout; endostome absent or present, basal membrane low, segments 16, narrow, keeled and lightly papillose, cilia absent or reduced. **Calyptra** cucullate or conic-mitrate, smooth or roughened. **Spores** unicellular to multicellular, spherical to ovoid, papillose.

DISCUSSION. The Cryphaeaceae contain eight genera and about 80 species of mostly tropical to subtemperate regions; in the Neotropics five genera and 21 species. The family is placed in the Leucodontales. Members of the family are commonly epiphytic in montane forests, with the exception of *Dendrocryphaea* which is restricted to rocks in páramo streams. Distinguishing features include the rather stiffly erect or loose pendent, irregularly branched secondary stems, thick-walled, oval to oblong laminal cells, well differentiated alar cells, and immersed capsules on terminal branches or appearing sessile along lateral stems.

LITERATURE. Manuel, M. G. 1981. Studies in Cryphaeaceae V. A revision of the family in Mexico, Central America and the Caribbean. Journal of the Hattori Botanical Laboratory 49: 115–140 [keys, illustrations, maps].

1. Leaf apices acute-rounded, margins entire, or finely crenulate by projecting papillae; capsules subglobose; plants aquatic, on rocks; Colombia ..... **Dendrocryphaea**
1. Leaf apices acute to more commonly short to long acuminate, margins entire or dentate to sharply serrate; capsules ovoid, ovoid-cylindrical to elliptical; plants epiphytic, rarely saxicolous and then in dry sites 2

2. Secondary stems pendent; leaves usually biplicate at base; peristome teeth smooth throughout **Dendropogonella**
2. Secondary stems erect; leaves mostly smooth, not plicate; peristome teeth papillose to smooth throughout or only at base 3
3. Sporophytes borne terminally on short branches and stems; stems erect or pendent; peristome single ..... **Schoenobryum**
3. Sporophytes borne laterally on short branches; stems erect; peristome double 4
4. Urn broadly ovoid to narrowly ellipsoid; exostome teeth papillose throughout; spores unicellular (not endosporic) ..... **Cryphaea**
4. Urn ellipsoid to broadly ellipsoid; exostome teeth smooth at base, papillose distally; spores multicellular (endosporic) .....**Sphaerotheciella**

Cryphaea (Fig. 103) - About 15 species in the Neotropics; a genus containing less than 50 species altogether, distributed in the tropical highlands and extending somewhat into temperate regions.

HABITAT. Epiphytic, on trunk or branches of trees and shrubs, rarely on rocks; montane forests, (100–)300–3900 m.

DESCRIPTION. **Plants** forming loose to dense tufts, mostly dark green, occasionally yellowish-green. **Secondary stems** stiff, ca. 3–6(–8) cm long, regularly to irregularly pinnately branched, branches often short, flagellate branches occasional; in cross-section outer 4–6 rows of cells small, thick-walled, inner cells larger, ± thin-walled, central strand absent; pseudoparaphyllia foliose. **Leaves** ovate to short oblong-lanceolate, 1–3.2 mm long, to 1.4 mm wide, apex acute to more often short or long acuminate, base usually slightly clasping stem; margins plane or strongly recurved, entire to serrulate or coarsely and irregularly serrate distally; costa extending just beyond midleaf to ending in acumen, or as a piliferous tip; upper marginal cells often longer; median cells oval to oblong-oval, smooth or slightly papillose by distal projecting angle, thick-walled; alar cells subquadrate, thick-walled. **Perigonia** lateral, bud-like. **Perichaetia** lateral and appearing sessile, often several in a row on one side of stem, leaves oblong, concave convolute, awn short to long piliferous. **Seta** very short, 0.2–0.25 mm long. **Capsule** with urn obloid-cylindrical to cylindrical or ellipsoid, 1.4–2 mm long. **Operculum** conic-short rostrate. **Peristome** double, exostome usually papillose throughout or smooth at base; endostome basal membrane low, segments finely to coarsely papillose, cilia absent. **Calyptra** cucullate, smooth or distally papillose-roughened. **Spores** unicellular, papillose.

DISCUSSION. The genus is characterized by the typically epiphytic, rarely saxicolous, erect habit, the several to somewhat numerous sporophytes borne laterally on very short branches, the broadly ovoid to narrowly ellipsoid capsule that appears sessile, papillose exostome teeth, rarely smooth at extreme base, and unicellular spores.

LITERATURE. León V., Y. & D. G. Horton. 1996. Las especies andinas de *Cryphaea*. Anales del Instituto de Biologia, Universidad Nacional Autónoma de México, Serie Botánica 67: 27–33.

Dendrocryphaea (Fig. 104) - A single species recorded for the Neotropics, *D. latifolia* D. G. Griffin, Gradst. & J. Aguirre, known only from two localities in Colombia; a genus containing six species, the remaining five confined to southern Argentina and Chile, and Tasmania.

HABITAT. On rocks in fast flowing shallow streams; subpáramo to páramo, at elevations from 3080–3400 m.

DESCRIPTION. **Plants** large to robust, forming loose to somewhat dense tufts, dark green to blackish-green. **Secondary stems** and branches erect, usually regularly pinnately branched; in cross-section outer 6–8 cell rows small and thick-walled, inner cells progressively larger and thin-walled, central strand absent. **Stem leaves** erect to erect-spreading, broadly ovate to obovate, to 2 mm long, to 1.2 mm wide, apex broadly acute to obtuse, base clasping stem; margins plane distally, slightly recurved at base, entire to crenulate distally by projecting papillae; costa strong, subpercurrent; cells thick-walled, median cells oval to short rectangular-rounded, smooth to papillose by projecting cell angles, distal and marginal cells smaller, rhombic-oval, appearing smooth, lower and basal cells oblong-linear, alar region differentiated, in 4–5 rows. **Branch leaves** smaller, oblong or ovate, to 1.2 mm long. **Perigonia** bud-like. **Perichaetia** lateral, leaves oblong-ovate, costa excurrent as a subula, equaling lamina length or shorter, to ca. 1.5 mm long. **Seta** short, to 0.5 mm long. **Capsules** several to rather numerous, urn subglobose, 1–1.5 mm long; exothecial cells short rectangular to subquadrate, collenchymatous, thick-walled. **Operculum** conic-mammillate. **Peristome** double, exostome teeth smooth below, distally light papillose; endostome basal membrane low, segments narrow, appearing smooth to densely papillose. **Calyptra** mitrate. **Spores** unicellular, spherical, finely papillose.

DISCUSSION. Distinguishing features of the genus include the blackish-green coloration of the gametophytes, broadly ovate to obovate leaves, and the subglobose capsules. The genus is the only

aquatic member of the family. The range includes a rather remarkable disjunction between Colombia and Tierra del Fuego.

LITERATURE. Griffin III, D., S. R. Gradstein & J. Aguirre C. 1982. Studies on Colombian cryptogams XVII. On a new antipodal element in the neotropical páramos - *Dendrocryphaea latifolia* sp. nov. (Musci). Acta Botanica Neerlandica 31: 175–184.

Dendropogonella (Fig. 104) - A neotropical monotypic genus, with *D. rufescens* (Schimp.) E. Britton known from Mexico, Central America, and possibly northern South America.

HABITAT. Epiphytic, on branches and trunks of trees; mostly montane forests, 200–3000 m.

DESCRIPTION. **Plants** long pendent, rather soft, reddish-brown. **Stems** slender, to 30 cm or more long, irregularly pinnately branched, branches short, to 3 cm long. **Leaves** loosely erect with tips reflexed or not when dry, spreading when wet, long lanceolate, to 1.6 mm long, apex long acuminate, biplicate at base, base decurrent; margins plane, recurved near base, entire or serrulate near apex; costa rather slender, extending to midleaf to mostly ending in acumen; laminal cells thick-walled and smooth, apical and median cells fusiform to rhomboidal; inner basal cells elongate, weakly porose or not; alar region differentiated, cells subquadrate. **Perichaetia** terminal on short branches, leaves differentiated, ovate to obovate piliferous. **Seta** very short, ca. 0.2 mm long. **Capsule** with urn ovoid, to 1.3 mm long; stomata apparently absent. **Peristome** double, exostome teeth smooth, endostome shorter than exostome, basal membrane absent, segments slender and smooth. **Calyptra** mitrate, smooth . **Spores** unicellular.

DISCUSSION. The slenderly long pendent stems and narrowly long lanceolate leaves that are biplicate at the base differentiates this genus from other members of the family which are typically stiff and suberect or perpendicular to the substrate.

LITERATURE. Manuel, M. G. 1973. Studies in Cryphaeaceae II. A review of the monotypic genus *Dendropogonella* Britt. The Bryologist 76: 521–527.

Schoenobryum (Fig. 104) - Probably only two species in the Neotropics, *S. concavifolia* (Griff.) Gangulee and *S. rubricaulis* (Taylor) Manuel; a genus of about 10 species with a pantropical distribution.

HABITAT. Epiphytic, on branches or trunks of trees; submontane to montane forests, 80–2770 m.

DESCRIPTION. **Plants** small to medium sized, forming short loose tufts, light green to yellowish-green or golden. **Secondary stems** erect, usually regularly pinnate branched, branches short, julaceous; in cross-section outer 2–3 rows of cells small, thick-walled, inner cells larger, firm-walled, central strand absent. **Leaves** closely appressed, broadly ovate to somewhat ovate-oblong, 1–1.5 mm long, apex usually abruptly short acuminate, base slightly decurrent and clasping at base; margins strongly recurved, entire or weakly dentate-serrulate at apex; costa strong, 1/2–2/3 lamina length; laminal cells thick-walled, apical marginal cells oblong elongate, median cells oval to oblong-oval; inner lower and basal cells elongate, oblong to linear, porose, golden-yellow; alar cells irregularly-subquadrate. **Perigonia** lateral, bud-like, leaves ovate to ovate-short lanceolate. **Perichaetia** terminal on branch or stem, leaves obovate-lanceolate, short to long piliferous. **Seta** very short. **Capsule** with urn subglobose-ovoid, 1.2–1.8 mm long, somewhat asymmetric at base; exothecial cells irregularly subquadrate to rectangular, thin-walled; stomata at urn-neck juncture, superficial; annulus revoluble. **Operculum** rostrate. **Peristome** single, exostome teeth narrowly lanceolate, papillose. **Calyptra** mitrate, scabrous, distal cell angles projecting. **Spores** unicellular, spherical to ovoid, papillose.

DISCUSSION. The combined features of sporophytes borne terminally on stems and branches, and the single peristome, representing by an exostome with papillose teeth, aid in distinguishing the genus. The name *Acrocryphaea* was previously applied to the neotropical species. The two common species can be recognized as follows: *S. concavifolia* — perichaetial leaf apices short, not conspicuous, leaf apical cells ± short, (4–6:1), apex short acuminate, and *S. rubricaulis* **—** perichaetial leaf apices very long, conspicuous; leaf apical cells elongate (ca. 8–10:1), apex long acuminate.

Sphaerotheciella (Fig. 105) - Two neotropical species, *S. pachycarpa* (Schimp. ex Besch.) Manuel and *S. pinnata* (Bruch, Schimp. & W. Gümbel) Manuel, confined to Mexico, Central America, and northern South America; a genus of three species, two in the Neotropics, one in eastern Asia.

HABITAT. Epiphytic on branches and occasionally trunks of trees; montane forests, 700–3130 m.

DESCRIPTION. **Plants** medium sized, forming suberect tufts, light to dark green. **Secondary stems** to 10 cm long, irregularly pinnately branched, branches to 2 cm long. **Leaves** erect when dry, spreading when wet, ovate to ovate-short lanceolate, 1–2.2 mm long, apex acute to broadly short acuminate, base short decurrent; margins revolute below acumen, irregularly serrate to weakly crenulate distally or entire; costa rather strong, 3/4–4/5 lamina length; upper and median cells long

oval to oblong-elliptic, smooth; inner basal cells elongate, weakly porose or not; alar region differentiated, cells obliquely arranged, subquadrate, smooth. **Perichaetia** lateral, on short branches; leaves differentiated, obovate-oblong, costa excurrent. **Seta** very short. **Capsule** with urn ovoid to ellipsoidal, 1–1.5 mm long; stomata apparently absent. **Operculum** conic. **Peristome** double, exostome teeth smooth throughout to distally papillose; endostome basal membrane absent, segments short or rudimentary, weakly papillose. **Calyptra** short mitrate, smooth. **Spores** endosporic, appearing multicellular.

DISCUSSION. The primary feature is the multicellular spores. These "spores" are, in fact, endosporic and germinate within the urn producing a protonematal disc. In addition, the absence of both stomata and basal membrane distinguishes this genus from *Cryphaea*. The two neotropical species can be separated as follows: *S. pachycarpa* — leaves entire or weakly serrulate at leaf apex, and *S. pinnata* — leaves serrate above.

LITERATURE. Manuel, M. G. 1977. Studies in Cryphaeaceae III. *Sphaerotheciella* Fleisch. new to the Americas. Occasional Papers of the Farlow Herbarium 12: 35–40.

DALTONIACEAE

Plants small to occasionally medium sized, forming tufts or thin mats, glossy green to yellowish-green or golden. **Primary stems** short and inconspicuous, or conspicuous and creeping to spreading. **Secondary stems** erect to ascending, or stems and branches spreading or subascending, radiculose below; paraphyllia absent, pseudoparaphyllia absent? **Leaves** spirally arranged or complanate, ovate- to oblong-lanceolate or obovate-oblong and symmetric or asymmetric, apex acuminate, acute or obtuse-apiculate, base slightly decurrent on one or both sides; margins plane to recurved, entire to bluntly or sharply serrate or ciliate, limbate; costa single, 1/3–3/4 lamina length, sometimes forked along a short costa; laminal cells either short to ± long hexagonal and walls weak or lax, or cells oval to rhomboidal and walls firm; alar region undifferentiated (occasionally border cells at base numerous and extend part or fully across to costa). **Gemmae** absent or present in leaf axils, short to long cylindrical. **Autoicous**, rarely dioicous. **Perichaetia** lateral, leaves differentiated, usually smaller than stem leaves. **Seta** elongate, slender to rather stout, smooth, papillose distally or throughout, or ciliate distally. **Capsule** exserted, erect to pendulous, urn ovoid, neck distinct or not; exothecial cells collenchymatous; stomata present, at base of urn or on neck; annulus usually persistent, cells little differentiated. **Operculum** conic-rostrate. **Peristome** double, exostome teeth 16, papillose or striate and furrowed; endostome basal membrane low or high, segments 16, cilia reduced or absent. **Calyptra** mitrate or campanulate, smooth or sparsely hairy, base fringed with hairs. **Spores** lightly to densely papillose, rarely smooth.

DISCUSSION. The Daltoniaceae contain nine genera and more than 200 species with a pantropical distribution; in the Neotropics three genera and 37 species. Genera of the Daltoniaceae have been placed in the Hookeriaceae by previous authors. More recently, some authors have defined the family much more broadly than presented here (see family ref. under Pilotrichaceae).

1. Costa short, ca. 1/2 or less lamina length, often distally forked; seta ciliate distally .... **Calyptrochaeta**
1. Costa longer, 2/3 or more lamina length; seta smooth or papillose distally or throughout 2
2. Leaves loosely complanate, differentiated between lateral and median leaves, ovate or obovate; apices usually ± rounded-obtuse; cells large and rather lax ..... **Leskeodon**
2. Leaves spirally arranged, similar, mostly lanceolate; apices usually gradually acuminate; cells small, firm, not lax ..... **Daltonia**

Calyptrochaeta (Fig. 105) - About five species in the Neotropics; a pantropical genus of about 25 species.

HABITAT. In moist shaded sites on rock and soil covered rocks, possibly epiphytic; montane forests.

DESCRIPTION. **Plants** medium sized, forming short lax tufts or mats, glossy pale green. **Stems** suberect; in cross-section central strand absent. **Leaves** somewhat complanate, erect-spreading, broadly oblanceolate or obovate, 2–3.5 mm long, apex short to rather long acuminate, base slightly decurrent on lateral leaves; margins plane, limbate, sharply to rather bluntly serrate; costa single, short and forked along nerve, unequal; laminal cells smooth, median cells broadly to narrowly hexagonal; marginal cells linear forming a border of 1–4 rows. **Autoicous** or dioicous. **Perichaetia** lateral, leaves small, ovate-lanceolate. **Seta** 2–5 mm long, rather stout, papillose to spinose, and ciliate distally with multicellular hairs (to 1 mm long). **Capsule** pendulous, urn ovoid, to ca. 0.8 mm long, neck distinct. **Operculum** conic-rostrate (straight). **Peristome** with exostome furrowed, lamellae extending beyond

margin, endostome membrane high, segments narrow, keeled and perforate, lightly papillose, cilia reduced. **Calyptra** mitrate, smooth?, or roughened, fringed at base. **Spores** not observed.

DISCUSSION. The erect, complanate–foliate plants with plane, weakly bordered leaves with a toothed margin, short, single costa that is forked distally, and the distally ciliate seta are diagnostic for the genus. The name *Eriopus* Brid., *nom. illeg*., was used by previous authors; *Piloseriopus* Sharp is a further synonym.

Daltonia (Fig. 105) - Twenty-two species in the Neotropics; a genus containing some 60 species primarily pantropical in distribution.

HABITAT. Epiphytic, rarely on rocks; submontane to more commonly montane forests, particularly cloud forest, also extending into páramo and puna in gallery forests, 1000–4200 m.

DESCRIPTION. **Plants** mostly small to somewhat medium sized, usually forming small tufts, glossy pale green to golden-brown or yellow. **Primary stems** short, creeping, inconspicuous. **Secondary stems** erect or suberect, ca. 1.5–3 cm tall, several branched. **Leaves** crowded, broadly lanceolate to linear-lanceolate, mostly 2–4 mm long, apex acuminate, base rounded; margins plane or recurved one or both sides, entire or apices rarely serrulate, weakly to strongly limbate; costa single, 1/2–4/5 lamina length; laminal cells smooth, upper and median cells oval to fusiform, thick-walled, smooth; basal and insertion cells linear to oblong, often yellowish-brown to golden; marginal cells long linear, forming a distinct border of few to many rows. **Autoicous**. **Perichaetial** leaves much smaller than stem leaves, oblong- to ovate-short lanceolate. **Seta** 7–12 mm long, slender to stout, smooth to more commonly papillose-roughened throughout or distally. **Capsule** erect to suberect, urn ovoid; exothecial cells collenchymatous, or walls equally thickened; stomata on neck or urn base, superficial. **Operculum** conic-short rostrate. **Peristome** with exostome teeth narrowly lanceolate, papillose, not furrowed; endostome basal membrane low, segments linear, lightly to strongly papillose, keeled and perforate. **Calyptra** campanulate, base fringed with hairs, distally smooth to somewhat roughened. **Spores** spherical to ovoid, mostly lightly papillose.

DISCUSSION. The genus is characterized by the small to somewhat medium sized tufted plants; oblong-lanceolate to linear-lanceolate leaves; entire or rarely serrulate, weakly to strongly bordered margins that are plane or recurved; rather thick-walled, often oval or fusiform upper cells; differentiated basal and insertion cells; and the roughened to papillose, rarely smooth seta. *Daltonia* remains poorly collected largely due to the small size of the plants and equally small populations. *Daltonia* seldom forms abundant populations, rather these inconspicuous plants occur as a few individuals or as small tufts on bamboo (at branching nodes) or on branches of shrubs or small trees. It is rather common to find two or three species growing intermixed, e.g., *D*. *gracilis* and *D*. *longifolia*. The Andes are one of the major centers of diversity for this genus. The treatment provided by Bartram (1931) is functional; however, it is apparent that the distinctness of several species is not always clear, and several additional species have been described since that study. A reassessment of the genus is warranted.

LITERATURE. Bartram, E. B. 1931. A review of the American species of *Daltonia*. Bulletin of the Torrey Botanical Club 58: 31–48, plates 3, 4 [keys, illustrations]. - Griffin III, D. 1980. Studies on Colombian cryptogams. IX. *Daltonia fenestrellata* (Musci: Daltoniaceae), a new species from Colombia. Brittonia 32: 214–216.

Leskeodon (Fig. 106) - A genus containing about 20 species primarily neotropical in distribution.

HABITAT. Epiphytic, and on humus or logs; submontane to upper montane forests, infrequent in the wet lowland forests, in moist, shaded sites, particularly cloud forests, possibly from near sea level, 300–3500 m.

DESCRIPTION. **Plants** rather small and delicate, forming mats, glossy pale to somewhat dark green. **Stems** spreading or subascending, rusty-red. **Leaves** often crispate or undulate when dry, loosely complanate when wet, lateral leaves oblong-elliptical to nearly orbicular, 1–3 mm long, apex short acuminate to rounded, tips often cuspidate or aristate, occasionally twisted; margins plane, entire, limbate; costa 2/3–3/4 lamina length; laminal cells smooth, upper and median cells isodiametric to rhombic; basal cells oblong-rectangular, lax, juxtacostal cells larger, lax; marginal cells long linear forming a border of 1–3 rows. **Autoicous**, rarely dioicous. **Perichaetia** lateral, leaves small, ovate-long acuminate to subulate. **Seta** to 6 mm long, smooth to distally roughened. **Capsule** erect to inclined, urn ovoid to ovoid-short cylindrical; exothecial cells collenchymatous; stomata on neck, superficial. **Operculum** short rostrate. **Peristome** with exostome teeth papillose, not furrowed; endostome basal membrane low, segments linear, papillose, keeled and perforate. **Calyptra** mitrate, usually sparsely hairy, fringed at base. **Spores** spherical to ovoid, lightly papillose.

DISCUSSION. The genus is characterized by the spreading habit, ovate or oblong complanate leaves, the entire, bordered margins, elongate single costa, large, thin-walled, isodiametric median

cells, and the smooth to distally roughened seta. Species of *Leskeodon* were originally placed in *Distichophyllum* and reports of the latter genus in the Neotropics are largely referable to the former genus. Both genera are gametophytically similar but differ in their peristomial features.

DICRANACEAE

Plants small to large and often robust, mostly forming loose to dense tufts. **Stems** erect, simple to more often few to several branched by innovations, radiculose, often densely tomentose; central strand present; rhizoids reddish-brown. **Leaves** mostly crowded, occasionally falcate or falcate-secund, narrowly to somewhat broadly lanceolate, often differentiated between a ovate to oblong base and limb lanceolate-linear to subulate, often inflexed to incurved; margins entire to more often serrate, often sharply so; costa single, percurrent to short excurrent, rarely hyaline, at base costa often 1/2 or more width of lamina, in cross-section stereids above and below guide cells or with hyaline cells commonly above or occasionally below guide and stereid cells; laminal cells mostly smooth, occasionally bulging mammillose or papillose, cell walls smooth, occasionally porose or sinuose; lower and basal cells often elongate; alar region differentiated or not, when distinct cells ± enlarged, often golden or reddish-brown, border present in few species with linear hyaline cells. **Propagula** usually in the form of deciduous branches or leaves (mostly in *Campylopus*). **Dioicous** or autoicous. **Perichaetia** terminal, or occasionally appearing lateral by stem innovations, leaves often elongate and sheathing. **Seta** generally elongate, smooth to rarely roughened distally, erect or flexuose or cygneous, usually twisted. **Capsule** immersed to more commonly exserted, inclined, to suberect or erect, symmetric to asymmetric, urn short to ± long cylindrical to ovoid-cylindrical or ovoid, smooth or variously furrowed or ribbed; stomata present or absent; annulus present or absent. **Operculum** conic short- to long-rostrate. **Peristome** single, teeth 16, mostly divided 1/2 or more toward base, vertically striate-pitted or -ridged below, distally papillose to papillose throughout, rarely smooth. **Calyptra** cucullate, smooth, naked, base entire or fringed with hairs. **Spores** mostly spherical, lightly to somewhat coarsely papillose, rarely smooth.

DISCUSSION. The Dicranaceae have a worldwide distribution with nearly 50 genera and nearly 1000 species; in the Neotropics 34 genera and about 190 species. It is one of the largest families in the tropical America and a principal component of open montane and alpine environments. The family, as traditionally recognized, is a diverse assemblage of taxa that is unlikely to represent a monophyletic group. The distinctions between the Dicranaceae and Ditrichaceae are relatively subtle. Gametophytic features found in *some* of the Dicranaceae genera and not in the Ditrichaceae include: alar region differentiated, costa very broad at leaf base, and cells porose. Sporophytic features of the Dicranaceae include: stegocarpic capsules, with peristome teeth flat, entire or distally divided (rarely divided to base); in the Ditrichaceae features (trends) include: cleistocarpic or stegocarpic capsules. When the latter, peristome teeth are terete, not flat and often divided to near base.

Study guide. Leaves are the primary means for identification of many of the neotropical species although sporophytes may be necessary for various genera and several species. Care must be taken when removing the leaf to ensure that the basal portion is maintained intact. This will enable one to determine if alar cells are present. Often these cells are rather fragile and remain attached to the stem when the leaf is removed. It is useful to examine leaf bases on a portion of the stems with some of the leaves removed. A leaf cross-section is necessary in *Campylopus* and associated genera. It is made midway on the leaf, or if the leaf is differentiated with an expanded base and narrower upper limb, then a cross-section is made midway on each portion. Sporophyte features to examine include the seta, whether it is erect, flexuose or cygneous, and capsules, whether stomata are present or absent, and peristome teeth, where the degree of division of individual teeth and the ornamentation are noteworthy features.

LITERATURE. Frahm, J.-P. 1991. Dicranaceae: Campylopodioideae, Paraleucobryoideae. Flora Neotropica Monograph 54: 1–238 [keys, illustrations, maps]. Stech, M. 1999. A reclassification of Dicranaceae (Bryopsida) based on non-coding CPDNA sequence data. Journal of the Hattori Botanical Laboratory 86: 137–159. - Williams, R. S. 1913. Dicranaceae. North American Flora 15 (2): 77–158 [keys to taxa of North and Central America, useful but dated].

1. Alar region differentiated, cells often enlarged or subquadrate, firm and thick-walled to lax and thin-walled 2
1. Alar region undifferentiated 24
2. Costa at leaf base 1/3 or less total width 3
2. Costa at leaf base mostly greater than 1/3 total width 16
3. Leaf margins with a hyaline border, 1/3 to total length of leaf; upper laminal cells faintly to distinctly papillose or strongly porose and smooth 4

3. Leaf margins unbordered, of if bordered then confined to base; upper laminal cells mostly smooth, bulging or appearing finely striate 6
4. Costa very narrow, faint to nearly absent below; laminal cells smooth, porose; southeastern Brazil ..... **Dicranoloma**
4. Costa mostly strong; laminal cells papillose, not porose 5
5. Leaves narrowly lanceolate; leaf apex concolorous, not deciduous ..... **Leucoloma**
5. Leaves broadly lanceolate or ovate-short lanceolate; leaf apex a short hyaline awn, or tips deciduous; southeastern Brazil ..... **Sclerodontium**
6. Upper laminal cells appearing finely longitudinally striate, striations over and between cells; plants small, stems to 1.5 mm tall; leaves strongly crispate-curled when dry; capsules wrinkled when dry ..... **Dicranoweisia**
6. Upper laminal cells lacking longitudinal striations; plants larger; leaves crispate-flexuose to spreading; capsules smooth or furrowed 7
7. Upper laminal cells mostly isodiametric 8
7. Upper laminal cells elongate (mostly 3 or more times longer than wide) 10
8. Flagellate branches present, erect; stem leaves spreading, falcate-secund or crispate ..... **Orthodicranum**
8. Flagellate branches absent; stem leaves crispate to flexuose or curled appressed 9
9. Leaves crispate when dry, broadly to narrowly lanceolate ..... **Holomitrium** p.p.
9. Leaves appressed and curled or spirally curved when dry, lingulate to oblong or oblong-lanceolate; West Indies and Brazil ..... **Macrodictyum** p.p.
10. Laminal cell walls entire, not porose 11
10. Laminal cell walls porose; capsules smooth 12
11. Leaves falcate-secund, distally bistratose; capsules smooth; peristome entire, papillose on both surfaces; presently known only from Ecuador in the Neotropics ..... **Holodontium**
11. Leaves loosely erect, distally unistratose; capsule often furrowed and slightly twisted; peristome distal 2/3 divided or nearly to base, outer surface vertically to obliquely striate (or nearly smooth), inner surface coarsely papillose ..... **Atractylocarpus** p.p.
12. Plants pendent; leaves ± distant; submontane Chocó ..... **Schliephackea**
12. Plants erect to ascending, not pendent; leaves mostly crowded 13
13. Leaf costa becoming broader above base, appearing to expand at juncture of setaceous tip and expanded leaf base, appearing very long excurrent ..... **Chorisodontium**
13. Leaf costa equally narrow throughout or gradually narrowed distally, percurrent to short excurrent 14
14. Peristome divided distally ca. ½ length; perichaetial leaves not sheathing; plants terrestrial ..... **Dicranum**
14. Peristome entire, not divided distally; perichaetial leaves sheathing; plants epiphytic, if on soil or rock then confined to the tepuis of northeast South America 15
15. Leaves mostly crispate; laminal cells sinuose distally, porose below ..... **Holomitrium** p.p.
15. Leaves spirally contorted distally; laminal cells sinuose and porose distally ..... **Eucamptodontopsis**
16. Leaves in cross-section with leucocysts confined to the upper surface 17
16. Leaves in cross-section with stereid cells on the upper surface or leucocysts above and below a median band of stereids or chlorocysts 18
17. Leaves strongly falcate-secund; in cross-section leucocysts and chlorocysts alternating dorsally; upper cells elongate; basal cells thin-walled and slightly porose; rare, southeastern Brazil ..... **Paraleucobryum** p.p.
17. Leaves mostly erect to loosely erect-spreading; lacking the remaining combination of characters; widespread ..... **Campylopus** p.p.
18. Stems verticillate foliate, portion of stem with erect leaves separating a series of verticillate tufts of leaves (also found in *Campylopus huallagensis* & *C. weberbaueri* — both with porose inner basal cells) ..... **Bryohumbertia**
18. Stems equally foliate or with a comal tuft of leaves at stem tip 19
19. Leaves in cross-section with a single layer of leucocysts above and below a layer of chlorocysts 20
19. Leaves in cross-section lacking the above combination of characters, leucocysts absent or if present leaves often 4 mm or more long 21
20. Upper laminal cells narrowly elongate; seta erect; Mexico ..... **Paraleucobryum** p.p.
20. Upper laminal cells short and irregularly rectangular to suboval; spp. in tropical Andes & Mexico ..... **Campylopus** p.p.
21. Leaves relatively short, to 4 mm long; upper laminal cells short, 1:3–4; plants rare 22
21. Leaves elongate, 5 mm or longer; upper cells elongate, 1:5–15; plants rare to common 23

22. Leaves to 2.3 mm long; in cross-section leucocysts above and below stereid band; flagelliferous branches frequent; capsules exserted ..... **Campylopodiella**
22. Leaves 2.5–4 mm long; in cross-section stereid bands above and below guide cells, leucocysts absent; flagelliferous branches none; capsules immersed ..... **Sphaerothecium**
23. Inner basal cells hyaline; upper laminal cells much elongate, 1:10–15; leaves readily deciduous; plants apparently rare ..... **Dicranodontium**
23. Inner basal cells firm, not hyaline; upper laminal cells shorter, 1:5–6; leaves not fragile and deciduous; plants common ..... **Atractylocarpus** p. p.
24. Leaf base sheathing, usually distally differentiated from expanded base 25
24. Leaf base mostly spreading from base, not sheathing stems 31
25. Expanded leaf base with juxtacostal cells enlarged, hyaline, thin-walled and fragile, outer marginal cells thick-walled; leaf limb bistratose along margins; plants confined to páramos .... **Kingiobryum**
25. Expanded leaf base with cells usually uniform across, not enlarged or fragile; leaf limb unistratose along margins; submontane to páramo 26
26. Plants epiphytic; stems tomentose below; margins of leaf limb usually undulate .... **Symblepharis**
26. Plants terrestrial, on soil or rocks; stems below radiculose or naked; margins of leaf limb plane/flat ..... 27.
27. Upper cells of expanded leaf base isodiametric or short rectangular 28
27. Upper cells of expanded leaf base elongate, oblong-linear or -fusiform 29
28. Leaf limb crispate-curled when dry; laminal cells of leaf base subquadrate to short rectangular; peristome rudimentary, smooth or striate ..... **Camptodontium**
28. Leaf limb erect to somewhat flexuose when dry; laminal cells of leaf base elongate, mostly oblong-linear; peristome well developed, papillose to striate-pitted below, papillose above ..... **Dicranella** p.p.
29. Plant stems appearing julaceous ..... **Aongstroemia**
29. Plant stems not julaceous 30
30. Leaves strongly sheathing, with base ovate, 2.5–4 mm long; costa stout; seta curved or flexuose, 3–7 mm long ..... **Microcampylopus**
30. Leaves loosely sheathing, with base oblong, mostly more than 3 mm long; costa slender; seta erect twisted, 10 mm or more long ..... **Pilopogon**
31. Leaves lanceolate to linear-lanceolate or subulate from an ovate to oblong base; distal laminal cells subquadrate to short rectangular 32
31. Leaves oblong to ligulate; laminal cells isodiametric, subquadrate-rounded 38
32. Plants grayish-pale white or green, rather glossy; clustered brood leaves present in distal leaf axils; leaves to ca. 3 mm long; in cross-section with leucocysts present; upper laminal cells narrowly long rectangular; Mexico ..... **Brothera**
32. Plants mostly dark green to golden-yellow or brown; clustered brood leaves absent; leaves various lengths; leucocysts absent; upper laminal cells quadrate to short rectangular 33
33. Laminal cells papillose; leaves linear-lanceolate; bistratose along margin and in portions of intralamina ..... **Cynodontium**
33. Laminal cells smooth; combination of remaining characters lacking 34
34. Upper lamina partially to fully bistratose; puna of the central Andes 35
34. Upper lamina unistratose; more widespread from lowland to high páramo or puna 36
35. Plants aquatic or semiaquatic, rigid; leaves subulate from an ovate or short oblong to triangular base ..... **Hydrodicranum**
35. Plants of dry habitats, rather soft; leaves broadly lanceolate from an ovate to oblong base .... **Pseudohyophila**
36. Peristome short, less than 200 μm long, often ca. 100 μm; lamina continuous to leaf tip, costae mostly subpercurrent ..... **Microdus**
36. Peristome long, to 200 μm or more (to 290 μm); lamina continuous to leaf tip or appearing to end well below; costae subpercurrent to excurrent 37
37. Plants forming dense, compact tufts; seta stout, conspicuously elongate, to 20 mm long; peristome apparently smooth; puna of Bolivia ..... **Polymerodon**
37. Plants forming mostly loose tufts; seta mostly slender, less than 20 mm long; peristome variously ornamented; widespread ..... **Dicranella** p.p.
38. Leaf margins plane or slightly recurved below; laminal cells smooth; stem central strand absent; capsules 8-ribbed ..... **Rhabdoweisia**
38. Leaf margins recurved; laminal cells mammillose or smooth; stem central strand present; capsules not ribbed ..... **Oreoweisia**

Aongstroemia (Fig. 106) - Three species in the Neotropics, *A. filiformis* (P. Beauv.) Wijk & Margad. (West Indies, Mexico to Peru, also southern Africa, Madagascar), *A. julacea* (Hook.) Mitt. (Mexico, Central America, tropical Andes (also Eurasia to southern Africa), and *A. orientalis* Mitt. (Mexico, Central America, and southeastern Brazil, also Eurasia to Malesia); a genus of about 7 widely distributed species mostly from high elevations.

HABITAT. On soil, frequent on exposed banks and trails or road cuts in montane sites, or above treeline, inconspicuous and often associated with tuft-forming bryophytes; open submontane and montane, to zacatonal, páramo and puna, 1250–5000 m.

DESCRIPTION. **Plants** small, slender, forming loose tufts, dark green to yellowish-green. **Stems** erect and slender, julaceous or terete-foliate, few branched; central strand present. **Leaves** clasping and deeply concave, shortly ovate- to oblong-obtuse or -broadly acute, or leaves abruptly subulate from an obovate sheathing base 0.5–5 mm long; margins plane, entire to crenulate or strongly erose-dentate distally; costa subpercurrent or long excurrent, ca. 1/4–1/5 width of leaf base; laminal cells smooth, median cells linear or linear-vermicular, thick-walled; lower or basal cells short to long rectangular; alar cells undifferentiated. **Dioicous**. **Perigonia** appearing lateral distally on stems, bud-like. **Perichaetia** terminal or appearing lateral by innovations, leaves larger and strongly convolute. **Seta** elongate, 3–10 mm long, erect, smooth. **Capsule** erect, urn obloid or ovoid-cylindrical, to 2 mm long; annulus differentiated or not. **Operculum** long rostrate, oblique. **Peristome** absent (gymnostomous) or present, teeth divided 1/2–2/3 into 2–4 segments, perforate below, papillose distally. **Calyptra** cucullate, smooth. **Spores** spherical, lightly papillose.

DISCUSSION. The genus is characterized by slender plants with leaves erect-appressed whether dry or wet, narrow costa, thick-walled upper laminal cells, and undifferentiated alar cells. The three species can be differentiated as follows: *A. filiformis* (syn. *A. jamaicensis* Müll. Hal.) — costa long excurrent, typically of open montane habitats. The remaining two species have a subpercurrent to percurrent costa and all typical of zacatonal, páramo and puna habitats, *A. julacea* — margins erose-dentate, appearing bifid by adjoining projecting cells, apex erect, and *A. orientalis* — margins crenulate, apex secund.

Atractylocarpus (Fig. 114) - Three species in the Neotropics, the most common species is *Atractylocarpus longisetus* (Hook.) E.B. Bartram (Mexico, Central America, tropical Andes, and southeastern Brazil), the remaining two species are rare, known from one or two localities, *A. brasiliensis* (Müll. Hal.) R.S. Williams (southeastern Brazil), and *A. nanus* R. S. Williams (Peru); nine species with a mostly pantropical distribution.

HABITAT. On soil, humus, logs, and base trunk of trees; montane forests and shrubby páramo or puna; 1500–4300 m.

DESCRIPTION. **Plants** somewhat small to medium sized, soft and rather delicate, forming short tufts, mostly golden-yellow or -brown. **Stems** erect, few branched, tomentose; central strand present. **Leaves** equally foliate, erect-spreading to falcate-secund, setaceous-subulate from a short ovate base, 4–10 mm long, concave, apex rather blunt and toothed; margins entire below, distal tips dentate; costa excurrent, ca. (1/3)1/2–2/3 width of leaf base, in cross-section stereids above and below guide cells; laminal cells smooth, cells of subula narrowly long rectangular, base cells rectangular, thin-walled; alar cells weakly differentiated, few, reddish, often lost in dissection. **Autoicous**. **Perichaetia** terminal, leaves long setaceous from an elongate oblong convolute base. **Seta** elongate, 10–28 mm long, distal 1/3–1/2 twisted, yellow to golden-yellow. **Capsule** erect to suberect, urn oblong-short cylindrical, 1–2 mm long, furrowed and often slightly twisted when dry, stomata absent; annulus absent. **Operculum** conic-long rostrate and rather oblique. **Peristome** teeth divided ca. 2/3 length, outer surface vertically to obliquely striate, or nearly smooth, distally papillose, inner surface coarsely papillose. **Calyptra** cucullate, naked, entire at base. **Spores** papillose.

DISCUSSION. The genus is characterized by the often yellow or golden-brown color; the ovate-setaceous leaves; rather broad costa; stereids above and below guide cells; elongate and narrow upper laminal cells; erect, twisted seta; erect, symmetric capsule; absence of both stomata and annulus; and entire calyptra base.

Padberg and Frahm (1985) include *Metzerella* and *Metzleria* as synonyms in their treatment of *Atractylocarpus*. Allen (1994, see general ref.), in agreement with Williams (1913, see family ref.), synonymized *Atractylocarpus* with *Dicranodontium*, based on the similarity of the gametophyte, and the rather unimpressive seta difference which in the former is erect or flexuose and in the latter cygneous as in *Campylopus*.

LITERATURE. Frahm, J.-P. 1991 (see family ref.). - Padberg, M. & J.-P. Frahm. 1985. Monographie der Gattung *Atractylocarpus* Mitt. (Dicranaceae). Cryptogamie: Bryologie, Lichénologie 6: 315–341 [keys, illustrations].

Brothera (Fig. 107) - A monotypic genus, *B. leana* (Sull.) Müll. Hal., is known only from Mexico (also from eastern United States, East Asia, Himalayas).

HABITAT. On logs, base of trees, soil and occasionally on rocks; montane forests, 200–2500 m.

DESCRIPTION. **Plants** small, forming dense mats or tufts, pale green or yellow. **Stems** simple to few branched. **Leaves** erect-flexuose, linear-lanceolate, to 3 mm long, concave below, subtubulose above; margins incurved, entire, toothed at apex; costa long excurrent, ca. 1/3 width of leaf base, rarely more; lamina in cross-section with interrupted median chlorocysts, enclosed above and below by hyaline cells; laminal cells smooth, firm-walled, upper cells long rectangular; basal cells rectangular, firm to thin-walled along margin; alar cells little differentiated; clustered brood leaves often present in axil of distal stem leaves. **Dioicous**. **Sporophytes** not known from the Americas.

DISCUSSION. The genus is recognized by the small pale plants, clustered brood leaves present in axils of distal stem leaves, linear-lanceolate leaves (to 3 mm long), long excurrent costa that is ca. 1/3 the width of leaf base, enlarged hyaline cells above and below a row of interrupted, small green cells, and undifferentiated alar cells. The reports from Central America of *Brothera* are erroneous and refer to *Campylopus fragilis* (cf. Allen, 1994, see general ref.).

LITERATURE. Frahm, J.-P. 1991 (see family ref.).

Bryohumbertia (Fig. 107) - A single species, *B. filifolia* (Hornsch.) J.-P. Frahm, with two varieties, widespread in the Neotropics, locally abundant; a pantropical genus of three species.

HABITAT. On soil, humus and logs; montane and adjacent lowland forests, not uncommon in secondary open forests, from near sea level to 2700 m.

DESCRIPTION. **Plants** rather delicate and soft, medium sized, forming loose short to tall tufts, glossy dark green, occasionally yellowish-brown or golden. **Stems** erect, few branched, tomentose; in cross-section outer 3–4 cells small, thick-walled, inner cells larger rather thick-walled, central strand present; rhizoids rusty-red, smooth to papillose. **Leaves** usually alternating between 2–3 or more groups of verticillately arranged (whorled) larger leaves that are erect-spreading to spreading and internodal leaves erect to appressed and smaller; **verticillate leaves** long subulate from a short concave ovate base, 6–14 mm long, to 0.8 mm wide at base, apex long acuminate, base weakly auriculate; margins incurved, distal 2/3 serrate; costa strong, serrate on back distally; laminal cells smooth, upper expanded base and limb marginal cells elongate, mostly narrowly rectangular; basal cells large, short rectangular; alar cells oval-short rectangular, dark rusty-red; **internodal leaves** small, oblong-lanceolate, 2.2–3.5 mm long. **Dioicous**. **Perichaetia** terminal, leaves not clasping seta. **Seta** elongate, 12–14 mm long, usually erect when dry, flexuose and twisted when wet, smooth, yellow. **Capsule** asymmetric, urn cylindrical, 2–2.2 mm long, curved, often irregularly furrowed, base gibbous; annulus present, compound. **Operculum** conic-long rostrate, 1.5–1.6 mm long, oblique. **Peristome** teeth on outer surface striate, inner smooth. **Calyptra** cucullate, 2.5–3 mm long, smooth and naked, base fringed with long hairs. **Spores** lightly papillose.

DISCUSSION. The unusual leaf arrangement with whorls of larger spreading to erect-spreading leaves alternating with smaller internodal leaves that are erect to appressed, gives unmistakable definition to *Bryohumbertia*. In addition, the costa, broadened at the base, the upper rectangular-rounded laminal cells, entire basal cell walls, well differentiated alar cells, ± erect seta, presence of an annulus, and smooth inner surface of peristome teeth help to identify this genus. *Bryohumbertia* appears to be a weak segregate of *Campylopus*, differing by the erect, not cygneous seta, that is greater than 10 mm long.

LITERATURE. Frahm, J.-P. 1982. A reinterpretation of *Bryohumbertia* P. de la Varde et Thér. Cryptogamie: Bryologie, Lichénologie 3: 365–369 [keys]. - Frahm, J.-P. 1991 (see family ref.).

Camptodontium - Two species in the Neotropics, *C. fallax* (Herzog) Broth. and *C. flexipes* (Herzog) Broth., both from the central tropical Andes; a genus of three species confined to Peru, Bolivia, and Argentina (possibly Chile).

HABITAT. On rocks and soil, in exposed sites; high montane to puna, 3000–4400 m.

DESCRIPTION. **Plants** small to somewhat medium sized, forming dense tufts, yellowish-brown above, blackish brown or brown below. **Stems** erect, to 2 cm tall, few branched, radiculose below; in cross-section outer epidermal wall thick, inner cells large, thin, central strand weak; rhizoids smooth. **Leaves** crispate-curled above an appressed sheathing base when dry, spreading when wet, oblong-lanceolate or -ligulate, to ca. 2 mm long, somewhat broadly concave below, distally channeled or keeled, apex bluntly acute to obtuse-rounded; margins plane or slightly reflexed or recurved, entire; costa subpercurrent, rather weak; lamina unistratose; upper cells quadrate, smooth, thick-walled, lower and basal cells subquadrate or short-rectangular toward the margin, rectangular near the costa, somewhat thick-walled above, below lax and thin-walled; alar cells undifferentiated. **Perichaetia**

terminal or appearing lateral by innovations; leaves somewhat smaller, otherwise similar. **Seta** flexuose to erect, to 4 mm long, twisted, smooth. **Capsule** erect, urn ovoid, to ca. 1 mm long, smooth, neck short; exothecial cells elongate, thick-walled; stomata few in neck region, superficial; annulus large, in 2–3 rows, persistent. **Operculum** conic-apiculate, slightly oblique. **Peristome** smooth to striate, apparently rudimentary, inserted below the mouth. **Calyptra** not observed. **Spores** spherical, faintly papillose.

DISCUSSION. The genus does not appear readily distinct and may be best synonymized under *Dicranoweisia*. The neotropical species were originally placed there by Herzog (1916), but further investigation into the status of the Herzog species is needed.

LITERATURE. Brotherus, V. F. 1924 (see general ref.). Herzog, T. 1916 (see general ref.).

Campylopodiella (Fig. 108) - Two species in the Neotropics, *C. flagellacea* (Müll. Hal.) J.-P. Frahm & Isoviita (rather rare throughout its range, Mexico to Bolivia) and *C. stenocarpa* (Wilson) P. Müll. & J.-P. Frahm (Mexico and Central America); the remaining two species are known from Sikkim in the Himalayas and Southeast Asia.

HABITAT. On soil, logs, base of trees or rocks; probably associated with high open montane forest-páramo transition, 1100–4000 m.

DESCRIPTION. **Plants** small, forming tufts, yellowish-green. **Stems** erect, to 15 mm high, equally foliate, radiculose, flagelliferous branches absent or present in axils of distant leaves; central strand present. **Leaves** erect, oblong-lanceolate, 1.8–6 mm long, channeled in distal 2/3; margins erect to slightly incurved, apex entire or dentate; costa excurrent, 1/2–2/3 width of leaf base, in cross-section leucocysts ventral and dorsal, stereids forming a median band (and 2–4 stereids ventrally); upper laminal cells oblong-rectangular to subquadrate; alar cells differentiated or not, somewhat inflated or not. **Dioicous**. **Perichaetia** terminal. **Seta** elongate, 8–20 mm long, erect, flexuose. **Capsule** erect, urn cylindrical to ellipsoid, 2–3 mm long, smooth; stomata absent. **Operculum** long rostrate, oblique, about as long as urn. **Peristome** teeth divided to near base, papillose or striate at base, papillose distally; stomata absent. **Calyptra** cucullate, smooth and naked, entire at base. **Spores** spherical, smooth to lightly papillose.

DISCUSSION. The genus is allied with *Brothera* and *Campylopus* but differs from these by a leaf that in transverse section exhibits a median band of stereids with leucocysts above and below, and a few rather indistinct stereids positioned ventrally. Additional features of note are the often present flagelliferous branches, the broad costa, differentiated alar cells or not, flexuose, erect seta, smooth capsule, absence of stomata, and entire calyptra base. The terminal deciduous flagella, inflated alar cells and thick-walled laminal cells that gradually become quadrate toward the leaf base distinguish *C. flagellacea*, whereas *C. stenocarpa* differs by the absence of terminal flagella, undifferentiated alar cells, and thin-walled laminal cells that become rectangular toward the base.

LITERATURE. Frahm, J.-P. 1984. A review of *Campylopodiella* Card. The Bryologist 87: 249–250. - Frahm, J.-P. 1991 (see family ref.).

Campylopus (Fig. 108) - In the Neotropics about 65 species are presently recognized; a genus containing about 160 species.

HABITAT. On soil, humus, logs, rocks, and less commonly epiphytic on shrubs and trees; moist to semi-dry lowland to upper montane forests, páramos and punas, also savannas, from near sea level to 5300 m.

DESCRIPTION. **Plants** small to large and often robust, forming dense tufts, light to dark green, yellow or golden, occasionally blackish-brown. **Stems** erect, few to several branched by innovations, often densely tomentose; central strand present; rhizoids rusty-brown or occasionally whitish, smooth or papillose; brood branches (or leaves) occasionally present, usually terminal on stems and branches. **Leaves** isomorphic or gradually enlarged and forming a comal tuft, rarely verticilliate, erect-spreading to appressed, lanceolate to subulate from an ovate or lanceolate base, apex acute to more commonly long acuminate, tips hyaline or concolorous; margins erect to incurved, usually entire below, distally often serrulate to serrate; costa strong, percurrent to commonly long excurrent, usually 1/2–4/5 width of leaf base, back occasionally ribbed, distally often toothed, in cross-section with or without enlarged hyaline cells above or below; laminal cells smooth, distal cells usually thick-walled and variously shaped, oval, quadrate, or rhomboidal to short or long rectangular, often angled, occasionally suboblique, porose or not; lower and basal cells elongate, thin- or thick-walled, mostly rectangular; alar cells mostly differentiated, oval-short rectangular, hyaline or rusty-red. **Dioicous**. **Perichaetia** terminal, leaves differentiated or not. **Seta** elongate, smooth, cygneous (when wet, or often when dry). **Capsule** exserted, urn ovoid to obloid-cylindrical and curved, often strumose at base; exothecial cells thick-walled, stomata absent; annulus present. **Operculum** rostrate.

Peristome teeth divided from 1/2 to nearly to base, outer surface mostly striate, inner surface mostly papillose. **Calyptra** cucullate, smooth, base often fringed with long hairs. **Spores** papillose.

DISCUSSION. The genus is highly variable with regard to the gametophyte, and defined by a combination of characters. Gametophytically, plants have equally foliate stems or gradually larger leaves ending in a comal tuft, rarely verticillate-foliate. Propagula, when present, are in the form of brood branches or reduced leaves. Vegetative leaves have erect to incurved margins, a strong costa, 1/2 or more the width of the leaf base, leaf cross-section exhibiting enlarged hyaline cells or stereids above and/or below guide cells, often differentiated alar region with enlarged, thin- to thick-walled, firm-walled upper cells, and a dioicous sexual condition. Sporophytic features include the cygneous seta, absence of stomata, divided peristome from 1/2 to near base, and often fringed calyptra with long hairs.

According to Frahm about 700 species were considered legitimate names prior to his revisionary studies. The contribution by Frahm (1991) provides the most recent and important synoptic overview for the Neotropics. The keys, however, are only partially functional. The previous treatments by Frahm for Brazil (1979) and the Andes (1978) are often more useful for the identification of species, but necessarily supplemented by the latter overall treatment by Frahm (1991) for synonymy. The first volume of the Central American moss flora by Allen (1994, see general ref.) provides more complete data and functional keys for that region's species. In the study of *Campylopus*, a cross-section near mid-lamina is mandatory. Furthermore, care must be taken when stripping the leaves from the stem to do as little damage as possible in order to determine the presence of alar cells that may be hyaline or red, and if basal cells (just above the alar cells, if present) are thin- or thick-walled.

LITERATURE. Frahm, J.-P. 1978. Übersicht *Campylopus*-Arten der Anden. Journal of the Hattori Botanical Laboratory 44: 483–524 [keys, illustrations]. - Frahm, J.-P. 1979. Die *Campylopus*-Arten Brasiliens. Revue Bryologie et Lichénologie 45: 127–178 [keys, illustrations]. - Frahm, J.-P. 1987. A revised list of the *Campylopus* species of the world. Bryologische Beitraege 7: 1–117. - Frahm, J.-P. 1990. The origin and distribution of neotropical species of *Campylopus*. Tropical Bryology 3: 1–18. - Frahm, J.-P. 1991 (see family ref.).

Chorisodontium (Fig. 109) - Four species in the Neotropics, cordilleras of Central American and South America; a genus of ten species distributed in tropical montane and southern temperate America and circum-Antarctic regions.

HABITAT. On soil, humus, and logs, also epiphytic on shrubs and treelets; upper montane forests, páramo and puna, 2100–4300 m.

DESCRIPTION. **Plants** rather large, often robust, forming loose to dense tufts, glossy yellowish-green to golden brown. **Stems** erect, few branched by innovations; in cross-section outer 2–4 rows of cells small, thick-walled, inner cells large, rather thick-walled, central strand weak. **Leaves** loosely erect to spreading, somewhat flexuose, gradually long subulate from a broad ovate or lanceolate base, broadly concave below, setaceous distally, apex bluntly acute (or acuminate), smooth to mostly toothed, often sharply so, base slightly decurrent; costa long excurrent, filling subula above expanded base, 1/4–1/5 width of leaf base, in cross-section stereid cells on either side of guide cells; laminal cells of expanded based thick-walled, distally oval-elongate to oblong, entire or porose; basal and lower cells narrowly elongate, strongly porose; alar cells enlarged, quadrate to short rectangular, rusty-red. **Dioicous**. **Perichaetia** terminal, leaves sheathing, convolute, abruptly short aristate. **Seta** elongate, erect, rather stout, smooth. **Capsule** erect, slightly asymmetric, urn short to long cylindrical, smooth; exothecial cells irregularly short to somewhat long rectangular, thick-walled, rim cells subquadrate or oblate; stomata at urn base, superficial; annulus cells undifferentiated. **Operculum** conic-long rostrate, to as long as the urn. **Peristome** teeth vertically striate, papillose or not at tips, divided above, perforate or not below. **Calyptra** cucullate, smooth and naked. **Spores** unicellular and spherical or multicellular, variable in size (anisosporous), smooth or appearing ornamented.

DISCUSSION. The genus is distinguished by the loosely erect to spreading leaves, gradually long subulate tips from an ovate or lanceolate base, narrow costa expanding and filling the subula at juncture of limb and base, strongly porose basal laminal cells, and well differentiated alar cells. In aspect this genus may be confused with *Campylopus*, but differs by the very narrow costa at leaf base. Other genera, e.g., *Dicranum* or *Holomitrium*, exhibit a continuously narrow costa that is generally percurrent to short excurrent. There appears to be considerable variation and a number of intermediate forms among the neotropical species of *Chorisodontium*. A further assessment is needed for the neotropical species.

LITERATURE. Frahm, J.-P. 1981. Bestimmungsschlüssel und Illustrationen zu Gattung *Chorisodontium* Broth. Herzogia 5: 499–516 [keys, illustrations]. - Frahm, J.-P. 1989. The genus *Chorisodontium* (Musci, Dicranaceae) in the Neotropics. Tropical Bryology 1: 11–24 [keys, illustrations, maps]. - Hyvönen, J. 1991. *Chorisodontium* (Dicranaceae, Musci) in southern South America. Annales Botanici Fennici 28: 247–258.

Cynodontium (Fig. 110) - Three species in the Neotropics, *C. crassirete* Ångstr. (Brazil), *C. guatemalense* (E. B. Bartram) H. A. Crum (Guatemala), and *C. mexicanum* Ireland (Mexico); a genus of about 15 species primarily distributed in the Northern Hemisphere.

HABITAT. On soil, and on tree trunks (including *Pseudotsuga menziesii*); open montane, at elevations from 2000–3800 m.

DESCRIPTION. **Plants** rather small, forming tufts, green to yellowish green. **Stems** to 3 cm tall, few branched, radiculose below. **Leaves** crispate when dry, erect-spreading when wet, linear-lanceolate, to 6 mm long, apex acute, keeled distally; margins partially recurved, weakly serrulate to serrate distally; costa subpercurrent to percurrent, 1/4–1/5 width of leaf base, in cross-section stereids above and below guide cells; lamina bistratose along margins, partially so inward; upper laminal cells irregularly subquadrate, unipapillose on both surfaces; basal cells rectangular, somewhat laxly so toward margin; alar cells undifferentiated. **Autoicous**. **Perichaetia** terminal; inner leaves sheathing. **Seta** 3–7 mm long, straight to curved or cygneous (when wet), smooth. **Capsule** erect to suberect, urn obloid-cylindrical, 1–1.7 mm long, strongly furrowed when dry; annulus absent. **Operculum** conic-long rostrate, oblique. **Peristome** teeth inserted at or near mouth, distal 1/2–2/3 divided, vertically striate-pitted below, distally papillose. **Calyptra** cucullate, smooth and naked, base entire. **Spores** spherical, papillose.

DISCUSSION. The genus is distinguished by the crispate linear-lanceolate leaves, often bistratose, doubly serrate distal margins, narrow costa, unipapillose, subquadrate upper laminal cells, undifferentiated alar cells, furrowed, erect capsule, and vertically striate-pitted, divided peristome.

LITERATURE. Ireland, R. R. 1985. A new species of *Cynodontium* from Mexico. The Bryologist 88: 372–373.

Dicranella (Fig. 110) - Nearly 40 species recorded for the Neotropics, with possibly 20 or fewer being justified; a genus of more than 100 species with a worldwide distribution.

HABITAT. On exposed soil and soil covered rocks; mostly in open sites, from open lowland to high montane, páramos and punas, from near sea level to 4400 m.

DESCRIPTION. **Plants** mostly small, forming loose to dense tufts, less often gregarious, green, yellowish-green or brown. **Stems** erect, few branched by innovations, occasionally radiculose below; central strand present. **Leaves** small and ± distant below, distally larger and crowded, erect to erect-spreading flexuose, secund or not, often only slightly more spreading when wet, oblong- to ovate- or triangular-lanceolate to narrowly lanceolate-subulate, 1–4 mm long, apex acute to bluntly obtuse; margins plane to reflexed below, subula inflexed, incurved or channeled, entire to distally dentate-serrulate; costa subpercurrent or percurrent, rarely excurrent, 1/3 or less width of leaf base; laminal cells thick-walled, upper cells rectangular to quadrate or subquadrate, smooth or bulging papillose; lower and basal cells long rectangular, smooth; alar cells undifferentiated. **Dioicous**. **Perichaetia** terminal, leaves larger, subsheathing to convolute. **Seta** elongate, 5–15 mm long, erect, smooth. **Capsule** erect or occasionally inclined, symmetric or asymmetric and curved, urn subglobose to ovoid-cylindrical, 0.7–1.5 mm long, smooth or furrowed, neck sometimes distinct, occasionally gibbous. **Operculum** conic-short to long rostrate. **Peristome** teeth divided ca. 1/2 length or slightly more into 2–3 segments, vertically striate-pitted below, distally papillose or spiculose. **Calyptra** cucullate, smooth and naked, base entire. **Spores** lightly to coarsely papillose.

DISCUSSION. The genus is characterized by the small habit; the erect- to erect-spreading, flexuose or secund leaves; a subpercurrent to percurrent, narrow costa; undifferentiated alar cells; erect, smooth seta; and vertically striate-pitted below, papillose above peristome teeth. Various authors have included *Anisothecium* and *Microdus* in *Dicranella*. A worldwide revision is needed for *Dicranella* and related segregate genera.

Dicranodontium (Fig. 110) - Two species present in the Neotropics, *D. denudatum* (Brid.) E. Britton (Mexico, Central America, tropical Andes; widespread in the north temperate region), *D. pulchroalare* Broth. var. *pulchroalare* [syn. *D. meridionale* E. B. Bartram] (Mexico, Central America, tropical Andes) and var. *brasiliense* (Herzog) J.-P. Frahm (SE Brazil). A genus of nine species, primarily associated with the Northern Hemisphere.

HABITAT. On logs, epiphytic, and on rocks associated with streams or waterfalls; montane forests to open montane and páramo, 1100–3400 m.

DESCRIPTION. **Plants** medium sized, forming soft tufts, pale green to yellowish-green or -brown. **Stems** erect, to 5 cm tall, tomentose below; in cross-section outer 2–3 rows of cells ± thick-walled, inner cells large, thin-walled, central strand present. **Leaves** loosely erect to falcate, lanceolate-subulate, 4–13 mm long, to 0.35 mm wide above base, concave below; margins distally erect; costa long excurrent, ca. 1/3 width of leaf base, distally serrate, sharply so at apex, in cross-section stereids

above and below guide cells; laminal cells smooth, distally linear to linear-long rectangular, walls entire or porose; marginal cells forming an indistinct border, inner laminal cells larger; at base marginal cells linear, inner basal cells larger, long rectangular, thick- or thin-walled; alar cells toward margin ± thick-walled, pale reddish or hyaline, inner cells adjacent to costa hyaline and thin-walled. **Dioicous**. **Seta** elongate, to ca. 10 mm long, curved or cygneous when young, erect and twisted when mature, smooth. **Capsule** erect, urn ovoid to cylindrical, to 1.2 mm long, symmetric; annulus absent. **Operculum** long rostrate, as long as urn. **Peristome** teeth divided to base, vertically striate below, papillose distally. **Calyptra** cucullate, naked and smooth, entire or ciliate at base. **Spores** spherical, finely papillose.

DISCUSSION. The genus is characterized by the linear to linear-rectangular upper laminal cells, mostly thick-walled basal cells, differentiated alar cells, an elongate seta, cygneous when wet, absence of an annulus, teeth of peristome divided to near base, vertically striate below, papillose distally, and with a ciliate or entire calyptra base. The genus is treated more broadly by Allen (1994, see general ref.) to include *Metzleria* which likewise exhibits upper elongate laminal cells, but differs by an erect, flexuose seta.

The two neotropical species can be differentiated as follows: upper laminal cells porose — *D. denudatum*, and upper laminal cells straight, not porose — *D. pulchroalare*.

LITERATURE. Frahm, J.-P. 1991 (see family ref.). - Frahm, J.-P. 1997. A taxonomic revision of *Dicranodontium* (Musci). Annales Botanici Fennici 34: 179–204 [keys, illustrations].

Dicranoloma (Fig. 111) - One or possibly two species in the Neotropics, *D. billardieri* (Brid.) Paris, known from southeastern Brazil and reported from Peru, frequent in southern Argentina and Chile; a genus of about 90 species distributed in the Southern Hemisphere with the greatest diversity concentrated in Australasia.

HABITAT. On humus or soils, in boggy sites; forested to open montane, above 1700 m.

DESCRIPTION. **Plants** rather large to robust, forming tufts or cushions, dark green to golden-yellow or brown. **Stems** erect, to 11 cm tall, several branched; in cross-section outer 3–5 rows of cells small, thick-walled, inner cells large, thick-walled, central strand weak, moderately thick-walled. **Leaves** somewhat crowded, falcate-secund, ovate-narrowly lanceolate, to 7 mm long, concave, base rounded; margins plane below, inflexed, distal 1/3 rather sharply serrate, lower 2/3 limbate; costa narrow, weak to nearly absent below, ending in acumen, coarsely toothed on back; lamina unistratose; laminal cells smooth and thick-walled, apical cells somewhat broadly oblong, weakly porose or not; median cells oblong-linear, porose; marginal cells below serration forming a border in 3–4 rows, long linear, hyaline; basal cells between alar region and costa subrectangular, strongly porose, golden yellow; alar cells large, oblong-rectangular with a row of small subquadrate cells above, golden-red. [**Pseudoautoicous**? **Perichaetia** terminal. **Seta** elongate, smooth. **Capsule** curved, urn cylindrical, strongly asymmetric, strumose; exothecial cells elongate, thick-walled; stomata at urn base, superficial; annulus persistent. **Opercula** conic-long rostrate. **Peristome** teeth vertically striate-papillose, distally divided into 2–3 segments. **Calyptra** cucullate, smooth and naked. **Spores** spherical, papillose.]

DISCUSSION. The narrow hyaline border in combination with the porose laminal cells and enlarged alar cells that often form a single terminal row of small subquadrate cells is diagnostic. Sporophytes have not been observed in the Neotropics. Because the distinctions between species assigned to *Dicranum* and *Dicranoloma* are often unclear, particularly in Australasia, some authors place the latter genus in the former. Three additional species are recorded for the Neotropics, including *D. steyermarkii* E. B. Bartram from Venezuela, but their status is not known.

Dicranoweisia (Fig. 111) - Four species recorded for the Neotropics; about 20 species known, of mostly cool temperate regions of both hemispheres.

HABITAT. On base of trees and logs, possibly from somewhat exposed sites; open montane forests, extending into páramo and puna, 1850–4800 m.

DESCRIPTION. **Plants** rather small, forming dense tufts, yellowish- to brownish-green, dark brown below. **Stems** erect, to 1.5 mm high, several branched; in cross-section outer 1(–2) rows of cells small, thick-walled, inner cells large, thin-walled, central strand weak. **Leaves** crispate, strongly curled when dry, erect-spreading to spreading when wet, linear-lanceolate to subulate from a narrowly elliptical base, to 4 mm long, distally channeled to subtubulose, apex bluntly acute to obtuse; margins distally erect to slightly incurved, entire or weakly crenulate by projecting cell walls, often bistratose, smooth or appearing irregularly papillose due to cuticular thickening over one or more cells; costa subpercurrent, 1/5–1/4 width of leaf base, roughened on back by projecting cuticular thickenings or not; upper cells subquadrate, somewhat transverse elongate, few cells short rectangular, thick-walled, smooth or with faint longitudinal striations in surface view; lower and basal cells oblong-rectangular,

mostly thick-walled; alar region rather weakly differentiated, several rows of cells, cells quadrate-rounded to oblong-short rectangular. **Autoicous**. **Perigonia** just below perichaetia. **Perichaetia** terminal; outer leaves slightly longer and broader at base, inner leaves sheathing, convolute, oblong-obtuse. **Seta** to 12 mm long, slender, smooth, distally twisted. **Capsule** erect, urn ovoid to ovoid-short cylindrical, to 1.6 mm long, wrinkled, neck short; exothecial cells hexagonal to short rectangular, thin-walled; stomata at juncture of urn and neck, few, superficial; annulus absent or narrow and indistinct. **Operculum** long rostrate, oblique. **Peristome** inserted well below mouth, teeth entire, not divided, hyaline, faintly papillose. **Calyptra** cucullate, base entire, smooth and naked. **Spores** spherical, smooth to faintly papillose.

DISCUSSION. The genus is characterized by the strongly curled, crispate leaves; narrow, subpercurrent costa; longitudinal striations over and between upper laminal cells; differentiated alar cells in few rows; erect seta; slightly wrinkled capsule; insertion of peristome well below mouth; entire, hyaline and faintly papillose teeth; and entire calyptra base. Two of the more widespread north temperate species recorded from the Neotropics include *D. cirrata* (Hedw.) Lindb. ex Milde from Mexico and *D. crispula* (Hedw.) Lindb. ex Milde from Colombia; two additional species apparently endemic are *D. brunnea* Herzog from Bolivia (status unknown) and *D. fastigiata* (Mitt.) Paris from Ecuador. The species *D. calcarea* E. B. Bartram from Guatemala is *Gymnostomum jacksharpii* (H. A. Crum) B. H. Allen. *Dicranoweisia* is in need of a worldwide revision.

Dicranum (Fig. 111) - About six species in the Neotropics, *D. frigidum* Müll. Hal. is the most frequently encountered species; a genus of about 90 species distributed mostly in cool temperate regions.

HABITAT. Shaded to partly exposed sites on soil, humus, and logs; montane forests, 1600–4225 m.

DESCRIPTION. **Plants** large and often robust, forming loose or more commonly dense tufts, glossy light to dark green or golden-yellow. **Stems** erect, solitary or few branched, tomentose, usually densely so; central strand present; rhizoids whitish to dark rusty-red. **Leaves** flexuose, spreading to wide-spreading, falcate-secund or not, ovate-short lanceolate to lanceolate-subulate, 5–13 mm long, concave below, distally keeled or involute, apex narrowly long acuminate or acute, base short decurrent; margins entire or distal 1/2 serrate; costa subpercurrent to short excurrent, ca. 1/5 or less the width of leaf base, entire or toothed at back distally, in cross-section with stereid bands above and below guide cells; upper laminal cells oblong-linear, strongly porose, unistratose, smooth; basal or insertion cells golden-yellow; alar region differentiated, cells enlarged, quadrate or short to ± long rectangular, golden-brown. **Pseudoautoicous**. **Perigonia** attached to tomentum. **Perichaetia** terminal, leaves convolute, usually differentiated from stem leaves. **Seta** 1 to often 2–4 per perichaetium, elongate, 20–60 mm long, smooth. **Capsule** inclined and curved, rarely erect, urn cylindrical, 3–5 mm long, annulus absent or rarely present and persistent. **Operculum** long rostrate, often equal to urn length**. Peristome** single, inserted at mouth or nearly so, teeth distally divided to ca. ½ length, vertically striate-pitted below, distally papillose. **Calyptra** cucullate, naked. **Spores** spherical, papillose.

DISCUSSION. The genus is characterized by the flexuose, spreading, often falcate-secund leaves; narrowly winged or ridged costa; smooth, often porose upper laminal cells; well differentiated alar cells; pseudoautoicous sexual condition; frequently polysetous perichaetia; erect seta; curved, rarely erect capsule; a peristome that is positioned at or near the mouth and teeth that are divided above and striate-pitted below. *Orthodicranum*, sometimes placed in *Dicranum*, is treated as a separate genus. It is generally distinguished by the smaller stature, the frequent flagellate branches, and the erect capsule.

Eucamptodontopsis (Fig. 112) - A neotropical genus of three species, *E. brittonae* (E. B. Bartram) B. H. Allen (Costa Rica, Panama, and Venezuela), *E. pilifera* (Mitt.) Broth. (Cuba, Guadeloupe, Suriname, and Venezuela), and *E. tortuosa* H. Rob. (Guyana, Venezuela).

HABITAT. Epiphytic, on trunks and branches of trees, occasionally on soil or leaf litter; submontane to lower montane forests, 550–2400 m.

DESCRIPTION. **Plants** medium sized to rather large, forming tufts or cushions, yellowish-brown to golden or dark brown. **Stems** erect to suberect, mostly to ca. 5 cm long (to 10 cm or more long); in cross-section outer 1–2 rows of cells small, thick-walled, inner cells large, rather thick-walled, central strand weak. **Leaves** crowded, spirally contorted or erect-appressed and rugose when dry, short to long ovate-lanceolate, ca. 4–15 mm or more long, concave below, tubulose above, base decurrent or not, apex gradually long acuminate, tip hyaline or concolorous; margins incurved distally, entire to dentate or crenulate distally; costa narrow, rather faint, excurrent; lamina unistratose; laminal cells ± uniform throughout, oblong-linear, strongly porose, thick-walled; basal cells golden; alar cells in 5–12

rows, large, oblong-rectangular. **Perichaetia** terminal; leaves elongate, inner ones convolute, extending to capsules. **Seta** to 15 mm long. **Capsule** erect, urn cylindrical, to 4 mm long; exothecial cells firm-walled; stomata at urn base, superficial. **Operculum** conic-long rostrate, straight to slightly oblique. **Peristome** teeth papillose distally to throughout or smooth at base, perforate or entire. **Calyptra** cucullate, smooth and naked. **Spores** spherical, finely papillose.

DISCUSSION. The genus may be confused with *Holomitrium* and possibly *Schliephackea*; however, the former genus typically exhibits crispate, not spirally contorted, leaves, or if so then the margins are serrate, and lower and upper cells are sharply differentiated. The latter genus is pendent and with leaves distant. In South America, *Eucamptodontopsis* is often associated with tepuis. Allen (1990) has provided a short discussion of the genus and keys to the species. The three species can be differentiated as follows: *E. pilifera* — leaf apex hyaline, leaves broadly ovate-narrowly lanceolate, to 5 mm long; the two remaining species exhibit a concolorous apex and leaves linear-lanceolate from a short ovate base, 7–15 mm long; *E. brittonae* — leaves 10–15 mm long, greater than 1 mm wide at leaf base, margins faintly denticulate; and *E. tortuosa* — leaves 7–10 mm long, less than 1 mm wide at base, margins entire.

LITERATURE. Allen, B. 1990 (see family ref.).

Holodontium (Fig. 112) - A monotypic genus, *H. strictum* (Hook.f. & Wilson) Ochyra (syn.: *H. inerme* (Mitt.) Broth.) is known from Ecuador (also Tierra del Fuego and sub-Antarctica).

HABITAT. Probably on wet, rocky soil or rocks, possibly submerged; in páramo, to 4200 m.

DESCRIPTION. **Plants** medium sized, forming stiff and rigid tufts, yellowish- to golden-brown. **Stems** erect, 2.5 cm tall or more, simple or few branched; in cross-section outer 1–2 rows of cells small, thick-walled, central strand absent. **Leaves** crowded, falcate-secund, subulate from an ovate- to oblong-lanceolate base, 4–5 mm long, channeled distally, apex gradually long acuminate; margins erect, entire; costa strong, ca. 1/3 width of leaf base, excurrent, in cross-section stereid band below and above large guide cells, lamina unistratose, bistratose distally along margin, both lamina and costa appearing papillose, papillae due to cuticular thickenings; upper cells of lamina base subquadrate to shortly oblong-rectangular, thick-walled; inner basal cells quadrate to short or long rectangular, very thick-walled, outer basal cells forming an indistinct border, ca. 10 rows of linear, thin-walled cells; alar region well differentiated, extending to costa, cells enlarged, thin-walled and hyaline to somewhat thick-walled and reddish. **Autoicous**. **Perichaetia** terminal, leaves similar to slightly larger to those of stem. **Seta** elongate, 10–15 mm long, erect, smooth. **Capsule** erect, exserted, urn broadly obloid to short-cylindrical, 1–1.8 mm long, stomata few at urn base, annulus absent. **Operculum** long rostrate. **Prostome** present, hyaline, smooth. **Peristome** set below mouth, teeth entire, coarsely papillose on both surfaces. **Calyptra** cucullate, smooth, base entire. **Spores** spherical, papillose.

DISCUSSION. The genus is characterized by the rather rigid, wiry plants of aquatic habitats; falcate-secund, ovate-to oblong-subulate leaves; entire, bistratose margins; narrow costa; papillose appearance of lamina and costa; indistinct border along basal margin; well differentiated alar cells; erect, elongate seta; erect, smooth capsule; presence of a smooth, hyaline prostome; peristome set below mouth; and both surfaces of the teeth papillose. The genus is only known from the Neotropics from two Ecuadorian collections. It is very likely to be found in Peru and Bolivia. *Holodontium* is asserted by Ochyra (1995) to be a member of the Seligeriaceae based on the double, haplolepidous peristome, but assigned the subfamily Dicranoweisioideae, sharing with *Dicranoweisia* the strongly papillose peristome. A re-assessment is clearly needed of the dicranoid genera and phenetically associated families.

LITERATURE. Ochyra, R. 1995. Antipodal mosses: I. A revision of the genus *Holodontium* (Seligeriaceae). Fragmenta Floristica et Geobotanica 38: 75–98 [illustrations, maps].

Holomitrium (Fig. 112) - About 15 species in the Neotropics; a genus of 50 species mostly associated with the Southern Hemisphere, in both tropical and temperate regions.

HABITAT. Epiphytic on branches and trunks of trees and shrubs, rather frequent in canopy; mostly from lower to upper montane forests, uncommon in the lowlands (except possibly *H. aboreum* Mitt.), from near sea level to 3950 m.

DESCRIPTION. **Plants** medium sized to rather large, forming dense tufts, dark green, yellowish-green or golden-brown. **Stems** erect, few to several branched, usually densely tomentose; central strand present. **Leaves** crowded, crispate or flexuose, loosely erect-spreading when wet, narrowly lanceolate or subulate from a narrow to broad ovate or obovate base, sheathing or not, keeled or channeled above, concave below; margins plane, occasionally undulate, sharply serrate, less often dentate, crenulate, or entire, occasionally bistratose; costa usually strong, percurrent to short excurrent, ca. 1/4 or less width of leaf base, often toothed distally on back, in cross-section stereid

bands above and below guide cells, epidermal layer differentiated or not; limb (above base) cells thick-walled, usually appearing in rows, quadrate, subquadrate, and irregular to sinuose, or elongate and strongly porose; base cells (lower and basal) elongate and strongly porose; alar cells differentiated, large and mostly short rectangular, rusty-red or -brown, adjacent cells between costa often hyaline, lax and fragile. **Pseudoautoicous**. **Perigonia** bud-like, attached to stem or leaf tomentum. **Perichaetia** terminal, leaves usually very long, reaching to or exceeding capsule, convolute. **Seta** 1(–2) per perichaetium, elongate, smooth. **Capsule** erect, urn ovoid-short to long cylindrical, smooth, exothecial cells thick-walled, stomata at base of urn, superficial; annulus absent. **Operculum** conic-rostrate. **Peristome** teeth inserted below urn mouth, somewhat divided or entire, perforate, usually papillose. **Calyptra** cucullate, smooth, naked, base entire. **Spores** lightly papillose.

DISCUSSION. The genus is characterized by tufted epiphytic plants; leaves mostly crispate or spirally contorted, then margins distinctly serrate; narrow costa; upper and lower laminal cells sharply differentiated, infrequently similar; alar cells generally well differentiated; elongate perichaetial leaves reaching or exceeding the smooth, erect capsule; absence of an annulus; and partially divided or entire, perforate, papillose peristome.

Holomitrium is similar to *Eucamptodontopsis* (see discussion under that genus), and also *Schliephackea* which differs by the pendent habit and distantly spaced leaves. *Breedlovea chiapensis* H. A. Crum, a monotypic genus described from Chiapas, Mexico (Crum, 1986), is identical to *Holomitrium pulchellum* Mitt., as originally noted by B. Allen (1994, see general ref.), and confirmed by examination of the type at MO.

LITERATURE. Allen, B. 1990. A preliminary treatment of the *Holomitrium* complex (Musci: Dicranaceae) in Central America. Tropical Bryology 3: 59–71 [keys]. - Crum, H. 1986. Taxonomic and nomenclatural addenda to the Mexican moss flora. The Bryologist 89: 23–27. - Hegewald, E. 1978. Critical notes on *Holomitrium* (Dicranaceae) from the Antilles. The Bryologist 81: 524–531 [keys, illustrations].

Hygrodicranum (Fig. 113) - Two species in the Neotropics, *H. bolivianum* Herzog (Ecuador to Bolivia), and *H. herrerai* R. S. Williams (Peru); a genus of three species, the third occurring in the Falkland Islands.

HABITAT. On rocks, associated with streams; high elevations in the páramo and puna, 3550–4600 m.

DESCRIPTION. **Plants** rather elongate, slender and wiry, forming tufts, yellowish-brown or blackish. **Stems** erect, to 11 cm tall, few branched by innovations; in cross-section outer 1–3 rows of cells small, very thick-walled, inner cells large, thin-walled, central strand well developed. **Leaves** rather distant, loosely erect to spreading, tips flexuose and curled, long and stoutly subulate from a short ovate-triangular base, to 4 mm long, lamina base concave, channeled above, apex bluntly acute, tips often eroded or broken; margins plane below, erect above expanded lamina, entire; costa long excurrent, ca. 2/3 width of leaf base, in cross-section stereids weak or absent above guide cells, below well developed; lamina partially to full bistratose in distal lamina; laminal cells above short to somewhat long oblong-rectangular, juxtacostal cells at mid region larger, toward margin narrower; basal cells oblong rectangular; alar region undifferentiated. **Dioicous**. **Sporophytes** not observed.

DISCUSSION. *Hygrodicranum* is one of the few aquatic dicranoid genera, all rare in the Neotropics. The genus is characterized by leaves long-subulate from a short ovate-triangular base, appearing long excurrent, fully to partially bistratose above; stereids absent or weakly developed above guide cells; and undifferentiated alar cells. *Holodontium* is also aquatic, but differs by the often falcate-secund leaves, and well developed stereids above guide cells and below.

Kingiobryum (Fig. 113) - A monotypic genus, with *K. paramicola* H. Rob. confined to the Cordillera Oriental of Colombia and the Cordillera de Mérida of Venezuela.

HABITAT. On soil or thin soil over rock; humid páramos, at elevation from 3500–4200 m.

DESCRIPTION. **Plants** forming dense tufts, green to reddish-brown, or terminal shoots green and reddish-brown below. **Stems** erect, to 3.5 cm tall, few branched by innovations, weakly radiculose below; in cross-section hyalodermis present, outer 2–3 rows of cells small, thick-walled, central strand present. **Leaves** crowded, lance-acuminate from a sheathing obovate base, to 3.8 mm long; margins plane below, inflexed and channeled above, entire; costa strong, subpercurrent, ca. 1/4 width of leaf base, in cross-section stereid bands above and below guide cells; distal sheath and limb cells thick-walled, smooth or bulging-papillose at wall ends; lower and basal sheath cells differentiated, inner juxtacostal cells enlarged, rectangular, hyaline and fragile, marginal cells appearing to form a border of thick-walled narrow rectangular or fusiform cells. **Dioicous**, apparently. **Perichaetia** terminal, inner leaves sheathing seta, smaller than stem leaves, oblong-oval. **Seta** to 20 mm long, twisted. **Capsule**

erect, urn obloid, to 2 mm long; annulus compound, 2–3 rows. **Operculum** long-rostrate. **Peristome** apparently absent. **Calyptra** not observed. **Spores** spherical, weakly papillose.

DISCUSSION. The distinguishing feature of this genus is the cancellinae-like cells that are enlarged, hyaline and porose and similar to those of the Calymperaceae. The generic name honors Robert Merrill King (1930–), a United States botanist, specialist on neotropical Asteraceae.

LITERATURE. Zander, R. H. & A. M. Cleef. 1982. Studies on Colombian cryptogams XVI. Taxonomy and habitat of *Kingiobryum paramicola* (Dicranaceae, Musci). Proceedings of the Koninklijke Nederlandse Akademie van Wetenschappen series C, 85: 627–634 [illustrations, map].

Leucoloma (Fig. 113) - At least 12 species recorded for the Neotropics; about 100 species with a pantropical, primarily African and Madagascaran distribution.

HABITAT. Epiphytic, occasionally on logs or rock; lowland moist forests to montane forests, from near sea level to 2500(3650) m.

DESCRIPTION. **Plants** small to medium sized, forming rather soft and fragile loose to dense tufts, dark green to yellowish-green. **Stems** erect to suberect, few branched; central strand absent (at least in *L. cruegerianum*). **Leaves** loosely erect-spreading, flexuose and occasionally falcate when dry, lanceolate-linear or -subulate, base ± ovate to narrowly oblong, concave below, incurved to subtubulose above, apex broadly acute or acuminate, base subauriculate; margins entire to serrulate in distal 1/2 or less, usually toothed at apex, limbate, border extending from base to 1/2 or nearly the full length of the lamina; costa weak and slender, in cross-section stereids usually above and below guide cells; upper cells oblong-oval to quadrate, smooth or papillose on back; marginal cells long linear, hyaline and forming a border of several rows; lower and basal cells elongate, linear to rectangular, mostly smooth; alar cells differentiated, large and rectangular, golden-brown. **Dioicous**. **Perichaetia** terminal. **Seta** elongate, rather slender and occasionally flexuose. **Capsule** erect, urn obloid; annulus absent. **Operculum** rostrate. **Peristome** teeth divided ca. ½ length above, trabeculate below, distally papillose. **Calyptra** cucullate, naked, smooth below, distally roughened. **Spores** spherical, smooth.

DISCUSSION. The principal distinguishing feature in *Leucoloma* is the hyaline border of linear cells in combination with the short, pluripapillose upper laminal cells. *Dicranoloma* also has a hyaline border, but in that genus the laminal cells are elongate, strongly porose and smooth.

LITERATURE. La Farge–England, C. 1998. The infrageneric phylogeny, classification, and phytogeography of *Leucoloma* (Dicranaceae, Bryopsida). The Bryologist 101: 181–220.

Macrodictyum (Fig. 114) - A neotropical genus of two species; *M. wrightii* (Sull.) E. H. Hegew. (Cuba), and *M. proligerum* (Mitt.) E. H. Hegew. (Cuba, Dominican Republic and Brazil).

HABITAT. Epiphytic, possibly on logs; subtropical forests?, apparently at moderately low elevations, ca. 450–525 m.

DESCRIPTION. **Plants** rather small to medium sized, forming tufts, dark green to yellowish brown or golden brown. **Stems** erect, to 3 cm tall, few branched, tomentose below; in cross-section outer 1–2 rows of cells small, thick-walled, inner cells large, thin-walled, central strand weak; rhizoids rusty red, smooth. **Leaves** crowded, enrolled appressed, somewhat spirally curved or not when dry, erect-spreading when wet, narrowly oblong-lanceolate to oblong or lingulate, to 4 mm long, apex truncate-rounded and cuspidate to short acuminate or acute; margins plane, distal 1/3 sharply serrate, irregularly so; costa strong, short excurrent; lamina unistratose; apical cells oblong-rhomboidal; median cells oblong-rectangular to subquadrate, weakly to strongly porose; basal cells oblong-linear, strongly porose, golden-yellow to -brown; alar region undifferentiated or distinct, intramarginal cells short rectangular, hyaline or golden brown, thin- to thick-walled. **Perichaetia** terminal; leaves sheathing ca. 1/3–1/2 seta length. **Seta** to 15 mm long, somewhat flexuose, smooth. **Capsule** exserted, erect, urn ovoid-cylindrical to cylindrical, symmetric, exothecial cells thick-walled; stomata at urn base, superficial. **Operculum** conic-long rostrate. **Peristome** teeth papillose. **Calyptra** not observed. **Spores** slightly roughened.

DISCUSSION. *Macrodictyum* is segregated from *Holomitrium* based primarily on the gametophytic features of non-crispate, narrowly oblong-lanceolate or lingulate leaves (Hegewald, 1978). The species can be differentiated as follows: *M. wrightii* — leaves to 4.5 mm long, apex acute or short acuminate, and *M. proligerum* — leaves shorter, to 3 mm long, apex obtuse-rounded or truncate

LITERATURE. Hegewald, E. 1978. Critical notes of *Holomitrium* (Dicranaceae) from the Antilles. The Bryologist 81: 524–531 [keys, illustrations].

Microcampylopus (Fig. 114) - A single neotropical species, *M. curvisetus* (Hampe) Giese & J.-P. Frahm, widespread but locally rare in the Neotropics (absent from the lowlands); a small pantropical montane genus of three species.

HABITAT. On soil, often associated with disturbed sites; open lower to possibly high montane, from near sea level to 2650 m.

DESCRIPTION. **Plants** small (to 10 mm), forming low, loose tufts, yellow-green. **Stems** erect, few branched, central strand present. **Leaves** erect-spreading wet or dry, subulate from an ovate to ± obovate base, to 4 mm long, to 0.6 mm wide, base concave and sheathing, distally erect or channeled, acuminate with a blunt serrate tip; margins entire (except at apex); costa long excurrent, ca. 1/3 width of leaf base; laminal cells smooth, median and distal sheath cells narrowly long rectangular; basal cells enlarged, short-rectangular; alar cells undifferentiated. **Dioicous**. **Perichaetia** terminal, leaf bases oblong and sheathing seta. **Seta** curved and twisted distally, to 3 mm long (equal to slightly shorter than perichaetial leaves), yellow, smooth. **Capsule** somewhat emergent to immersed, with urn ovoid, ca. 1 mm long; exothecial cells irregularly oblong and thick-walled; annulus present, compound. **Operculum** conic-rostrate, oblique. **Peristome** teeth vertically striate below, divided ca. 2/3 length and perforate, rusty-red below, distally whitish. **Calyptra** cucullate, naked, base ± entire. **Spores** coarsely papillose, papillae large.

DISCUSSION. The genus is distinguished by small habit, a rather long subulate leaves from a concave, sheathing obovate base, undifferentiated alar cells, short, curved seta (to 3 mm), slightly emergent capsules, vertically striate peristome that is divided to 2/3 leghth, and absence of ciliate hairs at the base of the calyptra.

LITERATURE. Giese, M. & J.-P. Frahm. 1985. A revision of *Microcampylopus* (C. Muell.) Fleisch. Lindbergia 11: 114–124 [keys].

Microdus (Fig. 115) - About 22 species in the Neotropics, possibly 10 or fewer; a pantropical genus of far fewer than the some 40 species recognized.

HABITAT. On soil, apparently not uncommon in secondary vegetation associated with human disturbance, e.g., pastures and road banks; open submontane to possibly mid montane, from near sea level to ca. 2200 m.

DESCRIPTION. **Plants** small, solitary or forming short tufts. **Stems** erect; central strand present. **Leaves** erect to somewhat appressed, ovate- to triangular-lanceolate or ± subulate, or narrowly oblong-ligulate, to 2(–4) mm long, apex acute to obtuse-rounded, entire, dentate or serrate; margins partially inflexed to reflexed, entire to distally serrate; costa rather strong, ending below apex, 1/4–1/5 width of leaf base; median cells rectangular to subquadrate, smooth; lower and basal cells larger, rectangular; alar region undifferentiated. **Autoicous**. **Perichaetia** terminal, leaves similar or larger and elongate. **Seta** elongate, to 6 mm long, smooth, twisted or not. **Capsule** erect or suberect to horizontal; urn short ovoid-cylindrical to globose, 0.7–1.2 mm long; exothecial cells thick-walled; annulus present. **Peristome** teeth usually less than 200 µm, often to 120 µm, rarely absent, blunt, entire or divided irregularly to near base, often perforate, papillose to vertically striate-papillose. **Calyptra** cucullate, naked and smooth, base entire. **Spores** lightly or coarsely papillose.

DISCUSSION. The genus is essentially a diminutive *Dicranella* with mostly erect leaves, an often broadly acute to obtuse, dentate or serrate apex, and a short, generally papillose peristome, to 120 µm, or rarely longer. The neotropical species of this genus are poorly known, partly due to their inconspicuousness. Various authors include *Microdus* in *Dicranella*. Ochrya (1997) has established that *Microdus* should be replaced by the name *Leptotrichella*.

LITERATURE. Ochyra, R. 1997. *Leptotrichella* replaces *Microdus* (Musci, Dicranaceae). Fragmenta Floristica et Geobotanica 42: 559—565.

Oreoweisia (Fig. 115) - Six species in the Neotropics; a genus containing about 15 species with a pantropical distribution and extending into temperate regions.

HABITAT. On soil; mid to more commonly high open montane, zacatonal, páramo, and puna, (1200)2700–4600 m.

DESCRIPTION. **Plants** forming loose to dense tufts, green to yellowish-brown or golden. **Stems** erect, to 3 cm tall, few to several branched, radiculose below; in cross-section outer 1–2 rows of cells thick-walled, inner cells larger, thin-walled, central strand present; rhizoids smooth to appearing lightly papillose. **Leaves** crispate, distally curled when dry, loosely erect-spreading from an appressed based when moist, oblong-ligulate, ca. 1.5–3.5 mm long, apex acute to rounded acute, slightly decurrent; margins recurved, distal 1/4–1/2 serrate-dentate; costa strong, ending well below apex, ca. 1/4–1/5 width of leaf base, projecting on back; median cells subquadrate to quadrate or short rectangular and oblate, smooth or mammillose to papillose; lower and basal cells long rectangular, smooth; alar cells undifferentiated. **Autoicous** or paroicous. **Perichaetia** terminal but appearing lateral, leaf base clasping seta. **Seta** 4–7 mm long, smooth, often twisted distally. **Capsule** erect, urn ovoid to ovoid-cylindrical, to 1.5 mm long, smooth, neck, distinct, short; stomata at urn base, superficial; exothecial cells thick-walled, mostly irregularly elongate; annulus persistent. **Operculum**

conic-mammillate or short rostrate, erect or somewhat oblique. **Peristome** positioned below the mouth, teeth often appearing reduced, smooth to faintly striate, perforate. **Calyptra** cucullate, smooth, base mostly entire. **Spores** coarsely papillose.

DISCUSSION. The genus is distinguished by the presence of a stem central strand, oblong-ligulate leaves, acute to rounded-acute apex, rounded, subquadrate laminal cells, undifferentiated alar cells, smooth, erect capsules, and somewhat reduced peristome. *Rhabdoweisia* is rather similar to *Oreoweisia* but differs by the 8-ribbed capsule, plane to slightly recurved leaf margin, and absence of a stem central strand. The two common species can be differentiated as follows: *O. brasiliensis* Hampe (Venezuela to Bolivia; southeastern Brazil) — cells of upper lamina smooth to low-convex; and *O. erosa* (Müll. Hal.) Kindb. (Mexico, Venezuela to Bolivia; Africa) — cells of upper lamina papillose to conic-mammillose.

LITERATURE. Griffin, D. 1986a. *Oreoweisia* (Dicranaceae, Musci) in tropical America: An annotated key to species. Cryptogamie, Bryologie, Lichénologie 7: 433–438. - Griffin, D. 1989. *Oreoweisia erosa* (C. Muell.) Kindb., an African-neotropical disjunct. Cryptogamie, Bryologie, Lichenologie 10: 297–300.

Orthodicranum (Fig. 115) - Three species in the Neotropics, all are widespread in the Northern Hemisphere. *Orthodicranum flagellare* (Hedw.) Loeske, is the most common species in the Neotropics (Mexico, Central America, West Indies, and Colombia), with *O. montanum* (Hedw.) Loeske (Peru), and *O. rhabdocarpum* (Sull.) Holz. (Mexico, Central America, West Indies) being less common; *Orthodicranum* is a segregate genus of *Dicranum*, with about nine species primarily of the Northern Hemisphere.

HABITAT. On decaying logs and possibly tree trunks; montane forests, including *Quercus* woodlands, apparently to near sea level at higher neotropical latitudes, to 2000–3300 m.

DESCRIPTION. **Plants** small to somewhat medium sized, forming dense tufts, green to yellowish-brown. **Stems** erect, tomentose, flagellate branches usually present with leaves scale-like; in cross-section central strand present. **Leaves** spreading to strongly falcate-secund, ovate-long lanceolate, 2–3 mm long, apex acute to acuminate; margins distally concave-tubulose, weakly serrulate distally; costa percurrent to short excurrent, ca. 1/4–1/3 width of leaf base, in cross-section stereids above and below guide cells, costa back distally roughened or sharply toothed; upper cells subquadrate to short rectangular, smooth, thick-walled; lower cells short to long rectangular; alar region differentiated, cells extending to near costa, enlarged, quadrate to short rectangular, reddish-brown. **Dioicous**. **Perichaetia** terminal. **Seta** elongate, twisted. **Capsule** ± erect, urn cylindrical, slightly asymmetric, when dry slightly furrowed. **Operculum** conic-long rostrate, oblique. **Peristome** teeth with 2–3 divisions ca. 1/2 length, vertically pitted-striate below, papillose distally. **Calyptra** cucullate, naked and smooth. **Spores** lightly papillose.

DISCUSSION. *Orthodicranum* is characterized by the generally smaller plants, leaves 3 mm or less long, presence of flagellate branches (rarely lacking), and erect capsules. The genus is often placed in the genus *Dicranum* which is possibly justified if members are solely derived from within that genus. A further species can be included here, originally described from Peru as a *Dicranum*, *D. gregoryi* B. H. Allen (cf. Allen, 1988).

LITERATURE. Allen, B. H. 1988. A contribution to the moss flora of Peru, including a new species of *Dicranum*. The Bryologist 91: 91–94.

Paraleucobryum (Fig. 116) - Two species in the Neotropics, *P. enerve* (Thed. ex Hartm.) Loeske (Mexico, Costa Rica, rather widespread in the Northern Hemisphere) and *P. longifolium* ssp. *brasiliense* (Broth.) P. Müller & J.-P. Frahm (southeastern Brazil); an essentially holarctic genus of four species.

HABITAT. Typically on acidic soils, or soil covered rocks and rock crevices; high montane to alpine, 2500–4000 m.

DESCRIPTION. **Plants** somewhat medium sized, forming dense tufts, glossy yellowish to grayish green. **Stems** erect, to 2.5 cm tall, few branched, radiculose below; in cross-section outer 1–2 rows of cells small, thick-walled, inner cells large, firm and thick-walled, central strand weak. **Leaves** crowded, erect-spreading to falcate, long lanceolate, to 4–12 mm long, apex gradually acuminate; margins erect, subtubulose distally, entire or serrate at tips; costa excurrent, ca. (2/3–)3/4–4/5 width of leaf base, smooth or slightly ridged on back, in cross-section leucocysts in one layer above and below a median chlorocyst layer, or leucocysts and chlorocysts alternating dorsally, stereids absent; upper cells long linear-rectangular, basal cells larger, rectangular, weakly porose or not; alar region well developed, cells inflated, extending into costa. **Dioicous**. **Perichaetia** terminal, leaves sheathing, somewhat subulate from a broad ovate base. **Seta** erect, to 20 mm long, smooth. **Capsule** erect, urn cylindrical, to 2.5 mm long; exothecial cells thick-walled; stomata few at urn base, superficial; annulus

absent or in 2 rows and deciduous. **Operculum** long rostrate. **Peristome** teeth divided to ½ length or more, cross- to obliquely-striate below, papillose distally. **Calyptra** cucullate, smooth, base entire. **Spores** spherical to ellipsoid, papillose.

DISCUSSION. The genus is distinguished by the very broad costa, absence of stereids, presence of chlorocysts between upper and lower leucocysts or alternating with them below, elongate and narrow upper laminal cells, well defined alar cells, erect seta and capsule, divided peristome, and entire calyptra base. Sporophytes are apparently unknown from neotropical specimens. Reports of *P. albicans* (Schwägr.) Loeske from several localities in South America refer to *Leucobryum megalophyllum* Mitt. (cf. Frahm, 1991).

LITERATURE. Frahm, J.-P. 1991 (see family ref.). - Müller, P. & J.-P. Frahm. 1987. A review of the Paraleucobryoideae (Dicranaceae). Nova Hedwigia 45: 283–314.

Pilopogon (Fig. 116) - Six neotropical species, the most common being *P. guadeloupensis* (Brid.) J.-P. Frahm; a genus of eight species, in addition to the neotropical species, an additional species in Chile and another in central Africa.

HABITAT. Mostly exposed sites on soil and rock, not uncommon in secondary vegetation; open submontane to high montane, zacatonal, páramo and puna, from near sea level at higher neotropical latitudes, to more commonly at 1000–4900.

DESCRIPTION. **Plants** somewhat small to medium sized, forming loose to dense tufts, green, yellowish-green, to golden-brown. **Stems** erect and slender, few to several branched, ± radiculose below; central strand present. **Leaves** erect to appressed, slightly erect-spreading when wet, subulate from a lanceolate or oblong base, concave below, often channeled above, apex bluntly acute and serrate; margins entire, occasionally serrate at juncture with costa distally; costa strong, short to long excurrent, tip hyaline or concolorous, (1/3–)1/2 width of leaf base, in cross-section stereids above and below guide cells, smooth or weakly ribbed on back; upper laminal cells thick-walled, oblique, rhomboidal, oval, or short rectangular; lower and basal cells elongate, mostly long rectangular and thin-walled; alar cells undifferentiated or weakly differentiated. **Dioicous**. **Perichaetia** terminal, leaves elongate, sheathing seta, often 1/2 or more length of seta. **Seta** elongate, erect, often distally roughened or weakly papillose. **Capsule** erect, urn ovoid-short to long cylindrical, exothecial cells thick-walled, stomata absent; annulus present. **Operculum** long rostrate, erect. **Peristome** teeth entire to divided to near base, papillose. **Calyptra** cucullate, smooth and naked, base fringed with long hairs (ciliate). **Spores** usually lightly papillose.

DISCUSSION. The genus is characterized by the rather slender plants; lanceolate-subulate leaves; excurrent costa with stereids above and below; alar cells weakly differentiated or undifferentiated; sheathing perichaetial leaves to ca. 1/2 the seta length; smooth to distally roughened, erect seta; erect capsule; absence of stomata; presence of an annulus; entire to deeply divided, papillose peristome teeth; and basely ciliate, smooth calyptra. *Pilopogon* may be confused with *Campylopus*, but in that genus the perichaetial leaves are not sheathing, the seta is cygneous when moist, and the peristome teeth are striate; also many of the species of *Campylopus* exhibit a broader costa and differentiated alar cells.

LITERATURE. Frahm, J.-P. 1983. A monograph of *Pilopogon* Brid. Lindbergia 9: 99–116 [keys, illustrations, maps]. - Frahm, J.-P. 1991 (see family ref.).

Polymerodon (Fig. 116) - A monotypic genus, *P. andinus* Herzog is only known from Bolivia.

HABITAT. On soil or soil covered rocks, associated with wet sites; puna, 3600 m.

DESCRIPTION. **Plants** medium sized, forming dense tufts, yellowish-brown to golden brown. **Stems** erect, to 5 cm tall, few branched, somewhat tomentose below; in cross-section 1(–2) outer rows of cells small, thick-walled, inner cells large, thin-walled, central strand well developed, often collapsed. **Leaves** crowded, loosely erect with tips curved or flexed when dry, erect-spreading when wet, stoutly lanceolate-subulate from a short obovate or short oblong base, to 1.4 mm long, concave at base, channeled above, apex rather bluntly acute-rounded; margins erect above, plane below, entire or weakly denticulate by adjoining cell walls; costa stoutly short excurrent, ca. 1/4 width of leaf base; cells near shoulder subquadrate to short rectangular, 1:1–3; basal cells oblong-rectangular; alar region undifferentiated. **Dioicous**? **Perichaetia** terminal, leaves larger, otherwise similar. **Seta** to 20 mm long, flexuose, stout, smooth. **Capsule** erect, urn pyriform to broadly ovoid, to 1 mm long, mouth wide when deoperculate; exothecial cells thick-walled; stomata few at urn base, superficial; annulus apparently undifferentiated, or possibly weakly developed and persistent. **Operculum** conic long rostrate, oblique. **Peristome** teeth divided in distal 1/2 or less, appearing smooth. **Calyptra** cucullate, smooth and naked. **Spores** spherical, faintly papillose.

DISCUSSION. The genus is characterized by a habit of dense tufts; narrowly lanceolate leaves from an obovate or short oblong base with a bluntly acute-rounded apex; stoutly short excurrent costa;

undifferentiated alar region; conspicuously elongate, erect seta; pyriform or broadly ovoid, erect capsule; few stomata; absence of an annulus; and smooth peristome. This genus appears to be similar to the concept of *Anisothecium* circumscribed by Allen (1994, see gen. ref.). The peristome teeth are at least 530 µm long.

LITERATURE. Herzog, T. 1910. Beiträge zur Laubmoosflora von Bolivia. Beihefte zum Botanischen Centralblatt 26: 45–102.

Pseudohyophila (Fig. 117) - A monotypic genus, *P. peruviana* (R. S. Williams) Hilp. is presently known only from Juliaca, Peru.

HABITAT. On sandstone rock; puna region, at 3820 m.

DESCRIPTION. **Plants** medium sized, forming dense tufts, greenish-brown above, brown below. **Stems** erect, to 2 cm tall, few branched, weakly tomentose below; in cross-section outer row of cells small, thick-walled, inner cells large, thin-walled, central strand well developed. **Leaves** crispate when dry, erect-spreading when wet, lanceolate to ovate-lanceolate, to 2.4 mm long, somewhat concave below, keeled above, apex rather bluntly acute; margins plane to recurved on one side, entire; costa strong, subpercurrent, ca. 1/5 width of leaf base, in cross-section few stereids below guide cells; lamina unistratose or bistratose in patches, laminal cells smooth, mostly firm-walled, upper cells quadrate to short rectangular; upper marginal cells subquadrate or more often oblate oblong-rectangular; inner lower and basal cells rather large, short to long rectangular, toward margin cells progressively quadrate. **Autoicous**. **Perichaetia** terminal. **Seta** to 5 mm long. **Capsule** obloid, to 1.5 mm long; exothecial cells thin-walled; stomata at urn base, superficial; annulus large, fragile. **Operculum** long rostrate, oblique. **Peristome** absent. **Calyptra** cucullate, smooth and naked. **Spores** spherical, roughened.

DISCUSSION. The genus is characterized by ovate-lanceolate leaves, crispate when dry, concave below, keeled above, entire, mostly plane margins, narrow costa with few stereids below guide cells, smooth laminal cells that are quadrate above and unistratose or partially bistratose, somewhat enlarged and rectangular below, undifferentiated alar region, oblate oblong marginal cells above, rather short erect seta, and smooth, erect, gymnostomous capsule. Originally placed in *Hyophila* (Pottiaceae) by Williams (1903), and later associated with the Grimmiaceae. Churchill (1981, see family ref. under Grimmiaceae) excluded *Psuedohyophila* from the Grimmiaceae, and Zander (1993, see family ref. under Pottiaceae) likewise excluded the genus from the Pottiaceae, suggesting placement in the Dicranaceae, with many features shared with *Dicranoweisia*. Further studies are warranted to establish the relationship of this taxon, including consideration of it placement in the Ditrichaceae.

LITERATURE. Williams, R. S. 1903. Bolivian mosses. Part 1. Bulletin of the New York Botanical Garden 3: 104–134.

Rhabdoweisia (Fig. 117) - Three species in the Neotropics, *R. crenulata* (Mitt.) H. Jameson, *R. crispata* (With.) Lindb., and *R. fugax* (Hedw.) Bruch, Schimp. & W. Gümbel; a genus of eight species distributed in temperate and tropical montane regions.

HABITAT. On soil, also in rock crevices; open high montane to zacatonal, páramo, or puna, 2200–4300 m.

DESCRIPTION. **Plants** rather small, forming short tufts, green. **Stems** erect, to ca. 10 mm, few branched; central strand absent. **Leaves** somewhat crispate when dry, lanceolate-linear to oblong-lanceolate, 2–3 mm long, apex acuminate to acute or obtuse; margins plane to slightly recurved below, entire to irregular denticulate or serrate; costa ending below apex, ca. 1/4–1/5 width of leaf base; median and upper cells quadrate-rounded or transversely-short elongate, smooth; lower and basal cells elongate, rather lax; alar region undifferentiated. **Autoicous**. **Perichaetia** terminal, leaves larger or similar in size to stem leaves. **Seta** rather short to elongate, 2.5–5 mm long, smooth. **Capsule** erect, urn oval to short cylindrical, to 1 mm long, when dry 8-ribbed; exothecial cells short to long rectangular, walls firm; stomata 1-few at urn base, superficial; annulus absent or weakly differentiated and persistent. **Operculum** short rostrate, oblique. **Peristome** reduced, teeth smooth or obliquely striate, undivided. **Calyptra** cucullate, smooth and naked. **Spores** lightly to rather coarsely papillose.

DISCUSSION. The genus is characterized by linear- to oblong-lanceolate leaves, crispate when dry, plane to weakly recurved on one side, subentire to denticulate or serrulate distally; subquadrate upper laminal cells; undifferentiated alar cells; 8-ribbed capsule; and smooth to faintly obliquely striate peristome. The three neotropical species can be differentiated by the following: *R. crenulata* — leaves irregularly serrate, apex acute to obtuse; *R. fugax* — leaves entire to subentire, apex acuminate; and *R. crispata* — leaves irregularly serrulate, apex acuminate.

LITERATURE. Lawton, E. 1961. A revision of the genus *Rhabdoweisia*. The Bryologist 64: 140–155 [keys].

Schliephackea (Fig. 117) - A neotropical genus of two species, *S. meteorioides* (R. S. Williams) Broth. (Costa Rica, Panama, Colombia) and *S. prostrata* Müll. Hal. (Chocó of Colombia and Ecuador).

HABITAT. Epiphytic on branches and trunks of trees; moist to wet submontane to upper montane forests, 700–3000 m.

DESCRIPTION. **Plants** usually forming long loose pendent wefts, yellowish-green to golden. **Stems** slender and lax, reddish-brown; central strand weak. **Leaves** distant, wide-spreading, twisted and contorted, ovate-lanceolate to narrowly lanceolate-setaceous, 7–14 mm long, concave to concave-enrolled below, distally broadly enrolled to ± keeled, apex flexuose, narrowly acuminate, base clasping stem; margins plane or enrolled below, sharply serrate distally, serrulate to near base; costa percurrent to short excurrent, ca. 1/5 width of leaf base; laminal cells smooth, upper and median cells short to long rectangular, walls entire to weakly or strongly porose; lower and basal cells narrowly rectangular to linear, porose; alar region well differentiated, large, cells subquadrate to short rectangular, golden-red to yellowish-brown. **Autoicous** (pseudoautoicous). **Perichaetia** terminal, leaves sheathing. **Seta** elongate, to 14 mm long. **Capsule** erect, urn cylindrical, to 2.5 mm long. **Operculum** long rostrate. **Peristome** teeth papillose. **Calyptra** cucullate, naked and smooth.

DISCUSSION. *Schliephackea* is a genus guaranteed to keep you guessing as to what it might be until examined closely. The single unique feature of the genus is the pendent habit, an oddity for the Dicranaceae, at least in the New World. This is the moss genus that comes closest to being a Chocó endemic, although it extends from submontane to upper montane forests. The name honors Karl Schliephacke, colleague and personal friend of Johan Karl Müller. The two species can be differentiated by the following: *S. meteorioides* — leaves ovate-lanceolate, 7–10 mm long, 2–2.2 mm wide, narrowly acuminate above; upper laminal cells rounded-rectangular, strongly porose; and *S. prostrata* — leaves narrowly lanceolate-linear, 10–14 mm long, to 1 mm wide, apices long setaceous; upper laminal cells linear, weakly porose.

LITERATURE. Allen, B. 1990 (see ref. under *Holomitrium*). - Williams, R. S. 1913 (see family ref.).

Sclerodontium (Fig. 118) - A single species in the Neotropics, *S. clavinerve* (Müll. Hal. ex Broth.) H. A. Crum, from southeastern Brazil (also Australia); the only other species of this genus is from Australasia.

HABITAT. On rocks; at elevations from 100–500 m.

DESCRIPTION. **Plants** medium sized, forming mats, dull olive green or yellowish-green. **Stems** spreading, rather rigid, branches distally subascending and curled; in cross-section outer 2–3 rows of cells small, thick-walled, rusty red, inner cells larger, thin- to thick-walled, central strand weak or absent. **Leaves** often secund when dry, crowded, broadly lanceolate to ovate-lanceolate, 1.8–2.2 mm long, to 0.9 mm wide, apices acuminate or appearing acute, tips mostly swollen and deciduous, a few distal branch leaves with short to rather long hyaline, smooth awns; margins distally enrolled, limbate; costa percurrent to short excurrent; laminal cells subquadrate to short rectangular, extending in several rows along margin to alar region (narrower along both margin and costa above), multifid unipapillose on back, sinuose, thick-walled, juxtacostal cells in lower 1/4–1/3 smooth, nearly oblong-linear to -long rectangular; marginal cells long linear, smooth and hyaline, forming a border of 3–4 rows near midleaf, ending below apices and near base in 1–2 rows; alar region differentiated, cells enlarged, quadrate to short oblong-rectangular, reddish-orange, extending to near costa. **Sexual** condition and sporophytes unknown.

DISCUSSION. Distinguishing features for the genus include the spreading habit with distal stems and branches subascending and curled; hyaline or broken leaf tips; hyaline bordered margins (to midleaf) that are distally enrolled; sinuose, single multifid papillae over cell lumen and enlarged; reddish-orange alar cells that extend to near the costa. In aspect plants appear pleurocarpic, but leaf features are characteristic of the Dicranaceae. The deciduous leaf tips likely account for the dispersion of this species via asexual reproduction. The recently used name *Dicnemoloma* is replaced by the older name *Sclerodontium*.

LITERATURE. Crum, H. 1986. A survey of the moss genus *Sclerodontium*. Hikobia 9: 289–295.

Sphaerothecium (Fig. 118) - Two species in the Neotropics, *S. phascoides* (Hampe) Hampe only known from the vicinity of Bogotá, Colombia; and *S. reconditum* Thwaites & Mitt. recently reported from São Paulo, Brazil (previously known only from Sri Lanka); a genus of three species.

HABITAT. On sandy soil, in exposed sites; open lower montane to subpáramo, at low elevations in Brazil, elsewhere 2500–3400 m.

DESCRIPTION. **Plants** somewhat small, to 7 mm high, forming tufts. **Stems** to 5 mm high, radiculose below; central strand present. **Leaves** oblong-narrowly lanceolate, to 4 mm long, channeled above, apex narrowly long acuminate; margins erect to slightly incurved, entire below, serrate at tips; costa excurrent, ca. 1/2 width of leaf base, in cross-section ventral and dorsal stereid bands between small guide cells, or leucocysts above guide cells; laminal cells thick-walled, upper laminal cells oblong-rectangular to -linear, thick-walled; basal cells short rectangular; alar region differentiated, cells enlarged, irregularly oblong or short rectangular. **Dioicous**. **Perichaetia** terminal. **Seta** to 2(–4) mm long, curved, smooth. **Capsule** immersed, urn subglobose, 0.8–1 mm long; annulus large, dehiscent. **Operculum** short-rostrate. **Peristome** teeth reduced, basal membrane low, equal to or just exceeding mouth. **Calyptra** cucullate, naked and smooth, base ciliate. **Spores** finely papillose.

DISCUSSION. In the absence of sporophytes this genus is indistinguishable from *Campylopus*; *Sphaerothecium* differs from *Campylopus* in the Neotropics by the immersed sporophytes, subglobose capsules, enlarged annulus, short peristome, and relatively large spores (ca. 21 µm in diameter).

LITERATURE. Frahm, J.-P. 1986. A review of *Sphaerothecium* Hampe. The Bryologist 89: 152–154. - Frahm, J.-P. 1991 (see family ref.). - Williams, R. S. 1928. *Sphaerothecium* Hampe - A good genus. The Bryologist 31: 72–73.

Symblepharis (Fig. 118) - Two species in the Neotropics, *S. lindigii* Hampe (Costa Rica, Colombia to Bolivia); and *S. vaginata* (Hook.) Wijk & Margad. (Mexico, Central America, Peru; also China and India); about 10 species with a pantropical highland distribution.

HABITAT. Epiphytic on trunks and branches of shrubs and low trees, also on logs and occasionally on soil and rocks; montane forests and shrubby páramo and puna, 1850–4400 m.

DESCRIPTION. **Plants** medium sized, forming rather tall tufts, dark green, occasionally blackish. **Stems** erect, few to several branched, tomentose below; central strand present. **Leaves** distally spreading and crispate-curled or -squarrose above base when dry, lanceolate-subulate from an obovate sheathing base, 5–7 mm long, channeled above, apex acuminate; margins denticulate to serrate or entire, distally undulate or not; costa percurrent to short excurrent, ca. 1/5 width of leaf base; laminal cells smooth, cells of limb distally quadrate to subquadrate, thick-walled; sheathing base cells linear-rectangular, thin-walled; alar cells undifferentiated. **Autoicous**. **Perigonia** in leaf axils, below perichaetia. **Perichaetia** terminal, leaves ± short, long subulate from a convolute sheathing base. **Seta** 1–2 per perichaetium, elongate, exceeding perichaetial leaves, erect when dry, slightly curved or not when wet, 5–25 mm long, reddish-orange or yellow, distally twisted. **Capsule** erect or slightly oblique, urn oblong-cylindrical, 1.8–4.5 mm long, smooth; columella often slightly exserted; exothecial cells very thick-walled. **Operculum** long rostrate. **Peristome** teeth divided distally, rather fragile, vertically striate or papillose. **Calyptra** cucullate, entire at base, distally slightly roughened or not. **Spores** spherical, smooth to lightly papillose.

DISCUSSION. The genus is characterized by the crispate-curled or -squarrose leaves that are lance-subulate from an obovate leaf base, narrow costa, smooth laminal cells that are quadrate above, long rectangular below, undifferentiated alar cells, erect seta, and divided, vertically striate or papillose peristome teeth. *Symblepharis* may be confused with *Holomitrium*. Both are epiphytes and occur in similar habitats, the latter however exhibits long sheathing perichaetial leaves, entire peristome teeth, and generally distinct differentiated alar cells. *Symblepharis tenuis* R. S. Williams from Peru is a synonym of *Dicranella campylophyllum* Taylor (*Anisothecium*).

LITERATURE. Salmon, S. 1898. A revision of the genus *Symblepharis*, Montagne. Journal of the Linnaea Society, Botany 33: 486–501.

DIPHYSCIACEAE

A family containing three genera and about 20 species. The family is placed in the order Buxbaumiales.

Diphyscium (Fig. 119) - About six species in the Neotropics; a genus of about 18 species.

HABITAT. Exposed on clay or humic soils, decaying wood, and rocks; lowland to montane forests, possibly moderately disturbed forests, 80–2800 m.

DESCRIPTION. **Plants** rather small, to 1.5 cm tall, forming tufts, blackish-green. **Stems** erect, short, few branched, radiculose below; in cross-section central strand absent; rhizoids papillose. **Leaves** crowded, crispate and curled when dry, erect-spreading when wet, lingulate, to 5.5 mm long, weakly concave, apex obtuse-rounded to acute or acuminate, base slightly expanded and clasping, ca. 1/4–1/3 lamina length; margins plane or ± erect, irregularly dentate-serrate above, uni - to multistratose; costa strong, ending well below apex to shortly excurrent, in cross-section with guide

cells in a single row, stereids in several rows above or not and below guide cells, upper epidermal cells similar to laminal cells; lamina bistratose throughout (except at margins in some taxa), upper (adaxial) surface cells ovate-rounded (1–3:1) and projecting, lower surface (abaxial) cells smaller or not, subquadrate, very thick-walled, smooth, mammillose to uni- or pluripapillose; subsheathing base cells long rectangular, thick-walled, unistratose. **Dioicous** (typically male plants smaller than female). **Perichaetia** terminal, leaves strongly differentiated, often several times longer than stem leaves, to 6.5 mm long, lanceolate and erose distally at juncture with costa, costa long excurrent. **Seta** very short, smooth. **Capsule** immersed, erect, urn strongly asymmetric, obliquely and broadly ovoid, narrowed toward mouth, to 5.5 mm long. **Operculum** conic-short rostrate to sharply high conic. **Peristome** double, exostome teeth short and irregular, endostome elongate, membrane high and conic, keeled (16-plicate), papillose. **Calyptra** short mitrate, smooth. **Spores** finely papillose.

DISCUSSION. Distinguishing features of the genus include the sexual dimorphism between male and female plants, oblong-ligulate leaves that are bistratose distally, conspicuously larger, aristate perichaetial leaves, an immersed, asymmetric, ovoid capsule that is tapered toward the mouth, and unique peristomial arrangement.

LITERATURE. Allen, B. 1996. *Diphyscium pocsii* (Musci: Buxbaumiaceae), an African species new to Honduras. Nova Hedwigia 62: 371–375 [key to New World species].

DITRICHACEAE

Plants small to medium sized, forming loose to dense tufts. **Stems** erect, few to several branched by innovations, radiculose below; central strand present. **Leaves** crowded to distant, distinctly 2 or 3 ranked or spirally arranged, broadly to more commonly narrowly lanceolate, often distally linear or subulate; margins plane or recurved below, entire to more commonly dentate or serrulate distally, elimbate; costa usually strong, subpercurrent to short or long excurrent, at base mostly less than 1/2 width of lamina; lamina unistratose or bistratose (*Chysoblastella*); median cells subquadrate to ± irregularly short rectangular, smooth to bulging mammillose or papillose; lower and basal cells elongate rectangular, mostly smooth; alar region undifferentiated. **Asexual structures** apparently absent in neotropical taxa, elsewhere rhizoidal tubers and gemmae in leaf axils have been reported for some taxa. **Dioicous**, paroicous, or autoicous. **Perichaetia** terminal. **Seta** short to more commonly elongate and slender, smooth. **Capsule** immersed and cleistocarpous with urn subglobose or ovoid and peristome absent, or exserted and stegocarpous with urn often ovoid-cylindrical and often furrowed when dry; annulus usually present, persistent or revoluble. **Operculum** conic to long rostrate. **Peristome** single when present, teeth 16 but divided into terete segments to near base or perforate near base, smooth to commonly papillose distally. **Calyptra** cucullate, naked and smooth, or mitrate. **Spores** mostly spherical and lightly to densely papillose.

DISCUSSION. The Ditrichaceae contain come 25 genera and about 185 species distributed worldwide in temperate and subtropical regions; in the Neotropics 15 genera and ca. 42 species. The distinction between the Ditrichaceae and Dicranaceae as traditionally accepted is not impressive (see discussion under Dicranaceae). Matsui and Iwatsuki (1990) provide a useful overview of the family.

LITERATURE. Britton, E. G. 1913. Ditrichaceae. North American Flora 15(1): 55–67. - Matsui, T. & Z. Iwatsuki. 1990. A taxonomic revision of the family Ditrichaceae (Musci) of Japan, Korea and Taiwan. Journal of the Hattori Botanical Laboratory 68: 317–366. - Seppelt, R. D. 1982. *Ditrichum* and other genera of the Ditrichaceae in Australasia and the Pacific. Journal of the Hattori Botanical Laboratory 52: 107–112.

1. Capsule cleistocarpous or stegocarpous but gymnostomous, immersed to shortly exserted, often globose, ellipsoid- to ovoid-short cylindrical; plants relatively small, leaves 2 mm or less long (often to ca. 1 mm) 2
1. Capsule stegocarpous, mostly long exserted, rarely immersed (see *Garckea*), mostly long cylindrical or ovoid-cylindrical; plants relatively large, rarely small, leaves 1.5 mm or longer (often greater than 2 mm long) 8
2. Leaves distinctly 3-ranked, costa strong, short excurrent; above treeline in Mexico and the Andes ..... **Tristichum**
2. Leaves not ranked, costa strong to weak, subpercurrent to excurrent; lowland to high elevations 3
3. Leaves subulate to lanceolate from an ovate or oblong base or oblong-short lanceolate; costa short to long excurrent 4
3. Leaves ovate, obovate to short lanceolate; costa subpercurrent to percurrent, rarely somewhat minutely excurrent 6

4. Seta curved; capsule gymnostomous, pendent, hemispheric; exothecial cells bulging; leaf margins serrate above the shoulder ..... **Eccremidium**
4. Seta erect or appearing absent; capsules cleistocarpous; exothecial cells smooth, not bulging; leaf margins entire to subentire 5
5. Leaves erect to erect-spreading, usually unistratose, rarely bistratose, upper cells smooth, not projecting on back; locally widespread ..... **Pleuridium**
5. Leaves somewhat falcate when dry, distally bistratose, upper cells mammillose-projecting on back; southeastern Brazil ..... **Crumuscus**
6. Leaves ovate to obovate; leaf apex obtuse; margins erose-crenulate distally ..... **Astomiopsis**
6. Leaves ovate to short oblong-lanceolate or lanceolate; leaf apex acute or some leaves obtuse; margins entire 7
7. Leaf lamina distally unistratose; basal marginal cells similar to inner basal cells; capsules cleistocarpous, globose; southeastern Brazil ..... **Cladastomum**
7. Leaf lamina distally bistratose; basal marginal cells differentiated from inner basal cells; capsules gymnostomous, ovoid; Mexico, Guatemala, Peru ..... **Bryomanginia**
8. Leaves distinctly 2-ranked ..... **Distichum**
8. Leaves spirally arranged, not 2-ranked 9
9. Comal tuft of leaves terminating stems, comal leaves to 2 mm long, stem leaves to 1 mm long; seta short, to 0.5 mm long; capsules immersed; calyptra mitrate ..... **Garckea**
9. Comal tuft of leaves absent, leaves similar or gradually longer toward distal stems; seta elongate; capsules exserted; calyptra cucullate 10
10. Leaves bistratose, laminal cells strongly bulging-papillose ..... **Chysoblastella**
10. Leaf margins unistratose, laminal cells mostly smooth 6
6. Leaves lanceolate, gradually tapered above, base not sheathing stem; margins reflexed .... **Ceratodon**
6. Leaves subulate or lanceolate from an ovate to oblong base, or ligulate; margins plane, channeled or involute 7
7. Leaves lax, ligulate to oblong-ligulate; laminal cells large, rather lax, thin-walled, upper cells hexagonal to rhomboidal; peristome teeth obliquely or spirally papillose ..... **Wilsoniella**
7. Leaves rather rigid or flexuose, subulate or lanceolate from an ovate or oblong base; laminal cells firm- and thick-walled 8
8. Leaves falcate-secund; seta flexuose-curved when dry, strongly curved when wet; peristome irregularly divided, obliquely striate; rare, Mexico ..... **Cygniella**
8. Leaves erect to erect-spreading, flexuose, not falcate; seta erect, slightly flexuose or not; peristome horizontal to obliquely striate or papillose; locally to commonly widespread 9
9. Peristome teeth papillose or horizontally striate-pitted ..... **Ditrichum**
9. Peristome teeth strongly spiral-spiculose or papillose ..... **Rhamphidium**

Astomiopsis (Fig. 119) - Three species in the Neotropics, *A. amblyocalyx* Müll. Hal. (central Mexico, southern Bolivia), *A. exserta* (E. B. Bartram) J. Snider (Mexico), and *A. subulata* Müll. Hal. (southern Bolivia); six species of widely scattered subtropical high elevations.

HABITAT. On soil among grasses and sedges; high zacatonal and puna meadows, at elevations from 3520–4300 m.

DESCRIPTION. **Plants** very small, solitary or gregarious, yellowish green or yellow. **Stems** erect or erect-curved distally, to ca. 4 mm high, simple or few branched from base, derived from subterranean rhizome; in cross-section outer and inner cells little differentiated, central strand well developed. **Leaves** crowded, imbricate or appressed, lowest most bract-like, progressively larger upward, distally ovate to obovate or oblong-ovate, or ovate abruptly tapered to a broad subula, to 0.9 mm long, deeply concave, apex obtuse, cucullate or not; margins entire below, distally erose-crenulate; costa subpercurrent to percurrent; laminal cells smooth, apical cells rhomboidal; median cells quadrate, short-rectangular to rhomboidal, rather thick-walled; basal cells short to long rectangular, rather lax, thin-walled; marginal cells narrower. **Autoicous** (or paroicous). **Perichaetia** terminal; leaves somewhat similar to stem leaves but larger, to 1.3 mm long. **Seta** short, to 2 mm long, smooth. **Capsule** immersed to short exserted, erect, urn ellipsoid-cylindrical, to 1.7 mm long; stomata at urn base, superficial; annulus in 2–3 rows, persistent. **Operculum** bluntly conic to short-rostrate, oblique. **Peristome** absent. **Calyptra** cucullate, smooth. **Spores** spherical, granulose.

DISCUSSION. The genus is characterized by the minute habit; spirally arranged, ovate, oblong-ovate, or obovate leaves; distally erose-crenulate margins; subpercurrent to percurrent costa; and immersed or emergent, gymnostomous capsules. *Astomiopsis* is likely to be found elsewhere in intervening highland areas (above 3500 m) between Mexico and Bolivia.

LITERATURE. Snider, J. A. 1987. A revision of the moss genus *Astomiopsis* (Ditrichaceae). The Bryologist 90: 309–320 [keys, illustrations].

Bryomanginia (Fig. 119) - A monotypic genus, with *B. saint-pierrei* Thér. known from Mexico, Guatemala, and Peru.

HABITAT. On soil in compact tufts; zacatonal and puna, mostly from 4000–5000 m.

DESCRIPTION. **Plants** small, forming dense tufts, golden brown or reddish-brown. **Stems** erect, to 10 mm tall, solitary or few branched; in cross-section outer epidermal wall rather thick-walled, inner cells larger, thin-walled, central strand weak. **Leaves** stiffly erect, little different dry or wet, oblong-lanceolate, to ca. 1 mm long, concave below, channeled distally, apex cucullate, bluntly acute to obtuse; margins erect, entire; costa broad below, subpercurrent; lamina bistratose distally; laminal cells smooth, upper cells quadrate-rounded, thick-walled; basal cells laxly rectangular, hyaline, toward margin becoming narrowly long rectangular, extending slightly upward along margins and differentiated from inner thick-walled cells. **Autoicous**. **Perichaetia** terminal; leaves larger than stem leaves, to 1.5 mm long. **Seta** very short, to 0.3 mm long. **Capsule** immersed, erect, urn ovoid, to 0.4 mm long; exothecial cells thin-walled; stomata absent; annulus large and broad, in 2 rows, persisting. **Operculum** convex-apiculate. **Peristome** absent. **Calyptra** cucullate, smooth and naked. **Spores** proximally vermiculose, distally rugose.

DISCUSSION. The genus is characterized by small, slender plants; stiffly erect, oblong-lanceolate leaves; cucullate, obtuse to acute apex; bistratose, smooth laminal cells; slightly differentiated border at leaf base; immersed, gymnostomous, ovoid capsules; absence of stomata; and cucullate calyptra. Includes as synonyms *Melophyllum radiculosum* Herzog, and *Astomiopsis saint-pierrei* Thér. ex W. R. Buck from Mexico.

LITERATURE. Buck, W. R. 1979. A new species of *Astomiopsis* (Ditrichaceae) from Mexico. Brittonia 31: 488–490.

Ceratodon (Fig. 120) - Two species in the Neotropics, *C. purpureus* (Hedw.) Brid. and *C. stenocarpus* Bruch, Schimp. & W. Gümbel, both widespread, only the latter is commonly encountered in the tropics; the genus contains 4–5 species distributed worldwide.

HABITAT. On soil or rock, rarely on logs or tree trunks, often in disturbed and cleared sites; mostly open montane to zacatonal, páramo, and puna, 2000–4150 m.

DESCRIPTION. **Plants** small to medium sized, forming loose to dense tufts, dark green to blackish-green. **Stems** erect, several branched by innovations; central strand present. **Leaves** lanceolate or triangular-lanceolate, 1.5–2 mm long, keeled distally, apex short acuminate; margins reflexed, entire to distally dentate or irregularly serrate at apex; costa strong, subpercurrent to short excurrent, in cross-section stereids above and below guide cells; median cells quadrate to subquadrate, smooth, thick-walled; basal cells rectangular, thick-walled. **Dioicous**. **Perichaetia** terminal, leaves larger, sheathing at base. **Seta** elongate, to ca. 20 mm long, smooth. **Capsule** erect to suberect or horizontal, urn short to long ovoid to cylindrical, to 2 mm long, weakly to strongly curved, asymmetric, furrowed when deoperculate and dry; exothecial cells irregularly long rectangular, thin-walled; stomata few at urn base, superficial; annulus in 2–3 rows, revoluble. **Operculum** conic. **Peristome** single, teeth divided 2/3 or more to near base, thickened segments jointed or not, hyaline border absent to strong, papillose. **Calyptra** cucullate, smooth, naked. **Spores** spherical, lightly papillose.

DISCUSSION. The genus is characterized by triangular-lanceolate leaves; reflexed, often distally dentate margins; uniform, thick-walled laminal cells, quadrate above, rectangular at base; slender, elongate seta; erect to horizontal, slightly curved capsule; rather strongly papillose peristome teeth; and conic operculum. Burley and Pritchard (1990) recognize *C. stenocarpus* as a subspecies of *C. purpureus*, but in the present treatment they are recognized as separate species. In the Neotropics *C. stenocarpus* is by far the more common taxon. The two species can be separated by the following features: *C. purpureus* — seta purple; capsule horizontal, ovoid, strumose, sulcate when old, peristome divided ca. 2/3 length, strongly hyaline border; *C. stenocarpus* — seta pale-yellow or red; capsule erect to suberect, cylindrical, not strumose, smooth to weakly sulcate, peristome divided to near base, hyaline border indistinct and narrow or absent.

LITERATURE. Burley, J. S. & N. M. Pritchard. 1990. Revision of the genus *Ceratodon* (Bryophyta). Harvard Papers in Botany 2: 17–76 [keys, illustrations].

Chrysoblastella (Fig. 120) - A monotypic genus, with *C. chilensis* (Mont.) Reimers known from the West Indies, tropical Andes, southeastern Brazil, and New Zealand

HABITAT. Mostly exposed sites on soil; open montane to páramos and punas, 2300–4100 m.

DESCRIPTION. **Plants** medium sized, forming loose coarse tufts, olive to dark green. **Stems** erect, dark red, simple or few branched, radiculose below; in cross-section outer 1–2 rows small, ± thick-walled, inner cells progressively larger, thin-walled, central strand well developed, often collapsed; rhizoids appearing papillose. **Leaves** distant to rather crowded, leaf limb suberect-incurved, ±

flexuose when dry, narrowly lanceolate from an expanded base or triangular-lanceolate, to 4.5 mm long, to 0.5 mm wide, concave below, distally channeled and ± cucullate at apex, apex broadly or bluntly acute, toothed, base loosely sheathing; margins plane or slightly recurved below, distally ± erect, crenulate; costa strong, percurrent or filling acumen, in cross-section stereid few above guide cells, many below; lamina bistratose, at base unistratose; upper and median laminal cells quadrate or short rectangular, mammillose, ca. 2 mammillae per cell; lower and basal cells quadrate to mostly short rectangular, mostly smooth. **Dioicous**. **Perichaetia** terminal, outer leaves to 5 mm long, inner leaves much shorter. **Seta** elongate, 6–17 mm long. **Capsule** suberect, urn cylindrical, to 2.3 mm long, slightly curved and ± asymmetric, when dry smooth or slightly wrinkled; exothecial cells thin-walled; annulus poorly developed, deciduous or persistent. **Operculum** rostrate. **Prostome** present. **Peristome** single, teeth divided to near base, occasionally adnate at apex, papillose-spiculose. **Calyptra** cucullate, naked and smooth. **Spores** not observed.

DISCUSSION. The genus is readily recognized by the bistratose, strongly mammillose laminal cells (ca. 2 mammillae per cell). When sterile, *Chrysoblastella* is likely to be confused with members of the Pottiaceae.

LITERATURE. Buck, W. R. 1981. A review of *Cheilothela* (Ditrichaceae). Brittonia 33: 453–456.

Cladastomum (Fig. 120) - A neotropical genus of two species, *C. ulei* Müll. Hal. and *C. robustum* Broth., both restricted to southeastern Brazil.

HABITAT. On humic soil and soil covered rocks, in part associated with rock outcrops; primarily associated with páramo-like vegetation, 1200–2600 m.

DESCRIPTION. **Plants** small, forming tufts, green above, yellow-brown below. **Stems** erect, 2(4) cm tall, often much shorter, rather slender, radiculose, usually beneath soil layer; in cross-section outer 1–2 rows small, somewhat thick-walled, inner cells large, thin-walled, central strand well developed. **Leaves** distally crowded, somewhat distant below, erect above, erect-spreading and incurved below, somewhat narrow to broadly ovate, to 1.2 mm long, concave below, ± channeled above, apex acute; margins plane, entire; costa rather strong, particularly on lower leaves, percurrent to short excurrent, ending in a pellucid point, few stereids above and below guide cells; lamina unistratose; laminal cells weakly convex, smooth, firm- to rather thick-walled, upper subquadrate, some transversely short rectangular, basal cells subquadrate to short rectangular. **Dioicous**. **Perichaetia** terminal; leaves enlarged, elliptic-lanceolate, to 1.7 mm long, costa percurrent to short excurrent, upper laminal cells fusiform-rhomboidal, thick-walled, lower cells oblong-rectangular. **Seta** very short, appearing absent. **Capsule** immersed, cleistocarpous, spherical-apiculate, ca. 0.8 mm in diameter, smooth; exothecial cells somewhat firm-walled; stomata not observed. **Operculum** absent. **Peristome** absent. **Calyptra** not observed, stated to be mitrate, lobed at base. **Spores** mostly spherical, rather coarsely papillose.

DISCUSSION. This narrowly restricted genus is characterized by the slender julaceous stems and branches, well developed central strand, appressed, acute, short lanceolate leaves, unistratose, smooth laminal cells, cleistocarpic capsules, absence of stomata, and small mitrate calyptra. *Cladastomum ulei* has been collected in the states of Espírito Santo, Minas Gerais, Paraná, Rio de Janeiro, and Santa Catarina; *C. robustum* appears to be rare, and possibly represents a form of the former species. The genus has been discussed and illustrated by Schäfer-Verwimp (1996).

LITERATURE. Schäfer-Verwimp, A. 1996. New or interesting records of Brazilian bryophytes, V. Candollea 51: 283–302.

Crumuscus (Fig. 121) - A monotypic genus, *C. vitalis* W. R. Buck & Snider, is restricted to southeastern Brazil (Minas Gerais, Rio de Janeiro).

HABITAT. On soil covered rocks, associated with rocky cliffs; open montane, at 2120 m.

DESCRIPTION. **Plants** minute, forming short tufts. **Stems** to 8 mm tall (often only 2–3 mm exposed above soil surface), reddish, few branched below perichaetia; in cross-section outer 7 rows of small, thick-walled cells, central strand well developed; rhizoids smooth. **Leaves** erect and often somewhat falcate when dry, simply erect when wet, oblong-lanceolate, to 0.9 mm long, apex broadly long-acuminate; margins plane, subentire to crenulate; costa broad, strong, nearly filling acumen, excurrent, in cross-section stereids above and below a row of 4 guide cells; lamina bistratose distally, partially so below, at base unistratose; laminal cells rectangular, distally mammillose-prorulose on back, smooth below. **Autoicous** (paroicous). **Perichaetia** terminal; leaves strongly differentiated, lanceolate, often broadly so, to 2.5 mm long, costa subpercurrent to percurrent, laminal cells unistratose, smooth, upper cells quadrate to short rectangular, long rectangular below. **Seta** to 0.1 mm long. **Capsule** immersed, cleistocarpous, spherical to ovoid with a strong apiculate beak, to 0.85 mm long; exothecial cells of median region irregularly rectangular, firm-walled; stomata absent.

Operculum absent. **Peristome** absent. **Calyptra** mitrate, smooth or slightly roughened, naked. **Spores** subspherical, separating from tetrads, papillose to verruculose.

DISCUSSION. The genus is characterized by the distally bistratose, projecting mammillose laminal cells; spherical capsule; absence of stomata; and mitrate calyptra (the latter two features also shared by *Pleuridium lindigianum* (Hampe) S. P. Churchill of Colombia). *Crumuscus* appears to be closely related to *Pleuridium*, if not a member of that genus. The generic name honors the United States bryologist Howard Alvin Crum (1922–), author of numerous publications on American mosses, specialist on American *Sphagnum*, and co-author of *Mosses of Eastern North America* with L. E. Anderson.

LITERATURE. Buck, W. R. & J. A. Snider. 1992. *Crumuscus vitalis* gen. et sp. nov. (Ditrichaceae). Contributions from the University of Michigan Herbarium 18: 39–41.

Cygniella (Fig. 121) - A monotypic genus, with *C. sharpii* H. A. Crum only known from Chiapas, Mexico.

HABITAT. On soil bank and decaying wood; montane forest, at elevations from 1830–1950 m.

DESCRIPTION. **Plants** small, forming dense tufts, yellow. **Stems** to 7 mm tall. **Leaves** falcate-secund and flexuose-twisted when dry, less so when wet, subulate-lanceolate or long-setaceous from an oblong base, base concave, distally channeled; costa ± filling subula; upper laminal cells of subula (extending to near apex) linear; lower and basal cells oblong-rectangular; marginal cells near mid and base regions forming an indistinct border of long linear cells. **Autoicous**. **Perichaetia** terminal, leaves similar to upper leaves of stem. **Seta** slenderly flexuose-curved when dry, strongly curved when wet, to 8 mm long, smooth. **Capsule** erect, ellipsoid-cylindrical, 1–1.2 mm long; stomata absent; annulus absent**. Operculum** long rostrate**. Peristome** teeth inserted below mouth, irregularly divided, forks terete, obliquely to sprially striate throughout. **Calyptra** cucullate, smooth and naked. **Spores** subspherical, finely papillose.

DISCUSSION. The genus is distinguished by the long subulate leaves from a narrow to somewhat broad oblong base; lamina extending the length of the subula; narrower, long-linear cells forming an indistinct border along the expanded leaf base; linear cells of the subula; slender, flexuose and curved seta; deeply inserted peristome; and teeth forked, terete, obliquely to spirally striate. The genus is only known from a single locality but given the plant's inconspicuous small size, it has probably been overlooked by general plant collectors.

LITERATURE. Crum, H. 1986. Taxonomic and nomenclatural addenda to the Mexican moss flora. The Bryologist 89: 23–27.

Distichium (Fig. 121) - A single species in the Neotropics, *D. capillaceum* (Hedw.) Bruch, Schimp. & W. Gümbel (widespread in the Northern Hemisphere, Mexico to Tierra del Fuego, South Africa, Australasia); a genus of about five species associated with cold temperate regions.

HABITAT. On soil, occasionally on exposed moist banks; grassy páramo and puna, 3000–4700 m.

DESCRIPTION. **Plants** rather small, soft and slender, forming dense tufts, glossy dark green or brownish-green. **Stems** erect, to 4 cm tall, several branched, somewhat tomentose below; central strand weak. **Leaves** 2-ranked, subulate from an elongate oblong sheathing base, 3–4.2 mm long, 0.4 mm wide, subula 2–3 times longer than sheathing lamina, concave; margin of sheathing base entire below, distally erose or dentate; costa strong, long excurrent, in cross-section stereids above and below guide cells; laminal cells smooth, obscure, distally subquadrate, rhomboidal to rhomboidal-oblong; basal cells linear-rectangular; costa cells roughened and bulging by adjoining cell walls. **Autoicous**. **Perichaetia** terminal, leaves similar to stem leaves. **Seta** elongate, 8–13 mm long, slender and usually twisted. **Capsule** erect to suberect, urn ovoid-cylindrical, 1.1–1.6 mm long; annulus in several rows. **Operculum** conic-short rostrate, long. **Peristome** single, teeth irregularly divided, smooth to obliquely striate below, often broken, stomata few at base of urn. **Calyptra** cucullate, smooth and naked. **Spores** spherical, lightly papillose.

DISCUSSION. The distinctly 2-ranked leaves with a stout, roughened long excurrent costa are diagnostic features that do not occur in other high elevational genera.

Ditrichum (Fig. 122) - Fourteen species recorded for the Neotropics, possibly 10; the genus is stated to contain 70 species of mostly temperate and subtropical regions.

HABITAT. On soil or rock, or rock in streams; mid to high open montane, zacatonal, páramo and puna, 2000–4700 m.

DESCRIPTION. **Plants** medium sized, forming loose to dense tufts, glossy or dull dark green to blackish- or yellowish-brown. **Stems** erect, often rather slender, few to several branched by innovations; central strand present. **Leaves** long subulate from an ovate or oblong base, 1.5–6.5 mm long, limb concave, channeled or flat, expanded base weakly to strongly sheathing, concave or

convolute; margins smooth, often serrate at tip; costa strong, percurrent to excurrent, often filling acumen; upper laminal cells of expanded base mostly thick-walled, irregularly short rectangular or subquadrate to oval or oblong-rhombic distally; lower and basal cells long and narrowly rectangular, walls entire to porose. **Dioicous** or autoicous. **Perichaetia** terminal, leaves similar to slightly larger than stem leaves. **Seta** elongate, 10–30 mm long, slender, often flexuose, smooth. **Capsule** suberect, slightly asymmetric and curved, urn cylindrical to obovoid-cylindrical, 1.4–2.8 mm long, smooth or slightly striate. **Operculum** short-rostrate. **Peristome** single, teeth usually divided to near base, coarsely papillose to spiculose. **Calyptra** cucullate, smooth, naked, base entire. **Spores** spherical, smooth or nearly so.

DISCUSSION. The genus is characterized by tufted, medium sized to rather large plants; leaves long subulate from an oblong to oblong-ovate subsheathing to sheathing base; by thick-walled, smooth laminal cells that are oval to short rectangular or oblong-linear in subula and expanded distal leaf base, and mostly long rectangular at base; by an elongate, slender seta; and cylindrical, slightly curved and asymmetric capsules with coarsely papillose peristome teeth, divided to near base. A critical worldwide revision is warranted for this genus.

LITERATURE. Anderson, L. E. & V. S. Bryan. 1958. Systematics of the autoicous species of *Ditrichum* subg. *Ditrichum*. Brittonia 10: 121–137. - Seppelt, R. D. 1982. *Ditrichum* and other genera of Ditrichaceae in Australasia and the Pacific. Journal of the Hattori Botanical Laboratory 52: 107–112. - Seppelt, R. D. & D. Griffin III. 1997. *Ditrichum* (Ditrichaceae, Musci) in the Americas. I. *Ditrichum venezuelanum* a synonym of *Ditrichum bogotense*. The Bryologist 100: 212–216.

Eccremidium (Fig. 122) - A single species in the Neotropics, *E. floridanum* H. A. Crum is known from Brazil (Bahia, Parana, Sergipe); a genus of six species primarily from Australia and New Zealand, also South Africa and United States (Florida & Georgia).

HABITAT. Moist sandy soil, shaded to exposed sites; caatinga and restinga vegetation, at near sea level to 50 m.

DESCRIPTION. **Plants** minute, gregarious, glossy bright light green or yellowish green. **Stems** erect, very short, to 3 mm tall, 1–2 subfloral innovations, radiculose at base. **Leaves** crowded, flexuose erect-spreading, linear-lanceolate from an expanded ovate or short oblong base, to 1.8 mm long; margins plane, entire below, serrate above shoulder; costa weak below, excurrent, filling the acumen; cells above expanded base linear, rather thick-walled, smooth; cells of expanded base oblong-rectangular, smooth. **Autoicous**. **Perichaetia** terminal; leaves similar, slightly longer. **Seta** short and curved, to 0.5 mm long. **Capsule** pendent, urn hemispheric, to 0.3 mm long, mostly flared at mouth when deoperculate; exothecial cells bulging, hexagonal, very thick-walled with central portion oval or oblong and thin-walled; stomata at urn base, superficial; annulus absent. **Operculum** hemispheric-apiculate. **Peristome** absent. **Calyptra** mitrate, weakly lobed. **Spores** large, to 100 µm in diameter, granulose-papillose.

DISCUSSION. The distinctive sporophytic features, pendent capsules, equal size and shape of the urn and opercula, and unique exothecial cells, are diagnostic. A brief but useful summary of the genus has been provided by Crum (1981) with a description of an additional new species, *E. floridanum* H. A. Crum. This species is mostly closely related to *E. exiguum* (Hook. f. & Wilson) Wilson ex Salm. which is known from Australia and South Africa.

LITERATURE. Crum, H. 1981. *Eccremidium*, a genus of Ditrichaceae new to the Americas. The Bryologist 84: 527–532. - Vital, D. M. & A. Egunyomi. 1984. *Eccremidium* (Ditrichaceae) new to South America. Journal of Bryology 13: 39–41.

Garckea (Fig. 122) - A single species in the Neotropics, *G. flexuosa* (Griff.) Margad. & Nork., known from Mexico, Panama, Suriname, and southeastern Brazil; a genus of about five species primarily of tropical and subtropical Asia.

HABITAT. Moist shady road banks or bare soil along seasonal streams, disturbed sites; at low elevations.

DESCRIPTION. **Plants** small, gregarious or forming loose tufts, yellowish-green. **Stems** erect, to 10 mm or more tall, simple, radiculose at base; in cross-section outer 4–5 rows of cells thick-walled, inner cells thin-walled. **Leaves** loosely appressed when dry, erect-spreading when wet, leaves below comal tuft lanceolate, ca. 1 mm long, comal tuft leaves to 2 mm long, apex bluntly acute; margins plane to slightly recurved, sinuate-denticulate; costa strong, subpercurrent to percurrent; lamina bistratose along margins and portions of lamina; laminal cells smooth, upper cells linear to oblong-linear; basal cells shorter and broader. **Dioicous**. **Perichaetia** terminal; leaves similar to comal leaves. **Seta** short, erect, to 0.5 mm long, rather stout. **Capsule** immersed, erect, urn ovoid-short cylindrical, to 1 mm long; exothecial cells thin-walled; stomata absent; annulus in 2 rows, deciduous in portions. **Operculum** convex-apiculate. **Peristome** single, inserted slightly below mouth, teeth articulate below,

entire or divided distally, coarsely papillose, vertically striate-papillose below. **Calyptra** mitrate, coarsely mammillose. **Spores** spherical, finely papillose.

DISCUSSION. The distal leaves, forming comal tufts, in combination with bistratose margins, long linear cells and immersed capsules are diagnostic. First reported from the Americas in 1953 by H. Crum from Panama, the genus is rare throughout the Neotropics. *Garckea phascoides* Müll. Hal. is a synonym.

LITERATURE. Crum, H. A. 1953. *Garckea phascoides* in Panama. The Bryologist 56: 204–207. - Yano, O. & D. M. Vital. 1977. Ocorrência do gênero *Garckea* C. Muell. (Ditrichaceae, Musci) no Brazil. Ciência e Cultura 30: 1464–1466.

Pleuridium (Fig. 123) - Ten species in the Neotropics; about 30 species of mostly temperate regions.

HABITAT. On soil, associated with exposed sites, e.g., pastures, cutbanks along trails and roads; open mid to high montane, extending into zacatonal and páramo, 300 to mostly 2000–4200 m.

DESCRIPTION. **Plants** very small, gregarious or forming short tufts, light or yellowish green. **Stems** erect, short, usually less than 8 mm, few branched by innovations. **Leaves** erect to erect-spreading wet or dry, those below smaller, often ovate, and ± distant, above much larger, crowded, gradually lanceolate-subulate or short to long subulate from an ovate base, rarely obovate to ovate-oblong, 0.5–4 mm long; margins distally erect to incurved, entire to serrulate; costa short to rather long excurrent; lamina unistratose, occasionally partially bistratose; laminal cells rhombic or linear to narrowly oblong-rectangular, smooth; basal cells often broader, oblong-rectangular. **Autoicous** or paroicous. **Perichaetia** terminal, leaves larger, oblong-narrowly lanceolate. **Seta** very short, 0.8 mm long, commonly shorter. **Capsule** immersed to occasionally emergent to shortly exserted, cleistocarpous, globose to ellipsoid-rounded, 0.5–0.8 mm long; exothecial cells large, short to elongate, stomata present or absent. **Operculum** and peristome absent. **Calyptra** cucullate or short mitrate, smooth to roughened distally. **Spores** weakly to more often densely to coarsely papillose, forming tetrads or not.

DISCUSSION. The genus is characterized by the gradually lanceolate-subulate leaves, and immersed to rarely shortly exserted, cleistocarpic capsules. The neotropical species of *Pleuridium*, of which several have been described, are in need of revision. Some of our species were previously placed in *Bruchia*.

LITERATURE. Griffin III, D. 1987. *Pleuridium venezuelanum*, a new species of moss from the South American páramos. Bulletin of the Torrey Botanical Club 114: 18–20.

Rhamphidium (Fig. 123) - Seven species recorded for the Neotropics, probably only 3–4; a small pantropical genus of some 17 species.

HABITAT. On soil or rocks in exposed, moist sites; open lowland to submontane, 400–1800 m.

DESCRIPTION. **Plants** rather small, forming dense tufts, somewhat dull light green. **Stems** erect, to 2.5(–3) cm tall, rusty-red, simple or few branched by innovations, radiculose below; in cross-section outer 2–3 rows of cells thick-walled, rusty-red, central strand large, mostly collapsed with central portion appearing hollow. **Leaves** spirally ranged, contorted and flexuose or incurved when dry, erect-spreading to spreading above clasping base when wet, rather broadly lanceolate above a oblong-obovate sheathing base, 1–2 mm long, to 0.5 mm wide, concave, deeply so below, above rather broadly so, apex bluntly acute; margins above sheathing base bluntly dentate; costa strong, percurrent, distal 1/5 papillose-dentate on back, in cross-section stereids above and below guide cells; cells of limb quadrate, few short rectangular, smooth to bulging on ventral surface; cells of sheathing base elongate, oblong-rectangular, insertion cells short, golden. **Dioicous**. **Perichaetia** terminal, leaves similar but longer, strongly sheathing. **Seta** elongate, 6–18 mm long, slender and somewhat flexuose, smooth. **Capsule** inclined, urn elliptical to short cylindrical, 0.9–1.5 mm long, neck short, exothecial cells irregular rectangular, ± thick-walled, stomata at base of urn, superficial. **Operculum** conic-long rostrate. **Peristome** single, teeth divided to near base, coarsely spiculose spiral-ridged above, at base nearly smooth to weakly striate-papillose. **Calyptra** cucullate, smooth and naked. **Spores** spherical to ovoid, appearing smooth.

DISCUSSION. Previously placed in the Pottiaceae, *Rhamphidium* presents various gametophytic and particularly sporophytic features that suggest an alignment with the Ditrichaceae (cf. Zander, 1993: 275, see family ref. under Pottiaceae). The genus may be confused with some members of *Dicranella* but differs in the broad distal lamina, ventral bulging cells, and the coarsely spirally-ridged peristome teeth. The neotropical species warrant a critical review.

Tristichium (Fig. 123) - Two species in the Neotropics (Mexico and Andes), *T. lorentzii* Müll. Hal. and *T. mirabile* (Müll. Hal.) Herzog; an additional species is reported from China.

HABITAT. Growing among tufts with other mosses such as *Bryum*, *Conostomum* and *Schizymenium*; in mid to high páramo and puna, 3400–4600 m.

DESCRIPTION. **Plants** small, forming short tufts, dark green to reddish-brown. **Stems** erect, 4–6 mm tall, few branched. **Leaves** distinctly 3-ranked, erect to erect-appressed, narrowly short to long lanceolate, apex usually blunt; margins plane, entire; costa strong, excurrent and filling acumen; median cells linear, ± vermicular, smooth; low and basal cells long rectangular. **Autoicous**? **Perichaetia** terminal, leaves somewhat similar or 1.5–2 times longer than stem leaves. **Seta** short to elongate. **Capsule** appearing sessile or immersed to short exserted, cleistocarpous or gymnostomous, urn globose to subglobose-ellipsoid, exothecial cells thick-walled. **Operculum** absent or present. **Peristome** absent. **Calyptra** cucullate.

DISCUSSION. The distinctly 3-ranked arrangement of leaves along the stem, strong percurrent to excurrent costa, and cleistocarpous or gymnostomous capsules are distinctive features of this genus. Herzog (1916: 12–13) has provided the only summary of the genus which includes useful illustrations.

LITERATURE. Herzog, T. 1916. Die Bryophyten meiner zweiten Reise durch Bolivia. Bibliotheca Botanica 87:1–347.

Wilsoniella (Fig. 124) - Two species in the Neotropics: *W. flaccida* (R. S. Williams) Broth. originally described as a new genus, *Teretidens* in the Pottiaceae, is from Bolivia (900 m); and *W. subvaginans* H. A. Crum & Steere known from Puerto Rico; a genus of about 10 species widely distributed in the tropics and subtropics, primarily from the Southern Hemisphere.

HABITAT. On clay banks; secondary open vegetation, at moderately low elevations, to 900 m.

DESCRIPTION. **Plants** somewhat small, forming loose, soft tufts, pale to brownish green. **Stems** ± erect, to 5 mm tall, few branched, radiculose below; in cross-section outer epidermal wall thick, inner cells ± uniform in size, central strand weak; rhizoids smooth. **Leaves** somewhat contorted when dry, wide-spreading and flaccid when wet, oblong-lanceolate or -ligulate, to 2.5 mm long, apex bluntly acute to obtuse, crenulate or bluntly toothed; margins plane, entire to bluntly serrulate in distal 1/3; costa subpercurrent (usually ending few to several cells below apex); lamina unistratose; laminal cells rather large, smooth, lax, thin-walled, apical cells short hexagonal to rhombic, median cells long hexagonal to rhomboidal; basal cells rectangular. **Autoicous**. **Perichaetia** terminal, leaves similar but slightly longer. **Seta** to 12 mm long, slender, somewhat flexuose or not, smooth. **Capsule** erect, urn obloid, cylindrical when dry, to 2 mm long, constricted below mouth or not when dry; neck distinct, short; exothecial cells elongate, thick-walled; stomata on neck, superficial; annulus large, revoluble. **Operculum** long rostrate. **Peristome** single, teeth divided to near base, segments spirally striate to papillose-striate. **Calyptra** mitrate, irregularly lobed at base, smooth and naked. **Spores** mostly spherical, finely papillose.

DISCUSSION. The genus is characterized by the rather flaccid, oblong-lanceolate or ligulate leaves; bluntly acute to obtuse apex; subpercurrent costa; thin-walled, lax, long hexagonal to rhomboidal median cells; elongate, rather flexuose seta; and spirally- to papillose-striate, divided peristome teeth.

ENCALYPTACEAE

The Encalyptaceae contain two genera and about 35 species primarily distributed in the Northern Hemisphere, in the tropics confined to montane regions. The family is placed in the order Encalyptales.

Encalypta (Fig. 124) - Four species in the Neotropics; 34 species primarily of the Northern Hemisphere.

HABITAT. On soil and rocks; open high montane to more commonly zacatonal, páramo and puna, (2350–) 2800–4600 m.

DESCRIPTION. **Plants** medium sized, forming tufts, dark green to yellowish-brown. **Stems** erect, solitary or few branched; central strand absent or weak. **Leaves** contorted and incurved when dry, erect-spreading when wet, ovate-oblong, oblong-elliptic to obovate, 1.8–5 mm long, occasionally undulate, apex broadly acute to obtuse, ± cucullate, mucronate or apiculate; margins plane, erect or inflexed distally, usually reflexed below; costa single, usually strong, subpercurrent to percurrent or short excurrent, back usually projecting; upper and median cells subquadrate, strongly pluripapillose, papillae branched; lower and basal cells large and short rectangular, smooth, walls dark brownish-orange; basal margin cells usually differentiated. **Autoicous** (gonioautoicous). **Perichaetia** terminal, leaves little differentiated. **Seta** elongate, (1–) 2–10 mm long, erect to ± flexuose, rather stout, smooth, often distally twisted. **Capsule** erect, urn usually long cylindrical, 1.2–4 mm long, smooth to furrowed and ± twisted; stomata present and superficial at base of urn; annulus undifferentiated.

Operculum rostrate from a plano-convex base. **Peristome** absent or present, teeth vertically-striate papillose, often fragile and deciduous. **Calyptra** mitrate-long cylindrical, apex constricted and rostrate, base fringed and lobed or not. **Spores** variously ornamented.

DISCUSSION. *Encalypta* is recognized by the cylindrical-campanulate calyptra and oblong-rectangular laminal cells at the base, smooth with cross walls thickened, and upper cells pluripapillose; the two former features may assist in separating various Pottiaceae from *Encalypta* with which it is likely to be confused. Two species are primarily restricted to the Neotropics, *E. asperifolia* Mitt. (Colombia to Argentina) and *E. flowersiana* Horton (Guatemala, Haiti, also Texas), the remaining two species, *E. ciliata* Hedw. and *E. rhaptocarpa* Schwägr., are widespread in the Northern Hemisphere.

LITERATURE. Horton, D. G. 1982. A revision of the Encalyptaceae (Musci), with particular reference to the North American taxa. Part I. Journal of the Hattori Botanical Laboratory 53: 365–418. - Horton, D. G. 1983. A revision of the Encalyptaceae (Musci), with particular reference to the North American taxa. Part II. Journal of the Hattori Botanical Laboratory 54: 353–532 [keys, illustrations, maps].

ENTODONTACEAE

Plants medium sized, forming loose to dense mats. **Stems** loosely to strongly complanate-foliate or julaceous, creeping to distally subascending, irregularly pinnately branched, radiculose beneath; central strand present, pseudoparaphyllia foliose; paraphyllia absent. **Leaves** imbricate, appressed to erect, ovate to oval or ovate- to oblong-lanceolate, usually concave, smooth or plicate, apex acute to short acuminate, occasionally apices reflexed, base slightly clasping or not; margins entire or distally serrulate or serrate, elimbate; costae usually very short and forked, or absent; laminal cells smooth, median cells linear to fusiform or rhomboidal; alar region differentiated, cells numerous, subquadrate, extending along margin 1/5–1/3 lamina length. **Asexual structures** apparently absent. **Autoicous**, less often dioicous. **Perichaetia** lateral, leaves elongate, mostly narrowly to somewhat broadly oblong-lanceolate. **Seta** elongate, smooth. **Capsule** exserted, erect, urn ovoid-cylindrical, symmetric, rarely and only slightly asymmetric, smooth; stomata absent or present at base of urn; annulus present or absent. **Operculum** conic short to long rostrate. **Peristome** double, inserted below mouth, exostome teeth 16, papillose or vertically to horizontally striate; endostome basal membrane absent or low, segments usually narrow, perforate, cilia absent. **Calyptra** cucullate, smooth and naked. **Spores** spherical, finely to coarsely papillose.

DISCUSSION. The Entodontaceae contain four genera and approximately 135 species of cool temperate and tropical regions; in the Neotropics three genera and about 30 species. The family is placed in the order Hypnales.

Study guide. Attention should be given to whether the stem and branch leaves are notably dimorphic, and for sporophytes the color of the seta and peristome ornamentation are often useful, if not critical, particularly for species of *Entodon*.

LITERATURE. Buck, W. R. 1980. A generic revision of the Entodontaceae. Journal of the Hattori Botanical Laboratory 48: 71–159.

1. Leaves plicate, not or slightly concave; seta light yellow; prostome present ..... **Mesonodon**
1. Leaves smooth, concave; seta reddish-orange to yellow; prostome absent 2
2. Leaves nearly as broad as long, broadly ovate; alar cells oblate, numerous and extending ca. 1/3 or more up lamina margin; annulus absent ..... **Erythrodontium**
2. Leaves half as broad as long, broadly lanceolate; alar cells subquadrate, extending 1/6–1/5(–1/4) up lamina margin; annulus generally present ..... **Entodon**

Entodon (Fig. 124) - About 28 species recorded for the Neotropics, probably closer to 20 or fewer are justified; a genus of some 100 species, of cool temperate regions and in the tropics often found in the highlands.

HABITAT. Epiphytic, on base of tree trunks, exposed roots and branches, also on logs, leaf litter, soil, or rocks; submontane to more commonly montane forests, 400–4000 m.

DESCRIPTION. **Plants** medium sized to rather large, forming loose to dense mats, often flattened, glossy light to dark green, golden-yellow. **Stems** creeping or occasionally subascending, irregularly pinnately to pinnately branched. **Leaves** weakly to strongly complanate, erect to erect-spreading, oblong-ovate to ovate- or oblong-lanceolate, 1.3–2 mm long, concave, apex acute to short or long acuminate, base not decurrent; margins plane or erect to reflexed below, entire to serrulate or serrate distally; costae double, short and forked, ca. 1/5–1/4 lamina length; laminal cells smooth, upper and median cells linear; alar region differentiated, extending upward along margin 1/6–1/5, rarely 1/4 the leaf length, often extending along base to costa, cells subquadrate, quadrate or short rectangular.

Autoicous, rarely dioicous. **Perichaetial** leaves oblong- to ovate-lanceolate. **Seta** 6–30 mm long, yellow or red, smooth, often distally twisted. **Capsule** with urn cylindrical, 3–4 mm long, symmetric to slightly curved and asymmetric; annulus generally present. **Operculum** short to long conic to short rostrate. **Peristome** with exostome teeth cross- to vertical-striate (or both) or papillose, often tips smooth, occasionally perforate distally; endostome basal membrane low, segments narrow, keeled and perforate, often reduced. **Spores** mostly finely papillose.

DISCUSSION. The genus is characterized by complanate-foliate, less often subjulaceous stems; concave, smooth, broadly lanceolate to oblong-lanceolate leaves; extension of alar cells along margin to ca. 1/5 the leaf length; low endostomial basal membrane; keeled and perforate segments; and finely papillose spores. A critical revision is needed for *Entodon*.

Erythrodontium (Fig. 125) - Five species in the Neotropics; about 15 species distributed throughout the tropics.

HABITAT. Epiphytic on trunks and branches of trees, less frequent on rocks or soil, often in exposed sites; moist to semi-dry, open submontane to montane forests, 450–2800 m.

DESCRIPTION. **Plants** somewhat small to medium-sized, forming mats, glossy green to yellowish-brown or golden. **Stems** creeping or short ascending and curled, julaceous or rarely somewhat complanate, radiculose beneath; rhizoids often clustered. **Leaves** appressed to erect-spreading, ovate-lanceolate to broadly ovate-oval or nearly orbicular, 0.7–1.8 mm long, deeply concave, apex abruptly or very short acuminate, base broadly short decurrent; margins entire to serrulate near apex; costa short and forked or absent; median cells linear to rhomboidal, smooth; alar cells numerous, usually 20 or more oblate quadrate-rounded to short oblong cells along margin. **Autoicous**. **Perichaetial** leaves mostly sheathing, oblong-lanceolate, abruptly acuminate, ecostate. **Seta** 10–15 mm long, dark red to yellow. **Capsule** with urn ovoid-cylindrical, 2–4 mm long; stomata at base, superficial; annulus absent. **Operculum** short rostrate. **Peristome** with exostome teeth striate, vertical and/or horizontal to papillose; endostome rudimentary, basal membrane absent, segments narrow. **Spores** rather coarsely papillose.

DISCUSSION. The genus is distinguished by the rather strongly julaceous branches, broadly ovate leaves, short acuminate apex, short decurrent leaf base, numerous alar cells, absence or a rudimentary basal membrane, segments neither keeled or perforate, and coarsely papillose spores. The two most common species can be separated by the following: *E. longisetum* (Hook.) Paris — leaves broadly ovate-lanceolate, 1.5–1.8 mm long, 0.75–0.85 mm wide, branches loosely julaceous, seta yellow; and *E. squarrosum* (Hampe) Paris — leaves broadly ovate to oval, 0.7–0.9 mm long, 0.5–0.6 mm wide, branches strongly julaceous, seta red.

Mesonodon (Fig. 125) - Two species in the Neotropics, *M. flavescens* (Hook.) W. R. Buck (northern Neotropics, also Africa and Asia), and *M. regnellianus* (Müll. Hal.) W. R. Buck (southeastern Brazil); the genus contains two species with a pantropical distribution.

HABITAT. Epiphytic on treelets and logs; presently known from submontane to lower montane forests, ca. 1000–1850 m.

DESCRIPTION. **Plants** medium-sized to rather large, forming mats, glossy bright green or yellowish-green. **Stems** creeping, tomentose beneath, distally stems and branches short, julaceous, ascending and somewhat falcate. **Leaves** ovate- to oblong-lanceolate, 1.3–2.8 mm long, to 1 mm wide, plicate, apex acuminate, base slightly decurrent; margins plane to recurved, ca. 2/3 lamina length from base, entire to serrate or serrulate at apex; costae absent, rarely short and double, separated; laminal cells smooth, median cells linear, vermicular or not; alar cells differentiated, numerous, quadrate or short rectangular. **Autoicous**. **Perichaetia** lateral. **Seta** to 30 mm long, erect, pale yellow. **Capsule** with urn cylindrical to ovoid-cylindrical, to 2.2 mm long; exothecial cells short rectangular to quadrate, thin-walled; stomata absent; annulus undifferentiated. **Operculum** short to long rostrate, oblique. **Prostome** present, adhering to front of exostome teeth, papillose on outer surface, inner surface smooth. **Peristome** with exostome teeth cross-striate below, midway becoming vertically striate, distally lightly papillose; endostome rudimentary, basal membrane absent and segments narrow, smooth, adhering to teeth. **Spores** coarsely papillose.

DISCUSSION. Distinguishing features include the plicate ovate-lanceolate to lanceolate leaves, not or slightly concave, ecostate or costate and short and double; numerous alar cells; light yellow seta; prostome present; exostome teeth finely cross-striate below, smooth above; and no basal membrane. The two species are differentiated as follows: *M. flavescens* — leaves ovate- to oblong-lanceolate, 2–2.8 mm long, broadest at 1/4–1/2 length above leaf base, alar cells 8–11 rows across the base, and *M. regnellianus* — leaves lanceolate, 1.25–1.85 mm long, broadest at leaf base, alar cells in 5–7 rows across the base.

EPHEMERACEAE

Plants ephemeral, minute, gregarious, light green. **Stems** very short from thick or somewhat thin protonematal mats, protonema persistent. **Leaves** few, contorted or not, linear- or ovate-lanceolate; apex acuminate to acute; margins plane, entire to serrate, often coarsely so, distally or to near base; costa none or occasionally weak; upper and median cells large, narrowly long hexagonal to rhomboidal, smooth to papillose by projecting distal cell angles; basal cells larger and broader, irregularly rectangular. **Autoicous**, dioicous, or polygamous. **Perichaetia** terminal, leaves larger. **Capsule** cleistocarpous, immersed, sessile or nearly so, ovoid to globose, apiculate or not, indehiscent or dehiscent near mid region, exothecial cells smooth to weakly or strongly bulging; stomata superficial, surrounded by 2 guard cells, restricted toward base or scattered throughout, occasionally absent. **Operculum** absent. **Peristome** absent. **Calyptra** mitrate, base weakly lobed or erose. **Spores** reniform, mostly large, papillose.

DISCUSSION. The Ephemeraceae contain three genera and about 35 species; in the Neotropics two genera and about 13 species. The family is placed in the order Funariales. These minute mosses develop on sparse to copious spreading protonematal mats with immersed cleistocarpic capsules which, as implied by the family name, are ephemeral and exhibit a rapid life cycle in temporal moist habitats.

LITERATURE. Bryan, V. S. & L. E. Anderson. 1957. The Ephemeraceae in North America. The Bryologist 60: 67–102 [a useful introduction to the family].

1. Calyptrae mitrate-campanulate, deciduous; leaves little contorted when dry, costate or nearly ecostate; laminal cells smooth or papillose; protonema usually abundant ..... **Ephemerum**
1. Calyptrae little differentiated, persistent; leaves shriveled or contorted when dry, ecostate; laminal cells smooth; protonema present but sparse ..... **Micromitrium**

Ephemerum (Fig. 125) - Seven species in the Neotropics, largely restricted to southeastern Brazil, Paraguay, Uruguay, and Argentina; a genus of about 25 species mostly associated with northern temperate regions.

HABITAT. On exposed moist soils, particularly alluvial; open sites associated with seasonal or periodic rains and possibly floods, at low elevations.

DESCRIPTION. **Plants** to 1 mm tall, gregarious, light green. **Stems** very short from thick protonematal mats. **Leaves** few, little contorted dry or wet, linear- or ovate-lanceolate, to ca. 1 mm long; apex acuminate; margins often coarsely serrate to near base; costa none (occasionally present); upper and median cells narrowly long hexagonal to rhomboidal, often papillose by projecting distal cell angles; basal cells larger and broader, irregularly rectangular. **Autoicous**, dioicous or polygamous. **Capsule** ovoid to globose, apiculate, to ca. 0.5 mm in diameter, indehiscent; stomata superficial, restricted toward base or scattered throughout. **Calyptra** mitrate, base weakly lobed or erose. **Spores** large, appearing coarsely papillose.

DISCUSSION. The genus is characterized by minute leafy plants occurring on thick protonematal mats, with leaves often contorted when dry, presence or absence of a single costa, and mitrate-campanulate calyptra. Schiavone and de Sarmiento (1985) have treated several of our species.

LITERATURE. Schiavone M., M. & M. N. R. de Sarmiento. 1985. Contribución al conocimiento de los musgos de la Argentina I. Género *Ephemerum* Hamp. Lilloa 36: 221–231 [keys, illustrations].

Micromitrium (Fig. 126) - Six species in the Neotropics; about 9 species of tropical and temperature distribution.

HABITAT. On exposed soil or sandy banks; open sites in tropical lowlands.

DESCRIPTION. **Plants** minute and inconspicuous, to 2 mm tall, pale to yellowish green; protonema forming thin mats. **Leaves** slightly contorted when dry, rather broadly lanceolate to oblong-lanceolate, 1(–2) mm long, apex bluntly acuminate; margins bluntly serrate; costa none; median cells large, smooth. **Capsule** globose, not apiculate, ca. 0.25 mm in diameter, dehiscent near mid region or rupturing in an irregular fashion, exothecial cells protruding and bulging; stomata absent or present. **Calyptra** minute, composed of remnants of the archegonium. **Spores** to 60 µm in diameter, appearing papillose or reticulate-papillose.

DISCUSSION. The genus is characterized by minute leafy plants borne on thin protonematal mats, with leaves little contorted when dry, absence of a costa, smooth laminal cells, and a minute calyptra. *Nanomitrium* is an earlier synonym. *Micromitrium austinii* Sull. in Austin is known from Mexico, Panama, Puerto Rico, and Brazil, *M. thelephorothecum* (Florsch.) Crosby is reported from the Amazon Basin. The remaining three species are from Brazil.

ERPODIACEAE

Plants somewhat small, in loose to somewhat dense mats, dull light to dark green. **Stems** creeping, irregularly pinnately branched, terminal stems and branches often ascending and curled, radiculose beneath. **Leaves** crowded, appressed to weakly complanate, occasionally appearing 4-ranked, ovate, oblong-ovate to nearly orbicular, symmetric to asymmetric, concave, elimbate, apex acuminate to acute, obtuse-rounded, apiculate or subpiliferous or not; margins plane, entire or crenulate by projecting papillae; costa none; laminal cells smooth or pluripapillose, apical cells elongate or isodiametric; median cells quadrate or rhombic to hexagonal and horizontally arranged or oblate; alar cells quadrate to oblong, oblately arranged. **Autoicous**. **Perichaetia** terminal on short lateral branches; leaves often enveloping sporophyte, oval to oblong. **Seta** erect, mostly short. **Capsule** immersed to short exserted, erect to subinclined, urn short-cylindrical; stomata absent or several at base of urn, superficial; annulus absent or compound and persistent. **Operculum** conic-rostrate or -apiculate. **Peristome** absent or single, teeth 16, poorly developed, short, papillose or irregular, pale segments. **Calyptra** mitrate to narrow and long campanulate, plicate, surface smooth to roughened. **Spores** spherical, smooth to finely papillose.

DISCUSSION. The Erpodiaceae contain four to six genera and some 25 species of mostly tropical and south temperate distribution; in the Neotropics two genera and 10 species are known. The family is placed in the Orthotrichales. The treatment here follows the family concept of Crum (1972); Stone (1997) presents a narrower family concept, recognizing *Aulacopilum* Wilson, *Wildia* Müll. Hal., and *Venturiella* Müll. Hal. as synonyms of *Erpodium* (Brid.) Müll. Hal.

LITERATURE. Crum, H. 1972. A taxonomic account of the Erpodiaceae. Nova Hedwigia 23: 201–224 [keys]. - Pursell, R. A. 1966. Notes on American Erpodiaceae, with description of two new species. The Bryologist 69: 461–471. - Stone, I. G. 1997. A revision of Erpodiaceae with particular reference to Australian taxa. Journal of Bryology 19: 485–502. - Vital, D. M. 1980. Erpodiaceae (Musci) do Brasil. Universidade Estadual de Campinas.

1. Calyptrae elongate and strongly twisted, campanulate, covering the entire capsule and upper portion of seta; laminal cells papillose ..... **Aulacopilum**
1. Calyptrae short, mitrate or somewhat cucullate, covering the operculum and upper portion of urn; laminal cells smooth or papillose ..... **Erpodium**

Aulacopilum (Fig. 126) - Three species recorded for the Neotropics, *A. glaucum* Wilson (Argentina, Brazil, also New Zealand), *A. schaeferi* H. A. Crum (southeastern Brazil), and *A. tumidulum* Thwaites & Mitt. (Mexico, Paraguay, Planalto, and southeastern Brazil, also Sri Lanka); a genus of seven species distributed in the Americas, Africa, and Asia.

HABITAT. On base and trunk of trees; semi-dry forests and areas of human occupation (including roadside trees, parks), from near sea level to 950 m.

DESCRIPTION. **Plants** small, forming thin mats, dull or glaucous olive green or brown. **Stems** creeping, irregularly pinnately branched, spreading complanate-foliate to subascending and terete; in cross-section outer 1–2 rows of cells rather small, thick-walled, inner cells large, thin-walled, central strand absent. **Leaves** appressed and weakly terete foliate when dry, loosely complanate when wet, ovate, to 0.6 mm long, mostly asymmetric, apex obtuse-rounded to bluntly acute or acute and ending in a hyaline apiculus or long piliferous tip; margins mostly plane, crenulate by projecting papillose cells; laminal cells hexagonal, pluripapillose over cell lumen, thin-walled, upper and median cells isodiametric; lower and occasionally marginal cells slightly elongate. **Perichaetial** leaves sheathing, slightly more elongate, to 0.8 mm long, apex acute to acuminate. **Seta** 0.7–1.2 mm long, smooth. **Capsule** exserted, urn short- to oblong-cylindrical to ovoid, 0.5–1 mm long; exothecial cells subquadrate, rather thick-walled; stomata absent or present in neck, superficial. **Operculum** conic-apiculate. **Peristome** absent. **Calyptra** campanulate, enveloping capsule (to 1.6 mm long), usually persistent, moderately twisted (spiral), longitudinally plicate and opening by slits, surface smooth to lightly papillose. **Spores** finely papillose.

DISCUSSION. The genus is characterized by the pluripapillose laminal cells, and twisted, elongate, smooth or lightly papillose, campanulate calyptra. The three species can be differentiated as follows: *A. schaeferi* — leaves obtuse-rounded to bluntly acute, calyptra surface smooth; *A. glaucum* — leaves mostly acute, apiculate or subpiliferous, calyptra surface lightly papillose; *A. tumidulum* — leaf apex inconspicuously hyaline-apiculate, perichaetial leaves acute, capsules oblong-obovoid, and leaf apex hyaline-subpiliferous, perichaetial leaves acuminate, capsules oblong-cylindrical.

LITERATURE. Crum, H. 1988. A new species of *Aulacopilum* from Brazil. The Bryologist 91: 191–192. - Yano, O 1984. Ocorrência de *Aulacopilum glaucum* Wils. (Erpodiaceae, Bryopsida) no Brasil. Anais Congresso da Sociedade de Botanica, Sao Paulo 4: 77–82.

Erpodium (Fig. 126) - Seven species in the Neotropics; 16 species widely distributed in tropical and subtropical regions.

HABITAT. Epiphytic, on tree trunks and exposed roots, also on rocks or logs, in shaded or partially exposed sites; semi-arid forests, from near sea level to 1700 m.

DESCRIPTION. **Plants** somewhat small, in loose to somewhat dense mats, dull light to dark green. **Stems** creeping, to 10 mm long, irregularly pinnately branched, terminal stems and branches often spreading to ascending and curled, radiculose beneath. **Leaves** appressed to weakly complanate, occasionally appearing 4-ranked, ovate, ovate-oblong to nearly orbicular, 0.5–1.2 mm long, symmetric to asymmetric, concave, apex acuminate to acute or rounded, apiculate or subpiliferous; margins plane, entire; laminal cells smooth or pluripapillose, apical cells elongate or isodiametric; median cells quadrate- to hexagonal-rounded and horizontally arranged or oblate; alar region differentiated, cells oblong, oblately arranged. **Perichaetial** leaves often enveloping sporophyte, oval to oblong. **Seta** short, 0.2–0.8 mm long. **Capsule** immersed to short exserted, erect to subinclined, urn short-cylindrical, 0.8–1.5 mm long; stomata absent or several at base of urn, superficial; annulus absent or compound and persistent. **Operculum** conic-rostrate. **Peristome** absent or poorly developed, papillose. **Calyptra** mitrate-short campanulate, plicate and lobed at base, or appearing cucullate, roughened or not. **Spores** smooth to lightly papillose.

DISCUSSION. The genus is characterized by the smooth or pluripapillose laminal cells, short, mitrate or somewhat cucullate calyptra covering the operculum and upper portion of urn.

EUSTICHIACEAE

A monotypic family, placed in the order Dicranales.

Eustichia (=*Diplostichum*) (Fig. 127) - Possibly a monotypic genus, in the Neotropics only *E. longirostre* (Brid.) Brid. is recognized in this treatment; distributed in Mexico, Central America, West Indies (Dominican Republic), Andes, southeastern Brazil; a genus stated to contain seven, but possibly all equal to the above species recorded from tropical America and Africa.

HABITAT. On rock or soil covered rocks; mid to upper montane forests, occasionally extending into subpáramo along gallery forests, 2360–3500 m; usually found in moist, shaded sites.

DESCRIPTION. **Plants** slender and small, forming loose to rather dense tufts, dull green or olive green. **Stems** erect, to 4 cm tall, freely branched, radiculose; in cross-section central strand present. **Leaves** 2-ranked above, spirally arranged scale-like leaves at stem base, erect to erect-spreading, conduplicate, short oblong-ovate, 0.5–0.8 mm long, apex inwardly hooked, short acuminate; margins plane, dentate throughout except at base; costa single, percurrent to short excurrent; laminal cells thick-walled, median cells subquadrate to short oblong-quadrate, pluripapillose on abaxial surface; basal cells short rectangular, smooth; marginal cells appearing mostly smooth; spirally arranged leaves on lower stems and branches ovate-short lanceolate, acuminate, costa rather long excurrent. **Dioicous**. **Perichaetia** appearing lateral, leaves convolute, oblong, apex abruptly narrow acuminate; costa rather long excurrent; laminal cells elongate. **Seta** elongate, to 15 mm long, smooth. **Capsule** mostly erect, urn short obloid, 0.8–1.2 mm long, when deoperculate usually ribbed with mouth flared; exothecial cells irregularly elongate; thick-walled, stomata several at base of urn, superficial. **Operculum** conic-long rostrate. **Peristome** single, teeth 16, joined at base, usually reduced, vertically striate-papillose. **Calyptra** cucullate, naked and smooth. **Spores** lightly papillose.

DISCUSSION. *Eustichia* is characterized by the strongly 2-ranked leaves with pluripapillose laminal cells and a short excurrent costa that is slightly incurved. Authors disagree on the number of species of *Eustichia* (one to seven), but no serious effort has been made to resolve the problem. The family is assigned to the Dicranales but further investigations are needed to elucidate its phylogenetic position among other higher taxa. *Eustichia longirostre* was previously placed in the genus *Diplostichum*.

FABRONIACEAE

Plants medium sized to mostly small, forming mats, glossy light to dark green. **Stems** creeping, distal stem and branch subascending, often curved; in cross-section central strand absent or weak; pseudoparaphyllia foliose. **Leaves** erect to imbricate when dry, erect-spreading to spreading when

wet, homomallous or not, orbicular, ovate to ovate- or oblong-lanceolate, weakly to strongly concave, acuminate to acute or rounded; margins plane or slightly erect, entire to serrate or ciliate distally; costa single, 1/2 lamina length to percurrent, slender to broad; laminal cells thin- to firm-walled, smooth, apical cells often shorter than median, upper and median cells oval, rhombic to rhomboidal or oblong-hexagonal; alar cells often oblate, few to rather numerous, extending to near cost or not, quadrate to quadrate-rounded or short rectanuglar. **Autoicous**. **Perichaetia** lateral, leaves usually differentiated. **Seta** elongate, twisted or not, smooth. **Capsule** erect, urn ovoid to cylindrical, constricted below mouth or not when deoperculate, neck short; stomata at urn base, superficial; annulus differentiated or not. **Operculum** short rostrate or conic-mammillate, oblique or straight. **Peristome** set below mouth, single or double, exostome teeth 16, paired or separate, hyaline or not, papillose; endostome, when present, rudimentary and adhering to exostome or with segments 8 or 16, shorter than exostome teeth, keeled, perforate, slightly roughened. **Calyptra** cucullate, smooth or roughened distally, naked. **Spores** spherical to ovoid, finely to coarsely papillose.

DISCUSSION. The Fabroniaceae contain about eight genera and 90 species, probably closer to 50, widely distributed in temperate and tropical regions; in the Neotropics with four genera and eight species. The family is placed in the order Hypnales. A redefined Fabroniaceae has been presented in a series of papers by Buck and Crum (1978) and Buck (1980, 1981), transferring several genera to an emended Myriniaceae.

LITERATURE. Buck, W. R. 1980. A re-interpretation of the Fabroniaceae: Additions and corrections. Journal of the Hattori Botanical Laboratory 47: 45–55. - Buck, W. R. 1981. A re-interpretation of the Fabroniaceae, III: *Anacamptodon* and *Fabronidium* revisited, *Mamillariella*, *Helicodontiadelphus* and *Bryobartlettia* gen. nov. Brittonia 33: 473–481. - Buck, W. R. & H. Crum. 1978. A re-interpretation of the Fabroniaceae with notes on selected genera. Journal of the Hattori Botanical Laboratory 44: 347–369.

1. Leaves broadly ovate to orbicular ..... **Dimerodontium**
1. Leaves ovate-lanceolate to oblong-lanceolate 2
2. Peristome single; leaf apices often narrowly and abruptly long acuminate; plants readily fragmenting when removing leaves ..... **Fabronia**
2. Peristome double, endostome shorter than exostome; leaf apices acute to broadly, sometimes ± narrowly, acuminate; plants sturdier, not readily fragmenting when removing leaves 3
3. Leaf margins entire or subentire; exostome papillose, endostome segments keeled and slightly roughened ..... **Anacamptodon**
3. Leaf margins distally serrate or serrulate; exostome hyaline, endostome rudimentary, adhering to exostome ..... **Levierella**

Anacamptodon (Fig. 127) - Two species in the Neotropics, *A. compactus* (Thér.) W. R. Buck (Mexico at moderate elevations), and *A. cubensis* (Sull.) Mitt. (Greater Antilles and tropical South America at low elevations); a genus of 12 species.

HABITAT. Epiphytic, base or trunk of trees, also knotholes; semi-dry to moist submontane or lower montane forests, at elevations from 200–2600 m.

DESCRIPTION. **Plants** small, glossy dark green. **Stems** creeping, distal stem and branch subascending, often curved; in cross-section outer row of cells rather small, firm-walled, inner cells large, thin-walled, central strand absent. **Leaves** erect and homomallous when dry, erect-spreading when wet, ovate-lanceolate, to ca. 1 mm long, weakly concave, gradually acuminate to acute; margins plane or slightly erect, entire to subentire; costa 1/2 lamina length to percurrent, slightly flexuose or not; laminal cells firm-walled, smooth, upper and median cells rhombic to rhomboidal or oblong-hexagonal; alar region differentiated, cells few, quadrate. **Perichaetial** leaves differentiated, oblong-lanceolate, gradually to abruptly acuminate, margins entire to rather coarsely serrulate, costate. **Seta** elongate, to ca. 8 mm long, slightly curved or flexuose, twisted or not, smooth. **Capsule** erect, urn ovoid to broadly short cylindrical, to 0.8 mm long, constricted below mouth when deoperculate, neck short; stomata at urn base, superficial; annulus little differentiated. **Operculum** bluntly short rostrate, oblique or straight. **Peristome** set below mouth, double, teeth strongly reflexed when dry, fused in pairs at base, broad, densely papillose on both surfaces, with a zig-zag median line; endostome segments 8 or 16, shorter than exostome teeth, keeled, perforate, slightly roughened. **Calyptra** smooth or roughened distally. **Spores** spherical or nearly so, finely papillose.

DISCUSSION. The genus is distinguished by the loose mats, subascending branches, broadly acuminate or acute apex, entire or subentire margins, few differentiated alar cells, capsule constricted below the mouth when deoperculated, papillose exostome, and keeled, slightly roughened endostome, shorter than exostome. The genus is similar to *Helicodontium* (Myriniaceae), the latter differing primarily by a peristome arising at the urn mouth, exostome cross-striate on outer surface, endostome basal membrane moderately high, and a tendency to form compact mats.

LITERATURE. Anderson, L. E. & P. G. Palmer. 1982. The peristome of *Anacamptodon splachnoides*. The Bryologist 85: 193–203. - Buck, W. R. 1980, 1981 (see family ref.).

Dimerodontium - Possibly two species in the Neotropics, the common one, *D. mendozense* Mitt., is found in southeast Brazil and Paraguay (also Argentine, Chile, and Uruguay); a genus represented in the tropics of America and Africa with 10 species, possibly 2-3.

HABITAT. Epiphytic, on trunk and exposed roots of trees, also logs; at elevations mostly below 300 m.

DESCRIPTION. **Plants** small, dull dark green. **Stems** creeping, irregularly branched, few to many branches; in cross-section central strand absent; rhizoids clustered beneath stems. **Leaves** crowded, imbricate to appressed when dry, spreading when wet, broadly ovate to orbicular, to 0.5 mm long, concave, apex acute-rounded; margins plane above, slightly reflexed at base, entire; costa subpercurrent, strong, conspicuously broad; laminal cells smooth, firm-walled; upper and median cells oval to quadrate-rounded, partly obliquely arranged; alar region differentiated, cells quadrate-round to short rectangular, oblate. **Perichaetial** leaves lanceolate; costa weak; laminal cells elongate, upper laminal cells fusiform, lower rectangular. **Seta** elongate, 3**–**7 mm long, erect, smooth. **Capsule** erect, urn ovoid to ovoid-cylindrical, ca. 1.1–1.4 mm long, exothecial cells rectangular, walls firm but thin; stomata rather numerous at base of urn, superficial; annulus absent or of undifferentiated cells. **Operculum** conic-mammillate. **Peristome** single, exostome teeth 16 in 8 pairs, strongly papillose. **Calyptra** smooth. **Spores** spherical, papillose.

DISCUSSION. The genus is characterized by the broadly ovate to orbicular, concave leaves; strong and broad costa; and strongly papillose, paired exostome teeth. The genus is well illustrated by Brotherus, V. F. (1924: fig. 646, see general ref.).

Fabronia (Fig. 127) - Four species in the Neotropics; a genus of 60 species of temperate and tropical regions.

HABITAT. Epiphytic, on trunks and branches of trees, less often on rocks, including concrete. *Fabronia ciliaris*, the most common species with several varieties, is often associated with human occupation and is frequent in cities and farms; in partially open montane, especially in semi-dry forests, extending into páramo and puna in wooded areas, 500–4400 m.

DESCRIPTION. **Plants** small, soft and delicate, glossy light green. **Stems** creeping, irregularly branched, few to many branches; in cross-section central strand absent; rhizoids clustered beneath stems, few. **Leaves** distant to somewhat crowded, loosely erect when dry, spreading when wet, ovate to ovate-lanceolate, 1 mm or less long, apex long acuminate; margins plane, entire or dentate to ciliate; costa ca. 1/2 lamina length, weak; laminal cells smooth, thin but firm-walled, apical and upper cells oblong-fusiform to linear; median cells rhomboidal; alar region differentiated, cells quadrate. **Perichaetial** leaves usually larger and longer than stem leaves. **Seta** somewhat elongate, to ca. 2 mm long, erect to slightly curved, smooth. **Capsule** erect, urn turbinate to ovoid, ca. 05.–1 mm long, exothecial cells quadrate to short rectangular with sinuate firm but thin walls; stomata few at base of urn, superficial; annulus absent or of undifferentiated cells. **Operculum** conic-mammillate. **Peristome** single, exostome teeth 16 in 8 pairs, bluntly rounded, papillose to cross-striate-papillose below, distally vertically, fragile, readily deciduous. **Calyptra** smooth. **Spores** spherical to ovoid, coarsely papillose.

DISCUSSION. The delicate, soft stems, small ovate or ovate-lanceolate abruptly narrowed leaves with a mostly long acuminate apex and weak single costa, the perichaetial leaves larger than stem leaves, and rather fragile single peristome are distinctive features of *Fabronia*.

LITERATURE: Buck, W. R 1983. A synopsis of the South American taxa of *Fabronia* (Fabroniaceae). Brittonia 35: 248–254 [keys, illustrations].

Levierella (Fig. 128) - A single species in the Neotropics, *L. perserrata* P. de la Varde & J.-F. Leroy, only known from Mexico (and Africa); a genus of four species (Mexico, Africa and India).

HABITAT. Epiphytic, on tree trunks, in shady sites of somewhat dry temperate montane forests; on *Juniperus* in *Quercus* and *Pinus* dominated woodlands, 1800–1930 m.

DESCRIPTION. **Plants** medium sized. **Stems** rather slender, irregularly pinnately branched, branches curled when dry. **Leaves** homomallous when dry, stem and branch leaves somewhat differentiated, stem leaves larger and more ovate, branch leaves oblong-lanceolate, 0.8–1.2 mm long, to 0.4 mm wide, apex acute; margins plane, distal 1/2 serrate to serrulate, sharply so at apex; costa ca. 1/2 lamina length; apical cells short hexagonal, 2:1, median cells long hexagonal, 5–6:1; alar region differentiated, cells quadrate, extending upwardly along margin, and to near or at costa. **Perichaetial** leaves lanceolate-triangular, ca. 2 times stem leaves. **Seta** elongate, to 12 mm long, twisted. **Capsule** erect, urn cylindrical, 2–3 mm long; annulus in 2–3 rows, deciduous. **Operculum**

conic-rostrate, oblique. **Peristome** double, exostome teeth hyaline, endostome rudimentary, adhering to exostome . **Calyptra** smooth. **Spores** spherical, finely papillose.

DISCUSSION. The genus is characterized by irregularly pinnate branching of the stems and the distally curled, homomallous foliage which is slightly dimorphic, stem leaves are ovate and branch leaves are short oblong-lanceolate, apex gradually acute, rather sharply serrate margins at apex, costa ending at or just below midleaf, long hexagonal median laminal cells, symmetric, suberect to erect capsule, hyaline exostome, and rudimentary endostome adhering to exostome. Delgadillo M. and Buck (1988) noted that the distribution exhibited by *Levierella*, tricentric disjunction (America–Africa–Himalaya), is apparently rare at least with regard to Mexico.

LITERATURE. Delgadillo M., C. & W. R. Buck. 1988. *Levierella* (Fabroniaceae), a moss genus new to the Americas. The Bryologist 91: 53–55 [illustrations].

FISSIDENTACEAE

A monotypic family, placed in the order Fissidentales.

Fissidens (Fig. 128) - About 100 species in the Neotropics; estimated at 500 species distributed worldwide but absent in arid regions.

HABITAT. Mostly in shaded, moist sites, on soil, rocks associated with streams, and lower trunks of trees, a few species truly aquatic; in moist or wet lowland to upper montane forests, also in open areas when sufficiently wet, extending into zacatonal, páramo, and puna, from near sea level to 4450 m.

DESCRIPTION. **Plants** very small to medium sized, 0.3–8 cm tall, mostly erect, forming tufts or solitary, dull to more commonly bright green, occasionally blackish-, reddish- or brownish-green. **Stems** simple or branched; in cross-section central strand present or absent. **Leaves** 2-ranked (distichous), median and upper leaves mostly oblong to ligulate or oblong-lanceolate, 0.5–6 mm long, composed of **vaginant laminae** (sheath-like), with **dorsal** (extending the length of the back part of leaf) and **ventral** (above the vaginant laminae) **lamina**; margins smooth, crenulate, or occasionally distally serrulate to irregularly sharply serrate, limbate, sometimes intramarginally, or elimbate, when limbate the limbidium uni- to multistratose; costa single, usually strong, (1/2–)2/3 to percurrent or short to long excurrent, lacking or weak in a few species; laminal cells smooth, mammillose or uni- or pluripapillose, border (marginal or intramarginal) cells when present linear and smooth. **Gemmae** mostly absent or present in leaf axils. **Autoicous**, synoicous or dioicous. **Perichaetia** terminal, occasionally lateral, leaves often differentiated. **Seta** 1(2–5) per perichaetium, 2–10 mm long, erect or variously curved, smooth. **Capsule** exserted, erect to horizontal, urn ovoid to broadly cylindrical, 0.3–2 mm long; annulus absent; exothecial cells short to long rectangular, longitudinal walls thick, collenchymatous or not; stomata at urn base, superficial. **Operculum** conic short to long rostrate. **Peristome** single, teeth 16, divided to half or more below, occasionally undivided or imperfectly divided, striate or papillose. **Calyptra** cucullate or short mitrate, naked, smooth or roughened. **Spores** spherical, smooth to lightly papillose.

DISCUSSION. The 2-ranked leaf arrangement along the stems with the distinctively modified leaves exhibiting vaginant lamina and dorsal and ventral laminae is diagnostic for the genus. *Fissidens* may be confused with *Diplostichum* (Eustichaceae) which also exhibits strongly 2-ranked leaves; however in the latter dorsal and ventral laminae are absent, and the costa is short excurrent and slightly incurved. *Sorapilla* (Sorapillaceae), only known from a single locality in Ecuador, is similar to *Fissidens* in leaf design, however this genus is pleurocarpic with hyaline bordered leaves and immersed capsules. *Mniomallia* may be mistaken for *Fissidens*, at least in aspect; however, the leaf margins are recurved, propagula commonly produced on terminal stems and branches, and a vaginant lamina is lacking. Because of its small size *Fissidens* is overlooked by most collectors and is generally poorly represented in herbaria. The recent treatments by Pursell in Allen (1994, see general ref.), and in Sharp *et al*. (1994, see general ref.), the latter with excellent illustrations, are very helpful since many of the species are widespread in the Neotropics.

Study guide. Leaves provide all the essential features needed for identifying species, however in a few species perichaetial leaves must be present to determine if a border is present. A cross-section of leaves is desirable, including the vaginant lamina, to determine cell ornamentation and if the limbidium is uni-, bi- or multistratose (the number of border cell layers or ornamentation can, with practice, be determined simply by focusing up and down at high power on an intact leaf).

LITERATURE. Bruggeman-Nannenga, M. A. 1973. The section *Pachylomidium* (genus *Fissidens*). I. The species of tropical and subtropical South America. Proceedings, Koninklijke Nederlandse Akademie van Wetenschappen, Series C, Biological and Medical 76: 172–189. - Bruggeman-Nannenga, M. A. 1979. The section *Pachylomidium* (genus *Fissidens*). II. The species of Central America, temperate South America (including the high Andes), Australia, New Zealand, and New

Guinea. Proceedings, Koninklijke Nederlandse Akademie Wetenschappen, Series C, Biological and Medical 82: 11–27. - Bruggeman-Nannenga, M. A. & W. Berendsen. 1990. On the peristome types found in the Fissidentaceae and their importance for the classification. Journal of the Hattori Botanical Laboratory 68: 193–234. - Bruggeman-Nannenga, M. A. & R. A. Pursell. 1990. The *Fissidens radicans* complex (Section *Amblyothallia*) in the Neotropics and Paleotropics. The Bryologist 93: 332–340. - Grout, A. J. 1943. Bryales. Fissidentaceae. North American Flora 15, part 3: 167–202, plates 1–10 [keys]. - Pursell, R. A. 1984. A preliminary study of the *Fissidens elegans* complex in the neotropics. Journal of the Hattori Botanical Laboratory 55: 235–252 [keys, illustrations]. - Pursell, R. A. 1987. A taxonomic revision of *Fissidens* subgenus *Octodiceras* (Fissidentaceae). Memoirs of the New York Botanical Garden 45: 639–660 [3 of 6 species in the Neotropics, keys, illustrations]. - Pursell, R. A. 1988. *Fissidens amazonicus* sp. nov. from Brazilian Amazonia, with comments on the relationship and taxonomy of subgenus *Fissidens* sections *Areofissidens*, *Weberiopsis* and *Reticularia* and subgenus *Aneuron* (Bryopsida: Fissidentaceae). Beiheft zur Nova Hedwigia 90: 345–355. - Pursell, R. A. 1994. Taxonomic notes on neotropical *Fissidens*. The Bryologist 97: 253–271. - Pursell, R. A. 1997. Taxonomic notes on neotropical *Fissidens*. II. An addendum. The Bryologist 100: 193–197. - Pursell, R. A. 1999. Taxonomic notes on neotropical *Fissidens*. III. Addendum II. The Bryologist 102: 125–127. - Pursell, R. A. & B. Allen. 1991. Distributional records of *Fissidens* in the Neotropics, with description of *F. panamensis* sp. nov. The Bryologist 94: 213–216. - Pursell, R. A. & B. H. Allen. 1991. A re-evaluation of *Fissidens* subgenus *Pachyfissidens*, with a detailed discussion of *Fissidens grandifrons* and *F. geijskesii*. Journal of the Hattori Botanical Laboratory 75: 15–22. - Pursell, R. A., M. A. Bruggeman-Nannenga & B. H. Allen. 1988. A taxonomic revision of *Fissidens* subgenus *Sarawakia* (Bryopsida: Fissidentaceae). The Bryologist 91: 202–213 [2 of 3 species in the Neotropics, keys and illustrations]. - Pursell, R. A. & W. D. Reese. 1980. The rediscovery of *Fissidens subulatus* Mitt. in Brazil. The Bryologist 83: 526. - Pursell, R. A. & D. M. Vital. 1986. Distributional adumbrations of *Fissidens* in the neotropics. The Bryologist 89: 300–301.

FONTINALACEAE

Primarily aquatic, the Fontinalaceae contain three genera and about 30 species, mostly of the north temperate region. The family is placed in the order Leucodontales.

Fontinalis (Fig. 128) - A single species known from the Neotropics, *Fontinalis bogotensis* Hampe, endemic to Colombia; about 20 species largely of the Northern Hemisphere.

HABITAT. Usually attached to rocks in small to medium sized, slow to fast flowing streams, in open montane and páramos (2000–3700 m).

DESCRIPTION. **Plants** aquatic, forming loose mats attached to substrate, dark green to blackish or brown. **Stems** usually elongate (to 50 cm long or more), irregularly pinnately branched; in cross-section outer 4–5 rows of cells small, thick-walled, inner cortical cells large, thin-walled, central strand absent. **Leaves** rather flaccid, 3-ranked or appearing 2-ranked, loosely spreading, ovate-lanceolate, 3.5–6 mm long, to 2.5 mm wide, concave, apex obtuse-rounded, base rounded to subauriculate; margins plane, entire; costa none, laminal cells thick-walled, smooth, upper and median cells broadly linear; basal cells rectangular-rounded; insertion cells often yellow or golden-brown; alar cells few, lax, subhexagonal to subquadrate. **Dioicous**. **Seta** very short. **Capsule** immersed, urn short-oblong cylindrical, to 1.5 mm long. **Operculum** not observed. **Peristome** double, exostome occasionally united in pairs at apex. **Calyptra** not observed. **Spores** spherical, smooth.

DISCUSSION. The genus is distinguished by its aquatic habitat, 3-ranked, ecostate leaves, firm-walled elongate cells, and immersed capsules. Sporophytes are rare, reproduction is likely by fragmentation of leafy stems and branches. Buck and Allen (1997) suggest that the Fontinalaceae belongs to the Leucodontales based on branching pattern, rhizoid-associated anatomy and axillary hairs.

LITERATURE. Buck, W. R. & B. Allen. 1997. Ordinal placement of the Fontinalaceae. Cryptogamie: Bryologie, Lichénologie 18: 227–234. - Welch, W. H. 1960. A monograph of the Fontinalaceae. Nijhoff, The Hague [keys, illustrations].

FUNARIACEAE

Plants small to somewhat medium sized, gregarious or forming loose tufts. **Stems** erect, short, simple or few branched, often weakly radiculose below; in cross-section central strand present. **Leaves** reduced below, distally crowded, often comose, usually contorted when dry, ovate- to oblong-lanceolate, obovate or oblanceolate, usually ± concave, apex acute or short acuminate to obtuse;

margins plane to somewhat inflexed distally, entire to rather bluntly serrate, limbate or elimbate; costa single, narrow, 4/5 the lamina length to short excurrent; laminal cells smooth, rather lax, upper and median cells broadly rhombic to hexagonal; lower and basal cells oblong to rectangular; alar region undifferentiated. **Asexual structures** absent. **Autoicous**, occasionally polygamous. **Perigonia** mostly bud-like, apex of paraphyses club-shaped. **Perichaetia** terminal, leaves somewhat enlarged. **Seta** elongate, rarely very short, erect or somewhat curved and hygroscopic, smooth or rarely papillose. **Capsule** exserted, rarely immersed, erect to pendent, urn pyriform or cupulate, symmetric and ± smooth to asymmetric and striate when dry; annulus revoluble or not, stomata 1-celled. **Operculum** flat to conic-rounded. **Peristome** double, single or absent, when double exostome teeth 16, papillose, trabeculate; endostome segments 16, cilia absent, or when peristome single to reduced, represented by the exostome. **Calyptra** cucullate and usually inflated or mitrate and lobed below, smooth and naked. **Spores** mostly spherical, papillose or smooth.

DISCUSSION. The Funariaceae contain some 16 genera and less than 250 species, distributed worldwide; in the Neotropics three genera and about 40 species. The family is placed in the order Funariales. The majority of species are often found in disturbed or open sites on bare soil. Sterile plants are not readily identified, even to genus; a few species exhibit distinctive vegetative features that allows one to name them. Fortunately members of the Funariaceae are autoicous and frequently fertile.

LITERATURE. Fife, A. J. 1985. A generic revision of the Funariaceae (Bryophyta: Musci). Part 1. Journal of the Hattori Botanical Laboratory 58: 149–196.

1. Capsule asymmetric, variously inclined to subpendent; peristome double, endostome well developed or somewhat rudimentary ..... **Funaria**
1. Capsule mostly symmetric and erect; peristome either single, rudimentary or absent 2
2. Capsule cupulate, mouth often flared when deoperculate; peristome absent; calyptra mitrate, base with few broad lobes ..... **Physcomitrium**
2. Capsule pyriform, mouth not flared when deoperculate; peristome present, single, rudimentary or occasionally absent; calyptra cucullate and inflated ..... **Entosthodon**

Entosthodon (Fig. 129) - About 15 species in the Neotropics; a genus of some 80 species.

HABITAT. On exposed soil; open montane, zacatonal, páramo and puna, 300 to more typically 2000–4650 m. Several of the common species, e.g., *Entosthodon bonplandii* (Hook.) Mitt., are very frequent in montane pasture slopes and along cutbanks of roads and mule trails.

DESCRIPTION. **Plants** small, solitary or forming small tufts, glossy green to golden-reddish brown. **Stems** erect, simple or few branched by innovations. **Leaves** distally comose, leafless or leaves reduced below, oblong- to obovate-lanceolate, 0.8–3.5 mm long, apex acute, short acuminate or obtuse; margins plane, entire or bluntly to rather sharply serrate; costa subpercurrent to short excurrent; upper and median cells large, broadly rhombic, short to long hexagonal; lower and basal cells oblong to rectangular, lax; marginal cells forming a border or not. **Autoicous**. **Perichaetia** terminal, leaves similar or somewhat larger. **Seta** elongate, 3–20 mm long, smooth or papillose distally or throughout. **Capsule** erect to inclined, urn short to somewhat long pyriform, 1–3 mm long. **Operculum** flat or convex. **Peristome** absent or present with exostome teeth straight or sigmoid; endostome usually not well developed, often peristome reduced and usually set below urn mouth. **Calyptra** cucullate, smooth. **Spores** variously ornamented.

DISCUSSION. The genus is characterized by an erect and elongate seta, symmetric, pyriform capsule with the mouth little altered when deoperculated, when present a single rather well developed or rudimentary peristome, and an inflated, cucullate calyptra. Species of this genus are likely more common than presently known for the Neotropics. Plants are small and readily overlooked by collectors.

Entosthodon is viewed by some authors as containing transitional species exhibiting a reduction series with regard to peristomial features from the typical double peristome of *Funaria* to the complete absence of a peristome. For that reason, the genus has been, and still is, placed in *Funaria* by some authors. We are in agreement with the treatment by Allan Fife.

LITERATURE. Fife, A. J. 1987. Taxonomic and nomenclatural observations on the Funariaceae. 5. A revision of the Andean species of *Entosthodon*. Memoirs of the New York Botanical Garden 45: 301–325 [keys, illustrations].

Funaria (Fig. 129) - Nearly 20 species recorded for the Neotropics, probably far fewer; a genus of about 80 species.

HABITAT. On soil and rocks, frequent in disturbed or open sites, including those recently burnt; lowland and submontane to zacatonal, páramo and puna, from near sea level to 4600 m.

DESCRIPTION. **Plants** medium sized, forming loose tufts, green to yellowish-green or brown. **Stems** erect, to 1.5 cm tall, simple or few branched by innovations, dark red, radiculose; in cross-section hyalodermis present, outer 1–2 rows of cortical cells thick-walled, inner cortical cells thin-walled, central strand well developed; rhizoids appearing smooth. **Leaves** contorted when dry, comose distally, often leafless below, loosely erect, oblong- to obovate-lanceolate, to 3.2 mm long, to 1.4 mm wide, concave, apex short acuminate to acute; margins plane or rather strongly incurved, entire to bluntly or strongly serrulate distally; costa subpercurrent to short excurrent; median cells large, subquadrate to short or long oblong-hexagonal, smooth; basal cells oblong-rectangular; marginal cells narrow and elongate, forming a somewhat distinct border. **Autoicous**. **Perigonia** on lateral branches or not, leaves smaller. **Perichaetia** terminal. **Seta** single, elongate, 20–55 mm long, yellow or golden-yellow, smooth, slender and wiry, usually hygroscopic. **Capsule** exserted, erect to inclined or occasionally horizontal, dark red or reddish-brown, urn pyriform, strongly asymmetric, 1.6–3.2 mm long, widest at mouth, deeply striate, mouth oblique, neck rather long, ± flattened; exothecial cells oblong-rectangular, thick-walled; stomata in neck region, superficial; annulus revoluble. **Operculum** low convex-rounded or -plano. **Peristome** double, exostome teeth broadly lanceolate, slightly curved and joined at tip by a central disk , oblique or vertically striate-papillose below, distally papillose, strongly appendiculate and trabeculate on back; endostome hyaline, lightly papillose, basal membrane high, segments narrowly lanceolate, keeled. **Calyptra** cucullate, inflated below, distally rostrate and as long or longer than inflated base, smooth. **Spores** spherical, smooth.

DISCUSSION. The genus is characterized by a long, slender, often hygroscopic seta, often a striate, subpendent to inclined, asymmetric capsule, often oblique mouth, double peristome with a well developed or slightly rudimentary endostome, and cucullate calyptra that is long rostrate from an inflated base. *Funaria calvescens* Schwägr., the most common species, is often treated as a variety of *F. hygrometrica* Hedw. by several authors. The two species can be separated by the following sporophytic characters: *F. calvescens* — capsules suberect to horizontal, neck often flattened (compressed); and *F. hygrometrica* — capsules horizontal to pendent, neck not flattened.

Physcomitrium (Fig. 129) - About 20 species recorded for the Neotropics, possibly only 10 or fewer are valid; 68 species worldwide, mostly associated with temperate moist regions.

HABITAT. On exposed soil, often associated with wet sites, e.g., along streams or rivers; open sites, from near sea level to ca. 2100 m.

DESCRIPTION. **Plants** mostly small, solitary or forming loose, tufts, light green to yellowish-green. **Stems** erect, to ca. 5 mm, few branched by innovations, radiculose below; in cross-section outer 1–2 rows of cells slightly differentiated, somewhat smaller, firm-walled, inner cells large, thin-walled, central strand mostly weak. **Leaves** progressively larger distally, often crispate when dry, erect-spreading to spreading when wet, oblong to obovate-oblong, mostly to 3 mm long, acuminate to acute or acute-rounded; margins plane or erect below, entire to more commonly serrate, limbate or elimbate; costa rather strong, ending well below apex to percurrent or short excurrent; laminal cells large, smooth, mostly thin-walled, median cells rectangular to oblong-hexagonal; basal cells more elongate, lax; marginal cells differentiated, narrower than inner laminal cells, or not. **Perichaetia** terminal, leaves similar to stem leaves but often larger. **Seta** short or elongate, to ca. 5 mm long, smooth. **Capsule** immersed to exserted, erect, urn cupulate, mostly 1–2 mm long (including neck), often flared at mouth when dry, neck usually distinct, short; stomata in neck region, superficial; annulus persistent or not. **Operculum** plano-apiculate or -short rostrate, erect or oblique. **Peristome** absent. **Calyptra** mitrate, inflated or not below, long beaked above, base irregularly lobed, smooth and naked. **Spores** coarsely papillose or spiculose.

DISCUSSION. The genus is characterized by a elongate, rarely subsessile, erect, cupulate capsule, often flared at the mouth when deoperculated, and the absence of a peristome. The majority of *Physcomitrium* species are separated ecologically from *Entosthodon* with which they may be confused, the former occurring in more temporal wet habitats and at lower elevations. *Physcomitrium* is in need of revision; it is likely that some of the reports or described species actually represent *Entosthodon*, e.g., *P. benoistii* Thér. = *E. laevis* (Mitt.) Fife. About 12 of the 20 neotropical species presently recognized are primarily from the southeastern region of Brazil. Probably no more than half of the neotropical species will prove to be valid.

GIGASPERMACEAE

Plants small, gregarious, or forming dense tufts, pale whitish- or yellowish-green or appearing silvery. **Stems** short, hyaline, few branched from a subterranean rhizome; rhizoids pale, smooth. **Leaves** erect, broadly ovate to ovate-subulate to oblong, apex gradually acuminate or obtuse to acute; margins entire; costa absent or single and short ending below midleaf, or long excurrent; laminal cells

moderately thick- to thin-walled; oblong or oblong-rhomboidal to rectangular. **Synoicous**, paroicous, or possibly dioicous? **Perichaetia** terminal. **Seta** short to somewhat elongate. **Capsule** cleistocarpic or gymnostomous, immersed to exserted, urn ellipsoid to globose, strongly wrinkled when dry or not. **Operculum** lacking or if present then plano-apiculate to conic or short-rostrate. **Peristome** absent. **Calyptra** mitrate or cucullate. **Spores** large, papillose to granulose or verrucose.

DISCUSSION. The Gigaspermaceae contain six genera and nine species distributed mainly in the Southern Hemisphere; in the Neotropics three genera and four species. The family is placed in the order Funariales. An overview of the family and its genera has been provided by Fife (1980).

LITERATURE. Fife, A. J. 1980. The affinities of *Costesia* and *Neosharpiella* and notes on the Gigaspermaceae (Musci). The Bryologist 83: 466–476.

1. Costa long excurrent; capsules cleistocarpic, operculum absent ..... **Lorentziella**
1. Costa absent or short, ending below midleaf; capsules gymnostomous 2
2. Leaves ovate, apex gradually short to long acuminate; capsules immersed; operculum plano-short apiculate ..... **Gigaspermum**
2. Leaves short oblong, apex rounded to bluntly acute; capsules exserted; operculum conic-apiculate ..... **Neosharpiella**

Gigaspermum (Fig. 129) - A single species in the Neotropics, *G. repens* (Hook.) Lindb., only known from central Mexico (also South Africa, Australia, and New Zealand); a genus of 2–3 species.

HABITAT. On soil; montane, at 2700 m elevation.

DESCRIPTION. **Plants** very small, gregarious, pale whitish-green or appearing silvery. **Stems** short, hyaline, few branched; rhizoids pale, smooth. **Leaves** progressively larger distally, crowded, erect, broadly ovate to ovate-subulate, to 2.5 mm long, broadly concave, apex gradually short to long and narrowly acuminate; margins entire; costa absent; laminal cells evenly thin-walled and lax; oblong-rhomboidal to rectangular. **Dioicous**? **Seta** short, erect to slightly curved. **Capsule** gymnostomous, immersed, urn wide-mouthed, spongy and strongly wrinkled when dry. **Peristome** absent. **Operculum** plano and minutely apiculate. **Calyptra** minute, mitrate. **Spores** angled, large (to 120 µm), densely papillose.

DISCUSSION. The genus is characterized by bud-like plants with large ovate-subulate, ecostate perichaetial leaves, immersed, strongly wrinkled, gymnostomous capsules, and large, angled, strongly papillose spores.

Lorentziella - A monotypic genus, *L. imbricata* (Mitt.) Broth. is known from Mexico, Uruguay, Paraguay, and Argentina.

HABITAT. On soil or sandy soil, in exposed moist sites; semi-arid areas, including in Mexico open secondary *Quercus* forests associated with *Mimosa* and *Opuntia*; in the southern Neotropics at low elevations, ca. 200–300 m, in Mexico at 2520 m.

DESCRIPTION. **Plants** small, forming dense tufts, pale green to glaucous-green. **Stems** with erect branches, to 5 mm tall. **Leaves** larger and crowded above, ovate, 1.5–4 mm long, deeply concave, apex acute; margins entire to serrulate at juncture with costa; costa single, slenderly long excurrent; upper and median cells oblong-hexagonal, firm-walled, corners somewhat thickened; lower cells oblong. **Paroicous**. **Perichaetial** leaves larger than stem leaves. **Seta** very short, ca. 0.2 mm long, smooth. **Capsule** cleistocarpic, immersed, ellipsoid and somewhat apiculate or not, 1–1.5 mm long, strongly wrinkled. **Operculum** and peristome absent. **Calyptra** conic-mitrate, covering tip of capsule. **Spores** large, ellipsoid or subglobose, finely granulose.

DISCUSSION. The genus is distinguished by the slender excurrent costa and wrinkled ellipsoid, cleistocarpic capsules. Given the present disjunct distribution at the extreme boundaries of the Neotropics, it is likely this species will eventually be found in intervening areas where appropriate habitats exist.

LITERATURE. Cárdenas S., A. & C. Delgadillo M. 1994. *Lorentziella imbricata* and *Oreoweisia delgadilloi* in Mexico. The Bryologist 97: 85–86. - Lawton, E. 1958. *Lorentziella*, a moss genus new to North America. Bulletin of the Torrey Botanical Club 80: 279–288.

Neosharpiella (Fig. 130) - A genus of two species largely confined to the Neotropics, *N. aztecorum* H. Rob. & Delgad. known only from central Mexico, and *N. turgida* (Mitt.) H. Rob. & Delgad. presently known from Ecuador, Bolivia, and Chile.

HABITAT. On soil, in exposed sites; semi-dry zacatonal and puna, 4200–4700 m.

DESCRIPTION. **Plants** small, pale yellowish-green. **Stems** rhizomatous with erect branches. **Leaves** oblong, to 1.5 mm long, apex obtuse to acute; costa absent or single and short, to ca. 1/3 lamina length, slender; upper and median cells oblong, rather thick-walled, corners somewhat

thickened or not; marginal cells smaller. **Synoicous** or paroicous. **Perichaetial** leaves similar or differentiated and somewhat larger than stem leaves. **Seta** rather elongate, to 6 mm long, smooth. **Capsule** gymnostomous, exserted, obovoid to globose, strongly wrinkled or not; stomata numerous (to ca. 40). **Operculum** bluntly conic to short-rostrate**. Calyptra** cucullate. **Spores** large, coarsely verrucose.

DISCUSSION. Fife (1980) characterized the stem of *Neosharpiella* as a fragile hyaline rhizome that gives rise to the observable "leafy plants." Additional characteristics of the genus include the obtuse to acute oblong leaves, absence or presence of a short costa, rather elongate seta, conic to short-rostrate operculum, and cucullate calyptra. The two species can be separated as follows: *N. aztecorum* — capsules spherical, stomates in 2–3 rows at base of capsule, Mexico, and *N. turgida* — capsules ellipsoid, stomates in 4–5 rows on lower third of capsule, Ecuador to Chile.

LITERATURE. Fife, A. 1980 (see family ref.). - Robinson, H. & C. Delgadillo M. 1973. *Neosharpiella*, a new genus of Musci from high elevations in Mexico and South America. The Bryologist 76: 536–540.

GRIMMIACEAE

Plants small to medium sized, forming cushions, dense mats or tufts, dark green, blackish-green or golden-brown. **Stems** erect or appearing spreading, branched by innovations. **Leaves** ovate-lanceolate to long-lanceolate, rarely obovate or oblong-ovate, often channeled distally, apex acute or long acuminate, hyaline awn present or absent; margins plane, recurved on one or both sides, rarely incurved, entire or serrate; lamellae absent or present (*Aligrimmia*); costa single, strong; lamina uni- or bistratose; median cells quadrate to rectangular, smooth or mammillose, walls straight or weakly to very strongly sinuose (papillose); basal cells short to long rectangular, often sinuose. **Autoicous**, cryptoicous or dioicous. **Perichaetia** terminal or terminal on short lateral branches, leaves often differentiated. **Seta** elongate or short, erect or curved, smooth, often twisted. **Capsule** exserted, emergent or immersed (*Schistidium*), erect or suberect, obloid to ovoid-cylindrical. **Operculum** short to long rostrate. **Peristome** single, teeth 16, often divided, perforate or not, mostly papillose. **Calyptra** cucullate and smooth, or mitrate to mitrate-campanulate, smooth or plicate, slightly to distinctly lacerated or deeply lobed at base. **Spores** spherical, smooth to papillose.

DISCUSSION. The Grimmiaceae contain about 15 genera and about 300 species of temperate regions, in the tropics confined to mountainous regions; in the Neotropics eight genera and about 50 species. The family is placed in the order Grimmiales. Members of this family are found almost exclusively on rocks, generally in exposed sites at mid to high elevations except at the extreme boundaries of the Neotropics. The treatments by Deguchi (1984, 1987) are useful reference for the Andes, although no keys are provided, the descriptions and illustrations are excellent. The treatment by Crum (in Sharp *et al*. 1994, see general ref.), although employing a broader generic concept, is useful north of South America.

Study Guide. Leaves provide nearly all the characters needed for determination of our species; a leaf cross-section is useful, made at midleaf and somewhat below the apex.

LITERATURE. Churchill, S. P. 1981. A phylogenetic analysis, classification and synopsis of the genera of the Grimmiaceae (Musci). *In* Funk, V. A. & D. R. Brooks (eds.), Advances in Cladistics. Pages 127–144. New York Botanical Garden, Bronx. - Deguchi, H. 1984. Studies on some Patagonian species of Grimmiaceae (Musci, Bryophyta). *In* H. Inoue (ed.), Studies on Cryptogams in Southern Chile. Pages 17–72. Kenseisha, Tokyo. - Deguchi, H. 1987. Studies on some Peruvian species of the Grimmiaceae (Musci, Bryophyta). *In* H. Inoue (ed.), Studies on Cryptogams in Southern Peru. Pages 19–74. Tokai University Press, Tokyo. - Murray, B. 1984. A revision of the monotypic genera *Indusiella*, *Aligrimmia* and *Coscinodontella* (Musci: Grimmiaceae), with comments on convergent xeromorphological features. The Bryologist 87: 24–36.

1. Upper surface of leaf with 8–11 rows of lamellae ..... **Aligrimmia**
1. Upper surface of leaf without lamellae 2
2. Costa with two stereid bands ..... **Ptychomitrium**
2. Costa with only one band of substereids or stereids on the dorsal side 3
3. Leaf cells strongly sinuose throughout, with spiral thickenings; plants cladocarpous; peristome teeth each divided in two prongs nearly to the base, occasionally appearing as 32 teeth ..... **Racomitrium**
3. Leaf cells smooth to sinuouse but without spiral thickenings; plants acrocarpous; peristome teeth, if present, triangular, entire to perforate, but not divided in two prongs 4
4. Calyptra campanulate, plicate, covering most of the capsule 5
4. Calyptra mitrate or cucullate, covering the opercula at the most 7

5. Leaf tips concolorous, hair-points lacking .....**Coscinodontella**
5. Leaf tips with hyaline hair-points 6
6. Leaves plicate .....**Coscinodon**
6. Leaves not plicate ..... **Jaffueliobryum**
7. Capsules immersed; columella falling attached to the operculum; calyptra minute, covering only the beak of the operculum ..... **Schistidium**
7. Capsules immersed to exserted; columella remaining attached to the urn; calyptra covering the capsule mouth .....**Grimmia**

Aligrimmia (Fig. 130) - A monotypic genus, with *A. peruviana* R. S. Williams only known from Peru.

HABITAT. On rocks; dry open montane, at 2250 m.

DESCRIPTION. **Plants** small, forming short tufts, dark green to blackish-green. **Stems** rather short, to 6 mm tall, erect; in cross-section central strand large and well developed. **Leaves** crowded, incurved when dry, erect-spreading when wet, oblong-ovate, to 1.2 mm long, apex cucullate, obtuse-acute; margins plane below, distal half incurved, entire; costa strong, 1/4–1/3 width of leaf base, percurrent, distal 4/5 upper surface covered by 8–11 rows of lamellae; lamina unistratose, outer wall of cells thicker on lower (back) surface, upper and median cells subquadrate to short oblong-rectangular, walls firm; lower and basal cells slightly larger, short-oblong rectangular; lamella cells mostly 4–10 cells high, terminal cells smaller, thickened on outer surface. **Autoicous** (cryptoicous). **Perichaetial** leaves similar, perigonia attached at base. **Seta** short, to 1.7 mm long, smooth, twisted when dry. **Capsule** slightly exserted, ovoid, to ca. 0.9 mm long; annulus large. **Operculum** conic-rostrate. **Peristome** teeth irregularly divided into 2–3 filiform segments, rather strongly papillose. **Calyptra** campanulate, smooth above, plicate below, base lobed. **Spores** spherical, finely papillose.

DISCUSSION. The genus is distinguished by the presence of lamellae in 8–11 rows on the upper distal surface of the leaf, a feature encountered elsewhere only in the Polytrichaceae and in a few genera in the Pottiaceae; a fine example of convergent evolution. Additional features characterizing the genus include the cucullate, obtuse-acute apex, cryptoicous sexual condition, short seta, slightly exserted capsules, irregularly divided 2–3 filiform segmented peristome, and lobed, plicate campanulate calyptra.

LITERATURE. Deguchi, H. 1987 (see family ref.). - Murray, B. 1984 (see family ref.).

Coscinodon (Fig. 130) - A single species in the Neotropics, from the central Andes: *C. boliviana* Broth.; a genus of about five species.

HABITAT. On rocks or thin soil-covered rocks, exposed sites; puna, at elevations above 3500 m.

DESCRIPTION. **Plants** medium sized, forming dense cushions. **Stems** erect, to 10 mm tall, few branched by innovations; outer row of cells small, thick-walled, inner larger, thin-walled, central strand absent. **Leaves** erect, lanceolate to ovate-lanceolate, to ca. 1.2 mm long, appearing biplicate throughout or in distal half, apex a short to long hyaline tip, to 1/3 lamina length; margins erect, entire or appearing crenulate by bulging cell walls; costa long excurrent, tip smooth to weakly toothed, an additional costa on either side of the principal costa distally, extending toward or reaching base; lamina fully to partially bistratose distally; upper and median cells quadrate- to short rectangular-rounded, thick-walled, cells of plication differentiated, mostly long rectangular; basal cells laxly rectangular. **Dioicous**. **Perichaetial** leaves larger, broadly ovate-lanceolate, hyaline tip near equal to lamina length. **Seta** short, to 1.1 mm long. **Capsule** immersed, ovoid, ca. 1 mm long. **Peristome** teeth perforate. **Calyptra** mitrate-campanulate, to 1.6 mm long, base deeply lobed, strongly plicate. **Spores** smooth.

DISCUSSION. The genus is distinguished by the biplicate, hyaline, lanceolate leaves, long rectangular, longitudinally plicate cells, immersed capsule, and deeply lobed, strongly plicate calyptra. The species *C. trinervis* (R. S. Williams) Broth. in Herzog is, as originally described, a *Grimmia*; *C. pseudocribrosus* Hastings is likely a synonym of *C. boliviana* Broth. in Herzog.

LITERATURE. Churchill, S. P. 1981 (see family ref.). - Deguchi, H. 1987 (see family ref.). - Hastings, R. I. 1996. The genus *Coscinodon* (Bryopsida, Grimmiaceae) in South America, including a new species. The Bryologist 99: 418–427 [keys, illustrations].

Coscinodontella (Fig. 131) - A monotypic genus, with *C. bryanii* R. S. Williams only known from Peru.

HABITAT. On soil, probably soil covered rock; open dry montane, at ca. 2460 m.

DESCRIPTION. **Plants** small, forming short cushions. **Stems** erect, to 4 mm tall, few branched by innovations; in cross-section central strand present. **Leaves** crowded, somewhat incurved when dry, erect-spreading when wet, oblong-obtuse, slightly differentiated between base and limb, to 1.6 mm

long; margins plane below, incurved above, entire; lamina in lower half unistratose, distal half mostly bistratose; laminal cells subquadrate to rectangular. **Autoicous** (cryptoicous). **Perichaetial** leaves similar. **Seta** rather short, to 0.8 mm long, smooth, twisted when dry. **Capsule** erect, urn ovoid, to ca. 0.7 mm long; stomata at urn base, superficial; annulus in ca. 2 rows. **Operculum** conic-rostrate. **Peristome** teeth irregularly perforate, papillose. **Calyptra** mitrate-campanulate, plicate and deeply lobed. **Spores** spherical, finely papillose.

DISCUSSION. The genus is characterized by a differentiated incurved, cucullate upper limb that equals or is slightly longer than the broader oblong base, bistratose above, unistratose below, shortly exserted, ovoid capsules, and deeply lobed, strongly plicate calyptra.

LITERATURE. Deguchi, H. 1987 (see family ref.). - Murray, B. 1984 (see family ref.).

Grimmia (Fig. 131) - Approximately 22 species recorded for the Neotropics, with maximum diversity concentrated in Mexico and the central Andes; a genus of about 75 species.

HABITAT. On rocks, in exposed sites; open montane to zacatonal, páramo and puna.

DESCRIPTION. **Plants** medium sized, forming dense tufts or cushions, blackish- or brownish-green. **Stems** erect, few branched by innovations; central strand present, rarely absent. **Leaves** loosely erect to appressed, ovate- to oblong-lanceolate, 1–2.5 mm long, apex mostly acuminate, often ending in a short to long hyaline awn, broadly concave below, distally keeled or concave; margins plane to recurved on one or both sides, entire; costa strong, percurrent to long excurrent, awn smooth to toothed; lamina unistratose to partially or fully bistratose distally, occasionally with lamina unistratose and margins bistratose, upper cells mostly isodiametric, often irregular, thick-walled; median cells similar or short rectangular, sinuose or not; lower and basal cells short to long rectangular, walls plane to sinuose. **Gemmae** absent or present in leaf axils, on costa or at base of upper laminal surface of stem leaves. **Autoicous** or dioicous. **Perichaetial** leaves elongate, usually longer than stem leaves. **Seta** short to elongate, 0.2–4 mm long, erect to slightly or strongly curved, often twisted. **Capsule** immersed to more commonly emergent or shortly exserted, erect, urn ovoid to elliptical or subglobose, 0.8–1.6 mm long, smooth or striate or ribbed. **Operculum** short to long rostrate, rarely plane; columella not attached to the operculum. **Peristome** present or absent, when present teeth entire to perforate above or cribrose throughout, papillose throughout or smooth at base. **Calyptra** cucullate or short mitrate and irregularly or regularly lobed at base. **Spores** spherical, smooth to papillose.

DISCUSSION. The genus exhibits considerable variation and is defined solely by a combination of characters (polythetic by definition): mostly oblong- to ovate-lanceolate, often hyaline tipped, often distally keeled, with thick-walled, isodiametric upper laminal cells, weakly sinuose or entire cell walled at midleaf or toward base, mostly elongate, somewhat curved or erect seta, generally emergent or exserted capsules, and cucullate to short mitrate calyptra.

LITERATURE. Deguchi, H. 1984, 1987 (see family ref.). - Greven, H. C. 1999. A synopsis of *Grimmia* in Mexico, including *Grimmia mexicana* sp. nov. The Bryologist 102: 426–436 [unbelievable] - Muñoz, J. 1998. Materials toward a revision of *Grimmia* (Musci: Grimmiaceae): nomenclature and taxonomy of *Grimmia longirostris*. Annals of the Missouri Botanical Garden 85: 352–363. - Muñoz, J. 1999. A revision of *Grimmia* (Musci: Grimmiaceae) in the Americas. 1: Latin America. Annals of the Missouri Botanical Garden 86: 118–191 [keys, illustrations, maps].

Jaffueliobryum (Fig. 131) - Two species in the Neotropics: *J. arsenei* (Thér.) Thér. endemic to central Mexico, and *J. wrightii* (Sull.) Thér. known from a single locality in Bolivia, widespread in central and southwest United States, northern Mexico, and disjunct to central northern Asia; a genus of three species of the Americas and northern Asia.

HABITAT. On rocks and soil covered rocks, often calcareous; dry lowland to high montane.

DESCRIPTION. **Plants** somewhat small to medium sized, forming loose to more commonly dense cushions. **Stems** erect, to ca. 10 mm tall, few branched by innovations; in cross-section outer 1-3 rows of cells small, thick-walled, inner cells large, thin-walled, central strand present. **Leaves** crowded, appressed when dry, erect to erect-spreading when wet, oval, obovate to oblong-obovate, 0.6–1.3 mm long (excluding hair point), concave, apex obtuse-rounded; margins plane, entire to serrate or erose near juncture with costa; costa excurrent as a short to long hair point, often equal to or longer than leaf lamina; lamina unistratose; median cells oval to oblong-oval or irregular to regular quadrate, hexagonal or rectangular; basal cells quadrate to somewhat rectangular, rather lax and thin-walled; marginal cells elongate and hyaline, or quadrate to short rectangular and smaller than inner cells. **Autoicous** or cryptoiocus. **Perichaetial** leaves similar but larger. **Seta** short (0.3 mm) to somewhat elongate (to 1.25 mm), smooth. **Capsule** immersed to short exserted, erect, ovoid, to 1 mm long; stomata at base or lower 1/3 of urn, superficial; annulus revoluble or persistent. **Operculum** short to long rostrate. **Peristome** teeth usually divided into 3 variously fused segments or simply

perforate, spiculose. **Calyptra** mitrate-campanulate, base erose or deeply lobed. **Spores** spherical, granulate or ruminate.

DISCUSSION. Distinguishing features of the genus include the short obovate leaves, long to short hyaline hairpoint, unistratose lamina, upper laminal cells mostly oval to oblong-oval, somewhat lax quadrate basal cells, spiculose, perforate, sometimes segments fused, peristome teeth, and the erose or deeply lobed mitrate-campanulate calyptra.

LITERATURE. Churchill, S. P. 1987. Systematics and biogeography of *Jaffueliobryum* (Grimmiaceae). Memoirs of the New York Botanical Garden 45: 691–708 [keys, illustrations, maps].

Ptychomitrium Fig. 132) - Fourteen species in the Neotropics, possibly 10 or fewer valid; about 40–50 species largely distributed in the Southern Hemisphere.

HABITAT. On rocks, rarely on logs, in open sites; montane to zacatonal, páramo, and puna, 1100–4400 m.

DESCRIPTION. **Plants** small to somewhat large, forming dense tufts, dark green to blackish-green. **Stems** erect, few to several branched; central strand present. **Leaves** strongly crispate when dry, erect-spreading to spreading when wet, ovate- to oblong-narrowly or broadly lanceolate, 2.5–6 mm long, lower portion subsheathing and slightly concave, plicate, limb keeled distally, apex acuminate to obtuse; margins plane to recurved or reflexed below, limb entire or sharply serrate; costa somewhat strong, percurrent, in cross-section stereids above and below guide cells; lamina unistratose below, limb margin and part of lamina bistratose to fully bistratose; upper laminal cells quadrate to quadrate-rounded, smooth to bulging-papillose on upper surface or both surfaces, thick-walled, walls straight to weakly sinuose; lower cells long rectangular, thick-walled and distinctly sinuose; basal cells large, rectangular, somewhat lax. **Gemmae** absent. **Autoicous** or cryptoicous. **Perigonia** and perichaetia in separate gametoecia, each stalked, leaves differentiated, smaller than stem leaves. **Seta** 1–4 per perichaetium, 2.5–8 mm long, stout, smooth. **Capsule** erect, urn short ovoid or ovoid cylindrical, older ones mostly cylindrical, 1–3 mm long. **Operculum** long rostrate. **Peristome** teeth divided into 2–3 narrow and long segments to near base, perforate at base of segments, papillose-spiculose. **Calyptra** mitrate to mitrate-campanulate, covering most of capsule, deeply lobed, distally scabrous or roughened, plicate. **Spores** spherical, lightly papillose.

DISCUSSION. The genus is recognized by the leaves crispate and contorted when dry, with rather strongly or moderately differentiated base and limb, often plicate near base; thick-walled quadrate or quadrate-rounded upper cells; perigonia situated below the perichaetia; peristome teeth fissured to near base in 2–3 forks, and deeply lobed; and plicate mitrate or mitrate-campanulate calyptra. Previously placed in the Orthotrichales (cf. Brotherus, 1925, see general ref.); however, recent authors consider an independent Ptychomitriaceae close to the Grimmiaceae, or, as presented here, included within the family.

LITERATURE. Deguchi, H. 1984, 1987 (see family ref.). Schiavone, M. M. & A. B. Biasuso. 1997. El género *Ptychomitrium* (Grimmiaceae, Musci) en el Noroeste Argentino. Lilloa 39: 101-112 [keys, illustrations].

Racomitrium (Fig. 132) - Ten species in the Neotropics, possibly only 6–8; about 75 species worldwide, often associated with aquatic habitats in cool temperate regions.

HABITAT. On rock, equally common in dry exposed sites or wet sites associated with streams; open montane, zacatonal, páramo, and puna, (300–)1500–4600 m.

DESCRIPTION. **Plants** medium sized to somewhat robust, in loose to dense mats or tufts, dark green to blackish-green or yellowish-brown to golden. **Stems** spreading to ascending, often with several to many short lateral branches; central strand absent. **Leaves** ovate- to oblong-lanceolate to narrowly lanceolate, 1.8–3.5 mm long, apex acuminate to obtuse-rounded, distally keeled or cucullate; margins recurved on one or both sides, entire or irregularly erose-dentate; costa subpercurrent to long excurrent as a hyaline awn; lamina unistratose, or bistratose partially or fully distally; median cells long rectangular, walls finely sinuose, marginal base cells often differentiated as enlarged short to long rectangular cells with smooth walls. **Dioicous**. **Perichaetia** terminal on short lateral branches. **Seta** elongate, 4–10 mm long, slender, smooth, often twisted. **Capsule** erect, urn obloid-cylindrical to cylindrical, 2–2.5 mm long. **Operculum** rostrate. **Peristome** teeth divided to near base, often perforate at base, papillose to smooth below, papillose distally. **Calyptra** short mitrate, smooth, lacerated or slightly lobed at base. **Spores** spherical, lightly papillose.

DISCUSSION. The distinctive sinuose cells of the leaf lamina are diagnostic (except at the basal margin), as are the often numerous short lateral branches can not confused with any other neotropical genus. The genus *Bucklandiella* is included in *Racomitrium*.

LITERATURE. Bednarek-Ochyra, H., R. Ochyra & W. R. Buck. 1999. The genus *Racomitrium* (Grimmiaceae) in Brazil, with the first report of *R. subsecundum* in South America. Brittonia 51: 93-

105 [keys, illustrations]. - Deguchi, H. 1984, 1987 (see family ref.). - Frisvoll, A. A. 1988. A taxonomic revision of the *Racomitrium heterostichum* group (Bryophyta, Grimmiales) in N. and C. America, N. Africa, Europe and Asia. Gunneria 59: 1–289. - Lawton, E. 1973. *Rhacomitrium crispulum* and some related species. Bulletin of the Torrey Botanical Club 100: 230–235. - Vitt, D. H. & C. Marsh. 1988. Population variation and phytogeography of *Racomitrium lanuginosum* and *R. pruinosum*. Beiheft zur Nova Hedwigia 90: 235–260.

Schistidium (Fig. 132) - At least five to as many as 20 or 30 species in the Neotropics; a genus containing 50 or more species, widely distributed in temperate regions.

HABITAT. Exposed sites on rock; confined to high elevations, usually associated with zacatonal, páramo and puna, 2500–4600 m.

DESCRIPTION. **Plants** rather small to medium sized, forming dense short cushions or tufts, dark green to black or brown. **Stems** erect, few branched by innovations; central strand absent or weakly defined. **Leaves** erect to erect-spreading, narrowly to broadly oblong-lanceolate, to 2.5 mm long, apex broadly acute to acuminate, base rather short decurrent; margins recurved on one or both sides, entire or apices roughed to serrate; costa strong, projecting at back, in cross-section cells little differentiated, all very thick-walled, guide cells absent; laminal cells thick-walled, upper cells subquadrate to short oblong and oblate; lower cells subquadrate or short rectangular, usually slightly sinuose; basal cells larger, quadrate to short rectangular. **Autoicous**. **Seta** short, to 0.5 mm long, erect. **Capsule** immersed, erect, ovoid to ovoid-short cylindrical, 0.6–1.5 mm long. **Operculum** conic-mammillate, the columella remaining attached to the operculum upon dehiscence. **Peristome** teeth subentire, usually perforate, dark red, densely papillose. **Calyptra** short cucullate, naked and smooth, entire at base. **Spores** spherical to ovoid, lightly papillose.

DISCUSSION. The single feature that readily distinguishes *Schistidium* from several other neotropical genera of this family, particularly *Grimmia*, is the columella that remains attached to the operculum when the latter separates from the urn. The species concept presented by Bremer is now thought to be to broad, thus the number of species is expected to exceed 10 or more for the Neotropics.

LITERATURE. Bremer, B. 1980. A taxonomic revision of *Schistidium* (Grimmiaceae, Bryophyta) 1. Lindbergia 6: 1–16. - Bremer, B. 1980. A taxonomic revision of *Schistidium* (Grimmiaceae, Bryophyta) 2. Lindbergia 6: 89–117. - Bremer, B. 1981. A taxonomic revision of *Schistidium* (Grimmiaceae, Bryophyta) 3. Lindbergia 7: 73–90. - Deguchi, H. 1984, 1987 (see family ref.).

HEDWIGIACEAE

Plants medium sized, forming tufts or cushions, glaucous to dark green, brown to grayish or blackish. **Stems** spreading to ascending or erect, several branched, weakly radiculose at base; central strand absent; pseudoparaphyllia filamentous or foliose. **Leaves** imbricate, spirally arranged, appressed to erect when dry, spreading to wide-spreading or squarrose when wet, ovate, obovate, narrowly to broadly lanceolate or oblong-short lanceolate, apex acute to acuminate, hyaline or not; margins plane to recurved below or throughout, entire or dentate at apex, elimbate; costa none; laminal cells quadrate to short rectangular, papillose, walls sinuose; insertion cells elongate and sinuose, papillae in rows, often golden-brown. **Autoicous**, rarely synoicous or polyoicous. **Perichaetia** terminal but appearing lateral, leaves elongate, broadly to rather narrowly lanceolate, margins ciliate or not. **Seta** short or elongate, smooth. **Capsule** immersed or exserted, erect, short cylindrical to ellipsoid or subglobose, often striate or ribbed when dry. **Operculum** plano-mammillate to short rostrate. **Peristome** absent. **Calyptra** cucullate or short and mitrate. **Spores** spherical, papillose, rarely multicellular.

DISCUSSION. The Hedwigiaceae contain three genera and about 30 species; in the Neotropics, three genera and 10 species. The family is recognized by the ecostate leaves, papillose laminal cells that are sinuose, and capsules that lack a peristome. The family is placed in the order Orthotrichales, previously with the Grimmiales and more recently with the Leucodontales. *Hedwigidium* is synonymized under *Hedwigia* by some authors. *Rhacocarpus*, until recent times, has been placed in the Hedwigiaceae; at present it is placed in its own family, the Rhacocarpaceae; see discussion and review by De Luna (1990b).

LITERATURE. De Luna, E. 1990a. Developmental evidence of acrocarpy in *Hedwigia ciliata* (Musci: Hedwigiaceae). Tropical Bryology 2: 53–60. - De Luna, E. 1990b. Protonemal development in the Hedwigiaceae (Musci), and its systematic significance. Systematic Botany 15: 192–204. - De Luna, E. 1995. The circumscription and phylogenetic relationships of the Hedwigiaceae. Systematic Botany 20: 347–373.

1. Leaf apex hyaline, to 1/4 of apex; margins plane or indistinctly recurved; margins of perichaetial leaf ciliate ..... **Hedwigia**
1. Leaf apex concolorous or weakly hyaline at tips; margins recurved; margins of perichaetial leaf not ciliate 2
2. Seta elongate, to 5–18 mm long; capsule exserted; leaves often distinctly plicate; plants saxicolous or epiphytic ..... **Braunia**
2. Seta short, 0.8–1.2 mm long, capsule immersed; leaves indistinctly plicate or not at all; plants saxicolous ..... **Hedwigidium**

Braunia (Fig. 133) - Eight species in the Neotropics; a genus containing about 20 species.

HABITAT. Epiphytic on tree trunks or branches, and on rocks; open to forested montane to zacatonal, páramo or puna, (500)1500–4400.

DESCRIPTION. **Plants** medium sized, forming loose to dense coarse mats or tufts, dull yellowish-brown to golden. **Stems** creeping, leaves mostly reduced, scale-like, appressed with tips spreading to recurved, frequently eroded from stem, distal stems and branches mostly ascending, several branched; pseudoparaphyllia foliose. **Leaves** imbricate, appressed with apices reflexed when dry, erect-spreading to spreading or squarrose when wet, ovate, obovate to oblong-ovate or lanceolate, 1.5–2 mm long, flat to concave, weakly to strongly plicate, apex short acuminate to abruptly long acuminate; margins entire below, apices irregularly dentate, erect to recurved throughout or partially, rarely plane; laminal cells thick-walled, upper and median cells short to long and narrowly rectangular, ± sinuose, papillose; lower middle and basal cells long rectangular, sinuose, papillose, papillae in single row; alar region differentiated, subquadrate to short-rectangular and oblate, walls rounded. **Synoicous**. **Perichaetia** appearing lateral, leaves elongate, narrowly oblong-lanceolate. **Seta** elongate, (3–)5–18 mm long, smooth, often twisted. **Capsule** exserted or emergent, erect to suberect, urn ovoid, cylindrical or ellipsoid to subglobose, 1.3–2.2 mm long, wrinkled or furrowed when dry, mouth slightly constricted. **Operculum** long rostrate, oblique. **Peristome** absent. **Calyptra** cucullate, smooth and naked. **Spores** spherical or multicellular, papillose.

DISCUSSION. *Braunia* is readily distinguished from the two remaining genera of the family by the elongate seta and mostly well exserted capsule. In the absence of sporophytes, however, the genera are difficult to distinguish. *Braunia* is found on rocks as well as shrubs and trees, whereas *Hedwigia* and *Hedwigidium* are restricted to rocks. Species diversity appears to be concentrated from Ecuador southward to Argentina.

LITERATURE. Biasuso, A. B. 1993. El género *Braunia* (Hedwigiaceae, Musci) en Tucumán. Lilloa 38: 5–21 [keys, illustrations].

Hedwigia (Fig. 133) - A single species in the Neotropics, *H. ciliata* (Hedw.) Ehrh. ex P.-Beauv.; a genus containing three species.

HABITAT. On rocks; open montane to zacatonal, páramo and puna, 500–3690 m.

DESCRIPTION. **Plants** medium sized, forming loose to dense tufts or cushions, grayish-green. **Stems** spreading to suberect; pseudoparaphyllia filamentous. **Leaves** appressed to erect when dry with distal apices spreading or recurved, spreading to erect-spreading when wet, ovate-lanceolate, 2–2.3 mm long, apex acuminate, upper 1/4 of apices hyaline and distinctly papillose; margins plane or slightly recurved below; costa absent; apical cells elongate, hyaline and indistinct, papillae in single row, to 8 or more; median cells short rectangular or quadrate, appearing sinuose, papillose, papillae 1–3, simple or branched; upper basal center cells long rectangular, papillae 3–6; lower basal center and insertion cells smooth, porose, often golden-brown. **Perigonia** bud-like, appearing lateral. **Perichaetia** on short terminal branches, appearing lateral, leaves narrowly lanceolate, distal margins long ciliate, cilia long and short branched, hyaline. **Seta** very short, 0.25–0.50 mm long, smooth. **Capsule** immersed, erect, urn short cylindrical, subglobose when deoperculate, 1–1.2 mm long, smooth. **Operculum** plano-mammillate. **Peristome** absent. **Calyptra** small, mitrate, smooth and hairy. **Spores** with trilete lines, coarsely rugose-papillose.

DISCUSSION. The hyaline leaf tips, ciliate margins of the perichaetial leaves, and immersed, and rather smooth capsules, in combination with the shared family features, distinguishes *Hedwigia*. Buck and Norris (1996) have suggested that neotropical collections called *H. ciliata* may in fact represent a different species, the oldest name being *H. nivalis* (Müll. Hal.) Mitt.

LITERATURE. Buck, W. R. & D. H. Norris. 1996. *Hedwigia stellata* and *H. detonsa* (Hedwigiaceae) in North America. Nova Hedwigia 62: 361–370.

Hedwigidium (Fig. 133) - A monotypic genus represented by *H. integrifolium* (P.-Beauv.) Dixon (Western Europe, pantropical at high elevations, Australia and New Zealand).

HABITAT. On rocks; open montane to zacatonal, páramo, and puna, 2000–4550 m.

DESCRIPTION. **Plants** medium sized, forming tufts or mats, green to dark reddish-brown. **Stems** erect or spreading; central strand absent; pseudoparaphyllia foliose. **Leaves** appressed, spreading to wide-spreading when wet, ovate to oblong-ovate, 1.5–2.2 mm long, weakly plicate or not, apex acute or short acuminate; margins strongly recurved, entire below, distally dentate or crenulate, occasionally weakly toothed; costa absent; apical cells elongate, median cells short rectangular to subquadrate, sinuose, papillose, papillae several along margin, appearing over lumen; central upper basal cells rectangular, porose, papillae few to several (7 or more) in single row (rarely double row); insertion cells at center smooth, golden-brown or yellow; cells of alar region quadrate, smooth. **Perichaetia** appearing lateral, but on terminal branches, leaves broadly lanceolate to oblong-lanceolate, to 5 mm long, plicate, short acuminate, upper margins not ciliate. **Seta** short, 0.8–1.2 mm long. **Capsule** immersed, erect, short obloid, 1–2 mm long, furrowed when dry or wet. **Operculum** short rostrate, oblique. **Peristome** absent. **Calyptra** small mitrate, smooth and naked. **Spores** with trilete lines, rugose-papillose.

DISCUSSION. The genus is characterized by the concolorous leaves, elongate, eciliate perichaetial leaves, furrowed, and immersed capsules.

HELICOPHYLLACEAE

The Helicophyllaceae is a monotypic family, placed in the Orthotrichales.

Helicophyllum (Fig. 134) - A monotypic genus represented by *H. torquatum* (Hook.) Brid., confined to and widespread in the Neotropics.

HABITAT. On tree trunks and exposed roots, logs and rocks, often in partly or fully shaded sites; typically of dry to semi-dry primary and secondary forests, from near sea level to 1050 m.

DESCRIPTION. **Plants** small, forming dense mats, dark green. **Stems** creeping usually with distal stems and branches short ascending, pinnately branched; central strand present; densely tomentose beneath, rhizoids reddish-brown, appearing smooth. **Leaves** differentiated between ventral (top) and dorsal (lower), each with median lateral leaves, when dry both ventral and dorsal lateral leaves strongly inrolled toward ventral stem side, when wet lateral leaves mostly widespreading; ventral lateral leaves oblong-lingulate, to 1.1 mm long, apex obtuse-rounded, base decurrent on basiscopic side; margins reflexed, bordered, ending below apex, appearing crenulate because of reflexed margins (obscuring border); costa strong, ca. 4/5 lamina length; median cells isodiametric, papillose, 1–2(3) papillae over cell lumen on both surfaces; alar cells on non-decurrent side rectangular, smooth or faintly papillose, marginal cells linear, smooth. **Median ventral and dorsal leaves** smaller, triangular. **Autoicous**, probably. **Perichaetia** terminal on ascending branches, leaves large, pale to golden-yellow. **Seta** very short, to 0.2 mm long. **Capsule** immersed, erect, urn short-cylindrical, to 1.2 mm long. **Operculum** plano-mammillate. **Peristome** absent. **Calyptra** not observed. **Spores** spherical or ovoid, papillose.

DISCUSSION. The dimorphic leaves, with the lateral leaves when dry strongly curled inward over stems, bordered margins, papillose laminal cells, and immersed eperistomate capsules are distinctive features of the genus.

LITERATURE. Yano, O. 1979. Contribuição ao inventário dos Musci brasileiros: Helicophyllaceae. Rickia 8: 7–16. - Yano, O. 1984. Novas ocorrências de *Helicophyllum torquatum* (Hook.) Brid. (Helicophyllaceae, Bryopsida) no Brasil. Rickia 11: 35–42.

HOOKERIACEAE

A family, in the strict sense, of six genera and about 50 species. Placed in the Hookeriales, members of this family are mainly distributed in the Southern Hemisphere.

Hookeria (Fig. 134) - A single species in the Neotropics, *H. acutifolia* Hook., rather widespread in the New World and Asia; a genus of two species of north temperate affinities.

HABITAT. Moist sites, usually in protected, shady places such as under rock ledges or lower banks, on soil or leaf litter; montane forests, from 600 m on islands, generally 1000 to 3075 m.

DESCRIPTION. **Plants** large, rather delicate, forming mats, somewhat dull to glossy light to dark green. **Stems** spreading, irregularly branched, branches short. **Leaves** loosely complanate, broadly ovate-lanceolate, 5–6(-7) mm long, apex acute to broadly acuminate; margins plane, entire; costa none; median cells large, hexagonal to fusiform, somewhat thick-walled. **Gemmae** often present on leaf tips and occasionally along margin, cylindrical, smooth or appearing lightly papillose. **Autoicous**.

Perichaetia lateral, leaves ovate-long acuminate, to 1.6 mm long. **Seta** elongate, to 9 mm long, stout and smooth. **Capsule** horizontal to pendent, urn cylindrical, ca. 1.2 mm long, exothecial cells collenchymatous, neck short. **Operculum** conic-rostrate. **Peristome** double, exostome teeth 16, cross-striate below, papillose distally, zig-zag median line, bordered and trabeculate; endostome lightly papillose, basal membrane high, segments 16, keeled and perforate, cilia absent. **Calyptra** conic-mitrate, smooth, base slightly lobed. **Spores** spherical, smooth.

DISCUSSION. *Hookeria* is characterized by the large, delicate plants forming soft mats, ovate-lanceolate complanate leaves, often bearing gemmae at leaf apex, and the absence of a costa. The 19th century concept of *Hookeria* included many of the genera of the Callicostaceae (as treated here), as in the treatment of Mitten (1869), that were largely segregated at the beginning of the 20th century by Brotherus (1901–1909, 1924–1925), among others. Previous authors have used the Hookeriaceae in a much broader sense to include the Adelotheciaceae, Pilotrichaceae (= Callicostaceae) and Daltoniaceae used in this treatment; see references under Pilotrichaceae. The genus is named for the renowned British botanist William Jackson Hooker (1785–1865), author of, among other works, *Musci Exotici*, director of the Royal Botanic Gardens, Kew, and father of Joseph Dalton Hooker.

LITERATURE. Welch, W. H. 1976. Hookeriaceae. North American Flora II, 9: 1–133

HYDROPOGONACEAE

Plants medium sized to somewhat small, forming loose to rather dense mats, pale to dark green. **Stems** lax to rigid, spreading to pendent; in cross-section outer 1–2 rows of cells small, thick-walled, inner cells progressively larger, thin-walled, central strand absent. **Leaves** distant along stem, crowded at stem and branch tips, oblong, elliptical to obovate, rigid or flaccid, apex acute to obtuse; margins plane or recurved below, entire to serrulate or serrate distally; costa absent or short and forked; laminal cells smooth, apical cells shorter than median, median cells oblong-fusiform to fusiform-rhomboidal or long hexagonal; alar cells weakly differentiated, quadrate to short rectangular, not inflated. **Perichaetia** lateral or terminal on short branches; leaves imbricate and sheathing, oblong-lanceolate, acuminate. **Seta** very short, erect, smooth. **Capsule** immersed to slightly emergent, erect, urn ovoid, ellipsoid to short cylindrical, annulus absent. **Operculum** conic-mammillate to short rostrate. **Peristome** absent or present with exostome teeth 16, striate, endostome absent. **Calyptra** mitrate, base slightly laciniate. **Spores** spherical, smooth to papillose.

DISCUSSION. The Hydropogonaceae contain two monotypic neotropical genera, *Hydropogon* and *Hydropogonella*, both found in aquatic or semi-aquatic habitats and distributed primarily in the upper Amazon Basin. This family, in the order Hypnales, appears to be related to the Sematophyllaceae. Further investigation is needed to clarify its phylogenetic relationship.

LITERATURE. Welch, W. H. 1943. The systematic position of the genera *Wardia*, *Hydropogon* and *Hydropogonella*. The Bryologist 46: 25–46 [keys, illustrations, map].

1. Leaves oblong, elliptical or oblanceolate; margins entire; costa none; peristome absent .... **Hydropogonella**
1. Leaves ovate to obovate; margins serrulate; costa short and forked, or none, at least some leaves costate; peristome present, single ..... **Hydropogon**

Hydropogon (Fig. 134) - A single neotropical species, *H. fontinaloides* (Hook.) Brid. distributed in Suriname and French Guiana, scattered throughout the upper Amazonia tributaries.

HABITAT. Usually epiphytic, on trees often associated with inundated forest sites along rivers; wet lowland forests, 100–250(600) m.

DESCRIPTION. **Plants** forming mats, dark dull green. **Primary stems** creeping. **Secondary stems** spreading or more often pendent, often devoid of leaves or leaves often distant, more crowded on distal branches and gametangia. **Leaves** oblong to oblong-obovate, 1.5–3 mm long, to 1.2 mm wide, apex acute; margins recurved below, plane distally, serrulate to serrate in distal 1/2–2/3 of lamina; costae absent or short and forked; median cells oblong-fusiform to fusiform rhomboidal; insertion cells often golden-yellow; alar cells rounded-quadrate to -rectangular, not inflated. **Perichaetia** lateral. **Seta** ca. 0.1 mm long. **Capsule** immersed, urn ovoid, 0.6–0.8 mm long. **Operculum** conic-mammillate. **Peristome** single, exostome teeth striate, apex obtuse. **Calyptra** not observed. **Spores** finely papillose.

DISCUSSION. This Amazonian lowland genus of inundated sites can be recognized by the combination of pendent habit, slender leafy stems becoming noticeably crowded toward the tips, oblong-obovate to short oblong leaves, few alar cells, immersed capsules, and single peristome. The distribution of *Hydropogon* was discussed and mapped by Churchill (1991).

LITERATURE. Churchill, S. P. 1991 (see general ref.). – Welch, W. H. 1943 (see family ref.).

Hydropogonella (Fig. 135) - A monotypic genus, *H. gymnostoma* (Bruch & Schimp.) Cardot is confined to upper Amazon Basin, the Guianas, and Panama.

HABITAT. Submerged, attached to rocks, branches and trunks of shrubs and trees; lowland forests, ca. 100–300 m.

DESCRIPTION. **Plants** rather small, forming loose, mats, pale green. **Stems** creeping or spreading, lax, to 15 cm long, irregularly pinnately branched. **Leaves** 3-ranked, distant or somewhat crowded on stem or branch tips, elliptical to obovate or oblanceolate, to 2.2 mm long, flaccid, apex bluntly acute to obtuse, occasionally apiculate; margins plane, entire; costa none; laminal cells pellucid, smooth and firm-walled, apical cells short, 1–2:1; median cells oblong-fusiform or long hexagonal; alar cells oblong-short rectangular to subquadrate; marginal cells subquadrate to short-rectangular, forming an indistinct border. **Autoicous**. **Perichaetia** terminal on short branches. **Capsule** immersed to slightly emergent, urn ellipsoid or short cylindrical, to 1 mm long; annulus absent. **Operculum** short-rostrate. **Peristome** absent. **Calyptra** mitrate, base slightly laciniate. **Spores** smooth.

DISCUSSION. The genus is characterized by the flaccid and soft habit, oblong, elliptical or oblanceolate leaves, entire margins, and absence of a costa and peristome. *Hydropogonella* is often separated ecologically from *Hydropogon*, the latter being typically an epiphyte of inundated sites, while the former is submerged in streams on rocks or exposed tree roots.

LITERATURE. Welch, W. H. 1943 (see family ref.).

HYLOCOMIACEAE

Plants medium sized to large and robust, forming loose to dense mats or tufts. **Stems** spreading to ascending or erect, rarely subpendent, regularly to irregularly pinnately branched; in cross-section central strand present or absent; paraphyllia and pseudoparaphyllia present or absent. **Leaves** erect to widespreading, falcate or not, oblong-lanceolate or broadly ovate to nearly oval, concave, plicate, smooth or rugose, apex broadly acute to rounded or gradually to abruptly acuminate, base cordate-auriculate or not; margins plane or recurved, entire to serrate or serrulate; costae double, 1/4–1/3(–1/2) lamina length or single; laminal cells smooth or some cells papillose at cell angles, median cells oblong-linear, fusiform or linear, weakly porose or not; lower and basal cells elongate, strongly porose; alar cells differentiated or not. **Dioicous**. **Perichaetia** lateral. **Seta** elongate, smooth. **Capsule** erect to inclined or horizontal, urn ovoid-cylindrical to ellipsoid, ± curved and asymmetric. **Operculum** conic to conic-apiculate or rostrate and oblique. **Peristome** double, exostome teeth 16, smooth or cross-striate below, distally papillose, trabeculate on back; endostome lightly papillose, basal membrane high, segments 16, keeled and perforate, cilia 1–3, or absent to rudimentary. **Calyptra** cucullate, naked and smooth. **Spores** spherical, finely papillose.

DISCUSSION. The Hylocomiaceae, order Hypnales, contain 12 genera and some 26 species distributed worldwide but largely of the north temperate regions; in the Neotropics four genera and five species.

LITERATURE. Rohrer, J. R. 1985a. A phenetic and phylogenetic analysis of the Hylocomiaceae and Rhytidiaceae. Journal of the Hattori Botanical Laboratory 59: 185–240. - Rohrer, J. R. 1985b. A generic revision of the Hylocomiaceae. Journal of the Hattori Botanical Laboratory 59: 241–278.

1. Costa single; leaves rugose when dry; some laminal cells on back of leaf with strongly projecting spine-like papillae ..... **Rhytidium**
1. Costa double or occasionally absent; leaves smooth to weakly undulate or plicate when dry; laminal cells smooth or if papillose then papillae weak, rounded 2
2. Stem leaves abruptly long acuminate from a broadly ovate leaf base; paraphyllia filiform, branched ..... **Loeskeobryum**
2. Stem leaves broadly ovate to oblong-ovate or elliptical with apices acute-rounded to obtuse; paraphyllia absent 3
3. Leaf margins serrulate to serrate above base; alar cells lax, thin-walled, hyaline .... **Leptohymenium**
3. Leaf margins entire or faintly serrulate at apex; alar cells firm, thick-walled reddish-brown .... **Pleurozium**

Leptohymenium (Fig. 135) - A single species in the Neotropics, *L. tenue* (Hook.) Schwägr., known from Mexico, Guatemala, and Southeast Asia. A genus with two species.

HABITAT. Epiphytic on branches and trunks of trees, also on moist rocks and soil; montane forests (*Quercus* and *Pinus*), 1400–2750 m.

DESCRIPTION. **Plants** medium sized, forming coarse mats, glossy yellowish- to golden-green or golden-brown. **Stems** spreading with ascending and arching stems, 1–2 pinnately branched; paraphyllia absent; pseudoparaphyllia ovate to deltoid. **Stem leaves** loosely erect-spreading to squarrose, broadly ovate, to 1.5 mm long, concave, smooth to irregularly and weakly plicate, apex acute to short acuminate or obtuse, base short decurrent; margins plane, reflexed at base, serrulate to serrate distally, serrulate or entire at base; costae double, very short to 1/2 lamina length, separated at base, slightly diverging; median cells oblong-linear, smooth to weakly papillose by projecting distal cell angles; basal cells larger, porose; alar region differentiated, cells enlarged, oval to oblong, lax and thin-walled. **Branch leaves** erect to spreading, ovate to elliptic, to 1.1 mm long, slightly decurrent; alar cells less differentiated. **Dioicous**. **Perichaetia** lateral. **Seta** to 23 mm long, smooth. **Capsule** erect, urn cylindrical to ovoid-cylindrical, to 3.5 mm long, smooth or weakly wrinkled. **Operculum** long conic to obliquely rostrate. **Peristome** double, inserted below mouth, exostome teeth ± smooth; endostome smooth, basal membrane high, segments short, keeled and perforate, cilia absent or rudimentary. **Calyptra** unknown. **Spores** finely papillose.

DISCUSSION. A genus characterized by ascending and arching stems that are 1–2 pinnately branched; squarrose to erect spreading, broadly ovate stem leaves; serrulate to serrate throughout along margin; double costae; thin-walled and lax, enlarged alar cells; erect cylindrical capsules; smooth exostomial teeth; and short endostomial segments set on a high basal membrane. *Leptohymenium* may be confused with members of the Hypnaceae, but the fundamental differences in the peristome readily separate the two. Further distinctions of help are the combination of broadly, somewhat wrinkled ovate leaves, elongate double costa, and oblong-linear cells that are often weakly projecting at distal cell angles.

LITERATURE. Rohrer, J. R. 1986. *Leptohymenium tenue* and *Elmeriobryum guatemalense*, sp. nov. in Mexico and Central America. The Bryologist 89: 28–31.

Loeskeobryum (Fig. 135) - Two species in the Neotropics, *L. brevirostre* (Brid.) M. Fleisch. *ex* Broth. recorded from Mexico, Guatemala, and Haiti (rather widespread in the Northern Hemisphere) and *L. giganteum* (E. B. Bartram) J. R. Rohrer known only from Guatemala and Colombia. A genus, segregated from the more traditional *Hylocomium*, containing three species primarily confined to the Northern Hemisphere.

HABITAT. On soil, logs, or rocks, somewhat pendent from shrubs and over humus; upper montane forest and shrubby páramo, 2800–3570 m.

DESCRIPTION. **Plants** large and robust; forming loose mats, glossy green. **Stems** loosely spreading to subpendent, to 22 cm long, reddish, irregularly pinnately branched; in cross-section central strand absent; paraphyllia numerous, filiform, few to many branched, smooth. **Stem leaves** wide-spreading to squarrose, oval to broadly ovate, nearly as wide as long, 3–3.8 mm long, to 3 mm wide, ± plicate, apex abruptly narrowly acuminate, base cordate-auriculate, clasping stem; margins plane, coarsely serrate distally, often sharply so, serrulate below; costae double, ca. 1/3 lamina length; median laminal cells oblong-linear, somewhat vermicular, weakly porose; basal and insertion cells oblong-rectangular, strongly porose, golden-yellow or -brown. **Branch leaves** erect-spreading, ovate, 2.3–2.6 mm long, 1.2–1.5 mm wide, concave, apex short acuminate. **Dioicous**. **Perichaetia** lateral. **Seta** elongate, smooth. **Capsule** inclined, ovoid-short cylindrical. **Operculum** conic-rostrate. **Peristome** double, exostome teeth cross-striate below, distally papillose,, trabeculate; endostome papillose, basal membrane high, segments keeled and perforate, cilia 2–3. **Calyptra** cucullate, smooth and naked. **Spores** finely papillose.

DISCUSSION. Distinguishing features include the large stature of the plants, abundant branched, filiform paraphyllia, leaves clasping stem, abruptly narrow acuminate apex from a broadly ovate leaf base, sharply and coarsely serrate margins, and strong double costae. Rohrer (1985b), although recognizing *L. giganteum*, suggests that it may only be a robust form of *L. brevirostre*. Sporophytes are unknown in the Neotropics.

LITERATURE. Rohrer, J. R. 1985b (see family ref.).

Pleurozium (Fig. 136) - A monotypic genus, with *P. schreberi* (Brid.) Mitt. (Mexico, Central America, Andes) primarily distributed in the Northern Hemisphere.

HABITAT. On humus and soil, in somewhat dry sites, also associated with semi-dry margins of bogs or marshes; mostly high open montane to zacatonal, páramo, and puna, 2650–4000 m.

DESCRIPTION. **Plants** medium to somewhat large, forming mats or tufts, rather glossy green to yellowish-brown or golden; paraphyllia none. **Stems** spreading to more commonly ascending, to 10 cm or more long, julaceous, dark red, regularly to irregularly pinnately branched; in cross-section outer cell rows small and thick-walled, inner cells larger, thin-walled, central strand present. **Stem leaves** suboval to ovate or oblong-ovate, 2–3 mm long, to 1.7 mm wide, deeply concave, apex broadly acute

to rounded, reflexed at base; margins plane, entire; costae short and double, ca. 1/4–1/3 lamina length; median cells fusiform to linear, porose; alar cells inflated, and somewhat excavate, thick-walled, short to long oblong or quadrate, golden-yellow or reddish-brown. **Branch leaves** smaller, ovate, enrolled distally, apex acute; margin entire to weakly serrulate distally. **Seta** often twisted. **Capsule** inclined, urn ellipsoid and curved, exothecial cells subquadrate to oblong, ± thick-walled, stomata present at base of urn, superficial; annulus absent. **Operculum** conic. **Peristome** with exostome teeth faintly reticulate; endostome cilia 2–3.

DISCUSSION. The ascending habit, dark red stems, strong, short and forked leaf costa, and the porose, thick-walled, usually dark reddish-brown alar cells aid in distinguishing *Pleurozium*. The genus may be confused with *Calliergonella* and *Calliergon* from which it differs by the absence of a hyalodermis, and the strongly forked costa, thick-walled alar cells; also, these two Amblystegiaceae are common in very wet marshy or boggy sites, whereas *Pleurozium* is found in drier sites. Although *Pleurozium* is quite common at high elevations in the tropics, it remains to be seen just how the plants are dispersed, since no apparent asexual structures are known, and sporophytes have not been observed, to our knowledge, in the Neotropics.

LITERATURE. Rohrer, J. R. 1985b (see family ref.).

Rhytidium (Fig. 136) - A monotypic genus, with *R. rugosum* (Hedw.) Kindb. widespread in the Northern Hemisphere. In the Neotropics the species is known from Mexico, Guatemala, and Bolivia.

HABITAT. Exposed sites on rock or thin soil over rock, often associated with escarpments and calcareous habitats; open montane to puna, 1830–4600 m.

DESCRIPTION. **Plants** rather robust, forming loose tufts, somewhat glossy yellowish- to golden-brown. **Stems** stiffly erect-ascending, to 5 cm or more tall, regularly to irregularly pinnately branched, branches short, often oriented towards one side, tips curved or hooked; paraphyllia none. **Leaves** crowded, falcate, loosely erect when dry, erect-spreading when wet, oblong-lanceolate or elliptic-short lanceolate, to 4 mm long, both plicate and rugose, apex secund, gradually acuminate; margins revolute below apex, distally serrate; costa single, 2/3–3/4 lamina length; laminal cells oblong-linear, flexuose, smooth with some cells papillose at distal angles on back, porose, thick-walled; alar cells subquadrate to short rectangular and oblate, thick-walled, smooth. **Perichaetial** leaves lanceolate with spreading long acuminate apices. **Seta** to 25 mm long. **Capsule** horizontal, urn obloid-cylindrical, asymmetric, smooth, neck short; annulus in 2–3 rows. **Operculum** conic-apiculate or conic-short rostrate and oblique. **Peristome** with exostome teeth cross-striate below, papillose distally; endostome cilia 1–2, nodose.

DISCUSSION. The robust, ascending habit, falcate, rugose leaves, single costa, smooth median cells with some cells strongly papillose at upper cell angles, and thick-walled, subquadrate alar cells assist in the recognition of the genus. *Rhytidium* is placed in the Rhytidiaceae by some authors.

LITERATURE. Rohrer, J. R. 1985b (see family ref.).

HYPNACEAE

Plants small to mostly medium sized, forming mats. **Stems** creeping and spreading to ascending, regularly or irregularly pinnate or bipinnately branched, branches mostly short, occasionally secund. **Leaves** ovate, ovate-lanceolate, lanceolate or triangular, falcate or not, apex acute to long acuminate, base decurrent or not; margins plane, occasionally recurved below, entire to serrulate or serrate throughout or distally; costae short and forked, or less often absent; median cells rhomboidal to linear, smooth or papillose by projecting cell angles; alar region undifferentiated or more often differentiated with cells often oval, or small and quadrate, generally not inflated. **Asexual structures** infrequent in the form of gemmae in axils of leaves. **Autoicous** or dioicous. **Perichaetia** lateral, leaves mostly differentiated. **Seta** elongate, smooth, rarely roughened or papillose distally. **Capsule** erect to more commonly inclined or pendulous, ovoid or cylindrical to obloid-cylindrical, often curved. **Operculum** conic-short to -long rostrate, oblique. **Peristome** double, exostome teeth 16, cross-striate below, papillose distally; endostome basal membrane high, rarely low, segments 16, cilia 1–3, nodose, rarely rudimentary. **Calyptra** cucullate, smooth and naked, rarely hairy. **Spores** spherical, mostly finely papillose.

DISCUSSION. The Hypnaceae contain some 30–40 genera and far fewer than the nearly 1000 species attributed to this family; in the Neotropics 21 genera and about 70 species. Although taking a traditional phenetic approach, the discussion provided by Ando *et al*. (1984) is useful with regard to other families in the Hypnales related to the Hypnaceae, and subfamilies recognized within the family. Defining the relationship among genera and circumscribing the family as a natural monophyletic taxon is a major challenge for future bryologists.

Study Guide. Leaves provide most of the features needed to distinguish species; care should be given to the habit of the plants, and whether the pseudoparaphyllia are foliose or filamentous.

LITERATURE. Buck, W. R. 1984. Taxonomic and nomenclatural notes on West Indian Hypnaceae. Brittonia 36: 178–183. - Nishimura, N., M. Higuchi, T. Seki & H. Ando. 1984. Delimitation and subdivision of the moss family Hypnaceae. Journal of the Hattori Botanical Laboratory 55: 227–234.

1. Leaves erect to spreading, not falcate-secund, crowded to somewhat distant on stems, often weakly to strongly complanate 2
1. Leaves falcate secund, often crowded on stems, not complanate 19
2. Median laminal cells large, broadly or narrowly fusiform or rhomboidal, smooth and lax; leaves broadly ovate to lanceolate; plants often whitish-green or pale green, somewhat flaccid when wet ..... **Vesicularia**
2. Median laminal cells mostly linear, often vermicular, smooth or papillose; leaves lanceolate, oblong, to triangular; plants light to dark green, yellowish-brown or golden, generally not flaccid when wet 3
3. Leaves of stem dimorphic, lateral and upper median leaves ovate or ovate- to oblong-lanceolate, underside leaves narrowly lanceolate ..... **Rhacopilopsis**
3. Leaves of stem monomorphic, underside and lateral leaves similar in shape and size (differing, if at all, in leaf symmetry; median symmetric and lateral asymmetric) 4
4. Median laminal cells smooth, or weakly and indistinctly papillose at distal cell angles 5
4. Median laminal cells papillose, or if smooth then leaves obtuse or acute 14
5. Leaves complanate 6
5. Leaves not complanate, loosely spreading to erect and often appressed when dry, homomallous or not; distal branches curved or not 10
6. Stem leaves broadly ovate, acute, plicate, distally incurved on some leaves, costa rather strong and usually separated at base; branch leaves elliptical or ovate ..... **Elmeriobryum**
6. Stem and branch leaves similar, the latter smaller, mostly ovate-lanceolate or lanceolate, apex short to long acuminate; costa usually joined at base 7
7. Leaves squarrose spreading, cultriform; gemmae when present clustered near branch tips, twisted with few (to 5) prongs ..... **Pseudotaxiphyllum**
7. Leaves erect to erect-spreading; gemmae absent 8
8. Apical cells shorter than median cells ..... **Taxiphyllum**
8. Apical cells similar in length to median cells 9
9. Basal cells in alar region ± inflated; peristome erect when dry, to 600 µm long, endostome segments longer than exostome teeth ..... **Syringothecium**
9. Basal cells not inflated; peristome spreading when dry, to 350 µm long, endostome segments often equal to or shorter than exostome teeth ..... **Isopterygium**
10. Leaves distally serrate, serrulate below ..... **Herzogiella** p.p.
10. Leaves entire or serrulate to dentate above, mostly entire below 11
11. Alar cells numerous, extending to broadest width of leaf, and to costa; capsules erect ..... **Platygyriella**
11. Alar cells few, not extending to broadest width of leaf, nor extending to costa; capsules erect or inclined 12
12. Brood branchlets present distally on branches ..... **Platygyrium**
12. Brood branchlets absent 13
13. Capsules erect, symmetric; distal branches often strongly curled ..... **Pylaisiella** p.p
13. Capsules inclined, asymmetric; distal branches weakly curved or not ..... **Homomallium**
14. Leaf apex mostly truncate; laminal cells with papillae over cell lumen (serially) and projecting at cell angles ..... **Phyllodon**
14. Leaf apex acuminate to acute or obtuse, occasionally truncate, laminal cells with papillae projecting at cell angles 15
15. Stem leaves ± complanate, lateral leaves oblong-lanceolate to oblong, folded, apices mostly acute to obtuse ..... **Taxiphyllum**
15. Stem leaves not complanate, leaves ovate-lanceolate, apices acuminate, rarely obtuse or acute 16
16. Leaves plicate; alar cells porose ..... **Puiggariopsis**
16. Leaves smooth; alar cells not porose 17
17. Plants soft, glossy green or more commonly yellow; stem leaves squarrose-recurved, base broadly decurrent ..... **Ctendium** p.p.
17. Plants rather wiry, not conspicuously glossy; stem leaves suberect to erect-spreading, or squarrose, base not decurrent or narrowly so 18

18. Stems stipitate, often arching or ascending; secondary stem and branch leaves dimorphic, stem or stipe leaves abruptly and narrowly long acuminate; laminal cells projecting as papillae only at distal angles ..... **Mittenothamnium**
18. Stems prostrate and spreading, not stipitate; secondary stem and branch leaves similar, not strongly differentiated, stem leaves ovate-lanceolate, gradually acuminate; laminal cells projecting at distal and proximal angles ..... **Chryso-hypnum**
19. Leaf margins toothed throughout, serrate above, serrulate below 20
19. Leaf margins entire to more commonly serrulate distally, entire below 21
20. Stem leaves somewhat abruptly acuminate from a broadly ovate decurrent base; laminal cells papillose, papillae projecting at cell angles ..... **Ctendium** p.p.
20. Stem leaves ovate-lanceolate, not decurrent; laminal cells smooth ..... **Herzogiella** p.p.
21. Alar cells not or weakly differentiated ..... **Ectropothecium**
21. Alar cells mostly numerous, cells small quadrate and thick-walled or ± enlarged, oval or rectangular, porose or not 22
22. Leaves ovate-subulate; margins entire or ± somewhat serrulate; alar cells small, thick-walled, quadrate-rounded, mostly less than 20 cells; capsules erect ..... **Pylaisiella** p.p.
22. Leaves lacking above combination of characters, mostly ovate-lanceolate or -subulate; margins serrate distally, serrate or serrulate towards base; alar cells small to large, inflated or porose and rectangular cells, or if of small thick-walled quadrate cells then greater than 20 cells; capsules inclined and curved 23
23. Leaves broadly ovate, ending in a subulate tip; margins strongly serrate throughout; median cells papillose by projecting cell angles ..... **Ctenidium** p.p.
23. Leaves ovate-lanceolate or -subulate, short to long acuminate, serrate distally, sometimes serrulate to base; median cells smooth 24
24. Plants often complanate; alar cells in 1–2 rows, slightly inflated and firm-walled; autoicous .... **Pylaisiadelpha**
24. Plants not complanate; alar cells in several rows, not inflated or if so then hyaline and thin-walled 25
25. Stem leaves weakly plicate just above base or smooth; alar cells oval and hyaline, thin-walled or quadrate with firm, entire walls ..... **Hypnum**
25. Stem leaves distinctly plicate, plication extending to midleaf; alar cells irregularly rectangular, thick-walled and strongly porose ..... **Caribaeohypnum**

Caribaeohypnum (Fig. 136) - A monotypic genus, with *C. polypterum* (Mitt.) Ando & Higuchi confined to the highlands of the Neotropics (Mexico, Central America, West Indies, northern Andes).

HABITAT. Typically on trunks and branches, occasionally on logs and over humus; lower to more commonly upper montane forests, 1000–3500 m.

DESCRIPTION. **Plants** large to rather robust forming mats, golden-brown or -yellow to light green, ± glossy. **Stems** spreading, pinnately to subpinnately branched, occasionally tripinnate; in cross-section with outer 5–7 rows of cells small, thick-walled, rusty red, inner cells larger, hyaline, central strand absent; pseudoparaphyllia foliose, lanceolate. **Stem leaves** crowded, strongly falcate-secund, ovate-lanceolate, 2.4–3 mm long, to 1.2 mm wide, concave below, distally channeled, plicate, plication extending to midleaf, apex acute or occasionally acuminate, base auriculate; margins serrulate throughout or dentate at base; costae double, ca. 1/3 lamina length, set apart at base; laminal cells porose, median cells linear and ± vermicular, smooth, ± thick-walled; alar region excavate, cells irregularly rectangular, thick-walled, strongly porose, golden. **Dioicous**. **Perichaetial** leaves lanceolate-subulate. **Seta** 30–40 mm long, smooth. **Capsule** suberect to inclined, urn long-cylindrical, 2.5–4 mm long, slightly curved; exothecial cells rectangular, ± thin-walled, weakly collenchymatous; annulus weakly differentiated. **Operculum** conic-apiculate. **Peristome** with exostome teeth striate-papillose below, distally papillose; endostome basal membrane rather low, segments papillose, weakly keeled and lacking perforations, cilia rudimentary or absent. **Spores** roughly papillose.

DISCUSSION. While sharing with *Hypnum* falcate-secund leaves, it differs from that genus in the larger habit, strong plications extending well above the leaf base, particularly noticeable when dry, and irregularly rectangular, strongly porose and thick-walled excavate alar cells. Sporophytes are apparently rare for both genera; in *Caribaeohypnum* the exostome teeth are papillose throughout, striate-papillose below, the basal membrane rather low, segments weakly keeled and not perforate, with cilia rudimentary or absent. In *Hypnum* the teeth are cross-striate below, and only papillose distally, the basal membrane is high, segments keeled and perforate, with cilia 1–3. The genus was previously placed in *Hypnum* and *Stereodon*.

LITERATURE. Ando, H. & M. Higuchi. 1984. *Caribaeohypnum*, a new genus for a northern Latin American moss, *Hypnum polypterum* (Mitt.) Broth. Cryptogamie: Bryologie, Lichénologie 5: 7–14 [illustrations].

Chryso-hypnum (Fig. 137) - About five species in the Neotropics, the most common species is *C. diminutivum* (Hampe) W. R. Buck; a genus of some 10-12 species that are also present in the Paleotropics.

HABITAT. On soil, logs, and rocks; moist to semi-dry lowland forests adjoining mountains, to lower montane forests, 300–2600 m.

DESCRIPTION. **Plants** small, forming mats, pale to rather dark green, or yellow. **Stems** procumbent, distally stems and branches spreading to ascending, subpinnately to pinnately branched, branches short; in cross-section with outer 2–3 rows of cells small, thick-walled, golden-yellow to rusty-red, inner cells larger, thin-walled, central strand absent; pseudoparaphyllia filamentous to subfilametous; rhizoids clustered beneath, rusty red. **Stem leaves** ovate-lanceolate, 0.6–0.9 mm long, to 0.35 mm wide, apex acuminate, often narrowly so; margins plane above, reflexed near base, serrulate in distal 2/3 or more, dentate below; costae short and forked or appearing single, ca. 1/5 lamina length, occasionally absent; median cells oblong-linear, both lower and upper angles projecting; alar region weakly differentiated, cells few, quadrate. **Branch leaves** similar, often complanate, progressively smaller. **Autoicous**. **Perigonia** to 0.4 mm long. **Perichaetial** leaves ovate-subulate, to 1.2 mm long. **Seta** 9–12 mm long, slender. **Capsule** pendent, urn ovoid, ca. 0.6–1 mm long, curved; exothecial cells irregularly short rectangular to subquadrate, thick-walled. **Operculum** conic-apiculate. **Peristome** with exostome teeth finely striate below, distally papillose; endostome basal membrane high, segments keeled, perforate, papillose, cilia 2–3. **Calyptra** naked or with few hairs. **Spores** lightly papillose.

DISCUSSION. *Mittenothamnium*, as presently recognized, is similar to *Chryso-hypnum* but differs in having a primary stipe-like stem, lanceolate pseudoparaphyllia, and leaf cells usually projecting only at distal angles. *Chryso-hypnum***,** segregated from *Mittenothamnium*, is poorly known. In both genera there are an inflated number of species described mostly from the Neotropics, and less so from Africa and associated islands. There may be only 5–10 species. The genus was previously placed in *Mittenothamnium*, and earlier in *Microthamnium* and *Stereohypnum*.

LITERATURE. Buck, W. R. 1984 (see family ref.). - Fleischer, M. 1908. Grundlagen zu einer Monographie der Gattung *Stereohypnum* (Hpe.). Hedwigia 47: 271–299 [marginally useful illustrations].

Ctenidium (Fig. 137) - A single species in the Neotropics, *C. malacodes* Mitt.; about 21 species distributed in tropical highlands and temperate boreal regions of the world, excluding Africa.

HABITAT. On soil, humus, logs and base of trees and shrubs; submontane to high montane forests, extending into zacatonal, páramo, and puna along forested canyons and valleys, 1700–3600 m.

DESCRIPTION. **Plants** small to medium sized, forming soft loose mats, glossy green, yellowish-green to -brown. **Stems** creeping, irregularly to regularly pinnately branched, branches spreading and numerous; in cross-section outer 4–5 rows of cells small, thick-walled, inner cells progressively larger, thin-walled, central strand present; pseudoparaphyllia foliose. **Stem leaves** loosely erect-spreading, broadly ovate-abruptly lanceolate or subulate, to 2.2 mm long, to 0.8 mm wide, mostly falcate, plicate below, apex long acuminate, base auriculate and decurrent; margins plane, occasionally undulate, recurved at base, sharply serrate throughout; costae short and forked; median cells linear, thick-walled, toward margin broader and shorter, mostly oblong to fusiform, distinctly papillose by projecting distal cell ends; alar region well differentiated, cells rectangular to quadrate. **Branch leaves** differentiated, narrowly ovate-lanceolate to lanceolate-subulate; margins sharply serrate. **Dioicous**. **Perichaetial** leaves oblong-lanceolate, abruptly setaceous. **Seta** to 30 mm long, slender and wiry, smooth. **Capsule** inclined to pendulous, urn short cylindrical, ca. 1–1.5 mm long, curved, asymmetric; exothecial cells rectangular-rounded; stomata at urn base, superficial; annulus in 1–3 rows, revoluble. **Operculum** conic-short rostrate or apiculate. **Peristome** with exostome teeth broadly lanceolate, finely cross-striate below, lightly papillose above; endostome basal membrane high, segments keeled and perforate, faintly papillose, cilia 1–2. **Calyptra** naked. **Spores** lightly papillose.

DISCUSSION. The broadly ovate abruptly acuminate, falcate leaves with strongly serrulate margins, faint forked costa, and strongly projecting laminal cells are diagnostic. *Ctenidium* is a common element of open and marginal montane forests.

LITERATURE. Nishimura, N. 1985. A revision of the genus *Ctenidium* (Musci). Journal of the Hattori Botanical Laboratory 58: 1–82 [illustrations, map].

Ectropothecium (Fig. 137) - Probably fewer than five species in the Neotropics, the most common and widespread is E. leptochaeton (Schwägr.) W. R. Buck; a pantropical genus stated to contain over 200 species with the primary diversity in tropical Asia.

HABITAT. On soil, humus, and logs; wet lowland to upper montane forests, 230–2800 m.

DESCRIPTION. **Plants** medium sized, forming mats, glossy light green to yellowish-green. **Stems** creeping, irregularly to regularly pinnately short branched; in cross-section outer 2–3 rows of cells small, thick-walled, inner cells larger, ± thin-walled, firm, central strand weak; pseudoparaphyllia foliose, linear-lanceolate. **Leaves** weakly to strongly falcate-secund, narrowly to broadly ovate-lanceolate, 1–1.4 mm long, apex short to long acuminate; margins plane to reflexed, distally serrulate to serrate; costae absent or short and forked; laminal cells smooth, median cells linear; basal cells shorter and broader, narrowly oblong, porose; basal marginal cells few, quadrate to short rectangular. **Branch leaves** smaller, lanceolate-subulate, strongly falcate-secund, occasionally circinate. **Autoicous**. **Perichaetial** leaves differentiated, ovate-oblong and abruptly long acuminate to subulate. **Seta** 12–20 mm long, slender, smooth. **Capsule** inclined or pendulous, urn ovoid, ca. 1 mm long, strongly constricted below mouth when deoperculate; exothecial cells quadrate-rounded to short oblong, thin-walled, weakly collenchymatous; stomata few at urn base, superficial; annulus present. **Operculum** mammillate. **Peristome** with exostome teeth finely cross-striate with zig-zag median line, distally papillose; endostome basal membrane high, segments papillose, cilia 1–2. **Spores** lightly papillose.

DISCUSSION. *Ectropothecium* may be possibly confused in aspect with the leafy gametophytes of *Pylaisiella* or even the falcate-secund species of *Sematophyllum*, but these genera exhibit well differentiated alar cells, and the capsules are usually cylindrical or ovoid-cylindrical. The genus is very much in need of a worldwide revision; in the Neotropics there are probably no more than 2–3 species.

Elmeriobryum (Fig. 138) - A single species in the Neotropics, *E. guatemalense* J. R. Rohrer, apparently restricted to Central America (Guatemala, El Salvador, and Costa Rica); one additional species is recorded from the Philippines and Taiwan.

HABITAT. Epiphytic, on branches and trunks of trees, rarely on leaves, also on soil; moist montane forests, at elevation from 1800–3100 m.

DESCRIPTION. **Plants** rather robust, forming loose mats, glossy yellow- to golden-green or golden-brown. **Stems** spreading, to 10 cm long, irregularly 1–2 pinnately branched; paraphyllia absent; pseudoparaphyllia broadly ovate to deltoid; rhizoids few, along stems and tip of branches. **Stem leaves** erect to erect-spreading when dry, spreading when wet, broadly ovate to oblong-ovate, to 1.8 mm long, nearly as wide, concave, plicate, apex abruptly apiculate, base not decurrent; margins plane to broadly enrolled distally, serrulate to nearly entire; costae double, 1/4–1/2 lamina length, parallel, separated at base; median cells narrowly elliptic to linear, smooth to weakly papillose by projected distal cell angles; basal cells larger, porose; alar region little differentiated, cells slightly broader than inner basal cells. **Branch leaves** smaller and narrower, ovate to elliptic, to 1.5 mm long, less plicate. **Dioicous**? **Perichaetia** unknown. **Sporophytes** unknown.

DISCUSSION. Distinguishing features of the genus include the plicate, apiculate ovate to oblong-ovate leaves, parallel double costae separated at the base, and weakly differentiated alar cells.

LITERATURE. Rohrer, J. R. 1986. *Leptohymenium tenue* and *Elmeriobryum guatemalense*, sp. nov. in Mexico and Central America. The Bryologist 89: 28–31.

Herzogiella (Fig. 138) - A single species in the Neotropics, *H. cylindricarpa* (Cardot) Z. Iwats. (Mexico, Central America, tropical Andes; also Africa); about eight species largely confined to temperate regions of the Northern Hemisphere.

HABITAT. On base of trees, humus, and logs; montane forests, 1800–3500 m.

DESCRIPTION. **Plants** rather small, forming soft mats, glossy light green to yellowish-green or golden. **Stems** and branches creeping to subascending, irregularly branched, radiculose; central strand absent. **Leaves** weakly complanate, spreading to wide-spreading, lanceolate, often narrowly so, 1–1.5 mm long, apex narrowly acuminate, often flexed, base weakly decurrent; margins plane, recurved at base, serrate distally, below serrulate to base or nearly so; costae short and forked, weak; laminal cells smooth, median cells linear; basal cells similar or shorter and wider, porose; alar region weakly differentiated, 3–5 quadrate to short rectangular cells. **Autoicous**. **Perichaetial** leaves oblong-short lanceolate, sheathing. **Seta** 14–20 mm long, twisted, smooth. **Capsule** erect, urn cylindrical, 1.5–3 mm long, slightly asymmetric; annulus present. **Operculum** conic-short rostrate, oblique. **Peristome** with exostome teeth cross-striate below, papillose distally; endostome papillose, basal membrane high, segments keeled, cilia absent. **Spores** lightly papillose.

DISCUSSION. The genus is characterized by a combination of characters, glossy plants with complanate, lanceolate leaves, margins plane and serrate above, serrulate below to near base, and

with erect capsules. Previously placed in *Ctenidiadelphus* (cf. Bartram, 1948), and more recently in *Sharpiella*); *H. boliviana* (Broth.) M. Fleisch. is a synonym. The generic name honors the German bryologist Theodor Herzog (1880–1961), who contributed significantly to knowledge of neotropical bryophytes, particularly of Bolivia.

LITERATURE. Ireland, R. R. 1990. Scanning electron microscopy of spores of *Herzogiella*. Lindbergia 16: 169–179. - Ireland, R. R. 1993. Synopsis of the genus *Herzogiella* for North America. Lindbergia 17: 111–115.

Homomallium (Fig. 138) - Two species in the northern Neotropics (Mexico), *H. mexicanum* Cardot and the less common *H. sharpii* Ando & Higuchi; a genus of about 10 species mostly of the Northern Hemisphere.

HABITAT. On tree trunks, rocks, or less often on soil; apparently frequent in montane *Quercus* forests, at elevations from 1900–3000 m.

DESCRIPTION. **Plants** medium sized, forming mats, glossy light green to yellowish or brownish green. **Stems** creeping, to 4 cm long, regularly to irregularly pinnately branched, branches ascending, radiculose below; in cross-section central strand weak; pseudoparaphyllia foliose. **Leaves** of stem and branch similar or differentiated, homomallous or not, ovate- to oblong-lanceolate, to 1.3 mm long, smooth or weakly plicate, apex gradually to abruptly long acuminate, margins recurved below or erect to weakly involute, subentire to weakly serrulate at apex; costae short and forked; upper and median cells rhomboidal- to oblong-linear, smooth to weakly projecting at distal cell angles; alar region differentiated, cells subquadrate in several to many rows (8–30), in extreme angles somewhat enlarged and rectangular. **Autoicous**. **Perichaetial** leaves oblong-lanceolate, weakly plicate or not, gradually to somewhat abruptly long acuminate, entire or nearly so. **Seta** to ca. 15 mm long, smooth. **Capsule** suberect to horizontal, urn obloid-cylindrical, to 2 mm long, curved and rather asymmetric, constricted below mouth when dry; exothecial cells elongate, moderately thick-walled; annulus present. **Operculum** conic-apiculate or short rostrate. **Peristome** with exostome teeth cross-striate below, finely papillose distally, trabeculate; endostome basal membrane high, segments free, keeled and perforate, cilia 1–2(3), nodose. **Spores** smooth to finely papillose.

DISCUSSION. A genus of little apparent distinction, primarily characterized by the leaves with a subentire or at best weakly serrulate distal leaf margin, distinct alar group of subquadrate cells, suberect to horizontal capsules, and well developed hypnoid peristome. *Homomallium* is likely to be confused with those non-falcate members of *Pylaisiella*, likewise confined to neotropical Mexico. The latter exhibits strongly curled branches, erect, symmetric capsule, and endostomial segments adnate or free of the exostome. Both species are restricted to the northern boundary of the Neotropics, essentially north temperate in affinity. The two species can be differentiated as follows: *H. mexicanum* — alar cells of branch leaf 20–30 along margins, stem and branch leaves similar, ± short acuminate; and *H. sharpii* — alar cells of branch leaf 8–12 along margins, stem and branch leaves ± differentiated, long acuminate.

LITERATURE. Ando, H. & M. Higuchi. 1983[1984]. *Homomallium sharpii*, a new species from Mexico. The Bryologist 86: 374–377.

Hypnum (Fig. 139) - About four or five species in the Neotropics; about 40 species distributed worldwide with the highest diversity found in the Northern Hemisphere.

HABITAT. On soil, rock, humus and leaf litter, rarely on logs or tree bases; mostly open montane to zacatonal, páramo and puna, ca. 1800–4400 m.

DESCRIPTION. **Plants** medium sized to somewhat large, forming mats, glossy green to more typically golden yellow or brown. **Stems** spreading to subascending, regularly to irregularly pinnately branched; in cross-section outer 2–4 rows of cells small, thick-walled, inner cells large, thin-walled, central strand weak, often absent in branches; pseudoparaphyllia foliose, short ovate to linear-lanceolate. **Stem leaves** crowded, loosely erect to falcate-secund, broadly ovate-lanceolate or lanceolate-subulate, 1.2–2.5 mm long, smooth or plicate at base, concave, apex short to long acuminate, base rounded to subauriculate, weakly decurrent or not; margins dentate to serrate, often sharply so distally; costae forked, 1/5–1/3(–1/2) lamina length, rarely absent; laminal cells smooth, acumen cells shorter or equal in length to median cells, walls entire, median cells mostly linear, weakly porose or not; basal cells oblong-linear, weakly to strongly porose; insertion cells often golden-yellow; alar region differentiated, cells small and quadrate, thin- to thick-walled, or inflated and suboval, thin-walled **Branch leaves** often smaller and narrower. **Dioicous**. **Perichaetial** leaves usually differentiated. **Seta** 10–20 mm long, smooth. **Capsule** suberect to horizontal, urn cylindrical, 2–3 mm long, curved, asymmetric. **Operculum** short apiculate. **Peristome** with exostome teeth cross-striate below, distally papillose, trabeculate on back; endostome lightly papillose, basal membrane high, segments weakly or not perforate, cilia 1–3. **Spores** lightly papillose or appearing smooth.

DISCUSSION. The genus is characterized by the rather large glossy plants, falcate-secund leaves, well defined, small subquadrate and thick-walled or enlarged oblong-rectangular, thin-walled alar cells, the inclined to horizontal, cylindrical capsules, and well developed hypnoid peristome. Gametophytically, *Caribaeohypnum* is similar to *Hypnum* in aspect, but differs by the strongly plicate leaves and thick-walled, strongly porose, excavate alar cells; see further comments under the former genus. Sporophytes of *Hypnum* have not been observed in the Neotropics. Two of the common species can be differentiated as follows: *H. cupressiforme* Hedw. — leaves ovate-lanceolate, short to rather long acuminate, acumen cells shorter and broader than median cells, alar cells quadrate and numerous; and *H. amabile* (Mitt.) Hampe — leaves ovate-subulate, long acuminate, acumen cells similar to median cells, alar cells inflated and oval.

LITERATURE. Ando, H. 1972. Distribution and speciation in the genus *Hypnum* in the circum-Pacific region. Journal of the Hattori Botanical Laboratory 35: 68–98. - Ando, H. 1989. Studies on the genus *Hypnum* Hedw. (VI). Hikobia 10: 269–291.

Isopterygium (Fig. 139) - Eight species reported from the Neotropics; reported to contain 150 species, probably no more than 30 are valid (see below).

HABITAT. On soil, base of tree trunks and logs, occasionally on rocks (limestone and sandstone); moist to wet lowland to lower montane forests, rarely found in upper montane forests, from near sea level to 2600(–3200) m.

DESCRIPTION. **Plants** small to medium sized, forming soft mats, glossy green to yellowish green. **Stems** spreading, irregularly branched; in cross-section cortical stem cells thick-walled and small, inner cells larger, thin-walled, central strand absent pseudoparaphyllia filamentous, 3–6-celled; rhizoids smooth, inserted below leaf insertion. **Leaves** loosely complanate, spreading, ovate to narrowly or broadly lanceolate, 0.5–3 mm long, apex acuminate; margins plane to erect, entire below, serrulate at apex; costae double and forked, weak, occasionally absent; apical cells shorter than median cells or not, median cells linear to linear-fusiform, flexuose, smooth; basal cells weakly porose or not; alar region differentiated, cells few, quadrate to subquadrate or short rectangular. **Gemmae** occasionally present on simple or branched stems, filamentous, multicellular, cells papillose. **Autoicous**, rarely dioicous. **Perichaetial** leaves ovate-subulate, equal to or longer than stem leaves. **Seta** 5–30 mm long, slender, smooth, twisted or not. **Capsule** inclined to horizontal or pendulous, rarely erect, urn short ovoid to short cylindrical or ellipsoid, 0.5–1.5 mm long, straight or slightly curved; exothecial cells irregularly isodiametric; annulus absent. **Peristome** with exostome teeth finely cross-striate below, distally papillose, bordered, trabeculate on back; endostome basal membrane low to high, segments keeled, perforate or not, cilia 1–3, rarely absent. **Spores** smooth to lightly papillose.

DISCUSSION. The genus is characterized by filamentous pseudoparaphyllia, leaf margins subentire or serrulate near apex, few subquadrate or short rectangular alar cells, filamentous, papillose gemmae, autoicous sexual condition, and absence of an annulus.

Isopterygium, widely distributed in the tropics and temperate regions, has been reported to contain more than 230 species, however that estimate has dramatically changed with the recent studies by Ireland (1991, 1992) of neotropical members where 92 species were reduced to eight, with *I. tenerum* containing some 45 names! A similar trend can be expected for the Paleotropics. *Isopterygiopsis muelleriana* (Schimp.) Iwats. has been reported from Mexico (on rock, at 3140 m). *Isopterygiopsis* and *Pseudotaxiphyllum* are segregates from *Isopterygium*; the former genus is differentiated by the papillose rhizoids, stem hyalodermis, and distinctly symmetric leaves. Buck (1989) placed *Syringothecium* in synonymy under *Isopterygium*; however Ireland (1992) maintains that the former genus warrants recognition (see discussion under the former genus).

LITERATURE. Buck, W. R. 1989 (see ref. under *Syringothecium*). - Ireland, R. R. 1991. A preliminary study of the moss genus *Isopterygium* in Latin America. Caldasia 16: 265–276 [keys; table comparing related genera]. - Ireland, R. R. 1992. The moss genus *Isopterygium* (Hypnaceae) in Latin America. Tropical Bryology 6: 111–132 [keys, illustrations].

Mittenothamnium (Fig. 139) - *Mittenothamnium*, excluding *Chryso-hypnum*, is stated to contain about 70 species, a more realistic estimate is 10–20 species. The genus is confined primarily to the Neotropics with a few taxa recorded for Africa and associated islands.

HABITAT. Epiphytic, on trunks and branches of trees, soil, logs and rocks; mostly from submontane to upper montane forests and open sites at forest margins in secondary sites, infrequent in lowland forests, 150–3400 m.

DESCRIPTION. **Plants** small to large, forming loose to dense mats, often coarsely so, light to dark green, yellowish-brown or golden. **Primary stems** creeping, radiculose beneath, leaves distant, often eroded. **Stipitate**, stipe inconspicuous to rather elongate. **Secondary stems** arching or

subascending, irregularly 1–3-pinnately branched; central strand weak; pseudoparaphyllia foliose. **Leaves** of stem and branches dimorphic, **stem leaves** ± distant, spreading to wide-spreading or squarrose, mostly broadly ovate- to triangular-lanceolate, rarely ovate-oblong, 0.8–2 mm long, apex acuminate, rarely acute or rounded, base short to ± long decurrent; margins plane or occasionally erect near apex, at base reflexed, serrulate to serrate distally, rarely entire; costae short and double, occasionally strong, or single, to 1/2 lamina length; median cells linear, appearing smooth to weakly or strongly projecting at distal angles; alar region differentiated, cells few, mostly oblong-rectangular to subquadrate, smooth; **branch leaves** often weakly to strongly complanate, commonly shorter or rarely longer than secondary stem leaves, oblong, oblong-ovate to narrowly oblong-lanceolate or lanceolate, rarely ovate or oblong, 0.7–1.5 mm long, often coarsely serrate, costae weaker or absent, laminal cells usually strongly papillose by projecting distal angles. **Autoicous** or dioicous. **Perichaetial** leaves ovate- to triangular-long subulate. **Seta** 20–30 mm long, slender, smooth, often twisted. **Capsule** suberect to subpendulous, urn ovoid or ovoid-short cylindrical, 2–3 mm long, usually constricted below mouth when deoperculate. **Operculum** conic-short rostrate or beaked. **Peristome** with exostome teeth cross-striate below , distally papillose, endostome basal membrane high, segments keeled and perforate, lightly papillose, cilia 2–3. **Spores** papillose.

DISCUSSION. *Mittenothamnium* is characterized by the arching stipitate stems with leaves of stipe differing from those of stems and branches, pseudoparaphyllia lanceolate, and laminal cells usually projecting only at distal angles. Similar genera include *Chryso-hypnum* which is procumbent, stems not stipitate, pseudoparaphyllia filamentous, and laminal cells projecting as papillae at both lower and upper cell angles, and *Puiggariopsis* which exhibits plicate leaves, and porose alar cells.

A notoriously difficult genus, Bartram (1949, see general ref.) best expressed the difficulties in delimiting the species of *Mittenothamnium* (including *Chryso-hypnum*) “After studying this group for a year or more I believe Fleischer acknowledged that it was a time-consuming task. I have no reason to disagree with him.” The treatment by Fleischer (1908) is a useful reference, but dated and based on very limited collections. The generic name honors William Mitten (1819–1906), author of the single most important bryological work on the New World tropics of the 19th-century *Musci austro-americani*, published in 1869, treating the known mosses of Latin America (reprinted and available from the Missouri Botanical Garden). The generic name *Microthamnium* Mitt. *hom. illeg*. and *Stereohypnum* have been used previously.

LITERATURE. Buck, W. R. 1984 (see family ref.). Fleischer, M. 1908. Grundlagen zu einer Monographie der Gattung *Stereohypnum* (Hpe.). Hedwigia 47: 271–299 [illustrations].

Phyllodon (Fig. 140) - A single species in the Neotropics, *P. truncatulus* (Müll. Hal.) W. R. Buck; at least three and possibly more species with a pantropical distribution.

HABITAT. On tree trunks, logs, and rocks; wet lowland to lower montane forests, 100–1700 m.

DESCRIPTION. **Plants** forming thin mats, pale to somewhat dark green or yellowish-green, ± glossy. **Stems** spreading, irregularly pinnately branched; in cross-section outer 2–3 rows of cells small, thick-walled, golden-yellow, inner cells larger, thin-walled, hyaline, central strand weak or appearing absent; pseudoparaphyllia foliose; rhizoids clustered beneath. **Leaves** ± complanate, spreading, differentiated, **lateral leaves** asymmetric, oblong-ovate, to 0.9 mm long, to 0.4 mm wide, broadly concave, apex obtuse to truncate; margins plane or recurved on one side below, one side narrowly folded, coarsely serrulate in distal 2/3; costae double, short, ca. 1/5–1/4 lamina length, or absent; apical and distal marginal cells short, with 3–4 sharp papillae; median cells oblong-linear, papillose, papillae projecting at cell angles and 2–3(–4) papillae over cell lumen; basal cells smooth; alar cells few, rectangular, smooth; **median leaves** symmetric, otherwise similar to lateral leaves. **Autoicous** or dioicous. **Perichaetial** outer leaves ovate-oblong, irregularly truncate, inner leaves oblong-ligulate, acumen ± broad, apex acute to rounded. **Seta** to 18 mm long, slender, reddish-orange to dark red, smooth to distally roughened. **Capsule** horizontal to inclined, urn ovoid, to 1 mm long, curved and constricted below mouth when deoperculate; exothecial cells rectangular-rounded, thick-walled; stomata few at junction of urn and neck, superficial; annulus revoluble, in 2–3 rows. **Operculum** conic-apiculate. **Peristome** with exostome teeth finely cross-striate below, distally hyaline and papillose, with a zig-zag median line, trabeculate on back; endostome basal membrane low, segments keeled, perforate, papillose, cilia rudimentary or 1. **Spores** lightly papillose.

DISCUSSION. The complanately arranged oblong-ovate leaves with an obtuse to truncate apex, seriate papillae (2–4) over cell lumen and projecting at distal cell angle, and weakly differentiated alar cells characterize *Phyllodon*. This species was previously placed in *Glossadelphus* (cf. Tixier, 1988). The genus is placed in the Sematophyllaceae by some authors.

LITERATURE. Buck, W. R. 1987. Notes on Asian Hypnaceae and associated taxa. Memoirs of the New York Botanical Garden 45: 519–527. - Tixier, P. 1988. Le genre *Glossadelphus* Fleisch. (Sematophyllaceae, Musci) et sa valeur. Nova Hedwigia 46: 319–356 [keys, illustrations].

Platygyriella (Fig. 140) - Two species in the Neotropics, *P. densa* (Hook.) W. R. Buck (Mexico, Central America, northern Andes, southeastern Brazil) and *P. pringlei* (Cardot) W. R. Buck (Mexico northern Central America); a pantropical genus of six species, two of which are African and two Asian.

HABITAT. Epiphytic, on tree bases or trunks, also on rocks; lower montane forests, 700–2100 m.

DESCRIPTION. **Plants** small to rather large, forming mats, glossy green to golden-brown. **Stems** creeping or spreading, irregularly pinnately branched, flagellate branches infrequent; in cross-section outer 2–4 rows of cells small, thick-walled, inner cells larger, thin-walled, central strand absent; pseudoparaphyllia filamentous. **Leaves** imbricate to erect-spreading, ovate-lanceolate or broadly ovate, 0.4–1.2 mm long, concave, apex gradually long to abruptly short acuminate, base short decurrent; margins erect, entire to finely serrulate; costa short and forked; cells smooth, linear; alar region differentiated, cells rather numerous, often extending to near costa, quadrate to short rectangular and oblate; decurrency cells slightly enlarged. **Dioicous**. **Perichaetial** leaves oblong-lanceolate, acuminate. **Seta** to 20 mm long, smooth, slightly twisted. **Capsule** erect, urn cylindrical, 2–4 mm long, smooth; annulus absent. **Operculum** conic to short rostrate. **Peristome** with exostome teeth cross-striate to papillose below, smooth to finely papillose distally; endostome basal membrane moderately high, segments finely to coarsely papillose, flat, not keeled, cilia absent. **Spores** finely papillose.

DISCUSSION. The genus is characterized by erect leaves, slightly enlarged cells in the decurrent part of the leaf, entire to finely serrulate margins, smooth laminal cells, rather numerous alar cells, erect, symmetric capsules, rather high basal membrane with flat, narrow segments and absence of cilia. Our two species can be differentiated as follows: *P. densa* (Hook.) W. R. Buck — leaves erect-spreading, ovate-lanceolate, apex gradually acuminate; and *P. pringlei* (Cardot) W. R. Buck — leaves imbricate, broadly ovate, abruptly short acuminate.

LITERATURE. Buck, W. R. 1984. *Bryosedgwickia*, a new synonym of *Platygyriella* (Hypnaceae). Brittonia 36: 86–88.

Platygyrium (Fig. 140) - A single species in the Neotropics, *P. fuscoluteum* Cardot, rather widespread in Mexico and extending to the southwestern United States; a north temperate genus of four species.

HABITAT. On base and trunk of trees, logs, infrequent on rocks or soil; temperate montane forests, associated with *Abies*, *Pinus*, and *Quercus*, at elevations from 2200–2800 m.

DESCRIPTION. **Plants** small to medium sized, forming mats, glossy green to yellow-brown. **Stems** creeping, rather strongly attached to substrate by dense rhizoids, regularly to irregularly 1–2-pinnately branched, branches subjulaceous, distally curved or not, axillary brood branches produced distally; in cross-section outer rows of cells small, thick-walled, inner cells larger, thin-walled, central strand absent. **Leaves** erect, oblong-lanceolate, to 1.5 mm long, weakly plicate or not, apex mostly gradually acuminate; margins entire, recurved below; costa weakly short and forked or on some leaves absent; cells smooth,
linear-rhomboidal; alar cells in several rows (to ca. 10), quadrate. **Dioicous**. **Perichaetial** leaves oblong-lanceolate, long acuminate and serrulate. **Seta** to 15 mm or more long. **Capsule** erect, urn cylindrical, to 2.5 mm long, smooth; annulus persistent, in 1–2 rows. **Operculum** rather long rostrate. **Peristome** with exostome teeth cross-striate below, smooth to roughened distally, strongly trabeculate on back; endostome basal membrane low, segments shorter than exostome, narrow and smooth, keeled, cilia 1, rudimentary. **Spores** faintly roughened.

DISCUSSION. This species is characterized by the typically adherenrt habit, distal branches with clustered brood branches, erect leaves, costa weak and forked, erect capsules, and an indistinct endostomial basal membrane.

Pseudotaxiphyllum (Fig. 141) - Two species in the Neotropics, *P. distichaceum* (Mitt.) Z. Iwats. (Mexico, Costa Rica, tropical Andes and southeastern Brazil), and *P. richardsii* (E. B. Bartram) Ireland (Mexico: Nayarit & Sonora); also from eastern North America, Asia, and Australia. A genus of about nine species rather widely distributed, particularly in Asia.

HABITAT. On moist soil, humus or soil over rocks; montane forests to páramo, 1200–3700 m.

DESCRIPTION. **Plants** small to somewhat medium sized, forming mats, somewhat glossy yellowish-green. **Stems** creeping, irregularly branched; in cross-section outer 1–2 rows of cells small, thick-walled, inner cells large, thin-walled, central strand weak; pseudoparaphyllia absent; rhizoids smooth. **Leaves** complanate, mostly distant, spreading to wide-spreading or squarrose, ovate or ovate- to oblong-lanceolate, to 1.8 mm long, to 0.5 mm wide, symmetric to asymmetric, apex acuminate, base rounded or not; margins plane or reflexed at base, narrowly folded on one side, serrate to serrulate in distal 1/2, weakly serrulate or entire below; costae forked, ca. 1/5–1/3 lamina length, asymmetric; median cells linear, smooth; alar region well differentiated or not, cells numerous

or few (2–3), quadrate to short rectangular. **Gemmae** absent or present in leaf axils, to ca. 0.4 mm long, cylindrical and twisted with 3–5 peg-like structures at distal end. **Dioicous**. **Sporophytes** observed only in *P. richardsii* — seta to 7 mm long, capsules inclined, urn elliptic, ca. 1 mm long.

DISCUSSION. The genus is characterized by a stem cortex of 1–2 outer rows of small, thick-walled cells (viewed in cross-section), smooth rhizoids, pseudoparaphyllia absent, weakly to distinctly complanate, spreading to squarrose leaves, smooth laminal cells, similar apical and median cells, and inclined capsules. Members of this genus were placed previously in *Isopterygium*. The two species are differentiated as follows: *P. distichaceum* — alar cells few (2–3), leaves strongly asymmetric, apex acuminate; and *P. richardsii* — alar cells numerous, leaves symmetric, acute to short acuminate.

LITERATURE: Iwatsuki, Z. 1987. Notes on *Isopterygium* Mitt. (Plagiotheciaceae). Journal of the Hattori Botanical Laboratory 63: 445–451 [table and illustrations of this and related genera].

Puiggariopsis (Fig. 141) - A monotypic neotropical genus, with *P. aurifolia* (Mitt.) Menzel known from Mexico, Central America, Venezuela, Peru, and southern Brazil.

HABITAT. Usually epiphytic on tree trunks and branches, rarely on rocks or logs; adjacent to or in low montane forests, 950–2000 m.

DESCRIPTION. **Plants** medium sized to rather robust, forming mats, yellowish-green or -brown. **Stems** arching or subascending, irregularly pinnately branched, occasionally flagellate; in cross-section outer 2–3 rows of cells small, thick-walled, inner cells larger, central strand weak; paraphyllia absent or present, lanceolate, occasionally branched near base; pseudoparaphyllia foliose. **Stem leaves** crowded, erect, broadly ovate-lanceolate, to 2.2 mm long, distinctly plicate (3–5 plications), apex acuminate, often half twisted, base slightly cordate, short decurrent; margins plane or reflexed at base, serrulate throughout; costae forked, short, ca. 1/4 lamina length or absent; upper and median cells linear, distal cells papillose by projecting cell angles on back; basal cells somewhat larger and shorter, porose; alar region weakly differentiated, cells oblong to short rectangular, thick-walled and porose. **Branch leaves** either smaller or somewhat larger than stem leaves, remaining features similar. **Dioicous**. **Perichaetial** leaves acuminate from an obovate base. **Seta** to 18 mm long, smooth. **Capsule** inclined to horizontal, urn ovoid, to 1.5 mm long, strongly constricted below mouth when dry. **Operculum** conic-rostrate, oblique. **Peristome** with exostome teeth finely papillose-cross-striate below, distally papillose; endostome basal membrane low, smooth, segments keeled and narrowly perforate, weakly papillose, cilia rudimentary (1–2) or absent. **Calyptra** densely hairy. **Spores** verrucose-papillose.

DISCUSSION. In the Neotropics *Puiggariopsis* may possibly be confused with *Mittenothamnium* or *Ctenidium*, but neither of the latter exhibit strongly plicate leaves or alar cells that are both thick-walled and porose. *Puiggariopsis* replaces the name *Puiggariella*.

LITERATURE. Nishimura, N. 1989. A taxonomic study of *Puiggariella* (Hypnaceae, Bryopsida) from the Neotropics. Bulletin of the National Science Museum, Series B (Botany) 15: 125–133 [illustrations].

Pylaisiadelpha (Fig. 141) - Five species in the Neotropics (Mexico, Central America, West Indies and southeastern Brazil); a genus of 30 or more species, largely distributed in the Northern Hemisphere.

HABITAT. On tree trunks and logs; montane forests, at elevations from 1250–3100 m.

DESCRIPTION. **Plants** small to medium sized, forming mats, glossy green to yellow or golden. **Stems** creeping, irregularly to regularly pinnately branched, branches spreading to curved; pseudoparaphyllia filamentous. **Leaves** erect-spreading, complanate, ovate- to oblong-lanceolate, 0.6–1.5 mm long, abruptly to gradually acuminate, secund; margins reflexed to recurved below, distally serrate or serrulate; costa absent or short and forked; laminal cells smooth, upper and median cells narrowly rhomboidal to linear; alar cells subquadrate or a few cells inflated, oval to oblong; branch leaves similar or differentiated. **Autoicous**. **Seta** elongate, 9–18 mm or more, smooth. **Capsule** erect to suberect, urn obloid-cylindrical; exothecial cells not collenchymatous. **Operculum** conic-short to long rostrate. **Peristome** with exostome teeth cross-striate below, with a median zig-zag line, not furrowed; endostome basal membrane high, segments keeled, cilia absent or 1–2. **Spores** finely roughened or papillose.

DISCUSSION. Some authors place the genus in the Sematophyllaceae, based in part on the slightly inflated alar cells and occasional absence of a short, forked costa in some of the species. *Pylaisiadelpha* is placed in the Sematophyllaceae by some authors.

LITERATURE. Ando, H., T. Seki & W. B. Schofield. 1989. Generic distinctness of *Brotherella* from *Pylaisiadelpha*. The Bryologist 92: 209–215. - Buck, W. R. 1984. *Pylaisiadelpha* replaces *Brotherella* (Sematophyllaceae). Yushania 1: 11–13.

Pylaisiella (Fig. 142) - Three species in the Neotropics with a single widespread species, *P. falcata* (Bruch, Schimp. & W. Gümbel) Ando; the remaining two species, *P. polyantha* (Hedw.) Grout and *P. selwynii* (Kindb.) H. A. Crum, Steere & L. E. Anderson, confined to Mexico; a genus of about 15 or more species primarily from the north temperate region.

HABITAT. On tree trunks and branches, also logs; lower to upper montane and transition to páramo forests, 1600–3700 m.

DESCRIPTION. **Plants** somewhat small to medium sized, forming mats, pale green to golden- or yellowish-brown. **Stems** spreading, distal stems and branches mostly ascending, somewhat curved, pinnately branched, branches short, rather numerous; in cross-section outer 2–3 rows of cells small and thick-walled, rusty red, inner cells large and thin-walled, central strand weak; pseudoparaphyllia foliose. **Leaves** strongly falcate-secund, concave, ovate- to lanceolate-subulate, 1.6–2.2 mm long, to 0.4 mm wide, apex long acuminate; margins plane or slightly recurved, entire to faintly serrulate distally; costae absent or indistinctly short and forked; median cells linear-vermicular, smooth; alar region differentiated, cells subquadrate to short rectangular, rounded, thick-walled, often dark golden-brown. **Autoicous**. **Perigonia** lateral, leaves ovate-lanceolate, narrowly acuminate. **Perichaetial** leaves sheathing seta, oblong-subulate, to 3.5 mm long. **Seta** to 30 mm long, slender, twisted, strongly so distally. **Capsule** erect to suberect, urn obloid-cylindrical, ca. 1.8–2.2 mm long; exothecial cells subquadrate to short rectangular, thick-walled; stomata few in neck region, superficial. **Operculum** conic-short rostrate, ca. 0.6 mm long, oblique. **Peristome** inserted below mouth, exostome teeth smooth-lamellate (not striate or papillose), trabeculate, distally granulate, endostome basal membrane low, segments adhering to exostome, granulate, cilia 1. **Spores** spherical, some rather ovoid, densely papillose.

DISCUSSION. The curved short branches, crowded, imbricate, homomallous or falcate-secund leaves with quadrate to subquadrate alar cells in a well defined group, erect cylindrical capsules with the endostome often adhering partially or fully to the exostome, distinguish *Pylaisiella*.

LITERATURE: Ando, H. 1978. *Pylaisiella falcata* (B.S.G.) Ando, a moss of East Asia-Latin American distribution. Phyta 1: 14–23 [illustrations].

Rhacopilopsis (Fig. 142) - A single species in the Neotropics, *R. trinitensis* (Müll. Hal.) E. Britton & Dixon; extending to tropical Africa. A genus of five species.

HABITAT. On tree trunks and logs; moist lowland and submontane forests, 200–1250 m.

DESCRIPTION. **Plants** small, forming mats, golden-yellow or brown. **Stems** spreading to subascending, irregularly pinnately branched; in cross-section outer 3–4 rows of stem cells small, thick-walled, rusty-red, inner cells larger, ± thin-walled, central strand absent; pseudoparaphyllia foliose, narrowly lanceolate, or subfilamentous; rhizoids clustered beneath, appearing smooth, reddish-brown. **Leaves** loosely complanate, dimorphic; **upper median and lateral leaves** asymmetric, broadly ovate- to oblong-lanceolate, 1–1.3 mm long, to 0.6 mm wide, apex abruptly short to long acuminate, apices often with a half twist; margins plane, reflexed at base, occasionally on one side distally, distal 1/3–2/3 serrulate, often sharply toothed near apex, occasionally subentire; costae short and forked or absent; median cells oblong-linear, smooth, ± thick-walled; alar cells subquadrate to rectangular, few cells ± inflated, rectangular-rounded, occasionally dark golden-brown; basal cells weakly porose; **underside leaves** small, ± symmetric, ovate to ovate-lanceolate; median branch leaves similar, underside leaves lanceolate, often narrowly so, to 0.9 mm long, to 0.3 mm wide. **Dioicous**. **Perichaetial** leaves narrowly lanceolate, to 1.4 mm long, long acuminate. **Sporophytes** not observed.

DISCUSSION. The dimorphism exhibited between the larger upper median and asymmetric lateral leaves and the smaller ventral leaves aid in the recognition of this genus. *Rhacopilopsis* may be monospecific, found in both the Neotropics and Africa, however W. R. Buck (pers. comm.) believes that a careful review may result in the recognition of several species.

LITERATURE. Dixon, H. N. 1922. *Rhacopilopsis trinitensis* E. G. Britt. & Dixon. Journal of Botany 60: 86–88. - Reese, W. D. 1984. *Calymperes* and *Syrrhopodon* (Musci: Calymperaceae) in the Serra do Cachimbo, Brazil, and *Rhacopilopsis trinitensis* (C. M.) Britt. & Dicks. new to Brazil. Lindbergia 10: 123–126.

Syringothecium (Fig. 142) - A neotropical genus of two species, *S. sprucei* Mitt. (Colombia to Bolivia) and *S. brasiliense* Broth. (Brazil).

HABITAT. On leaf litter; submontane to lower montane forests, 800–2100 m.

DESCRIPTION. **Plants** forming loose mats, light green to yellowish green. **Stems** spreading, irregularly branched; in cross-section outer 1–2 rows of small golden thick-walled cells, inner cells much larger, hyaline, central strand absent; pseudoparaphyllia filamentous. **Leaves** loosely complanate, ovate-lanceolate to lanceolate, 1–1.4 mm long, to 0.4 mm wide, apex narrowly

acuminate; margins weakly serrulate distally, entire below; costae short and forked or appearing absent on branch leaves; median cells linear, smooth; basal cells (in single row) ± enlarged, oblong, above with a few subquadrate cells. **Autoicous**. **Perichaetial** leaves narrowly long lanceolate, to 2 mm long, cells at base forming 3–4 rows of enlarged cells. **Seta** to 16 mm or more long, smooth. **Capsule** erect to suberect, urn ovoid to short cylindrical, 0.9–1.8 mm long; exothecial cells subrectangular; stomata several at urn base, superficial. **Operculum** conic-long rostrate. **Peristome** with exostome teeth narrowly lanceolate, finely papillose-striate below; endostome membrane high, segments keeled, narrowly perforate or not, cilia single and short or absent. **Spores** finely papillose.

DISCUSSION. The genus is similar to *Isopterygium*, according to Ireland (1992), but differs in the following characters: alar region with a single row of inflated cells at leaf base, capsules suberect, and peristome teeth erect when dry, to 600 µm long, with endostome segments longer than exostome teeth. Care must be taken in removing the leaves so that the basal cells remain attached. The genus was recently treated as *Isopterygium* (Buck, 1989). The two species can be differentiated as follows: *Syringothecium sprucei* — leaves ovate, rather abruptly short acuminate, margins plane; and *S. brasiliense* — leaves lanceolate, gradually long acuminate, margins erect.

LITERATURE. Buck, W. R. 1989. The status of the South American moss genus *Syringothecium*. The Bryologist 92: 529–532 [keys, illustrations]. - Ireland, R. R. 1992 (see ref. under *Isopterygium*).

Taxiphyllum (Fig. 143) - Five species in the Neotropics; about 30 species primarily of subtropical and tropical distribution.

HABITAT. On soil, rocks, base of trees or logs; lower montane, often in semi-dry sites of open forests, 200–1700 m.

DESCRIPTION. **Plants** small to somewhat medium sized, forming thin to dense mats, glossy green to yellowish-green. **Stems** spreading, irregularly branched; in cross-section outer 1–2 rows of cells small, thick-walled, inner cells larger, thin-walled, central strand present or absent; pseudoparaphyllia foliose, triangular-linear, acuminate, serrate; rhizoids clustered beneath stem, reddish-brown, smooth to lightly papillose. **Leaves** of stem and branch similar, mostly complanate, erect- to wide-spreading, ovate- or oblong-lanceolate to oblong-ligulate, 1–2.5 mm long, somewhat asymmetric, apex obtuse-rounded, truncate, or broadly acute to short acuminate, sometimes abruptly so; margins plane to recurved; lateral leaves folded on one side at base; margins serrulate to serrate throughout or nearly so, teeth simple or bifid; costae short and forked or appearing absent on some leaves; apical cells usually shorter than those below; median cells linear-vermicular, smooth or papillose with papillae projecting at cell angles; alar region weakly to notably differentiated, cells few, quadrate to rectangular. **Dioicous**. **Perichaetia** lateral. **Seta** smooth. **Capsule** horizontal, urn short-ovoid; annulus persistent. **Operculum** conic-rostrate, oblique. **Peristome** with exostome teeth cross-striate below, distally papillose, bordered, trabeculate on back; endostome basal membrane high, segments keeled and perforate, cilia 1–3. **Spores** smooth to lightly papillose.

DISCUSSION. The reinterpretation of *Glossadelphus* by Buck (1987, see ref. under *Phyllodon*) with regards to the American species resulted in a redistribution of species among *Taxiphyllum* and *Phyllodon*. Both genera exhibit relatively few quadrate to short rectangular alar cells; in *Taxiphyllum* the papillae, when present, project from the cell angles, and in *Phyllodon* the papillae are both project from the cell angles and are seriate (a row of several papillae over the cell lumen). The genus *Irelandia* W. R. Buck (Buck, 1984), here included in *Taxiphyllum*, is distinguished by julaceous stems, broadly recurved leaf margins, and well differentiated alar cells.

LITERATURE. Buck, W. R. 1984 (see family ref.). - Ireland, R. R. 1969. A taxonomic revision of the genus *Plagiothecium* for North America, north of Mexico. National Museum of Natural Sciences, Publications in Botany 1: 1–118. - Ireland, R. R. 1986. Synopsis of the genus *Taxiphyllum* for North America. Lindbergia 12: 153–157.

Vesicularia (Fig. 143) - About 17 species recorded for the Neotropics, possibly only 2–3, *Vesicularia vesicularis* (Schwägr.) Broth. is the common widespread species, with two common varieties, var. *portoricensis* (Brid.) W. R. Buck and var. *rutilans* (Brid.) W. R. Buck, the latter previously known as *V. amphibola*; a pantropical genus stated to contain over 100 species, probably far fewer.

HABITAT. On soil, humus, logs, base of trees and rocks, often found in moist shaded sties; wet lowland to submontane or lower montane forests, from near sea level to ca. 2000 m.

DESCRIPTION. **Plants** somewhat small to medium sized, forming mats, glossy pale to dark green, occasionally yellowish-brown. **Stems** spreading, irregularly pinnately branched; in cross-section outer 1(2) rows of cells somewhat small and thick-walled, inner cells progressively larger and thin-walled, central strand present; pseudoparaphyllia foliose, linear-lanceolate; rhizoids clustered beneath stem, smooth to lightly papillose, reddish-brown. **Leaves** weakly to strongly complanate, crispate and often homomallous whey dry, secund, **lateral leaves** ovate-lanceolate to broadly ovate, asymmetric, to 1.2

mm long, apex abruptly short acuminate; margins plane, entire to bluntly dentate distally, ecostate or occasionally short and forked; median cells fusiform, rhomboidal to hexagonal, somewhat lax, smooth; lower and basal cells fusiform-hexagonal; distal marginal cells usually differentiated, narrow and linear, or similar though at time progressively smaller toward margin; **median leaves** symmetric, broadly ovate to ovate-lanceolate, smaller than lateral leaves. **Autoicous**. **Perichaetial** leaves ovate- to oblong-subulate. **Seta** somewhat flexuose, slender, smooth, to 18 mm long. **Capsule** horizontal to pendent, urn ovoid, 0.8–1 mm long; exothecial cells short, rounded, weakly collenchymatous; stomata few at urn base, superficial; annulus present, persistent. **Operculum** short rostrate, oblique. **Peristome** with exostome teeth cross-striate below, distally papillose, bordered, trabeculate on back, endostome basal membrane high, segments keeled and perforate, papillose, cilia 1–3. **Spores** lightly papillose.

DISCUSSION. The genus is characterized by pale green or whitish-green, lax plants, weakly complanate, somewhat differentiated lateral and ventral leaves, bluntly toothed margins, weak or absent costa, large, lax and thin-walled, fusiform, rhomboidal to hexagonal median and upper cells, and undifferentiated alar cells. While several species and even more names have been used in the Neotropics, probably no more than a couple of species are valid. *Leucomium* (Leucomiaceae) may be mistaken for *Vesicularia*, see comments under the former genus.

LITERATURE. Buck, W. R. 1984 (see family ref.). - Salmon, E. S. 1904. A revision of some species of *Ectropothecium*. Bulletin of the Torrey Botanical Club 31: 309–324 (pls. 13–14).

HYPOPTERYGIACEAE

Plants medium sized to somewhat large, forming loose frondose tufts, rather dark green to yellow or light golden-brown. **Primary stems** mostly elongate, creeping; leaves scale-like, broadly ovate-apiculate, laminal cells large, laxly hexagonal, elimbate; tomentose, rhizoids weakly papillose. **Secondary stem** stipitate, 1(2)-pinnately branched; in cross-section central strand present or absent. **Secondary stem leaves** differentiated, crispate when dry, erect spreading and complanate when wet, **lateral leaves** ovate, asymmetric, apex short acuminate, base short decurrent on one side; margins plane, serrate distally, serrulation extending further down on acroscopic side, limbate, border extending throughout; costa single, 2/3 lamina length to excurrent, often flexuose or forked; laminal cells rather uniform, smooth, rhombic to hexagonal; basal cells oblong to broadly rectangular, weakly to strongly porose; marginal border cells linear, porose; **amphigastrial** (underside) **leaves** smaller, symmetric, orbicular, ovate-triangular to -lanceolate; costa ending below acumen or rather long excurrent. **Asexual structures** absent. **Autoicous**. **Perichaetia** lateral on secondary stems or primary branches; leaves sheathing seta, broadly lanceolate to ovate-narrowly acuminate. **Seta** elongate to rather short (to 4 mm long), curved or erect, stout, smooth or roughened. **Capsule** pendent to suberect, urn obloid to short cylindrical; exothecial cells collenchymatous. **Operculum** conic-long apiculate or rostrate. **Peristome** double, exostome teeth 16, cross striate-papillose, distally papillose; endostome finely papillose, basal membrane moderately high, segments 16, keeled, perforate, cilia present or absent. **Calyptra** narrowly mitrate or cucullate, smooth, naked or sparsely hairy. **Spores** spherical, finely papillose.

DISCUSSION. The Hypopterygiaceae contain four genera and some 70 species, largely of the Southern Hemisphere but extending somewhat into the Northern Hemisphere; in the Neotropics two genera and four species are known. The family is currently placed in the order Hypnales, but previously associated with the Hookeriales. Distinguishing features of the neotropical members of this family include the frondose habit, bordered leaves, differentiated between the larger asymmetric lateral leaves and smaller symmetric ventral median leaves, and smooth laminal cells.

LITERATURE. Matteri, C. M. 1973. Revisión de las Hypopterygiaceae (Musci) austrosudamericanas. Boletín de la Sociedad Argentina Botánica. 15: 229–250.

1. Lateral leaf costa 2/3–3/4 lamina length; secondary stem frond broad or umbellate; central strand well developed; seta elongate, to 16 mm long; widespread in montane and submontane ..... **Hypopterygium**
1. Lateral leaf costa short excurrent; secondary stem frond oblong in outline, pinnate to bipinnate; stem central strand absent; seta short, to 6 mm long; southeastern Brazil ..... **Lopidium**

Hypopterygium (Fig. 143) - About eight species in the Neotropics, possibly no more than 2–3 species; about 55 species of mostly cool temperate and highland tropics.

HABITAT. Typically on logs, over humus or leaf litter, occasionally on base trunk of trees or over rocks, in shaded sites; lower to upper montane forests, 300 to more commonly 900–3200 m.

DESCRIPTION. **Plants** medium sized, forming loose frondose tufts, dark green. **Stipes** wiry, tomentose below, leaves few and distant, often eroded, broadly ovate to orbicular, short acuminate, margins bordered, entire to serrate distally, costa ca. 1/2–2/3 lamina length, forked distally. **Secondary stems** erect-arching, fronds broad, rather umbellate, regularly branched; in cross-section epidermal and cortical cells moderately thick-walled and firm, epidermal cells ± larger than outer cortex cells, inner cortical cells larger, central strand well developed, cells numerous, ± thin-walled; pseudoparaphyllia foliose, short-lanceolate (3- or 4-celled). **Secondary stem lateral leaves** secund when dry, ovate, to 2 mm long, apex short apiculate; margins plane, acroscopic side sharply serrate to near base, basiscopic side smooth below distally serrate at apex; costa 2/3–3/4 lamina length, often forked distally; median cells rhombic to hexagonal; basal cells broadly rectangular, lax, weakly porose; marginal border on acroscopic side in 2 rows, basiscopic side in 3 rows below, distally 2, cells long linear, hyaline, often weakly porose; **amphigastrial leaves** orbicular, symmetric, ca. 1 mm long, apex abruptly cuspidate; margins smooth or weakly serrulate distally; costa usually excurrent; border of 1–2 cell rows. **Perichaetial** leaves ovate to oblong, long acuminate, to 2.2 mm long, ecostate or costate, laminal cells elongate. **Seta** to 16 mm long, smooth. **Capsule** inclined to pendulous, urn ovoid to short cylindrical; exothecial cells rounded; stomata at urn base, appearing immersed. **Operculum** conic-long rostrate, to 2.5 mm long, oblique. **Peristome** with exostome teeth striate-papillose below, distally papillose, bordered, strongly trabeculate on back; endostome cilia 2–3. **Calyptra** cucullate, occasionally appearing short mitrate, sparsely hairy.

DISCUSSION. The frondose habit with fronds broad and spreading, dimorphic bordered leaves, elongate seta, and presence of endostomial cilia are diagnostic. *Hypopterygium tamarisci* (Bird.) Brid. ex Müll. Hal. is the common and widespread neotropical species. *Hypopterygium* is in need of a critical worldwide revision. The well known and long employed name *H. tamariscinum* (Hedw.) Brid., has been demonstrated to represent an unrelated element that is restricted to New Zealand (Kruijer, 1995).

LITERATURE. Kruijer, H. 1995. *Canalohypopterygium tamariscinum* (Hedw.) Kruijer: typification and synonymy of a new combination. Lindbergia 20: 85–88.

Lopidium (Fig. 144) - A single species in the Neotropics, *L. concinnum* (Hook.) Wilson (syn. *L. plumarium* (Mitt.) Hampe) known from southeastern Brazil, also Argentina, Chile, New Zealand, and Tasmania; a genus of about 15 or more species with the greatest diversity in western Asia.

HABITAT. Mostly epiphytic on tree trunks; submontane forests, at recorded elevations from 250–1000 m.

DESCRIPTION. **Plants** medium sized to somewhat large, forming loose tufts, rather dark green to yellow or light golden-brown. **Primary stems** tomentose, with leaves broadly ovate-apiculate, laminal cells large, laxly hexagonal, elimbate; rhizoids weakly papillose. **Secondary stem** erect or perpendicular to surface, to 8 cm tall/long, dark red to brown, 1(–2) pinnately branched; in cross-section outer 2–3 rows of cells small, thick-walled, inner cells large, thin-walled, central strand absent. **Secondary stem leaves** differentiated, crispate when dry, erect spreading and complanate when wet, **lateral leaves** ovate, to 2.5 mm long, asymmetric, flat, apex short acuminate, base short decurrent on one side; margins serrate distally, serrulation extending further down on acroscopic side; costa strong, often flexuose, short excurrent; laminal cells rather uniform, stellate-hexagonal, collenchymatous, appearing weakly porose; basal cells in 2–4 rows, oblong, strongly porose; insertion cells golden-red; marginal border cells linear, porose, becoming rhomboidal near apex; **branch leaves** narrower, ovate-oblong, margins often sharply serrate distally on acroscopic side; **amphigastrial leaves** smaller, ovate-triangular on secondary stems, to ca. 1.4 mm long, ovate-lanceolate on primary branches, to ca. 1.8 mm long; costa rather long excurrent, otherwise similar. **Perichaetial** leaves broadly lanceolate, to 2.4 mm long, laminal cells rhomboidal above, oblong below, strongly porose. **Seta** rather short, 3–6 mm long, curved, often strongly so, roughened throughout. **Capsule** with urn obloid to short cylindrical, 1.5–2 mm long; exothecial cells collenchymatous. **Operculum** rather conic-long apiculate. **Peristome** with exostome teeth cross striate-finely papillose, distally papillose; endostomial cilia absent. **Calyptra** narrowly mitrate, smooth and naked.

DISCUSSION. *Lopidium concinnum* is characterized by the pinnate to bipinnate, oblong-frondose secondary stems, absence of stem central strand, short excurrent costa of lateral leaves, curved, short and stout seta, and absence of endostomial cilia. Matteri (1973) has provided a full account with illustrations and a map of the local species.

LITERATURE. Matteri, C. M. 1973 (see family ref.).

LEPTODONTACEAE

Plants medium sized, forming tufts, green to yellowish-green or golden-brown. **Primary stems** creeping, radiculose beneath; leaves scale-like; rhizoids reddish-brown. **Secondary stems** ascending, stipitate or not, erect or curved, irregularly pinnately branched, distal branches bearing slender microphyllous branches from leaf axils or not; in cross-section outer 3–8 rows of cells small, thick-walled, deeply rusty-red, inner cells larger, thin-walled, pale yellow, central strand absent. **Secondary stem leaves** imbricate, appressed to erect, ovate- to oblong-short lanceolate, apex apiculate to acuminate; margins plane to partially recurved, entire to distally serrulate; costa single, 1/2–3/4 lamina length, occasionally with some costae short and forked; median cells fusiform to oval or elliptic, smooth to indistinctly papillose by projecting cell angles; alar cells well developed, quadrate to subquadrate or rounded, oblate; branch leaves similar, smaller, microphyllous branches present or absent. **Dioicous**, autoicous or synoicous. **Perichaetia** lateral, leaves lanceolate. **Seta** short to elongate. **Capsule** immersed to exserted, cylindrical to ovoid. **Peristome** double or single, exostome teeth 16, smooth to granulose; endostome absent or reduced. **Calyptra** cucullate. **Spores** smooth to finely papillose.

DISCUSSION. The Leptodontaceae contain 3–4 genera and 16 or more species rather widely distributed in temperate and tropical forested regions; in the Neotropics two genera and four species. The family is placed in the order Leucodontales Genera of the Leptodontaceae have been, and still are, placed in the Leucodontaceae by some authors.

LITERATURE. Buck, W. R. 1980. Animadversions of *Pterigynandrum* with special commentary on *Forsstroemia* and *Leptopterigynandrum*. The Bryologist 83: 451–565.

1. Median laminal cells fusiform, smooth or weakly unipapillose, papillae projecting at cell angles, firm-walled; microphyllous branches commonly present; plants dioicous ..... **Pseudocryphaea**
1. Median laminal cells oval to elliptical or rhombic-rounded, smooth, very thick-walled; microphyllous branches lacking; plants autoicous or synoicous ..... **Forsstroemia**

Forsstroemia (Fig. 144) - Three species present in the Neotropics, *F. coronata* (Mont.) Paris (southern edge of the Neotropics), *F. producta* (Hornsch.) Paris, and *F. trichomitria* (Hedw.) Lindb. (Mexico and disjunct to the southern edge of the Neotropics and further south; the latter also present in the Dominican Republic); 10 species in temperate regions of both hemispheres.

HABITAT. Epiphytic on tree trunks or branches, occasionally on rocks or logs; subtemperate and montane forests, 100–1500 m.

DESCRIPTION. **Plants** medium sized, forming tufts. **Primary stems** creeping; rhizoids clustered beneath. **Secondary stems** erect or curved, irregularly pinnately branched; in cross-section outer 3–5 rows of cells small, thick-walled; pseudoparaphyllia foliose, narrowly lanceolate. **Stem leaves** crowded, erect to appressed when dry, erect-spreading to spreading when wet, ovate to ovate-short lanceolate, 1–3 mm long, concave, apex apiculate to acuminate, often twisted; margins plane to partially recurved on one or both sides mostly below midleaf, entire to serrulate distally; costa single or mixed with short and forked costae, 1/2–3/4 lamina length, occasionally spurred; apical cells in center of acumen oblong-flexuose or not; median cells oval to elliptic; basal cells weakly porose; alar cells quadrate to subquadrate, extending along margin to ca. 1/3 leaf length. **Propagula** absent. **Branch leaves** similar, smaller, complanate or not when dry. **Autoicous**, (gonioautoicous), rarely synoicous or polyoicous. **Perichaetial** leaves lanceolate, 2–4 mm long. **Seta** relatively short, 0.5–4.5 mm long, smooth, twisted. **Capsule** immersed to exserted, cylindrical, 0.8–2.3 mm long; stomata absent; annulus absent. **Operculum** conic-rostrate, erect or oblique. **Peristome** set below mouth, double or single, exostome teeth smooth and faintly papillose to granulose, occasionally perforate or cribrose distally; endostome absent or rudimentary, basal membrane and cilia absent, segments fragmentary, adhering to exostome or not. **Calyptra** sparsely to rather densely hairy. **Spores** spherical, smooth to finely papillose.

DISCUSSION. The genus is characterized by concave ovate to short ovate-lanceolate leaves, often twisted, apiculate or acuminate apex, entire to serrulate distal leaf margins, single or mixed short and forked, occasionally spurred, costa, thick-walled, oval to oblong median cells, monoicous sexual condition, immersed to shortly exserted, cylindrical capsules, double or single peristome, with exostome smooth and faintly papillose or granulose, endostome segments fragmentary or absent, and absence of a basal membrane and cilia.

LITERATURE. Stark, L. R. 1987. A taxonomic monograph of *Forsstroemia* Lindb. (Bryopsida: Leptodontaceae). Journal of the Hattori Botanical Laboratory 63: 133–218 [keys, illustrations, maps].

Pseudocryphaea (Fig. 144) - A monotypic genus, with *P. domingensis* (Spreng.) W. R. Buck confined to the Neotropics.

HABITAT. Typically epiphytic, on trunks or branches of trees, occasionally on rocks; wet to semi-dry lowland and submontane open forests, 40–1800 m.

DESCRIPTION. **Plants** medium sized, forming tufts, green to yellowish-green or golden-brown. **Primary stems** creeping, radiculose; rhizoids reddish-brown; leaves scale-like, ovate-triangular, 0.5–0.8 mm long. **Secondary stems** ascending, substipitate, stiffly erect and rather frondose, often curved, to 6 cm long, irregularly pinnately branched, distal branches bearing slender microphyllous branches from leaf axils; in cross-section outer 6–8 rows of cells small, thick-walled. **Secondary stem leaves** imbricate, appressed to erect, ovate- to oblong-short lanceolate, 2–2.4 mm long, to 1.2 mm wide, apex short acuminate; margins plane, entire to distally serrulate; costa single, rather weak, ca. 2/3–3/4 lamina length; median cells fusiform, smooth to indistinctly unipapillose by projecting cell angles; alar region distinct, cells subquadrate or rounded, ± sinuose. **Branch leaves** 1.2–1.8 mm long, 0.6–0.8 mm wide. **Microphyllous branches** slender, to 4 mm or more long; leaves much reduced, ovate-lanceolate, to 0.2 mm long; ecostate. **Dioicous**. **Sporophytes** not observed.

DISCUSSION. The stiffly erect, stipitate plants with leaves weakly, single costate, plane margins, and occasionally with faint projecting cell angles, the numerous microphyllous branches with highly reduced leaves are diagnostic. The microphyllous branches serve as propagulae, the primary means of reproduction. The sporophyte has been described as having an elongate seta and ovoid capsule with exostome teeth smooth (cf. Florschütz, 1964; see general ref.). *Pseudocryphaea flagellifera* (Brid.) E. Britton of previous authors, has been replaced by an older name, given above. The genus has been placed previously in the Leucodontaceae. The generic name literally means false *Cryphaea*, in reference to the similarities exhibited by that genus with regard to the leafy gametophytes of *Pseudocryphaea*.

LITERATURE. Buck, W. R. 1980 (see family ref.).

LEPYRODONTACEAE

A family containing two genera, *Dichelodontium* and *Lepyrodon*, placed in the Leucodontales (Allen, in press).

Lepyrodon (Fig. 145) - A single species in the Neotropics, *L. tomentosus* (Hook.) Mitt. is common from the cordilleras of Mexico to Tierra del Fuego, also Dominican Republic and southeastern Brazil; a genus of seven species with an Austral-Antarctic distribution.

HABITAT. On shrubs, logs and rocks; upper montane forest to shrubby zacatonal, páramo and puna, (1900–)2900–4600 m.

DESCRIPTION. **Plants** medium sized to somewhat robust, forming soft dense cushions or mats, glossy green to golden-brown. **Primary stems** short, creeping, densely tomentose; rhizoids appearing finely papillose, younger branches smooth. **Secondary stems** erect, 3–6 cm tall, few to several branched, flagellate branches occasionally present; in cross-section outer 2–3 rows of cells small, thick-walled, inner cortical cells large, hyaline, central strand well developed. **Leaves** oblong-lanceolate to narrowly lanceolate, 4.5–6 mm long, to 1 mm wide, plicate, apex narrowly acuminate ending in a long flexuose hyaline capillary tip; margins plane to recurved at base, serrulate throughout; costa single, weak, 1/4–2/3 lamina length; median cells linear, vermicular, smooth, porose; basal cells short to long rectangular-rounded, strongly porose; alar region weakly differentiated, cells few, short. **Dioicous**. **Perichaetia** lateral, leaves oblong, abruptly erose-cuspidate. **Seta** elongate, 10–15 mm long, reddish-orange, smooth, twisted. **Capsule** erect to suberect, urn obloid-cylindrical, 1.8–3 mm long, mouth slightly flared when deoperculate; exothecial cells irregularly quadrate to short rectangular, thick-walled; stomata several at urn base, immersed. **Operculum** conic-long rostrate, oblique. **Peristome** single, exostome absent, endostome poorly developed, often deciduous, basal membrane low, segments 16, perforate, hyaline and lightly papillose, cilia absent. **Calyptra** cucullate, smooth. **Spores** lightly papillose.

DISCUSSION. The densely tomentose stems, soft plicate leaves that terminate in a long flexuose hyaline capillary tip, and exserted, erect sporophytes with the peristome represented only by a partially developed endostome are diagnostic for *L. tomentosus*. A small form referred to as *L. duellii* H. A. Crum, is a small, depauperate form of *L. tomentosus* (Allen, in press), characterized by ovate-short lanceolate to oblong-ovate leaves to 3 mm long, ecostate or costate with costae short and forked. *Lepyrodon* is a characteristic element of the shrubby transitional high montane and zacatonal, páramo, and puna zones.

LITERATURE. Allen, B. 1999. A revision of the moss genus *Lepyrodon* (Leucodontales: Lepyrodontaceae). Bryobrothera 5: 23-48.

LESKEACEAE

Plants small, forming loose to dense mats, dark green to yellowish or golden-brown. **Stems** coarse and stiff to rather lax and soft, irregularly to regularly pinnately branched; central strand present, weak; paraphyllia absent or present and simple, not papillose. **Leaves** mostly ovate-lanceolate, often plicate, apex short to long acuminate; margins often reflexed below, plane above, serrulate or dentate above base; costa single, ca. 2/3 lamina length, distally strong or weak or costa forked distally; median cells oval to oblong-oval or rhomboidal and smooth or indistinctly projecting at upper angle, or cells isodiametric and unipapillose, papillae confined to back; alar region differentiated, cells subquadrate, usually numerous. **Asexual structures** absent. **Autoicous**. **Perichaetia** lateral, leaves usually differentiated, long lanceolate. **Seta** elongate, smooth, often twisted. **Capsule** erect or inclined to horizontal, urn cylindrical and ± symmetric or ovoid-short cylindrical and asymmetric. **Operculum** conic or conic-short rostrate. **Peristome** double, exostome teeth 16, mostly cross-striate below and papillose at tips or nearly papillose throughout but cross-striate at extreme base, rarely smooth; endostome variously reduced, basal membrane low or absent, rarely high, segments 16 or absent. **Calyptra** cucullate, naked and smooth. **Spores** spherical, lightly to rather coarsely papillose.

DISCUSSION. The Leskeaceae contain about 20 genera and nearly 150 species primarily distributed in the temperate regions, extending into the montane tropics; in the Neotropics six genera and 13 species. A member of the order Hypnales, the family appears to be polythetic, lacking defining (unique) characters, and is characterized by trends, e.g., rather simple paraphyllia, laminal cells mostly short, often mammillose or papillose, and with varying degrees of peristome reduction.

Study Guide. Stems should be examined with some leaves removed to observe whether paraphyllia are absent or present, and if so whether they are simple or branched, and smooth or papillose. Sporophytes are useful to determine if the capsules are erect or curved, and also peristomial features, particularly the exostomial ornamentation.

LITERATURE. Buck, W. R. 1981. A re-interpretation of the Fabroniaceae. III. *Anacamptodon* and *Fabronidium* revisited, *Mamillariella*, *Helicodontiadelphus* and *Bryobartlettia* gen. nov. Brittonia 33: 473–481. - Buck, W. R. & H. Crum. 1990. An evaluation of familial limits among the genera traditionally aligned with the Thuidiaceae and Leskeaceae. Contributions to the University of Michigan Herbarium 17: 55–69.

1. Costa forked distally, ca. 1/3 of total costa length, occasionally a few leaves of the same stem or branch also with costa single or forked at base ..... **Leptopterigynandrum**
1. Costa single, occasionally spurred below 2
2. Laminal cells smooth 3
2. Laminal cells weakly to strongly unipapillose 5
3. Alar cells extending to costa; peristome smooth or nearly so; plants forming thin, loose mats, rather delicate; rare, known only from Guatemala ..... **Fabronidium**
3. Alar cells not extending to costa; peristome ornamented or absent; plants relatively coarse, often forming dense mats; occasional or common within the taxon range 4
4. Plants rather soft, glossy yellowish-green to golden brown; leaf costa distally weak; leaf apices often rather slender and long acuminate ..... **Leskeadelphus**
4. Plants coarse and stiff, dull dark green to golden or brown; leaf costa distally strong; leaf apices rather abruptly short acuminate ..... **Leskea** p.p.
5. Capsules inclined, curved, strongly asymmetric; endostomial basal membrane high; leaves when wet erect ..... **Haplocladium**
5. Capsules erect, symmetric; endostomial basal membrane low; leaves when wet loosely erect or widespreading to nearly squarrose 6
6. Leaves narrowly acuminate from an ovate base, apex concolorous; exostome cross-striate at extreme base ..... **Leskea** p.p.
6. Leaves acute to short or rather long acuminate, if acuminate then apex with a hyaline hair point; exostome weakly papillose throughout, not striate ..... **Lindbergia**

Fabronidium (Fig. 145) - A monotypic genus, with *F. guatemaliense* (Müll. Hal.) W. R. Buck known only from Guatemala.

HABITAT. Apparently epiphytic; probably associated with lowland forests, ca. 380 m.

DESCRIPTION. **Plants** small, forming thin mats, glossy light green. **Stems** creeping, to 10 mm or more long, irregularly pinnately branched; rhizoids slightly roughened. **Leaves** somewhat crowded, loosely erect with tips flexuose when dry, erect-spreading when wet, lanceolate, to 0.8 mm long, apex gradually acuminate; margins plane, or slightly reflexed at base, distal 2/3 serrulate-dentate; costa ca. 2/3 lamina length, slender; median cells rhomboidal to oblong-hexagonal, smooth or slightly projecting at distal angles; alar region differentiated, tapering to widest part of leaf, and extending near to the

costa, in several rows, cells irregularly quadrate. **Autoicous**. **Seta** rather short, to 1.2 mm long, smooth. **Capsule** erect, urn short cylindrical, to 1.2 mm long; exothecial cells thick-walled; stomata at urn base, superficial; annulus in 2 rows, large, persistent. **Peristome** with exostome teeth reduced (to 165 µm), smooth to indistinctly papillose; endostome basal membrane low, segments shorter than exostome, smooth, keeled, not perforate, cilia absent. **Calyptra** unknown. **Spores** sparsely papillose.

DISCUSSION. The genus is characterized by the delicate habit, forming small, loose mats, the smooth, rhomboidal to oblong-hexagonal laminal cells, alar cells extending to costa, smooth to inconspicuously papillose short exostome teeth, and low endostomial basal membrane with segments shorter than the exostome.

Fabronidium was originally placed, as the generic name implies, in the Fabroniaceae; it is possibly to be confused with *Anacamptodon* and *Fabronia* of that family. Both of these genera having a somewhat shorter costa. The former exhibits a densely papillose exostome with teeth joined at the base, the latter has only an exostome with the 16 teeth paired. *Fabronidium guatemaliense* is known from the original collection made by Carl Bernoulli between the 1860's and 1870's near Mazatenango, Guatemala. Obviously, little is known of the ecology of this rare taxon.

LITERATURE. Buck, W. R. 1981 (see family ref.). - Buck, W. R. & H. Crum. 1978. A re-interpretation of the Fabroniaceae with notes on selected genera. Journal of the Hattori Botanical Laboratory 44: 347–369.

Haplocladium (Fig. 145) - Three species in the Neotropics; the most common one, *H. microphyllum* (Hedw.) Broth., is widespread in neotropical montane and subtemperate regions at higher latitudes (also Europe and Asia), *H. angustifolium* (Hampe & Müll. Hal. ex Müll. Hal.) Broth. is recorded from Mexico and Greater Antilles (also southern Europe, southern Africa, and eastern Asia), and *H. porphyropelma* Müll. Hal. from southeastern Brazil; about 15 species rather widely distributed in tropical and temperate regions.

HABITAT. On soil, rocks, tree trunks and logs, in shaded to partly exposed sites; semi-dry lowland to montane forests, 400–3100 m.

DESCRIPTION. **Plants** rather small, forming mats, light to dark green. **Stems** creeping, usually 1-pinnately branched, branches spreading; paraphyllia simple to foliose, smooth, often absent on branches. **Stem leaves** abruptly long acuminate from an ovate base, 0.85–1 mm long, to 0.5 mm wide, plicate, apex often curved, ending in a single sharp apical cell; margins plane to recurved or reflexed below, entire to serrulate, costa percurrent, ending in acumen; median cells mostly isodiametric, irregularly quadrate or short rectangular, unipapillose, papillae over cell lumen or projecting at upper ends. **Branch leaves** ovate-short lanceolate, to 0.55 mm long, to 0.3 mm wide. **Autoicous**. **Perichaetial** leaves lanceolate-subulate, to 2.2 mm long. **Seta** elongate, 10–17 mm long, slender, twisted. **Capsule** inclined to horizontal, urn cylindrical, 1.2–1.4 mm long, curved when deoperculate and flared at mouth. **Operculum** conic to conic-short rostrate, oblique. **Peristome** with exostome teeth cross-striate below, distally papillose, trabeculate on back; endostome lightly papillose, basal membrane high, segments keeled and perforate, cilia 3–4. **Spores** lightly papillose.

DISCUSSION. The genus is distinguished by the 1-pinnately branched plants, smooth, simple to foliose paraphyllia, narrowly long acuminate stem leaves, apex ending in a sharp pointed cell, percurrent costa, unipapillose, isodiametric upper and median laminal cells, the strongly asymmetric, curved and inclined capsule, and well developed hypnoid peristome.

The genus was previously associated with the Thuidiaceae, and may be confused with members of that family, but differs, in part, by the sharp, single cell of leaf apex and smooth paraphyllia. The name *Bryohaplocladium* has been used in recent times when it was thought that *Haplocladium* was previously applied to a red alga, fortunately it was discovered that the name as it was originally employed did not specify a rank to the alga.

Leptopterigynandrum (Fig. 146) - Two species in the Neotropics, *L. austro-alpinum* Müll. Hal., ranging from Peru to northern Argentina (also Mexico, Alaska, Colorado, and Africa), and *L. clavatum* W. R. Buck & H. A. Crum from Bolivia; a genus containing about 10 species.

HABITAT. Wet to dry sites, on soil, soil covered rocks, including vertical cliffs, rarely epiphytic on branches of shrubs; temperate zacatonal and puna, apparently extending into open montane, at elevations (2700–)3300–4660 m.

DESCRIPTION. **Plants** rather small, forming loose to more typically dense mats, light green to more commonly yellow- or golden-brown. **Stems** spreading to distally subascending, to 3 cm or more long, often subjulaceous, irregularly pinnately branched, tips of branches and stems often curved, clavate or not; in cross-section outer 2–4 rows of cells small, thick-walled, inner cells large, thin-walled, central strand present; paraphyllia small, irregularly triangular; pseudoparaphyllia foliose; rhizoids clustered beneath, reddish-brown. **Leaves** imbricate, tips often spreading to recurved, homomallous, often

abruptly short to long acuminate from a broadly ovate base, to ca. 0.5 mm long, concave, apex usually falcate, base short decurrent; margins plane or recurved at base, entire or subentire; costa mostly single and forked above, occasionally short and forked or single, (1/3–)1/2–2/3 lamina length; laminal cells thick-walled, indistinctly and finely pluripapillose, often appearing smooth, upper and median cells oblong-fusiform to rhomboidal or irregular rhombic; basal juxtacostal cells oblong-rectangular; alar region well developed, extending along margin to widest portion of leaf, cells quadrate to short rectangular and oblate, thin- to thick-walled. **Dioicous**? **Perichaetial** leaves strongly sheathing, inner oblong-lanceolate to lanceolate, gradually to abruptly long acuminate, ecostate or costate, elongate. **Seta** to 12 mm long, strongly twisted, smooth. **Capsule** erect, urn ellipsoid-cylindrical, to ca. 2 mm long. **Operculum** conic to conic-short rostrate, straight or oblique. **Peristome** with exostome teeth narrow, papillose, or smooth below; endostome basal membrane moderately low, segments ca. 1/2 or more exostome length, narrow, slightly keeled below, cilia absent. **Calyptra** not observed. **Spores** rather coarsely papillose.

DISCUSSION. The genus is distinguished by the shortly decurrent leaves, distally forked costa, divided ca. 1/3 of total costa length (some leaves with costa single or absent), indistinct minutely pluripapillose laminal cells, well defined and differentiated alar cells extending to the widest portion of leaf, erect capsules, and endostome segments ca. 1/2 of the exostome length. The two species can be differentiated as follows: *L. austro-alpinum* — median cells oblong-fusiform to rhomboidal, 3–5:1, branch tips not clavate; and *L. clavatum* — median cells irregular rhombic, mostly 1–2:1, branch tips clavate.

LITERATURE. Buck, W. R. 1980. Animadversions of *Pterigynandrum* with special commentary on *Forsstroemia* and *Leptopterigynandrum*. The Bryologist 83: 451–565.

Leskea (Fig. 146) - At least three species in the Neotropics, *L. angustata* Taylor (Mexico, Venezuela to Peru), *L. plumaria* Mitt. (tropical Andes), and *L. teretiuscula* Mitt. (Ecuador to Bolivia); about 20 or more species associated with cool temperate regions, primarily in the Northern Hemisphere.

HABITAT. Epiphytic on shrubs and trees, also on logs and over humus, possibly on rocks; open lower montane and upper montane forests, to near treeline, 1500–3500 m.

DESCRIPTION. **Plants** somewhat small, forming loose to more commonly dense and coarse mats, dark green. **Stems** creeping and spreading, irregularly pinnately branched; central strand weak; paraphyllia present or absent, when present simple or branched, cells smooth; pseudoparaphyllia foliose. **Leaves** rather abruptly short to long acuminate from an ovate base, weakly to strongly biplicate, apex often slightly curved, margins plane or reflexed below, serrulate distally; costa strong, ca. 3/4 lamina length, often ending below or in acumen; laminal cells thick-walled, median cells oval-elongate to rhombic-rounded, smooth or unipapillose with papillae over cell lumen; alar region differentiated, cells rather numerous, subquadrate to short rectangular and oblate. **Autoicous**. **Perichaetial** leaves differentiated, mostly narrowly oblong-lanceolate, laminal cells elongate. **Seta** elongate, smooth, twisted or not. **Capsule** exserted, erect to slightly inclined, urn cylindrical, straight or slightly curved; exothecial cells subquadrate to short rectangular, thin-walled; stomata few at urn base, superficial; annulus present or absent. **Operculum** conic or conic-short rostrate. **Peristome** with exostome teeth narrowly lanceolate, papillose or cross-striate near base; endostome basal membrane low, segments narrow, papillose. **Spores** lightly papillose.

DISCUSSION. The genus is characterized by the rather coarse, dull, dark green plants, leaves abruptly narrow to broad acuminate from an ovate base, strong costa not slender and tapering at apex, smooth or unipapillose laminal cells, papillose or cross-striate at base of exostome, and low endostomial basal membrane.

Two of the more common species can be differentiated as follows: *L. angustata* — paraphyllia absent on stems, laminal cells appearing smooth; and *L. plumaria* — paraphyllia present on stems, laminal cells unipapillose. Two of our species (*L. plumaria* and *L. teretiuscula*) have been placed in the genus *Rauiella* by some authors; previously associated with the Thuidiaceae.

LITERATURE. Robinson, H. 1959. *Leskea angustata* in Mexico. The Bryologist 62: 31–35.

Leskeadelphus (Fig. 146) - Probably monotypic, *L. bolivianus* (E. Britton) W. R. Buck, is confined to the tropical Andes.

HABITAT. Mostly in exposed sites on soil and rock, rarely on tree trunks; mid and high montane, extending into the páramo and puna, 1300–4000 m.

DESCRIPTION. **Plants** small, forming thin to somewhat dense mats, yellowish-green to golden brown. **Stems** creeping, subpinnately branched, often subjulaceous; paraphyllia absent. **Leaves** erect to erect-spreading when dry, spreading to wide-spreading when wet, ovate-lanceolate, 0.7–1.1 mm long, to 0.5 mm wide, weakly concave and biplicate below, apex somewhat abruptly acuminate,

straight to curved; margins plane or occasionally recurved at base on one side, entire to weakly serrulate distally; costa 3/4 lamina length to percurrent, strong below, distally tapering and weak; laminal cells smooth and thick-walled, median cells rhombic to rhomboidal; alar region differentiated, cells subquadrate to oblate rectangular-rounded. **Autoicous**. **Perichaetial** leaves differentiated, oblong-lanceolate, to 2 mm long. **Seta** elongate, 8–13 mm long, smooth, twisted. **Capsule** erect, urn cylindrical, 2.2–2.8 mm long, slightly curved. **Operculum** conic. **Peristome** inserted below mouth, exostome teeth narrow, papillose (occasionally cross-striate at base); endostome basal membrane absent, segments linear, papillose, cilia absent. **Spores** rather coarsely papillose.

DISCUSSION. The genus is characterized by the rather soft, glossy yellowish-green to golden plants, often rather slender and long acuminate leaf apex, distally tapered and weak costa, papillose, narrow exostome teeth, absence of an endostomial basal membrane, and linear segments. *Pseudodimerodontium* is a synonym.

Lindbergia (Fig. 147) - Three species in the Neotropics, *L. brachyptera* (Mitt.) Kindb. (Mexico and Bolivia; also eastern North America, northern Asia), *L. mexicana* (Besch.) Cardot (Mexico and Guatemala; also southwestern United States), and *L. ovata* Thér. (Michoacán, Mexico); stated to contain 17 species mostly of north temperate and southern African affinities.

HABITAT. Epiphytic, on trunks of trees, also on logs and rocks; semi-dry tropical montane forests, at elevations from 1000–3400 m.

DESCRIPTION. **Plants** somewhat small, forming loose thin mats, dull yellowish- to dark-green or brown. **Stems** creeping, irregularly pinnately branched; brood branches absent or present in leaf axils; pseudoparaphyllia foliose or absent. **Leaves** crowded, appressed when dry, wide-spreading when wet, ovate to ovate-short lanceolate, to 1.4 mm long, short to gradually long acuminate, hyaline tip present or not; margins plane, entire to weakly serrate near apex; costa 2/3 lamina length or ending in acumen, rather strong below; laminal cells firm- to thick-walled, hexagonal-rounded to rhombic, unipapillose, papillae over cell lumen; alar region differentiated, cells quadrate to short rectangular and oblate, thick-walled. **Autoicous**. **Perichaetial** leaves long acuminate from a sheathing base. **Seta** to 8(–11) mm long, smooth. **Capsule** erect, urn obloid-cylindrical, to 2 mm long, symmetric to weakly curved; annulus weakly differentiated or absent. **Operculum** bluntly conic. **Peristome** inserted below mouth, exostome teeth joined at base, weakly to densely papillose; endostome represented by a low basal membrane, finely papillose. **Spores** finely papillose.

DISCUSSION. The genus is characterized by widespreading leaves when wet, absence of paraphyllia, faintly to distinctly unipapillose, hexagonal-rounded to short rhombic laminal cells, erect capsules, and low endostomial basal membrane.

LEUCOBRYACEAE

Plants rather small to large or robust, forming loose to dense cushions or tufts, white or whitish-green, occasionally tinged with purple or red (particularly stem and leaf bases). **Stems** erect to suberect, simple or few branched by innovations. **Leaves** crowded, mostly with an upper lingulate to ligulate or linear-lanceolate limb from an expanded ovate or obovate to oblong base, limb channeled or flat, base often sheathing and concave, apex acute to rounded-apiculate; margins plane to erect or incurved, entire to weakly serrulate or dentate at apex; costa appearing absent but in fact single and occupying most of leaf, in cross-section composed of leucocysts (hyaline cells) above and below internal smaller single row of chlorocysts (green cells), leucocysts in 2–8 layers; lamina mostly restricted to basal flanges, cells smooth, mostly thin-walled, entire or porose. **Dioicous** or autoicous. **Perichaetia** terminal or appearing lateral by innovations. **Seta** erect, rather short to elongate, smooth. **Capsule** erect to inclined and curved, urn ovoid-cylindrical to cylindrical, neck strumose or not. **Operculum** rostrate. **Peristome** single or absent, teeth 8 or 16, entire to divided distally, smooth to variously ornamented. **Calyptra** cucullate or mitrate, smooth, base entire or fringed. **Spores** mostly spherical, smooth or lightly papillose.

DISCUSSION. The Leucobryaceae, presented here in the more-or-less traditional sense, contain eight genera and some 150 species primarily pantropical in distribution, extending into the temperate regions in both hemispheres. In the Neotropics there are five genera and about 30 species. The whitish appearance of the gametophytes with fleshy leaves appearing ecostate and multistratose, with chlorocysts between the hyaline, porose leucocysts, are among the distinctive features of the family. The family, a member of the order Dicranales, is closely related to the Dicranaceae, and placed in that family by some past and recent authors. Andrews (1947) provided some insightful comments on the Leucobryaceae, including the transfer of *Leucophanes* and *Octoblepharum* to the Calymperaceae (see that family for further comments, and particularly the reference by Ellis, 1985), and the return of *Leucobryum* to the Dicranaceae.

Study Guide. Leaf cross-sections are required for the two most common genera. A cross-section should be made for *Leucobryum* both at or near the leaf base and slightly above midway on the limb above the expanded base. For *Octoblepharum* a cross-section should be made midway on the limb.

LITERATURE. Andrews, A. L. 1947. Taxonomic notes VI. The Leucobryaceae. The Bryologist 50: 319–326. - Robinson, H. 1985. The structure and significance of the Leucobryaceous leaf. Monographs in Systematic Botany from the Missouri Botanical Garden 11: 111–120. - Robinson, H. 1990. A functional evolution of the Leucobryaceae. Tropical Bryology 2: 223–237. - Williams, R. S. 1913. Leucobryaceae. North American Flora 15 (2): 159–166 [keys; although outdated, still an essential reference]. - Yano, O. 1982. Distribuição geográfica de Leucobryaceae (Bryopsida) na Amazônia. Acta Amazonica 12: 307–321.

1. Costa with a narrow fascicle of stereids on dorsal side (appearing costate) .... **Leucophanes** see Leucophanaceae
1. Costa without a fascicle of stereids, appearing ecostate 2
2. Limb of leaves flat or plano-convex on upper surface; base of leaves often ovate or obovate .... **Octoblepharum**
2. Limb of leaves channeled with margins somewhat involute 3
3. Leaf base not expanded or indistinctly so; gemmae often at or near leaf tip; a single row leucocysts above and below a median row of chlorocysts; capsule immersed, broadly flared when dry .... **Ochrobryum**
3. Leaf base usually expanded; gemmae absent or present at leaf tip; leucocysts in 1 or more often 2 or more rows above and below chlorocyst row; capsule exserted, not flared when dry 4
4. Chlorocysts in cross-section 3-angled (triangular), alternating with leucocysts (only known from the Guayana Highlands) ..... **Steyermarkiella**
4. Chlorocysts in cross-section 4-angled, chlorocysts arranged in a row with leucocysts above and below 5
5. Chlorocysts, in cross-section near the base, nearer the lower surface, leucocysts in 1 layer above and below chlorocysts; capsules erect, symmetric; rare, restricted to the Guayana Highlands ..... **Holomitriopsis**
5. Chlorocysts, in cross-section near the base, nearer the upper surface, leucocysts in 2 or more layers above and below chlorocysts, if 1 layer of leucocysts then at base nearer the lower surface; capsule inclined, asymmetric; common and widespread in the Neotropics ..... **Leucobryum**

Holomitriopsis (Fig. 147) - A monotypic genus, with *H. laevifolia* (Broth.) H. Rob. endemic to the Guayana Highlands of Guyana and Venezuela.

HABITAT. Epiphytic on trees and treelets, and on soil or rich humic sandy soils; transitional lowland to base montane forests, including escarpments, at elevations from 950–2000 m.

DESCRIPTION. **Plants** rather large, forming dense tufts or cushions, whitish-green to dull yellowish-brown. **Stems** to 5 cm or more tall, dark red, appearing black, few branched; in cross-section outer 2 rows of cells small, very thick-walled, inner cells large, thin-walled, central strand absent. **Leaves** crowded, stiffly suberect, often clasping in appearance, rather broadly lanceolate, 3–4 mm long, apex obtuse rounded, cucullate near tip; margins entire, limbate; costa in cross-section with leucocysts in two layers throughout leaf, chlorocysts usually nearer lower surface from the base to a short distance below the apex; laminal cells mostly rectangular, porose; marginal cells long linear, strongly porose. **Perichaetial** leaves clasping seta at base, leaves elongate, to ca. 4.5 mm long, apex acute. **Seta** to 8 mm long, slender, bulging-roughened below urn. **Capsule** erect to suberect, urn cylindrical, to 2 mm long, smooth; exothecial cells somewhat spirally arranged, oblong-linear, thick-walled; stomata absent. **Peristome** teeth 16, variously divided or entire, papillose, papillae rather scattered, or faintly papillose-striate at base; prostome present. **Calyptra** cucullate, base entire, not fringed. **Spores** finely papillose.

DISCUSSION. The suberect capsules and the somewhat spirally arranged oblong-linear exothecial cells are further distinctive features of the genus. The position of the chlorocysts in relation to the leucocysts has been noted as closer to the lower (dorsal surface), however in the mid region they can actually be equal distance from the lower and upper surfaces. Originally placed in *Leucobryum*, and still so by some authors.

LITERATURE. Newton, A. E. & H. Robinson. 1994. The structure of the leaf and peristome of *Holomitriopsis laevifolia* (Broth.) H. Robins. illustrated with scanning electron microscopy. Tropical Bryology 9: 111–116.

Leucobryum (Fig. 147) - Approximately 30 species recorded for the Neotropics, probably only about 15 valid species. A genus containing about 80 species primarily tropical with regard to species diversity, extending into the temperate regions of both hemispheres.

HABITAT. On soil, humus, base of trees and logs; wet lowland to upper montane forests, 200–2900 m.

DESCRIPTION. **Plants** small to large and robust, forming cushions or tufts, very rarely solitary, whitish-green to pale green. **Stems** erect to suberect, few to several branched; in cross-section hyalodermis present or not, central strand absent or weak. **Leaves** crowded, loosely erect to erect-spreading, occasionally falcate-secund, lanceolate to somewhat subulate above from an ovate-oblong or -elliptical base, 1.5–20 mm long, base concave, limb channeled, apex acute to acuminate, rarely cucullate or obtuse apiculate; margins entire; costa extending width of leaf or nearly so, in cross-section composed of a single layer of quadrate or quadrangular chlorocysts with (1)2–3(5) layers of leucocysts above and below, chlorocysts near the base, nearer the upper surface, if 1 layer of leucocysts then chlorocysts at base nearer the lower surface; laminal cells thin-walled, often porose, quadrate above, rectangular to quadrate below; bordered along expanded base by linear hyaline cells. **Dioicous** or pseudoautoicous. **Perigonia** in tomentum between leaves of sterile perichaetia. **Perichaetial** leaves differentiated or not. **Seta** elongate, to 35 mm long, smooth. **Capsule** commonly inclined and curved, or rarely erect, urn cylindrical, 1.5–2 mm long, weakly to strongly furrowed when dry, strumose or not; stomata absent; annulus absent or rarely present. **Operculum** conic-rostrate. **Peristome** teeth 16, divided above to ca. 1/2, vertically striate-papillose below and distally papillose or striate below, smooth distally. **Calyptra** cucullate, smooth and naked. **Spores** spherical, finely papillose or appearing smooth.

DISCUSSION. *Leucobryum* is characterized by the broadly or deeply concave leaf base and erect to incurved leaf limb, leucocysts in 1 or more rows above and below the median row of chlorocysts, well exserted, generally curved and furrowed capsules, and peristome teeth distally divided, striate to striate-papillose at base. *Terrestria* W. Peterson (Mexico to Honduras) is included in the concept of *Leucobryum*, the former is distinguished from the latter by the erect, smooth capsules, and vertically striate ornamentation of the peristome teeth. *Leucobryum* is in need of revision in the Neotropics.

Ochrobryum (Fig. 148) - Three species in the Neotropics, *O. gardneri* (Müll. Hal.) Lindb. (widespread, but absent from the West Indies; also in Africa), *O. sessile* B. H. Allen (Central America, Colombia and Venezuela), and *O. subulatum* Hampe (Venezuela, Bolivia and Brazil; also in Africa and Asia); a pantropical genus of five species.

HABITAT. Epiphytic, at base of tree trunks or on logs; wet to semi-wet lowland and lower montane forests, 100–2200 m.

DESCRIPTION. **Plants** mostly small, forming loose to dense tufts, whitish-green. **Stems** erect, short, mostly less than 12 mm tall, simple to few branched; central strand absent. **Leaves** crowded, erect to erect-spreading, occasionally falcate, linear-lanceolate or lanceolate from a narrow ovate base, 2–7 mm long, channeled or subtubulose above base, apex bluntly acute or obtuse to acuminate, apiculate; margins entire, erect or incurved; costa appearing absent, in cross-section leucocysts in 2 layers, one above and below chlorocysts, distally leucocysts occasionally in 2 layers, chlorocysts 4-angled, at apex 1–2 layers of leucocysts above and 1 layer below chlorocysts; laminal cells of expanded base thin-walled, hyaline, in 4–6 rows, marginal cells long linear, inner cells short to ± long rectangular. **Gemmae** usually present, globose, on distal upper surface of leaves, in leaf axils, or extended stem or branch tips. **Dioicous**. **Seta** short, 1–1.5 mm long, rarely elongate, smooth. **Capsule** immersed to short exserted, urn obovoid, 0.5–1 mm long, broadly flared when dry; stomata absent; annulus adhering to urn mouth and operculum base. **Operculum** long rostrate. **Peristome** absent. **Calyptra** mitrate, often 2 times operculum length, naked and smooth, ciliate or laciniate at base. **Spores** spherical, smooth to lightly papillose.

DISCUSSION. The relatively small sized plants, presence of globose gemmae on the distal upper surface of leaves, very distinctive and unusual flared urn when dry, absence of a peristome, and fringed base of calyptra assist in the recognition of this genus.

LITERATURE. Allen, B. 1992. A revision of *Ochrobryum* (Leucobryaceae). Contributions from the University of Michigan Herbarium 18: 113–130.

Octoblepharum (Fig. 148) - Nine species in the Neotropics, *O. albidum* Hedw. being the most common species; a genus containing some 15 or more species with a pantropical distribution.

HABITAT. Epiphytic on trunks and branches of trees or lianas, also on exposed fibrous roots and logs, rarely on soil; moist or wet lowland and montane forests, from near sea level to 2800 m.

DESCRIPTION. **Plants** small to medium sized, forming loose to dense cushions or tufts, rarely solitary, glossy to somewhat dull white or whitish-green, often reddish or purplish at base of leaves.

Stems short or long, simple or few branched, radiculose below; central strand absent. **Leaves** erect-spreading to spreading, often fragile when dry, ligulate from a ± expanded suboval, ovate, or obovate base, 2–30 mm long, distally usually flat (plane) or rarely triangular-terete, base somewhat concave, apex rounded-apiculate; margins entire below, distally entire to serrate or serrulate at apex; costa in cross-section consisting of triangular to elliptical chlorocysts with 1–4(5) layers of leucocysts above and below. **Autoicous** or dioicous. **Perichaetia** terminal or appearing lateral by innovations. **Seta** rather short to elongate, 2–18 mm long, smooth. **Capsule** short to long exserted, urn short to long ovoid-cylindrical, 1–2.5. **Operculum** rostrate, oblique. **Peristome** teeth 8 or 16, entire, smooth to vertically striate or papillose and semicircular thickenings; prostome present. **Calyptra** cucullate, naked and smooth. **Spores** spherical or irregularly shaped, usually finely papillose or granulose.

DISCUSSION. The genus is characterized by the flat or plano-convex upper leaf surface, often ovate or obovate leaf base and ligulate limb, erect or suberect, ovoid-cylindrical capsules, entire, generally smooth, 8 or 16 peristome teeth; an additional feature, although not present in all species, is the reddish-pink to purple coloration of the leaf bases. Some authors place *Octoblepharum* in the Calymperaceae, associated with *Leucophanes*. For a discussion summarizing various views see Salazar Allen (1991).

LITERATURE. Salazar Allen, N. 1991. A preliminary treatment of the Central American species of *Octoblepharum* (Musci: Calymperaceae). Tropical Bryology 4: 85–97 [keys]. - Salazar Allen, N. 1992. Notas para la revisión de las especies de *Octoblepharum* del neotrópico. Tropical Bryology 6: 171–179.

Steyermarkiella (Fig. 148) - A monotypic genus, with *S. anomalodictya* H. Rob. endemic to the Guayana Highlands of Venezuela.

HABITAT. On tree branches; submontane forests, at 1000 m elevation.

DESCRIPTION. **Plants** forming rather stiff cushions, dirty pale brown. **Stems** suberect, to at least 20 mm tall. **Leaves** erect, ovate-lanceolate, to 6 mm long, apex long apiculate; margins erect below, involute above, limbate, border with several rows of linear, porose cells; costa in cross-section with 2 cell layers, leucocysts alternating with chlorocysts, chlorocysts 3-angled. **Dioicous**? **Sporophytes** unknown.

DISCUSSION. The genus is distinguished by the unique 3-angled (triangular) chlorocysts alternating with leucocysts. The generic name honors the foremost neotropical plant collector of the twentieth century and prolific author, Julian A. Steyermark (1909–1988).

LITERATURE. Robinson, H. 1965. Venezuelan bryophytes collected by Julian A. Steyermark. Acta Botanica Venezuelica 1: 73–83.

LEUCODONTACEAE

Plants medium sized to somewhat robust, forming tufts or mats, dark green to yellowish-brown or golden. **Primary stems** creeping; leaves small, scale-like. **Secondary stems** spreading to ascending or erect, curled or not; in cross-section outer 2–4 rows of cells small, thick-walled, reddish-orange, inner cells larger, firm- or thin-walled, central strand absent or present; pseudoparaphyllia foliose. **Leaves** appressed to erect when dry, erect-spreading to spreading when wet, ovate-short lanceolate to ± narrowly lanceolate, smooth or distinctly plicate, broadly concave, apex gradually to abruptly short acuminate; margins plane to weakly reflexed at base or occasionally along midleaf margin, entire or weakly serrulate to dentate at apex; costa none; laminal cells smooth, thick-walled, upper ones oblong-linear; median cells oblong-linear or rhomboidal or oval, porose or not; inner basal cells elongate; alar cells few to numerous, subquadrate to irregularly short rectangular and often oblate; insertion cells golden-red. **Dioicous**. **Perichaetia** lateral, inner leaves elongate, involute, oblong-lanceolate, acute or acuminate. **Seta** erect, short to more commonly elongate, smooth, twisted to the left. **Capsule** immersed to exserted, erect and symmetric to slightly curved and asymmetric, obloid, puckered at mouth, neck short, distinct. **Operculum** rostrate, oblique. **Peristome** double or single, exostome absent or teeth 16, papillose, endostome rudimentary or absent. **Calyptra** cucullate, naked. **Spores** spherical or ellipsoid, uni- or multicellular, smooth to faintly papillose.

DISCUSSION. The Leucodontaceae contain possibly six or eight genera and about 50 species distributed mostly in temperate regions of the Northern Hemisphere; two genera and five species in the Neotropics. Definition or naturalness of the family is currently in question. Akiyama (1994) has presented the most recent discussion of the problems in the classification of the Leucodontaceae. Five groups and eight genera are tentatively accepted, including *Forsstroemia* and *Pseudocryphaea* which are recognized as belonging to the Leptodontaceae in this treatment.

LITERATURE. Akiyama, H. 1994. Suggestions for the delimitation of the Leucodontaceae and the infrageneric classification of the genus *Leucodon*. Journal of the Hattori Botanical Laboratory 76:1–

12. - Manuel, M. G. 1974[1975]. A revised classification of the Leucodontaceae and a revision of the subfamily Alsioideae. The Bryologist 77: 531–550.

1. Leaves smooth; alar cells little differentiated, few; capsules erect, symmetric ..... **Felipponea**
1. Leaves weakly to rather strongly plicate; alar cells differentiated, rather numerous; capsule slightly curved and asymmetric ..... **Leucodon**

Felipponea (Fig. 159) - A single species in the Neotropics, *F. montevidensis* (Müll. Hal.) Hook., known from southeastern Brazil, Bolivia, Uruguay, and South Africa; a genus of three species.

HABITAT. On rocks, often associated with streams; in open lowland forests and meadows, at elevations from 150–700 m.

DESCRIPTION. **Plants** medium sized, forming mats, dark green. **Stems** creeping, to 5 cm long, with leaves scale-like. **Secondary stems** and branches spreading to ascending, julaceous, irregularly pinnately branched; in cross-section outer 2–4 rows of cells small, thick-walled, inner cells large, thin-walled, central strand absent. **Leaves** crowded, appressed with apices spreading when dry, wide-spreading when wet, broadly to narrowly ovate or ovate-oval, to 1.5 mm long, smooth, apex rather abruptly short acuminate or cuspidate; margins plane, entire or apex weakly dentate; apical cells oblong-linear; median cells oblong-rhomboidal to -oval; basal cells linear, porose, golden yellow; alar region weakly differentiated, cells oblate oblong-oval. **Perichaetial** leaves sheathing, to ca. 1/2 seta length, oblong-lanceolate, to 3 mm long, apex acute, ecostate, upper laminal cells linear, weakly porose, lower and basal cells rectangular. **Seta** to 4.5 mm long, twisted. **Capsule** erect, urn ovoid-cylindrical, to 1.8 mm long, symmetric, mouth somewhat constricted when dry; exothecial cells thick-walled; annulus absent? **Operculum** long rostrate. **Peristome** without exostome; endostome reduced. **Calyptra** cucullate, smooth and naked. **Spores** not observed.

DISCUSSION. The genus is characterized by julaceous branches, smooth, broadly to narrowly ovate or ovate-oval leaves with abruptly acuminate or cuspidate apices, few alar cells, and symmetric, erect capsules with the peristome apparently represented only by a reduced endostome.

LITERATURE. Akiyama, H. 1988. Rearrangement of two species of *Leucodon* (Leucodontaceae, Musci) with a note on *Felipponea*. Journal of Japanese Botany 63: 265–272.

Leucodon (Fig. 149) - Four or possibly three species in the Neotropics; a genus containing nearly 40 species of mostly temperate regions, extending into the montane tropics.

HABITAT. Epiphytic on tree trunks (including *Quercus* and *Weinmannia*) and branches, logs and occasionally on rocks; montane forests to shrubby subpáramos, (1220–)2000–3440 m.

DESCRIPTION. **Plants** medium sized to rather robust, forming rather stiff tufts, green or yellowish-brown to golden. **Primary stems** mostly short, creeping; leaves ovate and abruptly narrowly acuminate, some apices piliferous. **Secondary stems** suberect to erect, often curled, julaceous or not when dry, 4–10 cm long; in cross-section outer 3–4 rows of cells small, thick-walled, reddish-orange, inner cells larger, firm-walled, central strand absent or present; pseudoparaphyllia foliose. **Leaves** appressed to erect, erect-spreading to spreading when wet, ovate to ovate-lanceolate or ± narrowly lanceolate, 1.5–3.5 mm long, distinctly plicate, apex gradually to rather abruptly short acuminate; margins plane to reflexed at base or occasionally along midleaf margin, entire or weakly serrulate at apex; upper and median cells oblong-linear or -rhomboidal, thick-walled, usually porose; inner basal cells elongate; alar region differentiated, cells subquadrate to irregularly short rectangular and often oblate thick-walled; insertion cells golden-red. **Perichaetial** leaves ending below or exceeding the capsule, inner leaves involute, oblong-lanceolate, to 4.5 mm long, acuminate. **Seta** elongate or relatively short, 2.5–8 mm long, twisted to the left. **Capsule** immersed or exserted, suberect to erect, urn ovoid to obloid, ca. 1–3.5 mm long, puckered at mouth, neck short, distinct. **Operculum** short to long rostrate. **Peristome** with exostome papillose, entire or somewhat perforate; endostome rudimentary or absent. **Calyptra** smooth above, somewhat plicate at base. **Spores** spherical and unicellular or ellipsoid and multicellular, smooth to faintly papillose.

DISCUSSION. The genus is distinguished by erect to curled stems and branches, weakly to strongly plicate leaves, well differentiated alar cells, slightly curved and asymmetric capsules, and peristome double or single, papillose exostome, endostome rudimentary or absent. *Leucodon curvirostris* Hampe (synonyms include *L. peruvianus* Broth. and *L. subgracilis* Hampe) appears to be our most common or at least widespread species, from Mexico to Colombia and Peru; *L. cryptotheca* Hampe, endemic to Mexico, is similar but differs by the immersed capsules, and *L. julaceus* (Hedw.) Sull. of Mexico, Dominican Republic, and eastern North America differs from the two former species by the julaceous stems and branches.

LITERATURE. Akiyama, H. 1994 (see family ref.).

LEUCOMIACEAE

Plants somewhat small to large and robust, forming thin to dense lax or soft mats, pale to dark green to yellowish brown. **Stems** creeping and spreading, irregularly pinnately branched; in cross-section cells uniform, large and thin-walled, central strand absent; pseudoparaphyllia and paraphyllia absent. **Leaves** crowded to somewhat distant, lanceolate to ovate-lanceolate, apex acuminate to setaceous, often decurved; margins plane, entire or weakly to sharply serrate distally, elimbate; costa none or short and forked; cells rhomboidal, fusiform or linear, smooth, walls rather lax or firm; alar region undifferentiated. **Gemmae** absent or present. **Dioicous** or autoicous. **Perichaetia** lateral, leaves slightly differentiated. **Seta** elongate, slender, smooth or roughened or weakly papillose below urn. **Capsule** inclined to horizontal, ovoid-cylindrical to oblong; exothecial cells collenchymatous or longitudinal walls thicker; stomata at urn base, superficial; annulus not differentiated. **Operculum** conic-long rostrate, oblique. **Peristome** double, exostome teeth 16, striate below, papillose distally, furrowed; endostome basal membrane high, segments 16, keeled and perforate, cilia absent or rudimentary (1–2). **Calyptra** cucullate or rarely mitrate, naked or with a few hairs, smooth. **Spores** spherical, lightly papillose or smooth.

DISCUSSION. The Leucomiaceae contain about six genera and 11 species largely associated with the tropics; in the Neotropics there are three genera and seven species. The family is placed in the Hookeriales.

1. Plants submerged or emergent, apparently restricted to tank bromeliads; synoicous; leaves ecostate or costate (short & forked) ..... **Philophyllum**
1. Plants terrestrial, on soil, humus or logs; autoicous; leaves ecostate 2
2. Leaf margins entire ..... **Leucomium**
2. Leaf margins weakly serrulate to sharply serrate ..... **Rhynchostegiopsis**

Leucomium (Fig. 149) - A pantropical genus of two species. *L. strumosum* (Hornsch.) Mitt. widespread in the tropics, and *L. steerei* B. H. Allen & Veling presently restricted to the Guayana Highlands of Venezuela.

HABITAT. Mostly in shaded sites, on soil, leaf litter, logs, and exposed roots and base of trees; moist or wet lowland and submontane forests, rarely extending higher, from near sea level to 2000 m.

DESCRIPTION. **Plants** small to somewhat medium sized, forming rather soft, thin to dense mats, pale green to whitish- or yellowish-green. **Stems** creeping, to 3 cm long; rhizoids clustered beneath stems. **Leaves** loosely complanate, often secund distally, crispate and contorted when dry, differentiated between lateral ± asymmetric and variously folded, and median symmetric leaves, ovate-subulate to ovate- or oblong-lanceolate, 1–3 mm long, ± concave at least below, apex short to long acuminate or hyaline hair pointed; margins plane, entire; costa none; laminal cells smooth, median cells large, linear-fusiform to long hexagonal, wide; basal cells shorter, lax. **Gemmae** observed once, occurring on rhizoids. **Autoicous**, synoicous or polyoicous. **Perichaetial** leaves ovate-subulate. **Seta** slender, 8–20(–35) mm long. **Capsule** inclined to pendulous, urn ovoid to cylindrical, 0.8–2 mm long, constricted below mouth, neck short; exothecial cells collenchymatous; stomata rather numerous in neck region. **Peristome** with exostome teeth striate below, papillose distally, with a median zig-zag line, furrowed, bordered, strongly trabeculate on back; endostome membrane high, segments keeled and perforate, lightly papillose, cilia absent or rudimentary. **Calyptra** cucullate, smooth and naked or with a few scattered hairs. **Spores** appearing smooth to lightly papillose.

DISCUSSION. The genus is characterized by pale, whitish- to yellowish-green plants, loosely complanate leaves sometimes differentiated between lateral and median, entire margins, and large, rather lax laminal cells. The two species can be differentiated as follows: *L. strumosum* — leaf apex short to long acuminate or filiform, seta 8–20 mm long, common and widespread; *L. steerei* — leaf apex hyaline hair pointed, seta 25–35 mm long, restricted to the Guayana Highlands. *Leucomium* may be confused with *Vesicularia*, but the latter exhibits a differentiated stem cross-section with a weak central strand, pseudoparaphyllia present, weakly blunt serrations, and although usually ecostate, occasionally with a faint short and forked costa.

LITERATURE. Allen, B. H. 1987. A revision of the genus *Leucomium* (Leucomiaceae). Memoirs of the New York Botanical Garden 45: 661–677 [keys, illustrations, map].

Philophyllum (Fig. 150) - A monotypic neotropical genus, with *P. tenuifolium* (Mitt.) Broth. known from Guatemala, southeastern Brazil, and Peru.

HABITAT. Occurring in tank bromeliads, (e.g., *Vriesea* and *Nidularium*), submerged or emergent; submontane to lower montane forests, rare in lowland forests, 300–2200 m.

DESCRIPTION. **Plants** medium sized, forming loose mats or strands, green to reddish-brown. **Stems** prostrate, 3–4(–9) cm long, adhering to substrate, slender and flaccid, irregularly branched; in cross-section cells progressively large, central strand absent. **Leaves** complanate, lateral leaves spreading, median leaves erect, ovate-lanceolate, ca. 4 mm long, long acuminate, often twisted; margins plane, entire to distally serrulate; costa none or short and forked, or single and elongate, often with fork below; laminal cells long-hexagonal, thin-walled, smooth, insertion cells shorter; alar region undifferentiated. **Gemmae** absent. **Synoicous**. **Perichaetial** leaves shorter than stem leaves, 1 mm long. **Seta** 15–30 mm long, somewhat flexuose. **Capsule** inclined, short cylindrical, 1.5–2.5 mm long, constricted below mouth when old and dry; exothecial cells collenchymatous; annulus in ca. 6 rows, deciduous and fragmenting. **Peristome** with exostome teeth cross-striate-papillose, papillose distally, narrowly furrowed; endostome basal membrane high, segments keeled, not perforate, cilia rudimentary. **Calyptra** mitrate and deeply lobed or cucullate and weakly lobed, smooth. **Spores** finely papillose.

DISCUSSION. The habitat of *Philophyllum*, in tank bromeliads, is unique among mosses. Features of note are variable in their expression, including the absence or presence of a costa; when present, short and forked or somewhat elongate and single, and the mitrate or cucullate calyptra.

Given the disjunct distributional pattern of this species, suggests that this species may be far more common in the intervening areas. The genus has been previously associated with the Pilotrichaceae or, in the more traditional sense, the Hookeriaceae.

LITERATURE. Buck, W. R. 1992. A revision of *Philophyllum* (Hookeriales). The Bryologist 95: 334–337.

Rhynchostegiopsis (Fig. 150) - A neotropical genus with about four or five species.

HABITAT. On logs and leaf litter, base of tree trunks, occasionally on soil and rock; in montane forests, 1200–3450 m.

DESCRIPTION. **Plants** rather small and delicate to large and robust, forming loose to dense mats, light to dark green, yellowish-green or golden brown. **Stems** creeping, irregularly pinnately branched, radiculose below; rhizoids clustered. **Leaves** weakly to strongly complanate, often secund to falcate-secund and decurved, ovate-lanceolate to broadly lanceolate-subulate, 1.5–6 mm long, apex erect, flexuose or falcate, narrowly long to short acuminate or setaceous, tips often 1/2 twisted; margins plane or on lateral leaves partially folded, entire below, distal 1/3–1/2 weakly serrulate or strongly serrate; costa none; laminal cells smooth, median cells linear or long oblong-fusiform; lower and basal cells mostly enlarged, broadly fusiform to fusiform-hexagonal; marginal cells at base narrow, linear; insertion cells short and lax. **Gemmae** absent or present in a pedicellate cluster on adaxial surface toward leaf base, or sessile and clustered in leaf axils. **Dioicous**. **Perichaetial** leaves usually smaller than stem leaves. **Seta** 15–35 mm long, slender and somewhat flexuose. **Capsule** inclined to subpendent, short- to long-cylindrical, 1.5–3 mm long, constricted below mouth; exothecial cells thick-walled, slightly collenchymatous above urn base. **Peristome** with exostome teeth cross-striate, distally papillose, deeply furrowed; endostome basal membrane rather high, segments lightly papillose, cilia 1 or reduced. **Calyptra** cucullate, naked. **Spores** lightly papillose.

DISCUSSION. The genus is distinguished by the ovate-lanceolate leaves that are short to long acuminate, with serrulate to strongly serrate distal leaf margins and absence of a costa. The two most common species, *R. flexuosa* (Sull.) Müll. Hal. and *R. tunguraguana* (Mitt.) Broth. are widespread in Central America, West Indies, and northern South America, the latter extending to Bolivia; *R. costaricensis* H. Rob. & D. G. Griffin is known from Costa Rica and Colombia, and *R. carolae* Crosby, a distinctive robust species, is only known from Costa Rica.

LITERATURE. Crosby, M. R. 1976. *Rhynchostegiopsis carolae* (Musci, Hookeriaceae): A new species from Costa Rica. Annals of the Missouri Botanical Garden 63: 373–375.

LEUCOPHANACEAE

A monotypic family, placed in the Pottiales.

Leucophanes (Fig. 150) - In the Neotropics the single species, *L. molleri* Müll. Hal., is widespread (but apparently absent in the Greater Antilles). The genus contains 12 species, confined primarily to the Paleotropics.

HABITAT. Epiphytic on tree or treelet trunks and branches, also on trunks of palms and tree ferns, or on logs; moist to wet lowland forests, from near sea level to 800 m.

DESCRIPTION. **Plants** rather small, somewhat delicate and fragile, solitary or forming loose short tufts, pale green or whitish-green. **Stems** loosely erect, to 4 cm tall, often much less, reddish-brown.

Leaves erect and distally twisted when dry, erect-spreading to spreading when wet, narrowly lanceolate to linear-lanceolate, 2.5–5.3 mm long, distally ± channeled, apex broadly acute to obtuse-rounded; margins plane to slightly recurved, serrulate at apex, bordered, border cells linear, appearing in 2–3 rows; costa single, slender, subpercurrent to percurrent, in cross-section composed of a fascicle of stereids close to back surface; remaining lamina in cross-section with one layer of leucocysts above and below triangular-shaped chlorocysts, margin multistratose, composed of small, thick-walled cells; median cells rectangular; basal cells short rectangular to quadrate, hyaline, insertion cells golden. **Gemmae** often present on leaf apices, variously shaped, fusiform, clavate, elliptical, branched or unbranched, papillose cells. **Dioicous**. Male plants and sporophytes unknown for the Neotropics, in the Paleotropics - **Seta** elongate. **Capsule** erect, urn cylindrical**. Operculum** long rostrate. **Peristome** single, inserted below mouth, teeth 16, papillose; prostome short. **Calyptra** cucullate.

DISCUSSION. *Leucophanes* can be confused with the Calymperaceae or Leucobryaceae, but lacks the well-defined cancellinae and mostly thick-walled, isodiametric, unistratose upper laminal cells in the former family, and exhibits a longitudinally centered bundle of stereids that appear as a costa, a condition not found in the latter family.

The genus has been treated by various authors as a member of the aforementioned families, thus as a member of the order Pottiales, as treated here, or Dicranales. *Leucophanes* is probably rather common in the wet lowlands, but overlooked due to its rather small size.

LITERATURE. Salazar Allen, N. 1993a. A revision of the pantropical moss genus *Leucophanes* Brid. Bryophytorum Bibliotheca 46: 1–281 [keys, illustrations, maps]. - Salazar Allen, N. 1993b. Leucophanaceae. Flora Neotropica Monograph 59: 1–11 [illustrations, map].

MACROMITRIACEAE

Plants small to more commonly medium sized or large and robust, forming tufts or mats. **Stems** creeping with branches erect or rarely subpendent, few to many branched, often densely tomentose, particularly stems and lower secondary stems; central strand absent, pseudoparaphyllia and paraphyllia absent. **Leaves** often crispate or flexuose when dry, linear- to oblong-lanceolate or oblong-lingulate, smooth to occasionally rugose or undulate, often plicate usually on one side, apex acute to acuminate, rarely obtuse, base occasionally decurrent; margins plane to reflexed or recurved, entire to serrulate or serrate, elimbate or limbate with marginal border of linear cells usually below midleaf; costa single, usually strong, subpercurrent to long excurrent; laminal cells thick-walled, upper and median cells isodiametric to elongate, smooth, mammillose or papillose; basal cells elongate or similar to upper cells, occasionally tuberculate (strongly mammillose with thick walls), occasionally sinuose or porose; alar region rarely differentiated or only marginal cells at base. **Autoicous** (including pseudautoicous) or dioicous. **Perichaetia** terminal on erect branches, leaves often differentiated. **Seta** short to more commonly elongate, often twisted, smooth or papillose. **Capsule** exserted, mostly erect, urn ovoid or ovoid-cylindrical, ± symmetric, smooth or ribbed or furrowed, neck usually distinct; exothecial cells usually thick-walled; stomata superficial or immersed; annulus often persistent. **Operculum** short to long rostrate. **Peristome** double, single or variously reduced to absent, exostome teeth 16 or in 8 pairs, smooth to more often papillose; endostome often reduced, smooth or papillose. **Calyptra** mitrate or campanulate, rarely cucullate, base usually lobed, plicate or smooth, naked or hairy. **Spores** spherical, usually papillose.

DISCUSSION. The Macromitriaceae have been treated traditionally as a subfamily of the Orthotrichaceae; however the latter family appears to be paraphyletic (De Luna, 1995) with several minor families more closely related to the Orthotrichaceae as treated here and other families to the Macromitriaceae. A member of the order Orthotrichales, the Macromitriaceae have been recognized by Churchill and Linares C. (1995, see general ref.). In the Neotropics the family contains seven genera and about 100 species.

Study guide. Many species can be identified by leaves alone; however for *Macromitrium* care should be taken to remove sufficient number of leaves with intact bases so it can be determined if the basal margin is toothed or not. Important sporophytic features to observe include the seta (whether smooth or papillose), and capsules (furrowed or not). A cross-section, just above midleaf, is useful for examining the ornamentation of laminal cells.

LITERATURE. De Luna, E. 1995. The circumscription and phylogenetic relationships of the Hedwigiaceae. Systematic Botany 20: 347–373. - Goffinet, B., R. J. Bayer & D. H. Vitt. 1998. Circumscription and phylogeny of the Orthotrichales (Bryopsida) inferred from *rbc*-L sequence analyses. American Journal of Botany 85: 1324–1337. - Grout, A. J. 1946. Bryales. Orthotrichaceae. North American Flora 15A(1): 1–62, plates 1–5 [keys]. - Vitt, D. H. 1979. New taxa and new combinations in the Orthotrichaceae of Mexico. The Bryologist 82: 1–19. - Vitt, D. H. 1982a.

The genera of Orthotrichaceae. *In* P. Geissler & S. W. Greene (eds.), Bryophyte Taxonomy. Beihefte zur Nova Hedwigia 71: 261–268. - Vitt, D. H. 1982b. On neotropical Orthotrichaceae. *In* P. Geissler & S. W. Greene (eds.), Bryophyte Taxonomy. Beihefte zur Nova Hedwigia 71: 531–535.

1. Basal leaf cells short and rounded, somewhat larger than upper cells 2
1. Basal leaf cells much elongate, usually linear-rectangular 5
2. Leaves bordered 1/4–4/5 lamina length along margin ..... **Groutiella**
2. Leaves not bordered at base 3
3. Laminal cells strongly unipapillose, papillae high conic; cells of leaf decurrency large and inflated; leaf apices often fragile and deciduous ..... **Cardotiella**
3. Laminal cells smooth to bulging or weakly papillose; cells of leaf decurrency not inflated; leaf apices neither fragile or deciduous 4
4. Leaf costa ending well below apex; laminal cells smooth to weakly unipapillose; basal marginal cells isodiametric or oval and oblate; rather widespread ..... **Macrocoma**
4. Leaf costa percurrent; laminal cells papillose, papillae 3–5-branched; basal marginal cells elongate; southern Mexico ..... **Florschuetziella**
5. Seta short, to 4 mm long; peristome with exostome reduced to a membrane of 5–6 cells high and endostome segments rather well developed, united at base, perforate, finely and coarsely open papillose; prostome absent; calyptra mitrate, covering only the operculum; Costa Rica ..... **Ceuthotheca**
5. Seta elongate; peristome lacking, single or double, when double exostome well developed or if reduced and truncate, then endostome often represented by a reduced membrane; widespread 6
6. Calyptra mitrate, often plicate, deeply lobed, smooth or hairy; peristome lacking, single or double, teeth when present often truncate; basal laminal cells often tuberculate ..... **Macromitrium**
6. Calyptra campanulate, not plicate; peristome double, teeth long-linear with a median line; basal laminal cells smooth ..... **Schlotheimia**

Cardotiella (Fig. 151) - A single species in the Neotropics, *C. quinquefaria* (Hornsch.) Vitt presently known from Mexico, Guatemala, Guyana, northern Argentina, and southeastern Brazil; a genus of seven species, in addition to our species, the remaining species are from South Africa, Madagascar, and associated islands.

HABITAT. On tree trunks, including *Quercus;* deciduous and evergreen montane forests, to 1400 m.

DESCRIPTION. **Plants** rather medium sized, forming coarse intertwining mats. **Stems** creeping, branches stiff, ascending and curved. **Leaves** crowded, erect-appressed, somewhat secund when dry, spreading when wet, spirally 5-ranked, ovate-short lanceolate or ligulate from an ovate base, to 1.5 mm long, apices short acuminate, often bluntly so, often fragile, deciduous, long decurrent; margins plane distally, recurved below, entire to dentate by projecting cell papillae; costa single, strong below, ending below apex; upper and lower laminal cells similar, quadrate-rounded, thick-walled, unipapillose, papillae rather strongly projecting and often angled; decurrency cells inflated, tuberculate, hyaline. **Dioicous**? **Sporophytes** not known from the Neotropics.

DISCUSSION. The genus is distinguished by the coarse intertwining mats, ascending straight or curved branches, 5-ranked, spirally arranged, long decurrent, short ovate-lanceolate leaves, fragile and deciduous apex, strongly unipapillose, quadrate-rounded laminal cells and decurrent leaf bases of inflated cells. Paleotropical species exhibit an erect, smooth seta, with capsules erect, urn ovoid-cylindrical, 8-ribbed, operculum conic-rostrate, peristome double, exostome teeth partly fused to form 8 pairs, somewhat papillose, endostome segments 16, calyptrae mitrate-campanulate, smooth, sparsely hairy, base lobed; spores papillose. The generic name honors the French bryologist Jules Cardot (1860–1934).

LITERATURE. Vitt, D. H. 1981. The genera *Leiomitrium* and *Cardotiella* gen. nova (Orthotrichaceae). Journal of the Hattori Botanical Laboratory 49: 93–113.

Ceuthotheca (Fig. 151) - A monotypic genus, with *C. cryptocarpa* (E. B. Bartram) Lewinsky-Haapasaari only known from southern Costa Rica.

HABITAT. Epiphytic; submontane forests, at elevations between 700–900 m

DESCRIPTION. **Plants** somewhat large, forming mats, olive-green or yellowish-brown above, reddish-brown below. **Stems** creeping, branches erect, to 8 cm long. **Leaves** of branches crowded, contorted and twisted when dry, erect-spreading when wet, lanceolate, to 3.5 mm long, gradually and broadly acuminate; margins plane below, undulate distally, bluntly serrate at base, distally dentate or serrate; costa single, subpercurrent; laminal cells thick-walled, apical cells oblong-oval; median cells

quadrate-rounded, smooth but bulging; lower cells oblong-oval; basal cells linear, porose; marginal base cells oblong, larger than inner basal cells, hyaline. **Gemmae** present, cylindrical, slightly curved. **Dioicous**? **Perichaetia** terminal, appearing lateral; leaves oblong, costa long excurrent, awn toothed. **Seta** short, to 0.4 mm long. **Capsule** erect, urn obloid-elliptical, smooth; stomata at urn base, superficial; annulus of small, thick-walled quadrate cells. **Operculum** conic-short rostrate. **Peristome** double, exostome reduced to a membrane 5–6 cells high, coarsely papillose; endostome segments 16, rather well developed, united at base, perforate, finely and coarsely open papillose; prostome absent. **Calyptra** covering only the operculum, mitrate, plicate, with short, branched and toothed hairs, base lobed. **Spores** globose, anisosporous, finely papillose.

DISCUSSION. *Ceuthotheca* is characterized by elongate branches to 8 cm long, lanceolate leaves undulate above, with margins bluntly serrate below, distally dentate or serrate, upper laminal cells smooth, slightly bulging, toothed, long awned perichaetial leaves, very short seta, smooth, immersed capsules, rudimentary exostome and well developed coarsely papillose endostome, and a plicate, very short mitrate calyptra ornamented with branched and notched hairs.

This is new genus recently proposed by Lewinsky-Haapasaari (1994) to accommodate a species originally described as *Pleurorthotrichum cryptocarpum* E. B. Bartram. Apparently rare and only known from three collections from Costa Rica.

LITERATURE. Lewinsky-Haapasaari, J. 1994. The genus *Pleurorthotrichum* Broth. Lindbergia 19: 11–24.

Florschuetziella (Fig. 151) - A single species in the Neotropics, *F. steerei* Vitt known only from Chiapas, Mexico; a genus of two species, the remaining species is known from China.

HABITAT. On tree trunks; open montane forests, at 2330 m elevation.

DESCRIPTION. **Plants** small, to 1 cm tall, slender, forming dense mats, olive-green, somewhat glaucous. **Stems** somewhat procumbent, irregularly branched, branches erect to ascending; in cross-section 5-angled, outer rows of cells small, thick-walled, inner cells larger, thin-walled, central strand absent; rhizoids at base of stems. **Leaves** stiffly erect-appressed when dry, wide- to recurved-spreading when wet, 4–5 ranked, short lanceolate to narrowly ovate-lanceolate, to 1.5 mm long, apex narrowly obtuse, somewhat keeled below; margins recurved to near apex, crenulate by projecting papillose cells; costa single, strong, subpercurrent to percurrent; upper and lower laminal cells similar, irregularly quadrate-rounded, rather thin-walled, pluripapillose, papillae conical or forked, 3–5 over cell lumen, simple to C-shaped; marginal cells at base elongate, oblong-rectangular. **Dioicous**. **Perichaetia** terminal on branches; leaves narrowly lanceolate, to 2 mm long. **Seta** 4–4.5 mm long, smooth, twisted. **Capsule** long exserted, erect, urn cylindrical, ca. 1.3 mm long, strongly 8-ribbed; exothecial cells differentiated along ribs; stomata at urn base and neck, superficial. **Operculum** conic-short rostrate. **Peristome** double, exostome teeth 8, reflexed-recurved when dry, whitish at tips, base reddish-orange, densely papillose; endostome segments 8, slightly shorter than exostome, incurved-erect when dry, hyaline, striate-papillose, obtusely keeled; prostome present. **Calyptra** covering entire capsule, mitrate, plicate, smooth to distally scabrous, naked. **Spores** spherical, appearing smooth (actually pitted).

DISCUSSION. *Florschuetziella* is distinguished by small, slender statured plants, to 1 cm tall, the appressed, acutely obtuse, broadly lanceolate leaves, pluripapillose, quadrate-rounded similar upper and lower laminal cells, well exserted, 8-ribbed capsule, presence of a prostome, exostome of 8 densely striate-papillose teeth, 8 hyaline segments, and plicate, distally scabrous calyptra enveloping the entire capsule.

The genus is named in honor of the Dutch bryologist Peter A. Florschütz (1923–1976), author of the first volume on the Suriname moss flora and co-author of *Index Muscorum*.

LITERATURE. Vitt, D. H. 1979 (see family ref.).

Groutiella (Fig. 152) - About 10 species in Neotropics; a genus primarily distributed in the Neotropics with several species recorded for the Paleotropics.

HABITAT. On tree trunks, logs, and occasionally on rocks; wet lowland to lower montane forests, from near sea level to 2070 m.

DESCRIPTION. **Plants** medium sized, forming dense mats, dark to blackish green. **Stems** creeping, branches usually simple, erect and short, densely tomentose; in cross-section outer 2–3 rows of cells small, thick-walled, inner cells larger, thick- to thin-walled, central strand absent; rhizoids smooth to papillose. **Leaves** contorted, typically spirally-twisted about the stem when dry, wide-spreading when wet, oblong-lingulate to oblong-lanceolate, smooth to rugose or undulate, often folded along costa, apex obtuse to obtuse-emarginate, mucronate or acute to acuminate, sometimes ending in a fragile, deciduous subula; margins plane, entire or serrulate-dentate below; costa single, strong, subpercurrent to short excurrent; upper and lower cells rather similar, quadrate-rounded to suboval

and often oblate, smooth, mammillate-bulging; basal cells with few differentiated, oblong to short rectangular-rounded, thick- to thin-walled, weakly porose or not; margins distinctly bordered, 1/3–3/4 lamina length, to 8 rows below, 1–2 rows distally, cells linear to short or long narrowly rectangular, smooth; insertion cells golden yellow. **Dioicous**. **Perichaetia** terminal on branches, leaves usually undifferentiated. **Seta** elongate, stout, smooth, often twisted. **Capsule** erect, urn ovoid or obloid elongate, neck short; exothecial cells short, thick-walled, rim cells often oblate, oval-elongate; stomata at urn base, superficial. **Operculum** long rostrate. **Peristome** reduced to a low membrane and papillose, or appearing absent. **Calyptra** mitrate-campanulate, naked, plicate or smooth, distally roughened or not, base deeply lobed. **Spores** spherical, smooth to densely papillose.

DISCUSSION. The bordered leaf margins are diagnostic for separating *Groutiella* from other genera of this family. Additional features are the spirally-twisted leaves, upper and lower laminal cells not conspicuously differentiated, papillose peristome reduced to a low membrane, and the naked, smooth or plicate, mitrate-campanulate calyptra.

Previously placed in *Micromitrium* Schimp. ex Besch. *hom. illeg.* and later *Craspedophyllum* Grout, *hom. illeg.* The genus is named in honor of the United States bryologist, Abel Joel Grout (1867–1947), editor and co-author of the *Moss Flora of North America*.

Macrocoma (Fig. 152) - Five species in the Neotropics; a genus of 10 species rather widespread in the subtropics and tropics, extending into the temperate regions of both hemispheres.

HABITAT. Epiphytic, on branches and trunks of shrubs and trees, rarely on rocks; in rather semi-dry, open montane forests, 1200–3400 m.

DESCRIPTION. **Plants** small to medium-sized, forming mats, dark green to brown. **Stems** creeping, often inconspicuous, branches erect, slender and wiry, irregularly pinnately branched; in cross-section outer 1–2 rows of cells small, thick-walled, inner cells larger, rather thick-walled, central strand absent. **Leaves** erect-appressed, plane, rarely twisted when dry, erect-spreading to spreading when wet, short lanceolate to ovate-lanceolate, ca. 1–2 mm long, apex obtuse to acute or acuminate; margins plane, recurved below, entire to crenulate; costa single, strong below, projecting at back, ending below apex, upper and lower laminal cells similar, oval-oblong or quadrate-rounded, often obliquely arranged, thick-walled, smooth to bulging-mammillose or papillose; juxtacostal cells near base often oblong. **Autoicous** (gonioautoicous). **Perichaetia** terminal on short branches, leaves usually elongate. **Seta** elongate, to 8 mm long, smooth. **Capsule** erect, urn cylindrical, short to long 8-ribbed or smooth; exothecial cells mostly short, thick-walled; stomata at urn base, superficial. **Operculum** conic short to long-rostrate. **Peristome** double, single, or absent, exostome rudimentary, teeth fused and forming a low membrane; endostome segments mostly reduced or absent. **Calyptra** mitrate-campanulate, smooth or weakly plicate, sparsely hairy. **Spores** spherical, lightly papillose.

DISCUSSION. The genus is distinguished by the slender, wiry habit, the intertwining stems, erect, imbricate, short ovate-lanceolate to lanceolate leaves, costa ending well below apex, similar upper and lower laminal cells smooth to weakly unipapillose, oblong juxtacostal cells, the mostly rudimentary single or double or absent peristome, and the smooth to weakly plicate calyptra.

LITERATURE. Vitt, D. H. 1973. A revisionary study of the genus *Macrocoma*. Revue Bryologique et Lichénologique 34: 205–220 [keys, illustrations]. - Vitt, D. H. 1980a[1981]. The genus *Macrocoma* I. Typification of names and taxonomy of the species. The Bryologist 83: 405–436. - Vitt, D. H. 1980b[1981]. The genus *Macrocoma* II. Geographical variation in the *Macrocoma tenue-M. sullivantii* species complex. The Bryologist 83: 437–450.

Macromitrium (Fig. 152) - Approximately 125 species recorded for the Neotropics, but probably less than 100; a genus of 350 or more species primarily distributed in the tropics and South Hemisphere.

HABITAT. Epiphytic, on trunks and branches of trees and shrubs, frequent in the canopy, occasionally on rocks; wet lowland forest to more commonly montane forests, occasionally extending into shrubby páramo and puna, 100–4000 m.

DESCRIPTION. **Plants** mostly medium-sized to large and robust, occasionally small, forming loose to dense mats or tufts, dark green to reddish-brown or golden. **Stems** short to long creeping, leaves often inconspicuous and hidden in dense tomentum, branches short to long erect, young shoots often bright green; in cross-section outer 4–8 rows of cells small, thick-walled, inner cells larger, thin- to thick-walled, central strand absent; tomentum occasionally extending upward along the branches. **Leaves** appressed or appressed-erect, variously contorted, usually crispate and often spirally twisted, erect-spreading to spreading when wet, linear-lanceolate, oblong-lanceolate to lingulate, often plicate with longitudinal fold along costa, apex obtuse or acute to short or long acuminate, rarely fragile; margins plane to recurved below, crenulate to dentate (occasionally at base), or distally serrate to serrulate at apex, basally occasionally with a toothed border of swollen hyaline cells; costa single,

usually strong and projecting on back, subpercurrent to long excurrent, rarely mucronate or with a hair point; laminal cells thick-walled, median cells oval, rounded-subquadrate or elongate (e.g., in apices), bulging mammillose or papillose, rarely smooth, walls entire to porose; basal cells often elongate and narrow, tuberculate or papillose, rarely smooth, often porose; alar cells undifferentiated. **Monoicous** or dioicous. **Perichaetia** terminal on stems or appearing on terminal branches, leaves differentiated or not. **Seta** elongate, erect to slightly flexuose, often twisted, smooth to papillose. **Capsule** exserted, erect, urn subglobose to ovoid-cylindrical, smooth to furrowed or ribbed; exothecial cells elongate, thick-walled; stomata at base, superficial; annulus undifferentiated. **Operculum** short- to long-rostrate, erect or oblique. **Peristome** mostly rudimentary (or absent), single or double, exostome often truncate and papillose; endostome membranous. **Calyptra** mitrate-campanulate, usually strongly lobed at base, naked or sparsely to densely hairy, plicate, rarely cucullate (sect. *Reverberatum*). **Spores** variously papillose.

DISCUSSION. *Macromitrium* is distinguished gametophytically, in part, by the elongate basal cells that are often tuberculate, marginal cells at base either undifferentiated or with a few enlarged, swollen cells that are bluntly toothed or not, and often plicate, mitrate calyptra. Sporophytically useful features include the elongate seta, peristome absent or, if present, then either single or double with exostome teeth often truncate.

Macromitrium appears to attain its greatest worldwide diversity in the tropical Andes within the Neotropics. As one of the largest genera encountered in the Neotropics, a critical revision is urgently needed.

LITERATURE. Allen, B. 1998. Five new species of *Macromitrium* (Musci: Orthotrichaceae), with a key to the species of *Macromitrium* in Central America. Novon 8: 113–123 [key to 30 species]. - Goffinet, B. 1993. Taxonomic and floristic notes on neotropical Macromitrioideae (Orthotrichaceae). Tropical Bryology 7: 149–154. - Grout, A. J. 1944. Preliminary synopsis of the North American *Macromitriae*. The Bryologist 47: 1–22.

Schlotheimia (Fig. 153) - About 56 species recorded for the Neotropics, of which probably 30 or fewer are justified; a tropical genus of fewer than the 120 species presently recognized.

HABITAT. Epiphytic, on tree trunks and branches, also on logs and rocks, in often partly to fully exposed sites; somewhat semi-dry to more commonly moist or wet lowland to lower montane forests, from near sea level to 2600 m.

DESCRIPTION. **Plants** medium sized, forming dense mats, dark green, occasionally blackish or brown. **Stems** creeping, often densely tomentose below, branches short and erect; in cross-section outer 2–3 rows of cells small, thick-walled, inner cells large, firm-walled, central strand absent; rhizoids smooth to papillose. **Leaves** of branches appressed and often spirally coiled about stem when dry, crispate, wide-spreading when wet, ovate-oblong to -lingulate, or abruptly narrowly lanceolate from an oblong base, 1.2–2.7 mm long, rugose or not, usually with a longitudinal fold, apex cuspidate, apiculate or abruptly long acuminate and often deciduous, base often with attached rhizoids; margins plane or recurved below, entire or crenulate; costa single, strong, often channeled, percurrent to short excurrent; median cells isodiametric, rhomboidal, quadrate-rounded or short rectangular, thick-walled; basal cells elongate, linear, thick-walled and porose, tubercula lacking; basal margin with a few quadrate or short rectangular cells. **Perichaetia** terminal on short lateral branches, leaves often differentiated from secondary stem leaves. **Seta** short to elongate, 2–12 mm long, stout, smooth. **Capsule** immersed or exserted, erect, ovoid to ovoid-cylindrical, 1.5–3 mm long; exothecial cells irregularly oblong-rectangular, thick-walled, or only longitudinal walls thick; stomata at urn base, superficial, or occasionally appearing immersed. **Operculum** short- to long-rostrate. **Peristome** double, often appearing rudimentary, exostome reflexed when dry, papillose; endostome segments 16, shorter than exostome, or reduced. **Calyptra** mitrate-campanulate, smooth or distally scabrous, base often lacerated or lobed. **Spores** spherical, papillose.

DISCUSSION. The genus is characterized by the smooth, elongate basal laminal cells; double peristome; long-linear teeth with a median line; and smooth or rarely roughened, non-plicate campanulate calyptra.

The greatest diversity, to judge solely by the number of names attributed to the flora, appears to be in southeastern Brazil. *Schlotheimia*, like *Macromitrium*, is in need of critical study in the Neotropics.

MEESIACEAE

The Meesiaceae contain three genera and 14 species primarily of the Northern Hemisphere. The family is placed in the Bryales.

Meesia (Fig. 153) - Two species in the Neotropics, *M. longiseta* Hedw. (Guatemala, Colombia, Ecuador; also reported from Honduras) and *M. triquetra* (L. ex Richt.) Ångstr. (Venezuela); about 10 species largely associated with the Northern Hemisphere.

HABITAT. In wet boggy areas; open montane to páramo sites, 2300–3800 m.

DESCRIPTION. **Plants** medium sized, in dense tufts, yellowish green or brown. **Stems** erect, 3–5(–10) cm tall, few branched by innovations, usually densely tomentose below; central strand present; rhizoids rusty-red, papillose. **Leaves** evenly and densely foliate, 3-ranked, erect-spreading to spreading, lanceolate to ovate- or oblong-lanceolate, 1.8–4 mm long, distally keeled, apex rather broadly acute to somewhat obtuse-acute, base decurrent; margins plane or reflexed to recurved from base to midleaf, entire to serrulate distally; costa single, strong below, subpercurrent, usually ending several cells below apex; laminal cells smooth, ± thick-walled, median and upper cells irregularly short rectangular; lower and basal cells long rectangular, lax; alar region undifferentiated. **Asexual structures** absent. **Synoicous** or dioicous. **Perichaetia** terminal, leaves elongate and enlarged or similar to stem leaves, to 4.5 mm long. **Seta** very much elongate, to 50(–100) mm long, slender, smooth. **Capsule** suberect, urn ± long pyriform, 2–4.5 mm long, curved, asymmetric; annulus not well differentiated. **Operculum** bluntly conic. **Peristome** double, inserted below mouth, exostome teeth 16, reduced, truncate, finely papillose; endostome well developed, 2–4 times longer than exostome teeth, basal membrane low, segments 16, narrow, keeled and perforate, smooth, cilia reduced or irregularly developed. **Calyptra** cucullate, smooth and naked. **Spores** spherical, lightly papillose to nearly smooth.

DISCUSSION. *Meesia* is characterized by the 3-ranked, ovate- to oblong-lanceolate leaves, broadly acute to obtuse-rounded apex, decurrent base, strong, subpercurrent costa, smooth and rather thick-walled laminal cells, irregularly short rectangular distal laminal cells, undifferentiated alar cells, slender, smooth, usually much elongate seta, asymmetric, pyriform capsules, and short, truncate exostome with endostome several times longer. The genus is rare in the Neotropics. Both of the species are relatively widespread in the Northern Hemisphere The two species can be differentiated as follows: *M. longiseta* exhibits entire or subentire leaf margins, and elongate perichaetial leaves, and *M. triquetra* differs by the margins distally serrulate, perichaetial leaves similar to stem leaves in length. *Meesia lavardei* Thér. from Colombia is referred to *Barbula lavardei* (Thér.) R. H. Zander & S. P. Churchill.

LITERATURE. Matteri, C. M. & R. Ochyra. 1999. The Meesiaceae (Musci) in southern South America, with notes on the subdivision of the family. Haussknechtia Beiheft 9: 225–242.

METEORIACEAE

Plants mostly medium sized to rather large, forming mats or wefts, **Primary stems** creeping or spreading. **Secondary stems** often pendent or spreading, irregularly to regularly pinnately branched, flagellate branches frequent; in cross-section outer 3–6 rows of cells small, thick-walled, inner cells thin- to somewhat thick-walled, central strand present or more often absent; paraphyllia and pseudoparaphyllia absent; rhizoids often clustered beneath. **Leaves** often differentiated between stem and branch, erect to wide-spreading, broadly ovate to lanceolate, concave or not, apex short acute to more commonly acuminate, costa single and weak or absent (*Pilotrichella*), median cells linear, smooth or various papillose, often porose, basal cells often porose, insertion cells often golden-yellow, alar region differentiated or not. **Propagula** in the form of flagellate branches, caducous leaves. **Dioicous**, rarely autoicous. **Perichaetia** lateral, leaves often differentiated. **Seta** short to somewhat elongate, smooth to distally papillose or roughened. **Capsule** immersed to exserted, erect to inclined, urn ovoid to broadly cylindrical; stomata usually present, at urn base, superficial. **Operculum** rostrate. **Peristome** double, exostome teeth 16, papillose to cross-striate below, papillose distally; endostome basal membrane low to ± high, segments 16, often keeled and perforate, lightly papillose, cilia absent or rudimentary. **Calyptra** mitrate or cucullate, base not lobed, smooth or hairy. **Spores** usually spherical, smooth to papillose.

DISCUSSION. The Meteoriaceae, in the traditional sense, contain some 15–20 genera and nearly 300 species; in the Neotropics 12 genera and about 40 species. The family is predominately montane, and in general, quite abundant in secondary forests. A distinguishing feature of the Meteoriaceae often stated is the pendent habit; however, it is apparent that this is a facultative feature. The pendent habit is useful in keys, and in some taxa it is the prevalent growth form.

Buck (1994) has proposed various new alignments and amendments to the Meteoriaceae. A total of 28 genera are recognized with the inclusion of *Trachypus* (Trachypodaceae of this treatment) and exclusion of *Pilotrichella* (including *Orthostichella*) and *Squamidium* (transferred to the Lembophyllaceae). We have maintained the more traditional concept of the family until a careful assessment can be made of the families and genera in light of phylogenetic studies. New genera or

transferred species proposed by Buck are noted under the individual genera treated below. See further comments under the Pterobryaceae with regard to the Meteoriaceae. As treated here the Meteoriaceae is placed in the Leucodontales; Buck (1998, see general ref.) places both the Lembophyllaceae and Meteoriaceae in the Hypnales, the latter close to the Brachytheciaceae.

Study guide. Leaves provide the essential features necessary for identification for most of the neotropical species, however attention must be given in some cases to differences between stem and branch leaves, and whether the leaves are clasping or sheathing the stem.

LITERATURE. Buck, W. R. 1994. A new attempt at understanding the Meteoriaceae. Journal of the Hattori Botanical Laboratory 75: 51–72 [keys to genera]. - Lewis, M. 1992. *Meteoridium* and *Zelometeorium* in Bolivia. Tropical Bryology 5: 35–55 [keys, illustrations, map]. - Visnadi, S. R. 1993. Meteoriaceae (Bryopsida) da mata tropical pluvial de encosta — "Mata Atlântica" — do estado de São Paulo. Mestre em Ciências Biológicas, Rio Claro, São Paulo [keys, illustrations].

1. Costa absent or if present then short, forked, or single but with the majority of the leaves ecostate 2
1. Costa present, single 5
2. Leaves long lanceolate, apex long acuminate to subulate 3
2. Leaves oblong-ovate or obovate, apex bluntly acute, laminal cells smooth 4
3. Leaves strongly plicate; laminal cells smooth ..... **Lepyrodontopsis**
3. Leaves smooth, not plicate; laminal cells with a single papillae over cell lumen .. **Barbella** p. p.
4. Leaves 1.5–3 mm long, ecostate, base distinctly auriculate; alar region excavate, cells dark golden-red or -brown; laminal cells strongly porose ..... **Pilotrichella**
4. Leaves ca. 1 mm long, ecostate and costate, short and forked (rarely short and single); base indistinctly auriculate; alar region weakly developed, cells few, not excavate; laminal cells weakly porose or not ..... **Orthostichella**
5. Upper leaf cells papillose 6
5. Upper leaf cells smooth 11
6. Cells unipapillose, papillae over cell lumen (occasionally mixed with a few cells with 2–3 papillae) ..... **Meteorium**
6. Cells distinctly pluripapillose 7
7. Laminal cells with papillae along margin of cell and over lumen (see also *Trachypus*, Trachypodaceae) 8
7. Laminal cells with papillae over cell lumen, seriate 9
8. Leaves erect and appressed, apices short acuminate to acute; laminal cells short oblong ..... **Papillaria** p.p.
8. Leaves widespread, apices very long acuminate; laminal cells linear ..... **Floribundaria**
9. Leaves linear-lanceolate; leaf base not auriculate ..... **Barbella** p.p.
9. Leaves ovate-lanceolate, leaf bases weakly to strongly auriculate or cordate 10
10. Leaves erect-spreading to wide-spreading, distally undulate ..... **Aerobryopsis**
10. Leaves loosely erect, not distally undulate ..... **Papillaria** p.p.
11. Branch leaves deeply concave, ovate to oblong-ovate; alar cells in a distinct group, often golden-yellow ..... **Squamidium**
11. Branch leaves not concave, narrowly lanceolate to ovate-lanceolate; alar cells absent or indistinct with a few cells oblong rectangular 12
12. Leaf base sheathing or clasping ..... **Zelometeorium**
12. Leaf base free, or if slightly sheathing then leaves long lanceolate 13
13. Leaves ovate-lanceolate; costa mostly 1/2–2/3 lamina length ..... **Meteoridium**
13. Leaves narrowly lanceolate; costa 1/4–1/3 lamina length..... **Lindigia**

Aerobryopsis (Fig. 153) - Two or three species in the Neotropics, two species occurring in the north, *A. longissima* (Dozy & Molk.) M. Fleisch. and *A. martinicensis* (Broth.) Spessard-Schueth, both distributed in Mexico, Central America, and West Indies, one or two species from southeastern Brazil, including *A. capensis* (Müll. Hal.) M. Fleisch.; a genus of four species, also found in Southeast Asia.

HABITAT. Epiphytic, on trunks or more commonly branches, also on leaf litter, rarely on rocks; moist montane forests, 680–1540 m.

DESCRIPTION. **Plants** rather medium sized to large, forming loose mats or pendent, glossy green or yellowish-green, usually black or brown tinged. **Stems** spreading or pendulous, to 30 cm long, irregularly pinnately branched; in cross-section outer 4–5 rows of cells small, thick-walled, inner cells large, rather firm-walled, central strand absent. **Leaves** loosely complanate or not, erect-spreading to wide-spreading, lanceolate to oblong-lanceolate, to 3 mm long, concave below, apex rather abruptly long acuminate, flexuose, ending in a filiform, sometimes capillary, tip; base auriculate; margins undulate distally, finely serrulate throughout by projecting cells; costa single, slender, 1/2–2/3 leaf

length; median cells linear, flexuose, papillose, papillae 1–4 over cell lumen; basal cells larger, irregularly oblong, porose. **Dioicous**. **Sporophytes** apparently unknown in the Neotropics.

DISCUSSION. The genus is characterized by the somewhat complanate, erect-spreading to wide-spreading, distally undulate or smooth, auriculate leaves, flexuose, narrowly long acuminate leaf apex, slender, single costa, and 1–4 papillae over cell lumen. *Aerobryopsis* may be mistaken for *Papillaria*, but the latter exhibits leaves mostly appressed, erect or erect-spreading, and margins papillose-serrulate or -dentate.

Buck (1994), while retaining *A. longissima* in *Aerobryopsis*, would place *A. martinicensis* (*A. wallichii* (Brid.) M. Fleisch. of reports from the Neotropics in *Pseudotrachypus*, as *P. martinicensis* (Broth. in Urban) W. R. Buck.

LITERATURE. Spessard-Schueth in Sharp et al. (1994, see general ref.). - Buck 1994 (see family ref.).

Barbella (Fig. 154) - Five species recorded for the Neotropics, possibly only 2–3 are valid; a genus containing 20 or more species primarily distributed in Southeast Asia.

HABITAT. Epiphytic on branches and occasionally on treelet trunks; submontane to upper montane forests, 60–2800 m.

DESCRIPTION. **Plants** rather small to medium sized, forming loose pendulous strands from mats, light green to golden- or reddish-brown. **Primary stems** short to ± long creeping, leaves usually eroded from stem. **Secondary stems** mostly pendent, to 15 cm long, branches slender or becoming distally slender; in cross-section outer cells small and thick-walled (to 10 rows), inner cells larger, ± thin-walled, central strand weak. **Leaves** forming a multimorphic series, initially complanate, lateral leaves spreading to erect-spreading, median leaves loosely erect, or initial leaves larger and becoming slender or filiform, oblong-lanceolate to lanceolate-subulate, to 3.7 mm long, to 0.9 mm wide, apex short to more typically long and slender acuminate, base clasping stem, weakly decurrent; margins erect to incurved, serrulate, usually sharply dentate near base; costa none or single and slender; median cells linear to rhomboidal-elongate, ± thick-walled, uni- or pluripapillose, papillae (1–8) over cell lumen, indistinct (best observed on folded leaves) or distinct; alar region somewhat well defined, cells subquadrate to short or long rectangular, porose; distal stem leaves becoming slender and terete, often flagellate, leaves narrowly long lanceolate, concave, apex ending in a long capillary tip, secondary branches occasional, short, leaves then repeating in form that of initial leaf type. **Dioicous**. **Sporophytes** not observed.

DISCUSSION. The genus is characterized by the pendent habit, leaves ecostate or with slender single costa, and 1 to few papillae over cell lumen. *Barbella tenuissima* (Hook.f. & Wilson) M. Fleisch. is now placed in *Meteoridium*. The two common species are differentiated as follows: *B. pendula* (Sull.) M. Fleisch. — branches slenderly uniform throughout; *B. trichophora* (Mont.) M. Fleisch. — branches larger initially, becoming filiform distally.

LITERATURE. Streimann, H. 1993. *Barbella trichophora*, an older name for *B. cubensis* (Musci: Meteoriaceae). The Bryologist 96: 223–225.

Floribundaria (Fig. 154) - A single species recorded for the Neotropics, *F. flaccida* (Mitt.) Broth.; a genus of five species with a pantropical distribution, the greatest diversity found in Australasia.

HABITAT. Epiphytic on branches of treelets and trees; lowland forests to lower montane forests, 50–1700 m.

DESCRIPTION. **Plants** small to medium sized, forming loose, soft mats with often long pendent stems and branches (to 15 cm or more), yellowish-green. **Primary stems** creeping. **Secondary stems** often pendent, irregularly pinnately short branched; central strand weak. **Leaves** spreading to wide-spreading from a clasping base, narrowly long lanceolate from an ovate base, to 3 mm long, to 0.7 mm wide, apex long and narrowly acuminate ending in a capillary hair point, base concave and loosely clasping stem, auriculate; margins plane, denticulate by projecting papillae and serrulate to serrate throughout, distally teeth irregularly spaced; costa single, somewhat less than 1/2 to 2/3 lamina length; median cells linear, pluripapillose, papillae appearing over cell lumen and along adjoining walls; basal cells irregularly short to ± long rectangular or oblong, weakly porose; alar region undifferentiated or with a few subquadrate cells. **Dioicous**. **Seta** rather short, to 2.5 mm long, smooth to slightly roughened distally. **Capsule** erect, oblong, to ca. 1 mm long. **Operculum** short rostrate. **Peristome** finely papillose, cross-striate at base; endostome finely papillose, basal membrane low, segments narrow, keeled and perforate, cilia not observed. **Calyptra** and spores not observed.

DISCUSSION. The genus is characterized by the pendent habit, wide-spreading, narrowly ovate-lanceolate leaves, capillary hair tip, auriculate base, pluripapillose laminal cells with papillae over lumen and along adjoining walls, and little differentiated alar region. *Floribundaria* can be mistaken for

Papillaria, possibly *P. deppii* (Müll. Hal.) A. Jaeger which also exhibits a capillary hair point. The leaves of *Papillaria*, however, are typically erect to erect-spreading with a cordate to strongly auriculate base, plicate surface, costa ca. 2/3 lamina length, and with papillae positioned over the cell lumen. Data provided by Zacharia Magombo (pers. com.).

LITERATURE. Magombo, Z. L. K. In press. Revision of the tropical moss genus *Floribundaria* M. Fleisch. (Meteoriaceae).

Lepyrodontopsis (Fig. 154) - A monotypic neotropical genus, with *L. trichophylla* (Hedw.) Broth. found in the West Indies, Trinidad, Venezuela, Guyana, French Guiana, and from the Pacific region of Colombia.

HABITAT. On trunks and exposed roots of trees, and logs, rarely on rocks, in moist, shaded sites; lower montane forests, 450–1390 m.

DESCRIPTION. **Plants** medium sized, forming loose to dense mats, glossy yellow or golden. **Stems** creeping and arching, irregularly pinnately branches, branches ascending or suberect, attenuated flagellate branches often numerous; in cross-section outer 1–2 rows of cells small, thick-walled, inner cells large, thin-walled, central strand absent. **Leaves** of stem small, somewhat distant, branch leaves crowded, erect-spreading dry or wet, narrowly long lanceolate to linear-lanceolate, to 5 mm long, strongly biplicate (appearing as a double costa), apices gradually acuminate, often with a half twist, base subauriculate and decurrent; margins plane, serrate distally, dentate below to base; costa absent; laminal cells above base linear, strongly porose, smooth; basal cells short; alar region somewhat differentiated, few cells short rectangular or quadrate, not porose. **Gemmae** often present, clustered in axils upper leaves, short cylindrical. **Dioicous**. **Perichaetia** leaves differentiated, smaller, ovate-lanceolate, margins sharply serrate, ecostate. **Seta** elongate, to 25 mm long, straight to somewhat flexuose, smooth. **Capsule** erect, obloid from a short distinct neck, to 3 mm long; stomata at urn base, superficial. **Operculum** conic-rostrate. **Peristome** with exostome teeth narrow, papillose; endostome basal membrane low, segments slender, not perforate, papillose, cilia rudimentary or absent. **Calyptra** cucullate, smooth and naked. **Spores** finely papillose.

DISCUSSION. The genus is characterized by the creeping and arching habit, ascending or suberect branches, often numerous flagellate branches, gradually acuminate, biplicate, narrowly long-lanceolate branch leaves, absence of a costa, strongly porose laminal cells, short cylindrical gemmae in leaf axils, elongate seta, erect capsule, narrow, papillose exostome teeth and low basal membrane with slender papillose segments. Asexual reproduction, via propagula in the form of attenuated branches and gemmae, appears to be the common mode of reproduction in *Lepyrodontopsis*; sporophytes are exceedingly rare. Further investigations are needed to establish the phylogenetic relationship of this taxon. It has been placed in its own family, Lepyrodontopsidaceae, or in the Brachytheciaceae by some authors. Placement in the Meteoriaceae was suggested by W. R. Buck.

LITERATURE. Buck, W. R. 1981. The taxonomy of *Eriodon* and notes on other South American genera of Brachytheciaceae with erect capsules. Brittonia 33: 556–563.

Lindigia (Fig. 155) - A monotypic genus, with *Lindigia debilis* (Mitt.) A. Jaeger confined to the tropical Andes.

HABITAT. Epiphytic on branches of shrubs or small trees, montane forests, 1800–3500 m.

DESCRIPTION. **Plants** rather small, forming loose mat. **Primary stems** creeping. **Secondary stems** creeping to subpendent, to 6 cm long, irregular pinnately branched; in cross-section central strand weak. **Leaves** erect-spreading, 1.8–3.2 mm long, long lanceolate, apex narrowly long acuminate, base slightly clasping; margins plane or distally inflexed on one or both sides, serrate, often strongly so distally, base entire; costa single, 1/4–1/3 lamina length; laminal cells smooth, median cells fusiform to oblong or rhomboidal, ± thick-walled; lower and alar region little differentiated, cells subrectangular. **Autoicous**. **Perichaetial** leaves ovate long acuminate. **Seta** elongate, 4–7 mm long, smooth. **Capsule** suberect, cylindrical, 1.4–2 mm long, slightly curved. **Operculum** conic-short rostrate. **Peristome** with exostome teeth separate, papillose; endostome basal membrane low, segments narrow, papillose, cilia absent. **Calyptra** cucullate, smooth and naked. **Spores** papillose.

DISCUSSION. The genus is characterized by the often pendent habit, erect-spreading long-lanceolate leaves, distally serrate leaf margins, short single costa, autoicous sexual condition, and slightly curved, suberect capsules. The more familiar name, *Lindigia aciculata* (Taylor) Hampe = *Aerolindigia capillacea* (Hornsch.) M. Menzel, is now placed in the Brachytheciaceae (see discussion under *Aerolindigia* in that family — cf. Menzel, 1991; Visnadi & Allen, 1991). The name honors Alejandro Lindig about whom little is known except that many of the lichens, hepatics, mosses, and ferns that he collected between 1859–1865 in Colombia were described as new species.

LITERATURE. Menzel, M. 1991. A taxonomic review of the genera *Lindigia* Hampe (Meteoriaceae, Leucodontales) and *Aerolindigia* gen. nov. (Brachytheciaceae, Hypnales), Bryopsida. Nova Hedwigia

52: 319–335. - Visnadi, S. R. & B. Allen. 1991. A revision of the genus *Lindigia* (Musci: Meteoriaceae) in the Neotropics. The Bryologist 94: 5–15.

Meteoridium (Fig. 155) - An endemic neotropical genus with two rather widespread species, *M. remotifolium* (Müll. Hal.) Manuel and *M. tenuissima* (Hook.f. & Wilson) M. A. Lewis.

HABITAT. On trunks and branches of trees and treelets, logs, humus, soil, and rocks; mostly from submontane to high montane forests, rare in lowland forests, and then in areas adjoining mountain ranges, 50–3300 m.

DESCRIPTION. **Plants** small to medium sized, forming soft thin to dense mats or loose pendulous or spreading strands, occasionally forming tufts, glossy light green to yellowish-brown or golden, occasional older portions black. **Primary stems** short to long creeping. **Secondary stems** spreading to subascending or more commonly pendent, regularly to irregularly pinnately branched, branches short to elongate, flagellate branches not uncommon; in cross-section outer 2–4 rows of cells small and thick-walled, inner cells larger, thin-walled, central strand weak or absent; rhizoids when present clustered beneath stems. **Leaves** crowded to more commonly distant, erect spreading to wide-spreading, occasionally suberect, narrowly lanceolate to ovate-short or long lanceolate, 1–2.5 mm long, apex short to long acuminate, occasionally twisted, base weakly decurrent, not clasping stem or auriculate; margins recurved at base, plane above, serrulate to serrate distally; costa single, slender, (1/3–)1/2–2/3 lamina length; laminal cells smooth, median cells linear to linear-vermicular, ± thick-walled; basal cells oblong-linear, porose; alar region weakly differentiated or not, cells few, rectangular, usually porose. **Dioicous**. **Perichaetial** leaves lanceolate- to ovate-subulate. **Seta** rather short, to 3 mm long, stout, smooth, twisted or not. **Capsule** exserted, urn ovoid to ovoid short cylindrical. **Operculum** conic-rostrate, oblique. **Peristome** with exostome teeth cross-striate below, distally papillose, trabeculate on back; endostome basal membrane ± low, segments keeled and perforate, cilia absent. **Calyptra** cucullate, smooth and naked. **Spores** appearing smooth to papillose.

DISCUSSION. *Meteoridium remotifolium* is likely to be confused with *Zelometeorium*; however, in the latter genus the stem leaves are distinctly sheathing or clasping. Some species of *Rhynchostegium* may likewise be confused with *Meteoridium* and they occasionally occur mixed together. *Rhynchostegium* usually exhibits a costa that ends in a dorsal spine, and with leaves that lack the often differentiated, slightly inflated inter basal cells typically of *Meteoridium*. Previously *Meteoridium remotifolium* was placed in *Meteoriopsis*, a genus that, as presently defined, is restricted to Asia. The two neotropical species can be differentiated by the following: *M. remotifolium* — secondary stem leaves ± crowded, ovate-lanceolate, 1.2–2.5 mm long, ± concave; and *M. tenuissima* — secondary stem leaves usually distant, widely spaced, lanceolate to narrowly-lanceolate, ca. 1–1.2 mm long, not concave.

LITERATURE. Lewis, M. 1992 (see family ref.). - Manuel, M. 1977. The genus *Meteoridium* (C. Müll.) Manuel, stat. nov. (Bryopsida: Meteoriaceae). Lindbergia 4: 45–55 [treating only *M. remotifolium*, illustrations, map].

Meteorium (Fig. 155) - Approximately 13 species recorded for the Neotropics, probably only 2–3 worth recognizing; a genus stated to contain some 30 species with a pantropical distribution.

HABITAT. Epiphytic on trunks and branches, also on logs, soil, humus and rocks; submontane to montane forests, occasionally extending into the páramo and puna along shrubby gallery forests, mostly 1000–3775 m.

DESCRIPTION. **Plants** medium sized to somewhat large, forming mats or wefts, occasionally pendent, glossy green, golden yellow, or yellowish-green often with portions of the stems and leaves black. **Primary stems** creeping. **Secondary stems** spreading or pendent, irregularly branched, branches short to elongate, often numerous, attenuate branches often present; central strand present. **Leaves** crowded, loosely erect, broadly ovate-short lanceolate, to 3.5 mm long, concave, plicate or rarely smooth, apex generally abruptly long acuminate, piliferous, often ending in a capillary tip or tips deciduous, rarely apiculate, base auriculate; margins plane, somewhat reflexed below, denticulate-serrulate in part by projecting papillae; costa 1/3–2/3 lamina length; median cells oblong to linear, porose, uni- to mixed with some cells pluripapillose (2–4 papillae), papillae over cell lumen; basal cells smooth, strongly porose; alar region little differentiated, few subrectangular cells present. **Dioicous**. **Perichaetial** leaves narrowly lanceolate to ovate-subulate, to 3 mm long, long acuminate. **Seta** elongate, 4–8 mm long, lightly roughened. **Capsule** exserted, ovoid to oblong-ovoid, 1.1–1.5 mm long. **Operculum** long rostrate, oblique. **Peristome** with exostome teeth papillose; endostome basal membrane low, segments papillose, cilia rudimentary. **Calyptra** cucullate, hairy. **Spores** lightly papillose.

DISCUSSION. The genus is characterized by the often plicate, concave, auriculate, broadly ovate to ovate-lanceolate leaves, single costa, mostly unipapillose laminal cells (occasionally some with 2–4 papillae), and little differentiated alar cells. *Meteorium* is similar to *Papillaria*, indeed the latter can be readily viewed as a weak segregate of the former. They differ primarily by the number of cell papillae, the former commonly with 1, but frequently some cells with 2–3 papillae, and the latter with 2–12. Both genera occur in similar habitats and are frequently found together at a particular site. Fertile plants of *Meteorium illecebrum* Sull (*M. sinuatum* (Müll. Hal.) Mitt. may be an older name for this species), the common neotropical species, are rare. Out of some 50 collections examined at NY from Colombia, only two contained sporophytes. The common mode of reproduction is probably via deciduous attenuate or flagellate branches.

Orthostichella (Fig. 156) - About five species in the Neotropics, probably fewer are valid. The most common species is *O. pentasticha* (Brid.) W. R. Buck; a genus of some 10 or fewer species distributed in the tropics of America and Africa.

HABITAT. Epiphytic, on trunks and branches of trees; moist lowland to upper montane forests, from near sea level to 2000(–3070) m.

DESCRIPTION. **Plants** pale olive to dark green, somewhat small, soft, pale green or yellowish green. **Primary stems** creeping; leaves appressed to erect, lanceolate, to 1 mm long, acuminate. **Secondary stems** usually pendent, freely branching; central strand absent. **Leaves** erect-spreading, ovate to short obovate, (0.5–)1–1.4 mm long, deeply concave, acute to short acuminate, base weakly auriculate; margins plane, serrulate mostly 1/2–1/3 lamina length; costa absent, rarely weakly short and either single or double; laminal cells smooth, median cells linear, ± vermicular; apical cells short; basal cells golden-yellow; alar region weakly differentiated, cells few, subquadrate to short oblong-rectangular, golden-yellow. **Dioicous**. **Perichaetial** leaves sheathing, oblong-acuminate, to 2 mm long. **Seta** rather short, to 4.3 mm long, ± curved, smooth, yellow to pale orange-yellow. **Operculum** conic-rostrate, oblique. **Capsule** exserted, erect, urn ovoid, to 1.2 mm long. **Peristome** with exostome teeth papillose; endostome basal membrane low, segments narrow, papillose, perforate to base. **Calyptra** not observed. **Spores** papillose.

DISCUSSION. The genus is distinguished by the slender stems and branches, and concave, ovate to obovate imbricate leaves that may or may not be slightly auriculate, ecostate or mixed with some leaves costate; when present costa short, forked or single, and few non-excavate subquadrate alar cells. Possibly to be confused in aspect with *Squamidium*, but the presence of a slender elongate costa and excavate, rather numerous alar cells aid in the separation of that genus. Members of this genus have long been placed in *Pilotrichella*. As presented in this treatment, the genus is now separated by the larger plants, auriculate leaf base, often strongly porose laminal cells, and excavate alar cells. The genus *Pseudopilotrichum* W. R. Buck & B. H. Allen (Buck, 1994, see family ref.) is now replaced by *Orthostichella* Müll. Hal. (Buck, 1994).

LITERATURE. Buck, W. R. 1994. The resurrection of *Orthostichella*. The Bryologist 97: 434–435.

Papillaria (Fig. 156) - About 37 species recorded for the Neotropics, probably fewer than 10; a genus, as traditionally defined, is stated to contain some 70 species (probably half would be maintained after a critical revision) with a pantropical distribution.

HABITAT. Epiphytic, on trunks, branches and exposed roots of trees, equally frequent on logs, soil and rocks; submontane to montane forests and adjacent associated lowlands, 20–3500 m.

DESCRIPTION. **Plants** small to mostly medium sized, forming rather coarse mats, often (sub) pendent, olive to dark green or golden-yellow, partly tinged with black. **Stems** creeping to pendent, irregularly to regularly pinnately branched; in cross-section outer 2–3 rows of cells small, thick-walled, inner cells larger, thin-walled, central strand weak. **Stem leaves** ovate, ovate- to triangular-lanceolate or oblong-lanceolate, 1–3 mm long, concave or weakly so, plicate, apex acute to more commonly acuminate, with a short to long capillary tip or not, distinctly auriculate or cordate or not; margins plane or slightly recurved below, usually dentate-serrulate; costa 1/2–3/4 lamina length; median cells oblong-oval to linear, pluripapillose, papillae in 1–2 rows, over cell lumen, sometimes at edge of lumen but not extending between cells, usually 2–6 or more per cell; alar cells little differentiated. **Branch leaves** small, distally often attenuate and flagellate with extremely reduced leaves. **Dioicous**. **Perichaetia** lateral. **Seta** short to rather elongate, to 7 mm long, roughened. **Capsule** emergent or exserted, urn oblong to ovoid. **Operculum** short rostrate. **Peristome** exostome teeth papillose or nearly smooth; endostome papillose. **Calyptra** mitrate hairy or cucullate and naked. **Spores** lightly papillose.

DISCUSSION. The genus is characterized by the creeping or pendent habit, plicate, ovate- to triangular-lanceolate leaves, cordate or auriculate leaf base, rather strong, single costa, pluripapillose laminal cells with papillae mostly 2–6, occasionally more, arranged in 1–2 rows over the center and edge of the cell lumen. See discussion under *Meteorium*, which can be confused with *Papillaria*.

Recently Buck (1994, see family ref.) relegated the majority of *Papillaria* species to *Meteorium* recognizing a new segregate genus, *Loxotis* W. R. Buck, to accommodate a certain suite of species, including in the Neotropics *P. imponderosa* (Taylor) Broth. This new genus departs from the traditional concept of *Papillaria* in the strongly auriculate leaf bases, twisted leaf apex, seriately papillose laminal cells, many-celled axillary hairs, nearly smooth exostome teeth, and naked, cucullate calyptra. It was discovered, however, that the generic name had been previously used, and so the name *Toloxis* (Buck, 1994, see family ref.), was substituted. The correct name for the local species is *T. imponderosa* (Taylor) W. R. Buck. *Cryptopapillaria* (M. Fleisch.) M. Menzel, a further segregate genus established by Menzel (1992), includes the widespread neotropical species *P. penicillata* (Dozy & Molk.) Broth.

LITERATURE. Buck, W. R. 1994. A nomenclatural correction in the Meteoriaceae. The Bryologist 97: 436. - Menzel, M. 1992. The bryophytes of Sabah (North Borneo) with special reference to the BRYOTROP transect of Mount Kinabalu. XVII. Meteoriaceae (Leucodontales, Bryopsida). Willdenowia 22: 171–196.

Pilotrichella (Fig. 156) - Three species in the Neotropics; about four species in the tropics of America and Africa.

HABITAT. Epiphytic, on trunks and branches of trees and shrubs, also on logs, occasionally on leaf litter; submontane to upper montane forests, 700–4000 m.

DESCRIPTION. **Plants** light green to golden brown, mostly large and robust, forming loose mats or pendulous. **Primary stems** short to long creeping; rhizoids clustered beneath, rusty-red; leaves erect to appressed, broadly ovate-oval, ca. 2 mm long, to 1.6 mm wide, obtuse-rounded. **Secondary stems** often pendent or spreading, to 30 cm or more long; in cross-section 4–5 outer cell rows small, thick-walled and reddish-orange, inner cells large, ± thick-walled, pale yellow. **Leaves** imbricate, erect-spreading, stem and branch leaves similar, those of the stem often somewhat smaller, broadly ovate to oblong-ovate, to 3 mm long, deeply concave, acute and often cuspidate with tips mostly reflexed, base strongly auriculate and clasping; margins incurved, usually strongly so distally, entire or serrulate distally; costa none; laminal cells strongly to weakly porose or occasionally walls entire, median cells linear; alar region strongly differentiated, excavate, cells subquadrate to short rectangular, thick-walled, weakly porose, usually dark red or reddish-orange; basal cells golden-yellow. **Dioicous**. **Perichaetial** leaves to ca. 3.5 mm long, sheathing. **Seta** elongate, to 15 mm long, distally roughened, rusty-red. **Capsule** exserted, erect, urn ovoid to ovoid-short cylindrical (broadly ovoid when deoperculate), to 2 mm long. **Operculum** long rostrate. **Peristome** double (not observed). **Calyptra** cucullate, hairy below, hairs ± erect. **Spores** not observed.

DISCUSSION. The genus is distinguished by the large, glossy plants; imbricate, concave, ecostate, acute to cuspidate ovate leaves; strongly auriculate base; weakly to strongly porose laminal cells; and excavate alar region. *Pilotrichella cuspidans* Renauld & Cardot, known only from Cuba and Hispaniola, is readily distinguished from all other species by the long cuspidate leaf tip; *P. quitensis* (Mitt.) A. Jaeger (Ecuador to Bolivia) is similar to *P. flexilis* (widespread in American and African tropical montane regions) but exhibits erect mucro, not reflexed, apices, branch leaves typically shorter, 1.4–1.6 mm long, with apices strongly serrulate, and laminal cells appearing weakly porose or with walls straight. The reports of *Weymouthia mollis* (Hedw.) Broth. from Peru are *Pilotrichella quitensis* (Mitt.) A. Jaeger., fide W. R. Buck.

Buck (1994, see family ref.) has suggested that *Pilotrichella* can be placed with *Squamidium* and *Weymouthia* in the Lembophyllaceae. *Pilotrichella* is subdivided by Buck with *P. flexilis* (Hedw.) Ångstr. maintained as the type species, and includes *P. quitensis* (Mitt.) A. Jaeger, whereas *P. pentasticha* (Brid.) Wijk & Margad. is placed in the genus *Orthostichella* (see discussion under *Orthostichella*).

Squamidium (Fig. 157) - An essentially neotropical genus of seven species, of which *S. brasiliense* (Hornsch.) Broth. is distributed both in South America and southwestern Africa.

HABITAT. Mostly epiphytic on trunks and branches, less often on logs, soil, and rocks; primary to secondary submontane to montane forests, extending into shrubby páramos, rarely found in moist or wet lowlands and then only when adjacent to highlands, from near sea level to more commonly higher, 600–3800 m.

DESCRIPTION. **Plants** medium to somewhat large, forming mats or pendulous strands, glossy green, yellowish-green or golden-brown, portions often tinged black or with blue sheen. **Primary stems** creeping; leaves broadly ovate-piliferous, base short to long decurrent. **Secondary stems** spreading to more often pendent; in cross-section outer 3–5 rows of cells small, thick-walled, inner cells larger, thin-walled, central strand weak; rhizoids clustered beneath prostrate stems, reddish-brown, smooth. **Stem leaves** narrowly to broadly oblong, ovate or ovate-lanceolate, 1–4 mm long,

deeply concave, apex short to long acuminate or piliferous, base weakly auriculate or cordate and decurrent or not; margins plane below, distally usually incurved, smooth or serrulate distally; costa ca. 3/4–4/5 lamina length, weak; apical cells short or long rhomboidal, median cells linear, often flexuose; insertion cells elongate, strongly porose, often golden-yellow or -brown; alar region differentiated, cells somewhat inflated and oval or quadrate, usually porose. **Branch leaves** broadly ovate to elliptical or oblong-cordate, 0.6–4.5 mm long, acute to broadly acute or piliferous. **Filiform stems** present or not, slender, leaves lanceolate or oblanceolate, piliferous, margins entire to distally coarsely toothed, teeth often sharply recurved. **Dioicous**. **Perichaetial** leaves differentiated. **Seta** shorter or somewhat longer than capsule, 0.2–3 mm long, rather stout, smooth. **Capsule** immersed to short exserted, ovoid-cylindrical, 2–2.7 mm long; exothecial cells rectangular, rather thick-walled; stomata at base or urn; annulus in several rows, deciduous. **Operculum** rostrate. **Peristome** with exostome teeth narrow, papillose or smooth below; endostome often shorter than exostome, lightly to densely papillose, basal membrane ± high, segments linear, variously perforate, cilia absent or rudimentary. **Calyptra** mitrate, often hairy. **Spores** lightly papillose.

DISCUSSION. The genus is characterized by the pendent or occasionally spreading or creeping habit, short to long acuminate or piliferous, deeply concave, smooth, ovate to oblong-ovate leaves, distally incurved, smooth to finely serrate margins, slender single costa, smooth linear laminal cells, and well defined alar region. Gametophytically, quite variable with regard to growth forms, resulting in a considerable number of names. The genus was reduced from 27 to seven species in the thorough revision by Allen and Crosby (1986).

LITERATURE. Allen, B. H. & M. R. Crosby. 1986. Revision of the genus *Squamidium* (Musci: Meteoriaceae). Journal of the Hattori Botanical Laboratory 61: 423–476 [keys, illustrations, maps].

Zelometeorium (Fig. 157) - A genus containing five species distributed in the tropics of America and Africa. Members of this genus were placed previously in *Meteoriopsis*.

HABITAT. Epiphytic on trunks and branches of trees and shrubs, occasionally epiphyllous, or less often on leaf litter, soil or rock; lowland to montane forests, from near sea level to 2700 m.

DESCRIPTION. **Plants** medium sized, forming loose mats or more often becoming pendulous, glossy green or yellowish-green. **Primary stems** creeping. **Secondary stems** often pendent, ca. 10–30 cm long or more, regularly to irregularly pinnately branched; in cross-section outer 2–3 rows of cells small, thick-walled, inner cells larger, thin-walled, central strand weak or absent; rhizoids clustered, beneath stems where attached to substrate, smooth or weakly papillose. **Stem leaves** erect to squarrose-recurved, ovate to ovate-lanceolate, 0.8–1.9 mm long, usually somewhat concave, apex acute to long acuminate, base cordate, sheathing or clasping stem; margins plane or recurved, serrulate distally; costa single, 1/2–3/4 lamina length; median cells linear-flexuose, smooth; lower and basal cells elongate, often porose; alar cells differentiated, rectangular-rounded, porose or not. **Branch leaves** erect to squarrose-recurved, broadly to narrowly ovate to elliptical or ovate-lanceolate, 0.5–1.6 mm long, apex broadly acute to long acuminate, base weakly clasping. **Dioicous**. **Perichaetial** leaves subsheathing, ovate to ovate-lanceolate, abruptly long acuminate, ecostate or rarely costate. **Seta** equal to, or less than, capsule length, smooth. **Capsule** shortly emergent, suberect, urn ovoid to obloid, 1.3–2.5 mm long, neck short; exothecial cells rectangular, longitudinal walls thick; stomata at urn base, superficial or occasionally appearing immersed, 2-celled or occasionally appearing 4-celled; annulus in 2–3 rows, deciduous. **Operculum** rostrate. **Peristome** with exostome teeth narrow, smooth below, distally lightly papillose; endostome lightly papillose, basal membrane ± high, segments linear, perforate, cilia appearing absent. **Calyptra** mitrate, sparsely hairy. **Spores** papillose.

DISCUSSION. The genus is characterized by the pendent habit, acute to long acuminate, broadly ovate to ovate-lanceolate secondary stem leaves with sheathing or clasping bases, slender costa, smooth, linear laminal cells, and little differentiated alar cells. See comments under *Meteoridium*, with which it can be confused. *Zelometeorium* was segregated by Manuel (1977) from *Meteoriopsis*.

LITERATURE. Manuel, M. 1977. A monograph of the genus *Zelometeorium* Manual gen. nov. Journal of the Hattori Botanical Laboratory 43: 107–126 [keys, illustrations, maps].

MNIACEAE

Plants somewhat small to medium sized, forming tufts or loose mats. **Stems** commonly erect, occasionally procumbent, few branched by innovations, radiculose to tomentose below; in cross-section central strand well developed. **Leaves** spirally arranged when erect, when procumbent appearing 2-ranked, crispate when dry, obovate to oblong or elliptical, apex acute to obtuse-rounded and mucronate or cuspidate, base narrowly decurrent; margins limbate, distal 2/3 serrate to dentate, teeth single or paired; costa single, subpercurrent to percurrent; lamina unistratose, cells smooth,

upper and median cells hexagonal-rounded to subquadrate, collenchymatous; basal cells rectangular-rounded or oblong; marginal cells linear, forming a border of 2 to several rows. **Synoicous** or autoicous. **Perichaetia** terminal. **Seta** elongate, smooth. **Capsule** exserted, pendent, obloid to obloid-cylindrical, neck short. **Operculum** conic-long rostrate, oblique. **Peristome** double, exostome teeth 16, finely papillose; endostome basal membrane high, segments 16, finely papillose, cilia 3(2–4), nodose. **Calyptra** cucullate, smooth and naked. **Spores** spherical, finely papillose.

DISCUSSION. The Mniaceae contain nine genera and about 70 species, the majority distributed in the north temperate region; in the Neotropics two genera and four species.

LITERATURE. Koponen, T. 1979. A synopsis of Mniaceae (Bryophyta, Musci.) I. South and Central American taxa. Journal of the Hattori Botanical Laboratory 46: 155–161. - Koponen, T. 1981. A synopsis of Mniaceae (Bryophyta). VII. List of species and their distribution. Annales Botanici Fennici 18: 113–115.

1. Leaf margins doubly toothed (teeth in pairs) ..... **Mnium**
1. Leaf margins singly toothed ..... **Plagiomnium**

Mnium (Fig. 157) - A single species in the northern Neotropics, *M. marginatum* (With.) Brid. *ex* P. Beauv. known from Mexico and Guatemala (widespread in Northern Hemisphere); a genus of 13 species primarily of the Northern Hemisphere.

HABITAT. On soil, in shaded sites; montane forests.

DESCRIPTION. **Plants** somewhat small to medium sized, forming loose tufts, green or brownish-green. **Stems** erect, to ca. 3 cm tall, dark red, few branched, radiculose below; in cross-section 5-angled, outer row of cells small, thick-walled, inner cells progressively larger, thin-walled, central strand well developed; rhizoids papillose. **Leaves** crisped or contorted when dry, erect-spreading when wet, oblong-ellipsoid, to 2.5–4 mm long, apex acute to acute-cuspidate, base narrowly decurrent; margins plane, distal 2/3 serrate, doubly toothed, teeth rather blunt; costa subpercurrent to percurrent, strong; laminal cells mostly uniform, subquadrate- to short rectangular-rounded, collenchymatous; basal most cells short rectangular-rounded; marginal border multistratose, cells linear. **Autoicous** (paroicous), rarely synoicous. **Seta** to 25 mm long. **Capsule** obloid-cylindrical to obloid, 3–4 mm long; stomata in neck, immersed**. Peristome** with exostome finely papillose, trabeculate; endostome finely papillose, cilia 3, occasionally 2 or 4, nodose.

DISCUSSION. The paired teeth along the margin readily separate this genus from *Plagiomnium* which exhibits a margin with unpaired teeth. *Mnium*, as well as the following genus, may possibly be confused with some Bryaceae, particularly *Bryum*; however, the collenchymatous, rounded, oblong-hexagonal cells that are arranged in longitudinal or oblique rows should assist in recognition.

Plagiomnium (Fig. 158) - Three species in the Neotropics, *P. cuspidatum* (Hedw.) T. J. Kop. (Mexico and Cuba), *P. medium* (Bruch, Schimp. & W. Gümbel.) T. J. Kop. (Mexico), and *P. rhynchophorum* (Hook.) T. J. Kop. (widespread in neotropical highlands); a genus of about 25 species distributed worldwide in moist cool temperate regions.

HABITAT. On soil, humus and decaying logs, less often on rock or epiphytic at base of trees, in full to partial shaded in moist sites; submontane to upper montane forests, 900–3200 m.

DESCRIPTION. **Plants** medium sized, forming tufts or mats, pale to dark green. **Stems** commonly erect, occasionally procumbent and leaves ± complanate, appearing 2-ranked, thinly to densely tomentose; central strand well developed; rhizoids papillose, rusty-red. **Leaves** crispate when dry, oblong to long-obovate or elliptical, to 8 mm long, apex obtuse-rounded and mucronate; margins plane to more commonly undulate, dentate to serrate, teeth single, blunt to rather sharp; costa percurrent; median cells rectangular- to hexagonal-rounded, obliquely arranged, juxtacostal cells enlarged; basal cells large and lax; marginal cells forming a border of 4–5 rows of oblong-linear cells, thick-walled, weakly porose. **Synoicous**. **Seta** 1–3, to 30 mm or more long, slender, pale yellow to reddish-orange. **Capsule** inclined to pendulous, cylindrical, to 3.5 mm long. **Peristome** with exostome finely papillose, coarsely so distally, reddish-orange; endostome papillose, cilia 2–3.

DISCUSSION. See discussion under *Mnium*.

MYRINIACEAE

Plants small, forming mats. **Stems** spreading, irregularly few to numerously branched; in cross-section central strand weak or absent; pseudoparaphyllia foliose. **Leaves** erect-spreading when wet, ovate to ovate-lanceolate or lanceolate, apex acute to acuminate, base short decurrent or not; margins plane, serrulate or serrulate-dentate above base; costa absent or single, 1/3–3/4 lamina length;

laminal cells smooth or papillose on back at upper cell angle, median cells rhomboidal to oblong-rhomboidal; alar cells few to rather numerous, subquadrate to short rectangular and oblate. **Perigonia** lateral, bud-like, leaves ovate. **Perichaetia** lateral; leaves narrowly lanceolate, costate or ecostate. **Seta** elongate to somewhat short, smooth to roughened. **Capsule** exserted, erect to suberect, short cylindrical to ovoid; exothecial cells quadrate to short rectangular; annulus mostly absent. **Operculum** rostrate. **Peristome** absent or present and double or single, when double exostome teeth 16, cross-striate below, papillose distally, endostome membrane low, segments 16, cilia absent or rudimentary; when single represented by endostome segments smooth or weakly papillose with basal membrane absent. **Calyptra** cucullate. **Spores** spherical, finely papillose.

DISCUSSION. The Myriniaceae contains about seven genera and some 30 species mostly of the tropics, extending somewhat into the temperate regions; in the Neotropics four genera and eight species. The family was emended and expanded by Buck and Crum (1978) with further refinements provided by Buck (1980).

LITERATURE. Buck, W. R. 1980. A re-interpretation of the Fabroniaceae: Additions and corrections. Journal of the Hattori Botanical Laboratory 47: 45–55. - Buck, W. R. & H. Crum. 1978. A re-interpretation of the Fabroniaceae with notes on selected genera. Journal of the Hattori Botanical Laboratory 44: 347–369.

1. Laminal cells papillose on back at upper angles; costa absent or faintly forked ..... **Schwetschkeopsis**
1. Laminal cells smooth; costa present, single 2
2. Leaf costa mostly 2/3–3/4 lamina length; peristome double ..... **Helicodontium**
2. Leaf costa ending below midleaf; peristome single or absent 3
3. Leaves narrowly lanceolate, ca. 0.6–0.8 mm long; costa projecting papillose on back; peristome absent ..... **Nematocladia**
3. Leaves ovate-short lanceolate, ca. 0.4 mm long; costa smooth on back; peristome single (endostomial) ..... **Austinia**

Austinia (Fig. 158) - A monotypic genus, with *A. tenuinervis* (Mitt.) Müll. Hal. locally widespread but apparently not common in the Neotropics (Mexico, Cuba, Peru, and Brazil), also Southeast Asia.

HABITAT. On tree trunks, occasionally on rocks or logs.

DESCRIPTION. **Plants** forming mats, glossy green. **Stems** creeping, several branched; in cross-section cells similar, rather thick-walled, central strand absent. **Leaves** erect to erect-spreading, ovate-short lanceolate, to 0.4 mm long, apex mostly short acuminate, base short decurrent; margins plane, serrulate-dentate above base; costa short, ca. 1/3 lamina length; laminal cells smooth, upper and median cells rhombic to oblong-rhomboidal; alar cells in 2–3 rows extending to below widest part of leaf, subquadrate; marginal cells mostly narrower and smaller. **Perichaetial** leaves narrowly lanceolate, costa present or absent. **Seta** to 5 mm long, smooth. **Capsule** erect to suberect, urn short-cylindrical, 0.75–0.85 mm long. **Operculum** long rostrate. **Peristome** single, endostome basal membrane absent, segments 16, variously perforate, faintly papillose, appearing smooth. **Calyptra** smooth or slightly roughened distally, naked or with a few hairs.

DISCUSSION. *Austinia* is distinguished by the short acuminate, ovate, short-lanceolate leaves with a slightly decurrent base, serrulate-dentate margins above base, short, single costa, smooth, short seta, erect capsules, and single peristome represented by smooth to weakly papillose segments. A detail discussion and revision of *Austinia* has been provided by Buck and Crum (1978). The genus is named for the United States bryologist, Coe Finch Austin (1831–1880).

LITERATURE. Buck, W. R. & H. Crum. 1978 (see family ref.).

Helicodontium (Fig. 158) - Possibly 4–5 species in the Neotropics; about 20 species distributed in the tropics of America and Africa.

HABITAT. On tree trunks, lianas, logs and rocks; mostly in semi-dry lowland to lower montane forests, 160–2400 m.

DESCRIPTION. **Plants** slender, forming thin mats or loose strands, dull light to dark green. **Stems** creeping or spreading, irregularly branched; central strand weak. **Leaves** erect to appressed when dry, ovate to ovate-lanceolate, 0.5–0.9 mm long, to 0.4 mm wide, weakly concave, often weakly plicate on one or both sides at base, apex acute, often bluntly so, or long acuminate; margins weakly serrulate in distal 2/3; costa (1/4–)1/2–2/3(–3/4) lamina length, ending in a distinct spine or not; median cells oval-rhomboidal, ± thick-walled; alar cells quadrate to short rectangular and oblate. **Perichaetial** leaves ovate-lanceolate, long acuminate, distal margins serrulate. **Seta** 5–7 mm long, yellowish-red, commonly roughened or scabrous, smooth below urn. **Capsule** erect, urn short ovoid to obloid, to ca. 1 mm long; exothecial cells irregularly short rectangular, ± thick-walled. **Operculum**

conic-rostrate, oblique. **Peristome** double, exostome teeth densely cross-striate below, distally papillose, hyaline and bordered, trabeculate on back; endostome basal membrane low, segments keeled, broadly perforate, sparsely papillose, cilia absent or rudimentary. **Calyptra** smooth and naked.

DISCUSSION. The genus is characterized by often weakly plicate, ovate to ovate-lanceolate leaves; plane, finely serrulate leaf margins; costa mostly 2/3–3/4 lamina length, ending in a short dorsal spine; roughened seta; erect, ovoid to obloid capsule; and double peristome with a low basal membrane and rudimentary or absent cilia. The most common and widespread species in the Neotropics appears to be *Helicodontium capillare* (Hedw.) A. Jaeger; Buck (1980) provides keys to the Central and northern South American species.

LITERATURE. Buck, W. R. 1980 (see family ref.).

Nematocladia - A monotypic genus, with *N. tesserata* W. R. Buck a peripheral member of the Neotropics, a narrow endemic only known from east central Mexico (San Luis Potosí and Tamaulipas).

HABITAT. On branches of *Quercus*; oak forests, ca. 600–1200 m.

DESCRIPTION. **Plants** small and slender, forming lax mats, glossy golden. **Stems** delicate and fragile, irregularly pinnately branched; in cross-section out layer rather thick-walled, inner cells in 2–4 rows, thin-walled, central strand weak; pseudoparaphyllia foliose. **Leaves** narrowly lanceolate, ca. 0.6–0.8 mm long, long acuminate; margins plane, serrulate above base; costa single, ending below midleaf, on back distally cells projecting, appearing somewhat spinose especially at costa tip; laminal cells smooth, median and upper cells oblong-rhomboidal, firm-walled; alar region well defined by quadrate cells, cells not extending to costa or so only extending up it by 3–5 cells, along margin to 18 rows of cells; branch leaves somewhat appressed and subjulaceous when dry, to 0.5 mm long; costa to midleaf or just beyond, alar cells reaching costa, extending up it by 1–3 cells, along margin extending up it by 10–13 rows. **Autoicous**. **Perichaetial** leaves triangular, margins serrulate to serrate distally; costa none. **Seta** rather short, ca. 3–4 mm long, smooth or appearing slightly roughened at mid length. **Capsule** erect, urn short cylindrical, ca. 1 mm long; exothecial cells long-rectangular, thin-walled, straight-walled; annulus absent; stomata few at extreme base of urn. **Operculum** conic obliquely short rostrate. **Peristome** none. **Calyptra** cucullate, naked.

DISCUSSION. In addition to the restricted distribution, *Nematocladia* is characterized by its narrow lanceolate leaves, papillose-roughened costa, long rectangular exothecial cells of capsule and lack of a peristome. *Fabronia* (Fabroniaceae) may be confused with *Nematocladia*, but the former genus exhibits leaf margins that are either entire or dentate, and a costa that general extends beyond midleaf.

LITERATURE. Buck, W. R. 1982. *Nematocladia tesserata* genus et species novae (Myriniaceae). Brittonia 34: 414–416 [illustration].

Schwetschkeopsis - A single representative in the Neotropics, *S. fabronia* (Schwägr.) Broth., only known from Cuba, elsewhere known from eastern North America, temperate Asia including Japan. A genus of four species primarily from temperate America and Asia.

HABITAT. On trunk of trees; submontane forests, 700–1000 m.

DESCRIPTION. **Plants** small and slender, forming soft dense mats, yellowish green to green. **Stems** creeping, terete foliate, irregularly pinnately branched, weak to distinctly complanate, flagellate tips occasionally present; in cross-section outer 2–3 rows of cells small, thick-walled, inner cells large, thin-walled, central strand absent; rhizoids clustered beneath. **Leaves** imbricate to erect when dry, somewhat erect-spreading when wet, ovate-short acuminate; to 0.7 mm long, margins plane, serrulate throughout; costa none or faint, very short, appearing forked or notched; laminal cells rather thick-walled, upper cells oblong-rhomboidal, papillose, papillae projecting at upper cell angle on back; basal marginal cells subquadrate in several rows. **Phyllodioicous** (dwarf males on stem leaves). **Seta** elongate, to ca. 7 mm long, smooth. **Capsule** erect to suberect, urn obloid-cylindrical, ca. 1 mm long, stomata and annulus absent. **Opercula** obliquely conic-rostrate. **Peristome** inserted near mouth, exostome teeth finely cross-striate below, appearing smooth or papillose above; endostomial basal membrane rather low, segments keeled and perforate, cilia rudimentary. **Calyptra** cucullate, smooth and naked. **Spores** finely papillose.

DISCUSSION. The genus is readily distinguished by the complanate foliate branches, absence of a costa or only faintly forked, and laminal cells papillose-projecting at upper angles on the back of the leaf. An illustration of this species can be found in Buck (1998, Plate 108, Fig. 8–13; see general ref.).

NECKERACEAE

Plants medium sized to rather large, forming tufts or mats, light to dark green, yellowish-green to golden-brown. **Primary stems** short to long creeping, leaves scale-like or eroded. **Secondary stems** ascending to pendent, irregularly to regularly pinnately branched, radiculose along primary stems; paraphyllia present or absent; pseudoparaphyllia foliose. **Leaves** mostly crowded, usually complanate, ovate- to oblong-lanceolate, oblong-lingulate, or cultriform, smooth or more commonly undulate, usually strongly asymmetric, apex obtuse to acute, truncate or acuminate, base often short decurrent on one side; margins plane to more commonly folded at base (usually along one side), entire below, distally entire or dentate, serrulate to serrate; costa single and 3/4–4/5 lamina length or short to somewhat long forked, occasionally absent; laminal cells smooth, linear and often vermicular, or rhomboidal to short hexagonal, walls firm, or porose. **Autoicous** or dioicous. **Perichaetia** lateral, leaves usually sheathing, strongly differentiated, with or without linear leaf-like ramenta on vaginula. **Seta** short to somewhat elongate, smooth. **Capsule** immersed or short exserted, rarely long exserted, erect, rarely horizontal or pendulous (*Isodrepanium*), urn ovoid to short cylindrical; annulus not differentiated. **Operculum** short to long rostrate, occasionally oblique. **Peristome** double, exostome teeth 16, papillose, rarely smooth or cross-striate below, distally papillose; endostome basal membrane low, segments 16, narrow, usually slightly perforate, cilia lacking. **Calyptra** cucullate or mitrate (-campanulate), smooth and naked. **Spores** spherical, usually papillose.

DISCUSSION. The Neckeraceae contain some 10 genera and possibly more than 150 species; in the Neotropics three genera and 14 species. *Porotrichum* (*Porothamnium*), *Thamnobryum* and related genera, traditionally placed in the Neckeraceae, are now placed in the Thamnobryaceae following Sastre-De Jesús (1987); see Enroth (1994) for an alternative view. The following taxonomic concepts are largely adapted from Sastre-De Jesús (1987) with the exception that *Isodrepanium* which is treated here in the Neckeraceae. Florschütz-de Waard (1986) has presented a persuasive argument for the inclusion of *Isodrepanium* in the Neckeraceae rather than as previous treatments which have placed this genus in the Hookeriaceae *s. l*.

Study guide. Most species can be identified by leaves alone, however stems should be examined for the presence of paraphyllia, and sporophytes are important in separating some species of *Neckera*.

LITERATURE. Enroth, J. 1994. On the evolution and circumscription of the Neckeraceae (Musci). Journal of the Hattori Botanical Laboratory 76: 13–20. - Florschütz-de Waard, J. 1986. (see general ref.). - Sastre-De Jesús, I. 1987. A revision of the Neckeraceae Schimp. and Thamnobryaceae Marg. & Dur. in the Neotropics. Ph. D. dissertation, City University of New York [keys, illustrations, maps].

1. Leaves cultriform, distal half strongly falcate; laminal cells often strongly porose ..... **Isodrepanium**
1. Leaves not cultriform, but asymmetric and slightly arching; laminal cells not porose, or only weakly so 2
2. Leaves broadly ovate-lanceolate, apex acute to acuminate; costae short and forked .. **Neckera**
2. Leaves broadly ligulate to oblong, apex truncate; costa single, ca. 3/4 lamina length ..... **Neckeropsis**

Isodrepanium (Fig. 159) - A monotypic genus, with *I. lentulum* (Wilson) E. Britton confined to the Neotropics, locally widespread.

HABITAT. Epiphytic, on branches and trunks of trees; submontane to montane forests, 500–2800 m.

DESCRIPTION. **Plants** medium sized, forming loose mats, glossy light to dark green or golden-green or -red. **Secondary stems** rather irregularly branched, often pendent; flagellate branches frequent; in cross-section outer 4–5 rows of cells small, thick-walled, inner cells larger, ± thin-walled, central strand absent; pseudoparaphyllia foliose, irregularly toothed, cells porose. **Leaves** strongly complanate, asymmetric, lateral more strongly so, wide-spreading to falcate, oblong-lanceolate, 2–3.2 mm long, to 1.2 mm wide, weakly to strongly cultriform (distal half nearly parallel to stem, arching backward), apex acute to short acuminate, based folded; margins plane, serrulate to serrate; costa absent or weakly short and forked or single; laminal cells smooth and porose, apical cells short; median cells linear, vermicular; insertion cells golden brown, strongly porose. **Flagellate branch leaves** 1 mm or less long, weakly asymmetric. **Dioicous**. **Perichaetial** leaves sheathing seta, oblong-lanceolate, ligulate-subulate. **Seta** elongate, to 4 cm long, smooth. **Capsule** horizontal to subpendulous, urn ovoid, ca. 2 mm long. **Operculum** conic-rostrate. **Peristome** with exostome teeth cross-striate, papillose distally, endostome papillose, basal membrane high, segments keeled and perforate, cilia rudimentary. **Calyptra** not observed. **Spores** smooth.

DISCUSSION. The genus is distinguished by the strongly complanate, distally falcate, cultriform leaves; costa absent or present and short and forked or single; and laminal cells smooth and porose. This genus may be confused with some members of *Lepidopilum* exhibiting sigmoid leaves, but that genus lacks the strongly porose median and upper cells found in *Isodrepanium*. Sporophytes of

Isodrepanium are rare and reproduction is probably facilitated by flagellate branches. Some authors place this genus in the Hookeriaceae *s. l.* (or as treated here in the Pilotrichaceae).

Neckera (Fig. 159) - About 10 species in the Neotropics; a pantropical genus of some 700 species, extending into the temperate regions.

HABITAT. Epiphytic on trunks and branches, occasionally on humus, logs or rocks; submontane, becoming more common in montane forests and extending into zacatonal, páramo, and puna in forested valleys, 1100–4500 m.

DESCRIPTION. **Plants** medium to somewhat robust, forming mats or wefts, glossy olive-green to golden-yellow. **Primary stems** creeping, leaves scale-like. **Secondary stems** spreading to more commonly ascending, often ± perpendicular to substrate or pendent, irregularly to regularly pinnately branched; paraphyllia few to abundant or appearing absent; pseudoparaphyllia filamentous to foliose. **Leaves** weakly to strongly complanate, suberect to spreading, undulate or occasionally flat, broadly ovate-lanceolate to oblong-ligulate, 2–5.5 mm long, asymmetric, apex obtuse to abruptly acute or short acuminate, base somewhat auriculate on proximal side; margins folded on proximal side at base, serrulate distally, rarely smooth; costae double, usually unequal, one costa much longer, to 1/5–1/3 lamina length; laminal cells smooth, porose or not, apical cells rhombic to fusiform; median cells linear, ± vermicular, smooth, insertion cells irregularly rectangular, porose; alar region weakly differentiated, cells subquadrate to short rectangular. **Autoicous**. **Perichaetial** leaves broadly lanceolate to oblanceolate, long acuminate to subulate. **Seta** short or somewhat elongate, 0.5–4 mm long, erect or slightly curved. **Capsule** immersed or shortly exserted, erect, urn short-cylindrical or ovoid to subglobose, 1–3.5 mm long; exothecial cells quadrate to rectangular, thick-walled; stomata at urn base, superficial. **Operculum** short to long rostrate, often oblique. **Peristome** with exostome teeth narrowly lanceolate, finely cross-striate at base, and occasionally just above vertically striate or smooth, distally papillose; exostome basal membrane low, segments linear, keeled and perforate, papillose. **Calyptra** cucullate or mitrate, smooth. **Spores** rather coarsely papillose.

DISCUSSION. The genus is characterized by the often undulate, broadly ovate- to ligulate-lanceolate leaves, acute to acuminate apex, short and forked costa, and immersed to shortly exserted capsules. The generic concept adapted here includes *Neckeradelphus*, segregated from *Neckera* mainly by the more abundant paraphyllia.

Neckeropsis (Fig. 159) - Three species in the Neotropics, two widespread species, *N. disticha* (Hedw.) Kindb. and *N. undulata* (Hedw.) Reichardt, the third *N. foveolata* (Mitt.) Broth. is rare (Costa Rica, Panama, Guyana, and SE Brazil); a genus of about 30 species with a pantropical distribution.

HABITAT. Epiphytic, on branches and trunks, rarely found on logs or rocks; moist or wet lowland to lower montane forests; from sea level to 2100 m.

DESCRIPTION. **Plants** rather small to medium sized, forming loose tufts, occasionally mats, light to dark green, occasionally golden-brown to blackish. **Primary stems** creeping, leaves scale-like, ovate-acuminate, base partially clasping; rhizoids clustered beneath. **Secondary stems** ascending, usually perpendicular to substrate, irregularly to regularly pinnately branched, occasionally distally flagellate; in cross-section outer 2–4 rows of cells small, thick-walled, inner cells larger, thin- to ± thick-walled, central strand absent; pseudoparaphyllia foliose. **Leaves** complanate, smooth to undulate, broadly lingulate, 1–2.5 mm long, asymmetric, apex truncate, base decurrent or not on one side; margins crenulate to weakly serrulate throughout or subentire near base; costa single, 3/4–4/5 lamina length; median cells irregularly rhomboidal or hexagonal, smooth. **Synoicous** or autoicous. **Perichaetial** leaves ovate- to oblong-subulate; ramenta, leaf-like paraphyses positioned along the vaginula, when present narrowly oblong- to linear-ligulate, ca. 2–3 mm long, often as long or longer than sporophyte. **Seta** short, 0.5–0.7 mm long, smooth. **Capsule** immersed to emergent, erect, short-cylindrical to oblong, 1–1.5 mm long; exothecial cells short rectangular to subquadrate, ± thick-walled; stomata absent; annulus absent. **Operculum** conic-long rostrate. **Peristome** with exostome teeth linear-lanceolate, papillose; endostome basal membrane low, segments linear, papillose, cilia absent. **Calyptra** mitrate-campanulate, smooth. **Spores** papillose.

DISCUSSION. The genus is distinguished by the strongly complanate, broadly lingulate, truncate leaves, single costa (3/4 lamina length), when present linear-ligulate ramental leaves, and immersed capsules. The two common species of *Neckeriopsis*, *N. undulata* and *N. disticha*, occur in the moist or wet lowland forests where both species can grow in proximity to each other; however, only *N. undulata* extends into the lower montane forests. Our species can be differentiated by the following:

a. Leaves smooth when dry, 1–1.4 mm long, to 0.7 mm wide	*N. disticha*
a. Leaves undulate when dry, 1.5–2.2 mm long, to 1 mm wide	b
b. Ramenta present, perichaetial leaves ca. 1 mm long.....	*N. undulata*
b. Ramenta absent, perichaetial leaves 3–4 mm long.....	*N. foveolata*

ORTHOTRICHACEAE

Plants small to large and robust, forming tufts. **Primary stems** erect, few to several branched; radiculose, occasionally tomentose; central strand usually absent; pseudoparaphyllia and paraphyllia absent. **Leaves** often crispate or flexuose when dry, linear- to oblong-lanceolate or oblong-lingulate, smooth to occasionally rugose or undulate, plicate or smooth, apex acute to acuminate, rarely obtuse, base occasionally decurrent; margins plane to reflexed or recurved, entire to serrulate or serrate, elimbate; costa single, usually strong, ending well below apex to long excurrent; laminal cells thick-walled, upper and median cells isodiametric to elongate, smooth, mammillose or papillose; basal cells usually elongate; alar cells rarely differentiated. **Autoicous** or dioicous. **Perichaetia** terminal on stems, leaves often differentiated. **Seta** short elongate, smooth, often twisted. **Capsule** immersed, emergent or exserted, mostly erect, urn ovoid or ovoid-cylindrical, ± symmetric, smooth or more often ribbed or furrowed, neck usually distinct; exothecial cells usually thick-walled; stomata superficial or immersed; annulus often persistent. **Operculum** short to long rostrate, less often mammillate. **Peristome** double, single or variously reduced to absent, exostome teeth 16 or in 8 pairs, smooth to more often papillose; endostome often reduced, smooth or papillose. **Calyptra** cucullate or mitrate to campanulate with base usually lobed, plicate or smooth, naked or hairy. **Spores** spherical, usually papillose.

DISCUSSION. In the Neotropics the Orthotrichaceae are represented by three genera and about 62 species. Traditionally, the Orthotrichaceae contained two major subgroupings, currently treated as families, the Orthotrichaceae and the Macromitriaceae. These were brought together under the single family, the Orthotrichaceae, by shared primitive characters (cf. De Luna, 1995). Presently, it is considered that the two families, while likely sharing a remote common ancestor, should be treated as separate evolutionary lines. In this sense, the Orthotrichaceae in the Neotropics is represented by *Orthotrichum* and *Zygodon*. The constituent genera of the Macromitriaceae (*Groutiella*, *Macrocoma*, *Macromitrium* and *Schlotheimia*) are discussed under that family.

Study guide. Many species can be identified by leaves alone, however sporophytic features (e.g., stomata type, immersed or superficial; and peristome type and ornamentation) are essential in *Orthotrichum* and *Zygodon*. A cross-section, just above midleaf, is useful for examining the ornamentation of laminal cells.

LITERATURE. De Luna, E. 1995. The circumscription and phylogenetic relationships of the Hedwigiaceae. Systematic Botany 20: 347–373. - Goffinet, B., R. J. Bayer & D. H. Vitt. 1998. Circumscription and phylogeny of the Orthotrichales (Bryopsida) inferred from *rbc*-L sequence analyses. American Journal of Botany 85: 1324–1337. - Grout, A. J. 1946. Bryales. Orthotrichaceae. North American Flora 15A(1): 1–62, plates 1–5 [keys]. - Vitt, D. H. 1979. New taxa and new combinations in the Orthotrichaceae of Mexico. The Bryologist 82: 1–19. - Vitt, D. H. 1982a. The genera of Orthotrichaceae. *In* P. Geissler & S. W. Greene (eds.), Bryophyte Taxonomy. Beihefte zur Nova Hedwigia 71: 261–268. - Vitt, D. H. 1982b. On neotropical Orthotrichaceae. *In* P. Geissler & S. W. Greene (eds.), Bryophyte Taxonomy. Beihefte zur Nova Hedwigia 71: 531–535.

1. Leaves distinctly crispate when dry 2
1. Leaves not crispate, often ± contorted or twisted when dry 4
2. Stomata immersed; basal marginal leaf-cells scarcely differentiated ..... **Orthotrichum** p.p.
2. Stomata superficial; basal marginal leaf-cells mostly either wider or narrower than adjoining cells 3
3. Papillae over cell lumen and walls of lamina; stems papillose; capsule emergent to slightly exserted ..... **Amphidium**
3. Papillae over cell lumen of lamina; stems smooth; capsule generally long exserted ..... **Zygodon** p.p.
4. Calyptra mitrate, conic-campanulate, often plicate or hairy or both ..... **Orthotrichum** p.p.
4. Calyptra cucullate, not plicate nor hairy ..... **Zygodon** p.p.

Amphidium (Fig. 160) - A single species in the Neotropics, *A. tortuosum* (Hornsch.) Cufod., found throughout the neotropical cordilleras and widespread in the Southern Hemisphere. A genus of about 10 or more species distributed in the temperate and tropical mountain regions.

HABITAT. On soil and in rock crevices; upper open montane to zacatonal, páramo, and puna, 2000–4550 m.

DESCRIPTION. **Plants** small, forming short tufts or cushions, olive to rather dark green. **Stems** erect, to 3–3.5 mm tall, few branched, sparingly radiculose below; in cross-section epidermal cells finely pluripapillose on outer surface, rather thick-walled, inner cells larger, firm-walled, central strand present. **Leaves** appressed below, distally spreading and crispate when dry, linear-lanceolate from an

oblong base, 2.5–3.5 mm long, to 0.3 mm wide, concave below, distally keeled, apex usually sharply acuminate, base weakly decurrent; margins mostly plane above, often recurved below, bluntly serrate or dentate in distal 1/2, occasionally extending to near base; costa single, not strong, sub- to percurrent; lamina unistratose, cells finely pluripapillose, papillae extending across cells and walls, median cells isodiametric, mostly subquadrate-rounded to quadrate, firm-walled; lower and basal cells elongate, mostly long-rectangular, faintly papillose, lax; alar cells undifferentiated. **Asexual** structures apparently absent. **Autoicous**. **Perichaetia** terminal; leaves not or little differentiated. **Seta** short, ca. 1 mm long, often curved, usually twisted distally. **Capsule** emergent to slightly exserted, urn pyriform, 0.5–0.6 mm long, ribbed, mouth flared when deoperculate; exothecial cells elongate and ± thick-walled, irregularly rectangular, some longitudinal rows broadly sinuate; annulus absent. **Operculum** mammillate to rostellate. **Peristome** absent. **Calyptra** cucullate, ca. 0.7 mm long, naked or slightly roughened at apex. **Spores** appearing ornamented.

DISCUSSION. The genus is characterized by small plants, long linear-lanceolate leaves, crispate when dry, bluntly serrate distal margins, subpercurrent to percurrent costa, finely pluripapillose stems and leaves, curved short seta, eperistomate, ribbed capsules. The papillose stems are possibly unique among mosses (also in *Heterocladium*), certainly so in the family. *Amphidium cyathicarpum* (Mont.) Broth. is apparently a synonym.

LITERATURE. Lewinsky, J. 1976. On the systematic position of *Amphidium* Schimp. Lindbergia 3: 227–231.

Orthotrichum (Fig. 160) - Twenty-four species in the Neotropics; a genus containing 116 species widely distributed but absent from deserts, grasslands, and lowland tropics.

HABITAT. Epiphytic on branches and trunks, occasionally on rocks; mostly montane forests to zacatonal, páramo, and puna, at high latitude in the Neotropics near sea level, at lower latitudes mostly 2000–5000 m.

DESCRIPTION. **Plants** mostly medium sized, forming loose to dense tufts, olive- or yellowish-green, brown below. **Stems** erect, few branched, radiculose below; in cross-section outer 2–3 rows of cells small, thick-walled, inner cells large, thin-walled, central strand absent. **Leaves** appressed to erect, contorted or twisted to crispate when dry when dry, erect-spreading to spreading when wet, narrowly lanceolate to oblong- or ovate-lanceolate, 0.8–5.5 mm long, often keeled distally, acuminate to acute or rounded, rarely apiculate, base undifferentiated or short decurrent; margins plane to more often recurved, occasionally undulate or flexuose, generally entire or denticulate at apex; costa single, usually strong, ending below apex, rarely excurrent; laminal cells mostly thick-walled, apical cells oval to elongate; median cells isodiametric to oblong, entire to nodose, unipapillose, papillae simple or 2–3 branched; basal cells short to long rectangular, smooth, thin- to thick-walled, entire, nodose or porose; alar cells occasionally differentiated, subquadrate-rounded. **Gemmae** occasionally present on leaves, short cylindrical. **Autoicous** (gonioautoicous). **Perichaetia** terminal; leaves differentiated or not. **Seta** short to elongate, 0.3–9 mm long, smooth, often twisted distally. **Capsule** immersed to somewhat long exserted, erect, urn oblong-ovoid cylindrical, 1.3–2.5 mm long, when dry and deoperculate often ribbed (usually 8), occasionally twisted, constricted below mouth; stomata on lower half of urn, immersed (cryptopore) or superficial. **Operculum** plano-convex, apiculate. **Peristome** double (rarely reduced and single), erect or reflexed when dry, exostome teeth 8 pairs, often splitting into 16, papillose, rarely smooth; endostome often reduced, segments mostly narrow to filiform 8 or 16, smooth, papillose or striate. **Calyptra** mitrate-campanulate, mostly plicate, rarely smooth, sparsely to rather densely hairy, or surface roughened. **Spores** papillose, often coarsely so.

DISCUSSION. The genus is characterized by the broadly to narrowly acuminate to acute, generally lanceolate to oblong-lanceolate leaves, plane to often recurved, mostly entire margins, papillose laminal cells, 1–4 papillae over cell lumen, or infrequently smooth, capsules often ribbed, immersed to shortly exserted, immersed to superficial stomata, often reflexed, mostly papillose, 8 to 16 exostome teeth, and smooth to ornamented, often plicate mitrate-campanulate calyptra.

One rather distinctive gametophytic feature, although by no means consistent in separating *Orthotrichum* from most members of this family, are the frequent presence of bipapillose conic laminal cells. Sporophytes are often essential for the identification of *Orthotrichum* species. The genus has been thoroughly treated for South America by Lewinsky (1984, 1987) and by Vitt for Mexico (1994, in Sharp et al., general ref.); a excellent world summary is given by Lewinsky (1993).

LITERATURE. Lewinsky, J. 1984. *Orthotrichum* Hedw. in South America 1. Introduction and taxonomic revision of taxa with immersed stomata. Lindbergia 10: 65–94 [keys, illustrations]. - Lewinsky, J. 1987. *Orthotrichum* (Orthotrichaceae) in South America 2. Taxonomic revision of taxa with superficial stomata. Memoirs of the New York Botanical Garden 45: 326–370 [keys, illustrations]. - Lewinsky, J. 1993. A synopsis of the genus *Orthotrichum* Hedw. (Musci, Orthotrichaceae). Bryobrothera 2: 1–59. - Lewinsky-Haapasaari, J. & L. Hedenäs. A cladistic analysis of the moss genus *Orthotrichum*. The Bryologist 101: 519–555.

Zygodon (Fig. 161) - About 37 species in the Neotropics; a genus of 90 species primarily distributed in the tropics and subtropics, extending into the temperate regions of both hemispheres.

HABITAT. Epiphytic, on branches and trunks of shrubs and treelets, occasionally on rocks and in rock crevices, shaded to exposed sites; montane forests to zacatonal, páramo, and puna, (500–)2000–4800 m.

DESCRIPTION. **Plants** small to medium sized, occasionally rather large, forming rather dense tufts, green to reddish- or golden-brown. **Stems** mostly erect, occasionally subascending, simple or few branched; usually radiculose or densely tomentose; in cross-section 5-sided, central strand absent. **Leaves** erect to suberect, contorted or ± crispate when dry, spreading to squarrose-recurved when wet, arranged in 5 distinct rows or not, oblong, elliptical to oblong-lanceolate or -linear, 0.6–2.7 mm long, apex acute to acuminate, rarely obtuse; margins plane or recurved below, entire to distally toothed, often sharply so; costa single, strong, projecting on back, subpercurrent to short excurrent; laminal cells papillose, papillae single or multiple, rarely smooth except at base, quadrate- to hexagonal-rounded; basal cells larger, mostly rectangular, firm-walled or lax and mostly hyaline. **Gemmae** occasionally present, on rhizoids or in leaf axils, clavate or ellipsoid. **Autoicous** or dioicous. **Perichaetia** terminal; leaves little differentiated. **Seta** elongate, 2–13 mm long, erect, smooth. **Capsule** erect, symmetrical, urn subcylindrical to narrowly pyriform, 0.7–2 mm long, 8-ribbed, neck short tapered; stomata superficial at base; annulus present and persistent. **Operculum** conic-rostrate. **Peristome** double or single (endostome), rudimentary or absent, prostome lacking; exostome teeth 16, joined in 8 pairs, papillose to papillose-striate; endostome segments 8 or 16, narrow, lightly papillose, striate or smooth. **Calyptra** cucullate, naked and smooth, rarely with few hairs. **Spores** smooth to papillose.

DISCUSSION. The genus is characterized by the often apiculate, oblong-lanceolate to linear-lanceolate or broadly elliptical-lanceolate leaves, finely pluripapillose laminal cells with papillae often minute and centric over the lumen, smooth, elongate seta, ribbed, well exserted capsules, and smooth, naked, cucullate calyptra.

LITERATURE. Griffin III, D. 1990. Two new pentastichous species of *Zygodon* from high elevation in Venezuela. Cryptogamie: Bryologie, Lichénologie 11: 163–168. - Malta, N. 1926. The genus *Zygodon* Hook. et Tayl. Latvijas Universitates Botaniská Dárza Darbi 1: 1–185 [dated, some keys and illustrations].

PHYLLODREPANIACEAE

Plants small to somewhat medium sized, forming loose, tufts or mats, dull to glossy dark green. **Stems** erect to somewhat prostrate and spreading, few branched or solitary, tomentose at base or extending up along stems and branches; central strand absent; rhizoids papillose. **Leaves** 4-ranked, complanate, strongly asymmetric, oblong- to ovate-lanceolate, distal side broad and convex, proximal side narrow and concave, apex acute to broadly short-acuminate; margins plane to recurved, entire or serrulate below, serrate distally; costa single, strong, subpercurrent to short excurrent, closer to proximal side; laminal cells oblong-rhomboidal to isodiametric, smooth, porose and collenchymatous or papillose and thick-walled. **Gemmae** present, on distal stem and branch tips, usually clustered, cylindrical, reddish-brown. **Dioicous**. **Sporophytes** rare for *Phyllodrepanium*, unknown for *Mniomalia*, see below.

DISCUSSION. The Phyllodrepaniaceae contain two genera and about four species with a pantropical distribution; in the Neotropics two genera and two species. The family is characterized by the four-ranked asymmetric leaves that are costate, and the presence of gemmae on terminal branch or stem tips. A member of the order Bryales, the family does not appear to have any obvious close relatives, nor do the constituent genera appear to be closely related.

LITERATURE. Yano, O. 1981. Contribuição ao inventário dos Musci brasileiros: 2. Phyllodrepaniaceae. Acta Amazonica 11: 505–509.

1. Plants dark dull green; leaf margins recurved; median cells isodiametric, unipapillose on back ..... **Mniomallia**
1. Plants glossy green; leaf margins plane; median cells rhomboidal, smooth .. **Phyllodrepanium**

Mniomallia (Fig. 161) - A single species in the Neotropics (excluding Mexico), *M. viridis* (Mitt.) Müll. Hal. About three species with a tropical American-Australasia distribution.

HABITAT. Epiphytic on tree trunks, and on logs; wet lowland forests, 100–720 m.

DESCRIPTION. **Plants** small, solitary or forming short tufts or mats, dark green to brownish-green. **Stems** often growing erect but parallel to substrate, to ca. 2 cm high, simple or few branched, tomentose, often densely so; outer 1–2 rows of cells thick-walled, inner cells larger, firm-walled, central strand absent; rhizoids extending along stems and branches to near tips, rusty-brown, papillose. **Leaves** appearing 4-ranked, complanate, often secund when dry, oblong-ovate, 0.6–1.2 mm long, to 0.3 mm wide, asymmetric, apex acute to rounded-apiculate, decurrent, longer on side toward base; margins rather strongly recurved, crenulate distally, apex often crenulate-dentate; costa single, strong, subpercurrent to percurrent, prominent on back; laminal cells thick-walled (marginal cells thicker), median cells ± isodiametric to short oblong, rounded, unipapillose on back, papillae usually strong, often appearing bifid by adjoining papillose cell walls; basal cells ± elongate. **Gemmae** often present, clustered on terminal stems and branches with reduced oblong leaves, cylindrical, to 0.6 mm long, rusty-brown, smooth. **Dioicous**. **Perichaetia** terminal; leaves elongate, narrowly oblong-ligulate, to 2.8 mm long. **Sporophytes** unknown.

DISCUSSION. *Mniomallia* may be mistaken for *Fissidens*, at least in aspect, owing to the leaves superficially appear 2-ranked; however, the recurved leaf margins and terminal cluster of gemmae readily separate the former from the latter (which exhibits a vaginant laminae that is absent in *Mniomallia*).

Phyllodrepanium (Fig. 161) - A monotypic genus, with *P. falcifolium* (Schwägr.) Crosby in Central America and northern South America.

HABITAT. Epiphytic on tree trunks, and on logs; wet lowland forests, from near sea level to 550 m.

DESCRIPTION. **Plants** rather small, forming thin mats, glossy light or somewhat dark green to golden. **Stems** often prostrate, to 2 cm long, tomentose at base, occasionally tomentum extending a short distance up stem; outer 3–4 rows of cells small, thick-walled, inner cells large, thin-walled, central strand absent; rhizoids rusty-brown, papillose. **Leaves** complanate, appearing 2-ranked (actually 4-ranked), oblong-lanceolate, to 2.2 mm long, ca. 0.6 mm wide, falcate, strongly asymmetric, apex broadly short-acuminate; margins mostly plane but folded below, weakly serrulate or entire below, strongly serrulate distally especially on convex side; costa single, strong, usually along or close to lower (concave) side, subpercurrent to short excurrent; median cells rhomboidal to oblong-rhomboidal, often porose, sometimes strongly so, collenchymatous, smooth, gradually elongate and becoming linear toward margin of convex side; lower and basal cells elongate, weakly porose, strongly so toward costa; terminal stems and branches often attenuate with reduced spathulate leaves. **Gemmae** cylindrical, clustered and appearing in a cup-like leafy sheath of reduced leaves. **Dioicous**. **Perichaetia** terminal, leaves longer but otherwise similar. **Seta** elongate, to 1.9 mm long, smooth. **Capsule** exserted, erect, urn short ovoid-cylindrical to subglobose, to 1.6 mm long; annulus absent. **Operculum** conic. **Peristome** single, teeth 16, irregular and reduced, papillose. **Calyptra** and **Spores** unknown.

DISCUSSION. The genus is distinguished by the strongly 4-ranked, complanate, falcate leaves, the position of costa along the lower concave side of leaf, and cup-shape smaller leaves surrounding a cluster of cylindrical gemmae. The genus was previously named *Drepanophyllum*, Crosby (1970) has reviewed the nomenclatural history. Variety *duidense* Pursell & B. H. Allen (Venezuela: Amazonas, Bolivar) differs from the typical form by the truncate to truncate-apiculate, strongly dentate-serrate leaf apices.

LITERATURE. Crosby, M. R. 1970. Some remarks on the genus *Drepanophyllum* Schwaegr. Revue Bryologique et Lichénologique 37: 345–353. - Pursell, R. A. & B. Allen. 1999. Commentary on *Phyllodrepanium* with *P. falcifolium* var. *duidense*, stat. et comb. nov. Journal of the Hattori Botanical Laboratory 87: 301–308 [illustrations].

PHYLLOGONIACEAE

A monotypic family placed in the Leucodontales.

Phyllogonium (Fig. 162) - Three species in the Neotropics, *P. fulgens* (Hedw.) Brid. (Mexico, West Indies, Suriname, tropical Andes), *P. viride* Brid. (Mexico, West Indies, Suriname, Bolivia, SE Brazil; Réunion), *P. viscosum* (P. Beauv.) Mitt. (Mexico, tropical Andes, South Africa, Réunion); the genus exhibits a tropical American-African distribution.

HABITAT. Commonly epiphytic on branches and occasionally trunks of trees, treelets and shrubs, less often on humus or leaf litter, particularly on steep banks; lowland adjoining submontane to more commonly in montane forests, 150–4200 m.

DESCRIPTION. **Plants** medium sized to rather large, forming long pendent strands from loose mats, glossy green, yellowish-green or golden-brown. **Primary stems** creeping; leaves scale-like. **Secondary stems** usually pendulous, to 50 cm or more, irregularly pinnately branched, few to many; in cross-section outer 2–4 rows of cells small, thick-walled, inner cells larger, rather thick-walled, central strand absent; pseudoparaphyllia foliose. **Leaves** loosely imbricate, usually appearing 2-ranked, ovate-oblong to oblong, 2.5–4.5 mm long, deeply concave and compressed laterally, smooth or undulate, apex rounded or truncate, apiculate and recurved or erect, base auriculate; margins plane, entire; costae absent or short and forked; laminal cells smooth and strongly porose throughout, median cells linear to oblong-rectangular; alar cells differentiated, shortly rectangular to subquadrate-rounded, strongly porose, usually rusty-red. **Dioicous**. **Perichaetia** lateral, leaves differentiated, abruptly long acuminate from an broadly ovate base. **Seta** short to somewhat elongate, 0.5–3.5 mm long, equal to or longer than capsule, smooth. **Capsule** shortly exserted or immersed, suberect, urn oblong-cylindrical to ovoid, 1.2–2.5 mm; exothecial cells mostly quadrate, ± thick-walled; stomata present or absent; annulus absent. **Operculum** conic-rostrate, oblique. **Prostome** present, represented by 1–3 layers adnate to the exostome. **Peristome** single or double, exostome teeth 16, smooth; endostome absent or if present represented only by a low, hyaline basal membrane **Calyptra** mitrate or cucullate, sparsely to densely hairy. **Spores** spherical, papillose.

DISCUSSION. *Phyllogonium* is characterized by the pendent habit, 2-ranked, oblong or oblong-ovate, conduplicate leaves, apiculate or truncate apex, auriculate base, short and forked costae, and strongly porose laminal cells. The genus is a typical element of montane forests, and is one of the more conspicuous pendent mosses. The species can be distinguished by the following features:

a. Leaves undulate, 3.8–4.7 mm long, apex truncate ..... *P. viscosum*
a. Leaves smooth, less than 3.6 mm long, apex cuspidate ..... b
b. Leaves ca. 3.6 mm long, apex cuspidate-recurved ..... *P. viride*
b. Leaves ca. 3 mm long, apex cuspidate-erect ..... *P. fulgens*

LITERATURE. Lin, S.-H. 1983. A taxonomic revision of Phyllogoniaceae (Bryopsida). Part I. Journal of the Taiwan Museum 36(1): 37–86 [keys, illustrations, maps].

PILOTRICHACEAE

Plants small to rather large. **Primary stems** creeping and spreading, leaves often reduced and scale like. **Secondary stems** spreading, ascending, or erect and frondose; in cross-section hyalodermis present, rarely absent, central strand absent. **Leaves** often complanate, ovate, ovate-oblong or -lanceolate, symmetrical, or if leafy stems complanate, then lateral leaves often asymmetrical and dorsal/ventral leaves symmetric; margins elimbate or limbate, plane to more often partially to fully recurved or reflexed, dentate to variously serrate, rarely entire; costae double, diverging or parallel, short or elongate, or absent (*Crossomitrium*); laminal cells isodiametric to linear, smooth or papillose, thin- to thick-walled, porose or not. **Propagula** occasionally present on the leaves or more often in leaf axils, occasionally produced on specialized branches or underside of stems, cylindrical. **Autoicous** or dioicous, rarely synoicous or polyoicous. **Perichaetia** lateral, leaves differentiated, mostly smaller than stem leaves. **Seta** short or elongate, smooth, papillose or spinose. **Capsule** exserted, erect to pendulous; annulus of persistent weakly differentiated cells. **Operculum** conic- short to long rostrate. **Peristome** double, exostome teeth 16, papillose and bordered or cross-striate and furrowed; endostome basal membrane usually low, segments 16, often keeled and perforate, cilia rudimentary or absent. **Calyptra** mitrate or mitrate-campanulate, smooth or hairy. **Spores** spherical, smooth to more often papillose.

DISCUSSION. The Pilotrichaceae, as defined here, contain some 23 genera with a mostly pantropical distribution; in the Neotropics 21 genera and about 200 species. The Neotropics are particularly rich in the number of genera unique to the region - 15 of the 21 presently recognized. The double costa, usually well developed, often in combination with the presence of a hyalodermis, and a seta that is sometimes ornamented are useful characters. The Pilotrichaceae has priority over the recently employed name Callicostaceae.

The Hookeriaceae in the broad sense (Brotherus, 1925; and followed by Welch, 1976) has been divided into several families, with little agreement between authors (cf. Miller, 1971; Crosby, 1974; Buck, 1987, 1988; Whittemore & Allen, 1989) as to the placement of various genera. A preliminary cladistic study has been provided by Hedenäs (1996). For the present, we have adopted the treatment of Buck (1987, 1988). The following key will separate the families assigned to the Hookeriales.

1. Costa absent 2
1. Costa present (absent in *Crossomitrium*) 3

2. Hyalodermis absent; leaf apex broadly acute; median cells large, rhomboidal ... **Hookeriaceae**
2. Hyalodermis present; leaf apex acuminate; median cells fusiform to linear ..... **Leucomiaceae**
3. Costa double, short or long ..... **Pilotrichaceae**
3. Costa single, or with a short single costa and basal or lateral spur 4
4. Branches not attenuate with deciduous leaves and gemmae; laminal cells hexagonal and rather thin-walled, or oval to oblong and thick-walled; seta elongate ..... **Daltoniaceae**
4. Branches attenuate, with deciduous leaves and gemmae; laminal cells stellate, thick-walled; seta short ..... **Adelotheciaceae**

LITERATURE. Buck, W. R. 1987. Taxonomic and nomenclatural rearrangement in the Hookeriales with notes on West Indian taxa. Brittonia 39: 210–224. - Buck, W. R. 1988. Another view of familial delimitation in the Hookeriales. Journal of the Hattori Botanical Laboratory 64: 29–36. - Crosby, M. R. 1974. Toward a revised classification of the Hookeriaceae (Musci). Journal of the Hattori Botanical Laboratory 38: 129–141. - Hedenäs, L. 1996. A cladistic overview of the “Hookeriales”. Lindbergia 21: 107–143. - Miller, H. A. 1971. An overview of the Hookeriales. Phytologia 21: 243–252. - Welch, W. H. 1976. Hookeriaceae. North American Flora II, 9: 1–133 [keys, less than functional, as are the species concepts adopted]. - Whittemore, A. & B. Allen. 1989. The systematic position of *Adelothecium* Mitt. and the familial classification of the Hookeriales (Musci). The Bryologist 92: 261–272.

1. Leaves ecostate; gemmae usually produced beneath leafy stems in clusters or on distal specialized branches ..... **Crossomitrium**
1. Leaves costate, costa double, short to long, occasionally absent; gemmae, if present, commonly in leaf axils or on leaves.....2
2. Laminal cells papillose, papillae over cell lumina or projecting at cell angles 3
2. Laminal cells smooth 11
3. Laminal cells unipapillose or pluripapillose, papillae over cell lumina 4
3. Laminal cells unipapillose, papillae mostly projecting at cell angles 7
4. Laminal cells unipapillose (rarely bipapillose but with most cells unipapillose) 5
4. Laminal cells pluripapillose 6
5. Leaf margins recurved; capsules erect; exostome papillose; high elevations of páramo or puna **Callicostellopsis**
5. Leaf margins plane; capsules inclined to pendent; exostome cross-striate below, papillose above; low elevations, mostly below the montane ..... **Callicostella** p.p.
6. Plants procumbent; costae strong, converging and ending at apex, strongly projecting on back; laminal cells isodiametric ..... **Pilotrichidium** p.p.
6. Plants procumbent or pendent; costa 1/4–3/4 lamina length, not strongly projecting, parallel to diverging; laminal cells elongate ..... **Hypnella**
7. Laminal cells long, 4–8 times longer than wide; leaves often falcate-secund .....**Trachyxiphium** p.p.
7. Laminal cells short (2–4 times longer than wide) or isodiametric 8
8. Alar region well differentiated, subquadrate cells numerous; branches subjulaceous and curved; central strand of stem present, weak; Mexico ..... **Curviramea**
8. Alar region lacking or with a few cells slightly differentiated; branches neither subjulaceous nor curved; central strand absent 9
9. Plants erect to suberect, stipitate, frondose; stem and branch leaves often dimorphic; laminal cells often oblong ..... **Pilotrichum**
9. Plants procumbent or forming short tufts, stems and branches spreading, not stipitate; leaves of stem and branches similar 10
10. Costa strong, often ending near apex, projecting on back; laminal cells ± isodiametric; seta often scabrous or papillose; plants common, of low elevations ..... **Callicostella** p.p.
10. Costa weak, ca. 1/2 lamina length; laminal cells 2–3 time longer than wide; seta smooth, plants rare, of mid elevations ..... **Helicoblepharum**
11. Plants forming short tufts, primary stems indistinct, short, appearing erect or ascending; seta papillose and/or spinose, occasionally only roughened or rarely smooth (see *Actinodontium*), capsules erect 12
11. Plants procumbent, often forming mats, stems creeping, secondary stems spreading to ascending or suberect to erect and perpendicular to substrate, to erect; seta smooth or variously papillose or spinose, capsules erect to horizontal or pendent 14
12. Leaves ovate to ovate-lanceolate; seta papillose throughout 13
12. Leaves oblong, ligulate; seta distally roughened or weakly papillose, rarely smooth ..... **Actinodontium**

13. Leaf apices narrowly acuminate; seta papillose and spinose ..... **Stenodesmus**
13. Leaf apices abruptly constricted above into a broad acumen, acute; seta papillose ..... **Helicoblepharum**
14. Leaves distinctly plicate, plications extending from base to about midleaf, obscuring the double costa..... **Hemiragis**
14. Leaves lacking plications, smooth, rugose or undulate 15
15. Leaves distinctly bordered by elongate cells 16
15. Leaves elimbate, marginal cells similar to inner laminal cells or gradually differentiated toward margin 20
16. Leaf border formed from costa merging along margin and continuing to into apex; Cuba and Jamaica ..... **Diploneuron**
16. Leaf border formed by marginal cells, generally similar to laminal cells, costa mostly weak, not merging with marginal border (occasionally reaching margin but not merging) 17
17. Marginal teeth often swollen and bifid..... **Thamniopsis** p.p.
17. Marginal teeth neither swollen nor bifid 18
18. Plants lax, somewhat flaccid 19
18. Plants not lax (rarely so, then leaves falcate-sigmoid) ..... **Lepidopilum** p.p.
19. Seta smooth, capsules pendent, exostome cross-striate .....**Cyclodictyon**
19. Seta papillose/spinose, capsules erect, exostome papillose .....**Amblytropis**
20. Laminal cells short, isodiametric to short oblong (2–3:1) 21
20. Laminal cells elongate (5–10 or more: 1) 22
21. Leaf margins serrate to dentate distally; costae not or weakly projecting on back, often toothed ..... **Callicostella** p.p.
21. Leaf margins entire; costae strongly projecting on back, often extending beyond lamina, smooth ..... **Pilotrichidium** p.p.
22. Plants radically and evenly foliate, not complanate; leaves often deeply concave .... **Stenodictyon**
22. Plants weakly to strongly complanate; leaves not or weakly concave 23
23. Plants often epiphytic, secondary stems ascending and often perpendicular to substrate; seta smooth to more commonly papillose/spinose, capsules erect to suberect, exostome papillose or cross-striate and furrowed 24
23. Plants often terrestrial, occasionally on base trunk of trees, mostly procumbent; seta smooth, capsules horizontal to pendent, exostome cross-striate 25
24. Exostome teeth papillose; seta papillose or spinose ..... **Lepidopilum** p.p.
24. Exostome teeth cross-striate and furrowed; seta smooth or papillose distally or throughout ..... **Lepidopilidium**
25. Stems with a distinct hyalodermis (epidermal cells enlarged, thin-walled, inner rows (outer cortex) of cells small, thick-walled), basal laminal cells differentiated from apical cells; leaves often dimorphic ..... **Thamniopsis**
25. Stems lacking a hyalodermis (or rarely present and weakly differentiated) basal and apical cells similar; leaves mostly monomorphic 26
26. Marginal teeth often bifid, swollen (occasionally teeth both single or bifid); laminal cell walls entire, or if porose then weakly so, often papillose by projecting cell angles; costa with or without prominent spines ..... **Trachyxiphium** p.p.
26. Marginal teeth usually simple, not swollen; laminal cells strongly porose or not, cells smooth, not papillose by projecting angles; costae usually smooth or with small spines 27
27. Costae short, 1/5–1/3 lamina length; laminal cells (except at base) not porose; plants mostly small; West Indies ..... **Hookeriopsis**
27. Costae elongate, 1/2 or more lamina length; laminal cells usually porose; plants often large; rather widespread in the Neotropics ..... **Brymela**

Actinodontium (Fig. 163) - Possibly only 2–3 species in the Neotropics; a small genus of some 9 species with a pantropical distribution.

HABITAT. Epiphytic on branches of trees and shrubs; adjacent lowland to lower montane forests, 200–2600 m.

DESCRIPTION. **Plants** small to somewhat medium sized, forming tufts, light to somewhat dark green, or yellowish-green. **Stems** erect or ascending, radiculose below; in cross-section central strand absent, hyalodermis present. **Leaves** loosely erect, crowded, weakly complanate, oblong-short- to somewhat long-lanceolate, ca. 1.5–2.7 mm long, occasionally with a single longitudinal plication, apex short acuminate, base rounded or subauriculate; margins partially to fully recurved on one or occasionally both sides, often indistinctly bordered, entire or serrulate to dentate at apex; costae 1/3–3/4 lamina length, parallel or slightly diverging; laminal cells smooth, upper cells narrowly

to broadly hexagonal or fusiform; lower and basal cells short to long rectangular, lax; marginal cells weakly differentiated or not. **Autoicous**. **Perichaetia** lateral. **Seta** elongate, ca. 5.5–9.5 mm long, weakly to rather strongly roughened distally. **Capsule** erect, urn ovoid, 1.2–1.5 mm long. **Operculum** conic-long rostrate. **Peristome** double, exostome teeth narrow, strongly papillose, bordered; endostome basal membrane low, segments papillose. **Calyptra** mitrate-short campanulate, plicate, base lobed. **Spores** papillose.

DISCUSSION. The tufted habit, rather similar to *Daltonia*, oblong-lanceolate leaves with partially to fully recurved margins, parallel double costae, distally roughened seta, and erect capsules with bordered, papillose exostome teeth characterize the genus. *Actinodontium* is related to *Lepidopilum* (particularly to *L. longifolium* Hampe and related species that have ± symmetric leaves), differing in part from the latter by the tufted habit and smooth to weakly papillose ornamentation of the seta; *Helicoblepharum* is likewise similar and related, exhibiting an abrupt but broad leaf apex that is often twisted, the rather thick-walled, oblong-oval laminal cells, and a seta papillose throughout or only in the distal portion.

Amblytropis (Fig. 163) - A neotropical genus of three species primarily of Central America and northwest South America.

HABITAT. On humus, leaf litter, logs, or soil; wet lowland forests adjacent to mountains, to lower montane forests, 35–2650 m.

DESCRIPTION. **Plants** somewhat small to medium sized, forming loose lax mats, mostly pale green or yellowish-green. **Stems** spreading and possible subascending, few to several branched, branches often short; in cross-section hyalodermis ± developed, central strand absent. **Leaves** loosely to somewhat strongly complanate, rather lax, erect-spreading to erect, lateral leaves asymmetric, ovate- to oblong-short lanceolate, 1.4–2.5 mm long, dorsal/ventral leaves symmetric, ovate to short oblong-lanceolate, apex apiculate or short to long acuminate and then acumen narrow to rather broadly lance-shaped; margins plane, lateral leaves mostly folded 2/3 lamina length, entire or serrulate to serrate in distal 1/5–1/3, limbate; costae 1/2–4/5 lamina length, gradually diverging, ± strong, ending in a short spine or not; upper and median cells broadly hexagonal, 1–1.5(–2) times longer than broad, occasionally short rectangular, lax and thin-walled; lower and basal cells short to more commonly long rectangular or oblong, lax, thin-walled; marginal border cells rather large and oblong-elongate to long linear, in 1–4(–6) rows. **Autoicous** or possibly dioicous. **Perichaetia** lateral. **Seta** elongate, 12–17 mm long, rather slender, spinose or hispid. **Capsule** suberect to inclined, urn short ovoid, 0.5–1.2 mm long; exothecial cells oblong-rectangular, rather thick-walled. **Operculum** conic-short rostrate. **Peristome** double, exostome teeth narrowly lanceolate, bordered, border hyaline, outer surface papillose; endostome somewhat longer than exostome, hyaline and papillose, basal membrane high, segments keeled, cilia rudimentary. **Calyptra** mitrate campanulate, somewhat plicate, smooth or with a few hairs or persistent archegonia, base lobed. **Spores** spherical, papillose.

DISCUSSION. The genus is characterized by the spreading or subascending stems, the lax, complanate leaves, bordered margins, the large hexagonal upper cells that are lax and thin-walled, distal portion of seta spinose-papillose, erect capsules, and hyaline bordered papillose exostome teeth. Gametophytically, similar to and likely to be confused with *Cyclodictyon*, as attested to by the species *C. jamesii* H. Rob. from Central America (= *A. hispidula* (Mitt.) Broth.), and sporophytically similar to *Lepidopilum* in the spinose seta. Of the three species, *A. ovata* (Mitt.) Broth. (only known from the type locality near Bogotá, Colombia) is maintained *inserta sedis* since sporophytes are unknown; the remaining two species can be differentiated as follows: *A. hispidula* (Mitt.) Broth. — leaves oblong-ligulate, upper margins entire (Costa Rica, Panama, Colombia, Ecuador); and *A. setosa* (Mitt.) Broth. — leaves oblong-lanceolate, upper margins serrate (Colombia, Ecuador).

Brymela (Fig. 164) - A neotropical genus of some 12–13 species.

HABITAT. On logs, humus and rocks, also epiphytic on treelets, shrubs and lianas; wet lowland to lower montane forests, rarely extending to upper montane forests, 100–2000(3400) m.

DESCRIPTION. **Plants** small to large and robust, forming loose to dense mats, glossy light or dark green to golden-brown. **Stems** and branches spreading to subascending; in cross-section central strand absent, hyalodermis absent. **Leaves** loosely erect-spreading to falcate-secund, oblong to oblong-short lanceolate, 0.8–8 mm long, smooth to undulate or rugose, apex acute, short acuminate or subobtuse, base weakly auriculate or not; margins reflexed or recurved in lower 1/3, or at midleaf, subentire to serrulate from about midleaf, often serrate at apex, elimbate or weakly limbate; costae double, 1/2–3/4 leaf length, parallel or slightly diverging, smooth to weakly or strongly serrulate along back; laminal cells smooth, apical cells shorter or not; median cells oblong-linear to linear, smooth to weakly or strongly porose; basal cells short, often golden-brown; marginal cells similar or forming a weak border of long linear cells. **Asexual structures** absent. **Perichaetia** lateral, leaves

differentiated, ovate-narrowly lanceolate, sharply serrate. **Seta** elongate, 10–45 mm long, slender to somewhat stout, smooth to more commonly weakly papillose or roughened below urn. **Capsule** inclined to horizontal, rarely subpendulous, urn ovoid-short cylindrical, 1–3 mm long, often somewhat flared below mouth when deoperculate. **Operculum** conic short to long rostrate. **Peristome** double, exostome teeth strongly furrowed, densely cross-striate, distal tips papillose; endostome basal membrane high, segments keeled and papillose. **Calyptra** mitrate-short campanulate, naked, lobed at base. **Spores** spherical, lightly papillose.

DISCUSSION. The genus is distinguished by the rather large habit, the absence of or little developed stem hyalodermis, the elimbate leaves with the serrated leaf margins of mostly simple teeth, and the ± homogeneous, firm- to thick-walled, porose laminal cells. Species of this genus were previously placed in *Hookeriopsis*. Further refinements are required in circumscribing *Brymela*. Members of this genus appears to be rather infrequent, due in large part to insufficient collecting, particularly in the submontane regions, except *B. parkeriana* (Hook. & Grev.) W. R. Buck which is rather widely distributed in the Guianas and the northern Amazon.

LITERATURE. Buck, W. R. 1987 (see family ref.). - Crosby, M. R. & B. H. Allen. 1985. *Brymela tutesona* (Musci: Hookeriaceae), a new genus and species from western Panama. Monographs in Systematic Botany from the Missouri Botanical Garden 11: 211–216.

Callicostella (Fig. 164) - Nearly 60 species recorded from the Neotropics, probably not exceeding more than 30 species; a pantropical genus containing far fewer than the some 97 species ascribed to it.

HABITAT. On soil, logs, and rock, often associated with streams; lowland to lower montane forests, from near sea level to 1200(–2400) m.

DESCRIPTION. **Plants** small to medium sized, forming mats, pale to dark green to yellowish or golden. **Stems** creeping and spreading; in cross-section lacking a hyalodermis, central strand absent. **Leaves** somewhat complanate, differentiated between lateral asymmetric leaves and dorsal/ventral symmetric leaves, the latter somewhat smaller, lateral leaves oblong, ovate- or oblong-short to rather long lanceolate, ligulate, 0.8–2.5 mm long, apex acute, often bluntly so, short acuminate, or truncate-apiculate; margins mostly plane or folded along one side, rarely reflexed below, distally regularly serrulate or dentate, or irregularly sharply serrate, teeth often bifid and swollen, elimbate; costae double, 2/3–4/5 lamina length, rarely extending to apex, mostly strong, usually toothed on back; upper and median cells hexagonal to rhombic, occasionally oblong, smooth to papillose with papillae over cell lumen or projecting at distal cell angle, ± thick-walled; basal cells oblong to rectangular-rounded, occasionally lax, smooth, porose or not. **Synoicous**, autoicous or dioicous. **Perichaetia** lateral, leaves strongly differentiated, often narrowly elongate. **Seta** elongate, 5–20 mm long, slender to rather stout, smooth to papillose or scabrous, distally or throughout. **Capsule** horizontal to subpendulous, urn ovoid to short cylindrical, 1–2 mm long, short neck, exothecial cells collenchymatous. **Operculum** conic-long rostrate, oblique. **Peristome** double, exostome teeth cross-striate and furrowed, endostome basal membrane high, segments keeled and perforate, lightly papillose. **Calyptra** mitrate-campanulate, plicate, scabrous distally, lobed at base. **Spores** spherical, lightly papillose.

DISCUSSION. The genus is characterized by the loosely complanate, ovate, narrowly to broadly oblong-ovate and unbordered leaves, the truncate-apiculate to broadly or narrowly acute apex, the irregularly to regularly serrate margins with teeth often bifid, strong and raised costa that is often toothed, thick-walled, short (1–2:1), smooth to papillose, rhombic, hexagonal upper laminal cells, smooth or papillose seta, cross-striate, furrowed exostome teeth, and high basal membrane. The older name, *Schizomitrium*, has been used again by recent authors; however, the name *Callicostella*, in long use, has been recently conserved. The genus is poorly known and in much need of revision in the Neotropics.

Callicostellopsis (Fig. 164) - A monotypic genus, with *C. meridensis* (Müll. Hal.) Broth. presently known only from Bolivia and Venezuela.

HABITAT. On wet or moist rocks or trunks of shrubs; open upper montane transition to subpáramo or puna, at high elevations, 3400–3650 m.

DESCRIPTION. **Plants** somewhat small, forming lax or soft mats, pale olive green to golden-brown or -yellow. **Stems** spreading to subascending, irregularly pinnately branched, branches few to many, tips bluntly obtuse; in cross-section hyalodermis weak, central strand absent; pseudoparaphyllia foliose, ovate. **Stem leaves** equally foliate to weakly complanate, crowded, flaccid or lax when wet, loosely erect, ovate-oblong to oblong, to 1.7 mm long, to 0.7 mm wide, concave, apex abruptly short acuminate, tips flexuose; margins recurved throughout except apex, weakly serrate or serrulate at apex or extending further below apex but obscured by recurved margins; costae double, 3/4–4/5

lamina length, usually separated at base, diverging gradually above; apical cells rhombic; median cells broadly fusiform-rounded or rhomboidal-rounded, thick-walled, ± collenchymatous, unipapillose, extending to near base, papillae over cell lumen; basal cells short to long rectangular, walls firms, smooth. **Branch leaves** similar but smaller. **Autoicous**? **Perichaetia** lateral, leaves lanceolate, cells smooth to weakly papillose distally. **Seta** dark rusty red, elongate, 12–30 mm long, mostly smooth below, roughened below urn. **Capsule** suberect to erect, urn ovoid-cylindrical to cylindrical (when deoperculate), to 2 mm long, exothecial cells short to ± long rectangular-rounded, thick-walled, collenchymatous, stomata few at urn base, set below surface, appearing absent; annulus undifferentiated. **Operculum** conic-long rostrate, ca. 1 mm long. **Peristome** double, exostome teeth narrowly lanceolate, papillose, appearing bordered; endostome basal membrane low, segments linear, ca. equal exostome, papillose, cilia absent. **Calyptra** mitrate-campanulate, naked, lobed at base. **Spores** spherical, finely papillose.

DISCUSSION. In aspect this species is somewhat similar to *Cyclodictyon* in the rather lax habit; however, *Cyclodictyon* exhibits a marginal border of elongate cells, smooth laminal cells, and, sporophytically, the seta is usually smooth, the exostome furrowed and cross-striate.

LITERATURE. Churchill, S. P. & E. L. Linares C. 1995 (see general ref.).

Crossomitrium (Fig. 165) - A genus of six species confined to, and widespread in, the Neotropics.

HABITAT. Commonly epiphyllous, also on branches and trunks of shrubs and treelets; frequent in wet lowland to lower montane forests; from near sea level to ca. 2000 m.

DESCRIPTION. **Plants** small to medium sized, forming loose, thin mats, glossy green, yellowish-green or golden. **Stems** creeping and spreading, irregularly pinnately branched; in cross-section central strand absent; paraphyllia and apparently pseudoparaphyllia absent; rhizoids often clustered below. **Leaves** crispate or not when dry, strongly complanate or erect and arching distally; stem leaves differentiated between dorsal and lateral, **lateral leaves** ovate, oblong, orbicular or ovate- to oblong-lanceolate, 0.5–2 mm long, to 1.2 mm wide, apex acute to short acuminate, often slightly keeled, base subauriculate to rounded; margins usually recurved in part or throughout, doubly-dentate or -serrate, occasionally single serrate between; ecostate; median cells linear to linear-vermicular, firm-walled, smooth; basal cells oblong-fusiform or -rhomboidal, porose; **dorsal leaves** shorter, usually broader, ovate, oval to orbicular. **Gemmae** present beneath stems or on specialized branches with differentiated leaves, cylindrical. **Dioicous**. **Perichaetia** lateral, leaves differentiated. **Seta** elongate, 4–12 mm long, papillose throughout or distally. **Capsule** suberect to inclined, urn ovoid to elliptical, 0.5–1.5 mm long, exothecial cells collenchymatous. **Operculum** conic-rostrate. **Peristome** double, exostome teeth papillose, endostome basal membrane low to high, segments weakly perforate and keeled, spiculose, cilia absent. **Calyptra** mitrate, base ciliate. **Spores** spherical, finely papillose.

DISCUSSION. Distinguishing features of *Crossomitrium* include the ecostate leaves, marginal bifid teeth, and cylindrical gemmae clustered beneath stems or on modified branch tips. This is the most common genus found on leaves of herbs, shrubs, and treelets. Although sporophytes are not uncommon, the primary means of reproduction is likely via asexual gemmae.

LITERATURE. Allen, B. H. 1990. A revision of the genus *Crossomitrium* (Musci: Hookeriaceae). Tropical Bryology 2: 3–34 [keys, illustrations, maps].

Curviramea (Fig. 165) - A monotypic genus, with *C. mexicana* (Thér.) H. A. Crum only known from Mexico.

HABITAT. On dry rocks in shaded sites; rather dry forests, at elevation from 150–900 m.

DESCRIPTION. **Plants** medium sized, forming loose mats, dull-green. **Primary stems** creeping; in cross-section outer 3–4 rows of cells thick-walled, inner cells large, thin-walled, central strand small and weak. **Secondary stems** spreading to subpendent, irregularly pinnately branched from a stipitate base, branches subjulaceous and curved; pseudoparaphyllia filamentous. **Leaves** erect when dry, erect-spreading when wet, broadly ovate, to 1.5 mm long, somewhat concave and biplicate, apex acute; margins somewhat revolute above base, plane above, serrate distally; costae double, ca. 2/3 lamina length, slightly divergent, weakly serrulate on back distally; upper and median cells oblong-hexagonal, papillose, papillae projecting at distal angles; alar region differentiated, cells subquadrate, in numerous rows. **Asexual reproduction** unknown. **Perichaetial** leaves slenderly acuminate. **Sporophytes** unknown.

DISCUSSION. The presence of pseudoparaphyllia, a central strand and differentiated alar cells, are characters that define *Curviramea* and are at variance with the features generally ascribed to the Callicostaceae. Noteworthy, as well, are the creeping primary and arching secondary stems and leaf lamina with prorate papillae. The relationship of this taxon to other members of the Pilotrichaceae or

even its inclusion in the family warrants further investigation; the discovery of sporophytes may resolve the problem.

Cyclodictyon (Fig. 165) - Approximately 70 species recorded for the Neotropics, more likely 30 or fewer species; a genus probably containing only half of the 90 species ascribed to it; widespread in the tropics of Africa and America.

HABITAT. Often on soil, humus or leaf litter, occasionally on rocks or epiphytic, mostly of moist or wet sites; lowland to upper montane forests, from near sea level to 3900 m.

DESCRIPTION. **Plants** medium sized, often rather lax, forming loose mats, mostly pale green to whitish-green, occasionally reddish. **Stems** creeping and spreading or subascending, irregularly branched, occasionally distal stems and branches with deciduous leaves; in cross-section hyalodermis usually present, cortical cells large and hyaline, central strand absent; rhizoids clustered beneath stems. **Leaves** crispate when dry, loosely complanate when wet, lateral and dorsal/ventral leaves differentiated, **lateral leaves** asymmetric, ovate to ovate-oblong, 0.5–2.8 mm long, apex short to long acuminate; margins entire to more often serrate or serrulate distally, limbate; costae double, 2/3–3/4 lamina length, slender; median cells large, hexagonal to broadly rhombic, smooth; basal cells large and lax; marginal cells forming a border of 1–5 or more rows, long-linear; **dorsal/ventral leaves** symmetric, often slightly smaller. **Gemmae** not observed. **Autoicous** or dioicous. **Perichaetia** lateral, leaves differentiated, abruptly long lanceolate or linear from an ovate base, distal cells often elongate. **Seta** 10–18 mm long, elongate, smooth. **Capsule** suberect to horizontal, urn ovoid to ovoid-cylindrical mm long, somewhat curved; exothecial cells rounded quadrate or rectangular, longitudinal walls often thick, collenchymatous or not; stomata represent by 4 or 6 subquadrate cells at urn base. **Operculum** conic-long rostrate, oblique. **Peristome** double, exostome teeth strongly furrowed, finely cross-striate below, distally papillose; endostome basal membrane moderately high, segments keeled, weakly perforate or not, lightly papillose, cilia absent. **Calyptra** mitrate, smooth, slightly laciniate at base. **Spores** spherical, lightly papillose.

DISCUSSION. The genus is characterized by the lax, spreading habit, the leaves crispate when dry and complanate when moist, differentiated between symmetric dorsal/ventral and asymmetric lateral ones, mostly ovate to oblong-ovate, margins limbate, large, thin-walled, hexagonal and rhombic median and upper cells, seta smooth, suberect to horizontal capsules, finely cross-striate, furrowed exostome teeth, and a smooth, mitrate calyptra with base somewhat laciniate. Although gemmae are unknown in the Neotropics, distal portion of branches have occasionally been observed with deciduous leaves in Colombia, possibly serving as propagula. A worldwide revision is urgently needed.

Diploneuron (Fig. 166) - A monotypic genus, with *D. connivens* E. B. Bartram known only from Cuba and Jamaica.

HABITAT. On logs and base of trees; lowland and submontane forests, at elevations from 60–980 m.

DESCRIPTION. **Plants** medium sized, forming mats, dull green to yellowish-red. **Stems** creeping, to 3 cm long, irregularly branched; in cross-section hyalodermis weakly differentiated, outer 2–3 rows of cells small, thick-walled, inner cells larger, thin-walled, central strand absent. **Leaves** complanate, ovate-lanceolate to narrowly lanceolate, to 3 mm long, apex acuminate, folded below, base rounded on one side; margins entire or weakly dentate; costae double, strong, merging near midleaf with margin and finally at apex to form a stout subulate tip (thus appearing distally bordered), in cross-section several layers of undifferentiated cells; laminal cells smooth, thick-walled, weakly porose, upper cells irregularly oblong-hexagonal or -rectangular; basal cells longer, oblong-rectangular; rounded side of leaf base with a somewhat distinct alar region, cells subquadrate. **Dioicous**. **Perichaetia** lateral, leaves somewhat similar but shorter. **Seta** elongate, to 28 mm long, smooth. **Capsule** horizontal, urn obloid, to 2 mm long, neck somewhat distinct; stomata in neck region, superficial. **Operculum** conic-short rostrate. **Peristome** double, exostome teeth finely cross-striate below, distally finely papillose; endostome basal membrane high, segments keeled and perforate, cilia absent. **Calyptra** mitrate, scabrous above, smooth below, base lobed. **Spores** spherical, smooth.

DISCUSSION. The strong double costa that merges with the margin forming a distal border and fusing at the apex to form a stout subula is unique to the family.

LITERATURE. Allen, B. H. & M. R. Crosby. 1986. A revision of the genera *Pilotrichidium* and *Diploneuron* (Musci: Hookeriaceae). Journal of the Hattori Botanical Laboratory 61: 45–64 [keys, illustrations].

Helicoblepharum (Fig. 166) - A neotropical genus of about four species.

HABITAT. Epiphytic, on branches of shrubs and treelets; submontane to possibly upper montane forests, 1200–2700 m.

DESCRIPTION. **Plants** rather small, forming loose tufts or thin mats, yellowish-green to golden. **Primary stems** short, creeping. **Secondary stems** ascending or spreading, equally foliate, leaves loosely erect, erect-spreading when wet. **Leaves** short oblong-lanceolate, 1–2 mm long, to 0.7 mm wide, concave, partially plicate along costa, apex gradually to ± abruptly acuminate, acumen ± broad, often with a half twist; margins plane to partially reflexed on one or both sides, often strongly so below apex tip, entire or nearly so; costae double, ca. 1/2 lamina length or somewhat less; laminal cells appearing smooth, occasionally with angles projecting, and mostly thick-walled, upper and median cells oblong to rhomboidal; basal cells irregular oblong-rectangular, those adjacent to costa appearing weakly porose; marginal cells at or near base forming a weak border of oblong-linear cells. **Dioicous**? **Perichaetia** lateral. **Seta** elongate, 5–10 mm long, papillose or roughened throughout excepted at base to distal 1/2. **Capsule** erect, urn ovoid, 0.8–1.3 mm long. **Operculum** not observed. **Peristome** double, exostome teeth spreading-recurved when wet, erect when dry, papillose and appearing bordered, endostome basal membrane appearing low, segments papillose. **Calyptra** and **spores** not observed.

DISCUSSION. The genus is related to *Lepidopilum*, sharing with it an ornamented seta, and a bordered, papillose exostome, but differing from that genus primarily by the erect habit with inconspicuous short primary stems, and short oblong-lanceolate leaves; it is also similar to *Actinodontium* (see comments under that genus). *Helicoblepharium* is likely far more common than the few records for the Neotropics would imply (fewer than 10 collections including types) due to its small size, and its tendency to often grow among other bryophytes.

Hemiragis (Fig. 167) - A monotypic genus, with *H. aurea* (Brid.) Renauld & Cardot confined to the Neotropics (Central America, West Indies, Guianas, Venezuela to Ecuador).

HABITAT. Epiphytic, leaf litter and on decaying logs; lowland forests and into lower montane forests, 480–1600 m.

DESCRIPTION. **Plants** rather large to somewhat robust, forming mats or tufts, glossy green to golden-yellow. **Stems** initially creeping, then spreading or more commonly ascending, to 10 cm long, irregularly pinnate branched; in cross-section hyalodermis present with 2–3 rows of small, thick-walled dark red cells, inner cells larger. **Leaves** densely crowded, erect-spreading, often secund, narrowly long-lanceolate, 3–4 mm long, to 0.6 mm wide, plicate in lower 1/2, 1–2 plications on either side of costa, and often along and obscuring costa, apex gradually long acuminate, slightly subauriculate; margins mostly plane, serrulate in lower 1/3, serrate above and distal 1/3 spinose; costae double (often obscured by plication), 3/4–4/5 lamina length, usually appearing to end in acumen, coarsely serrate on back; upper and median cells long linear-vermicular, smooth, thick-walled, strongly porose; lower and base cells becoming shorter and broader, porose; insertion cells golden-brown. **Autoicous**. **Perichaetia** lateral, leaves ovate-lanceolate or -subulate, costa double and short or absent. **Seta** elongate, smooth. **Capsule** inclined, urn short-cylindrical to ovoid, 1–2 mm long. **Operculum** conic rostrate. **Peristome** double, exostome teeth broadly furrowed, finely striate below, distal 1/4 with scattered papillae; endostome basal membrane high, segments keeled, and perforate, weakly papillose, cilia absent. **Calyptra** mitrate, to 4 mm long, smooth, lobed at base. **Spores** spherical, finely papillose.

DISCUSSION. The genus is distinguished by the large tufted plants, crowded, falcate, narrowly lanceolate strongly plicate leaves, with plicae obscuring the long parallel double costae, the strongly porose, linear laminal cells, a furrowed exostome finely striate below, papillose above, and high endostomial basal membrane. It was previously placed in *Harpophyllum*.

Hookeriopsis (Fig. 167) - Two species in the Neotropics, *H. leiophylla* (Besch.) A. Jaeger, and *H. luteo-rufescens* (Besch.) A. Jaeger, both confined to the West Indies.

HABITAT. On exposed roots and base of trees, logs, and rocks; montane cloud forests, at elevations from 940–1095 m.

DESCRIPTION. **Plants** small, forming mats, dark green to more commonly golden-brown or -red. **Stems** creeping, often subascending distally, irregularly pinnately branched; in cross-section outer 2–3 rows of cells small, thick-walled, inner cells few, large, thin-walled, central strand absent. **Leaves** somewhat distant to crowded, often homomallous, erect-spreading, falcate-secund or straight and erect, lanceolate to linear-lanceolate, to 1.3 mm long, concave below, apex gradually long acuminate, base often rounded; margins plane or incurved distally, reflexed at base, weakly serrulate, apex more notably serrulate, teeth simple, not swollen or bifid; costae short and double, ca. 1/5–1/3 lamina length, diverging; laminal cells rather uniform, gradually differentiated toward base, smooth, linear to oblong-linear, weakly porose; basal cells slightly larger. **Dioicous**. **Perichaetia** lateral. **Seta** to 15

mm long, slender, smooth. **Capsule** inclined to subpendent, urn cylindrical to ellipsoid, to ca. 1 mm long, constricted below mouth when dry. **Operculum** conic-rostrate. **Peristome** double, exostome teeth cross-striate below, distally papillose, furrowed, trabeculate; endostome ± equal exostome length, basal membrane high, segments perforate, cilia absent. **Calyptra** mitrate, smooth, base lobed. **Spores** not observed.

DISCUSSION. The genus, as circumscribed here, is distinguished by small, mat-forming plants with lanceolate to linear-lanceolate leaves that are often homomallous and falcate-secund, with distally serrulate margins with simple, not bifid teeth, short costae (to 1/3 the lamina length), linear to oblong-linear median and upper laminal cells, and cross-striate furrowed exostome teeth, and high basal membrane. *Hookeriopsis* is here narrowly defined (cf. Buck, 1987); previously, the genus included all of *Trachyxiphium* and most species assigned to *Brymela* and *Thamniopsis*. The genus is likely to be confused with *Trachyxiphium*; however, that genus differs in the elongate costa extending beyond midleaf, the bifid teeth along the leaf margin, and distal laminal cells often with prorose papillae. At present, there remain about 30 species assigned to *Hookeriopsis* whose status has yet to be determined.

LITERATURE. Buck, W. R. 1987 (see family ref.).

Hypnella (Fig. 167) - A neotropical genus of six species.

HABITAT. On soil, rock, leaf litter, logs, occasionally epiphytic; lowland to upper montane forests, 100–3000 m.

DESCRIPTION. **Plants** medium sized, forming mats, pale to dark green, yellowish-brown or red, usually rather dull, occasionally glaucous. **Stems** spreading, rarely subascending or pendulous, irregular to regularly pinnately branched; in cross-section hyalodermis present or outer 2–3 rows of cells small, rusty-red, inner cells large, hyaline, central strand absent. **Leaves** crowded, erect to erect-spreading, ovate-oblong to narrowly or broadly oblong, 0.5–1.7 mm long, concave, apex acute-apiculate and often recurved, or long piliferous; margins reflexed below, finely serrulate to denticulate; costae double, usually 2/3 lamina length, parallel or slightly diverging; median cells linear to linear-oblong, walls entire to weakly porose, pluripapillose, 3–6 simple or branched papillae in a row over cell lumen; basal cells larger, oblong-rectangular, porose or not; insertion cells often golden-red. **Perichaetia** lateral, leaves differentiated. **Autoicous** or dioicous. **Seta** elongate, to 30 mm long, often roughened or papillose distally. **Capsule** inclined to horizontal, urn obloid to cylindrical, 0.5–3 mm long, annulus present as undifferentiated cells. **Operculum** rostrate. **Peristome** double, exostome teeth finely cross-striate, furrowed or finely papillose, hyaline bordered with median zig-zag line; endostome basal membrane somewhat low to high, segments smooth to finely papillose, keeled and weakly perforate, cilia absent. **Calyptra** mitrate, smooth, base lobed. **Spores** spherical, lightly papillose.

DISCUSSION. The genus is easily distinguished and not to be confused with any other family or genus by the pluripapillose laminal cells with papillae arranged in a single row, and the costa of two parallel forks. Some authors have argued for the placement of this genus in the Sematophyllaceae (cf. Crosby et al., 1985), close to *Taxithelium* and *Glossadelphus* (= *Phyllodon*, Hypnaceae of our treatment); however, *Hypnella* lacks differentiated alar cells and a short, forked costa.

LITERATURE. Allen, B. H. 1986. The taxonomic status of *Hypnella punctata*. The Bryologist 89: 224–226 [revised keys, illustrations]. - Crosby, M. R., B. H. Allen & R. E. Magill. 1985. A review of the moss genus *Hypnella*. The Bryologist 88: 121–129 [keys, maps].

Lepidopilidium (Fig. 168) - About 5–6 species in the Neotropics (Central America, West Indies, Venezuela, southward to Brazil, also Bolivia and northern Argentina); a tropical American-African genus of some 15–20 species, from near sea level to 1800(–2800) m.

HABITAT. Epiphytic, on branches and trunks of trees; mostly lowland and submontane forests.

DESCRIPTION. **Plants** small to somewhat large, forming loose to dense mats, generally glossy, pale to dark green, or golden yellow to red. **Primary stems** creeping, leaves scale-like; rhizoids clustered beneath. **Secondary stems** creeping or more often ascending, few branched; in cross-section hyalodermis well developed, outer 2–3 rows of cells small, thick-walled, inner cells hyaline, thin-walled, central strand absent. **Leaves** complanate or less often terete foliate, crowded to distant, crispate to flexuose or not when dry, appressed to more commonly spreading; lateral and dorsal/ventral leaves differentiated, **lateral leaves** generally asymmetric, ovate, ovate-lanceolate, or oblong to narrowly lanceolate, 1.6–5 mm long, often somewhat sigmoid, acute to acuminate, base usually asymmetric; margins often folded and ± clasping at base, plane to revolute, elimbate, entire to commonly sharply serrate distally; costae double, at base set apart or occasionally joined, diverging to occasionally subparallel, 1/3–2/3 lamina length; laminal cells smooth, median cells rhomboidal to more commonly fusiform or linear-fusiform, thin- to occasionally thick-walled; basal cells irregularly short to

long rectangular, somewhat lax; marginal cells linear, not forming a distinct border; **dorsal/ventral leaves** symmetric, ovate, ovate- to oblong-lanceolate, acute to short acuminate, margins entire to more commonly serrate, costae double, 1/3–1/2 lamina length, median cells rhomboidal to fusiform. **Gemmae** often produced in leaf axils, cylindrical, smooth. **Autoicous** or dioicous. **Perichaetia** lateral, leaves ovate- to triangular-lanceolate, acuminate, costae absent. **Seta** short to elongate, 2–8.5 mm long, smooth to more commonly papillose, distally or throughout, papillae warty to distinctly projecting. **Capsule** erect to inclined, urn ovoid to obloid, 0.8–1.8 mm long, exothecial cells strongly collenchymatous; stomata superficial, few, confined to urn base; annulus appearing as 2 rows of differentiated cells. **Operculum** usually long rostrate. **Peristome** double, exostome teeth furrowed, striate below, distally papillose; endostome basal membrane ± high, segments keeled (and perforate?), lightly papillose, cilia absent. **Calyptra** mitrate, sparsely hairy, laciniate at base. **Spores** spherical, mostly lightly papillose.

DISCUSSION. Likely only to be confused gametophytically with those members of *Lepidopilum* that exhibit strongly complanate and asymmetric, falcate or sigmoid leaves, the sporophytic features readily separate the two genera. In *Lepidopilidium* the seta is smooth to weakly papillose or roughened below the urn, never spinose, and the exostome is furrowed, striate below and distally papillose.

Lepidopilum (Fig. 168) - Primarily a neotropical genus containing about 40 species. Two or three species are found in montane habitats of West Africa.

HABITAT. Mostly epiphytic, on trunks and branches of trees and shrubs, also on bamboo nodes and lianas, a few species are aquatic, occurring on rocks along and in streams; wet lowland to upper montane forests, rarely extending into subpáramo and puna, from near sea level to 3700 m.

DESCRIPTION. **Plants** small to rather large, forming loose to dense mats or tufts, light to dark green, occasionally golden. **Primary stems** short to long creeping, leaves scale-like; rhizoids clustered beneath stems. **Secondary stems** spreading to more commonly erect and perpendicular to substrate, irregularly pinnately branched; in cross-section hyalodermis well developed, outer 2–3 rows of cells small, thick-walled, inner cells hyaline, thin-walled, central strand absent. **Leaves** spirally arranged and symmetric to more often complanate with lateral and dorsal/ventral ones differentiated; **lateral leaves** mostly asymmetric, ovate-lanceolate, obovate to oblong or oblong-lanceolate, 1.4–8 mm long, some falcate and often sigmoid-shaped, apex acuminate to obtuse; margins plane to recurved, mostly serrate to serrulate distally, elimbate or limbate; costae double, 1/5–3/4 lamina length; laminal cells smooth, walls entire to weakly porose; median cells linear or fusiform or hexagonal; marginal cells similar or forming a distinct border of long linear cells; **dorsal/ventral leaves** usually smaller, symmetric. **Gemmae** often present in leaf axils, rarely along leaf apices, cylindrical, smooth to papillose; propagula in the form of deciduous leaves. **Autoicous** or dioicous. **Perichaetia** lateral, leaves differentiated, smaller. **Seta** short to elongate, 1.7–28 mm, papillose to more often spinose distally or throughout. **Capsule** suberect, urn ovoid or ovoid-cylindrical, 0.8–2.2 mm long. **Operculum** short to long rostrate. **Peristome** double, exostome teeth papillose with whitish colored bordered; endostome basal membrane low, segments keeled and papillose, cilia absent. **Calyptra** mitrate to campanulate, plicate or smooth, base usually lobed, naked to more often hairy. **Spores** spherical, mostly lightly papillose.

DISCUSSION. The genus exhibits considerable variation, both in features of the gametophyte and sporophyte. Plants are, in general, epiphytic or saxicolous, never (or very rarely) on soil, logs or leaf litter; primary and secondary stems are differentiated, the latter spreading or erect-ascending; leaves are strongly complanate and asymmetric, or ± terete-foliate and symmetric, with margins bordered or not, laminal cells linear to large and hexagonal; seta is always papillose or papillose and spinose, and the capsules are erect to slightly inclined with the exostome bordered and papillose, and the endostomial basal membrane low; the calyptra is campanulate or mitrate, plicate or not, and often ornamented. *Lepidopilum* is a fine example of excessive naming by late 19th- and early 20th-century bryologists. There are well over 125 described with only a third being valid. *Lepidopilum* is not well collected, possibly due to locally small population size, and the fact that many general plant collectors do not like collecting only a few individual bryophyte plants.

LITERATURE. Churchill, S. P. 1988. A revision of the moss genus *Lepidopilum* (Callicostaceae). Ph. D. dissertation, City University of New York. - Churchill, S. P. 1992. Clarification and review of *Lepidopilum affine* and *L. grevilleanum* (Callicostaceae). Brittonia: 44: 350–355.

Pilotrichidium (Fig. 169) - A neotropical genus of two species; *P. callicostatum* (Müll. Hal.) A. Jaeger distributed in the northern Neotropics and *P. antillarum* Besch. restricted to the West Indies and Honduras.

HABITAT. On rocks along streams, rarely on tree branches; moist submontane to lower montane forests, 700–1500 m.

DESCRIPTION. **Plants** small to medium sized, forming mats, pale green to blackish-green. **Stems** spreading, irregularly to subpinnately branched; in cross-section hyalodermis present, central strand absent. **Leaves** often contorted when dry, ovate-oblong to oblong-ligulate, to 1.8 mm long, to 0.25 mm wide, apex obtuse-acute to truncate; margins plane, crenulate; costae double, strong, subpercurrent to percurrent, gradually divergent at base, becoming parallel and converging at apex, terminating in a projecting blunt tooth; upper and median cells irregularly isodiametric, thick-walled, smooth or pluripapillose, papillae several over cell lumen, basal cells subrectangular, thick-walled, smooth. **Dioicous**. **Perichaetia** lateral, leaves ovate, acute, ecostate, laminal cells smooth. **Seta** elongate, to 15 mm long, smooth, twisted. **Capsule** suberect, urn oblong, exothecial cells rectangular, thick-walled; stomata apparently absent. **Operculum** rostrate. **Peristome** double, exostome teeth striate below, papillose distally; endostome basal membrane high, cilia absent. **Calyptra** not observed. **Spores** spherical, appearing smooth.

DISCUSSION. *Pilotrichidium* is likely to be confused only with *Callicostella*, but differs by the exceedingly strong, smooth projecting costa and pluripapillose or smooth laminal cells. *Callicostella* has a weakly projecting, often serrate costa and unipapillose or smooth laminal cells. *Pilotrichidium callicostatum* exhibits laminal cells that are pluripapillose, whereas in *P. antillarum* the cells are smooth, except at the apex.

LITERATURE. Allen, B. H. & M. R. Crosby. 1986. A revision of the genera *Pilotrichidium* and *Diploneuron* (Musci: Hookeriaceae). Journal of the Hattori Botanical Laboratory 61: 45–64 [keys, illustrations].

Pilotrichum (= *Callicosta*) (Fig. 168) - A neotropical genus of about 20 species with the greatest diversity centered in the Antilles.

HABITAT. Epiphytic on trunks and branches; wet lowland to lower montane forests, from near sea level to 2460 m.

DESCRIPTION. **Plants** forming thin or rather dense tufts, light to dark green, with age becoming reddish-brown. **Primary stems** creeping, leaves reduced, scale-like, often eroded. **Secondary stems** erect, frondose, 2–10 cm or more, pinnate or bipinnate (occasionally tripinnate), with determinate growth or indeterminate with additional new secondary stems arising; in cross-section epidermal and outer cortical cells small and thick-walled, central strand absent. **Leaves** of secondary stem somewhat larger than branches, rather spirally arranged, not differentiated between lateral and dorsal/ventral, broadly ovate to oblong-ovate, concave, 0.7–0.9 mm long, apex short-acute, base weakly auriculate; margins recurved below, distally ± channeled, often weakly inflexed, dentate to serrulate; costae strong, double, 2/3–4/5 lamina length, ± parallel to slightly converging distally, joined at base or shortly above base and forming a single costa to base, weakly to strongly serrate on back, ending in a short spine; median and distal cells oblong to oval, thick-walled, occasionally with papillae projecting at cell angles; alar region ± distinct, cells subquadrate to rectangular. **Gemmae** absent or present, on back of costa distally or at base, or in leaf axils, occasionally along leaf margin. **Synoicous**, autoicous or dioicous. **Perichaetia** lateral, leaves differentiated, costate. **Seta** short, 0.6–2 mm long, smooth. **Capsule** usually shortly exserted, erect, urn short oblong, 1–2 mm long, exothecial cells ± thick and evenly walled; annulus absent. **Operculum** rostrate. **Peristome** double, exostome teeth papillose, not furrowed, endostome basal membrane high, segments weakly keeled and papillose, cilia absent or rudimentary. **Calyptra** campanulate, hairy. **Spores** spherical, finely papillose.

DISCUSSION. The genus is readily distinguished by the frondose habit, strongly costate leaves, and short seta, mostly twice the length of the capsule or less. A surprising number of species, slightly more than half, are narrowly restricted to one or a few islands in the West Indies (Crosby, 1969b). The name *Callicosta*, used in recent years, predates the previously employed name *Pilotrichum* which was thought to be illegitimate (in part due to the ambiguous wording of the *Botanical Code*, Art. 63); however, *Pilotrichum* is the correct name.

LITERATURE. Crosby, M. R. 1969a. A revision of the tropical American moss genus *Pilotrichum*. The Bryologist 72: 275–343 [keys, illustrations, maps]. - Crosby, M. R. 1969b. Distribution patterns of West Indian mosses. Annals of the Missouri Botanical Garden 56: 409–416. - Crosby, M. R. 1978. New combinations in *Callicosta* (Musci), the correct name for *Pilotrichum*. The Bryologist 81: 435–437.

Stenodesmus (Fig. 169) - A monotypic genus, *S. tenuicuspis* (Mitt.) A. Jaeger, is known from the lower Andean slopes of eastern Ecuador and southwestern Colombia.

HABITAT. Epiphytic on tree branches; submontane moist forests, at 625–925 m elevation.

DESCRIPTION. **Plants** medium sized, forming tufts, glossy pale-pellucid green. **Stems** appearing erect to suberect, primary stems short, creeping, secondary stems ascending, irregularly branched; in cross-section stems with a hyalodermis, outer 1–3 rows rather thick-walled, inner cells large and thin-walled, central strand absent. **Stem leaves** crowded, erect-spreading to suberect, apices recurved outward, mostly symmetric with lateral leaves weakly differentiated and somewhat asymmetric with a fold, broadly ovate to oblong, to 2.8 mm long, deeply concave, apices abruptly long acuminate, somewhat flexuose or not; margins entire or apices weakly serrulate; costae double, slender and rather weak, ca. 2/3–3/4 lamina length, slightly diverging, separate or weakly joined at base; laminal cells thin-walled and smooth, apical cells of acumen long linear; median cells long hexagonal to oblong-rectangular; basal cells lax, marginal cells long linear, forming a somewhat indistinct border; **branch leaves** narrower, ovate- to oblong-lanceolate, to 2 mm long. **Gemmae** not observed. **Dioicous**? **Perichaetia** lateral; leaves (on vaginula) broadly ovate-acuminate to ± triangular, to 1.8 mm long, distally serrate, ecostate. **Seta** elongate, reddish-brown, appearing golden due to spines, to 24 mm long, rather slender, strongly spinose throughout intermixed with low papillae. **Capsule** erect, urn ovoid, to 1.4 mm long, symmetric and smooth; neck short; exothecial cells mostly oblong-rectangular, thick-walled, weakly collenchymatous; annulus undifferentiated. **Operculum** conic-long rostrate. **Peristome** double, exostome teeth appearing pale-white bordered, with a darker golden-yellow median region, finely papillose; endostome finely papillose, basal membrane rather high, segments longer than exostome teeth, keeled, cilia absent. **Calyptra** campanulate, lobed at base, naked or with a few multicellular hairs, somewhat roughed at apex, weakly plicate. **Spores** spherical, finely papillose.

DISCUSSION. The genus is characterized by soft tufted plants, weak differentiation between lateral and dorsal/ventral ovate to oblong, deeply concave leaves, flexuose long acuminate apex, indistinct laminal border, weak double costae, thin-walled hexagonal to oblong-rectangular median cells, spinose and papillose elongate seta, erect capsule, bordered papillose exostome, high endostomial basal membrane, and lobed, campanulate calyptra. Presently known only from the type locality of Canelos, Ecuador, originally collected by Richard Spruce in 1857.

Stenodictyon (Fig. 169) - A neotropical genus of two species, *S. pallidum* E. Britton ex H. A. Crum & Steere (Greater Antilles) and *S. wrightii* (Sull. & Lesq.) Crosby (Central America, Venezuela, Colombia and Ecuador).

HABITAT: On soil, humus, base of trees, and logs, in moist shaded sites; submontane to montane forests, 800–2500 m.

DESCRIPTION. **Plants** medium sized to somewhat large, forming mats, pale to yellowish green or golden-brown. **Stems** creeping and spreading, irregularly pinnate branched, rusty-red; in cross-section hyalodermis present, central strand absent. **Leaves** evenly spirally arranged, not complanate, loosely erect to erect-sheathing, ovate-short oblong to oblong, 1.4–1.6 mm long, to 0.5 mm wide, deeply concave, apex abruptly long and narrowly acuminate (to 0.4 mm long); margins entire, occasionally with apices weakly serrulate, elimbate; costae double, 1/2–2/3 lamina length, parallel to slightly diverging; upper cells linear, median cells linear to oblong-linear, vermicular or straight-walled, smooth, walls entire or weakly porose, ends rounded or tapered acute; basal cells lax, short rectangular, hexagonal or oblong; insertion cells golden-brown. **Gemmae** apparently rare, at base of leaves, hyaline, 1–4 cells long. **Dioicous** or autoicous. **Perichaetia** lateral, leaves short ovate-subulate. **Seta** elongate, to 45 mm long, slender, smooth, distally roughened below urn. **Capsule** horizontal to pendulous, urn ovoid to elliptical, with a short neck, ca. 2 mm long; exothecial cells short oblong, walls evenly thickened, rim cells short oblong, oblate, rusty-red; stomata represented by 4–6 short cells. **Operculum** conic-rostrate. **Peristome** double, exostome teeth striate below, distally papillose, with a median furrow; endostome basal membrane rather low to moderately high, segments keeled, papillose, cilia absent. **Calyptra** short mitrate, lobed, smooth. **Spores** spherical, lightly papillose.

DISCUSSION. Features characterizing the genus include the creeping habit, presence of a hyalodermis, concave, oblong-ovate spirally arranged leaves with an abruptly long acuminate apex, thin-walled laminal cells, the upper cells linear and the median cells oblong, the cross-striate, furrowed exostome teeth, and the smooth, lobed, mitrate calyptra. *Stenodictyon bisodalense* B. H. Allen, Crosby & Magill (type from Costa Rica) is *Lepidopilum longifolium*. The two species can be separated as follows: *S. pallidum* — laminal cells vermicular, ends acute tapered, autoicous, seta to 14 mm long; and *S. wrightii* — laminal cells straight walled, ends obtuse, dioicous, seta 20–40 mm long.

LITERATURE. Allen, B. H., M. R. Crosby & R. E. Magill. 1986. A review of the genus *Stenodictyon* (Musci). Lindbergia 11: 149–156 [keys, maps].

Thamniopsis (Fig. 170) - Ten species in the Neotropics; a pantropical genus of about 15 species.

HABITAT. On soil, rocks, and logs; wet lowland to mid, rarely upper, montane forests, from near sea level to 3400 m.

DESCRIPTION. **Plants** mostly medium sized to somewhat large, forming mats, pale to dark green, yellowish to golden. **Primary stems** creeping; in cross–section hyalodermis present, central strand absent. **Secondary stems** creeping, spreading, subpendent to ascending, stipitate or not. **Leaves** of stems and branches dimorphic, rarely monomorphic, usually weakly to strongly complanate, ovate, ovate-oblong or oblong-lanceolate, smooth or undulate, apex obtuse, acute or abruptly long acuminate, base often rounded or subauriculate; margins entire to more commonly serrate, often sharply so, teeth single or bifid, less often (on stem leaves) serrulate or dentate distally or entire; costae double, 1/2–2/3 (–4/5) lamina length, diverging or parallel, smooth or toothed on back; median cells linear or oblong-linear, narrowly rectangular, rarely rhomboidal or fusiform, smooth, walls usually weakly to strongly porose, rarely entire; basal cells usually differentiated, conspicuously enlarged, oblong or rectangular. **Autoicous**, rarely dioicous. **Perichaetia** lateral, leaves differentiated. **Seta** elongate, smooth. **Capsule** inclined to subpendent, urn cylindrical or ovoid-cylindrical. **Operculum** conic-long rostrate. **Peristome** double, exostome teeth densely cross-striate, distally papillose, with a strong median furrow; endostome basal membrane rather high, segments keeled and usually perforate, cilia absent. **Calyptra** mitrate, smooth, base lobed. **Spores** spherical, usually lightly papillose.

DISCUSSION. A distinctive feature in *Thamniopsis* is the strong leaf dimorphism exhibited between stems and branches for several of the species presently assigned to this genus (e.g., *T. diffusa* (Wilson) W. R. Buck and *T. killipii* (R. S. Williams) E. B. Bartram); leaf dimorphism of this type is rare among the other neotropical species of the family. Additional features characterizing the genus include the presence of a stem hyalodermis; weakly to rather strongly complanate leaves; smooth laminal cells; enlarged basal as compared to median and upper cells; smooth seta; and cross-striate, deeply furrowed exostome teeth. *Thamniopsis* has been emended recently (Buck, 1987, see family ref.) to include a number of species previously placed in *Hookeriopsis*.

Trachyxiphium (Fig. 170) - A neotropical genus containing about 10–15 species.

HABITAT. On humus, logs, exposed roots, trunks, and branches of treelets and trees, also in moist to wet sites on soil and rocks; mostly montane primary and secondary forests, rarely extending into the lowland forests, páramo, or puna, from near sea level to 3755 m.

DESCRIPTION. **Plants** mostly small to somewhat medium sized, forming mats, glossy light to dark green or reddish-brown to golden. **Stems** spreading or ascending; in cross-section hyalodermis absent or weakly present on stems but usually absent on branches, central strand absent. **Leaves** often homomallous, erect to falcate or falcate-secund, lanceolate to ovate- or oblong-lanceolate, to ca. 2 mm long, apex short to more commonly long acuminate, base usually rounded; margins usually strongly serrate, teeth bifid, swollen or not, rarely serrulate in apices; costae double, 3/4–4/5 lamina length, usually strong, parallel, occasionally one costa longer; upper and median cells linear, usually porose, smooth to more commonly projecting at distal angles; basal cells little differentiated, usually slightly broader and shorter. **Autoicous**, rarely dioicous. **Perichaetia** lateral, leaves differentiated, erect to falcate, ovate- to lanceolate-subulate. **Seta** elongate, 5–20 mm long, slender, smooth, occasionally distally papillose below neck. **Capsule** suberect to inclined, urn ovoid to ovoid-short cylindrical, 1 mm long; exothecial cells oblong, longitudinal walls often thicker, weakly collenchymatous; stomata represented by 4–6 subquadrate cells. **Operculum** conic-short to long rostrate. **Peristome** double, exostome teeth finely cross-striate, distal tips papillose, strongly furrowed; endostome basal membrane ± high, segments keeled and usually narrowly perforate, papillose. **Calyptra** mitrate-campanulate, smooth or weakly plicate at base, lobed at base. **Spores** spherical, lightly papillose or appearing smooth.

DISCUSSION. The genus is characterized by the typically small habit, absence of a hyalodermis, often falcate-secund, elimbate leaves, mostly long acuminate apex, bifid, often swollen, teeth, elongate double costae, usually linear median and upper laminal cells, a seta slenderly elongate, smooth or occasionally roughened distally, exostome finely cross-striate below, papillose above, furrowed, high endostomial basal membrane, and the naked calyptra. The genus is similar to *Hookeriopsis* (see comments under that genus). A recent segregate of *Hookeriopsis* (cf. Buck, 1987, see family ref.), *Trachyxiphium* is in need of reassessment. Several of the species, now relegated to synonym, may be valid.

PLAGIOTHECIACEAE

A monotypic family as presented here, placed in the Hypnales.

Plagiothecium (Fig. 171) - Four neotropical species; fewer than the 52 species attributed to this genus, distributed in temperate regions, in the tropics confined to montane zones.

HABITAT. On soil, humus, base of tree trunks, logs and rocks; lower montane forests to zacatonal, páramo, and punas, 1800–4350 m.

DESCRIPTION. **Plants** medium sized, forming loose to ± dense mats, glossy light to dark green, or yellowish-green. **Stems** spreading to subascending, simple to irregularly branched; in cross-section central strand present; pseudoparaphyllia and paraphyllia absent; rhizoids beneath, reddish-brown, smooth. **Leaves** weakly to strongly complanate, ovate to ovate-lanceolate, 0.9–2.6 mm long, asymmetric, folded on one side or not, weakly concave, apex acute to narrowly acuminate, base weakly to strongly decurrent; margins plane to reflexed or recurved below, entire or distally serrulate, elimbate; costae short and forked, occasionally absent; laminal cells smooth, median cells linear and ± vermicular, walls rather firm; alar region often differentiated, cells few, quadrate to oblong-short rectangular. **Propagula** occasionally present, cylindrical, smooth. **Autoicous** or dioicous. **Perichaetia** lateral, leaves elongate, sheathing. **Seta** elongate, 10–25 mm long, often twisted distally, smooth. **Capsule** suberect to horizontal, urn obloid-cylindrical, 1.5–2.5 mm long, neck short; exothecial cells isodiametric, thick-walled; annulus in 2–3 rows, deciduous. **Operculum** conic to conic short rostrate. **Peristome** double, exostome teeth 16, cross-striate below, distally papillose, bordered, trabeculate on back; endostome basal membrane high, segments 16, keeled and perforate, cilia 1–3, nodose. **Calyptra** cucullate, smooth and naked. **Spores** mostly spherical, smooth or lightly papillose.

DISCUSSION. *Plagiothecium* is characterized, gametophytically, by rather soft, glossy mats, the asymmetrical, often complanate, ovate to ovate-lanceolate leaves, acuminate or acute apex, decurrent base, entire or weakly serrulate margins, short and forked costa, linear upper laminal cells, and few oblong or quadrate alar cells. The Plagiotheciaceae, as treated here, is monotypic, containing only *Plagiothecium*. Previously classifications have include several other genera in the family. For a historical overview see Buck and Ireland (1985).

Study guide. Leaves are sufficient for identification; however, care must be taken when removing leaves so that the base is left intact to examine the degree of decurrency. Leafy stems with some of the leaves removed can also be used to examine this feature.

LITERATURE. Buck, W. R & R. R. Ireland. 1985. A reclassification of the Plagiotheciaceae. Nova Hedwigia 41: 89–125. - Ireland, R. R. & W. R. Buck. 1989. Plagiotheciaceae. Flora Neotropica Monograph 50: 1–22 [keys, illustrations, maps].

POLYTRICHACEAE

Plants small to very large and robust, often coarse. **Stems** erect, solitary or few branched. **Leaves** oblong- to lingulate-lanceolate or differentiated with a narrow to broad lanceolate limb from a clasping sheathing base that is broadly oblong to obovate-oblong; margins plane, erect or incurved or folded, often serrate to spinose, teeth single or double, sometimes limbate; costa single, usually strong, narrow to nearly width of limb, percurrent to somewhat long excurrent, often with teeth on abaxial side; sheathing base cells mostly elongate-rectangular; limb cells isodiametric, thick-walled; lamellae on adaxial side, in continuous or discontinuous rows over the costa, few to several cells high, terminal lamella cells variously shaped, rounded, truncate, U-shaped or pyriform, smooth or papillose. **Dioicous**, rarely autoicous. **Perichaetia** terminal; leaves differentiated. **Seta** mostly elongate, stout and wiry. **Capsule** suberect to inclined, urn cylindrical, terete or 2–4-sided. **Operculum** usually long rostrate, oblique. **Peristome** single, teeth mostly 32 or 64, joined terminally to an exserted columella (epiphragm). **Calyptra** smooth to slightly scabrous distally, or densely hairy. **Spores** variously ornamented.

DISCUSSION. The Polytrichaceae contain about 18 genera and some 200 or more species with a worldwide distribution; in the Neotropics 10 genera and about 40 species. The family is distinguished by the presence of longitudinal lamellae on the upper leaf surface, formation of an epiphragm from the columella, and multicellular peristome appearing single and commonly with 32 or 64 teeth. Plant size is remarkably variable. Several species can range from 0.5 to 30 cm or more in height. Many members of this family are some of the earliest colonizers of disturbed montane sites such as landslides, exposed banks, and roadside cuts.

Study guide. Identification requires in most cases a cross-section of the leaf, midway on limb or if leaves are undifferentiated between limb and sheath then just above midleaf, to examine the lamellae (extent of rows covering the upper lamina, number of cells high, and ornamentation and shape of the

terminal cells); it is also useful to scrape the upper surface to remove the lamellae to obtain a side-view.

LITERATURE. Hyvönen, J., T. A. Hedderson, G. L. Merrill, J. G. Gibbings, S. Koskinen. 1998. On phylogeny of the Polytrichales. The Bryologist 101: 489–504. - Schiavone, M. M. 1978. Las Polytrichaceae del noroeste Argentino. Lilloa 35: 31–65 [keys, illustrations]. - Schiavone, M. M. 1993. Bryophyta Musci: Polytrichiales. Flora Criptogámica de Tierra del Fuego 14(12): 1–61 [keys, illustrations]. - Smith, G. L. 1971. A conspectus of the genera of Polytrichaceae. Memoirs of the New York Botanical Garden 21: 1–83 [keys to genera, limited illustrations, no generic descriptions; a long time student of the Polytrichaceae, Gary Smith, has recently published under the name G. S. Merrill].

1. Leaf margins bordered 2
1. Leaf margins not bordered or indistinctly so 3
2. Margins singly toothed; cells of border lightly pluripapillose ..... **Steereobryon**
2. Margins doubly toothed; cells smooth, not papillose ..... **Atrichum**
3. Margins folded and obscuring upper surface of limb *or* terminal cells of lamellae U-shaped ....**Polytrichum** p.p.
3. Margins plane or incurved, upper surface usually observable; terminal cells of lamellae variously shaped, rounded, truncate or pear-shaped 4
4. Lamellae restricted to upper costa surface ..... **Oligotrichum**
4. Lamellae extending over costa and lamina surface 5
5. Stems distally branched, branches to 7 cm long; leaves to 12 mm long; ?Peru, southern South America ..... **Dendroligotrichum**
5. Stems unbranched; leaves mostly less than 10 mm long 6
6. Leaves strongly differentiated between sheath and limb, sheath obovate to oblong-obovate; peristome teeth 64 or absent..... 7
6. Leaves not differentiated, or slightly differentiated with a sheath and limb, sheath ovate, slightly broader than limb width; peristome teeth 32 10
7. Peristome absent; seta rather short, to 6 mm long; urn subglobose, to 2.4 mm long, strongly wrinkled when dry; stomata absent; restricted to montane southeastern Brazil ..... **Itatiella**
7. Peristome present; seta mostly much longer; urn cylindrical or obloid and/or variously angled; stomata present; geographical range broader 8
8. Terminal lamellae cells conic, coarsely papillose; leaf limb lacking an orange spot; capsules 4-angled ..... **Polytrichastrum**
8. Terminal lamellae cells pear-shaped, smooth 9
9. Leaf limb with a distinct orange spot; capsules 2-angled ..... **Polytrichadelphus**
9. Leaf limb lacking an orange spot; capsules strongly 4-angled ..... **Polytrichum** p.p.
10. Leaves usually piliferous or cucullate; margins entire or weakly dentate at juncture with piliferous tip; capsules ± bilaterally compressed, asymmetrical; calyptrae smooth below, sparsely hairy at apex ..... **Notoligotrichum**
10. Leaves mostly acute, not piliferous; margins serrate or dentate distally; capsules terete, ± symmetrical; calyptrae densely hairy ..... **Pogonatum**

Atrichum (Fig. 172) - Four or five species in the Neotropics; about 20 species of temperate regions, particularly the Northern Hemisphere.

HABITAT. On soil, in partly or fully shaded sites, frequent along stream banks; submontane to upper montane forests or associated with marginal and open forests, at elevations mostly from 1000–2600(–3000) m, at high latitudes in the Neotropics probably less than 1000 m.

DESCRIPTION. **Plants** medium sized, forming loose tufts, dark green to blackish-green or -brown. **Stems** erect, simple to few branched, radiculose; central strand well-developed; rhizoids reddish-brown or pale white. **Leaves** crispate, narrowly- to oblong-lanceolate, 5–10 mm long, often weakly to strongly undulate, usually toothed on back of lamina and costa, apex acute to short acuminate, base little differentiated, weakly sheathing; margins plane, limbate, doubly toothed; costa narrow, percurrent, in cross-section with stereid bands above and below guide cells; laminal cells oblong-short rectangular to subquadrate, thick-walled; basal cells rectangular, thick-walled; margins cells elongate; lamellae 4–6, confined to costa, in few rows, 3–6 cells high, terminal cell rounded. **Dioicous** or autoicous. **Perichaetia** terminal; leaves differentiated. **Seta** 1–3(4), elongate, smooth. **Capsule** suberect to inclined, urn cylindrical, asymmetric, slightly to somewhat strongly curved; exothecial cells rectangular, thick-walled. **Operculum** conic long-rostrate, oblique. **Peristome** teeth 32. **Calyptra** cucullate, roughened distally. **Spores** papillose.

DISCUSSION. The genus is characterized by the crispate and contorted leaves when dry, not or weakly differentiated leaf base, narrow costa, 4–6 rows of lamellae, doubly toothed and bordered margins, and 32 peristome teeth. The only other genus likely to be confused with *Atrichum* is

Steereobryon - the latter is readily differentiated by the finely pluripapillose and bluntly, single toothed margins. Two of the most common species can be distinguished by the following: *A. oerstedianum* (Müll. Hal.) Mitt. — plants dioicous, leaves broadly oblong-lanceolate, often undulate, often frequently spinose on back; and *A. polycarpum* (Müll. Hal.) Mitt. — plants autoicous; leaves mostly narrowly lanceolate, rarely undulate, dorsal side with few or no teeth.

LITERATURE. Nyholm, E. 1971. Studies in the genus *Atrichum* P. Beauv. Lindbergia 1: 1–33 [includes *Steereobryon*; keys, illustrations].

Dendroligotrichum (Fig. 172) - A single species possibly represented in the Neotropics, *Dendroligotrichum dendroides* (Hedw.) Broth., reported from Peru but not confirmed. A genus of two species, with a circum-Antarctic distribution.

HABITAT. On soil, possibly bank slopes; habitat unknown, expected in open montane to puna, at high elevations.

DESCRIPTION. **Plants** large and robust, solitary or forming tufts. **Stems** erect, dendroid, to 25 cm or more tall, tomentose at base, branches suberect and often curled distally, to 7 cm long; rhizoids dull white. **Leaves** of branches somewhat spreading and flexuose-curled from an appressed base when dry, limb erect-spreading to spreading when wet, linear-lanceolate from an obovate or ovate sheathing base, to 12 mm long (base ca. 2 mm long); margins of sheathing base plane, of limb erect, sharply serrate; costa narrow in base, expanding in limb, distally on back sharply toothed; lamellae 2–3 cells high, toward margin one cell high, terminal cell rounded; margin cells of limb subquadrate, thick-walled; sheathing base cells linear to linear-long rectangular, walls thin but firm. **Dioicous**. **Perichaetia** terminal on branches. **Seta** to 5 cm long. **Capsule** suberect to inclined, urn short cylindrical, to 2 mm long; stomata immersed, scattered throughout. **Operculum** long rostrate, oblique. **Peristome** teeth 64, distally attached to an epiphragm, basal membrane somewhat high. **Calyptra** sparsely hairy or naked. **Spores** papillose.

DISCUSSION. The genus is readily distinguished by its large size (to 25 cm), dendroid habit and cylindrical capsule. The report of this species from Peru has not been confirmed; based on a collection by *Philippi s.n.* cited by Jaeger (Ber. Thätigk. St. Gallischen Naturwiss Ges. 1873–74: 257. 1875). Given the conspicuous large size of this species, it is likely to have been collected by general plant collectors but this appears not to have been the case. We suspect that this species does not occur in the Neotropics. This is inferred from the above observations and the fact that it has not been reported for Bolivia nor has it been recorded by Schiavone (1978) for northern Argentina. *Dendroligotrichum* is well documented from temperate sites of Argentina and Chile, also Juan Fernandez and New Zealand.

LITERATURE. Schiavone, M. M. 1978, 1993 (see family ref.).

Itatiella (Fig. 172) - A single species in the Neotropics, *I. ulei* (Broth. ex Müll. Hal.) G. L. Sm., from southeastern Brazil.

HABITAT. On soil banks, along trails and stream banks; open montane forest and non-forested sites, at elevations from 2100–2500 m.

DESCRIPTION. **Plants** rather small, gregarious or small tufts, dark green to blackish. **Stems** erect, to 1.5 cm tall, tomentose at base; rhizoids whitish. **Leaves** crowded, limb spreading-incurved from an appressed base, lanceolate-ligulate from an ovate or elliptical sheathing base, to 2.8 mm long, apex broadly acute and apiculate, cucullate and curved; margins of base plane, limb inflexed, entire; costa somewhat narrow in base, expanding in limb, toothed on back near apex, teeth large and rather blunt; cells of base distally subquadrate to short rectangular and rounded, collenchymatous, basal cells short to long rectangular; lamellae 6–7 cells high in central part, terminal cell somewhat rounded. **Dioicous**. **Perichaetia** terminal; leaves larger. **Seta** to 6 mm long, stout. **Capsule** exserted, suberect, urn subglobose, to 2.4 mm long, strongly wrinkled when dry; stomata absent. **Operculum** long rostrate, oblique. **Peristome** absent. **Calyptra** sparsely hairy. **Spores** spherical to somewhat ellipsoid, finely papillose.

DISCUSSION. The genus is characterized by the typically small plants, leaves to 2.8 mm long, cucullate and inflexed distally, strongly wrinkled capsule when dry, and both stomata and peristome absent. *Itatiella* and *Notoligotrichum* are segregates from the previously broadly and ill defined *Psilopilum* by Smith (1971).

LITERATURE. Smith, G. L. 1971 (see family ref.).

Notoligotrichum (Fig. 173) - Two species in the Neotropics, *N. mexicanum* (G. L. Sm.) G. L. Sm. (central Mexico), and *N. trichodon* (Hook.f. & Wilson) G. L. Sm. (Andes); a genus of about 10 species of the Southern Hemisphere.

HABITAT. On soil, in exposed sites; zacatonal, páramo and puna, at elevations above treeline, 4000–4500 m.

DESCRIPTION. **Plants** rather fragile, often growing in short dense tufts, reddish to golden-brown. **Stems** erect, 2–5 cm tall. **Leaves** erect to appressed, ovate-narrowly lanceolate or -subulate to oblong-ovate, 4–5 mm long, to 1.4 mm wide near base, apex short acuminate, often piliferous or cucullate and obtuse-rounded, smooth or roughened on back distally; margins plane, occasionally inflexed to erect and channeled near apex, entire or weakly dentate at juncture with excurrent costa; costa percurrent to excurrent as a short piliferous tip; median cells irregularly quadrate or short rectangular and often oblate, thick-walled; basal cells quadrate to mostly rectangular, lax and thin-walled; lamellae in distal 1/3–1/2 of leaf, over costa and lamina in many rows, 5–7 cells high, terminal cells rounded, smooth. **Dioicous**. **Seta** elongate 14–18 mm long, stout, smooth. **Capsule** suberect to inclined, urn asymmetric, bilaterally-compressed, ovoid, appearing subglobose when deoperculate; stomata appearing sunken at urn base. **Operculum** long rostrate, oblique. **Peristome** teeth 32, reduced, tapering hyaline. **Calyptra** cucullate, apex sparsely hairy, smooth below.

DISCUSSION. The genus is characterized by 32 hyaline, reduced peristome teeth and the sparsely hairy tipped calyptra. The two species can be differentiated as follows: *N. mexicanum* — leaves obtuse-rounded, toothed at back distally, with cucullate apex, and *N. trichodon* — leaves piliferous, smooth at back, with acuminate apex. Members of this genus were previously placed in the genus *Psilopilum*.

LITERATURE. Smith, G. L. 1971 (see family ref.).

Oligotrichum (Fig. 173) - Three or four species in the Neotropics; about 25 species associated with the Southern Hemisphere.

HABITAT. On soil, in exposed sites usually associated with other tufted bryophytes; open upper montane to páramo and puna, (1050–)2600–4000 m.

DESCRIPTION. **Plants** small, forming low tufts, dark green to reddish-brown. **Stems** erect, to 1 cm tall. **Leaves** somewhat crispate when dry, erect when wet, upper leaves obovate-lanceolate, 4–5 mm long, to 2 mm wide, lower leaves oblong or obovate-oblong, apex acute, base weakly sheathing stems; margins plane to distally incurved at apex, denticulate in distal 1/2; costa rather strong, percurrent; median cells isodiametric, rather collenchymatous; basal cells short to rather long rectangular-rounded, somewhat lax; upper marginal cells firm, thick-walled; lower 1/3–1/2 of leaf with cells short to long rectangular, thick-walled; lamellae in 6–7 rows, 4–5 cells high, terminal cell rounded. **Dioicous**. **Perichaetia** terminal; leaves strongly enveloping seta, longer that stem leaves. **Seta** elongate, to 40 mm long, wiry. **Capsule** suberect, ovoid-cylindrical, to 4 mm long, indistinctly 6–8 angled; stomata numerous, superficial. **Opercula** conic-long rostrate, oblique. **Peristome** teeth 32. **Calyptra** cucullate, sparsely hairy or smooth, slightly roughed at apex.

DISCUSSION. The species are separated geographically, *O. aligerum* Mitt. (Mexico, Central America, and West Indies), the recently described *O. denudatum* G. L. Sm. Merrill (Brazil), and *O. erosum* (Hampe) Lindb. (Colombia to Peru).

LITERATURE. Merrill, G. L. S. 1991. *Oligotrichum denudatum* (Polytrichaceae), a new moss from Minas Gerais, Brazil. Novon 1: 107–109. - Mullen, D. & T. C. Frye. 1947. Middle and South American species of *Oligotrichum*. The Bryologist 50: 67–79.

Pogonatum (Fig. 173) - Ten species in the Neotropics; about 52 species distributed worldwide, generally associated with temperate and montane regions.

HABITAT. On soil or soil covered rocks, frequent on exposed landslides and roadcuts; open montane and páramo areas, from near sea level to more commonly 1000–4750 m.

DESCRIPTION. **Plants** small to large, solitary or forming tufts, dark green to reddish-brown or blackish. **Stems** mostly erect, occasionally distally curved. **Leaves** rather crowded, contorted or crispate when dry, mostly weakly differentiated between sheath and limb, base slightly expanded and slightly sheathing, or not, ovate to short oblong, limb oblong-lanceolate or lingulate-lanceolate; margins plane, dentate to somewhat sharply serrate; costa weak to mostly strong, percurrent; median cells isodiametric, thick-walled; lamellae extending over lamina and costa, 2–6 cells high, terminal cells single or paired, truncate, rounded or pear-shaped. **Dioicous**. **Perichaetia** terminal. **Seta** elongate, stout and smooth. **Capsule** suberect to inclined, urn short to long cylindrical, terete, not angular, ± symmetrical. **Operculum** conic-mammillate. **Peristome** teeth 32. **Calyptra** densely hairy. **Spores** variously ornamented.

DISCUSSION. The genus is rather variable and necessarily defined by a combination of characters including a differentiated leaf base, absence of a hyaline margin in the leaf sheath, numerous rows of lamellae over a broad costa, often thick-walled or paired terminal lamellae cells, densely hairy calyptra, cylindrical capsules with 32 peristome teeth, roughened-papillose exothecial cells and

absence of stomata. Three characters considered by Hyvönen (1989) to be uniquely derived (synapomorphies) defining *Pogonatum* as a monophyletic group included: exothecial cells roughened-papillose, absence of stomata, and strongly pigmented 32 compound peristome teeth. The worldwide treatment by Hyvönen (1989) is very useful for the Neotropics, and includes analyses of the phylogeny and geography of the genus.

LITERATURE. Hyvönen, J. 1989. A synopsis of the genus *Pogonatum* (Polytrichaceae, Musci). Acta Botanica Fennica 138: 1–87 [keys, illustrations]. - Menzel, M. 1985 [1986]. Die Gattung *Pogonatum* P. Beauv. (Polytrichales, Musci) in Lateinamerika 1. Taxonomie und Geographie von *Pogonatum campylocarpum* (C. Müll) Mitt. und *P. subflexuosum* (Lor.) Broth. Lindbergia 11: 134–140. - Menzel, M. 1986. The genus *Pogonatum* P. Beauv. (Musci: Polytrichales) in Latin America 2. Taxonomy and geography of the section *Cephalotrichum* (C. Muell.) Besch. Lindbergia 12: 43–46.

Polytrichadelphus (Fig. 174) - About 22 species recorded in the Neotropics, possibly fewer than 10 (Costa Rica, Andes, and southeastern Brazil); a genus stated to contain 25 species, confined to the Southern Hemisphere, primarily to South America and Australasia.

HABITAT. On soil, not infrequent along bank slopes, including roadcuts; open montane to páramo and puna, 1100–4200 m.

DESCRIPTION. **Plants** mostly medium sized to very large and robust, solitary to forming loose or dense tufts, dark green to mostly rusty-red or deep, dark red. **Stems** simple or few branched by innovations, 3–30 cm tall; central strand well developed. **Leaves** erect to appressed when dry, erect- to wide-spreading when wet, differentiated with a basal oblong (ovate-oblong) to obovate-oblong sheath, reddish-orange semi-circle extending down 1/3–1/2 from the base-limb junction, distal limb narrow to broadly ligulate-lanceolate, apex acute to acuminate, sheathing base concave and clasping; margins of sheathing base plane, limb plane more commonly erect to incurved, serrate, bluntly so at times, to spinose or ciliate; costa above sheath base expanding and extending across limb, back distally smooth to roughened by short projecting papillae or strongly toothed; cells of sheathing base long and narrowly rectangular, junction between sheath and limb with strongly compressed oblate oblong-rectangular cells; lamellae extending across limb, ca. 8 cells high, terminal cell pear-shaped, smooth. **Dioicous**. **Seta** elongate, 15–85 mm long, stout, smooth. **Capsule** suberect to inclined, urn 2-angled, 2.5–5.5 mm long. **Operculum** long rostrate from a plano-convex base. **Peristome** teeth 64, attached to an oval or round epiphragm. **Calyptra** cucullate, naked (occasionally fringed with paraphyses). **Spores** appearing lightly papillose.

DISCUSSION. A distinguishing feature of this genus is the orange or reddish-orange spot found on the distal sheathing base. The genus is considered to be diverse in the northern Andes, an area of "secondary evolution" (Smith, 1971); however given the variability and polymorphism within and among between populations, the justifiable diversity may be less than the number of published names would suggest.

LITERATURE. Proctor, M. C. F. 1992. Scanning electron microscopy of lamella-margin characters and the phytogeography of the genus *Polytrichadelphus*. Journal of Bryology 17: 317–333. - Smith, G. L. 1971 (see family ref.).

Polytrichastrum (Fig. 174) - Two species in the Neotropics, *P. alpinum* (Hedw.) G. L. Sm. and *P. tenellum* (Müll. Hal.) G. L. Sm.; a genus of about 10 or more species of cool temperate regions.

HABITAT. On soil in exposed sites; open montane to páramo or puna, 1200–4400 m.

DESCRIPTION. **Plants** medium sized to rather large, forming loose tufts, dark reddish-brown. **Stems** 4–15 cm tall, erect to erect-spreading, somewhat stiff; central strand well developed. **Leaves** when dry appressed to spreading above base, when wet erect-spreading or spreading-recurved, strongly differentiated between sheathing base and limb, base ovate to ovate-oblong, 1.6–3 mm long, to 2.6 mm wide, limb narrowly lanceolate, 2.6-12 mm long, apex long acuminate; margins erect to slightly inflexed, base entire, limb sharply toothed; costa percurrent; limb cells mostly quadrate, thick-walled; cells between junction of limb and base oblate oval-elongate, very thick-walled; sheathing base cells long rectangular, somewhat tapering or rounded, thin-walled; lamellae covering costa and lamina, in cross-section 6–8 cells high, terminal lamellae cells distinctly papillose, papillae large. **Dioicous**. **Capsule** indistinctly 4-angled. **Operculum** rostrate, oblique. **Peristome** single, teeth ca. 40, attached to epiphragm, marginal teeth on epiphragm. **Calyptra** cucullate, pilose.

DISCUSSION. The genus is similar to *Polytrichum* sharing the differentiated limb and base, with lamellae extending over both the costa and lamina, the peristome teeth attached to an epiphragm, and the densely hairy calyptra. It differs from that genus by the thickened terminal lamellae that are conic, smooth or papillose, weakly 4-angled cylindrical capsules, weak or absent constriction between neck and hypophysis, fewer than 64 (ca. 40) peristome teeth, and erect, denticulate epiphragm processes attached to back of peristome teeth. *Polytrichastrum tenellum* (Müll. Hal.) G. L. Sm. is distinguished

from *P. alpinum* (Hedw.) G. L. Sm. by the terminal lamellae (as viewed from the side) which in the former are crenulate, and in the latter entire. Members of this genus were previously assigned to *Pogonatum*.

LITERATURE. Smith, G. L. 1971 (see family ref.).

Polytrichum (Fig. 174) - About 12 species in the Neotropics, probably half or fewer are valid; a widespread genus of some 40 species.

HABITAT. On soil and soil covered rocks, common in disturbed sites; open montane to zacatonal, páramo and puna, mostly 500–4700 m.

DESCRIPTION. **Plants** variable in size, mostly medium sized to large and robust, gregarious or forming compact tufts, dark green to reddish-brown. **Stems** erect, simple (branched?), reddish-brown; central strand well developed. **Leaves** erect-appressed to -spreading when dry, erect- to wide-spreading when wet, leaf differentiated between sheathing base and limb, base ovate-oblong and sheathing, limb oblong- or ligulate-lanceolate, apex broadly acute to acuminate; margins of limb erect to broadly folded and forming a flap covering adaxial surface of limb, base entire, limb entire with apices toothed or limb sharply serrate; costa ± narrow in leaf base, expanding in limb to 2/3–4/5 of width, percurrent to short excurrent, often toothed distally on back, in cross-section stereids above and below guide cells; cells at transition between limb and base oblong-oblate, compressed and thick-walled base cells long rectangular, thin-walled; lamellae cells in many rows, 6–7 cells high, terminal cell pear- or U-shaped. **Dioicous**. **Perigonia** terminal; leaves strongly differentiated, short and broadly oval to ovate. **Perichaetia** terminal; leaves similar to stem leaves. **Seta** elongate, erect or weakly flexuose, rather stout. **Capsule** suberect to horizontal, urn somewhat longer than wide, strongly 4-angled; neck short and compressed, constricted below urn base. **Operculum** rostrate from a plano-convex base. **Peristome** single, teeth 64, teeth attached to a thick oval epiphragm, teeth alternating with short segments or lobes beneath epiphragm. **Calyptra** cucullate, densely hairy. **Spores** appearing smooth.

DISCUSSION. The genus is characterized by the differentiated limb and base, U- or pear-shaped lamellae extending over the costa and lamina, strongly 4-angled capsules, strongly constricted hypophysis below neck, 64 peristome teeth attached to an epiphragm, lower margin of epiphragm divided into lobes alternating with peristome teeth, and densely hairy calyptra. One of the most commonly encountered neotropical mosses of open montane and alpine sites, *P. juniperinum* Hedw., is readily distinguished by limb margins extending over and nearly enclosing the upper leaf surface. The leafy plants are highly variable with several rather distinct forms and a considerable number of synonyms (cf. Messmer & Frye, 1947; Walther, 1934).

LITERATURE. Messmer, L. & T. C. Frye. 1947. The *Polytrichum juniperinum* group between South America and the United States. The Bryologist 50: 259–268. - Smith, G. L. 1976. Neotropical Polytrichaceae IV. The Bryologist 79: 93–95. - Walther, K. 1934. Untersuchungen Über die variabilität innerhalb des formenkreises von *Polytrichum juniperinum* Willd. Annales Bryologici 7: 121–156.

Steereobryon (Fig. 174) - Two species confined to the Neotropics, *S. subulirostrum* (Schimp. ex Besch.) G. L. Sm. (Mexico, Central America, Greater Antilles, tropical Andes), and *S. elamellosum* (Herzog) M. Menzel (Bolivia).

HABITAT. On soil, often rocky or sandy, exposed to partly shaded sites; marginal or open montane forests, 1700–2615 m.

DESCRIPTION. **Plants** small, gregarious or forming loose short tufts, dark-green to brownish-green. **Stems** erect, simple, to 10 mm tall, reddish; in cross-section central strand present. **Leaves** progressively larger from base, ± distantly spaced, crispate and curled when dry, erect-spreading when wet, elliptical to oblong-obovate, 1.3–2.9 mm long, to 1 mm wide, unistratose, subcucullate, apex broadly acute to obtuse, base slightly clasping; margins plane, distal 1/2–2/3 bluntly serrate, limbate; costa single, subpercurrent to percurrent, in cross-section stereids above and below guide cells; lamellae absent or when present with 2–4 rows over costa, interrupted, in cross-section 1–3(4) cells high; median cells subquadrate to oblong-short rectangular, smooth, ± thick-walled; lower and basal cells short to long rectangular, rather lax; border cells oblong-vermicular, yellowish-brown, faintly pluripapillose, unistratose. **Dioicous**. **Perichaetia** terminal. **Seta** elongate, slender and ± flexuose, to 23 mm long. **Capsule** suberect, urn long cylindrical, slightly curved, ca. 2–3.2 mm long. **Operculum** long rostrate, ca. 1 mm long. **Peristome** teeth 32. **Calyptra** cucullate, naked and smooth. **Spores** not observed.

DISCUSSION. The genus is characterized by crispate, oblong-obovate or elliptical bluntly serrate leaves, with limbate margins, narrow costa without or with 2–4 rows of 1–3 cells high lamellae, finely pluripapillose border cells, cylindrical capsule, and 32 peristome teeth. It remains to be demonstrated

whether this taxon is most closely related to *Atrichum* or simply evolved within that genus. Both of our species were treated by Nyholm (1971), and can be differentiated as follows: *S. subulirostrum* — lamellae present on upper (adaxial) surface of costa, and *S. elamellosum* — lamellae absent. The generic name honors the United States bryologist William Campbell Steere (1907–1989), author of numerous floristic articles ranging from the extremes of the frigid Arctic to tropical Ecuador.

LITERATURE. Nyholm, E. 1971 (see ref. under *Atrichum*). - Smith, G. L. 1971 (see family ref.).

POTTIACEAE

Plants small to medium sized, rarely large, forming short turfs or dense to loose tufts, often dark green to brown or black. **Stems** erect, simple to few branched by innovations, radiculose, occasionally densely tomentose; in cross-section hyalodermis present or absent, outer cortical cells differentiated or not, central strand usually present. **Leaves** mostly crowded, narrowly to broadly lanceolate, lingulate or ligulate, apex acute to acuminate, occasionally obtuse-rounded, base decurrent or more often not; margins plane to more commonly recurved or incurved, entire to crenulate or irregularly serrate; limbate or more commonly elimbate; costa single, strong, subpercurrent to excurrent, occasionally as a hyaline, smooth or toothed awn, superficial cells quadrate to rectangular, in cross-section with 1 or 2 stereid bands, guide cells in 1–2, rarely more, layers; lamellae, filaments or a pad of cells absent or present on upper surface of costa; median and distal cells mostly isodiametric, smooth to more commonly mammillose, uni- to pluripapillose, thin- or more commonly thick-walled; lower and basal cells commonly elongate, uniform across or extending along the margin, mostly rectangular, thin- or less commonly thick-walled, alar region undifferentiated. **Asexual structures** occasionally present in the form of gemmae, usually produced in leaf axils or lamina apex or fragile, deciduous laminal fragments. **Monoicous** or dioicous. **Perichaetia** terminal; rarely lateral on short terminal branches (e. g., *Anoectangium*, *Molendoa*, *Pseudosymblepharis*), leaves often differentiated. **Seta** short to more commonly elongate, smooth, twisted or not. **Capsule** immersed to mostly exserted, erect to suberect, stegocarpous or occasionally cleistocarpous, mostly cylindrical, less often short to long ovoid-cylindrical or subglobose; annulus present or absent. **Operculum** mostly conic short- or long-rostrate, often oblique. **Peristome** absent, rudimentary or more commonly single, teeth 16, commonly divided to near base, erect or spirally twisted, papillose to spiculose, occasionally with a low or less frequently high basal membrane. **Calyptra** cucullate, rarely campanulate, naked, smooth or less often roughened to mammillose. **Spores** spherical, usually variously papillose.

DISCUSSION. The Pottiaceae contain seven subfamilies, six tribes, 77 genera and 1457 species; in the Neotropics 55 genera and 361 species, with probably on the order of about 250 valid species. The majority of neotropical taxa are found in open, often rather dry, habitats with the greatest diversity occurring in the mountainous regions.

The following treatment is, in large part, adapted from Zander's *Genera of the Pottiaceae: Mosses of Harsh Environments* (1993). This is the first notable analysis of a large moss family based on monophyletic taxa. Numerous comments related to neotropical taxa are provided in addition to full descriptions combined with excellent illustrations by Patricia Eckel of many of our species. The treatment is indispensable for the study of the Pottiaceae in the Neotropics. Several large genera, e.g., *Barbula*, *Didymodon*, *Syntrichia*, *Trichostomum*, *Tortula*, and *Weissia*, present in the Neotropics require a thorough regional revision that will likely result in a significant reduction in the number of recognized species.

The following provides a sequenced phylogenetic placement of the subfamilies, tribes, and genera given by Zander (1993) that are recognized for the Neotropics. The number in parentheses represents the total number of genera recorded for the subfamilies or tribes worldwide.

Subfamily **Timmielloideae** (1 genus): *Timmiella*.
Subfamily **Erythrophyllopsoideae** (2 genera): *Erythrophyllopsis*, *Erythrophyllastrum*.
Subfamily **Gertrudielloideae** (1 genus): *Gertrudiella*.
Subfamily **Chionolomoideae** (3 genera): *Pseudosymblepharis*.
Subfamily **Trichostomoideae** (8 genera): *Eucladium*, *Trichostomum*, *Tuerckheimia*, *Streptocalypta*, *Pleurochaete*, *Calyptopogon*, *Tortella*.
Subfamily **Merceyoideae**: Tribe **Bryoerythrophylleae** (5 genera) - *Rhexophyllum*, *Mironia*, *Bryoerythrophyllum*, *Pseudocrossidium*. Tribe **Leptodontieae** (7 genera) - *Hymenostylium*, *Trachyodontium*, *Streptotrichum*, *Leptodontiella*, *Leptodontium*. Tribe **Barbuleae** (9 genera) *Anoectangium*, *Streptopogon*, *Barbula*, *Gymnostomum*, *Scopelophila*, *Gymnostomiella*, *Didymodon*.

Subfamily **Pottioideae**: Tribe **Hyophileae** (19 genera) - *Hymenostyliella*, *Hyophiladelphus*, *Molendoa*, *Hyophila*, *Plaubelia*, *Teniolophora*, *Weissia*, *Weissiodicranum*, *Quaesticula*, *Ganguleea*, *Weisiopsis*, *Luisierella*, *Crossidium*, *Globulinella*, *Aloina*, *Aloinella*. Tribe **Pottieae** (21 genera) - *Tetrapterum*, *Trachycarpidium*, *Uleobryum*, *Tortula*, *Saitobryum*, *Hennediella*, *Dolotortula*, *Acaulon*, *Chenia*, *Syntrichia*, *Sagenotortula*.

Study guide. The identification of Pottiaceae usually requires leaf cross-sections (see section on methods to study mosses in the introduction), usually at or just below midleaf region. This is useful to determine if the lamina surface is smooth, bulging, or ornamented (e.g., mammillose; papillose – unipapillose or pluripapillose; and shape of the papillae - simple or branched, etc.); if the costa contains outgrowths (lamellae, filaments, or a pad of cells) on the upper surface or not; if stereid bands are above and/or below the guide cells, if the costal epidermal cells are differentiated and, if so, the number of cells across and their ornamentation; and also the number of guide cells and layers. Stem sections are often useful and should be routinely made in order to determine the presence or absence of a central strand and a hyalodermis. Zander (1993) recommends using a 2 % KOH solution (1–2 drops on a slide) to observe color reactions for leaves and cross-sections; this technique is required in the use of the generic keys given below.

LITERATURE. Delgadillo M., C. 1973a. A new species, nomenclatural changes, and generic limits in *Aloina*, *Aloinella* and *Crossidium* (Musci). The Bryologist 76: 271–277. - Delgadillo M., C. 1973b. A quantitative study of *Aloina*, *Aloinella* and *Crossidium* (Musci). The Bryologist 76: 301–305. - Delgadillo M., C. 1975. Taxonomic revision of *Aloina*, *Aloinella* and *Crossidium* (Musci). The Bryologist 78: 245–303 [keys, illustrations, maps]. - Zander, R. H. 1977a. *Rhabdoweisia crenulata* and *Erythrophyllopsis andina* from Colombia. The Bryologist 80: 158–160. - Zander, R. H. 1977b. The tribe Pleuroweisieae (Pottiaceae) in Middle America. The Bryologist 80: 233–269. - Zander, R. H. 1978. A synopsis of *Bryoerythrophyllum* and *Morinia* (Pottiaceae) in the New World. The Bryologist 81: 539–560. - Zander, R. H. 1979. Notes on *Barbula* and *Pseudocrossidium* (Bryopsida) in North America and an annotated key to the taxa. Phytologia 44: 177–214. - Zander, R. H. 1981. Descriptions and illustrations of *Barbula*, *Pseudocrossidium* and *Bryoerythrophyllum* (p.p.) of Mexico. Cryptogamie, Bryologie & Lichénologie 2: 1–22. - Zander, R. H. 1989. Seven new genera in Pottiaceae (Musci) and a lectotype of *Syntrichia*. Phytologia 65: 424–436. - Zander, R. H. 1993. Genera of the Pottiaceae: Mosses of harsh environments. Bulletin of the Buffalo Society of Natural Sciences 32: 1–378 [keys to subfamilies, tribes and genera, illustrations]. - Zander, R. H. 1996. Conservation of evolutionary diversity in Pottiaceae (Musci). Anales del Instituto de Biologia, Universidad Nacional Autónoma de México, Serie Botánica 67: 89–97.

1. Ventral costal stereid band absent (costa with a single stereid band, below guide cells) 2
1. Ventral costal stereid band present (costa with two stereid bands, above and below guide cells) 34
2. Ventral costal outgrowths absent 3
2. Ventral costal outgrowths present, a pad of cells, lamellae or filaments 27
3. Stem central strand absent 4
3. Stem central strand present 12

Costa with one stereid band, costal outgrowths absent, central strand absent

4. KOH color reaction of upper laminal cell walls essentially yellow or orange 5
4. KOH color reaction of upper laminal cells essentially red, usually a definite brick red 9
5. Superficial walls of upper laminal cells similarly shaped on both sides of lamina; leaves when dry occasionally channeled but not distinctly tubulose..... 6
5. Superficial walls of upper laminal cells ventrally bulging-mammillose, weakly convex dorsally; leaves tubulose when dry 8
6. Medial upper laminal cells small to medium sized, 7–14 µm wide ..... **Scopelophila**
6. Medial upper laminal cells large, commonly more than 14 µm wide 7
7. Leaf margins recurved to revolute; cross-section of dorsal costal stereid band round to semicircular; hydroid strand absent; stem hyalodermis absent; commonly epiphytic, widespread montane ... **Streptopogon** p.p.
7. Leaf margins plane to incurved or involute; cross-section of dorsal costal stereid band clearly flattened or ventrally indented, reniform or crescent-shaped; hydroid strand present; stem hyalodermis present, occasionally indistinct; rheophytic, rare (Ecuador) ... **Calyptopogon** p.p.
8. Basal cell group differentiated as a “V”, with at least laterally differentiated cells rising higher marginally as a tapering border; cross-section of dorsal costal stereid band clearly flattened or ventrally indented, reniform or crescent-shaped; ventral and dorsal costal epidermis absent; leaf base clearly differentiated in shape ..... **Luisierella**

8. Basal cell group differentiated straight across leaf or rising medially; cross-section of dorsal costal stereid band round to semicircular; ventral and dorsal costal epidermis present; leaf base little differentiated in shape; Brazil ..... **Ganguleea**
9. Medial upper laminal cells small to medium sized, 7–14 µm wide 10
9. Medial upper laminal cells large, commonly more than 14 µm wide 11
10. Dorsal costal epidermis absent; basal cell group clearly differentiated, usually larger, less papillose, walls thinner; urn ovoid to cylindrical; capsule stegocarpous; leaves usually widest at or above midleaf ..... **Syntrichia** p.p.
10. Dorsal costal epidermis present; basal cell group not or little differentiated from upper medial cells; urn spherical; capsule cleistocarpous; leaves widest below midleaf ..... **Acaulon** p.p.
11. Leaf margins plane to incurved or involute; length to width ratio of medial upper laminal cells 1–2:1; rheophytic, rare (Ecuador) ..... **Calyptopogon** p.p.
11. Leaf margins recurved to revolute; length to width ratio of medial upper laminal cells 2–4:1 or more; commonly epiphytic, widespread montane ..... **Streptopogon** p.p.

Costa with one stereid band, costal outgrowths absent, central strand present

12. Medial upper laminal cells small to medium sized, 7–14 µm wide 13
12. Medial upper laminal cells large, commonly more than 14 µm wide 22
13. Dorsal costal epidermis absent 14
13. Dorsal costal epidermis present 15
14. KOH color reaction of upper laminal cell walls essentially yellow to orange **Streptocalypta** p.p.
14. KOH color reaction of upper laminal cell walls red, usually a definite brick red **Syntrichia** p.p.
15. Superficial walls of upper laminal cells similarly shaped on both sides of lamina 16
15. Superficial walls of upper laminal cells ventrally bulging-mammillose, weakly convex dorsally 20.
16. Ventral costal epidermis absent 17
16. Ventral costal epidermis present 18
17. Leaf ventral surface above midleaf nearly plane to broadly channeled; leaves widest at or above midleaf; rather deep, narrow groove along costa absent; perichaetium terminal on main axis; seta less than 1 cm ..... **Gymnostomiella** p.p.
17. Leaf ventral surface above midleaf keeled; leaves widest below midleaf; rather deep, narrow groove along costa present; perichaetium lateral on main axis at ends of very short branches; seta 1 cm or longer ..... **Anoectangium** p.p.
18. Hydroid strand present ..... **Pseudocrossidium** p.p.
18. Hydroid strand absent 19
19. Perichaetium lateral on main axis at ends of very short branches; leaves usually strongly keeled ..... **Anoectangium** p.p.
19. Perichaetium terminal on main axis; leaves usually broadly channeled across the ventral surface ..... **Didymodon** p.p.
20. Leaf margins revolute to near apex; cross-section of dorsal costal stereid band clearly flattened or ventrally indented, reniform or crescent-shaped; guide cells commonly more than 6; stem hyalodermis present (sometimes indistinct); Andes ..... **Gertrudiella**
20. Leaf margins plane to incurved or involute; cross-section of dorsal costal stereid band round to semicircular; guide cells 2–6; stem hyalodermis absent 21
21. Leaf margins plane or very weakly incurved; cross-section of costa round or ovate or elliptical; hydroid strand absent; leaf base clearly differentiated in shape ..... **Weisiopsis**
21. Leaf margins clearly incurved or involute; cross-section of costa semicircular; hydroid strand present; leaf base little differentiated in shape ..... **Plaubelia** p.p.
22. Leaf margins plane to incurved or involute 23
22. Leaf margins recurved to revolute 25
23. Cross-section of dorsal costal stereid band clearly flattened or ventrally indented, reniform or crescent-shaped; upper laminal papillae absent ..... **Sagenotortula**
23. Cross-section of dorsal costal stereid band round to semicircular; upper laminal papillae present 24
24. Ventral costal epidermis absent; hydroid strand absent; superficial walls of upper laminal cells strongly convex to bulging on both sides of lamina ..... **Gymnostomiella** p.p.
24. Ventral costal epidermis present; hydroid strand present; superficial walls of upper laminal cells flat or very weakly convex ..... **Hennediella**
25. KOH color reaction of upper laminal cell walls essentially yellow or orange ..... **Tortula** p.p.
25. KOH color reaction of upper laminal cell walls essentially red, usually a definite brick-red ... 26
26. Basal cell group not or little differentiated from upper medial cells ..... **Dolotortula**
26. Basal cell group clearly differentiated, usually larger, walls thinner ..... **Chenia**

Costa with one stereid band, costal outgrowths present

27. KOH color reaction of upper laminal cell walls essentially yellow or orange 28
27. KOH color reaction of upper laminal cells walls essentially red, usually a definite brick red ..32
28. Ventral costal outgrowths differentiated as filaments or lamellae 29
28. Ventral costal outgrowths differentiated as a bulging pad of cells 31
29. Cross-section of dorsal costal stereid band round to semicircular; cross-section of costa round to semicircular ..... **Crossidium**
29. Cross-section of dorsal costal stereid band clearly flattened or ventrally indented, reniform or crescent-shaped; cross-section of costa distinctly flattened, usually reniform 30
30. Leaf margins plane to incurved or involute; leaf apex cucullate; leaves tubulose when dry .... **Aloinella**
30. Leaf margins recurved to revolute; leaf apex flattened, channeled or keeled; leaves when dry occasionally channeled but not distinctly tubulose ..... **Pseudocrossidium** p.p.
31. Leaf margins plane to incurved or involute; medial upper laminal cells 7–14 µm in width; leaf apex cucullate; upper laminal papillae absent ..... **Globulinella** p.p.
31. Leaf margins recurved to revolute; medial upper laminal cells commonly larger than 14 µm in width; leaf apex flattened, channeled or keeled; upper laminal papillae present .... **Tortula** p.p.
32. Ventral costal outgrowths differentiated as filaments or lamellae; median upper laminal cells commonly larger than 14 µm in width; cross-section of dorsal costal stereid band clearly flattened or ventrally indented, reniform or crescent-shaped; leaf base clearly differentiated in shape; cross-section of costa distinctly flattened, usually reniform ..... **Aloina**
32. Ventral costal outgrowths differentiated as a bulging pad of cells; medial upper laminal cells small to medium sized, 7–14 µm in width; cross-section of dorsal costal stereid band round to semicircular; leaf base little differentiated in shape; cross-section of costa round to semicircular 33
33. Stem central strand absent; leaf margins plane to incurved or involute; number of rows of cells across ventral surface of costa usually 2 (to 4); medial upper laminal cells medium sized, 11–14 µm in width; leaf apex obtuse or acute to acuminate ..... **Acaulon** p.p.
33. Stem central strand present; leaf margins recurved; number of rows of cells across ventral surface of costa commonly 4 or more; medial upper laminal cells small, 7–10 µm in width; leaf apex broadly rounded ..... **Saitobryum**

Costa with two stereid bands, upper laminal cells KOH yellow or orange, central strand absent

34. KOH color reaction of upper laminal cell walls essentially yellow or orange 35
34. KOH color reaction of upper laminal cells walls essentially red, usually a definite brick red 125
35. Stem central strand absent 36
35. Stem central strand present 45
36. Leaf margins entire or minutely and evenly crenulate 37
36. Leaf margins denticulate or serrulate to toothed 39
37. Ventral costal epidermis absent ..... **Hymenostylium**
37. Ventral costal epidermis present 38
38. Basal cell group differentiated as a “V”, with at least laterally differentiated cells rising higher marginally as a tapering border ..... **Tortella** p.p.
38. Basal cell group differentiated straight across leaf or rising higher medially **Trichostomum** p.p.
39. Leaf margins denticulate only near leaf base or upper sheathing portion of leaf .... **Eucladium**
39. Leaf margins denticulate, serrulate or serrate near apex or throughout 40
40. Leaf margins plane to incurved or involute; leaf ventral surface above midleaf nearly plane to broadly channeled; rather deep, narrow groove along costa absent ..... **Trichostomum** p.p.
40. Leaf margins recurved; leaf ventral surface above midleaf keeled; rather deep, narrow groove along costa present 42
41. Basal cell group not or little differentiated from upper medial cells ..... **Leptodontiella** p.p.
41. Basal cell group clearly differentiated, usually larger, less papillose, walls thinner 43
42. Papillae per lumen 2–6, usually bifid or multifid 44
42. Papillae per lumen many, usually 6 or more, simple or bifid 45
43. Urn short, less than 1.5 mm long ..... **Leptodontiella** p.p.
43. Urn longer, usually more than 1.5 mm long ..... **Leptodontium**
44. Upper marginal cells in same number of layers as medial cells, not longer than medial cells (sometimes larger); seta less than 1 cm; urn usually 1.5–3.5 mm long; marginal cell walls not thicker than those of medial cells ..... **Streptotrichum**

44. Upper marginal cells differentiated as a bistratose border, rectangular and clearly longer than medial cells; seta 1 cm or longer; urn more than 3.5 mm long; marginal cell walls thicker than those of medial cells ..... **Trachyodontium**

Costa with two stereid bands, upper laminal cells KOH yellow or orange, central strand present

45. Leaf margins entire or minutely and evenly crenulate 46
45. Leaf margins denticulate or serrulate to toothed 107
46. Hydroid strand absent 47
46. Hydroid strand present 95
47. Inflated, banana-shaped alar cells present and decurrent as a pad on the stem; Mexico, West Indies, Galapagos ..... **Weissiodicranum**
47. Inflated, banana-shaped alar cells absent or alar cells merely swollen and rounded 48
48. Superficial walls of upper laminal cells similarly shaped on both sides of lamina 49
48. Superficial walls of upper laminal cells ventrally bulging-mammillose, weakly convex dorsally 86
49. Ventral costal stereid band smaller than the dorsal or of nearly equal size 50
49. Ventral costal stereid band distinctly larger than the dorsal 85
50. Leaf margins plane to incurved or involute 51
50. Leaf margins recurved to revolute 79
51. Leaf margins plane or very weakly incurved 52
51. Leaf margins clearly incurved to involute 77
52. Dorsal costal epidermis absent 53
52. Dorsal costal epidermis present 64
53. Capsules cleistocarpous, i.e., rupturing irregularly 54
53. Capsules stegocarpous, i.e., dehiscing by an operculum 56
54. Basal cell group differentiated straight across leaf or rising higher medially (occasionally rising weakly along extreme basal margin as a line of elongate cells) ..... **Trichostomum** p.p.
54. Basal cell group differentiated as a “V”, with at least laterally differentiated cells rising higher marginally as a tapering border 55
55. Leaf base little differentiated in shape; stem hyalodermis absent; capsule less than 1.5 mm long, surface evenly mammillose or with distinct protuberances of strongly bulging cells basally or throughout ..... **Trachycarpidium** p.p.
55. Leaf base clearly differentiated in shape; stem hyalodermis present (sometimes indistinct); capsule more than 1.5 mm long, surface nearly smooth ..... **Tortella** p.p.
56. Cross-section of dorsal costal stereid band round to semicircular 57
56. Cross-section of dorsal costal stereid band flattened or ventrally indented, reniform or crescent-shaped 59
57. Costal ventral cells longitudinally elongate, 3:1 or more ..... **Gymnostomum** p.p.
57. Costal ventral cells quadrate to very short rectangular 58
58. Costa ending before the leaf apex ..... **Gymnostomum** p.p.
58. Costa percurrent to excurrent ..... **Trichostomum** p.p.
59. Guide cells commonly more than 6; stem length less than 10 mm, usually less than 6 mm ..... **Streptocalypta** p.p.
59. Guide cells 2–6; stem length usually 10 mm or more 60
60. Stem hyalodermis absent 61
60. Stem hyalodermis present 62
61. Medial upper laminal cells small, 7–10 µm wide; leaf apex obtuse to broadly acute; costa ending before the leaf apex ..... **Gymnostomum** p.p.
61. Medial upper laminal cells medium sized, 11–14 µm wide; leaf apex narrowly acute to acuminate; costa percurrent to excurrent ..... **Tuerckheimia** p.p.
62. Basal cell group differentiated as a “V”, with at least laterally differentiated cells rising higher marginally as a tapering border; perichaetial leaves distinctly different in size or morphology, sometimes strongly sheathing ..... **Tortella** p.p.
62. Basal cell group differentiated straight across leaf or rising higher medially; perichaetial leaves similar to stem leaves or occasionally smaller or somewhat enlarged 63
63. Costa ending before the leaf apex ..... **Gymnostomum** p.p.
63. Costa percurrent to excurrent ..... **Trichostomum** p.p.
64. Cross-section of costa round to semicircular 65
64. Cross-section of costa distinctly flattened, usually reniform 76
65. Capsule cleistocarpous, i.e., rupturing (usually) irregularly 66
65. Capsule stegocarpous, i.e., dehiscing by an operculum 68

66. Basal cell group differentiated straight across leaf or rising higher medially **Trichostomum** p.p.
66. Basal cell group differentiated as a “V”, with at least laterally differentiated cells rising higher marginally as a tapering border 67
67. Stem hyalodermis absent; capsule surface evenly mammillose or with distinct protuberances of strongly bulging cells basally or throughout; theca short, less than 1.5 mm .... **Trachycarpidium** p.p.
67. Stem hyalodermis present; capsule surface smooth, theca longer, usually more than 1.5 mm .....**Tortella** p.p.
68. Stem outer cortical cells not or little differentiated 69
68. Stem outer cortical cells clearly differentiated 73
69. Stem hyalodermis absent 70
69. Stem hyalodermis present 71
70. Medial upper laminal cells small, 7–10 µm wide; leaf apex obtuse to broadly acute; costa ending before the leaf apex ..... **Gymnostomum** p.p.
70. Medial upper laminal cells medium sized, 11–14 µm wide; leaf apex narrowly acute to acuminate; costa percurrent to excurrent ..... **Tuerckheimia** p.p.
71. Basal cell group differentiated as a “V”, with at least laterally differentiated cells rising higher marginally as a tapering border; perichaetial leaves distinctly different in size or morphology, sometimes strongly sheathing ..... **Tortella** p.p.
71. Basal cell group differentiated straight across leaf or rising higher medially; perichaetial leaves similar to stem leaves or occasionally smaller or somewhat enlarged 72
72. Costa ending before the leaf apex ..... **Gymnostomum** p.p.
72. Costa percurrent to excurrent ..... **Trichostomum** p.p.
73. Perichaetium lateral on main axis at ends of very short branches ..... **Molendoa** p.p.
73. Perichaetium terminal on main axis 74
74. Costal ventral cells longitudinally elongate, 3:1 or more ..... **Barbula** p.p.
74. Costal ventral cells quadrate to very short rectangular 75
75. Leaf base little differentiated in shape; leaves widest at or above midleaf ..... **Hyophila** p.p.
75. Leaf base clearly differentiated in shape; leaves widest below midleaf .... **Trichostomum** p.p.
76. Perichaetium terminal on main axis ..... **Trichostomum** p.p.
76. Perichaetium lateral on main axis at ends of very short branches ..... **Molendoa** p.p.
77. Cross-section of dorsal costal stereid band round to semicircular ..... **Quaesticula** p.p.
77. Cross-section of dorsal costal stereid band flattened or ventrally indented, reniform or crescent-shaped 78
78. Upper leaf margins not sharply and narrowly infolded; leaf base little differentiated in shape; leaves widest at or above midleaf; stem outer cortical cells clearly differentiated ..... **Hyophila** p.p.
78. Upper leaf margins sharply and narrowly infolded; leaf base clearly differentiated in shape; leaves widest below midleaf; stem outer cortical cells not or little differentiated ..... **Weissia** p.p.
79. Stem outer cortical cells not or little differentiated ..... **Gymnostomum** p.p.
79. Stem outer cortical cells clearly differentiated 80
80. Perichaetium lateral on main axis at ends of very short branches ..... **Molendoa** p.p.
80. Perichaetium terminal on main axis 81
81. Cross-section of dorsal costal stereid band round to semicircular 82
81. Cross-section of dorsal costal stereid band clearly flattened or ventrally indented, reniform or crescent-shaped 83
82. Leaf plane to broadly channeled ventrally, costa lacking a ventral groove ..... **Didymodon** p.p.
82. Leaf channeled or keeled, costa with a rather deep, narrow groove ventrally ..... **Barbula** p.p.
83. Leaf channeled or keeled, costa with a rather deep, narrow groove ventrally ..... **Barbula** p.p.
83. Leaf plane to broadly channeled ventrally, costa lacking a ventral groove 84
84. Leaves widest at or above midleaf; peristome teeth absent; leaves tubulose when dry .... **Hyophila** p.p.
84. Leaves widest below midleaf; peristome teeth present; leaves occasionally channeled but not distinctly tubulose when dry ..... **Didymodon** p.p.
85. Stem hyalodermis present (sometimes indistinct) ..... **Pseudosymblepharis** p.p.
85. Stem hyalodermis absent ..... **Didymodon** p.p.
86. Basal cell group differentiated as a “V”, with at least laterally differentiated cells rising higher marginally as a tapering border 87
86. Basal cell group differentiated straight across leaf or rising higher medially 89
87. Ventral costal stereid band distinctly larger than the dorsal ..... **Pseudosymblepharis** p.p.
87. Ventral costal stereid band smaller than the dorsal or of nearly equal size 88
88. Upper leaf margins not sharply and narrowly infolded; guide cells commonly more than 6

..... **Streptocalypta** p.p.
88. Upper leaf margins sharply and narrowly infolded; guide cells 2–6 ..... **Weissia** p.p.
89. Cross-section of dorsal costal stereid band round to semicircular ..... **Quaesticula** p.p.
89. Cross-section of dorsal costal stereid band clearly flattened or ventrally indented, reniform or crescent-shaped 90
90. Cross-section of costa round or ovate or elliptical 91
90. Cross-section of costa semicircular..... 93
91. Upper leaf margins sharply and narrowly infolded, leaf not bordered intramarginally by differentiated cells; leaf base clearly differentiated in shape; leaves widest below midleaf; stem hyalodermis present (sometimes indistinct) ..... **Weissia** p.p.
91. Upper leaf margins not sharply and narrowly infolded; leaf base little differentiated in shape; leaves widest at or above midleaf; stem hyalodermis absent; West Indies 92
92. Intramarginal border of elongate cells present; stem outer cortical cells clearly differentiated; basal cells along margin firm, not distinctly inflated; gemmae present ..... **Teniolophora** p.p.
92. Intramarginal border of elongate cells absent; stem outer cortical cells little differentiated; basal cells along margin lax and inflated; gemmae absent ..... **Hyophiladelphus**
93. Perichaetium lateral on main axis at ends of very short branches; upper laminal cell walls clearly trigonous or porose, lumina irregularly angular or stellate; Brazil ..... **Hymenostyliella** p.p.
93. Perichaetium terminal on main axis; upper laminal cell walls thin to evenly thickened, lumina quadrate to rounded 94
94. Upper leaf margins not sharply and narrowly infolded; leaf base little differentiated in shape; stem outer cortical cells clearly differentiated; leaves widest at or above midleaf ..... **Hyophila** p.p.
94. Upper leaf margins sharply and narrowly infolded; leaf base clearly differentiated in shape; stem outer cortical cells not or little differentiated; leaves widest below midleaf ..... **Weissia** p.p.
95. Ventral costal outgrowths absent 96
95. Ventral costal outgrowths present as a pad of cells, lamellae or filaments 108
96. Dorsal costal epidermis absent 97
96. Dorsal costal epidermis present 100
97. Basal cell group differentiated as a “V”, with at least laterally differentiated cells rising higher marginally as a tapering border 98
97. Basal cell group differentiated straight across leaf or rising higher medially 99
98. Leaf margins plane or very weakly incurved; upper leaf margins not sharply and narrowly infolded; leaf base little differentiated in shape; costal ventral cells longitudinally elongate 3:1 or more; stem hyalodermis absent ..... **Trachycarpidium** p.p.
98. Leaf margins clearly incurved to involute; upper leaf margins sharply and narrowly infolded; leaf base clearly differentiated in shape; costal ventral cells quadrate to very short-rectangular; stem hyalodermis present (sometimes indistinct) ..... **Weissia** p.p.
99. Cross-section of dorsal costal stereid band round to semicircular ..... **Uleobryum**
99. Cross-section of dorsal costal stereid band clearly flattened or ventrally indented, reniform or crescent-shaped ..... **Weissia** p.p.
100. Capsules cleistocarpous 101
100. Capsules stegocarpous 103
101. Basal cell group differentiated straight across leaf or rising higher medially ..... **Weissia** p.p.
101. Basal cell group differentiated as a “V”, with at least laterally differentiated cells rising higher marginally as a tapering border 102
102. Leaf margins plane or very weakly incurved; upper leaf margins not sharply and narrowly infolded; leaf base little differentiated in shape; costal ventral cells longitudinally elongate 3:1 or more; stem hyalodermis absent ..... **Trachycarpidium** p.p.
102. Leaf margins incurved to involute; upper leaf margins sharply and narrowly infolded; leaf base clearly differentiated in shape; costal ventral cells quadrate to very short-rectangular; stem hyalodermis present ..... **Weissia** p.p.
103. Costal ventral cells longitudinally elongate 3:1 or more ..... **Barbula** p.p.
103. Costal ventral cells quadrate to very short-rectangular 104
104. Cross-section of dorsal costal stereid band round to semicircular ..... **Plaubelia** p.p.
104. Cross-section of dorsal costal stereid band clearly flattened or ventrally indented, reniform or crescent-shaped 105
105. Upper leaf margins sharply and narrowly infolded ..... **Weissia** p.p.
105. Upper leaf margins not sharply infolded 106
106. Cross-section of costa round to semicircular; peristome teeth absent; leaves widest at or above midleaf; leaves tubulose ..... **Hyophila** p.p.
106. Cross-section of costa distinctly flattened, usually reniform; peristome teeth present; leaves widest below midleaf; leaves when dry occasionally channeled but not distinctly tubulose

..... **Pseudocrossidium** p.p.
107. Ventral costal outgrowths differentiated as filaments or lamellae; margins recurved to revolute; cross-section of dorsal costal stereid band clearly flattened or ventrally indented, reniform or crescent-shaped; leaf apex flattened, channeled or keeled; cross-section of costa distinctly flattened, usually reniform ..... **Pseudocrossidium** p.p.
107. Ventral costal outgrowths differentiated as a bulging pad of cells; margins plane to incurved or involute; cross-section of dorsal costal stereid band round to semicircular; leaf apex cucullate; cross-section of costa round to semicircular ..... **Globulinella**
108. Leaf margins denticulate only near leaf base or at top of leaf sheath ..... **Molendoa**
108. Leaf margins denticulate or serrulate to toothed near apex or throughout 109
109. Dorsal costal epidermis absent 110
109. Dorsal costal epidermis present 113
110. Perichaetium lateral on main axis at ends of very short branches; perichaetial leaves distinctly differentiated in size or morphology, strongly sheathing the seta ..... **Pleurochaete** p.p.
110. Perichaetium terminal on main axis; perichaetial leaves similar to stem leaves or occasionally smaller or somewhat enlarged 111
111. Guide cells commonly more than 6; length of stem less than 10 mm, usually less than 6 mm ..... **Streptocalypta** p.p.
111. Guide cells 2–6; length of stem 10 mm or more 113
112. Stem hyalodermis absent ..... **Tuerckheimia** p.p.
112. Stem hyalodermis present ..... **Trichostomum** p.p.
113. Superficial walls of upper laminal cells similarly shaped on both sides of leaf 114
113. Superficial walls of upper laminal cells ventrally bulging-mammillose, weakly convex dorsally .... 120.
114. Rather deep, narrow groove along costa present ..... **Barbula** p.p.
114. Rather deep, narrow groove along costa absent 115
115. Leaf margins plane to incurved or involute 116
115. Leaf margins recurved to revolute 119
116. Perichaetium lateral on main axis at ends of very short branches; upper marginal cells rectangular and clearly longer than medial cells; perichaetial leaves distinctly different in size or morphology, strongly sheathing the seta ..... **Pleurochaete** p.p.
116. Perichaetium terminal on main axis; upper marginal cells not longer than medial cells (sometimes larger); perichaetial leaves similar to stem leaves or occasionally smaller or somewhat enlarged 117
117. Leaves widest at or above midleaf ..... **Hyophila** p.p.
117. Leaves widest below midleaf 118
118. Stem hyalodermis absent ..... **Tuerckheimia** p.p.
118. Stem hyalodermis present ..... **Trichostomum** p.p.
119. Leaves widest at or above midleaf; peristome teeth absent; leaves tubulose when dry ..... **Hyophila** p.p.
119. Leaves widest below midleaf; peristome teeth present; leaves when dry occasionally channeled but not distinctly tubulose ..... **Didymodon** p.p.
120. Hydroid strand absent 121
120. Hydroid strand present 124
121. Basal cell group differentiated as a “V”, with at least laterally differentiated cells rising higher marginally as a tapering border; leaf base clearly differentiated in shape .... **Pleurochaete** p.p.
121. Basal cell group differentiated straight across leaf or rising higher medially; leaf base little differentiated in shape 122
122. Cross-section of costa round or ovate or elliptical; upper marginal cells differentiated intramarginally as a bistratose border; upper marginal cells rectangular and clearly longer than medial cells; marginal cell walls thicker than those of medial cells; West Indies **Teniolophora** p.p.
122. Cross-section of costa semicircular; upper laminal cells in same number of layers as medial cells; upper marginal cells not longer than medial cells (sometimes larger); marginal cell walls not thicker than those of medial cells 123
123. Leaves widest at or above midleaf; upper laminal cell walls thin to evenly thickened, lumina quadrate to rounded; perichaetium terminal on main axis; widespread ..... **Hyophila** p.p.
123. Leaves widest below midleaf; upper laminal cell walls clearly trigonous or porose, lumina irregularly angular or stellate; perichaetium lateral on main axis at ends of very short branches; Brazil ..... **Hymenostyliella** p.p.

124. Leaf base clearly differentiated in shape; guide cells commonly more than 6; seta 10 mm or longer; upper laminal cells medially bistratose, the cells staggered, not one directly above the other in section ..... **Timmiella**
124. Leaf base little differentiated in shape; guide cells 2–6; seta less than 10 mm; upper laminal cells medially unistratose 125
125. Cross-section of dorsal costal stereid band round to semicircular; peristome teeth present .... **Plaubelia** p.p.
125. Cross-section of dorsal costal stereid band clearly flattened or ventrally indented, reniform or crescent-shaped; peristome teeth absent ..... **Hyophila** p.p.

Costa with two stereid bands, upper laminal cells KOH red
126. Leaf margins denticulate or serrulate to toothed 127
126. Leaf margins entire or minutely and evenly crenulate 130
127. Ventral costal epidermis absent ..... **Rhexophyllum**
127. Ventral costal epidermis present 128
128. Stem hyalodermis present (occasionally indistinct) ..... **Bryoerythrophyllum**
128. Stem hyalodermis absent 129
129. Hydroid strand absent; costal groove absent; 2 to occasionally 4 rows of cells across ventral surface of costa; in cross-section laminal cell walls strongly convex to bulging on both surfaces ..... **Didymodon** p.p.
129. Hydroid strand present; costal groove deep and narrow; 4 or more rows of cells across ventral surface of costa; in cross-section laminal cell walls flat or very weakly convex on both surfaces ..... **Mironia** p.p.
130. Cross-section of dorsal costal stereid band clearly flattened or ventrally indented, reniform or crescent-shaped 131
130. Cross-section of dorsal costal stereid band rounded to semicircular 133
131. Stem outer cortical cells not or little differentiated ..... **Erythrophyllopsis**
131. Stem outer cortical cells distinctly differentiated 132
132. Hydroid strand absent; costal groove absent; 2 to occasionally 4 rows of cells across ventral surface of costa; in cross-section laminal cell walls strongly convex to bulging on both surfaces ..... **Didymodon** p.p.
132. Hydroid strand present; costal groove deep and narrow; 4 or more rows of cells across ventral surface of costa; in cross-section laminal cell walls flat or very weakly convex on both surfaces ..... **Mironia** p.p.
133. Leaf margins plane to incurved or involute; costal hydroid strand present .... **Erythrophyllastrum**
133. Leaf margins recurved to revolute; costal hydroid strand absent .....**Didymodon** p.p.

Acaulon (Fig. 175) - Three species in the Neotropics, *A. nanum* Müll. Hal. (Brazil), *A. schimperianum* (Sull.) Sull. (Mexico, Dominican Republic), and *A. uleanum* Müll. Hal. (Brazil); 19 species widely distributed, primarily in arid temperate regions.

HABITAT. On soil, in exposed to slightly shaded sites; semi-dry to dry vegetation at moderately low elevations.

DESCRIPTION. **Plants** very small, gregarious or scattered, yellowish brown or reddish. **Stems** very short, to 0.5 mm tall, unbranched; in cross-section hyalodermis absent, cells uniform, central strand absent. **Leaves** appressed with apices often reflexed, broadly ovate, to 1.5 mm long, deeply concave, apex broadly acute; margins plane, entire to dentate; costa short excurrent, apiculate or mucronate, rarely percurrent or as a short awn, superficial cells above and below elongate, usually smooth, ventrally 3–4 rows across at midleaf, in cross-section round, ventral stereid band generally absent, dorsal present but weak, guide cells 2–4 in 1 layer; upper laminal cells quadrate-rounded to rhomboidal, convex, thick-walled, smooth to papillose, papillae over cell lumen; basal cells rectangular, thin-walled. KOH leaf color reaction red. **Dioicous**. **Perichaetia** terminal. **Seta** very short, to 0.2 mm long. **Capsule** immersed, cleistocarpous, spherical, to ca. 0.5 mm in diameter, not apiculate; exothecial cells thin-walled; stomata at base, superficial. **Operculum** absent. **Peristome** absent. **Calyptra** mitrate, often lobed at base. **Spores** large, to 30 µm or more in diameter, finely papillose or warty.

DISCUSSION. The genus is characterized by the minute stature of the plants, strongly appressed, deeply concave, broadly ovate leaves, mostly short excurrent costa, and immersed, cleistocarpic, non-apiculate capsules.

LITERATURE. Zander, R. H. 1993 (see family ref.).

Aloina (Fig. 175) - Six species in the Neotropics; 12 species of rather wide distribution.

HABITAT. On soil and soil covered rocks, often in exposed to partially shaded, dry sites; plains at lower elevations ranging up slope to upper open montane, páramo or puna, 300–4570 m.

DESCRIPTION. **Plants** very small, gregarious or forming thin tufts, dark green to brown above. **Stems** erect, but often buried in soil with only tips exposed, 2–6 mm tall, simple or few branched, radiculose below, beneath soil; in cross-section hyalodermis absent, epidermal wall somewhat thickened, inner cells rather uniform, thin-walled, central strand present or absent; rhizoids pale. **Leaves** appressed-incurved when dry, slightly spreading when wet, ovate-lingulate or short lingulate, 0.5–2.5 mm long, often deeply channeled, apex obtuse to rounded, cucullate, piliferous or not, base subauriculate, sheathing; margins strongly enfolded, entire or distally crenulate or denticulate; costa undifferentiated or single, percurrent to rather long excurrent, superficial cells ventrally represented in distal half by photosynthetic filaments extending beyond costal region, mostly 4–8 cells high, terminal cell distally thickened, dorsally long rectangular or distally short rectangular or quadrate, in cross-section broadly reniform, stereids below guide cells, dorsal epidermis weakly differentiated, guide cells 6–12 in 1(–2) layer; lamina partially bistratose; upper cells transversely oblong-rectangular or elliptical, thick-walled; basal cells rectangular, thin-walled. KOH leaf color reaction red. **Dioicous** or autoicous. **Perichaetia** terminal; leaves mostly similar, margins plane, not enfolded. **Seta** elongate, 6–20 mm long, twisted, smooth. **Capsule** erect, urn cylindrical or ovoid-cylindrical, 1–3 mm long; exothecial cells rectangular, thin-walled; stomata at urn base, superficial; annulus 1–3 rows, revoluble to persistent. **Operculum** long conic or rostrate, erect to slightly oblique. **Peristome** single, teeth straight to twisted, variously divided, spiculose, basal membrane absent or present, low to high. **Calyptra** cucullate, smooth and naked. **Spores** spherical, finely to coarsely papillose.

DISCUSSION. Distinguishing features include the half or more buried plants, strongly folded distal margins that cover the ventral costal filaments, and medially bistratose lamina. Several *Aloina* species are concentrated within both Mexico and the Central Andes as well as being widely distributed outside the Neotropics, e.g., *A. rigida* (Hedw.) Limpr.; other species however are restricted in their distribution: *A. apiculata* (E. B. Bartram) Delgad. from Jamaica, and from the central Andes *A. catillum* (Müll. Hal.) Broth. and *A. roseae* (R. S. Williams) Delgad. The generic name refers to liliaceous genus *Aloë* with its fleshy leaves.

LITERATURE. Delgadillo M., C. 1973a, b, 1975 (see family ref.).

Aloinella (Fig. 175) - Six species in the Neotropics, primarily confined to Andean South America.

HABITAT. On exposed soil; zacatonal, páramo, and puna, 2700–5300 m.

DESCRIPTION. **Plants** very small, forming tufts, yellowish green. **Stems** erect, to 2 cm tall, several branched; in cross-section hyalodermis absent, outer (1)2 rows of cells small, thick-walled, inner cells large, firm-walled, central strand well developed. **Leaves** appressed when dry, erect-spreading or not when wet, fleshy, ovate to obovate or orbicular, to 1 mm long, deeply concave distally, base undifferentiated, strongly to weakly cucullate distally, apex obtuse-rounded; margins weakly to strongly incurved, entire or denticulate to serrulate distally or throughout; costa subpercurrent to percurrent, 1/4–1/3 width at base, superficial cells dorsally elongate, ca. 12 rows across at midleaf, in cross-section reniform, stereid band below guide cells, filaments present on ventral costal surface, to 6 cells high, terminal cells thin-walled, epidermis undifferentiated or weakly so dorsally, guide cells 2–6 in 1 layer; lamina unistratose; upper cells rhomboidal to rectangular, smooth to pluripapillose medially, papillae several over cell lumen, thick-walled; basal cells rectangular, thin- to thick-walled, smooth. KOH leaf color reaction golden yellow. **Dioicous**. **Perichaetia** terminal or appearing lateral; leaves sheathing, ovate to oblong. **Seta** to 10 mm long, twisted. **Capsule** erect to inclined, urn cylindrical to ovoid-cylindrical, to 2 mm long; exothecial cells thin-walled; stomata at urn base, superficial; annulus in 1–2 rows. **Operculum** conic-rostrate, straight to oblique. **Peristome** single, teeth short, entire or divided above, spiculose, basal membrane absent. **Calyptra** cucullate, smooth and naked. **Spores** spherical, finely papillose.

DISCUSSION. The genus is characterized by the strongly appressed, deeply cucullate leaves, ventral filaments over the costa, not developing from the lamina as in *Aloina*.

LITERATURE. Delgadillo M., C. 1973a, b, 1975 (see family ref.).

Anoectangium (Fig. 176) - Five neotropical species, *A. aestivum* (Hedw.) Mitt. is the common species in the Neotropics; a genus of about 47 species, primarily tropical, extending into the temperate mountainous regions and the Arctic.

HABITAT. On soil, soil covered rock, and rock, frequently calcareous, often associated with moist or wet sites including waterfalls; open montane, zacatonal, páramo, and puna, (300–)1100–4700 m.

DESCRIPTION. **Plants** small, forming tufts, green to yellowish-green, brown below. **Stems** erect, to ca. 10 mm tall, simple to few branched, weakly radiculose to densely tomentose; in cross-section hyalodermis absent, central strand present. **Leaves** rather distant to crowded, often forming comal tufts, appressed to erect-spreading, incurved, spiral or secund distally when dry, spreading when wet, oblong to ligulate or lanceolate, 1–1.6 mm long, keeled distally, adaxially grooved along costa, apex acute to obtuse, usually mucronate with 1–3 hyaline cells; margins plane or weakly reflexed at midleaf, entire or crenulate by projecting cells; costa subpercurrent to percurrent, superficial cells ventrally elongat
e or occasionally short rectangular or quadrate near apex, 2–3 cells across at midleaf, elongate dorsally, in cross-section reniform to oval, stereids only below guide cells, 2–4 guide cells in 1 layer; upper laminal cells oval to subquadrate or hexagonal, thick-walled, papillose, papillae usually strong, simple or multiple; basal cells differentiated medially to costa, short rectangular, thick-walled. KOH leaf color reaction yellow to yellow-orange. **Dioicous**. **Perichaetia** terminal on short lateral branches, leaves sheathing. **Seta** elongate, to 8 mm long, twisted. **Capsule** erect, ovoid to elliptical, 0.5–1 mm long, neck short; annulus in 2 rows. **Operculum** long rostrate, oblique. **Peristome** absent. **Calyptra** cucullate, smooth and naked. **Spores** spherical, lightly to densely papillose.

DISCUSSION. The genus is distinguished by the sporophytes borne terminally on short lateral branches, often ligulate leaves, costa deeply grooved, absence of a ventral stereid band, and laminal cells usually strongly bulging-pluripapillose. A worldwide revision is needed for this genus.

LITERATURE. Zander, R. H. 1977b, 1993 (see family ref.).

Barbula (Fig. 176) - About 45 species recorded for the Neotropics, probably on the order of 20 or less; a genus containing about 200 species with a worldwide distribution.

HABITAT. On soil, soil covered rocks, and rocks, including limestone, rarely found on bark, moist to dry exposed sites, frequently associated with disturbed areas; infrequent in lowlands, more commonly found in open montane, zacatonal, páramo, and puna, from near sea level to 4570 m.

DESCRIPTION. **Plants** forming loose turfs, yellowish-brown or blackish-brown. **Stems** erect, solitary or few branched; central strand generally well-developed. **Leaves** ovate, spathulate to ovate- or triangular-lanceolate, 1–3 mm long, ventrally broadly concave or narrowly channeled, apex rounded to acute, base weakly differentiated to sheathing; margins plane to recurved, entire, infrequently dentate distally; costa subpercurrent to short excurrent as a mucro, superficial cells ventrally and dorsally elongate, occasionally quadrate, papillose or smooth, 2–3(–5) cells across ventrally at midleaf, in cross-section semicircular to oval, stereid bands 2, dorsal stereid band well-developed, ventral band weakly differentiated, guide cells 2–4 in 1 layer; lamina unistratose, rarely bistratose; upper laminal cells quadrate to short rectangular, thin- to thick-walled, firm, flat on both surfaces to weakly convex or bulging adaxially, epapillose or papillose, papillae solid or hollow, over cell lumen, often multiplex; basal cells differentiated across leaf or higher medially, rectangular, smooth to weakly papillose. KOH leaf color reaction yellow, occasionally yellow-orange. **Gemmae** when present on rhizoids or in leaf axils, stalked, clavate to ovoid, armed or not. **Dioicous**. **Perichaetia** terminal; leaves similar or often enlarged and elongate. **Seta** elongate, twisted. **Capsule** erect, ovoid or short- to long-cylindrical; stomata at urn base; annulus in 1–2 rows, persistent or occasionally revoluble to deciduous. **Operculum** short- to long-conic. **Peristome** weakly to strongly twisted, teeth divided into 32 filaments, spiculose; basal membrane low. **Calyptra** cucullate, naked and smooth. **Spores** finely papillose.

DISCUSSION. The genus can be confused with *Didymodon*, however, *Barbula* generally exhibits an apex that ends frequently in an apiculus of one to few cells. The laminal cells exhibit distinct papillae that obscure the cell lumen and readily observable along the leaf margin. A world revision is very much needed for this genus. The neotropical species will possibly be reduced by one third or one half after careful review.

LITERATURE. Zander, R. H. 1979, 1981 (see family ref.).

Bryoerythrophyllum (Fig. 176) - About 12 species in the Neotropics; a genus containing 27 species with a nearly worldwide distribution. In the tropics largely confined to the highlands.

HABITAT. On soil and rock, including calcareous, infrequently found on logs, often in disturbed sites; open montane, zacatonal, páramo and puna, (600–)1400–4800 m.

DESCRIPTION. **Plants** medium sized, forming loose to dense tufts, often dark brown, reddish-brown, or distally green. **Stems** erect, few branched, radiculose below; in cross-section hyalodermis usually absent, central strand generally present and well developed. **Leaves** somewhat distant to crowded, when dry appressed incurved or twisted above base, erect-spreading when wet, ovate to oblong or oblong-lanceolate, 1–5 mm long, channeled to keeled, apex acute to obtuse-rounded; margins plane to more commonly recurved at mid leaf, or reflexed throughout, entire to distally

dentate-serrate, apical cells short-toothed, hyaline; costa percurrent to short-excurrent, in cross-section epidermal cells 2–6 across costa at midleaf, upper stereids weak to strong, lower stereids strong, guide cells 2–4 in 1 (rarely 2) layer; upper laminal cells subquadrate, short-rectangular or oval, usually thick-walled, pluripapillose, papillae simple or bifid; basal cells well differentiated or not, usually rectangular, hyaline, smooth to weakly bulging. KOH leaf color reaction red to orange-red. **Gemmae** absent or present in distal leaf axils. **Dioicous**, rarely autoicous. **Perichaetia** terminal; leaves sheathing, similar or longer than stem leaves. **Seta** 1(–2) per perichaetium, elongate, twisted. **Capsule** erect, ovoid-cylindrical to elliptical, symmetric, or inclined with urn short to ± long-cylindrical, curved, asymmetric, 0.8–2.5 mm or more long; annulus in 1–2 rows, often revoluble or deciduous in pieces. **Operculum** short conic to rostrate. **Peristome** absent, rudimentary to more commonly well developed with teeth usually divided into 32 weakly to strongly papillose (or spiculose) segments, basal membrane low or absent. **Calyptra** cucullate, smooth and naked. **Spores** spherical, smooth to lightly papillose.

DISCUSSION. The genus is characterized by the red coloration of the stems and often the leaves, papillae of upper laminal cells usually crowded and bifid, and basal cells well defined.

LITERATURE. Zander, R. H. 1968. *Barbula inaequalifolia* Tayl. new to North America. The Bryologist 71: 41–44. - Zander, R. H. 1978 (see family ref.). - Zander, R. H. 1986. Notes on *Bryoerythrophyllum* (Musci). The Bryologist 89: 13–16 [revised keys].

Calyptopogon (Fig. 177) - A monotypic genus, with *C. mnioides* (Schwägr.) Broth. exhibiting an Austral-Antarctic Andean distribution, in the Neotropics apparently only known from Ecuador.

HABITAT. On rocks, in streams; unknown but presumably from high elevations.

DESCRIPTION. **Plants** medium sized, forming tufts or mats, yellowish-green. **Stems** erect, to 4 cm high, few branched, radiculose, sometimes densely so; in cross-section hyalodermis present, inner 1–2 rows of cells small, thick-walled, inner cells larger, firm-walled, central strand absent. **Leaves** crowded, incurved and conspicuously undulate along margins when dry, wide spreading and reflexed when wet, ovate- to elliptical-lanceolate, to 4.5 mm long, weakly keeled or not, apex acute, base clasping; margins plane, entire, minutely crenulate by projecting walls or papillae, intramarginal border present, with 3–4 rows of cells; costa strong, short excurrent, superficial cells above in 4 rows, short rectangular and distally papillose, in cross-section ovate, stereids below guide cells, absent above, guide cells 2–4(–6) in 1 or occasionally 2 layers, upper epidermal surface bulging, lower surface undifferentiated; lamina unistratose; laminal cells distally elliptic-oval to irregularly hexagonal-rounded, corners thickened, porose, papillose, papillae 1–4, over cell lumen; basal cells long rectangular, extending and merging toward intramarginal border; marginal cells mostly short oblong-rectangular, thick-walled, not porose; upper intramarginal border cells oblong-linear, smooth, porose. KOH leaf color reaction red to yellow with red blotches or yellow-orange. **Gemmae** when present multicellular, on upper surface of costa. **Dioicous**. **Perichaetia** terminal; leaves strongly differentiated, sheathing and convolute, linear-lanceolate, to 13 mm long, cells rectangular to long rhomboidal, thick-walled, porose. **Seta** to 5 mm long, twisted. **Capsule** erect, urn cylindrical, to 2.2 mm long, slightly curved; exothecial cells rectangular, evenly thickened; stomata at urn base, superficial; annulus in 3–4 rows, persistent. **Operculum** long conic. **Peristome** teeth divided into 32 filaments, twisted once, densely spiculose, basal membrane high. **Calyptra** cucullate, smooth. **Spores** spherical, appearing smooth.

DISCUSSION. The intramarginal border consisting of smooth, porose cells, and papillose laminal cells, and presence of a dorsal stereid band, in combination with habitat are diagnostic. In the Neotropics this species is apparently only known from a single collection made in the previous century by Jameson from Ecuador labeled “Andes Quitenses.” This distinctive moss is likely rare in our region, or possibly it merely reflects that rheophytic habitats have not been adequately explored by collectors.

LITERATURE. Zander, R. H. 1993 (see family ref.).

Chenia - Two species in the Neotropics, *C. leptophylla* (Müll. Hal.) R. H. Zander widespread (Mexico, Bolivia, and southeastern Brazil) and *C. subobliqua* (R. S. Williams) R. H. Zander known only from Peru; a genus of three species.

HABITAT. On soil, rocks, stone walls, in moist areas; lowland subtemperate to open montane sites, from sea level to 2900 m.

DESCRIPTION. **Plants** rather small, forming tufts, green above, brown below. **Stems** erect, to 10 mm tall, seldom branched, weakly radiculose below; in cross-section hyalodermis absent, inner and outer cells somewhat uniform, central strand well developed. **Leaves** crowded, appressed, somewhat contorted, ligulate to spathulate, to 2.5 mm long, apex broadly acute to rounded, often apiculate with terminal cell thickened; margins plane or weakly recurved at base, rather strongly crenulate or dentate distally, outer walls thickened and appearing papillose; costa slender, mostly subpercurrent, superficial

cells on both surfaces short rectangular, in cross-section guide cells 2 in 1 row, stereids few below or absent; upper and median cells isodiametric, hexagonal, bulging, smooth, thin-walled; basal cells uniform across lamina, short rectangular; marginal cells smaller. KOH leaf color reaction red. **Gemmae** occasionally present on rhizoids, irregularly spherical or clavate. **Dioicous**. **Perichaetia** terminal; inner leaves similar, outer larger. **Seta** short (0.2 mm) to elongate, to 12 mm long, twisted. **Capsule** cleistocarpous, spherical and beaked, or stegocarpous, urn ovoid to cylindrical, to 2 mm long; stomata at urn base, superficial; annulus in 2–3 rows, persistent. **Operculum** short to long conic. **Peristome** when present single, divided into 32 filaments with several articulations, straight or twisted, spiculose, basal membrane short. **Calyptra** cucullate (stegocarpic condition), or mitrate and 3-lobed at base (cleistocarpic condition). **Spores** spherical, smooth to finely papillose.

DISCUSSION. The genus is characterized by leaf margins toothed, denticulate or dentate, with a slender costa and smooth laminal cells. The genus is closely related to *Syntrichia* (Zander, 1993). The two neotropical species are differentiated by the following features: *C. leptophylla* — leaves narrowly elliptical, leaf margins finely and evenly denticulate; *C. subobliqua* — leaves somewhat obovate, leaf margins irregularly dentate. Species of *Chenia* were previously aligned with *Phascum* and *Tortula*. The generic name honors the Chinese bryologist Chen Pan-chieh (1907–1970), author of *Genera Muscorum Sinicorum*.

LITERATURE. Zander, R. H. 1989, 1993 (see family ref.).

Crossidium (Fig. 177) - Two species in Mexico and the central Andes, *C. crassinervium* (De Not.) Jur. (Mexico, also southwest United States, Europe, northern Africa, and India) and *C. rosei* R. S. Williams (Peru); a rather widespread xerophyte genus of 13 species.

HABITAT. On soil, often calcareous, in exposed sites; associated with xerophytic vegetation, 600–1000 m.

DESCRIPTION. **Plants** very small, scattered or forming small tufts, hoary green. **Stems** erect, to 5 mm tall, simple or few branched, sparsely radiculose; in cross-section hyalodermis absent, central strand present. **Leaves** appressed when dry, erect-spreading when wet, oblong-ovate to short ligulate, to 1.5 mm long, broadly concave, apex obtuse to broadly acute, with short to long hair point; margins recurved below, involute near apex; costa excurrent, ventral surface with branched filaments present on distal 1/2 of costa, to 12 cells high, terminal cells smooth to weakly papillose, papillae 2–4, superficial cells 3–6 rows across, dorsally cells elongate, in cross-section round to elliptical, single stereid band present, epidermis weakly present on dorsal surface or absent, guide cells 2–5 in 1(–2) layer; lamina unistratose; upper cells subquadrate to short rectangular, smooth or papillose, papillae C-shaped; basal cells differentiated across, extending higher medially, rectangular, lax, thin-walled, smooth. KOH leaf color reaction yellow, orange in older leaves, occasionally with medial red blotches distally. **Dioicous** or autoicous (cladautoicous). **Perichaetia** terminal; leaves clasping, similar to stem leaves. **Seta** to 12 mm long. **Capsule** erect, urn ovoid-cylindrical, to 2.2 mm long; exothecial cells rectangular, thin-walled; stomata at urn base, superficial; annulus in 2 rows. **Operculum** conic-rostrate, straight or oblique. **Peristome** single, teeth divided into 32 segments, spiculose, basal membrane low to moderately high. **Calyptra** cucullate, smooth and naked. **Spores** spherical, nearly smooth to papillose.

DISCUSSION. The genus is distinguished by the short ovate or ligulate leaves, multicellular photosynthetic filaments present on distal ventral surface of costa, hair point or mucronate leaf tip, unistratose lamina, enlarged, lax basal cells that extend upward along costa, elongate seta and peristomate capsule.

LITERATURE. Cano, M. J., J. Guerra & R. M. Ros. 1993. A revision of the moss genus *Crossidium* (Pottiaceae) with the description of the new genus *Microcrossidium*. Plant Systematics and Evolution 188: 213–235. - Delgadillo M., C. 1973a, b, 1975 (see family ref.).

Didymodon (Fig. 178) - About 37 species recorded for the Neotropics, probably near 20; a large genus of some 120 species exhibiting a worldwide distribution with primary diversification in the temperate and highlands regions.

HABITAT. On soil, soil covered rocks and rocks, including calcareous, limestone and sandstone, in exposed to somewhat shaded, dry, occasionally moist, sites, rather frequent in disturbed areas; open montane, zacatonal, páramo and puna, 500 to more commonly 2000–4855 m.

DESCRIPTION. **Plants** forming tufts or cushions, dark green to blackish-brown. **Stems** erect, ca. 5–20 mm tall, few-branched; in cross-section hyalodermis generally absent, outer 2–3 cell rows small, thick-walled, inner cells larger, ± thin-walled, central strand usually well developed. **Leaves** ovate- or triangular-short to -long lanceolate, ca. 1–3 mm long, apex narrowly to bluntly acute, base often subsheathing, channeled distally; margins plane distally, often recurved to reflexed below, entire to dentate or crenulate at apex; costa subpercurrent to long-excurrent, superficial cells ventrally quadrate

to elongate, 2–4(–8) cells across at midleaf, dorsally cells short rectangular above midleaf, in cross-section ovate, semicircular or reniform, stereids usually above and below guide cells, or occasionally absent ventrally, epidermis ventrally present, rarely absent, dorsally weakly present, guide cells 2–6(–8) in 1 layer; lamina unistratose, occasionally bistratose throughout or in patches; upper laminal cells subquadrate- to hexagonal-rounded, thin to thick-walled, bulging or with papillae, either simple or bifid; basal cells weakly differentiated across, often confined to near leaf insertion, quadrate or rectangular, smooth or weakly papillose. KOH leaf color reaction yellow or red. **Dioicous**. **Perichaetia** terminal; leaves often enlarged, loosely sheathing. **Seta** elongate, 5–20 mm long, twisted. **Capsule** erect, urn ovate to long cylindrical, 1–3 mm long; stomata few at base; annulus persistent. **Operculum** conic or conic-rostrate. **Peristome** single, teeth usually divided into 32 filaments and often twisted, or reduced and short, papillose or spiculose, basal membrane absent or low. **Calyptra** cucullate, naked and smooth. **Spores** spherical, nearly smooth to papillose.

DISCUSSION. This genus, along with *Barbula*, is in need of a critical revision in the Neotropics. For distinctions between *Barbula* and *Didymodon*, see discussion under the former genus. The genus as defined by Zander (1993), still remains somewhat heterogeneous and further genera may be recognized after additional studies. Species previously assigned to *Husnotiella* are now placed in *Didymodon*; *Husnotiella glossophylla* Herzog - status unknown, type lost (fide R. Zander).

LITERATURE. Robinson, H. 1970. A revision of the moss genus *Trichostomopsis*. Phytologia 20: 184–191. - Zander, R. H. 1978. New combinations in *Didymodon* (Musci) and a key to the taxa in North America north of Mexico. Phytologia 41: 11–32. - Zander, R. H. 1981. *Didymodon* (Pottiaceae) in Mexico and California: taxonomy and nomenclature of discontinuous and nondiscontinuous taxa. Cryptogamie: Bryologie, Lichénologie 2: 379–422. - Zander, R. H. 1993 (see family ref.). - Zander, R. H. 1998. A phylogrammatic evolutionary analysis of the moss genus *Didymodon* in North America north of Mexico. Bulletin of the Buffalo Society of Natural Sciences 36: 81–115.

Dolotortula (Fig. 178) - A monotypic genus, previously placed in *Tortula*. *D. mniifolia* (Sull.) R. H. Zander is confined to and rather widespread in the Neotropics.

HABITAT. On soil and rock, along banks of streams and falls, fully to partially exposed, moist sites; sparsely wooded lowland to lower montane, 35–2050 m.

DESCRIPTION. **Plants** medium sized, forming loose soft tufts, dull dark green to brownish-green. **Stems** erect, to ca. 15 mm tall; weakly radiculose below; in cross-section hyalodermis absent, little differentiation between epidermis and cortex cells, central strand present. **Leaves** loosely erect and contorted when dry, erect- to wide-spreading when wet, ligulate to more commonly spathulate, (2–)2.5–5.5 mm long, to 1.5 mm wide, flat, apex obtuse-rounded, bluntly apiculate; margins plane or weakly recurved below midleaf, entire, limbate; costa slender, subpercurrent to percurrent, superficial cells ventrally long rectangular with 2 rows of cells at midleaf, dorsally narrowly elongate, in cross-section round, stereids few below guide cells, epidermis present ventrally and dorsally, guide cells 2 in 1 layer; lamina unistratose; upper and median laminal cells large, oblong-hexagonal to short rectangular-rounded, thin-walled, smooth; basal cells not strongly differentiated, rectangular, lax; marginal cells long linear, forming a border, multistratose, 4 stereids in thickness. KOH leaf color reaction red. **Dioicous**. **Perichaetia** terminal; leaves similar but slightly larger. **Seta** elongate, to 12 mm long, twisted. **Capsule** erect, urn cylindrical, 1.2–2 mm long; annulus in 3–4 rows, persistent. **Operculum** long-conic. **Peristome** teeth divided into 32 filaments, spiculose, basal membrane low. **Calyptra** cucullate, naked and smooth. **Spores** lightly papillose.

DISCUSSION. The genus, rather rare, is distinguished by the obtuse-rounded, spathulate leaves with a strong, multistratose border and large upper laminal cells. Gametophytically, the Mniaceae is rather similar to *Dolotortula*, however this genus exhibits a combination of features, e.g., multistratose and subentire or entire margins, not found in neotropical Mniaceae.

LITERATURE. Zander, R. H. 1989, 1993 (see family ref.).

Erythrophyllastrum (Fig. 178) - A monotypic genus with *E. andinum* (Sull.) R. H. Zander, as the specific name implies, restricted to the Andes (Colombia to Bolivia).

HABITAT. On soil, usually in dense tufts; páramo and puna, 3000–4550 m.

DESCRIPTION. **Plants** medium sized, forming loose or somewhat dense tufts, dark green, black or brown. **Stems** erect, to 4.5 cm tall, reddish-brown, few branched; in cross-section hyalodermis present, inner 3–5 rows of cells small, thick-walled, inner cells larger, central strand well developed. **Leaves** crowded, erect-appressed and curled when dry, widespread when wet, lanceolate, 2–3 mm long, distally keeled or channeled, broadly sheathing below, apex acute; margins plane, entire; costa strong, percurrent, superficial cells ventrally quadrate, short rectangular at apex or not, papillose, 10–16 rows of cells across at midleaf, dorsally quadrate at apex, rectangular below, in cross-section

semicircular, stereids above and below guide cells, guide cells (4–)6 in 1 layer; lamina unistratose to partially or fully bistratose; laminal cells of limb subquadrate or short-rectangular-oval; cells of sheathing base similar across, forming an enlarged area of lax rectangular cells; marginal cells forming a border of long rectangular cells. KOH leaf color reaction red. **Dioicous**. **Perichaetia** terminal. **Seta** elongate, to 10 mm long. **Capsule** erect, urn elliptical, to 2 mm long; stomata at urn base, superficial; annulus in 1–2 rows. **Operculum** long conic to conic-rostrate. **Peristome** teeth short and irregularly divided, perforate, papillose. **Calyptra** cucullate, smooth and naked. **Spores** finely papillose.

DISCUSSION. The genus is similar to *Erythrophyllopsis*, see comments under that genus. Zander (1977a, see family ref.) noted that the Colombian populations differed from those of Bolivia, exhibiting a mostly unistratose lamina or partially bistratose margin rather than a typical bistratose lamina.

Erythrophyllopsis (Fig. 179) - A monotypic genus, with *E. fuscula* (Müll. Hal.) Hilp. only known from Bolivia and Argentina.

HABITAT. On moist rocks; apparently rare, high elevations in puna.

DESCRIPTION. **Plants** somewhat large, forming tufts or cushions, dark green to reddish brown above. **Stems** to 3 cm tall, few branched; in cross-section a hyalodermis present, often collapsed, outer 2–3 rows of cortical cells somewhat small, thick-walled, inner cells larger, thin-walled, central strand well-developed. **Leaves** crowded, appressed below, incurved above, squarrose-spreading when wet, long lanceolate from a strongly sheathing oblong base, 3.5–4.5 mm long, broadly channeled or keeled distally, apex acuminate to narrowly acute; margins plane, entire to weakly denticulate at apex; costa percurrent or appearing to end in acumen, strong, upper surface cells above base elongate, in cross-section stereids in several rows above and below guide cells; upper laminal cells bistratose, cells along marginal shoulder and above quadrate, papillose, papillae bifid, several over lumen, thick-walled; basal cells differentiated, those toward the sheathing shoulders narrowly rectangular and often thick-walled, intralaminal cells of sheath and base long rectangular, thin-walled. KOH leaf color reaction red. **Dioicous**. **Perichaetia** terminal; leaves similar to stem leaves. **Seta** elongate, to 15 mm long, twisted. **Capsule** erect, urn ca. 3.3 mm long; stomata at urn base, superficial; annulus in 3–4 rows, persistent. **Operculum** conic-rostrate. **Peristome** single, teeth short, 16 or reduced, papillose, straight. **Calyptra** unknown. **Spores** spherical, appearing smooth.

DISCUSSION. The genus is characterized by the differentiated leaf limb and base, the base distinctly shouldered, plane margins and bistratose lamina limb. *Erythrophyllastrum* is similar but differs by the 1–3 layers of hyalodermis cells, shorter leaves (2–3 mm), and upper lamina unistratose to partially or fully bistratose.

LITERATURE. Zander, R. H. 1993 (see family ref.).

Eucladium (Fig. 179) - A monotypic genus, with *E. verticillatum* (Brid.) Bruch & Schimp. known in the Neotropics from Mexico, West Indies, Central America and recently reported for southeastern Brazil; also occurring in North America, Europe, Africa, and Asia.

HABITAT. On calcareous rocks, often associated with waterfalls and entrance to caves; infrequent in our area, to 860 m.

DESCRIPTION. **Plants** rather small, forming tufts, bright green to dark green above. Stems erect, irregularly branched, weakly radiculose below or not; hyalodermis weakly differentiated, central strand absent. **Leaves** incurved when dry, recurved-spreading to spreading when wet, linear- to narrowly oblong-lanceolate, 1.5–2.5 mm long, apex narrowly to broadly acute; margins plane, entire above, denticulate below; costa short excurrent as a strong mucro, superficial cells ventrally quadrate to elongate, bulging, 6 rows across at midleaf, dorsally cells elongate, in cross-section semicircular to elliptical, stereids above and below the 4–7 guide cells, epidermis present ventrally and dorsally, smooth; lamina unistratose; upper cells subquadrate, appearing smaller along the margins, rather thick-walled and often weakly bulging, pluripapillose, papillae low, mostly simple, occasionally multifid; basal cells strongly differentiated across, oblong-rectangular, thin-walled. KOH leaf color reaction yellow. **Dioicous**. **Perichaetia** terminal; leaves ovate-lanceolate. **Seta** elongate, to 6 mm long, twisted or not. **Capsule** erect, urn ovoid to short cylindrical, to 1 mm long; stomata at urn base, superficial; annulus in 2 rows. **Operculum** conic-long rostrate. **Peristome** teeth cleft or entire, usually somewhat rudimentary, papillose, basal membrane low. **Calyptra** cucullate. **Spores** spherical, smooth.

DISCUSSION. The genus is best distinguished by the toothed lower leaf margins in combination with the absence of a central strand, weakly differentiated hyalodermis, plane leaf margins and pluripapillose upper laminal cells with simple, low papillae.

LITERATURE. Zander, R. H. 1993 (see family ref.).

Ganguleea (Fig. 179) - A monotypic genus, with *G. angulosa* (Broth. & Dixon) R. H. Zander known from southeastern Brazil and Himalayas of India and Nepal.

HABITAT. On soil over rocks; open montane, 160–700 m.

DESCRIPTION. **Plants** small, forming loose tufts, green above, dark brown or blackish below. **Stems** rosulate, to 3 mm high, several branched; in cross-section hyalodermis absent, outer 1–2 rows of cells small, thick-walled, inner cells larger, rather thin-walled, central strand absent; rhizoids few. **Leaves** incurved and tubulose when dry, spreading when wet, oblong-elliptical to spathulate, 1.5–2 mm long, apex rounded apiculate to broadly acute; margins incurved, entire; costa subpercurrent to short excurrent as a sharp mucro, strong, superficial cells ventrally quadrate-rounded, bulging, 2–4 rows across at midleaf, dorsally cells elongate, in cross-section circular, stereids below the 2 guide cells, epidermis present ventrally and dorsally smaller, smooth; lamina unistratose; cells thick-walled, mostly quadrate-rounded, bulging on upper surface, lower surface flat; juxtacostal cells near base enlarged, oblong-rectangular. KOH leaf color reaction yellow. **Autoicous** (paroicous). **Perichaetia** on short lateral branches; leaves differentiated, oblong-short lanceolate. **Seta** elongate, to 5.5 mm long, slender, twisted. **Capsule** erect or suberect, urn ovoid, to 0.8 mm long, plicate, plications several; stomata at urn base, superficial; annulus in 2 rows. **Operculum** conic-long rostrate. **Peristome** absent. **Calyptra** long conic, smooth to slightly roughened distally base cleft. **Spores** spherical, smooth or nearly so.

DISCUSSION. The genus is characterized by leaves narrowing toward the base, sporophytes produced laterally, and plicate, eperistomate capsule. *Ganguleea angulosa* is an exceedingly rare moss. In Brazil, only known from a single locality above Rio de Janeiro. It was previously placed in *Merceyopsis* and *Weisiopsis*. The generic name honors the Indian bryologist Hirendra C. Gangulee (1914–), author of *Mosses of Eastern India and Adjacent Regions*.

LITERATURE. Zander, R. H. 1989, 1993 (see family ref.).

Gertrudiella (Fig. 180) - A monotypic genus, with *G. validinervis* (Herzog) Broth. only known from Bolivia.

HABITAT. On rocks; dry lowland to puna, at elevations from 300–3200 m.

DESCRIPTION. **Plants** medium sized, forming cushions, green above, brown to reddish- or blackish-brown below. **Stems** to 2 cm long, several branched; in cross-section hyalodermis differentiated, cells rather firm, outer 1–3 rows of cells small, thick-walled, inner cells large, thin-walled, central strand well developed. **Leaves** crowded, contorted or curled and weakly spreading when dry, squarrose from a short sheathing base when wet, long lanceolate from a weakly differentiated elliptical base, 3.5–4.5 mm long, broadly channeled distally, apex narrowly acute or appearing gradually acuminate; margins revolute to near apex, entire or weakly dentate at apex; costa percurrent to short excurrent, in cross-section semicircular, stereids well developed in several rows below guide cells, reniform in shape, guide cells also in several rows, upper epidermal cells differentiated, papillose; lamina unistratose; upper laminal cells subquadrate to irregularly hexagonal, firm-walled, upper surface mammillose-bulging, lower surface flat in median portion; basal juxtacostal cells large and rectangular, somewhat thin-walled; marginal cells in 10–20 rows bulging and papillose on both surfaces. KOH leaf color reaction orange. **Dioicous**? **Sporophytes** unknown.

DISCUSSION. Distinguishing features include the recurved leaf margins, unistratose lamina with cells bulging on upper surface and flat on the lower median surface, margins with up to 20 rows of cells that are bulging and papillose on both surfaces. The costa exhibits several important features, including the strong reniform single band of stereids below the several rows of guide cells. *Gertrudiella* is placed in a separate subfamily of the Pottiaceae, the Gertrudielloideae. The generic name, originally *Gertrudia*, was given by T. Herzog in dedication to his wife, Gertrude.

LITERATURE. Herzog, T. 1916 (see general ref.). - Zander, R. H. 1993 (see family ref.).

Globulinella (Fig. 180) - Two species largely confined to the Neotropics; *G. benoistii* (Thér.) Magill is only known from Ecuador and *G. globifera* (Hampe) Steere is distributed from the southwestern United States to Central America.

HABITAT. On soil; open dry montane, 2000–2800 m.

DESCRIPTION. **Plants** small, gregarious or forming short tufts, green above, light brown below. **Stems** to 6 mm high, simple or few branched by subperichaetial innovations; in cross-section hyalodermis absent, central strand well developed. **Leaves** appressed when dry, slightly spreading when wet, ovate, spathulate or orbicular, to 1.3 mm long, distally concave to broadly channeled, apex broadly rounded, usually cucullate; margins plane to incurved; costa subpercurrent, strong and rather broad, spurred or not, superficial cells ventrally quadrate to short rectangular, bulging, 2–6 rows across at midleaf, dorsally elongate, in cross-section round to elliptical, stereids present below guide cells, ventral and dorsal epidermis present, guide cells 2–4 in 1 layer; laminal cells of distal 1/2–2/3

subquadrate to short-rectangular, irregularly thick-walled, weakly bulging, more so on upper surface, smooth; basal cells weakly differentiated across, oblong-rectangular, firm-walled, smooth, rarely weakly porose. KOH leaf color reaction yellow. **Gemmae** uncommon, in leaf axils, spherical to short clavate. **Dioicous**. **Perichaetia** terminal; leaves rather similar or slightly larger. **Seta** to 8 mm long, twisted. **Capsule** erect, urn ovoid to ellipsoid, to 1.6 mm long; stomata at urn base, superficial; annulus in 2 rows. **Operculum** rostrate, slightly oblique. **Peristome** teeth irregularly cleft or fused, densely spiculose. **Calyptra** cucullate, smooth. **Spores** spherical, smooth to weakly papillose.

DISCUSSION. The genus is distinguished by the appressed, concave, obovate to spathulate leaves, broadly acute, often cucullate apex, bulging ventral costa, thick-walled distal laminal cells and well exserted, peristomate sporophytes. *Globulinella peruviana* (R. S. Williams) Steere is now placed in *Saitobryum*.

LITERATURE. Magill, R. E. 1977. A reexamination of *Globulinella* (Musci; Pottiaceae). The Bryologist 80: 76–82.

Gymnostomiella - A single species in the Neotropics, *G. vernicosa* (Harv.) M. Fleisch. (= *G. orcuttii* E. B. Bartram) is known from Mexico, Central America, West Indies, Galápagos Islands, Brazil, and Australasia); five species largely associated with Africa and Australasia.

HABITAT. On wet limestone rocks, apparently associated with cyanobacteria; open lowland to submontane, from near sea level to 1500 m.

DESCRIPTION. **Plants** minute, forming low tufts, dull green to brown. **Stems** loosely erect, to 3 mm tall, simple or few branched, radiculose at base; in cross-section hyalodermis absent, central strand well developed, large. **Leaves** distant to somewhat crowded distally, laxly erect to spreading when dry, spreading to wide-spreading when wet, oblong-obovate, to 0.4 mm long, apex obtuse to broadly rounded; margins plane, crenulate-papillose in distal half; costa ca. 3/4 lamina length, weak, superficial cells on both surfaces elongate, 2 cells across ventrally at midleaf, in cross-section elliptical, cells undifferentiated or guide cells positioned centrally, 2 in 1 layer; lamina unistratose; laminal cells lax, upper cells (distal half) hexagonal, papillose, 1–3 simple papillae over lumen; basal cells differentiated across, rectangular, smooth. KOH leaf color reaction yellow, or variously negative to black or pink to deep purple. **Gemmae** present in distal leaf axils, ellipsoid. **Dioicous**. **Perichaetia** terminal; leaves larger, spathulate, sheathing, laminal cells nearly smooth. **Seta** to 6 mm long. **Capsule** erect, urn broadly ovoid to short ellipsoid, to 0.8 mm long; annulus little differentiated. **Operculum** low conic-long rostrate, oblique. **Peristome** absent. **Calyptra** cucullate, smooth and naked. **Spores** spherical, finely papillose.

DISCUSSION. The genus is characterized by the small stature, obovate-oblong leaves, weak costa extends to ca. 3/4 the leaf length, a centrally positioned stereid band, rather large, laminal cell with 1–3 papillae, and absence of a peristome.

LITERATURE. Arts, T. 1998. A revision of the moss genus *Gymnostomiella* Fleisch. Journal of Bryology 20: 411–427. - Redfearn, P. L., Jr. 1991. *Gymnostomiella* (Musci: Pottiaceae) in the neotropics and eastern Asia. The Bryologist 94: 392–395.

Gymnostomum (Fig. 180) - About three species in the Neotropics: *G. aeruginosum* J. E. Sm. is the most common species in our area, *G. calcareum* Nees & Hornsch. is widespread (and likely a synonym of the former) and *G. jacksharpii* (H. A. Crum) B. H. Allen occurs in Central America; a widespread genus of 24 species.

HABITAT. On soil and rocks, frequently calcareous, in moist or wet, often shaded sites; submontane to upper montane, 700–2900 m.

DESCRIPTION. **Plants** erect, forming tufts or cushions, light to dark green or olive green. **Stems** erect, to 25 mm tall, few to several branched, mostly radiculose; in cross-section hyalodermis present or absent, central strand generally present. **Leaves** distant, rarely crowded above, appressed to somewhat erect-spreading when dry, spreading when wet, oblong to oblong-ligulate, ca. 0.5–1 mm long, apex broadly acute to acute-rounded, apiculate or not, base not decurrent; margins plane, rarely recurved on one side, entire or finely crenulate by projecting papillae; costa rather strong, subpercurrent, superficial cells ventrally quadrate to short rectangular, dorsally elongate, 2–4(6) rows of cells ventrally at midleaf, in cross-section ovate to semicircular, stereid bands weakly represented ventrally and dorsally, ventral epidermis present, 2–4 guide cells in 1 layer; upper laminal cells mostly subquadrate, pluripapillose, papillae simple or bifid, usually hollow; basal cells differentiated across leaf base or higher medially, subquadrate to short rectangular. KOH leaf color reaction yellow to yellow-orange, occasionally with red blotches. **Dioicous**. **Perigonia** terminal on short branches. **Perichaetia** terminal; inner leaves larger than stem leaves, sheathing below. **Seta** elongate, to 6 mm long. **Capsule** erect, urn ovoid to short cylindrical, to 0.8 mm long; annulus in 1–3 rows. **Operculum**

rostrate. **Peristome** absent. **Calyptra** cucullate, naked and smooth. **Spores** spherical, smooth to papillose.

DISCUSSION. The genus is characterized by the rather small plants, the distant, somewhat appressed, ligulate leaves, subpercurrent costa, generally weak stereid bands, finely pluripapillose laminal cells, firm-walled basal cells, and eperistomate capsules. Zander (in Sharp et al. 1994 - see generally ref.) has noted that *Gymnostomum* may be confused with *Molendoa sendtneriana*, but the latter differs in having the leaves arranged in distinct spirals and laminal cells with papillae solid, not hollow as in the former.

LITERATURE. Zander, R. H. 1977b, 1993 (see family ref.).

Hennediella (Fig. 181) - About eight species in the Neotropics, primarily distributed in Mexico and the Andes; 20 species rather widespread but with the greatest diversity in the Southern Hemisphere.

HABITAT. On moist to wet soil, or possibly rocks; mid open montane to páramo and puna, 2200–4800 m.

DESCRIPTION. **Plants** mostly medium sized, forming loose tufts olive to light green above, brown or brownish black below. **Stems** erect, occasionally laxly so, few several branched, radiculose; in cross-section hyalodermis absent or present with cells collapsed or not, outer 2–3 rows slightly differentiated with cells smaller and somewhat thick-walled, inner cells larger, thin-walled, or cells ± uniform, central strand weak; rhizoids appearing smooth. **Leaves** appressed to incurved above an appressed sheathing base when dry, erect-spreading to spreading when wet, broadly lanceolate to oblong-spathulate, to ca. 5 mm long, flat to channeled distally, apex narrowly to broadly acute or rounded and apiculate or not; margins plane to rarely recurved, dentate to serrate, often sharply so, limbate; costa percurrent to short excurrent, rarely subpercurrent, upper superficial cells mostly short rectangular, smooth or papillose, lower cells elongate, smooth, in cross-section a single stereid band below guide cells, upper surface cells distinct; upper cells quadrate, short rectangular or hexagonal, thin- to firm-walled, smooth to more commonly pluripapillose, papillae simple to bifid; basal cells long rectangular, rather lax, thin-walled; marginal cells forming a border of 2–12 rows, mostly long rectangular, smooth. KOH leaf color reaction red. **Autoicous** or dioicous. **Perichaetia** terminal; leaves slightly larger, otherwise similar. **Seta** to 15 mm or more long, rather slender, twisted. **Capsule** erect to slightly curved, cylindrical, to 4 mm long; exothecial cells rectangular, thin-walled; stomata at urn base, superficial; annulus in 2–3 rows, persistent. **Operculum** long-conic to -rostrate. **Peristome** absent or single thin- to firm-walled, teeth divided into 32 filaments, long, spirally arranged, spiculose, basal membrane high. **Calyptra** cucullate, smooth and naked. **Spores** ± spherical, faintly to distinctly papillose.

DISCUSSION. The broad spathulate or lanceolate leaves usually with a distinct border and rather sharply toothed margins characterizes several of our species. The genus is most closely related to *Dolotortula*. The genus, as defined by Zander (1993), contains elements previously placed in *Desmatodon*, *Pottia* and *Tortula*. The generic name honors the Scottish phycologist, Roger Hennedy (1809–1877).

LITERATURE. Zander, R. H. 1993 (see family ref.).

Hymenostyliella (Fig. 181) - A single neotropical species, *H. alata* (Herzog) H. Rob. known from southeastern Brazil; a genus of three species, the remaining two are from India and Philippines.

HABITAT. On soil, associated vegetation and elevation unknown.

DESCRIPTION. **Plants** forming dense tufts, dark green. **Stems** to 1.5 cm tall, few branched; in cross-section central strand present. **Leaves** rather crispate incurved when dry, spreading to widespreading when wet, crowded, narrowly oblong-lanceolate to ligulate from a slightly ovate base, ca. 2.5 mm long, 0.3 mm wide, channeled-concave, apex acute to somewhat obtuse, cucullate, occasionally mucronate, base only slightly broader, short elliptical; margins involute; costa percurrent, bearing 2 prominent lamellae (wings) on upper surface, in cross-section ventral lamellae ca. 12 cells high, 1 cell wide, stereid bands well developed below guide cells, fewer above, 3–4 guide cells in 1 layer; upper laminal cells rather strongly mammillose on ventral surface, flat on dorsal surface; basal cells rectangular, yellowish, subpellucid. **Dioicous**? **Sporophytes** unknown.

DISCUSSION. This species is readily distinguished by the presence of ventral lamellae in two rows over the costa in combination with the strongly mammillose cells on the upper leaf surface. Originally placed in *Timmiella* by Herzog (1925), this species is known from a single collection made by Lützelburg from an unknown locality in Brazil. The above description is adapted from Herzog (1925) and Robinson (1971). The KOH leaf color reaction may be yellow.

LITERATURE. Herzog, T. 1925. Contribuições ao conhecimento da Flora Bryologica do Brasil. Archivos de Botanica do Estado de S. Paulo 1: 27–105. - Robinson, H. 1971. A revision of the moss genus, *Hymenostyliella*, with description of sporophyte. Phytologia 21: 1–3.

Hymenostylium (Fig. 181) - Two species in the Neotropics: *H. recurvirostrum* (Hedw.) Dixon is the most common and widespread species in our area, *H. contextum* Herzog is only known from Bolivia. A genus containing 18 species distributed worldwide.

HABITAT. On rocks, often associated with streams and waterfalls; open montane to zacatonal, páramo and puna, 500–4500 m.

DESCRIPTION. **Plants** rather small, forming dense tufts, glossy, occasionally glaucous green above, light brown below. **Stems** erect, several to many branched, radiculose or tomentose, flagellate branches often present; in cross-section hyalodermis usually absent, outer 2–4 rows of cells small, thick-walled, inner cells larger, thin-walled, central strand absent or weak; rhizoids red. **Leaves** distant or somewhat crowded, appressed- to spreading-incurved when dry, spreading to widespreading when wet, narrowly oblong- to ligulate-lanceolate, 2–3 mm long, keeled, apex acute, to acute-rounded, base weakly decurrent or not; margins plane or broadly recurved on one or both sides, dentate to crenulate; costa subpercurrent to short excurrent and ending in a short mucronate point, superficial cells elongate above, 2–4 cells across at midleaf, in cross-section semi-circular or circular, stereids 2–3 above guide cells or absent, stereids below 3–6, guide cells 2–4 in 1 layer; lamina unistratose, rarely bistratose in patches; upper laminal cells subquadrate to irregularly short rectangular, papillose, papillae low, 1–3 over lumen; marginal cells slightly elongate; basal cells differentiated across, elongate, rectangular, ± thick-walled and porose or not; basal marginal cells rectangular and hyaline. KOH leaf color reaction yellow. **Dioicous**. **Perichaetia** terminal; leaves similar or slightly differentiated. **Seta** elongate, to 10 mm long, twisted. **Capsule** erect, urn ovoid, ca. 1 mm long; stomata at urn base, superficial; annulus weakly differentiated. **Operculum** long rostrate, oblique, often remaining attached to columella. **Peristome** absent. **Calyptra** cucullate, naked and smooth. **Spores** lightly papillose.

DISCUSSION. The genus is characterized by the usual absence of a hyalodermis and central strand, the oblong-lanceolate or ligulate-keeled leaves, with the laminal cells bearing one or more low papillae not obscuring lumen, absence of ventral epidermis on costa, presence of two stereid bands, columella remaining attached to the operculum, after dehiscence or not, and eperistomate capsule. The species were placed in *Gymnostomum* by past and some recent authors.

LITERATURE. Zander, R. H. 1977, 1992 (see family ref.).

Hyophila (Fig. 182) - Twenty-five species recorded for the Neotropics, probably only about five with *H. involuta* (Hook.) A. Jaeger the only common species; a genus containing some 80 species in temperate and tropical regions.

HABITAT. On rock and soil, frequent along streams or moist or wet cut banks, partially to fully exposed sites; lowland and montane, from near sea level to 2000 m, rarely to 2700 m.

DESCRIPTION. **Plants** small to medium sized, forming dense to loose tufts, dull green, often blackish- or brownish-green. **Stems** erect, radiculose; central strand present. **Leaves** incurved and tubulose when dry, oblong-obovate to ± spathulate, 1.5–2.5 mm long, to 0.8 mm wide, narrowed to base, apex broadly acute to obtuse, often apiculate or mucronate; margins plane, entire below or throughout, distally irregularly serrate or dentate; costa rather strong, subpercurrent to percurrent, superficial cells ventrally short rectangular or occasionally quadrate, 2–6 rows of cells across at midleaf, cells elongate dorsally, in cross-section semicircular, stereids above and below guide cells, ventral and dorsal epidermis present, guide cells 4(–6) in 1 layer; lamina unistratose, bulging on ventral surface; upper laminal cells quadrate-rounded to oval, thick-walled, mammillose; basal cells differentiated across or medially, confined to leaf insertion, short rectangular, ± thin-walled and lax. KOH leaf color reaction yellow, occasionally with red medially above midleaf, at base occasionally red. **Gemmae** occasionally present in distal leaf axils, clavate or stellate, produced terminally on cylindrical stalks. **Dioicous**. **Perichaetia** terminal; leaves similar to stem leaves. **Seta** elongate, to ca. 4–7 mm long, slender. **Capsule** erect, urn cylindrical, 1–2.2 mm long; annulus in 1–3 rows, persistent or deciduous. **Operculum** conic-rostrate. **Peristome** absent. **Calyptra** cucullate, naked and smooth. **Spores** spherical, smooth to lightly papillose.

DISCUSSION. The genus is characterized by a combination of features: spathulate to ligulate leaves; laminal cells bulging on ventral side, dorsally somewhat convex, lacking papillae; little differentiated basal cells or only slightly so at leaf insertion; armed or slightly branched gemmae and absence of a peristome. A review of the neotropical species would likely result in a reduction to less than half of the species presently recorded. The name *H. tortula* (Schwägr.) Hampe, widely used in the Neotropics, is a synonym of *H. involuta*.

Hyophiladelphus - A monotypic genus, with *H. agrarius* (Müll. Hal.) R. H. Zander known from the Caribbean region and southeastern United States (Florida).

HABITAT. On calcareous soil, limestone and sandstone rock, not infrequently associated with disturbed sites on brick or concrete; coastal regions, from sea level to ca. 350 m.

DESCRIPTION. **Plants** small, blackish green. **Stems** very short, to 2 mm tall; central strand present. **Leaves** appressed, involute when dry, weakly spreading when wet, oblong-obovate, elliptical or spathulate, 1.2–2 mm long, concave to broadly channeled above, apex broadly acute; margins entire, occasionally serrulate at apex; costa percurrent to short excurrent, superficial cells ventrally and dorsally elongate and smooth, in cross-section stereids above and below guide cells, guide cells 2 in a single layer; lamina unistratose to partially bistratose along margin or median region; upper laminal cells subquadrate to subrectangular, thin-walled, smooth, not papillose, bulging on upper surface, plane on lower surface; basal cells differentiated across leaf, from near base to 1/3 lamina length, rectangular and rather curved, thin-walled; alar cells often distinctly differentiated, bulging. KOH leaf color reaction strongly yellow-orange. **Gemmae** absent. **Dioicous**. **Perichaetia** terminal; leaves similar to stem leaves. **Seta** elongate, 4–10 mm long. **Capsule** erect, urn cylindrical to ellipsoid, to 1.7 mm long, frequently sulcate; annulus in 1–2 rows, revoluble. **Operculum** long conic. **Peristome** teeth divided into 32 filamentous segments, spiculose, articulations numerous, granulate to spiculose, basal membrane low. **Calyptra** cucullate, naked and smooth. **Spores** spherical, lightly papillose.

DISCUSSION. The genus is characterized by the oblong-obovate to spathulate leaves that are tubulose when dry, ventral and dorsal surface of costa with cells elongate and smooth, stereid bands above and below guide cells, and adaxial surface of lamina bulging. *Hyophiladelphus*, allied with the subfamily Pottioideae and most closely related to *Hymenostyliella*, was previously placed in *Barbula*.

LITERATURE. Zander, R. H. 1995. Phylogenetic relationships of *Hyophiladelphus* gen. nov. (Pottiaceae, Musci) and a perspective on the cladistic method. The Bryologist 98: 363–374.

Leptodontiella (Fig. 182) - A monotypic genus, with *L. apiculata* (R. H. Zander) R. H. Zander & E. H. Hegew. endemic to Peru.

HABITAT. Epiphytic, on trunks and branches of shrubs and trees, also on rocks; open submontane forests and puna, at elevations from 600–4236 m.

DESCRIPTION. **Plants** medium sized, forming loose tufts or mats, greenish-brown. **Stems** suberect, to 3 cm high, several branched, sparsely tomentose below; in cross-section hyalodermis present, often collapsed, appearing fluted, outer 2–3 rows of cortical cells small, thick-walled cells, inner cells larger, thin-walled, central strand absent. **Leaves** distant, appearing 3-ranked, erect and flexuose when dry, spreading-recurved when dry, ovate- to oblong-lanceolate, to 2.5 mm long, apices acuminate to narrowly acute, ending in a long pellucid cell, decurrent; margins weakly recurved below, plane distally, distal 1/3 irregularly sharply serrate or dentate; costa subpercurrent to percurrent, superficial cells elongate ventrally and dorsally, in cross-section stereids above and below guide cells, 4(–6) guide cells in 1 layer; lamina unistratose; laminal cells irregularly quadrate to short rectangular, firm-walled, pluripapillose, papillae simple or bifid, several over lumen; basal cells differentiated, several rows along margin slightly larger, quadrate to short rectangular, juxtacostal cells slightly enlarged, hyaline and thin-walled. KOH leaf color reaction yellow to yellow-orange. **Gemmae** occasionally present on stems, cylindrical, uniseriate. **Dioicous**. **Perichaetia** terminal; leaves to 6 mm long, sheathing nearly total length of seta. **Seta** short, to 2 mm long, twisted. **Capsule** erect, ovoid to short-ellipsoid, to 1.2 mm long; stomata absent; annulus in 1–2 rows, persistent. **Operculum** conic-rostrate. **Peristome** teeth divided to near base into 3–4 filaments, weakly fused below, faintly spirally striate. **Calyptra** cucullate, smooth and naked. **Spores** spherical, finely papillose.

DISCUSSION. *Leptodontiella* can be mistaken for *Leptodontium*; however, the former differs by the uniseriate propagula, short seta (to 2 mm) and urn (to 1.2 mm), and a peristome with the teeth each divided to the base in 3–4 segments; see comments under *Streptotrichum* which is also similar.

LITERATURE. Zander, R. H. 1972 (see ref. under *Leptodontium*). - Zander, R. H. & E. Hegewald. 1976. *Leptodontiella* gen. nov. and *Leptodontium* from Peru. The Bryologist 79: 16–21.

Leptodontium (Fig. 182) - Nineteen species in the Neotropics; a large genus containing 39 species with the greatest diversity found in tropical mountains, with only a few species extending into the temperate regions

HABITAT. Frequent on soil and rock, occasionally epiphytic on trunks and branches of shrubs or small trees; a common element of the open montane to zacatonal, páramo, and puna, at high latitudes in the tropics from 100–600 m, at low latitudes commonly from 1000–4700 m.

DESCRIPTION. **Plants** small to commonly large or robust, forming short tufts or loose to dense tufts, light to dark green, brownish-yellow or golden. **Stems** often stiff and rigid, mostly erect, 1–10(20)

cm tall, simple to several branched; in cross-section hyalodermis present (often collapsed, fluted) or absent, then composed of small stereid cells, central strand absent; rhizoids usually present, often forming a dense tomentum. **Leaves** short or long-lanceolate, with an oblong sheathing base, occasionally leaves oblong, (1–)2–8(–12) mm long, apex narrowly to broadly acute to obtuse, base decurrent or not; margins plane to commonly recurved or reflexed, entire to more commonly serrate or dentate distally or to near base, often sharply so; costa strong, subpercurrent to short excurrent, superficial cells ventrally and dorsally elongate, in cross-section reniform, semicircular or elliptical, stereid bands below and above guide cells, epidermal cells absent both ventrally and dorsally, guide cells 2–4 in 1 layer; lamina unistratose; upper and median cells isodiametric, mostly subquadrate, often obscured by papillae, pluripapillose, or papillae crown-shaped and terminally branched; basal cells medially large, narrowly rectangular to oblong-rectangular, thin-walled, often weakly porose and papillose, outer basal cells often differentiated, oblong to short rectangular. KOH leaf color reaction yellow, or less often yellow with red blotches. **Asexual structures** in the form of gemmae or flagellate branches, gemmae often present on stems, leaf apices or leafless branches, obovoid to claviform, often short stalked. **Dioicous**, rarely autoicous. **Perichaetia** terminal; leaves mostly elongate, long sheathing. **Seta** 1–2 per perichaetium, elongate, (8)10–15 mm long. **Capsule** erect to inclined, urn cylindrical, ca. 1.5–3 mm long; stomata absent or present at base, superficial; annulus in 2-several rows. **Operculum** conic to conic-rostrate. **Peristome** single, teeth usually irregularly divided or perforate, smooth to striate. **Calyptra** cucullate, naked and smooth. **Spores** papillose (di- or monomorphic).

DISCUSSION. This is one of the most frequently encountered pottiaceous genera in the highlands, *Leptodontium* is characterized by the relatively large, coarse habit (not all species), absence of a central strand, presence or absence of a hyalodermis, strongly recurved leaf margins, absence of an costal epidermis, and smooth or striate peristome teeth. *Leptodontiella* and *Streptotrichum*, both rare, are similar. See discussion under those genera. *Zygodon* (Orthotrichaceae) may also be mistaken, at least in aspect, to *Leptodontium*; however, in the former the laminal basal cells are not conspicuously differentiated from the upper cells, and the costa lacks two stereid bands, rather it is either undifferentiated or if stereids present then found dorsally.

LITERATURE. Zander, R. H. 1972. Revision of the genus *Leptodontium* (Musci) in the New World. The Bryologist 75: 213–280 [keys, illustrations].

Luisierella (Fig. 183) - A monotypic genus, with *L. barbula* (Schwägr.) Steere recorded from Mexico, West Indies, and Brazil, also from Java and Japan.

HABITAT. On moist calcareous rock, often associated with crusted cyanobacteria, open sites; at low elevation, from near sea level to 1650 m.

DESCRIPTION. **Plants** very small, gregarious, dull green or blackish-green. **Stems** short, erect, to 2 mm high, infrequently branched; in cross-section cells uniform, hyalodermis absent, central strand absent. **Leaves** contorted and tubulose when dry, spreading-recurved when wet, long ligulate, 1–2 mm long, apex obtuse-rounded to broadly acute; margins plane to erect-incurved, crenulate by projecting cells; costa strong below, weak above, subpercurrent, superficial cells ventrally similar to laminal cells, 4–6 cells across at midleaf, dorsally elongate, in cross-section stereids below guide cells, epidermis present ventrally, absent dorsally, guide cells 2–4 in 1 layer; laminal cells rounded, strongly bulging on upper surface, flat on lower surface; basal cells strongly differentiated, forming a V-shape (extending a short distance along margin), inflated, oblong-rectangular, hyaline and thin-walled. KOH leaf color reaction light yellow to orange, occasionally negative. **Synoicous** or with only perigonial plants. **Perichaetia** terminal; leaves smaller than those on stem. **Seta** elongate, to 5 mm long, twisted. **Capsule** erect, urn cylindrical, to 2 mm long, straight or slightly curved; stomata at urn base, superficial; annulus in 2 rows, persistent. **Operculum** long conic. **Peristome** variable, absent, rudimentary or teeth divided to near base, densely papillose to spiculose. **Calyptra** cucullate, smooth and naked. **Spores** spherical, appearing smooth.

DISCUSSION. The genus is characterized by the small, blackish green plants, narrowly oblong or ligulate leaves, subpercurrent ventrally bulging costa, dorsally flat laminal cells, and sharply differentiated inflated, hyaline basal cells that extend distally along the margin. The genus is named in honor of the French bryologist, Rév. Père Alphonse Luisier (1872–1957).

LITERATURE. Deguchi, H. 1987. *Luisierella* (Pottiaceae, Musci), a moss genus with a disjunctive distribution in Neotropics and Japan. Journal of Japanese Botany 62: 7–15.

Mironia (Fig. 183) - A genus of three species restricted to the cordilleras of the Neotropics; *M. ehrenbergiana* (Müll. Hal.) R. H. Zander is the most frequently encountered species (Mexico, Guatemala, Venezuela to Bolivia), the remaining two are known from the northern Neotropics, *M.*

crassicuspis (H. Rob.) R. H. Zander (Mexico, Guatemala) and *M. stenotheca* (Thér.) R. H. Zander (Mexico).

HABITAT. On soil and rock, occasionally on bark or humus; open upper montane to zacatonal, páramo, and puna, 2530–4350 m.

DESCRIPTION. **Plants** forming tufts, rusty-brown, medium sized. **Stems** erect, to 4–5 cm tall, simple or with few short branches, loosely radiculose below; in cross-section hyalodermis absent, central strand present; rhizoids papillose. **Leaves** loose erect and twisted or curved from a sheathing base when dry, erect-spreading to squarrose when wet, ovate- to oblong-short lanceolate, (1.5–)3–3.5 mm long, usually keeled distally, apex acute, often broadly so, occasionally fragile; margins recurved to near apex, weakly to strongly dentate near apex, rarely entire; costa strong, percurrent to short excurrent as a mucro, in cross-section reniform, stereids below and above guide cells, those above often weak, guide cells 2–5 in 1 layer; laminal margins bistratose; upper and median cells distally subquadrate, pluripapillose, papillae granular to multifid; cells of lower sheathing base elongate, rectangular, weakly papillose to smooth. KOH leaf color reaction red, rarely olive or yellow. **Dioicous**. **Perichaetia** terminal; leaves narrowly oblong, convolute, to 7 mm long. **Seta** elongate, 12–15 mm long, twisted. **Capsule** erect to slightly curved, urn narrowly long cylindrical, 3–4(6) mm long; annulus in 1–3 rows, deciduous; stomata at urn base, superficial. **Operculum** long conic. **Peristome** teeth divided into 32 segments, spirally twisted, segments papillose-spiculose, basal membrane low. **Calyptra** cucullate, naked and smooth. **Spores** spherical, lightly papillose.

DISCUSSION. The genus is similar to *Bryoerythrophyllum* and *Leptodontium*, but differs from the former by leaves keeled, margins bistratose and leaf tips occasionally fragile, and from the latter by the presence of a stem central strand and differentiated costal epidermis. The genus was previously called *Morinia*.

LITERATURE. Zander, R. H. 1978, 1993 (see family ref.).

Molendoa (Fig. 183) - Five species recorded for the Neotropics, primarily from montane regions in Mexico, Central America, the tropical Andes, and southern Brazil; *M. sendtneriana* (Bruch, Schimp. & W. Gümbel) Limpr. is the common species in the Neotropics. A genus of 15 species widely distributed in montane or boreal regions of the world.

HABITAT. On soil and rock, often in disturbed sites; open lower and upper montane to páramo and puna, 2100–4650 m.

DESCRIPTION. **Plants** rather small, forming dense tufts, light to dark green, occasionally glaucous. **Stems** erect, to 40 mm tall, simple to few branched, often somewhat tomentose; in cross-section hyalodermis weakly developed or more commonly absent, outer cortical cells in few rows, small, thick-walled, central strand distinct. **Leaves** crowded, appressed incurved when dry, spreading when wet, oblong- or linear-lanceolate to ligulate, 1–2(–4) mm long, flat to broadly grooved along costa, apex acute-rounded, occasionally cucullate; margins plane, occasionally recurved below, entire to faintly crenulate; costa sub- to percurrent, superficial cells quadrate to elongate on both sides, ventrally 2–7 rows of cells across at midleaf, in cross-section circular to semicircular or reniform, absent or few (2–4) stereids ventrally, dorsally well developed, flattened, guide cells 2–4 in 1 layer; lamina distally fully to partially in patches bistratose; upper cells subquadrate to oval, pluripapillose, papillae 3–4 over lumen, simple or multiple, low; basal cells differentiated across or extending medially, rectangular, smooth to weakly papillose. KOH leaf color reaction light yellow. **Dioicous**. **Perichaetia** terminal on short lateral branches. **Seta** rather short, 2–7 mm long, twisted. **Capsule** erect, urn ovoid to cylindrical, to 1.5 mm, when old rugose and mouth somewhat flared; annulus present, in 2–3 rows. **Operculum** long rostrate, oblique. **Peristome** absent. **Calyptra** cucullate, naked and smooth. **Spores** smooth to lightly papillose.

DISCUSSION. The genus is rather similar to *Anoectangium* with its lateral perichaetia and lack of a peristome, but differs by the presence of a ventral stereid band (sometimes weak or absent), as well as glaucous upper leaves in some species, and upper margins bistratose. The generic name honors the German bryologist, Ludwig Molendo (1833–1902).

Plaubelia (Fig. 184) - A single rather widespread species in the Neotropics, *P. sprengelii* (Schwägr.) R. H. Zander, found in Mexico, Central America, West Indies, Venezuela, and Brazil; in addition to our species, one species in Africa and another in Asia.

HABITAT. On calcareous and sandstone rocks, stream banks, mostly in exposed sites; from near sea level to 700(–1000) m.

DESCRIPTION. **Plants** small, forming short tufts, green. **Stems** short, to ca. 4 mm tall, few branched; in cross-section hyalodermis absent, outer row of cells somewhat small, thick-walled, inner cells larger, central strand well developed; rhizoids few at base. **Leaves** larger and crowded distally, spreading-incurved when dry, wide-spreading when wet, somewhat rosulate, oblong-elliptical, to 3.2

mm long, somewhat broadly concave, apex obtuse-rounded to broadly acute, narrowed toward base; margins plane to somewhat erect, entire to denticulate at apex; costa strong, subpercurrent to percurrent, superficial cells ventrally rounded-hexagonal and bulging, ca. 4 rows across at midleaf, dorsally cells elongate, in cross-section rounded, stereids above and below guide cells, or upper stereids absent or weak, epidermis ventrally well developed, dorsally less so, guide cells 2–4 in 1 layer; lamina unistratose; laminal cells quadrate- to hexagonal-rounded, bulging to papillose on ventral surface, papillae 1–2, usually weak, lower surface flat; juxtacostal basal cells somewhat differentiated, short oblong-rectangular, inflated. KOH leaf color reaction yellow on upper leaves, often orange-brown on lower leaves. **Dioicous**. **Perichaetia** terminal; inner leaves shorter, ovate-lanceolate to ligulate, weakly sheathing. **Seta** to 6 mm long. **Capsule** erect, urn ellipsoid, to 1.7 mm long; stomata at urn base, superficial; annulus persistent or detaching in fragments, rarely revoluble. **Operculum** rostrate. **Peristome** single, teeth divided to near base, not twisted, spiculose, basal membrane absent. **Calyptra** cucullate, smooth and naked. **Spores** spherical, lightly papillose.

DISCUSSION. The genus is similar to *Hyophila*, particularly *H. involuta*, with rosulate, oblong to somewhat spathulate leaves, and cells of the lamina and costa bulging on the ventral side, and dorsally flat; however, *Plaubelia* differs by the rounded-quadrate ventral costal cells and presence of a peristome. The single neotropical species was previously placed in *Neohyophila*. The generic name is apparently in honor of the mycologist Plaubel.

LITERATURE. Zander, R. H. 1983. A reevealuation of *Neohyophila* Crum (Pottiaceae). The Bryologist 86: 134–139.

Pleurochaete (Fig. 184) - A single taxon in the Neotropics, *P. squarrosa* (Brid.) Lindb. var. *luteola* (Besch.) R. H. Zander, known from Mexico, West Indies, Central America, and Colombia to Bolivia; a genus containing four species widely distributed.

HABITAT. Exposed sites on soil and rocks; open montane to páramo and puna, 1800–2800 m.

DESCRIPTION. **Plants** mostly large and robust, forming dense tufts or cushions, dull light to dark green or yellowish-green. **Stems** erect to suberect, to 6 cm tall, several branched, not radiculose; in cross-section hyalodermis weak but present, central strand present. **Leaves** crowded, crispate-contorted when dry, wide-spreading to squarrose-recurved above a sheathing base when wet, 4.5–6 mm long, to 1.5 mm wide, long and gradually lanceolate from a broadly ovate sheathing base, broadly channeled above shoulders, apex acute, base concave, and ± plicate; margins plane to erect distally, wavy below, limbate, expanded base serrulate, limb serrulate-crenulate; costa strong, short excurrent, superficial cells quadrate to short rectangular, papillose, 6–8 rows across on upper surface, in cross-section semicircular or reniform, stereids well developed above and below guide cells, 4–6 guide cells in a single rows; upper laminal cells short rectangular to quadrate, pluripapillose; lower and basal cells oblong-rectangular, smooth; marginal cells forming a border, 2/3–3/4 lamina length, at widest point of 8–10 rows, hyaline, smooth, rectangular, or oblong. KOH leaf color reaction deep yellow to orange. **Dioicous**. **Perichaetia** terminal. **Seta** elongate. **Capsule** erect, urn ovoid-cylindrical, symmetric. **Operculum** long conic. **Peristome** teeth divided into 32 filaments from a basal membrane, weakly spirally twisted, densely papillose. **Calyptra** cucullate, smooth and naked. **Spores** spherical, lightly papillose.

DISCUSSION. The genus is characterized by the distinct border that extends somewhat above the shoulders (to 7 rows), toothed margins, two stereid bands, best developed below, and pluripapillose laminal cells.

Pseudocrossidium (Fig. 184) - Eight species in the Neotropics. Only *P. replicatum* (Taylor) R. H. Zander is frequent in our area, the remaining species are mostly locally distributed in the Andes; a genus containing 16 species, rather widely distributed in highland regions.

HABITAT. On soil or rock; associated with dry vegetation or in slightly drier exposed montane to zacatonal, páramo, and puna, 400 to more commonly 1500–4550 m.

DESCRIPTION. **Plants** forming loose to dense tufts, dark green to blackish- or brownish-green. **Stems** erect, 3–20 mm tall, few branched, weakly radiculose; hyalodermis usually absent or weak, central strand present. **Leaves** erect to spirally-twisted when dry, erect-spreading when wet, oblong-ligulate, ovate or ligulate to lanceolate, 0.5–3 mm long, apex obtuse to acute; margins recurved distally and plane below, or strongly spirally-revolute, entire; costa strong, subpercurrent or short excurrent and mucronate or with a short smooth awn, superficial cells quadrate to short rectangular, upper cells papillose, differentiated as a pad of papillose, thin-walled filaments, in cross-section reniform to circular, stereid band strong below, weak or absent above, guide cells 2–4 (rarely more) across, epidermal cells large; laminal cells subquadrate to hexagonal, generally papillose, papillae crowded, bifid to multiplex; basal cells differentiated medially or across, rectangular, thin to rather thick-walled. KOH leaf color reaction yellow to orange, occasionally with red blotches. **Gemmae** infrequent, when

present on upper surface of leaf costa or axils, clavate or spherical. **Dioicous**. **Perichaetia** terminal; leaves undifferentiated or more commonly strongly differentiated, often elongate, convolute-sheathing, and awned. **Seta** elongate, ca. 10–15 mm long, twisted. **Capsule** erect, urn cylindrical to elliptical, ca. 1.6–3 mm long; exothecial cells short rectangular; stomata few at urn base; annulus in 2–4 rows, persistent. **Operculum** short to long conic or short rostrate. **Peristome** single, teeth divided into 32 filaments to base, twisted or occasionally erect, spiculose, basal membrane absent or low. **Calyptra** cucullate, smooth and naked. **Spores** spherical, nearly smooth to lightly papillose.

DISCUSSION. The genus is distinguished, in part, by the poorly developed (sometimes absent) upper stereid band and strongly developed, often crescent shaped lower stereid band with very thick-walled epidermal layer below. Two further notable features present in some but not all species are the development of photosynthetic tissue in the form of filaments on the adaxial surface of the costa, and strongly revolute-rolled leaf margins. The concept of *Pseudocrossidium* has been modified considerably by Zander (1979, 1981, 1993) from previous workers (e.g., R. S. Williams); it now includes a number of the species placed in *Barbula*.

LITERATURE. Churchill, S. P. 1990. *Pseudocrossidium steerei*, a new species from Ecuador. The Bryologist 93: 353–356. - Zander, R. H. 1979, 1981, 1993 (see family ref.).

Pseudosymblepharis (Fig. 185) - Three species in the Neotropics. *Pseudosymblepharis schimperiana* (Paris) H. A. Crum is the most common species in our area; less wide-ranging are *P. angustifolia* (H. A. Crum & Steere) R. H. Zander from the West Indies, and *P. cavernarum* (Broth.) R. H. Zander from southeastern Brazil. A tropical or subtropical genus of 11 species.

HABITAT. On soil, rock, or tree trunks, in exposed sites, not uncommon in disturbed areas; submontane to upper montane, ca. 1000–4000 m.

DESCRIPTION. **Plants** medium sized, forming dense tufts. **Stems** simple or few branched, to 1.5 cm tall, radiculose below; in cross-section hyalodermis present, outer cells somewhat small than inner cells, central strand weak. **Leaves** crispate and contorted when dry, spreading when wet, linear to linear-lanceolate from a rather narrow to broad oblong sheathing base, 5–7 mm long, 0.5–0.6 mm wide at base, sheathing base concave, yellowish-hyaline, apex acuminate; margins erect to slightly inflexed, crenulate; costa strong, short excurrent as a smooth, sharp point, superficial cells ventrally quadrate to short rectangular, ca. 8–15 rows of cells across at midleaf, dorsally cells elongate, in cross-section semicircular to ovate, stereids above and below guide cells, epidermis present ventrally, absent or present dorsally, smooth, not papillose, guide cells 6–9 in 1 layer; laminal cells above quadrate-rounded, thick-walled, pluripapillose, papillae bulging over cell lumen; cells at junction of limb and sheath elongate, thick-walled and weakly porose near costa; lamina sheath cells mostly long rectangular, smooth, thin-walled below; cells at shoulder usually extending a short distance along margin with inner cells typical of limb cells. KOH leaf color reaction golden yellow-orange, occasionally deep yellow. **Dioicous**. **Perichaetia** terminal; leaves similar, erect. **Seta** elongate, slender. **Capsule** erect, urn cylindrical; annulus absent. **Operculum** conic-rostrate, oblique. **Peristome** single, inserted below mouth, teeth erect, irregularly divided into 2–3 partly fused segments, papillose. **Calyptra** cucullate, naked and smooth. **Spores** spherical, lightly papillose.

DISCUSSION. *Pseudosymblepharis schimperiana* is rather similar to *Trichostomum tenuirostris*, especially the narrow leaf base forms of the former; however, the upper basal cells near the costa in *Trichostomum* are not porose. A further feature, noted by Zander (1993), to distinguish both *Tortella* and *Trichostomum* subgen. *Oxystegus* from *Pseudosymblepharis* is the ventral stereid band distinctly larger than the dorsal band.

LITERATURE. Crum, H. A. 1952. *Pseudosymblepharis* in Middle America. The Bryologist 55: 137–142. - Zander, R. H. 1993 (see family ref.).

Quaesticula (Fig. 185) - A monotypic genus, with *Q. navicularis* (Mitt.) R. H. Zander restricted to Mexico and the West Indies.

HABITAT. On rocks, rarely on tree or palm trunks, associated with streams and waterfalls; apparently montane, at moderate elevations.

DESCRIPTION. **Plants** small, forming low, dense tufts, light to dark green above, light brown below. **Stems** short, to 0.6 mm tall, few branched; in cross-section hyalodermis absent, cells firm-walled, progressively larger inwardly, central strand well-developed. **Leaves** contorted, incurved and tubulose when dry, spreading when wet, ligulate to ligulate-lanceolate, 1.5–2 mm long, apex rounded, weakly cucullate; margins plane at base, distal 1/2–2/3 incurved to involute, entire or crenulate by projecting cell walls; costa strong, subpercurrent, superficial cells quadrate-rounded, 3–6 rows across at midleaf, in cross-section circular to ovate, superficial cells strongly bulging on upper surface, smooth on lower surface, stereids above and below guide cells, occasionally absent above, well developed below, guide cells (2–)4 in a single row; laminal cells above base quadrate-rounded to hexagonal, evenly

thick-walled, mostly unipapillose, papillae large and bulging, more so on upper surface; inner basal cells large, rectangular, thin-walled; marginal cells of leaf base forming a rather distinct border of narrow linear cells. KOH leaf color reaction yellow. **Dioicous**. **Perichaetia** terminal; leaves slightly longer than stem leaves, sheathing at base. **Seta** single, elongate, to 12 mm long, twisted. **Capsule** erect, urn ellipsoidal, to 1.3 mm long; stomata at urn base, superficial; annulus in 3 rows, persistent. **Operculum** long conic. **Peristome** single, teeth divided into 32 long filamentous twisted segments, spiculose, basal membrane low. **Calyptra** cucullate, smooth. **Spores** spherical, smooth.

DISCUSSION. The genus, recently described by Zander (1993), is characterized by the little differentiated cortical cells of stem (as viewed in cross-section), rounded, ligulate leaves, incurved to involute entire margins, bulging cells of upper lamina surface, and twisted filamentous peristome teeth. The name, *Quaesticula*, according to the author, is in reference "to the long and careful evaluation required for placing the new genus in proper taxonomic perspective..." The single species had previously been placed in four genera, including *Weissia* and *Tortula*.

LITERATURE. Zander, R. H. 1993 (see family ref.).

Rhexophyllum (Fig. 185) - A monotypic genus, with *R. subnigrum* (Mitt.) Thér. ex Hilp. only known from Mexico, Peru, Bolivia, and northern Argentina in the Neotropics; also the southwestern United States.

HABITAT. On soil and rock, occasionally on trees; open montane, 2300–4300 m.

DESCRIPTION. **Plants** medium sized, forming tufts, green to blackish-green above, reddish-brown below. **Stems** erect, to 4 cm tall, few branched; in cross-section hyalodermis present, appearing fluted, outer 2–3 rows of cells thick-walled, inner larger, central strand well developed. **Leaves** folded distally, twisted to incurved when dry, widespreading to squarrose when moist, lanceolate to ovate-lanceolate, to 3 mm long, sheathing at base, short decurrent, keeled above, apex acute, fragile; margins plane above, broadly recurved below, distal 1/4–1/2 serrate-dentate, teeth irregular; costa excurrent as short smooth mucro, upper surface cells distally rectangular to quadrate, 3–4 cells across at midleaf, below distally papillose by projecting cell angles, in cross-section reniform, stereids above and below guide cells; lamina bistratose in patches, rarely 3–4 stratose above; laminal cells above base quadrate- to hexagonal-rounded, thin-walled, pluripapillose, papillae crowded, multifid; basal cells rectangular, smooth; marginal cells at base smaller than inner cells. KOH leaf color reaction red. **Dioicous**. **Perichaetia** terminal; inner leaves conspicuously differentiated, convolute-sheathing, longer than stem leaves. **Seta** elongate, to 10 mm long, twisted distally. **Capsule** erect, urn ellipsoidal to cylindrical, to 3.5 mm long; stomata at urn base, superficial; annulus in 2 rows, deciduous. **Operculum** long conic. **Peristome** absent. **Calyptra** cucullate, smooth. **Spores** spherical, weakly papillose.

DISCUSSION. The genus is characterized by the blackish-green distal section stems, presence of a hyalodermis, well developed central strand, oblong-lanceolate leaves that are squarrose when wet, distal leaf margins somewhat irregularly, sharply toothed, lamina mostly bistratose in patches, and perichaetial leaves strongly differentiated. Gametophytically, *Rhexophyllum* can be mistaken for *Leptodontium*, but differs by the blackish-green upper portion of the plants and partially bistratose lamina.

LITERATURE. Zander, R. H. 1993 (see family ref.).

Sagenotortula (Fig. 186) - A monotypic genus, with *S. quitoensis* (Taylor) R. H. Zander confined to the Neotropics (Mexico, tropical Andes).

HABITAT. On humic soil and rocks; upper montane forest to zacatonal, páramo, and puna, 2500–4200 m.

DESCRIPTION. **Plants** medium sized, forming somewhat dense tufts, brownish-green. **Stems** erect, to 3 cm tall, simple to few branched, branches mostly distal, radiculose, occasionally weakly tomentose; in cross-section hyalodermis absent, cells little differentiated, somewhat progressively larger toward center, central strand strong, occasionally collapsed. **Leaves** appressed, incurved, contorted especially branch leaves when dry, erect to erect-spreading when wet, broadly lingulate to spathulate, 3–5 mm long , concave, somewhat cucullate distally, apex obtuse or obtuse-apiculate; margins plane, entire or bluntly toothed by bulging cells; costa subpercurrent to percurrent, superficial cells ventrally quadrate to hexagonal to short-rectangular, 2(–3) cells across at midleaf, dorsally rectangular, in cross-section ± rounded, stereids weakly developed, epidermis ventrally present, dorsally absent, guide cells 2 in 1 layer; upper and median cells subquadrate to short hexagonal, thin-walled, corners somewhat thickened, smooth; basal cells differentiated in lower 1/4, across leaf or medially, rectangular, lax, often fragile toward costa. KOH leaf color reaction red. **Gemmae** borne on tomentum of perigoniate plants. **Dioicous**. **Perichaetia** terminal. **Seta** elongate, to 25 mm long, twisted distally. **Capsule** erect, urn cylindrical, 3–4 mm long; annulus in 2–3 rows, deciduous.

Operculum conic. **Peristome** single, teeth divided into 32 filaments from a low basal membrane, teeth papillose-spiculose. **Calyptra** cucullate, naked and smooth. **Spores** spherical, smooth.

DISCUSSION. The genus is distinguished by the obovate-oblong or spathulate leaves, large, smooth laminal cells, nearly entire, elimbate margins. The single species was previously placed in *Tortula*; the more familiar name, *Tortula mniadelphus* (Müll. Hal.) Broth., is a synonym. When sterile, plants may be confused with the Splachnaceae, e.g., *Tayloria*.

LITERATURE. Zander, R. H. 1989, 1993 (see family ref.).

Saitobryum (Fig. 186) - A monotypic genus, with *S. peruvianum* (R. S. Williams) R. H. Zander known from Mexico, Ecuador, and Peru.

HABITAT. On soil cover rock, including volcanic rock; high elevations including zacatonal, páramo and puna, 4100 m.

DESCRIPTION. **Plants** very small, forming dense, short tufts, deep reddish brown above. **Stems** to 4 mm, few branched, weakly radiculose below; in cross-section hyalodermis absent, central strand distinct. **Leaves** imbricate, appressed when dry, erect-spreading when wet, obovate to oblong-obovate or suborbicular, to 0.6 mm long, widest above midleaf, concave, apex broadly rounded; margins plane above, recurved below, distally crenulate by projecting cell walls, broadly bordered; costa subpercurrent, rather broad, superficial cells above quadrate to short rectangular, papillose, 4–5 rows of cells across at midleaf, cells elongate below, smooth or papillose, in cross-section stereid cells below, guide cells absent, upper epidermal cells bulging; lamina unistratose; distal lamina cells rhomboidal, subquadrate to short rectangular, thick-walled, smooth, forming a border of up to 18 cells wide, medially cells papillose, papillae several over cell lumen, bifid; basal, lower half, cells subquadrate to short rectangular, thin-walled. KOH leaf color reaction deep red. **Sexual** features and sporophytes unknown.

DISCUSSION. The genus is distinguished by the obovate leaves, strong costa, absence of guide cells, presence of a single stereid band on dorsal side of leaf and a wide band (to 18 rows) of smooth laminal cells along margin in upper half of leaf, giving way to pluripapillose cells in the medial zone of the upper lamina. *Saitoella* is likely to be found in intervening tropical highlands. The genus was originally described as *Saitoa* R. H. Zander, *hom. illeg.*, and re-named *Saitoella* Menzel, *hom. illeg*. (cf. Zander, 1997). The generic name honors the Japanese bryologist Kamezo Saito (1947–), a specialist in the Pottiaceae.

LITERATURE. Zander, R. H. 1989, 1993 (see family ref.). - Zander, R. H. 1997. Three nomenclatural changes in Pottiaceae (Musci). The Bryologist 100: 520–521.

Scopelophila (Fig. 186) - Two species in the Neotropics, *S. cataractae* (Mitt.) Broth. and *S. ligulata* (Spruce) Spruce, both rather widespread, including Mexico and the tropical Andes; a rather widespread genus of three species.

HABITAT. On soil or soil over rock, usually associated with highly mineralized soils; open montane, 1500–3300 m.

DESCRIPTION. **Plants** mostly medium sized, forming loose to dense tufts, green or brownish-green above. **Stems** simple to rarely few branched, to 4 cm high; in cross-section hyalodermis absent, cells little differentiated, outer 1–2 rows of cells somewhat small, firm-walled, inner cells slightly larger, thin-walled, central strand absent; rhizoids sparse or forming a tomentum. **Leaves** often crowded, contorted or not, incurved when dry, erect-spreading to spreading when wet, ligulate to lingulate or oblong-spathulate, to 4 mm long, keeled, apex acute to short acuminate or rounded, base slightly decurrent or not; margins plane above, occasionally undulate at least when dry, recurved below, entire or weakly crenulate distally; costa subpercurrent to percurrent, superficial cells ventrally rectangular or quadrate with 2–4 rows of cells across at midleaf, short-rectangular to elongate dorsally, in cross-section semicircular to round, stereid band below, epidermis absent or present ventrally, present dorsally, guide cells 2(–4) in 1 layer; lamina unistratose; upper laminal cells subquadrate or quadrate-rounded, short-rectangular or hexagonal, bulging ventrally or appearing flat, smooth; basal cells differentiated across, extending higher medially, rectangular, hyaline, thin-walled; marginal cells distally often thickened and appearing as a border, lower marginal base bordered by 1 or more rows of narrowly rectangular cells. KOH leaf color reaction yellow to yellow-orange. **Gemmae** rare, stalked from stems, clavate or ellipsoid. **Dioicous**. **Perichaetia** terminal; leaves undifferentiated. **Seta** to 6 mm long. **Capsule** erect, urn short cylindrical, to 2.2 mm long; annulus in 1–3 rows, deciduous in segments. **Operculum** long-rostrate, oblique. **Peristome** absent. **Calyptra** cucullate, smooth. **Spores** faintly papillose.

DISCUSSION. The genus is characterized by the absence of both a central strand and hyalodermis, oblong-spathulate or lingulate leaves, slightly bulging, smooth distal laminal cells, the dorsal costal epidermis and absence of a peristome. Our two species may be differentiated as follows: *S.*

cataractae exhibits acute to short acuminate leaf tips with stems tomentose, whereas in *S. ligulata* the leaf tips are obtuse or rounded, and stems have a few rhizoids. The generic name refers to the rocky habitat of the plants.

LITERATURE. Zander, R. H. 1967. The New World distribution of *Scopelophila* (= *Merceya*). The Bryologist 70: 405–413.

Streptocalypta (Fig. 187) - Three species in the Neotropics, *S. lorentziana* Müll. Hal. (Bolivia and Argentina), *S. santosii* (E. B. Bartram) R. H. Zander (Mexico), and *S. tortelloides* (Cardot) R. H. Zander (Mexico); a genus of four species.

HABITAT. On soil or rock, along stream banks and exposed slopes; montane, including secondary forests, 1420–1950 m.

DESCRIPTION. **Plants** small, forming low tufts, green above, brown below. **Stems** erect, to 6 mm tall, few branched; in cross-section hyalodermis weakly developed or absent, outer and inner cells ± similar, central strand present, occasionally absent. **Leaves** crowded, incurved when dry, spreading when wet, ligulate to lingulate, to ca. 3 mm long, apex acute to rounded, apiculate; margins plane or weakly incurved; costa subpercurrent to short excurrent, superficial cells above quadrate, rectangular below, in cross-section stereids weak or absent above and present below, 2–4 rows of guide cells; lamina unistratose; upper laminal cells subquadrate, pluripapillose, several papillae over cell lumen; basal cells extending upward along margin in a "V," rectangular, smooth, lax and thin-walled; marginal cells distally similar to inner laminal cells or 1–3 rows of fusiform, smooth cells. KOH leaf color reaction yellow or light olive. **Autoicous**, synoicous or dioicous. **Perichaetia** terminal; leaves similar to stem leaves. **Seta** to 10 mm long, twisted. **Capsule** erect, urn cylindrical to ellipsoid, to 1.5 mm long; stomata at urn base or neck, superficial; annulus 1–3 rows, deciduous in portions. **Operculum** long conic to long rostrate, oblique. **Peristome** absent or present and single, teeth divided into 32 filaments, straight to slightly twisted, papillose or spiculose, basal membrane low. **Calyptra** cucullate, smooth and naked. **Spores** spherical, papillose.

DISCUSSION. The genus is characterized by the several layers of guide cells, ventral stereids absent or nearly so; *Tortella* is closely related, sharing features that include the plane leaf margins and distinct “V” of the basal cells. *Streptocalypta* is apparently rather rare, known only from a few collections but likely to be found elsewhere in the Neotropics.

LITERATURE. Zander, R. H. 1982. The genus *Streptocalypta* C. Muell. (= *Barnesia* Card.). Lindbergia 8: 161–165 [keys, illustrations].

Streptopogon (Fig. 187) - Five to seven species in the Neotropics; about seven species distributed in the American tropics, central and southern Africa, Madagascar, and Hawaii.

HABITAT. Epiphytic on branches and trunks of treelets and shrubs, often co-occurring with *Daltonia*, *Lepidopilum*, *Orthotrichum*, etc., infrequently found on rocks; mostly montane forests, extending into shrubby zacatonal, páramo, and puna, 1000–4050 m.

DESCRIPTION. **Plants** medium sized, solitary or forming small tufts, dark green to reddish-brown. **Stems** erect, simple or more often few branched, radiculose below, occasionally weakly tomentose; in cross-section hyalodermis absent, outer 2–3 rows of cells small, thick-walled, inner cells larger, central strand absent. **Leaves** appressed-incurved to weakly contorted when dry, spreading when wet, broadly lanceolate to oblong- ovate, 2–6 mm long, apex acuminate and awned or rounded to abruptly cucullate; margins recurved, or if cucullate then appearing incurved above, entire to distally serrate and often sharply so, limbate or elimbate; costa rather strong, long excurrent and smooth or toothed, or percurrent, superficial cells ventrally and dorsally elongate, 2 rows of cells ventrally at midleaf, in cross-section rounded, stereids few to many rows below guide cells, 2 guide cells ventrally across midleaf; lamina unistratose; laminal cells smooth, short or long hexagonal to rectangular; basal cells little differentiated, rectangular, somewhat lax to firm-walled; marginal cells, if forming a border, long linear, hyaline. KOH leaf color reaction usually red, occasionally yellow to yellow-orange. **Gemmae** absent or if present then on upper distal leaf surface or at and around apex, rarely along upper leaf margin, clavate or cylindrical. **Dioicous** or autoicous. **Perichaetia** terminal; leaves little differentiated or somewhat larger. **Seta** somewhat short, 0.5–8 mm long. **Capsule** emergent, erect, urn long ellipsoid, 3–3.5 mm long; annulus in ca. 4 rows, persistent. **Operculum** long conic. **Peristome** teeth 16 or divided into 32 segments, papillose-spiculose, basal membrane somewhat short to high. **Calyptra** mitrate, lobed below, roughened or scabrous distally. **Spores** spherical, strongly papillose.

DISCUSSION. The genus is characterized by a combination of features of reddish or reddish-brown plants or a least below, leaves rather lax, costa rather strong with superficial cells elongate, smooth laminal cells that are little differentiated above and below, often with gemmae present on leaves, and with capsules often emergent on a relatively short seta. In the Neotropics *Streptopogon* is one of the few epiphytic genera in the Pottiaceae that is confined to primary and secondary montane forests.

LITERATURE. Salmon, E. S. 1903. A monograph of the genus *Streptopogon* Wils. Annals of Botany (London) 17: 107–150 [illustrations]. - Zander, R. H. 1993 (see family ref.).

Streptotrichum (Fig. 187) - A rare monotypic genus, with *S. ramicola* Herzog only known from Bolivia.

HABITAT. On nodes of bamboo; upper montane forests, at elevations from 3140–3400 m.

DESCRIPTION. **Plants** rather large, forming loose tufts, green above, light brown below. **Stems** to 4 cm high, several branched, sparsely tomentose; in cross-section hyalodermis present, outer 2–3 rows of cortical cells small, thick-walled, inner cells large, thin-walled, central strand absent. **Leaves** spreading-twisted when dry, squarrose-recurved when moist, lanceolate to oblong-lanceolate, to 3.3 mm long, keeled distally, apex acute, base sheathing to 1/3 of leaf length; margins recurved below, distally dentate; costa subpercurrent, superficial cells elongate on both surfaces, 4–7 rows of ventral cells at midleaf, in cross-section reniform, stereids above and below guide cells, epidermal cells absent, guide cells 4 in 1 layer; lamina unistratose; laminal cells quadrate to short rectangular, thick-walled, faintly pluripapillose, papillae simple, several over lumen; basal cells (below shoulder) differentiated across leaf base, short to long rectangular, firm but thin-walled. KOH leaf color reaction yellow, occasionally with red blotches. **Dioicous**. **Perichaetia** terminal or subterminal; leaves strongly differentiated, long lanceolate, to 8 mm long, convolute-sheathing most of seta. **Seta** 1(2) per perichaetium, rather short, to 7 mm long, not twisted. **Capsule** erect, urn cylindrical, to 3 mm long; stomata absent; annulus in 1–2 rows, persistent. **Operculum** conic-rostrate. **Peristome** single, teeth divided to near base, occasional with short filamentous segments present along tooth margins, straight to weakly twisted, strongly branching-spiculose, basal membrane low. **Calyptra** cucullate, smooth. **Spores** large (ca. 20 µm), spiculose-papillose.

DISCUSSION. The genus, similar in aspect and gametophytic morphology to *Leptodontium* and *Leptodontiella*, differs by the unique peristomial features, 16 highly divided, spiculose teeth with short filamentous segments along the margins. *Trachyodontium* is also similar to *Streptotrichum*, and both genera are found on bamboo nodes, but the former differs in having a distinct marginal border on the leaves. It is apparently very rare, known from the Bolivian Cordillera Oriental, original collection by T. Herzog northeast of Cochabamba in the early part of this century, and recently northeast of La Paz.

Syntrichia (Fig. 188) - About 24 species in the Neotropics; a widespread genus with approximately 82 species.

HABITAT. On soil, rocks, logs or epiphytic, on trunks and branches of shrubs and trees; mostly open lower montane to zacatonal, páramo and puna, at elevations from 300–4900 m, but commonly at 2500–3500 m.

DESCRIPTION. **Plants** small to rather large, forming loose to dense tufts, light to dark green, yellowish-green or reddish-brown. **Stems** erect, simple to few branched, to 4 cm or more tall, radiculose to tomentose; in cross-section hyalodermis absent or present, often fluted, outer few rows of cells small and thick-walled, inner cells larger, thin-walled, central strand present, often weak, rarely absent. **Leaves** closely to loosely twisted and appressed when dry, erect- or wide-spreading to squarrose when wet, oblong-lanceolate or -obovate to spathulate, ca. 2–7 mm long, apex acute to rounded, rarely cucullate; margins plane to partially to full recurved, entire, or occasionally crenulate to serrate at apex; costa strong, usually projecting on back, percurrent, apiculate to short or somewhat long excurrent, hyaline point when present smooth or toothed, superficial cells ventrally quadrate-rounded, papillose, rarely elongate and smooth, 2–4 rows of cells at midleaf, dorsally elongate and often smooth, in cross-section round, less often semicircular, stereids present below, rarely above, guide cells 2–4 per 1–4 layers; median and upper laminal cells isodiametric, hexagonal to subquadrate, rather thick-walled, collenchymatous or not, pluripapillose, papillae bifid, often appearing C-shaped; basal cells often sharply differentiated from upper cells, differentiated across leaf, extending medially, somewhat firm-walled or lax, mostly long rectangular, basal cells often fragile. KOH leaf color reaction brick red. **Asexual structures** when present represented by gemmae present on upper leaf surface or costa, rhizoidal tubes or fragile and deciduous lamina. **Dioicous** or autoicous. **Perichaetia** terminal; leaves usually similar. **Seta** elongate, 10–30 mm long, often twisted distally. **Capsule** erect to suberect, urn long cylindrical, 2–6 mm long, straight to more commonly curved slightly. **Operculum** short to long conic or conic-rostrate, usually curved; annulus in 2–4 rows, persistent. **Peristome** teeth divided into 32 filaments either divided to base or forming a short to ± long basal membrane, spiculose. **Calyptra** cucullate, naked and smooth. **Spores** spherical, papillose.

DISCUSSION. The genus is characterized by the spathulate to obovate-oblong leaves, elimbate, frequently recurved leaf margins, and often excurrent costa with a single dorsal stereid band. The

majority of our species which have been traditionally placed in *Tortula* and are now placed in *Syntrichia*; cf. Zander, 1993.

LITERATURE. Kramer, W. 1988. Beiträge zur Systematik und Bryogeographie einiger Sippen von *Tortula* Hedw. sect. *Rurales* De Not. (Pottiaceae, Musci) unter besonderer Berücksichtigung der Südhemisphäre. Journal of the Hattori Botanical Laboratory 65: 81–144. - Mishler, B. D. 1985a. Biosystematic studies on the *Tortula ruralis* complex. I. Variation of taxonomic characters in culture. Journal of the Hattori Botanical Laboratory 58: 225–253. - Mishler, B. D. 1985b[1986]. The phylogenetic relationships of *Tortula*: an SEM survey and a preliminary cladistic analysis. The Bryologist 88: 388–403. - Zander, R. H. 1989, 1993 (see family ref.).

Teniolophora (Fig. 188) - A monotypic genus, with *T. fluviatile* (R. S. Williams) W. D. Reese only known from the West Indies (Haiti and Puerto Rico).

HABITAT. On moist or wet rocks associated with streams and waterfalls; to ca. 800 m.

DESCRIPTION. **Plants** medium sized, forming thick tufts, dark green above, brown below. **Stems** erect, few branched; in cross-section outer rows of cells thick-walled, small, inner cells larger, central strand well developed. **Leaves** appressed, incurved-tubulose when dry, spreading when wet, oblong-elliptic, to 2.5 mm long, apex broadly acute to rounded, often apiculate and reflexed; margins plane to incurved, entire to weakly denticulate near apex, intramarginal border present, extending from just above narrowed base to below apex; costa strong, percurrent, in cross-section stereids above and below guide cells, upper surface cells bulging; lamina unistratose; laminal cells subquadrate- to short rectangular-rounded, basal cells rectangular, progressively larger toward costa, firm-walled, upper surface bulging-unipapillose, lower surface flat; intramarginal border cells rectangular, bistratose. KOH leaf color reaction dark yellow on upper leaves, dark yellow-orange on lower leaves. **Gemmae** present, on stalks in upper leaf axils, multicellular, obovoid to ellipsoid. **Dioicous**? **Perichaetia** terminal; leaves little differentiated. **Sporophytes** unknown.

DISCUSSION. The single species is similar to *Hyophila involuta* but differing by the intramarginal border. The name, *Teniolophora*, refers to the intramarginal border, which is similar to the teniolae of *Calymperes*. The original name, *Teniola,* is invalid.

LITERATURE. Reese, W. D. 1959. *Teniola*, a new genus of mosses. The Bryologist 62: 221–224. - Reese, W. D. 1962. *Teniolophora*, a new name for the genus *Teniola*. The Bryologist 65: 67.

Timmiella (Fig. 188) - Two species in the Neotropics, *T. anomala* (Bruch, Schimp. & W. Gümbel) Limpr. (Mexico, Central America) and *T. barbuloides* Mönk. (southern Andes); a genus of 13 species of dry or mountainous regions of North and South America, Europe, Asia, and Africa.

HABITAT. On soil and rock, often calcareous, occasionally on base trunk of trees; open dry vegetation, from ca. 1800–3000 m.

DESCRIPTION. **Plants** rather small, forming tufts or cushions. **Stems** erect, to 1.5 cm tall, simple or few branched; in cross-section hyalodermis present, 1–2 rows of small, thick-walled cells, inner cells larger, central strand well developed. **Leaves** crowded, incurved and tubulose when dry, spreading when wet, broadly lanceolate to long-elliptical, 3.5–5 mm long, somewhat narrower above subsheathing base, apex acute; margins plane to weakly incurved, serrulate to denticulate above base, apex serrate; costa strong, percurrent, in cross-section stereids above and below guide cells, upper surface cells bulging, similar to upper laminal cells but smaller, lower surface cells smooth; lamina bistratose except at margin; upper and lower cells slightly alternating, laminal cells above subsheathing base subquadrate, bulging on upper surface, smooth on lower surface, thick-walled; subsheathing base cells rectangular to long hexagonal, thin-walled. KOH leaf color reaction yellow. **Dioicous**, autoicous or synoicous. **Perichaetia** terminal; leaves similar to stem leaves. **Seta** elongate, 1–2 cm long, twisted. **Capsule** erect, urn long cylindrical, 3–5 mm long; stomata superficial at urn base; annulus present. **Operculum** long rostrate, erect. **Peristome** single, teeth divided to near base, straight or twisted (clockwise), papillose or spiculose, basal membrane smooth or striate. **Calyptra** cucullate, smooth and naked. **Spores** spherical, lightly papillose.

DISCUSSION. The genus is characterized by the presence of a hyalodermis, well developed central strand, distally dentate or serrate, plane or slightly incurved leaf margins, medially bistratose lamina with upper surface cells strongly bulging and positioned not directly over lower row of cells, and lower surface flat. The generic name refers to the resemblance to the moss genus *Timmia*.

LITERATURE. Zander, R. H. 1993 (see family ref.).

Tortella (Fig. 190) - About 10 species in the Neotropics; a widespread genus of 53 species.

HABITAT. On soil and rocks (calcareous or limestone), or on base trunk of trees, occasionally on logs; somewhat open montane vegetation, 500–3080 m.

DESCRIPTION. **Plants** rather small to medium sized, forming loose or dense tufts. **Stems** erect, solitary or few branched, radiculose below; in cross-section outer hyalodermis mostly present, inner 3–4 rows ± thicker, central strand present or absent. **Leaves** crispate and contorted when dry, erect-spreading to spreading when moist, linear- to oblong-lanceolate or lingulate from an erect base, 2.5–7 mm long, rather broadly channeled, apex obtuse to narrowly or broadly acute and often apiculate, rarely caducous, fragile and readily deciduous; margins plane, occasionally broadly incurved, entire to crenulate by projecting papillae, or irregularly denticulate; costa strong, percurrent to more commonly short excurrent, 2–6 rows of cells across on upper surface, in cross-section semicircular or ovate, stereid band above and below guide cells, those above weak to strong, strong below, guide cells 4–6 in 1 layer; median and upper cells thick-walled, subquadrate to short rectangular or rounded-hexagonal, pluripapillose, papillae usually appearing dense; basal cells forming a V-shape extension toward and along marginal shoulder, rectangular, thin- to occasionally thick-walled, smooth. KOH leaf color reaction mostly yellow, occasionally yellowish orange or reddish brown. **Dioicous** or autoicous. **Perichaetia** terminal; leaves little differentiated. **Seta** elongate, 7–30 mm long. **Capsule** stegocarpic, rarely cleistocarpic; erect, urn cylindrical, rarely ellipsoidal, (1.5)2–3 mm long, slightly curved; annulus in 1–4 rows, persistent. **Operculum** high conic. **Peristome** inserted near mouth, teeth divided into 32, linear segments twisted clockwise, spiculose-branched. **Calyptra** cucullate. **Spores** smooth to papillose.

DISCUSSION. The genus is characterized by the V-shape arrangement of the basal cells of the leaf, a feature found most commonly in *Pseudosymblepharis* and *Trichostomum* (subgen. *Oxystegus*). The former generally exhibits leaves that are narrow and elongate above a broadly sheathing base, the latter is not so readily separated in some of its forms, but usually the V-shaped basal cells are not as clearly distinct as in *Tortella*. The caducous leaf apices of *Tortella alpicola* Dixon (syn. *T. tortelloides* (S. W. Greene) H. Rob. in G. A. Llano) likely serves as asexual propagules.

LITERATURE. Eckel, P. M. 1998. Re-evaluation of *Tortella* (Musci, Pottiaceae) in conterminous U.S.A. and Canada with a treatment of the European species of *Tortella nitida*. Bulletin of the Buffalo Society of Natural Sciences 36: 117–191 [keys, illustrations].

Tortula (Fig. 189) - About 23 species recorded for the Neotropics, possibly five or fewer that are valid; a rather widespread genus of far fewer than the presently recognized 163 species.

HABITAT. On soil and rocks, in exposed, dry sties; at moderately high elevations.

DESCRIPTION. **Plants** very small, forming loose to dense tufts, green to yellowish brown. **Stems** short or elongate, few branched; in cross-section hyalodermis absent, outer 1–2 rows of cells slightly small, ± thick-walled, or cells uniform and thin-walled, central strand weak. **Leaves** contorted and curved when dry, erect to erect-spreading, 2.5–4 mm long, oblong-lanceolate to -obovate or spathulate, flat to concave, apex apiculate, broadly acute or rarely short acuminate; margins revolute, less often reflexed, entire; costa short to long excurrent, superficial cells ventrally often quadrate to short rectangular, 3–4(–5) rows across at midleaf, dorsally elongate, in cross-section circular to semicircular, stereid bands weak or absent ventrally, dorsally well developed, ventral epidermal cells often modified, enlarged, guide cells 1(–2) cells in 1(–2) layers; upper laminal cells quadrate-rounded to hexagonal, pluripapillose, papillae several over lumen, often C-shaped; basal cells differentiated across or extending medially, laxly rectangular, thin-walled. KOH leaf color reaction usually yellow, occasionally medially red or negative. **Gemmae** absent. **Dioicous** or autoicous. **Perichaetia** terminal; leaves little differentiated. **Seta** very short (0.1 mm) and somewhat curved, to elongate (to 20 mm or longer), twisted or not. **Capsule** cleistocarpic or stegocarpic, immersed or exserted, subglobose or ellipsoid and apiculate, or short to long cylindrical; exothecial cells rectangular, thin-walled; stomata few at urn base, superficial; annulus in 1–2 rows, usually persistent. **Operculum** absent or present, often long conic. **Peristome** absent or present, teeth divided into 32 filaments from a short to long basal membrane, twisted or straight, spiculose. **Calyptra** cucullate, smooth and naked. **Spores** spherical to subspherical, densely papillose.

DISCUSSION. The genus, as recently emended, is characterized by the presence of a central strand, absence of a hyalodermis, obovate to spathulate leaves, with entire, recurved lower margins, a stereid band that is dorsally well developed and ventrally weak or absent, and rather large, distal laminal cells. A number of the neotropical species originally described in *Tortula* have not been studied, thus whether they represent members of *Syntrichia* or another genus, or in fact are synonyms, awaits further studies. *Tortula*, as defined by Zander (1993), includes *Phascum cuspidatum* Schreb. ex Hedw. (*Tortula atherodes* R. H. Zander). *Pottia*, in the traditional sense as *Tortula* sect. *Pottia* (Zander, 1993). The status and disposition of about seven neotropical species described or assigned to *Pottia* remain unclarified.

LITERATURE. Zander, R. H. 1993 (see family ref.).

Trachycarpidium (Fig. 190) - A single species in the Neotropics, with *T. lonchophyllum* (Roth) R. H. Zander known from southeastern Brazil; a pantropical genus of five species.

HABITAT. On partly sandy soil, exposed moist sites, associated with Ephemeraceae in sods; at low elevations.

DESCRIPTION. **Plants** very small, to 2 mm tall, forming loose tufts, light green. **Stems** erect, to 0.5 mm tall, few to several subfloral branched, radiculose at base; in cross-section hyalodermis absent, central strand weak. **Leaves** contorted-curled when dry, somewhat erect-spreading to spreading when wet, linear, to ca. 1.4 mm long, apex short acuminate; margins involute when dry, ± plane when wet, crenulate by projecting cell papillae; costa rather strong, short excurrent as a short mucro or awn, superficial cells ventrally elongate, ca. 4–6 rows across at midleaf, dorsally elongate, in cross-section semicircular to ovate, stereids few, above and below guide cells, epidermis ventrally weakly developed, dorsally absent or weak, guide cells 2 in 1 layer; lamina unistratose; upper cells hexagonal to subquadrate, rather thick-walled, pluripapillose, papillae several over cell lumen, bifid; basal cells differentiated across and extending upward along margin forming a "V," rectangular, lax, thin-walled. KOH leaf color reaction yellow. **Autoicous**. **Perichaetia** terminal; leaves longer, to 2.2 mm long, otherwise similar to stem leaves. **Seta** very short, to 0.2 mm long. **Capsule** cleistocarpous, spherically beaked, ca. 0.3 mm in diameter, cells bulging (not on the beak). **Calyptra** mitrate, smooth and naked. **Spores** densely fine papillose.

DISCUSSION. The genus is characterized by long lanceolate, awned leaves with entire, plane margins, pluripapillose distal laminal cells, basal cells extending upward along margin (forming a "V"), and immersed, apiculate, cleistocarpic capsules with bulging exothecial cells. The single neotropical species is rare, apparently only known from a collection by E. Ule in July 1889 from Tubarão, Santa Catharina, Brazil.

LITERATURE. Zander, R. H. 1993 (see family ref.).

Trachyodontium (Fig. 191) - A monotypic genus, with *T. zanderi* Steere only known from Ecuador along the slopes of Volcán Pichincha.

HABITAT. On nodes of *Chusquea* sp., and "living" fence posts of *Gliciridia sepium*; probably secondary montane forests, at 2650 m.

DESCRIPTION. **Plants** rather large, forming tufts, yellowish-green above to brownish below. **Stems** erect, to 3 cm tall, simple, ± tomentose below; in cross-section hyalodermis well developed, often fluted, outer 1–3 rows of cells small, thick-walled, inner cells progressively larger, central strand absent. **Leaves** flexuose-twisted when dry, wide-spreading to squarrose when wet, oblong-lanceolate, 4–6 mm long, widest at shoulders, keeled, sheathing at base, acute; margins recurved below, distally bordered, irregularly serrate distally, serrulate below; costa strong, percurrent, superficial cells elongate and papillose on both surfaces, 4–6 rows of cells across upper surface at midleaf, in cross-section reniform, stereids above (few), below guide cells well developed; median and upper cells subquadrate or short rectangular or hexagonal, pluripapillose, papillose several over lumen, simple; basal cells differentiated across, long rectangular, smooth, further up becoming increasingly pluripapillose; margins bistratose, cells elongate, finely pluripapillose. KOH leaf color reaction yellow with occasional red patches. **Gemmae** absent. **Dioicous**. **Perichaetia** terminal; appearing lateral by innovations; leaves sheathing below, as long as seta or capsule, linear to linear-lanceolate, costa excurrent. **Seta** single, to 14 mm long, slender. **Capsule** erect, urn cylindrical, 5.5–6 mm long, slightly curved and tapered at ends; stomata absent; annulus deciduous. **Operculum** not observed. **Peristome** single, teeth divided into 64 filaments, not twisted, strongly spiculose. **Calyptra** cucullate, smooth and naked. **Spores** spherical, punctate.

DISCUSSION. The genus is characterized by the presence of well developed stem hyalodermis, absence of a central strand, bordered leaves, superficial cells of costa elongate above and below and with 2 stereids bands, undifferentiated epidermis (seen in cross-section) and spiculose, 4-paired peristome teeth. See comments under *Streptotrichum*.

LITERATURE. Steere, W. C. 1986. *Trachyodontium*, a new genus of the Pottiaceae (Musci) from Ecuador. The Bryologist 89: 17–19.

Trichostomum (Fig. 191) - About 43 species in the Neotropics, possibly 20 or fewer are valid; a large and widespread genus of about 130 species.

HABITAT. On soil, rock and occasionally base of tree trunks; moist or semi-dry lowland to upper montane forest sites, frequent in open, often disturbed sites.

DESCRIPTION. **Plants** small to medium sized, to 3 cm tall, forming dense tufts, somewhat dark green to brown. **Stems** erect, simple or few branched, radiculose below; in cross-section hyalodermis present or absent, central strand present or absent. **Leaves** when dry arching (catenulate), slightly crispate and curved, curled and contorted or reflexed distally from an appressed base, when wet

erect-spreading to spreading or squarrose, oblong- to ligulate-lanceolate or narrowly lanceolate to linear-lanceolate, 1.8–4 mm long, to 0.5 mm wide, apex acute (and apiculate) or short acuminate, base slightly sheathing and broadly concave or not, distally flat or broadly channeled; margins plane to erect, smooth or wavy, crenulate-papillose, occasionally dentate below; costa strong, short excurrent, tip occasionally stout, in cross-section semicircular, reniform or ovate in shape, stereids above and below guide cells, upper band equal to or smaller than lower, guide cells 2–4 in a single row, epidermal surface papillose; median and distal laminal cells subquadrate, thick-walled, pluripapillose, papillae over lumen on both surfaces, bifid, crowded; basal cells differentiated across or weakly extending upward along margin, mostly long rectangular, smooth, yellowish-hyaline, those along costa and above base narrowly long rectangular, not porose, short rectangular to oblong cells occasionally extending a short distance along margin, hyaline and lax, thin-walled. KOH leaf color reaction mostly orange to yellowish orange. **Dioicous**. **Perichaetia** terminal. **Seta** elongate, ca. 5–15 mm long, smooth. **Capsule** stegocarpic, rarely cleistocarpic; erect, urn short to somewhat long cylindrical, rarely ellipsoidal. **Operculum** short to long rostrate, slightly oblique. **Peristome** single, teeth distally divided and jointed below or to base, usually short and fragile, papillose. **Calyptra** cucullate, naked and smooth. **Spores** finely to rather coarsely papillose.

DISCUSSION. The genus is highly variable with regard to gametophytic features and not readily characterized. The leaves are often curled and crispate, the base not shouldered, margins plane to erect, costa with upper epidermal surface differentiated, and papillose, 2 stereid bands ± equally developed, and lamina generally unistratose and pluripapillose on both surfaces. A critical revision of the neotropical species would likely reduce the number of species by more than half. As treated here, *Oxystegus* is included in *Trichostomum*.

LITERATURE. Zander, R. H. 1993 (see family ref.).

Tuerckheimia (Fig. 191) - Three species from Mexico and Central America; four species rather narrowly distributed, southeastern United States, Alaska, Central America, and eastern Asia.

HABITAT. On moist to wet rocks in shaded sites, often associated with streams; open forests.

DESCRIPTION. **Plants** medium sized, forming tufts, light to dark green above, often glaucous. **Stems** simple to few branched, to 2.5 cm high; in cross-section hyalodermis mostly undifferentiated, central strand present. **Leaves** spreading and incurved, twisted or crisped when dry, spreading when wet, oblong- to linear-lanceolate, to ca. 3 mm long, broadly concave to keeled or not, apex acute to acuminate, often mucronate, base little differentiated; margins plane, entire to coarsely dentate in distal half; costa percurrent to excurrent, often mucronate, upper epidermal surface of 4–6 cells, papillose, lower surface smooth, in cross-section circular to ovate, stereids above and below guide cells, 2 or more guide cells in a single row; lamina unistratose or interrupted bistratose distally; cells above subquadrate to short-rectangular or hexagonal, papillose, papillae large, bifid to multifid, over cell lumen, thick-walled; basal cells weakly differentiated, only at extreme base, oblong-rectangular, thin- to thick-walled, smooth; marginal cells at base weakly differentiated or not. KOH leaf color reaction yellow. **Dioicous**? **Perichaetia** terminal; leaves sheathing below. **Seta** elongate. **Capsule** erect, urn cylindrical. **Operculum** long rostrate. **Peristome** absent or rudimentary? **Calyptra** not observed. **Spores** not observed.

DISCUSSION. The genus is characterized by the strongly mucronate leaves with plane margins, the coarse papillae centered over the cell lumen, and poorly developed basal cells. *Tuerckheimia valeriana* (E. B. Bartram) R. H. Zander is the most widespread species, known from Mexico, Guatemala and Panama; the distal, sharply dentate teeth separate this species from other members of the genus. Sporophytic features are not well known in the American species. The genus is named in honor of Hans von Türckheim (1853–1920), plant collector of the later ninetieth and early twentieth century in Guatemala and the West Indies.

LITERATURE. Zander, R. H. 1978. Synopsis of the genus *Tuerckheimia* (Pottiaceae). Miscellanea Bryologica et Lichenologica 8: 25–28.

Uleobryum (Fig. 192) - A genus with two species in the Neotropics, *U. occultum* (Roth) R. H. Zander (West Indies) and *U. peruvianum* Broth. (Central America, West Indies and tropical Andes); three species of the Neotropics and Australia.

HABITAT. On soil, in exposed to shaded sites; at low elevations to 1450 m.

DESCRIPTION. **Plants** small, forming loose tufts or occurring solitary, green above, brown below. **Stems** short, to 2 mm tall, few branched; in cross-section hyalodermis absent, central strand present. **Leaves** appressed and incurved when dry, spreading when wet, spathulate to elliptical, to ca. 1 mm long, apex acute to rounded, mucronate; margins plane, crenulate to bluntly serrate by projecting cell walls; costa strong, percurrent, superficial cells above and below elongate, 2–6 rows of cells above at midleaf, in cross-section rounded to semicircular, stereids above (occasionally absent) and below

guide cells, 2–4 guide cells in 1 layer; lamina unistratose; laminal cells subquadrate to short rectangular, uni- to pluripapillose, papillae over lumen; basal cells differentiated across leaf or occasionally extending along margin, rectangular, smooth, thin-walled. KOH leaf color reaction yellow. **Autoicous**. **Perichaetia** terminal. **Seta** very short, to 0.04 mm long. **Capsule** cleistocarpous, immersed, erect, globose-apiculate, to 0.5 mm in diameter; stomata few at base, superficial; annulus absent. **Operculum** absent. **Peristome** absent. **Calyptra** short mitrate or conic mitrate, slightly roughened or mammillose. **Spores** large, to 0.3 mm in diameter, spiculose.

DISCUSSION. The genus is distinguished by the minute habit, spathulate or elliptical leaves, plane margins, well developed costa, distal pluripapillose cells, and globose-apiculate cleistocarpic capsules. The generic name honors the German botanist Ernst Ule (1854–1915), one of the ardent plant collectors of tropical South America at the turn of the century.

LITERATURE. Zander, R. H. 1993 (see family ref.).

Weisiopsis (Fig. 192) - Three species in the Neotropics, *W. norrisii* R. H. Zander and *W. oblonga* Thér. both recorded from Mexico, and *W. bahiensis* (Müll. Hal.) Broth. from the Planalto of Brazil; a total of seven species, the remaining four species occurring in the Paleotropics.

HABITAT. On soil; in open, dry vegetation, at elevations to 1830 m.

DESCRIPTION. **Plants** small, forming short tufts, light green or yellowish-brown. **Stems** short, to 3 mm tall, simple to few branched, radiculose at base; in cross-section hyalodermis absent, outer and inner cells similar, firm-walled, central strand weak. **Leaves** crowded, incurved and curled, often tubulose when dry, spreading when wet, ligulate to spathulate, to ca. 2 mm long, apex bluntly acute to obtuse-rounded, cucullate or not; margins plane to somewhat incurved, crenulate by projecting cells; costa subpercurrent to percurrent, superficial cells ventrally and dorsally elongate, smooth, or ventrally quadrate-rounded and bulging, ca. 2 cells across at midleaf, in cross-section rounded, stereid band below guide cells, epidermis ventrally often absent, dorsally present, guide cells 2(–4) in 1 layer; upper and median cells quadrate- or hexagonal-rounded, thick-walled, bulging on ventral surface, extending partially down along margin; basal cells abruptly differentiated across or notably extending medially along costa, rectangular, smooth, firm above, lax and thin-walled below. KOH leaf color reaction yellow. **Autoicous**. **Perichaetia** terminal; leaves somewhat larger, otherwise similar. **Seta** elongate, 4–6 mm long, slender, smooth. **Capsule** ovoid-cylindrical to ovoid, to 0.6 mm long; exothecial cells elongate; stomata at urn base, superficial; annulus in 2–3 rows, or poorly developed. **Operculum** long conic or short rostrate. **Peristome** absent or single, teeth inserted below the mouth, very slender and widely spaced, finely spiculose, basal membrane absent. **Calyptra** cucullate, smooth and naked. **Spores** spherical, smooth or nearly so.

DISCUSSION. This small genus is characterized by the small habit, the tubulose, ligulate to spathulate leaves with plane to slightly incurved margins, somewhat flattened guide cells, single stereid band, single peristome set below mouth or peristome absent, and widely spaced, finely spiculose teeth.

LITERATURE. Zander, R. H. 1993 (see family ref.).

Weissia (Fig. 192) - About 19 species recorded for the Neotropics, possibly only 10 that are valid; a genus of nearly 100 species distributed worldwide.

HABITAT. Open submontane to upper montane; in disturbed sites, on soil.

DESCRIPTION. **Plants** small, forming short, small tufts. **Stems** erect, to 10 mm high, few branched; in cross-section hyalodermis weak to well differentiated, central strand present. **Leaves** tubulose, contorted and twisted when dry, spreading when wet, narrowly oblong-lanceolate, to 2.5 mm long, apex acute to subulate, mucronate; margins involute to strongly incurved, rarely erect or plane, entire; costa short excurrent as an apiculate pellucid awn, superficial cells above quadrate to short rectangular, 4–8(–10) cells across, cells below elongate, in cross-section ovate to semicircular, stereid cells above and below guide cells, 4–6(–8) guide cells across at midleaf; upper laminal cells subquadrate to hexagonal, pluripapillose, papillae mostly bifid; basal cells differentiated across leaf, short-rectangular, smooth, thin to thick-walled. KOH leaf color reaction mostly pale yellow. **Autoicous** or dioicous. **Perichaetia** terminal; leaves similar to stem leaves. **Seta** elongate, 10–12 mm long. **Capsule** erect, urn ovoid, obloid-short cylindrical or less frequently subcylindrical, 1–2 mm long, stegocarpous or cleistocarpous. **Operculum** absent to present and long rostrate, oblique. **Peristome** absent or single, teeth partially to fully divided, fragile or often rudimentary, mostly papillose to spiculose, low basal membrane present or absent. **Calyptra** cucullate, naked and smooth. **Spores** lightly papillose.

DISCUSSION. The genus is characterized by the presence of a stem hyalodermis and central strand, leaf margins strongly involute, rarely erect or plane, laminal cells pluripapillose, and 2 stereid

bands. The sporophytes range from capsules that are cleistocarpic and ovoid to stegocarpic and cylindrical, with or without a peristome.

LITERATURE. Anderson, L. E. & B. E. Lemmon. 1972. Cytological studies of natural intergeneric hybrids and their parental species in the moss genera *Astomum* and *Weissia*. Annals of the Missouri Botanical Garden 59: 382–416. - Stoneburner, A. 1985(1986). Variation and taxonomy of *Weissia* in southwestern United States. II. Taxonomic treatment. The Bryologist 88: 293–314. - Zander, R. H. 1993 (see family ref.).

Weissiodicranum (Fig. 193) - A monotypic genus, with *W. insularum* W. D. Reese only known from the Greater Antilles (Puerto Rico and Jamaica) and the Galapagos Islands of Ecuador.

HABITAT. On mostly calcareous soil in exposed sites; open lowland, 150–250 m.

DESCRIPTION. **Plants** forming low tufts, green above, light brown below. **Stems** erect, to ca. 0.5 cm tall, few branched, weakly radiculose below; in cross-section hyalodermis absent, outer cells small, becoming progressively larger, central strand well developed. **Leaves** incurved and contorted when dry, spreading when wet, linear-lanceolate, to 2.5 mm long, apex narrowly acute; margins incurved to involute, entire; costa short excurrent as a mucronate tip, superficial cells quadrate, ca. 4 rows across on upper surface, in cross-section nearly rounded, elliptical or ovate, stereids above and below guide cells, upper surface cells weakly unipapillose; lamina unistratose, cells quadrate-rounded, upper surface bulging, lower surface flat; basal cells short to somewhat long rectangular, thin but firm-walled; alar region differentiated, cells in 1–3 rows, extending ca. 2/3 way to costa, inflated, oblong. KOH leaf color reaction yellow. **Dioicous**? **Perichaetia** terminal; leaves little differentiated. **Sporophytes** unknown.

DISCUSSION. The generic name is derived from the similar aspect of plant and leaves to *Weissia*, and the inflated basal cells ("banana shaped") exhibited by some members of the Dicranaceae.

LITERATURE. Reese, W. D. & W. R. Buck. 1991. *Weissiodicranum insularum* gen. et sp. nov. The Bryologist 94: 308–310.

PRIONODONTACEAE

The Prionodontaceae contain three tropical genera and about 20 species. The family is placed in the Leucodontales.

Prionodon (Fig. 193) - About 5–6 species primarily distributed in the Neotropics, also present in montane tropical Africa.

HABITAT. Epiphytic, occasionally on leaf litter, humus or rocks; montane forests, occasionally extending into páramo and puna in protected ravines, ca. 800–4000 m.

DESCRIPTION. **Plants** medium to robust, forming loose to dense tufts, pale to dark green, blackish-green or golden-brown. **Primary stems** usually short, occasionally long, creeping, leaves often eroded. **Secondary stems** suberect to pendent, 6–25 cm long or more, irregularly to regularly pinnately branched, branches few to many, occasionally simple. **Leaves** broadly ovate-lanceolate, 4–9 mm long, broadly short to somewhat long acuminate, apices often fragile and deciduous, base slightly clasping, plicate; margins mostly plane, coarsely serrate to spinose; costa ending in acumen or rarely short excurrent; median cells irregularly rhombic or rectangular, porose or not, unipapillose, often faintly so; alar cells usually differentiated, cells isodiametric or oval, often stellate and oblate, or cells elongate and porose. **Dioicous**. **Perigonia** lateral, leaves bud-like. **Perichaetia** lateral, leaves shorter and broader than stem leaves, abruptly subulate. **Seta** short, 1–3 mm long, usually as long as capsules or shorter, smooth. **Capsule** shortly exserted, urn broadly ovoid to subglobose, ca. 2–3 mm long; annulus present, revoluble. **Operculum** conic-rostrate, oblique. **Peristome** double, exostome teeth 16, papillose; endostome segments partially adnate, cilia absent. **Calyptra** cucullate, short, covering the operculum, smooth. **Spores** lightly papillose.

DISCUSSION. *Prionodon* is characterized by pendent or suberect secondary stems, crowded, ovate-lanceolate leaves, often deciduous apices, plicate below, unipapillose, stellate laminal cells, alar region usually well differentiated, and capsules immersed or emergent. Neotropical species of *Prionodon* exhibit a good deal of polymorphism with regard to the gametophytes, particularly in size and degree of branching. This has lead to an extreme number of names for the genus. The excessive variation encountered in this genus would make an excellent subject of a combined morphological and molecular study.

Study guide. Particularly care and attention should be given to removing the leaves from the stem so that the basal portions remain intact.

LITERATURE. Griffin, III, D. 1970 (1971). Notes on the tropical genus *Prionodon* (Musci). Revue Bryologique et Lichénologique 37: 653–656. - Griffin, III, D. 1973. *Prionodon luteo-virens* (Tayl.) Mitt. and *P. dichotomus* Hampe. Taxon 22: 257–258. - Griffin, III, D. 1994. *In* Sharp et al. (see general ref.).

PTERIGYNANDRACEAE

The Pterigynandraceae contain about five genera and 20 species; primarily of the Northern Hemisphere. The definition and circumscription of the family, a member of the Hypnales, was outlined by Buck and Crum (1990). Reports of *Heterocladium* for the Neotropics have not been verified, and thus are excluded here. *Pterigynandrum filiforme* Hedw. is known from just beyond the northern neotropical boundary in Mexico; it is distinguished by slender, julaceous branches, elliptic to oblong-ovate leaves (to 1 mm long), apices acute, short and forked costa, and the cells strongly projecting at both ends.

Trachyphyllum (Fig. 193) - A single species in the Neotropics, *T. dusenii* (Müll. Hal. ex Broth.) Broth. known from the Planalto of Brazil (Distrito Federal, Goiás, Minas Gerais); a pantropical genus of seven species.

HABITAT. Epiphytic, on tree trunks and bases, occasionally on rocks (limestone); gallery forests in cerrados, at elevations from 400–1250 m.

DESCRIPTION. **Plants** somewhat small to medium sized, forming rather dense mats, brownish green to yellow. **Stems** creeping, 1-pinnately branched, branches short, suberect and curved; in cross-section outer 2–3 rows of cells small, thick-walled, inner cells larger, thin-walled, central strand weak; rhizoids clustered beneath stems, appearing smooth. **Leaves** of stem loosely erect to erect, broadly ovate-lanceolate, to 1.2 mm long, apex gradually long acuminate; margins plane or slightly reflexed at base, appearing denticulate at mid region; costae short and forked, joined at base; apical cells long linear, smooth or nearly so; median cells linear (shorter than apical cells), rather strongly papillose by projecting cell angles; basal cells adjoining costa oblong-rectangular, porose; alar region well differentiated, cells numerous, extending to, or just beyond broadest portion of leaf, oblate short rectangular to subquadrate; marginal cells at mid leaf shorter and broader; branch leaves smaller, narrowly ovate-lanceolate, apex slenderly long acuminate. **Dioicous**. **Perichaetia** lateral; leaves abruptly long acuminate from an oblong base, costae single or double, margins strongly serrate, teeth sometimes multicellular. **Seta** elongate, smooth, twisted. **Capsule** exserted, inclined, urn short-cylindrical, asymmetric, constricted below mouth when dry; exothecial cells quadrate to rectangular, not collenchymatous; stomata at urn base, superficial; annulus absent. **Operculum** short rostrate. **Peristome** double, exostome teeth 16, densely cross-striate below, distally papillose, median zig-zag line present, trabeculate on back; endostome nearly equal exostome length, basal membrane rather high, segments 16, keeled and perforate, finely papillose, cilia well-developed, 1–3. **Calyptra** cucullate, smooth and naked. **Spores** spherical, finely papillose.

DISCUSSION. The genus is recognized by the broadly ovate-lanceolate leaves, gradually long acuminate apex, short and forked double costa, upper long, smooth, linear apical cells, projecting papillae at distal angle of median cells, and well differentiated alar cells that extend to the broadest width of the leaf.

The gametophytes of *Trachyphyllum* can be mistaken for *Erythrodontium* (Entodontaceae), but readily separated by the strong projecting papillae at the distal cell angles of the former genus, and smooth laminal cells of the latter. *Trachyphyllum dusenii* was only recently reported in the Americas, previously known from central west Africa (Buck & Griffin, 1984).

LITERATURE. Buck, W. R. 1979. A revision of the moss genus *Trachyphyllum* Gepp (Thuidiaceae). Brittonia 31: 379–394 [keys, illustrations]. - Buck, W. R. & H. Crum. 1990. An evaluation of familial limits among the genera traditionally aligned with the Thuidiaceae and Leskeaceae. Contributions to the University of Michigan Herbarium 17: 55–69. - Buck, W. R. & D. Griffin, III. 1984. *Trachyphyllum*, a moss genus new to South America with notes on African-South American bryogeography. Journal of Natural History 18: 63–69.

PTEROBRYACEAE

Plants small to more commonly medium sized or large and robust, forming tufts or mats. **Primary stems** creeping, leaves usually differentiated, often scale like. **Secondary stems** erect and frondose or dendroid, occasionally simple, or spreading and often pendulous, radiculose beneath; in cross-section outer 2–5 or more rows of cells small and thick-walled, central strand absent; paraphyllia

absent; pseudoparaphyllia filamentous. **Leaves** imbricate, complanate, equally spirally arranged or 5-ranked, often differentiated between primary (stolon) and secondary stems, the latter between stipe (if present) and secondary stems and branches, broadly to narrowly ovate- to oblong-lanceolate, mostly symmetric, smooth or plicate, apex acute to acuminate, occasionally piliferous, base often auriculate; margins plane to reflexed (recurved), entire or serrulate to sharply serrate; costa single to short and double or absent (*Hildebrandtiella*), when single 1/2 lamina length to percurrent; median cells oblong to ± linear, smooth to weakly unipapillose or prorulose, often porose; alar cells usually weakly to strongly differentiated, subquadrate, porose; insertion cells often golden-brown or yellow. **Gemmae** often present, in leaf axils, short to long cylindrical. **Dioicous** or rarely autoicous. **Perichaetia** lateral, leaves usually differentiated. **Seta** short to somewhat elongate, smooth or roughened distally. **Capsule** immersed to exserted, erect to suberect, urn ovoid to ovoid-cylindrical, smooth; annulus absent or cells undifferentiated to differentiated and revoluble. **Operculum** conic short to long rostrate. **Peristome** generally single, often reduced, rarely double, exostome teeth 16, often fused, smooth or papillose below and distally papillose; endostome absent or reduced, basal membrane low, segments rudimentary, cilia absent; prostome (continuous or discontinuous ring of irregular short segments of cells ± adhering to outer base of exostome) present or absent. **Calyptra** mitrate or cucullate, smooth or sparsely hairy. **Spores** mostly spherical, usually papillose or granulate, occasionally large and polymorphic.

DISCUSSION. The Pterobryaceae contain about 27 genera with less than 160 species distributed primarily in the tropics (Buck & Vitt, 1986; Magill, 1982); in the Neotropics 10 genera and about 35 species. Almost exclusively epiphytic, this family exhibits a variety of growth forms, i.e., pendent, dendroid or frondose.

Due to the occasional difficulty in distinguishing the families Meteoriaceae and Pterobryaceae, Allen (1987) has noted that pseudoparaphyllia are apparently absent in the Meteoriaceae whereas in the Pterobryaceae pseudoparaphyllia are present and filamentous. See also a discussion by Argent (1973) detailing additional distinguishing features between the two families. Another aspect shared by the Meteoriaceae and Pterobryaceae is that they are primarily dioicous and sporophytes are rarely produced, suggesting that asexual strategy has been the primary mechanism for reproduction in these two families. A notable difference, however, is that gemmae are a common feature in many Pterobryaceae species, whereas in the Meteoriaceae they are absent or very rare, although attenuate or flagellate branches are common. The Meteoriaceae tend to be more abundant in montane forests, while the Pterobryaceae are more typical of submontane forests.

Study guide. Attention must be given first to the habit and branching pattern of the plant, and second, comparison the leaves of the secondary stem and branch, and the leaves of the stipe (if present).

LITERATURE. Allen, B. 1987. On distinguishing Pterobryaceae and Meteoriaceae by means of pseudoparaphyllia. Bryological Times 42: 1–3. - Argent, G. C. G. 1973. A taxonomic study of the African Pterobryaceae and Meteoriaceae I. Pterobryaceae. Journal of Bryology 7: 353–378. - Arzeni, C. B. 1954. The Pterobryaceae of the southern United States, Mexico, Central America, and the West Indies. The American Midland Naturalist 52: 1–67 [keys, illustrations]. - Buck, W. R. 1991. Notes on neotropical Pterobryaceae. Brittonia 43: 96–101 [key to *Orthostichopsis*]. Buck, W. R. & D. Vitt 1986. (see general ref.). - Magill, R. E. 1982. On the circumscription of Pterobryaceae. Beihefte zur Nova Hedwigia 71: 273–279.

1. Leaves ecostate or costae minute, short and forked 2
1. Leaves costate, costa single, occasionally mixed with a few leaves variously forked 3
2. Leaves strongly ranked, in 5-spiral rows; costa absent ..... **Hildebrandtiella**
2. Leaves spirally arranged, not ranked, or weakly so; costa minutely short and forked, occasionally single, or if costa absent, then leaf apex abruptly narrow and long acuminate ..... **Renauldia**
3. Plants pendulous; secondary stems and/or branches often piliferous or very long acuminate .. 4
3. Plants frondose to dendroid or occasionally simple, secondary stem leaves mostly acute to acuminate, rarely piliferous 5
4. Secondary stem leaves widespreading, broadly ovate-long lanceolate; leaf base clasping stem ..... **Spiridentopsis**
4. Secondary stem leaves erect, oblong to oblong-ovate; leaf base not clasping stem .... **Orthostichopsis**
5. Leaves strongly plicate; capsules immersed ..... **Pterobryon**
5. Leaves smooth, not plicate or indistinctly so; capsules immersed to exserted 6
6. Leafy stems and branches complanate ..... **Calyptothecium**
6. Leafy stems and branches not complanate 7
7. Secondary stem leaves erect-spreading, base auriculate; costa single, not variable; laminal cells smooth or papillose 8

7. Secondary stem leaves squarrose-spreading, base not or weakly auriculate; costae variable, single or short and double; laminal cells smooth ..... **Jaegerina**
8. Stem and branch leaves imbricate, broadly ovate; alar cells numerous `..... **Pterobryopsis**
8. Stem and branch leaves usually not noticeably imbricate, ovate-lanceolate to oblong-lanceolate; alar cells few to somewhat numerous 9
9. Plants usually frondose, occasionally simple; leaf margins plane or weakly recurved; laminal cells smooth or papillose with papillae projecting at cell angles ..... **Pireella**
9. Plants mostly with secondary stems solitary or few branched; leaf margins recurved; laminal cells papillose, papillae 1–2 over cell lumen ..... **Henicodium**

Calyptothecium (Fig. 194) - Five, but possibly only three, species in the Neotropics; a tropical genus of some 30 species primarily confined to Asia and less so in Africa and the Americas.

HABITAT. Epiphytic; semi-dry to moist lowland to lower montane forests, 600–2600 m.

DESCRIPTION. **Plants** somewhat small to rather large, forming loose tufts, glossy green. **Primary stems** creeping, wiry; leaves scale-like, usually eroded. **Secondary stems** erect, simple and unbranched, or frondose and several branched. **Leaves** rather complanate, somewhat differentiated between median mostly symmetric leaves and lateral asymmetric leaves, concave, strongly so with lateral leaves, broadly ovate-short lanceolate, apex acute or broadly short acuminate, base auriculate; margins plane or incurved distally, entire to weakly serrulate distally; costa single, ca. 2/3 lamina length, usually forked below; median cells linear, somewhat vermicular, smooth, weakly porose; insertion cells golden-brown; alar cells differentiated, subquadrate, porose. **Gemmae** present in leaf axils, mostly on distal stem and branches, cylindrical, smooth. **Dioicous**. **Perichaetial** leaves oblong-lanceolate, convolute. **Seta** short to somewhat elongate. **Capsule** immersed to shortly exserted, urn ovoid-cylindrical. **Operculum** conic-rostrate. **Peristome** double although often rudimentary or absent. **Calyptra** mitrate. **Spores** not observed.

DISCUSSION. The genus is characterized by the simple to frondose habit, complanate leafy stems and branches and costate leaves. *Calyptothecium* has previously been placed in the Neckeraceae. The two species known to us can be differentiated as follows: *C. duplicatum* (Schwägr.) Broth. — plants frondose, several branched; sporophyte immersed (Mexico, Central America, Greater Antilles, tropical Andes, to Peru, and southeastern Brazil); and *C. planifrons* (Renauld & Paris) Argent — plants simple, rarely branched; sporophytes shortly exserted (outer reaches of the Amazon Basin in Colombia and Brazil; also Africa); the latter species has been placed in the genus *Orthorrhynchidium* by some authors.

Henicodium (Fig. 194) - A single species in the Neotropics, *H. geniculatum* (Mitt.) W. R. Buck. The genus seems to be monotypic and with a pantropical distribution.

HABITAT. Epiphytic on tree trunks and branches, occasionally on logs; moist to semi-dry lowland to lower montane forests, from near sea level to 1800 m.

DESCRIPTION. **Plants** small, forming loose short tufts, glossy green to yellowish-green. **Primary stems** creeping, tomentose. **Secondary stems** mostly simple, rarely branched, distally often attenuated with small ovate-triangular leaves. **Leaves** erect to distally appressed when dry, erect-spreading to spreading when wet, ovate- to oblong-short lanceolate, 1.4–2 mm long, to 0.6 mm wide, somewhat concave, plicate when dry, clasping at base, apex rather bluntly acuminate to acute, base slightly decurrent; margins strongly revolute, at times to below apex, occasionally plane on one side or partially so, distally denticulate to serrulate; costa 2/3 lamina length; median cells linear to linear-fusiform, 1–2 papillose, papillae appearing over lumen, often indistinct; juxtacostal basal and insertion cells irregularly rectangular and porose, golden-brown; alar region differentiated, cells extending to widest portion of leaf, oblate rectangular- or quadrate-rounded, smooth. **Gemmae** often present in leaf axils, cylindrical, smooth. **Dioicous**. **Seta** elongate, to ca. 4 mm long, twisted, smooth. **Capsule** exserted, erect, urn oblong-cylindrical, ca. 1.7 mm long. **Operculum** rostrate. **Peristome** reduced and single, exostome teeth blunt, smooth. **Calyptra** and spores not observed.

DISCUSSION. *Henicodium* is readily distinguished by the erect to distally appressed, oblong-short lanceolate leaves, strongly revolute margins, slender, single costa, 1–2 papillae over cell lumen, and well defined alar region. The papillae are often rather indistinct, but are readily observed along the recurved margins. *Leucodontopsis* is now replaced by the older name *Henicodium*.

LITERATURE. Buck, W. R. 1989. *Henicodium* replaces *Leucodontopsis* (Pterobryaceae). The Bryologist 92: 534.

Hildebrandtiella (Fig. 194) - A single species in the Neotropics, *H. guyanense* (Mont.) W. R. Buck, rather widespread; about five species distributed in the tropics of America and Africa.

HABITAT. Epiphytic, on branches and trunks of trees and treelets; wet lowland to lower montane forests, 100–2000 m.

DESCRIPTION. **Plants** medium sized to more commonly large and robust, forming mats or tufts, glossy green to golden-green. **Primary stems** creeping; rhizoids clustered beneath; rusty-red, leaves scale-like, erect and distally spreading, triangular-acuminate, 0.35–0.5 mm long. **Secondary stems** spreading to pendent, irregularly pinnately branched. **Secondary stem leaves** seriate, in 5 rows, oblong, 2.5–3 mm long, to 1.5 mm wide, deeply concave, apex short acuminate to acute, base subauriculate; margins incurved distally, entire to indistinctly serrulate distally (upper 1/5–1/4); costa none; median cells linear, porose, smooth; alar region not well developed, cells few (ca. 10–15), quadrate-rounded to short rectangular, thick-walled and porose; insertion cells (and alar cells) golden-brown. **Branch leaves** similar but smaller, strongly seriate, 1.2–2 mm long, 0.7–0.9 mm wide. **Gemmae** present in leaf axils, cylindrical, smooth, elongated tips often appearing papillose. **Dioicous**. **Perichaetial** leaves oblanceolate to oblong, narrowly acuminate, to 5 mm. **Seta** short, 0.5–0.6 mm long, roughened or papillose. **Capsule** immersed, erect, urn short cylindrical to ovoid, ca. 2 mm long. **Operculum** rather long rostrate, to 0.9 mm long. **Peristome** set below mouth, reduced, prostome present, appearing as a hyaline smooth double ridge in front of exostome tooth, exostome teeth smooth. **Calyptra** appearing mitrate, smooth. **Spores** smooth or nearly so.

DISCUSSION. The genus is distinguished by the rather robust, golden-brown, irregularly branched secondary stems; 5-spirally ranked leaves; and absence of a costa. The single neotropical species previously placed in *Orthostichidium* (Buck, 1991 - see family ref.).

Jaegerina (Fig. 195) - Two species in the Neotropics, the rather widespread *J. scariosa* (Lorentz) Arzeni and *J. guatemalensis* E. B. Bartram from Central America and Jamaica; about 10 species distributed in the tropics, primarily in Africa and Asia.

HABITAT. Epiphytic on tree trunks and branches; moist to semi-dry lowland to lower montane forests, 100–2600 m.

DESCRIPTION. **Plants** medium sized, forming short loose tufts, yellowish-green to golden-brown. **Primary stems** short, creeping; leaves scale-like, often eroded. **Secondary stems** erect, to 5 cm tall, simple or 1–2 branched. **Leaves** crowded, spreading to wide-spreading, ovate to ovate-long lanceolate, 2–5.5 mm long, to 1.5 mm wide, concave, plicate, slightly sheathing, apex short to long acuminate, tips slightly reflexed, base somewhat auriculate; margins plane, slightly reflexed below apices, entire to indistinctly or distinctly serrulate throughout; costa single, weak, 2/3–3/4 lamina length or ending in subula, occasionally short forked or notched along costa length; apical cells rhomboidal; median cells oblong-linear, smooth or indistinctly papillose at cell angle, weakly porose; basal cells irregularly oblong-short rectangular, strongly porose, golden-brown. **Gemmae** present in leaf axils, short cylindrical. **Dioicous**. **Perichaetial** leaves somewhat differentiated. **Seta** somewhat to distinctly elongate, 4–8 mm long, smooth. **Capsule** erect, urn ovoid-short cylindrical to ellipsoid, ca. 2 mm long. **Operculum** long-rostrate. **Peristome** single, teeth fragile and reduced, short, papillose or not, blunt. **Calyptrae** and spores not observed.

DISCUSSION. The genus is characterized by simple or sparingly branched secondary stems, squarrose-spreading secondary stem leaves, leaf base weakly auriculate or lacking auricles, single costa or costa variable, single or short and double in leaves from the same stem, and laminal cells smooth to weakly projecting at cell angles. Our two species can be differentiated as follows: *J. guatemalensis* — leaves lanceolate, to 5.5 mm long, and *J. scariosa* — leaves ovate, to ca. 2.5 mm long. The generic name honors the Swiss bryologist August Jaeger (1842–1877), compiler, with F. Sauerbeck, of *Genera et species muscorum systematice disposita seu adumbratio florae muscorum totius orbis terrarum* published over a period of 10 years (1870–1880).

Orthostichopsis (Fig. 195) - About four species in the Neotropics; stated to contain some 17 species (probably 10 or fewer valid species) distributed in tropical America and Africa.

HABITAT. Epiphytic on branches and trunks of trees and treelets; from wet lowland to lower montane forests, from near sea level to 1970 m.

DESCRIPTION. **Plants** medium sized, forming soft mats with secondary stems usually pendent, glossy green to golden-green. **Primary stems** creeping; rhizoids clustered beneath; leaves reduced or eroded. **Secondary stems** long pendent, irregularly to regularly pinnately branched, with several short branches, distally often attenuated and elongate. **Stem leaves** ranked in 5 spiral rows, oblong to oblong ovate, to 3.5 mm long, smooth or plicate, apex rather abruptly short to long acuminate, base weak to somewhat strongly auriculate; margins incurved distally, serrulate in distal 1/4–1/3; costa 2/3–3/4 lamina length, weak to strong, occasionally short and single or forked; laminal cells smooth, median cells linear to oblong-linear, vermicular, porose; insertion cells often golden-brown; alar cells few to numerous, in radiating rows reaching the margins, irregularly subquadrate. **Branch leaves**

narrowly oblong and acuminate to abruptly long acuminate. **Dioicous**. **Perichaetial** leaves much elongate. **Seta** short to somewhat elongate, to ca. 5 mm long. **Capsule** immersed to exserted, erect, urn ovoid to long elliptical, to 3 mm long. **Operculum** conic-short rostrate, oblique. **Peristome** double, prostome present, exostome teeth 16, smooth; endostome rudimentary. **Calyptra** cucullate, sparsely hairy. **Spores** spherical.

DISCUSSION. The genus is characterized by the pendent habit, erect, non-clasping, oblong to oblong-ovate secondary stem leaves; cuspidate or piliferous branch leaves; single costa or mixed with a few short and forked. *Orthostichopsis* may be confused with some members of *Squamidium* (Meteoriaceae), however in that genus the leaves are not distinctly ranked in 5 spiral rows, alar cells of leaf enlarged and are excavate, and pseudoparaphyllia are absent. Buck (1991) has provided a discussion and keys of the American species.

LITERATURE. Buck, W. R. 1991 (see family ref.).

Pireella (Fig. 195) - A genus of 14 species largely confined to the Neotropics, extending into the coastal southeastern United States.

HABITAT. Primarily epiphytic, on trunks and branches, occasionally on logs; lowland to lower montane forests, from near sea level to 2000 m or possibly higher.

DESCRIPTION. **Plants** often forming loose or dense turfs, olive to dark green. **Primary stems** creeping; rhizoids clustered beneath; leaves scale like, lanceolate, long acuminate. **Secondary stems** simple to more commonly frondose from a distinct stipe, 1–9 cm long; stipe leaves appressed, loosely erect or squarrose. **Leaves** of stem (1–5.3 mm long) and branch (0.8–2.5 mm long) oblong- or ovate-lanceolate, concave, apex mostly abruptly acuminate, base decurrent or not, auricles absent or present, weak to strong; margins serrulate usually throughout or entire; costa ca. 1/2 lamina length or percurrent to subpercurrent; median cells oval to oblong-linear, appearing smooth or weakly papillose by projecting distal cell angles; alar region usually differentiated, cells few to several, subquadrate. **Gemmae** often present in dense clusters on branch primordia, rarely on leaf tips. **Dioicous**. **Seta** short to elongate, 0.5–12 mm long, smooth or distally roughened. **Capsule** immersed or exserted, erect, urn ovoid to ovoid-cylindrical, 1.4–3 mm long. **Operculum** short conic to short or long rostrate. **Peristome** single or double and reduced, exostome often appearing to form 8 pairs of teeth, smooth or roughened distally; endostome often absent or adhering to back of exostome; prostome often present. **Calyptra** very short mitrate or cucullate, naked or sparsely hairy. **Spores** small, spherical or larger and polymorphic, granulate.

DISCUSSION. The genus is characterized by the frondose, rarely simple, habit, the smooth to weakly prorose, oblong-linear to oval upper laminal cells, and few to several subquadrate alar cells. The excellent and thorough treatment by Newton (1993) defines *Pireella* as a monophyletic group based on the following synapomorphies: short leaf cells, presence of supra-alar cells, cell wall pits reduced in the upper leaf lamina, and notched or ciliate perichaetial leaves. The original name given by Cardot, *Pirea hom*. *illeg*. is replaced by *Pireella* Cardot; the name honors Louis Piré (1827–1887), a Belgain bryologist and Cardot's father-in-law.

LITERATURE. Newton, A. E. 1993. Phylogenetic systematics of the tropical moss genus *Pireella* (Pterobryaceae: Musci). Ph. D. dissertation. Duke University, Durham.

Pterobryon (Fig. 196) - Two species in the Neotropics, *P. densum* (Schwägr.) Hornsch. (Mexico, Central America, West Indies (Dominican Republic), Andes and southeastern Brazil) and *P. excelsum* Müll. Hal. (Colombia); the latter species is distinguished from the former by its narrowly lanceolate, undulate leaves. A genus of about 5–6 species apparently with a pantropical distribution.

HABITAT. Epiphytic on trunks and branches of trees and treelets; submontane to upper montane forests, 1500–3070 m.

DESCRIPTION. **Plants** large, often robust, forming loose to dense dendroid tufts, glossy green to golden-brown. **Primary stems** forming stolons, wiry; leaves scale-like. **Stipe** appearing naked or with closely appressed leaves distally. **Secondary stem** regularly to irregularly pinnately branched; in cross-section epidermal surface appearing faintly papillose. **Secondary stem leaves** ovate-short lanceolate to lanceolate, weakly to rather strongly plicate, apex short acuminate, base weak to strongly auriculate and decurrent; margins plane to weakly recurved below, distal 1/3–1/4 serrate; costa single, subpercurrent (ca. 7/8 lamina length); median cells fusiform-flexuose, smooth, weakly porose; insertion cells strongly porose, golden-brown. **Branch leaves** smaller, broadly to more commonly narrowly lanceolate, strongly plicate, usually 2 long and often 1–2 short plications near base, rarely undulate, apex acute; margins plane above, recurved below, dentate to serrulate below, distally serrate; laminal cells weakly porose. **Gemmae** usually abundant in leaf axils of distal stem and branch tips, long cylindrical, smooth. **Dioicous**. **Perichaetial** leaves broadly elliptical, abruptly setaceous, costa excurrent, equal to or slightly shorter than lamina length, margins faintly serrulate.

Seta very short, ca. 0.5 mm long. **Capsule** immersed, erect, urn broadly ovoid-elliptical; exothecial cells irregularly short rectangular- or subquadrate-rounded, thick-walled; stomata absent; annulus revoluble. **Operculum** conic-short rostrate. **Peristome** appearing single, teeth smooth, yellow, incomplete hyaline furrows at base. **Calyptra** short mitrate, naked and smooth. **Spores** spherical to irregularly ovoid, appearing lightly papillose.

DISCUSSION. The genus is distinguish by its stipitate, dendroid habit, strongly plicate, ovate-lanceolate leaves, serrulate margins, subpercurrent costa, cylindrical propagula nearly always present in axils of distal leaves, and immersed capsules.

LITERATURE. Churchill, S. P. 1988a (see general ref.) [keys].

Pterobryopsis (Fig. 196) - Two species in the Neotropics, *P. mexicana* (Schimp.) M. Fleisch. (Mexico to Panama) and *P. stolonacea* (Müll. Hal.) Broth. (Peru to northern Argentina, and southeastern Brazil). A genus of about 30 species of Australasia and America.

HABITAT. Epiphytic, base and trunk of trees, logs, and rocks; deciduous and evergreen montane forests, at elevations from 800–2200 (3000) m.

DESCRIPTION. **Plants** medium sized to large and robust, forming tufts, dark green to yellowish brown. **Primary stems** creeping; leaves small, rather inconspicuous, often eroded. **Secondary stems** erect to subpendent, to 12 cm tall, frondose, stipitate or not, irregularly pinnately branched. **Leaves** imbricate, erect-appressed to erect-spreading, smooth or weakly plicate when dry, erect-spreading when wet, broadly ovate, to 2.5 mm long, concave, apex acute, base auriculate, short decurrent; margins plane, entire to serrulate at apex; costa single, 2/3–4/5 lamina length, often spurred, occasionally long forked; median cells oblong- to rhomboidal-fusiform, smooth, rather strongly to weakly porose; basal cells near costa oblong-fusiform, strongly porose, golden yellow; alar region differentiated, cells numerous, quadrate to few short rectangular, thick-walled, weakly porose; branch leaves smaller, narrower, apex acute to short acuminate, often distinctly serrulate. **Gemmae** in distal stem and branch leaf axils, short-cylindrical or -elliptical, smooth. **Dioicous**. **Sporophytes** unknown in the Neotropics.

DISCUSSION. The densely foliate frondose plants with broadly ovate leaves, single costa and numerous alar cells help to distinguish this genus. The difference between the two species is not impressive, plants from northern populations, particularly in Mexico, tend to be larger.

LITERATURE. Arzeni, C. B. 1954 (see family ref.).

Renauldia (Fig. 196) - Three or four species in the Neotropics, *R. mexicana* (Mitt.) H. A. Crum (Mexico), *R. paradoxica* B. H. Allen (Panama, Guyana, French Guiana), *R. peruvianum* (Mitt.) Broth. (Peru). A genus of about 10 species distributed in the tropics of America and Africa.

HABITAT. Epiphytic, on branches and possibly trunks of trees (including *Quercus*); submontane to lower montane forests, at elevations from 350–2555 m.

DESCRIPTION. **Plants** medium to large, forming loose tufts, green, yellowish-green or brown. **Primary stems** creeping; leaves scale-like. **Secondary stems** subfrondose or pendent, to 15 cm long, lacking a distinct stipe, irregularly 1–2 pinnately branched. **Leaves** of stem and branch similar or branch leaves smaller and narrower, apices more distinctly serrulate or not, crowded, erect to erect spreading, broadly ovate to obovate, to ca. 4 mm long, concave, apex flat and acute or abruptly long acuminate and somewhat flexuose, base auriculate, decurrent or not; margins incurved distally, distally serrulate; costae short and forked, to 1/6 lamina length, or absent; laminal cells strongly porose and smooth, apical cells rhomboidal-fusiform, median cells linear; alar region strongly differentiated, cells few, subquadrate to short rectangular, golden-yellow. **Autoicous**. **Perichaetia** on primary branches; leaves differentiated, broadly lanceolate to long acuminate from an oblong or ovate base. **Seta** nearly absent to 0.4 mm long, smooth. **Capsule** immersed, erect; urn ovoid-short cylindrical, 1.2–1.7 mm long; exothecial cells firm, thin-walled; annulus revoluble, in 2–3 rows. **Operculum** short rostrate. **Peristome** set below mouth, single, teeth smooth. **Calyptra** mitrate, naked. **Spores** ellipsoid to obloid, granular.

DISCUSSION. The genus is characterized by the subdendroid or pendent secondary stems, spirally-foliate leaves, not ranked, and the costa absent or single or short and forked. The three *Renauldia* species are separated geographically. The generic name honors the French bryologist Ferdinand Renauld (1837–1910).

LITERATURE. Allen, B. H. 1987. *Renauldia paradoxica* Allen sp. nov. (Musci, Pterobryaceae). Journal of Bryology 14: 677–680.

Spiridentopsis (Fig. 197) - A monotypic genus, with *S. longissima* (Raddi) Broth. known from Central America and southeastern Brazil.

HABITAT. Epiphytic, on tree branches; moderately moist submontane forests, at elevations from 340–1100 m.

DESCRIPTION. **Plants** large and robust, pendent, light yellowish-green to golden brown. **Primary stems** creeping; rhizoids clustered beneath, appearing smooth; leaves small, scale-like, abruptly subulate from a broad ovate base. **Secondary stems** pendent, irregularly pinnately branched, branches mostly short. **Leaves** crowded, wide-spreading, differing little when dry or wet, broadly ovate-lanceolate, rather abruptly narrowed into a long capillary hair point, longer than leaf lamina, concave, base auriculate, clasping; margins incurved distally, denticulate below, hair point serrulate; costa single, slender, ca. 2/3 lamina length (excluding hair point); laminal cells thin-walled, smooth and porose; apical and hair point cells longer and wider than median cells; median cells linear; alar region somewhat differentiated, few cells quadrate to short rectangular-oblong, strongly porose, golden-yellow. **Perichaetial** leaves oblong-piliferous, to 3 mm long, costate, laminal cells porose. **Seta** 1–2 per perichaetium, to 4 mm long, smooth, distally roughened. **Capsule** slightly exserted, erect, urn ovoid-ellipsoid, to 1.8 mm long, symmetric. **Operculum** long rostrate, oblique. **Peristome** reduced to hyaline fragments. **Calyptra** cucullate, hairy, long capillary hairs erect-spreading. **Spores** large, spherical, smooth.

DISCUSSION. This is a truly beautiful moss distinguished by the pendent habit, wide-spreading, ovate-lanceolate leaves with an abruptly long, serrulate, capillary hair point, a slender, single costa, and little differentiated alar cells.

RACOPILACEAE

The Racopilaceae contain two genera and about 30 species with a pantropical distribution. The family is placed in the Leucodontales.

Racopilum (Fig. 197) - Two species in the Neotropics, *R. intermedium* Hampe (Venezuela to Bolivia) and *R. tomentosum* (Hedw.) Brid. (SE United States, Mexico to northern Chile and Argentina); about 50 tropical and subtropical species (probably 15 or fewer valid species).

HABITAT. On trunks and branches of trees and shrubs, logs, soil and rock; moist to wet forests from low to high elevations, near sea level to 3400 m.

DESCRIPTION. **Plants** medium sized, forming loose to somewhat dense mats, mostly dark green. **Stems** creeping and spreading, irregularly to regularly pinnately branched, often densely tomentose; in cross-section outer 2–3 rows of cells small, thick-walled, inner cells larger, thin-walled, central strand present; rhizoids rusty-red, smooth or appearing lightly papillose. **Leaves** dimorphic, dorsal (upper) leaves small and symmetric, narrowly triangular, 1.5–2 mm long, apex narrowly acuminate; margins distally serrate; costa single, long excurrent; lateral leaves ovate- to oblong-lanceolate, 2–3 mm long, asymmetric, apex acute to broadly acuminate; margins plane, serrate distally, rather coarsely so; costa single, short excurrent; median cells irregularly isodiametric, hexagonal or rhomboidal, thick-walled, smooth to weakly papillose. **Monoicous** or dioicous. **Perichaetia** lateral, leaves ovate-long acuminate. **Seta** elongate, 10–30 mm long, smooth. **Capsule** often curved, urn cylindrical, 2.5–4 mm long, smooth to furrowed, neck short; exothecial cells oblong-rectangular, thick-walled; stomata at urn base, superficial. **Operculum** short or long rostrate. **Peristome** double, exostome striate below, papillose distally, endostome basal membrane short to high, cilia 2–4, nodose. **Calyptra** cucullate, sparsely hairy. **Spores** spherical, lightly papillose.

DISCUSSION. *Racopilum* is characterized by the creeping habit, with dimorphic leaves, the upper leaves triangular and symmetric, the lateral leaves ovate to broadly oblong-lanceolate and asymmetric, distally serrate, elimbate margins, single and excurrent costa, firm-walled and smooth laminal cells, land cylindrical, slightly curved capsules. The two species can be differentiated by the following: *R. intermedium* — capsules smooth, not furrowed, opercula very long rostrate, endostome basal membrane reduced, stems regularly branched, phyllodiocous (male plants very small, nested on female plants); and *R. tomentosum* — capsules furrowed, opercula short rostrate, basal membrane high (to half the length of the exostome teeth), stems remotely pinnate, monoicous.

The recent investigations by de Vries et al. (1989), based in part on electrophoretic data, suggest that the widespread neotropical *Racopilum tomentosum* is likely an autopolyploid (n = 20), and although as yet unknown, *R. intermedium* has not replicated its chromosome number, thus probably n = 10.

LITERATURE. Vries, A. de, J. P. J. Bramer, B. O. van Zanten, A. Hoffman & R. Bijlsma. 1989. Allozyme variation in populations of four *Racopilum* species, including the polyploid *R. tomentosum*. Lindbergia 15: 47–59.

REGMATODONTACEAE

Regmatodontaceae contain two genera and 4–5 species. The family is placed in the Hypnales.

Regmatodon (Fig. 197) - A single species in the Neotropics, *R. orthostegius* Mont. (= *R. polycarpa* (Griff.) Mitt.) known from Mexico and Central America to Bolivia and southeastern Brazil, Paleotropics; a genus of two species with a pantropical distribution.

HABITAT. Epiphytic on trunk and branches of trees, or occasionally on logs; semi-dry montane forests, 1000–3000 m.

DESCRIPTION. **Plants** small to medium sized, forming loose to dense mats, dark green to brownish. **Stems** creeping, distal stems and branches ascending to erect, irregularly subpinnately branched, branches several, radiculose beneath; in cross-section outer 2–3 rows of cells ± thick-walled, inner cells larger, thin-walled, central strand weak. **Leaves** erect when dry, erect-spreading when wet, ovate-short lanceolate, 0.5–1.2 mm long, to 0.5 mm wide, somewhat asymmetric, apex short acuminate; margins entire, partially reflexed; costa single, ca. 2/3 lamina length, strong, occasionally weakly forked; laminal cells smooth and ± thick-walled, median cells rhomboidal to oblong, ± obliquely arranged; marginal and basal cells subquadrate to short rectangular. **Autoicous**. **Perichaetia** lateral; leaves elongate, ovate-lanceolate, to 2.2 mm long, acuminate, cells oblong, some porose. **Seta** elongate, 5.5–12 mm long, rather stout, smooth or roughened. **Capsule** erect to inclined, urn oblong-cylindrical, 2–3 mm long, somewhat asymmetric, smooth; neck short; exothecial cells mostly irregularly rectangular, longitudinal walls thick; stomata few at urn base, superficial; annulus undifferentiated. **Operculum** conic. **Peristome** double, set below mouth, exostome teeth 16, tips obtuse, cross-striate with a zig-zag line, trabeculate on back, ca. 1/2 or less endostome length; endostome basal membrane low, segments 16, broadly keeled, perforate below, punctate. **Calyptra** cucullate, smooth and naked. **Spores** spherical, granulose.

DISCUSSION. The genus is characterized by ascending to erect distal stems and branches, somewhat asymmetric, ovate-short lanceolate leaves, short acuminate apex, entire margins, a strong to occasionally weakly forked costa ca. 2/3 lamina length, smooth and thick-walled laminal cells, rhomboidal to oblong, somewhat obliquely arranged median cells, and subquadrate to short rectangular marginal and basal cells. The peristome aids most in distinguishing this taxon. The exostome is ca. 1/2 or less endostome length, and the endostomial basal membrane is low. The genus may be confused with the Leskeaceae, but differs by the peristomial differences previously discussed. The more familar name, *R. polycarpus*, is predated by *R. orthostegius* by only a few months (Eakin & Allen, 1999).

LITERATURE. Eakin, D. A. 1998. A taxonomic revision of the moss genus *Rhegmatodon*. Nova Hedwigia 67: 139–152. - Eakin, D. A. & B. Allen. 1999. A nomenclatural note on *Regmatodon*. Nova Hedwigia 69: 1–2. - Schultze-Motel, W. 1984. Studies in South American species of the genus *Regmatodon* (Musci, Regmatodontaceae). Journal of the Hattori Botanical Laboratory 55: 303–305.

RHACHITHECIACEAE

Plants small, solitary or more commonly forming short tufts. **Stems** erect, simple or few branched by innovations, radiculose below. **Leaves** crispate or curled when dry, erect-spreading when wet, mostly oblong to oblong-lanceolate or spathulate, acute to obtuse-rounded, apiculate or not; margins plane to erect or slightly incurved, entire or crenulate; costa single, 2/3 lamina length to short excurrent; median cells mostly subquadrate, occasionally rhombic to short oblong-rectangular or hexagonal, smooth or pluripapillose; basal cells quadrate to more commonly oblong-rectangular, smooth, lax or not. **Autoicous**. **Perichaetia** terminal; leaves differentiated or not. **Seta** single, short to somewhat elongate, erect or curved, smooth. **Capsule** immersed to shortly exserted, urn short cylindrical, ovoid or subglobose, strongly 8-ribbed or not; stomata at base of urn, superficial; annulus often enlarged, persisting or deciduous. **Operculum** plano-mammillate to conic-apiculate or rostrate and often oblique. **Peristome** absent or if present then single, teeth 8 or 8 pairs, smooth or vertically ornamented. **Calyptra** cucullate to possibly mitrate, smooth or distally roughened, naked. **Spores** spherical to ellipsoid, granulate to finely papillose.

DISCUSSION. The Rhachitheciaceae contain seven genera and about 15 species distributed, in addition to the Neotropics, through Africa and eastern Asia; in the Neotropics six genera and seven species. The family is allied to the Orthotrichales. Characteristics of the family include the small habit, leaves oblong-lanceolate to broadly or narrowly spathulate, upper laminal cells mostly subquadrate, seta short, capsules immersed to short exserted, and when present, 16 peristome teeth in 8 pairs, and the urn smooth or strongly 8-ribbed. The family was established by Robinson (1964) and recently examined in detail by Goffinet (1997).

LITERATURE. Goffinet, B. 1997. The Rhachitheciaceae: Revised circumscription and ordinal affinities. The Bryologist 100: 425–439. - Robinson, H. 1964. New taxa and new records of bryophytes from Mexico and Central America. The Bryologist 67: 446–458.

1. Upper laminal cells papillose 2
1. Upper laminal cells smooth 4
2. Upper lamina fully to partially bistratose; cells above uni- to bipapillose ..... **Uleastrum**
2. Upper lamina unistratose; cells above pluripapillose, several papillae over cell lumen 3
3. Leaves narrowly oblong-lanceolate, margins entire; peristome present, teeth 8; operculum conic-apiculate ..... **Hypnodontopsis**
3. Leaves spathulate, margins crenulate; peristome absent; operculum long rostrate .... **Tisserantiella**
4. Costa of leaf subpercurrent to short excurrent; seta very short, inconspicuous; capsule subglobose; peristome absent ..... **Jonesiobryum**
4. Costa of leaf 2/3–4/5 lamina length; seta 2 or more times the urn length; capsule ovoid-cylindrical to cylindrical; peristome present 5
5. Leaf apices broadly obtuse-rounded; perichaetial leaves little differentiated; capsules smooth when dry ..... **Zanderia**
5. Leaf apices obtuse-rounded with some or most leaves apiculate; perichaetial leaves long sheathing, extending nearly the full length of the seta; capsules 8-ribbed when dry ..... **Rhachithecium**

Hypnodontopsis (Fig. 198) - A single species in the Neotropics, *H. mexicana* (Thér.) H. Rob. is endemic to Mexico. The only other member of the genus is found in Asia.

HABITAT. Epiphytic, on bark of trees; montane forests, at 2300 m elevation.

DESCRIPTION. **Plants** small. **Stems** to 3 mm tall, few branched, weakly radiculose. **Leaves** crispate when dry, erect-spreading to spreading when wet, narrowly oblong-lanceolate, to 1.4 mm long, apex bluntly acute to obtuse-rounded; margins erect, entire; costa subpercurrent; lamina unistratose; upper cells irregularly quadrate-rounded, thick-walled, pluripapillose, papillae over lumen; basal cells of the lower 1/4-1/3 differentiated, extending upward along margin a short distance, oblong-rectangular, smooth. **Perichaetial** leaves sheathing at base, to 1.5 mm long, otherwise similar to stem leaves. **Seta** curved or twisted when dry, curved when wet, ca. 1 mm long. **Capsule** slightly exserted, urn subcylindrical and strongly 8-ribbed when dry, ellipsoid when wet, ca. 0.6 mm long; exothecial cells differentiated between rib and inter-rib bands; stomata at urn base, superficial; annulus broad, deciduous. **Operculum** low conic, obliquely apiculate. **Peristome** single, teeth 8, coarsely vertical marked below. **Calyptra** cucullate, smooth. **Spores** spherical, finely roughened.

DISCUSSION. The genus is characterized by narrowly oblong-lanceolate leaves, erect, entire margins, pluripapillose laminal cells, strongly 8-ribbed capsules, 8 peristome teeth coarsely vertically marked below, and an obliquely apiculate low conic operculum. Our species is apparently only known from the type collection originally made by Brother Arsène Brouard (1867–1938), an important collector of Mexican bryophytes in the early part of this century.

LITERATURE. Iwatsuki, Z. 1957. The genus *Hypnodon* and its allies. The Bryologist 60: 299–310.

Jonesiobryum (Fig. 198) - Two species from the Planalto of Brazil, *J. cerradense* Vital ex B. H. Allen & Pursell and *J. termitarum* Vital ex B. H. Allen & Pursell. An additional species is recorded from western Africa.

HABITAT. Epiphytic, on tree trunks and on termite nests; cerrados of Brazil, at elevations probably below 500 m.

DESCRIPTION. **Plants** solitary or forming small tufts, yellowish-green. **Stems** to ca. 1 mm tall, radiculose at base; in cross-section cells of nearly equal size, rather thin-walled, central strand weak; rhizoids smooth. **Leaves** crowded, erect-appressed when dry, erect-spreading when wet, progressively larger above, oblong to obovate or orbicular, to ca. 1 mm long, apex bluntly acute to obtuse-rounded; margins erect to somewhat incurved, entire; costa strong below, subpercurrent to short excurrent; upper laminal cells irregularly subquadrate to rhombic, smooth, thin-walled, rather lax; basal cells slightly differentiated, quadrate. **Perichaetial** leaves larger, obovate, to 1.3 mm long, apex bluntly acute and slightly reflexed, costa prominent on back. **Seta** very short, hardly observable. **Capsule** immersed, urn subglobose to broadly ovoid, to ca. 0.6 mm long; exothecial cells elongate, thin-walled; stomata at urn base, superficial or appearing slightly immersed; annulus well developed, persistent, ca. 3 outer layers of small isodiametric cells, inner row of much elongate narrowly oblong cells (to 55 µm long). **Operculum** plano-mammillate, ca. 0.2 mm long. **Peristome** absent. **Calyptra** not observed, possibly mitrate. **Spores** spherical, somewhat spaced coarsely papillose (granulate).

DISCUSSION. The genus is characterized by oblong to obovate or orbicular leaves erect-appressed when dry, costa subpercurrent to short excurrent, smooth, little differentiated distal and proximal laminal cells, very short inconspicuous seta, subglobose capsule, large annulus, and absence of a peristome. *Jonesiobryum* was placed previously in the Funariaceae. Reasons for placement in the Rhachitheciaceae are explored in depth by Allen and Pursell (1991). The two Brazilian species are differentiated by the following: *J. cerradense* — leaves oblong to somewhat obovate with apices obtuse-rounded and costa subpercurrent; and *J. termitarum* — leaves orbicular mucronate with costa short excurrent. The genus is named in honor of Eustace Wilkinson Jones (1909–1992), long time student of the west African hepatics.

LITERATURE. Allen, B. & R. A. Pursell. 1991. A reconsideration of the systematic position of *Jonesiobryum*. The Bryologist 94: 438–442. - Vital, D. M. 1983. Two new species of *Jonesiobryum* (Musci) from the Brazilian cerrado regions. Journal of Bryology 12: 383–391.

Rhachithecium (Fig. 198) - A single species in the Neotropics, *R. perpusillum* (Thwaites & Mitt.) Broth. known from Mexico, Brazil (Planalto and southeast) and Argentina. A genus of four species with a tropical to subtropical distribution.

HABITAT. Epiphytic on base or trunk of trees, in Mexico on *Alnus* and *Quercus*, in Brazil on some seven tree genera including *Aspidosperma*, *Ficus*, and *Ligustrum*; open semi-dry (including cerrado) to moist montane forests.

DESCRIPTION. **Plants** solitary or forming short tufts, green or yellowish green. **Stems** short, to ca. 1 mm tall, radiculose below. **Leaves** contorted and curled, lower leaves shorter and somewhat lingulate, upper leaves oblong-spathulate, to 2 mm long, apex obtuse-rounded and at least some leaves apiculate; margins plane, entire; costa strong below, to 2/3–4/5 lamina length; lamina unistratose; laminal cells smooth, upper cells quadrate- to rectangular-rounded or irregularly hexagonal; basal 1/4 with cells laxly rectangular. **Gemmae** occasional, in upper leaf axils, obloid, multicellular. **Perichaetial** leaves strongly differentiated, narrowly oblong-lanceolate, to 2 mm or more long. **Seta** to 2.5 mm long, erect when dry, curved distally when wet, twisted. **Capsule** slightly exserted, urn cylindrical, to 1.2 mm long, strongly 8-ribbed when dry, ovoid to ellipsoid when wet, mouth flared when deoperculate; exothecial cells thin-walled; stomata at urn base, superficial; annulus deciduous. **Operculum** apiculate, slightly oblique. **Peristome** single, set below mouth, reflexed when dry, inflexed when wet, teeth fused into 8 pairs, distally divided, smooth. **Calyptra** cucullate, roughened. **Spores** ellipsoid, finely punctate, appearing smooth.

DISCUSSION. The genus is characterized by the upper, oblong-spathulate leaves, curled-contorted when dry; some leaves of every plant with apiculate apices, costa 2/3–4/5 leaf length, smooth upper laminal cells, short seta ca. two times the urn length, usually curved when wet, cylindrical capsule, 8-ribbed when dry, and smooth, distally divided 8-paired peristome teeth. Yano (1985) provides a good review of *R. perpusillum* for Brazil accompanied by illustrations and a distribution map.

LITERATURE. Yano, O. 1985. Contribuição ao inventário dos musci brasileiros. 4. Rhachitheciaceae. Rickia 12: 29–34.

Tisserantiella (Fig. 199) - A single species in the Neotropics, *T. minutissima* (Mitt.) R. H. Zander known from the Planalto of Brazil and apparently eastern Bolivia; an additional species is recorded from western Africa.

HABITAT. Epiphytic, on tree bark, associated with *Helicophyllum*; Brazilian region of Serra de Santa Brida, apparently from semi-dry vegetation, in Bolivia reported from lower mountain slopes at 700 m.

DESCRIPTION. **Plants** forming short tufts, olive to yellowish green. **Stems** to 1–2 mm tall, weakly radiculose below. **Leaves** crowded, strongly crispate, contorted-incurved when dry, erect-spreading when wet, spathulate, to 1 mm long, somewhat channeled above, apex broadly obtuse-rounded; margins plane to distally erect, crenulate; costa strong below, subpercurrent, in cross-section stereids below guide cells; lamina unistratose; laminal cells strongly differentiated with upper cells subquadrate, rather thick-walled, pluripapillose, papillae several over lumen; basal 1/4–1/3 with cells oblong-rectangular, smooth, lax. **Perichaetial** leaves somewhat differentiated, larger, to 1.85 mm long, apex often notched. **Seta** to ca. 2.3 mm long, slender. **Capsule** erect, urn ovoid to ovoid cylindrical, to 0.6 mm long; remaining features not observed (immature capsules). **Operculum** long rostrate, erect to somewhat oblique. **Peristome** stated to be absent. **Calyptra** not observed. **Spores** not observed.

DISCUSSION. The genus is distinguished by the spathulate leaves, crenulate margins, the strongly differentiated laminal cells with the upper cells being isodiametric, incrassate and pluripapillose while the lower cells are lax, thin-walled and smooth, absence of a peristome, and long rostrate operculum. The type collection, by Gardner, was described by Mitten (1869, see gen. ref.) and placed in *Weissia*,

later placed in a new genus, *Macroglossum* Hilp. *nom. illeg*. Zander (1993) excluded *Tisserantiella* from the treatment of the Pottiaceae, suggesting alignment with the Rhachitheciaceae.

LITERATURE. Zander, R. H. 1993. Genera of the Pottiaceae: Mosses of Harsh Environments. Bulletin of the Buffalo Society of Natural Sciences 32: 1–378.

Uleastrum (Fig.199) - One or possibly two species in the Neotropics, *U. palmicola* (Müll. Hal.) R. H. Zander, recorded from the Planalto and southeastern Brazil. A genus of at least two species, distributed in South America.

HABITAT. On soil, or shaded sandy banks along rivers; exposed sites, open forests, to 800 m.

DESCRIPTION. **Plants** small, forming tufts, dark green to yellowish-green. **Stems** to 3 mm tall, radiculose at base; in cross-section cells similar, thin-walled, central strand absent. **Leaves** crowded, erect-appressed, contorted-incurved when dry, erect-spreading when wet, ligulate to oblong-elliptical, to 1.7 mm long, broadly keeled above, apex broadly acute to apiculate, rarely a few leaves obtuse; margins plane or slightly reflexed (usually on one side), finely crenulate above, entire or slightly notched below (just below juncture with upper papillose cells); costa single, strong, ending several cells below apex; lamina above in cross-section bistratose, unistratose along margin; upper and median cells subquadrate, 1–2 papillose, papillae over cell lumen, thick-walled; basal cells of lower 1/4–1/3 of leaf laxly rectangular, thin-walled; marginal cells at base extending upward in several rows (4–8), oblong-rectangular, rather thick-walled. **Autoicous**. **Perichaetia** leaves sheathing seta, similar or larger than stem leaves. **Seta** erect, to ca. 2 mm long, slightly twisted, smooth. **Capsule** exserted, urn ovoid, to 0.8 mm long; exothecial cells thick-walled, elongate; annulus in ca. 2 rows, large, deciduous in parts. **Operculum** rostrate, oblique. **Peristome** single, set below mouth, teeth 8-paired, short and blunt, smooth, perforate. **Calyptra** cucullate, smooth and naked. **Spores** small to large, coarsely papillose.

DISCUSSION. The genus is characterized by the small stature of the plants, apiculate, bistratose, ligulate to oblong-elliptical leaves, uni- to bipapillose, subquadrate upper laminal cells, erect seta, and the single peristome of 16 smooth teeth in 8 pairs.

Zander (1993) excluded *Uleastrum* (*Ulea hom. illeg.*) from the Pottiaceae, suggesting transfer to the Orthotrichaceae but not ruling out the Ptychomitriaceae or the Rhachitheciaceae. Subsequently Goffinet (1997) has provided convincing evidence for placement of the genus in the Rhachitheciaceae. The generic name honors the German plant explorer Ernst Heinrich Georg Ule (1854–1915), one of the foremost plant collectors in tropical South America, particularly in Brazil, at the turn of the century.

LITERATURE. Goffinet, B. 1997 (see family ref.). - Zander, R. H. 1993. Genera of the Pottiaceae: Mosses of harsh environments. Bulletin of the Buffalo Society of Natural Sciences 32: 1–378 [keys, illustrations].

Zanderia - A monotypic genus, with *Z. octoblepharis* (A. Jaeger) Goffinet known from the Brazilian Planalto and southeast region.

HABITAT. On soil, or shaded sandy banks along rivers, possibly epiphytic; exposed sites, open forests, at elevations below 500 m.

DESCRIPTION. **Plants** small, forming tufts, dark green to yellowish-green. **Stems** to 2 mm tall, radiculose at base; in cross-section outer epidermal cell wall somewhat thick, inner cells similar, thin-walled, central strand absent. **Leaves** crowded, crispate when dry, spreading when wet, lingulate to oblong-spathulate, to 1.5 mm long, broadly keeled above, apex obtuse-rounded; margins plane or slightly reflexed (usually on one side), entire; costa single, strong, ending several cells below apex; lamina in cross-section unistratose; upper and median cells subquadrate, smooth, thick-walled; basal cells of lower 1/4–1/3 of leaf laxly rectangular to subquadrate, thin-walled. **Dioicous**. **Perichaetia** leaves similar or larger than stem leaves. **Seta** curved, to ca. 1.5 mm long, smooth. **Capsule** exserted, urn ovoid to ovoid-short cylindrical, to 0.9 mm long, smooth; exothecial cells quadrate to hexagonal, firm-walled; annulus not differentiated; stomata at urn base. **Operculum** conic-rostrate, oblique. **Peristome** single, set below mouth, teeth 8-paired, somewhat long lanceolate, smooth, perforate. **Calyptra** cucullate, smooth and naked. **Spores** small to large, finely papillose but appearing smooth.

DISCUSSION. The genus is characterized by the small stature of the plants, obtuse-rounded, unistratose, lingulate to oblong-spathulate leaves, smooth subquadrate upper laminal cells, and the single peristome of 16 smooth teeth in 8 pairs.

Goffinet (1997) recently segregated *Zanderia* from *Uleastrum*. The generic name honors the United States bryologist, Richard Zander (1941–), world specialist on the family Pottiaceae and author of *Genera of the Pottiaceae: Mosses of harsh environments*.

LITERATURE.. Goffinet, B., 1997 (see family ref.).

RHACOCARPACEAE

A family containing two genera and nine species, placed in the Leucodontales.

Rhacocarpus (Fig. 200) - Five species in the Neotropics; a tropical and subtropical genus containing seven species.

HABITAT. Typically on rocks, soil and humus, rarely on tree branches; open montane to zacatonal, páramo and puna, ca. 500–4600 m.

DESCRIPTION. **Plants** mostly medium sized, forming loose to dense mats, pale olive green to yellowish-brown or pale golden. **Stems** spreading to subascending, occasionally pendent, irregularly to regularly pinnately branched, stem and branches tips attenuate; in cross-section outer 4–6 rows very small and thick-walled, inner cells larger, thick-walled, central strand absent. **Leaves** distant to crowded, rather orbicular, obovate to oblong-lanceolate with a gradual to abrupt long piliferous tip, or apex acute to apiculate, to 3.5 mm long, to 1.1 mm wide, concave, base slightly decurrent; margins serrulate distally, usually appearing bordered, piliferous tip smooth to weakly toothed; costa none; laminal cells strongly porose, median cells linear-oblong, appearing finely pluripapillose, papillae numerous over lumen and walls; marginal cells linear, usually forming a distinct often rusty red border; alar region differentiated, cells short to rather long rectangular, often dark rusty red or occasionally hyaline. **Dioicous**. **Perichaetia** appearing lateral, on short terminal branches; leaves sheathing seta, oblong-lanceolate. **Seta** elongate, to 28 mm long, smooth below, roughened below capsule, usually twisted distally. **Capsule** erect to suberect, urn broadly ovoid-short cylindrical, to 2 mm long, strongly to weakly ribbed when deoperculate; exothecial cells thick-walled, subquadrate-rounded to short oblong, cells below urn mouth oblate, smaller and walls thicker. **Operculum** long rostrate, oblique. **Peristome** absent. **Calyptra** cucullate, naked and smooth. **Spores** trilete, appearing finely papillose.

DISCUSSION. The distinguishing features of the genus include the broadly ovate or orbicular, ecostate stem leaves, distinct to indistinct border of smooth, linear cells, laminal cells appearing finely pluripapillose over and between the lumen, enlarged alar cells, elongate seta and gymnostomous capsules. The common and widespread neotropical species (also found in Africa and Australia) *Rhacocarpus purpurascens* (Brid.) Paris, as presently understood, is highly polymorphic with regards to gametophytic features. Further studies are needed, specifically to determine morphological limits and the possible influence of environmental factors. In addition to the above mentioned species, which exhibits a long piliferous leaf tip, *R. inermis* (Müll. Hal.) Lindb., from southeastern Brazil, exhibits a short acute or cuspidate leaf apex. Frahm (1996) has recently provided a synopsis of the genus. Buck (1995) has suggested that *Rhacocarpus* is acrocarpous, i.e., the sporophyte is produced terminally. Furthermore, the genus is argued to be better positioned in the Dicranales, close to the family Dicnemonaceae.

LITERATURE. Buck, W. R. 1995. The systematic position of the moss genus *Rhacocarpus*. Fragmenta Floristica et Geobotanica 40: 127–131. Frahm, J.-P. 1996. Revision der Gattung *Rhacocarpus* Lindb. (Musci). Cryptogamie: Bryologie, Lichénologie 17: 39–65 [keys, illustrations].

RHIZOGONIACEAE

Plants small to rather large, forming loose to dense tufts. **Stems** mostly erect, few branched, radiculose, often densely tomentose; central strand well developed. **Leaves** spirally arranged or appearing 2-ranked, distant to rather crowded, ovate to narrowly or broadly oblong-lanceolate, or linear-lanceolate, apex acute to acuminate, base decurrent or not; margins plane or reflexed to recurved, crenulate, dentate or sharply serrate, teeth single and margins unistratose or double and margins bistratose; costa single, strong, percurrent to short excurrent, entire or toothed on back distally; laminal cells mostly isodiametric and smooth, or bulging mammillose, walls firm and entire; alar region undifferentiated. **Gemmae** in leaf axils of distal stems and branches (absent in *Pyrrhobryum*), cylindrical, smooth to papillose. **Autoicous** or dioicous. **Perigonia** bud-like, usually below perichaetia. **Perichaetia** lateral at base or at mid stem, or terminal, leaves small and differentiated. **Seta** elongate, wiry, smooth. **Capsule** erect to horizontal, urn short to rather long cylindrical, symmetric to asymmetric, curved or straight. **Operculum** conic or short rostrate, oblique. **Peristome** double or absent, exostome teeth 16, cross-striate below, papillose above, or papillose throughout; endostome basal membrane moderately high, segments 16, keeled, cilia usually present. **Calyptra** cucullate, naked and smooth. **Spores** spherical, lightly papillose.

DISCUSSION. The Rhizogoniaceae contain about eight genera and some 35 species with a pantropical distribution; in the Neotropics five genera and eight species. The family is placed in the Bryales. The distinguishing feature of the Rhizogoniaceae is that the sporophytes occur laterally near

the base or midway along the erect stems (but terminal in *Leptotheca*). Manuel (1980) segregated *Pyrrhobryum* from *Rhizogonium*, a subdivision that appears well supported from several lines of evidence (cf. Inoue & Iwatsuki, 1976). Koponen (1988) has presented a classification in which *Leptotheca* and *Pyrrhobryum*, among the neotropical taxa, are placed in an amended Mniaceae. Only *Hymenodon* and *Rhizogonium* are retained in the Rhizogoniaceae. This study has merit. Certainly the traditional concept of the Mniaceae, the Rhizogoniaceae, and related families needs critical reassessment, however the cladistic analyses presented by Koponen only weakly support the new classification.

LITERATURE. Inoue, S. & Z. Iwatsuki. 1976. A cytotaxonomic study of the genus *Rhizogonium* Brid. (Musci). Journal of the Hattori Botanical Laboratory 41: 389–403. - Koponen, T. 1988. The phylogeny and classification of Mniaceae and Rhizogoniaceae (Musci). Journal of the Hattori Botanical Laboratory 64: 37–46. - Manuel, M. G. 1980. Miscellanea bryologica II. Classification of *Rhizogonium* Brid., *Penzigiella hookeri* Gangulee, and some nomina nuda. Cryptogamie: Bryologie, Lichénologie 1: 67–72.

1. Leaf margins crenulate; laminal cells strongly bulging mammillose; peristome absent .... **Hymenodon**
1. Leaf margins dentate to serrate; laminal cells smooth or appearing slightly bulging; peristome present 2
2. Leaves doubly-serrate, margins bistratose; exostome cross-striate ..... **Pyrrhobryum**
2. Leaves singly-serrate, margins unistratose; exostome papillose 3
3. Costa ending several cells below leaf apex; leaf cells elongate, ca. 4–5:1 ..... **Goniobryum**
3. Costa percurrent to excurrent; leaf cells ± isodiametric 4
4. Leaves appearing 2-ranked, complanate, ovate to broadly elliptical; gemmae infrequent and inconspicuous; perichaetia lateral ..... **Rhizogonium**
4. Leaves spirally arranged, not complanate, linear-lanceolate to narrowly oblong-lanceolate; gemmae often very numerous, bottle-brush appearance on distal stems; perichaetia terminal ..... **Leptotheca**

Goniobryum (Fig. 200) - A single species in the Neotropics, *G. subaloma* Herzog, from Bolivia; a genus of two species, the other species found in Subantarctica.

HABITAT. Stated to be possibly submerged; puna, at 4700 m.

DESCRIPTION. **Plants** rather large, glossy green, lower portions yellow . **Stems** to 6 cm long, simple or few branched by innovations; in cross-section outer 2 rows of cells somewhat small, rather thick-walled, inner cells large, thin-walled, central strand weak. **Leaves** contorted when dry, lax and flaccid, remaining somewhat contorted when wet, oblong to somewhat elliptic-lanceolate, 5–6 mm long, 1–1.5 mm wide, apex acute; margins plane, weakly serrulate-denticulate; costa slender, ending several cells below apex; laminal cells large and lax, upper cells long-hexagonal to rectangular, 85–110 µm long, 25–30 µm wide, larger and thin-walled toward the costa; basal cells irregularly rectangular, to 200 µm long, to 30 µm wide; marginal cells at base forming a weak border with 3–4 rows of narrowly oblong cells. **Gemmae** absent. **Sex** and sporophytes unknown.

DISCUSSION. Our species is characterized by lax and rather flaccid elliptic-lanceolate leaves that are contorted when dry, weakly serrulate-dentate distal margins, slender subpercurrent costa, large and lax long-hexagonal to rectangular upper cells, and weak border of narrowly oblong cells at basal margin. *Goniobryum subaloma* is only known from the original collection near Illampu, Cordillera Real, Bolivia (Herzog, 1934). The only other member of the genus, *G. subbasilare* (Hook.) Lindb., is known from temperate forests of Argentina and Chile, often associated with evergreen *Nothofagus* forests in Tierra del Fuego (also from Tasmania, Australia and New Zealand), and growing exclusively on decaying wood.

LITERATURE. Herzog, T. 1934. Die Bryophyten der Andenreisen von C. Troll. Musci. Hedwigia 74: 97–114.

Hymenodon (Fig. 201) - Two species in the Neotropics, *H. aeruginosus* (Hook.f. & Wilson) Müll. Hal. (Brazil, possibly Argentina and Colombia) and *H. reggaeus* Kart. & S. Bäck (Greater Antilles); five species, two American and three Australasian.

HABITAT. On tree trunks, particularly tree ferns, e.g., Cyatheaceae, *Hemitelia* and *Nephelea*; submontane to lower montane forests, 150–1480 m.

DESCRIPTION. **Plants** small, forming delicate tufts, pale green to yellowish-green or brown. **Stems** prostrate to suberect, to ca. 12 mm long, simple, radiculose at base; in cross-section outer row of cells small, thick-walled, inner cells larger, thick-walled, progressively thin, central strand present, appearing collapsed; rhizoids papillose. **Leaves** erect and slightly twisted when dry, erect to erect-spreading

when wet, oblong to oblong-lanceolate, 0.8–1.2 mm long, to 0.3 mm wide, apex acute with a long piliferous point (ca. 0.2 mm long); margins plane to weakly flexed, crenulate throughout or entire at base; costa rather long excurrent; median cells irregularly isodiametric, bulging, mammillose; basal cells subquadrate to short rectangular weakly mammillose or smooth. **Dioicous**. **Perichaetia** at base of stems; leaves differentiated, ovate-lanceolate, costa excurrent, distally cells rectangular. **Seta** elongate, to 15 mm long, slender, smooth. **Capsule** erect, urn ovoid to short cylindrical, 1.6–2 mm long, neck short; exothecial cells short to somewhat elongate, thin-walled; stomata on lower 1/4 of urn, superficial; annulus in several rows. **Operculum** conic-long rostrate, ca. 0.7 mm long, oblique. **Peristome** absent. **Calyptra** cucullate. **Spores** spherical, lightly papillose.

DISCUSSION. The genus is readily recognized by the piliferous-tipped, short to rather elongate oblong leaves; crenulate margins; strongly mammillose, isodiametric laminal cells; sporophytes positioned at stem base; and absence of a peristome. The two species can be differentiated as follows: *H. aeruginosus* — leaves 3–4 times longer than wide, piliferous tip 1/4 lamina length, gemmae absent; and *H. reggaeus* — leaves 6–7 times longer than wide, piliferous tip 1/6 lamina length, gemmae generally present.

LITERATURE. Karttunen, K. & S. Bäck. 1988. Taxonomy of *Hymenodon* (Musci, Rhizogoniaceae). Annales Botanici Fennici 25: 89–95.

Leptotheca (Fig. 201) - Two species in the Neotropics, *L. boliviana* Herzog (Jamaica, Honduras to Bolivia) and *L. hamiltonii* H. A. Crum (Peru); a genus of three species, distributed in the tropical American cordilleras and circum-Antarctic region.

HABITAT. Epiphytic on branches and trunks of trees and shrubs, also on trunks of tree ferns; in moist or wet montane forests, 1500–3100 m.

DESCRIPTION. **Plants** rather small to medium sized, forming tufts, light to dark green. **Stems** erect, to 3 cm tall, often densely tomentose below; in cross-section 5-sided, outer 2–3 rows of cells small, thick-walled, on corners rows to 5, inner cells larger, thick-walled, central strand well differentiated; rhizoids rusty-red, distinctly papillose. **Leaves** linear-lanceolate, 2–2.3 mm long, apex acuminate, base slightly decurrent; margins plane above, recurved below, serrate in distal 1/2, teeth single, sharply toothed to spinose distally; costa strong, short excurrent, toothed on back; laminal cells smooth, thick-walled, median cells isodiametric or oval to irregularly rectangular-rounded; basal cells similar or those associated with propagula cells long rectangular-rounded. **Gemmae** nearly always present on terminal stems in leaf axils, often in a dense cluster (like a bottle-brush), each long cylindrical, golden-red, lightly papillose. **Dioicous**. **Perichaetia** terminal; leaves lanceolate-acuminate, costa short to rather long excurrent, not serrate, upper cells similar, lower and basal cells short rectangular, lax, golden red. **Sporophyte** unknown.

DISCUSSION. This epiphytic genus is distinguished by the bottle-brush appearance of clustered, papillose, cylindrical gemmae on distal portion of stems; additional features include the often very tomentose lower stems, spirally arranged leaves, and single toothed serration of the leaf margin.

LITERATURE. Churchill, S. P. & W. R. Buck. 1982. A taxonomic investigation of *Leptotheca* (Rhizogoniaceae). Brittonia 34: 1–11 [keys, illustrations, maps].

Pyrrhobryum (Fig. 201) - Two species in the Neotropics, *P. mnioides* (Hook.) Manuel (Costa Rica, Venezuela to Chile and Argentina, also Australia and New Zealand.) and *P. spiniforme* (Hedw.) Mitt. (pantropical); a pantropical genus of 12 species.

HABITAT. On tree trunks, logs and soil or humus, leaf litter covered banks; wet lowland to upper montane forests, from near sea level to 3670 m.

DESCRIPTION. **Plants** medium sized to somewhat large, forming loose to dense tufts, dark green. **Stems** erect or curved; in cross-section outer 2–3 rows of cells small, thick-walled, inner cells larger, moderately thick-walled, central strand distinct; rhizoids often forming a dense tomentum below. **Leaves** linear-lanceolate to broadly lanceolate, 4–8 mm long, apex acuminate, base decurrent or not; margins plane, bistratose and doubly-serrate to near base; costa strong, percurrent to excurrent, toothed on back, in cross-section stereids above and below guide cells; laminal cells uniform throughout except at base, isodiametric, rounded to 4–6 sided, thick-walled, smooth; juxtacostal basal cells often weakly differentiated, enlarged, short to rather long rectangular, lax or not. **Gemmae** absent. **Synoicous**. **Perichaetia** lateral, confined to base or lower part of stem; leaves oblong-lanceolate, marginal teeth single or double, upper cells elongate, oblong-rectangular, lower cells larger, lax, golden. **Seta** elongate, 2–6 cm long, smooth. **Capsule** inclined to horizontal, urn cylindrical, 1.5–3 mm long, usually curved, becoming striate and flared at the mouth when deoperculate; exothecial cells quadrate- to rectangular-rounded, moderately thick-walled, somewhat weakly collenchymatous at base; stomata at urn base, superficial. **Operculum** conic-rostrate, oblique. **Peristome** double, exostome teeth lanceolate, appearing cross-striate (actually finely striate-

papillose), distally papillose; endostome basal membrane rather high, segments keeled and perforate, cilia 2–3. **Calyptra** cucullate, smooth. **Spores** spherical, lightly papillose.

DISCUSSION. The genus is characterized by the elongate stems; distal and spirally arranged broadly to narrowly lanceolate or linear-lanceolate leaves; doubly toothed, bistratose leaf margins; costa distally toothed on the back; mostly isodiametric laminal cells uniform to near base; and sporophytes positioned somewhat midway on stem or near the base. The local species were previously placed in the genus *Rhizogonium*. The two species may be differentiated by the following: *P. mnioides* — leaves strongly decurrent, leaf base 0.75–1 mm wide, gametangium in axil of leaf, not confined to base, upper montane (2700–3670 m); and *P. spiniforme* — leaves not decurrent, leaf base 0.25–0.50 mm wide, gametangium confined to near base of stem, lowland to low montane (50–2550 m).

Rhizogonium (Fig. 202) - A single species in the Neotropics, *R. novae-hollandiae* (Central America, Dominican Republic, tropical Andes, southeastern Brazil; also Australasia); in the strict sense *Rhizogonium* contains about 10 species, primarily distributed in Australasia.

HABITAT. On soil banks, base and trunk of trees including tree ferns (*Blechnum*, *Dicksonia*), in moist, shaded sites; submontane to upper montane forests, 1200–3250 m.

DESCRIPTION. **Plants** small and delicate, forming loose tufts, occasionally solitary, pale green. **Stems** erect, to 2 cm tall, simple to few branched; outer 2–3 rows of cells small, thick-walled, inner cells larger, rather thick-walled, central strand present; rhizoids confined to stem bases. **Leaves** scale-like near base, spiral and distant, above leaves appearing 2-ranked and complanate, more closely spaced, spreading, ovate to elliptical, 1–1.2 mm long, to 0.7 mm wide, apex acute and mucronate, base asymmetric; margins plane to slightly recurved, irregularly serrate 1/3–1/2 distally, teeth single; costa percurrent to short excurrent, smooth; laminal cells thick-walled, median cells isodiametric, subquadrate-rounded, bulging; basal cells short to rather long rectangular-rounded; marginal cells often small and elongate, often bistratose near base. **Gemmae** occasionally present in leaf axils, cylindrical, to 1 mm long. **Perichaetia** lateral, at base of stems; leaves differentiated, ovate-lanceolate, acuminate, costa 2/3 lamina length to percurrent, upper cells elongate, occasionally appearing weakly porose or ornamented, lower cells broadly rectangular or subquadrate, lax, rusty-red. **Seta** elongate, 2–3.5 cm long, slender. **Capsule** inclined, urn short cylindrical, 1–1.5 mm long; exothecial cells subquadrate to short rectangular-rounded, thick-walled; stomata at urn base, superficial. **Operculum** conic-short rostrate, ca. 0.5 mm long. **Peristome** double, exostome teeth papillose cross-striate below, distally hyaline and papillose; endostome basal membrane appearing rather low, segments shorter than exostome teeth, ± narrow, keeled and lightly papillose, cilia apparently 1. **Calyptra** cucullate, 2.5–3 mm long, smooth. **Spores** spherical, lightly papillose.

DISCUSSION. Small statured, pale green, soft plants; ovate to broadly elliptical, 2-ranked leaves along stem; distinctly single toothed margins near apex; smooth, short excurrent costa; and isodiametric laminal cells that appear slightly bulging, aid in the recognition of *Rhizogonium*. The frequently used name *R. lindigii* (Hampe) Mitt., is a synonym.

RIGODIACEAE

The Rigodiaceae as presently defined is a monotypic family, previously placed in the Lembophyllaceae. The family is placed in the Hypnales.

Rigodium (Fig. 202) - A single species in the Neotropics, *R. toxarion* (Schwägr.) A. Jaeger (Mexico, Central America, Hispaniola, Andes, southeastern Brazil). Seven species and one variety with a tropical to austral-temperate distribution.

HABITAT. Epiphytic on tree trunks and branches, also on logs and soil; lower to upper montane forests, 1200–3750 m, lowers elevations in southern Brazil, 30–100 m.

DESCRIPTION. **Plants** medium sized to somewhat large, forming loose tufts, dark green to blackish-green. **Primary stems** creeping. Secondary stems weakly to strongly stipate, stems above stipe suberect to arching and subdendroid, to 10 cm tall, usually rather stiff, several-pinnately branched, branches slender to filiform, usually becoming flagellate; in cross-section stem surface ridged or fluted, outer 3–4 rows of cells small, thick-walled, inner cells large, thin-walled, central strand well developed; pseudoparaphyllia and paraphyllia absent. **Leaves** differentiated; **stipe leaves** wide-spreading, broadly ovate and abruptly long acuminate, to 1.4 mm long, 1 mm wide, base somewhat decurrent, usually ecostate, or costa short and single or forked; **stem leaves** wide-spreading to squarrose, 1–1.2 mm long, to 0.8 mm wide, similar to stipe leaves but apex gradually narrowed and acute; costate, costa single, ending in or just below acumen; **branch leaves** short ovate-lanceolate, to

0.25 mm long or less; costa ending below or into acumen; margins usually serrulate throughout; laminal cells smooth and thick-walled, subquadrate- to oblong-rounded, smaller along margin; alar region not well differentiated, cells oblong-rectangular or subquadrate. **Dioicous**. **Perichaetia** lateral; leaves differentiated, elongate, oblong-subulate. **Seta** elongate, 10–25 mm long or more, smooth. **Capsule** inclined to horizontal, urn ovoid-cylindrical, 1.5 mm long, constricted below mouth when dry; exothecial cells thick-walled; annulus present, in 2 rows, deciduous. **Operculum** conic-long rostrate. **Peristome** double, exostome teeth 16, cross-striate below, distally papillose; endostome basal membrane high, segments 16, keeled and perforate, finely papillose, cilia 1–3. **Calyptra** cucullate, naked and smooth. **Spores** spherical, finely papillose.

DISCUSSION. The genus is distinguished by the subdendroid habit, stipitate with secondary stems often exhibiting long delicate, flagellate branches, differentiated stipe, stem and branch leaves, finely serrulate margins, and oval to oblong-oval laminal cells. *Rigodium* may be confused with *Eurhynchium praelongum* (Hedw.) Bruch, Schimp. & W. Gümbel, but in that species the intramarginal cells at the base of stem leaves are enlarged, oblong-oval, thin-walled and hyaline. Although sporophytes are occasionally present, it is likely that the common mode of reproduction in *Rigodium* is asexual by propagula in the form of distal flagellate branches and deciduous leaves.

LITERATURE. Crum, H. 1981. Taxonomic and nomenclatural notes on middle American mosses. The Bryologist 84: 390–393. - Zomlefer, W. B. 1993. A revision of *Rigodium* (Musci: Rigodiaceae). The Bryologist 96: 1–72 [keys, illustrations, maps].

SELIGERIACEAE

Plants small to somewhat medium sized, gregarious or forming rather dense tufts. **Stems** erect, branched by innovations, radiculose below; central strand present. **Leaves** rather loosely foliate, linear-lanceolate or subulate from an ovate to oblong or oblong-lanceolate base; margins plane and entire; costa single, stout, long excurrent; laminal cells somewhat elongate, lower cells ± long oblong-rectangular; alar cells differentiated or not. **Asexual structures** not observed, apparently absent. **Autoicous** or dioicous. **Perichaetia** terminal, leaves little or distinctly differentiated. **Seta** elongate and slender, erect, curved or cygneous, distally twisted, smooth. **Capsule** erect or subpendulous, urn short ovoid to short-cylindrical, smooth or ribbed; annulus present and well developed or absent. **Operculum** short rostrate, straight or oblique. **Peristome** absent or more commonly present, single, teeth 16, fragile and reduced or teeth shortly divided at apex, papillose or smooth; very low hyaline membrane surrounding and positioned outside peristome. **Calyptra** cucullate or mitrate-short campanulate. **Spores** spherical, mostly finely papillose.

DISCUSSION. The Seligeriaceae contain some 5–6 genera and about 55 species primarily of the temperate regions; in the Neotropics three genera and seven species. The family is placed in the Dicranales.

1. Plants small, gregarious, rarely in tufts; alar region undifferentiated, cells not enlarged; capsule striate or rarely smooth ..... **Brachydontium**
1. Plants large, in loose to dense tufts; alar region differentiated, cells enlarged; capsule smooth when deoperculate 2
2. Basal cells moderately thick-walled, not or weakly porose; capsules subcylindrical; annulus present; peristome papillose above a smooth base ..... **Hymenolomopsis**
2. Basal cells very thick-walled, walls as thick or thicker than cell lumen, porose; capsules pyriform; annulus absent; peristome smooth ..... **Blindia**

Blindia (Fig. 202) - Three species in the Neotropics, *B. acuta* (Hedw.) Bruch & Schimp. (Guatemala, widespread in Northern Hemisphere), *B. gradsteinii* J. K. Bartlett & Vitt (Colombia), and *B. magellanica* Schimp. (Andes, southeastern Brazil; circum-Antarctic); about 16 species widely distributed, in the tropics confined to high elevations.

HABITAT. On rock, along and in streams; moderately high open montane to páramo and puna, 2250–4200 m.

DESCRIPTION. **Plants** rather small to rather large, forming loose to more commonly dense stiff tufts or ascending mats, glossy brownish- to yellowish-green. **Stems** erect, wiry, to 10 cm tall, few to several branched by innovations. **Leaves** erect to erect-spreading, subulate from an ovate to obovate base, 1.5–5 mm long, apex aristate, base weakly auriculate; margins plane, entire to distally dentate or serrulate; costa strong, long excurrent; laminal cells thick-walled, median cells oblong-linear; distal cells and toward margin shorter; basal cells thick-walled, as thick or thicker than cell lumen, dark red; alar cells differentiated, outer cells inflated, oblong-rectangular, hyaline or yellowish, inner cells smaller, very thick-walled, dark red. **Dioicous**. **Perichaetia** terminal. **Seta** 3–13 mm long, flexuose

or cygneous, smooth. **Capsule** erect, urn pyriform, 0.5–1 mm long, smooth. **Opercula** low conic-rostrate, oblique. **Peristome** smooth, spreading when dry, dark red. **Calyptra** cucullate, naked and smooth. **Spores** spherical, lightly papillose.

DISCUSSION. The genus is characterized by the aquatic habitat, confined to rocks; the rather stiff habit; the short to long oblong upper and median laminal cells; dark red, well differentiated alar cells, pyriform capsules; and smooth, red peristome teeth. When sterile, the genus may be confused with members of the Dicranaceae, but in *Blindia* the leaf costa in cross-section is mostly composed of undifferentiated cells.

LITERATURE. Bartlett, J. K. & D. H. Vitt. 1986. A survey of species in the genus *Blindia* (Bryopsida, Seligeriaceae). New Zealand Journal of Botany 24: 203–246 [keys, illustrations, maps].

Brachydontium (Fig. 203) - Four species in the Neotropics; about 7–8 species, half associated with the montane tropics, the remaining either with the southern or northern temperate regions.

HABITAT. On soil and rock, possibly on bark; open montane, 2000–2900 m.

DESCRIPTION. **Plants** small and inconspicuous, gregarious or forming small tufts, yellowish-green to golden-yellow. **Stems** short and erect, 4–5 mm tall, few branched, radiculose at base; rhizoids rusty red, appearing smooth. **Leaves** progressively elongate from base (leaves at base ovate-acute, 0.2 mm long) to distally crowded, erect to erect-spreading, setaceous (subulate) from a short ± concave ovate to elliptical base, 1–3 mm long, apex bluntly acute to obtuse-rounded; margins entire; costa strong, excurrent, rarely percurrent; laminal cells of expanded base smooth, distally subquadrate to oblong-rectangular or rhombic, thick-walled; basal cells larger, oblong-rectangular, thin-walled and lax; alar cells undifferentiated. **Autoicous** or dioicous. **Perichaetia** terminal, leaves larger than stem leaves, nearly as long as seta. **Seta** 1–3 mm long, cygneous, distally twisted. **Capsule** somewhat pendent, urn ovoid-short cylindrical, 0.5–1 mm long, striate or smooth; stomata at urn base; annulus compound, exceeding or slightly shorter than the length of the peristome, outer row short, inner most row elongate, truncate or acute. **Operculum** short rostrate. **Peristome** absent, or present and reduced, papillose, pale. **Calyptra** mitrate-short campanulate, base lobed. **Spores** finely ornamented to nearly smooth.

DISCUSSION. The genus is characterized by the small habit, leaves subulate from an ovate or oblong base, undifferentiated alar cells, cygneous, rarely flexuose-curved, seta, striate, rarely smooth capsules, large and conspicuous compound annulus and short, pale, papillose peristome teeth.

The neotropical members of the genus are separated geographically: *B. curvisetum* H. A. Crum (Mexico), *B. flexisetum* (Hampe) Paris (Colombia), *B. notorogenes* W. R. Buck & Schaf.-Verw. (southeastern Brazil), and *B. olsonii* F. D. Bowers & B. H. Allen (Honduras). A review by Stone (1973) provides a useful overview of the genus. Three additional species have since been described (see Buck and Schäfer-Verwimp, 1992, for a summary).

LITERATURE. Buck, W. R. & A. Schäfer-Verwimp. 1992. *Brachydontium notorogenes* sp. nov. (Seligeriaceae) from southeastern Brazil. The Bryologist 95: 340–342. - Stone, I. G. 1973. A new species of *Brachydontium* from Australia. Journal of Bryology 7: 343–351.

Hymenolomopsis (Fig. 203) - A monotypic genus, with *H. tolucensis* Thér. only known from Mexico.

HABITAT. On moist soil or rock; zacatonal, at 3100 m elevation or possibly higher.

DESCRIPTION. **Plants** slender, forming tufts, glossy yellowish-green to yellow. **Stems** to 3 cm tall, numerous branched by innovations, radiculose at base. **Leaves** crisped and flexuose, erect-spreading when dry, loosely erect when wet, subulate from an oblong-lanceolate base, 3–3.5 mm long; marginal cells of subula short oblong-rectangular to subquadrate in 1–3 rows; upper cells of lamina base oblong-linear, thick-walled; alar cells subquadrate, firm- to thick-walled, adjoining basal cells not or weakly porose, walls narrower than cell lumen. **Autoicous**. **Perichaetial** leaves sheathing, stoutly subulate from an oblong base. **Seta** 5–10 mm long, pale yellow. **Capsule** erect, urn subcylindrical, ca. 1 mm long, smooth; stomata at juncture of urn base and seta; annulus conspicuous, in several rows, deciduous. **Operculum** stoutly long rostrate, oblique. **Peristome** red, smooth at base, distally papillose. **Calyptra** cucullate. **Spores** finely papillose.

DISCUSSION. The genus is recognized by the subquadrate alar cells; the moderately thick-walled, not or weakly porose basal cells; subcylindrical capsules; enlarged compound, deciduous annulus; the distally papillose peristome teeth smooth at the base.

SEMATOPHYLLACEAE

Plants small to somewhat large, forming loose to dense mats or short to ascending tufts, often glossy light to dark green or yellowish-green to golden. **Stems** short to long creeping or spreading to ascending, irregularly short or long branched, julaceous or homomallous, rarely complanate, radiculose; central strand present; pseudoparaphyllia ?, paraphyllia absent. **Leaves** crowded, occasionally distant, erect to erect-spreading, linear to broadly lanceolate, ovate, ovate-oblong, often concave, apex narrowly to broadly acuminate or acute, rarely obtuse, base undifferentiated or slightly auriculate; margins plane to reflexed or recurved, entire to serrulate or serrate distally; costa none or short and forked or double; laminal cells smooth or papillose, papillae single or several in a row, walls firm; alar region typically differentiated, cells usually inflated, oval to oblong-oval, thick-walled, often reddish-orange or golden. **Propagula** absent or if present then produced in distal branches and stems in leaf axils (*Aptychella*), cylindrical; reduced branch leaves (flagellate branches) in *Wijkia* possibly serve in asexual reproduction. **Dioicous**, occasionally autoicous. **Perichaetia** lateral, leaves often differentiated, elongate. **Seta** elongate, smooth or distally papillose. **Capsule** exserted, inclined or occasionally erect, urn ovoid or short cylindrical, often slightly curved and asymmetric, often constricted below mouth when deoperculate; exothecial cells mostly collenchymatous; stomata usually present at base of urn, superficial; annulus absent or persistent. **Operculum** mostly conic-long rostrate, usually oblique. **Peristome** double, or reduced and often single (exostome present), exostome teeth 16, cross-striate below, distally papillose, trabeculate, usually with a zig-zag median line, occasionally furrowed, or exostome single and smooth or papillose; endostome basal membrane generally high, segments keeled, cilia 1–3. **Calyptra** cucullate, smooth and naked. **Spores** spherical, smooth or lightly papillose.

DISCUSSION. The Sematophyllaceae contain 40-45 genera and 800-900 species, primarily of the tropics; in the Neotropics 20 genera and about 90 species. The family is rather broadly distinguished by the ecostate leaves or rarely with costa short and forked, with alar cells conspicuously enlarged, mostly oval or oblong and thick-walled. The two most common genera among those exhibiting smooth laminal cells, *Sematophyllum* and *Acroporium*, are widespread in the Neotropics, the remaining genera are by and large rare, or locally common in distribution. Critical revisions are needed on a worldwide scale for most of the larger genera.

Study guide. An adequate sample of both stem and branch leaves are needed to determine the variation in shape and whether the leaves are essentially mono- or dimorphic. Occasionally, the papillae in several species of *Trichosteleum* are difficult to observe. Such papillae can best be seen along leaf plications or on folded leaves. Many of the species can be identified by leaves alone, particularly when one becomes familiar with the local flora, however until that time sporophytes are essential with careful attention given to the peristome features.

LITERATURE. Hedenäs, L. 1996. A cladistic evaluation of relationships between the Hookeriales, the Sematophyllaceae and some other taxa. Lindbergia 21: 49–82. - Hedenäs, L. & W. R. Buck. 1999. A phylogenetic analysis of the Sematophyllaceae. Lindbergia 24: 103–132. - Seki, T. 1968. A revision of the family Sematophyllaceae of Japan with special reference to a statistical demarcation of the family. Journal of Science of the Hiroshima University, Series B, Division 2 (Botany) 12: 1–80.

1. Laminal cells papillose (in some species best observed on folded leaves), papillae over cell lumen 2
1. Laminal cells smooth or if papillose, papillae rather faint, projecting at cell angles 3
2. Leaf cells pluripapillose, papillae several in a row over cells lumen ..... **Taxithelium**
2. Leaf cells unipapillose, papillae single over cell lumen ..... **Trichosteleum**
3. Secondary stem and branch leaves dimorphic, branch leaves distinctly smaller and narrower than stem leaves 4
3. Secondary stem and branch leaves monomorphic, leaves generally of similar shape and nearly the same size 5
4. Leaf margins sharply serrate in distal 1/2; leaves 2–3 mm long, branch leaves mostly falcate ..... **Heterophyllium**
4. Leaf margins entire or serrulate in distal 1/4–1/3; leaves usually less than 1.6 mm long, branch leaves not falcate ..... **Wijkia**
5. Leaves costate, rather elongate single or double (to 1/3 or more the lamina length); alar cells small, subquadrate 6
5. Leaves ecostate or rarely costate, costa faint, short and forked, less than 1/4 the lamina length; alar cells either small and subquadrate or inflated and oval or oblong 7
6. Propagula commonly produced on terminal tips of stems and branches, or in leaf axils; leaves slenderly lanceolate to oblong-lanceolate, acuminate; leaf costa commonly single but occasionally some leaves with a single costa or ecostate; laminal cells smooth; epiphytic, usually branches, rarely on logs ..... **Aptychella**

6. Propagula lacking; leaves mostly ovate, acute to obtuse-acute; leaf costa double, 1/5–1/3 lamina length; laminal cells weakly papillose by projecting cell angles; on soil, rock, occasionally base of tree trunks ..... **Horridohypnum**
7. Alar cells obliquely angled (ca. 45°); exostome with a median furrow ..... **Acroporium**
7. Alar cells ± erect; exostome not furrowed, usually with a zig-zag median line or peristome single 8
8. Alar region with 2–3 rows of inflated cells, very thick-walled, dark rusty-red; leaves oblong (2–2.4 mm long), apex abruptly short to rather long acuminate and flexed ..... **Aptychopsis**
8. Alar region usually with 1 row of inflated cells, and above with supra-alar, or alar cells small and subquadrate; leaves ovate, ovate- to oblong-lanceolate, apex short to long acuminate or acute, or if oblong then apex acute, not flexed 9
9. Peristome single 10
9. Peristome double 12
10. Peristome smooth, with an indistinct hyaline border; sporophytes produced abundantly along one side of stem; eastern Andean slopes of Ecuador ..... **Allioniellopsis**
10. Peristome papillose, lacking a hyaline border; sporophytes few; somewhat widespread in the Neotropics 11
11. Alar cells of leaf inflated and thick-walled, mostly oval to short oblong; leaves 0.8–1.3 mm long, ecostate; exostome teeth hyaline to white, separated and widely spaced ..... **Meiothecium**
11. Alar cells of leaf quadrate, few, thin-walled; leaves small, 0.5–0.7 mm long, costate, short and forked; exostome teeth often appearing in pairs, closely spaced ..... **Pterogonidium**
12. Peristome double and fully developed, exostome teeth on the outer surface finely cross-striate or projecting, ellipical thickenings; endostome basal membrane high, segments subequal to exostome teeth, keeled 13
12. Peristome double with exostome or endostome, or both, variously modified and reduced; exostome on the outer surface often papillose or smooth; endostome basal membrane absent to moderately high 15
13. Outer surface of exostome with projecting, elliptical thick-walled plates; exostome teeth white; restricted to the highlands of Ecuador ..... **Timotimius**
13. Outer surface of exostome finely cross-striate; exostome teeth brown or reddish-brown; broadly distributed 14
14. Leaves broadly to narrowly ovate or lanceolate to oblong-lanceolate, acute to obtuse-rounded or short to long acuminate, often abruptly so; common throughout the Neotropics **Sematophyllum**
14. Leaves ligulate, obtuse-rounded; confined to Amazon Basin ..... **Potamium**
15. Exostome teeth paired; endostome represent only by cilia; Bolivia at 2200 m ... **Schroeterella**
15. Exostome teeth not paired; endostome with basal membrane absent to present and low to moderately high, segments mostly narrow, cilia absent 16
16. Leaves broadly ovate to obovate, bluntly and broadly acute to more commonly obtuse-rounded; exostome teeth abruptly slender distally from a broad base; confined to lowlands, primarily the Amazon Basin ..... **Colobodontium**
16. Leaves ovate- to oblong-lanceolate, apex acuminate to narrowly acute; exostome teeth gradually tapered or uniform in width; mostly montane 17
17. Endostomial segments divided and separate; Mexico ..... **Acritodon**
17. Endostomial segments not divided 18
18. Exostome teeth papillose; montane southeastern Brazil ..... **Paranapiacabaea**
18. Exostome teeth smooth or very faintly papillose 19
19. Exostome teeth moderately to distinctly elongate (250–400 µm long), obtuse; endostome basal membrane low, segments very slender, finely papillose ..... **Donnellia**
19. Exostome teeth short and truncate (ca. 110 µm long); endostome coarsely papillose, basal membrane moderately high, segments truncate, equal exostome length ..... **Pterogoniopsis**

Acritodon - A monotypic genus, with *A. nephophilus* H. Rob. confined to Oaxaca, Mexico.

HABITAT. Epiphytic on tree trunks and branches; montane cloud forests, 3000–3200 m.

DESCRIPTION. **Plants** forming dense mats, glossy golden or golden-brown. **Stems** creeping, irregularly pinnately branched, branches curved-ascending when dry, erect when wet; pseudoparaphyllia filamentous. **Leaves** oblong-ovate to oblong, 1.5–2 mm long, concave, apex rather abruptly long acuminate; margins plane or revolute at base or throughout, entire; costae short and forked; median cells linear, smooth; alar cells excavate, quadrate, thick-walled; branch leaves similar but homomallous, 1–1.8 mm long. **Autoicous**. **Perichaetial** leaves slenderly long acuminate. **Seta** 16–22 mm long, rather flexuose, smooth. **Capsule** erect, urn elliptical to oblong-cylindrical, 1.5–2 mm long; neck distinct; exothecial cells firm-walled, not collenchymatous; annulus ± persistent. **Operculum** conic mammillate. **Peristome** double, exostome teeth bluntly acute, papillose or weakly

cross-striate at base, bordered, trabeculate, with a fine zig-zag median line, not furrowed, yellowish-brown at base, hyaline above; endostome subequal to exostome teeth, hyaline, papillose, basal membrane low moderately high, segments divided to base of membrane; cilia 1, short to elongate or absent. **Calyptra** cucullate but apparently often remaining attached to seta. **Spores** finely papillose, stated to germinate in capsule.

DISCUSSION. *Acritodon* is characterized by the distally curved branches when dry, forked costa, excavate, thick-walled quadrate alar cells, papillose peristome, bluntly acute-rounded exostome apex, divided endostomial segments, and short to elongate single cilia. The systematic position of the genus warrants further study.

LITERATURE. Robinson, H. 1964. New taxa and new records of bryophytes from Mexico and Central America. The Bryologist 67: 446–458.

Acroporium (Fig. 203) - Four or five species in the Neotropics; about 70 species primarily of the Paleotropics.

HABITAT. Epiphytic on tree trunks and branches; wet lowland to upper montane forests; from near sea level to 3500 m.

DESCRIPTION. **Plants** usually forming tufts, glossy green, yellowish-green or golden. **Stems** initially short, creeping, then ascending to erect, usually cuspidate-foliate at apices; central strand absent. **Leaves** erect to erect-spreading, narrowly to broadly ovate to oblong-lanceolate, 1.5–3 mm long, concave, apex long acuminate, base usually somewhat auriculate; margins distally enrolled, entire to slightly serrulate; laminal cells smooth (rarely unipapillose), upper and median cells linear, porose or not; basal cells shorter, strongly porose; alar cells obliquely angled (45°), oblong-rectangular, inflated, thick-walled, usually golden-yellow or -brown. **Autoicous**. **Seta** elongate, slender and wiry, smooth or weakly papillose. **Capsule** inclined to erect, urn ovoid, mouth flared when deoperculate; exothecial cells collenchymatous; stomata at urn base, superficial. **Operculum** long-rostrate, oblique. **Peristome** double, exostome finely cross-striate, distally papillose, weakly to strongly furrowed or not; endostome basal membrane high, segments keeled and perforate. **Calyptra** cucullate, smooth and naked. **Spores** spherical, lightly to densely papillose.

DISCUSSION. *Acroporium* is distinguished by the tufted habit formed by ascending stems and branches, the deeply concave, distally tubulose leaves, strongly obliquely arranged, inflated, thick-walled, oblong alar cells, and exostome furrowed or not. *Acroporium estrellae* (Müll. Hal.) W. R. Buck & Schaf.-Verw., previously placed in *Schraderobryum* as *S. ulicinum* (Mitt.) M. Fleisch., is infrequent; the common neotropical species, *A. pungens* (Hedw.) Broth., ranges from lowland to upper montane.

LITERATURE. Buck, W. R. & A. Schäfer-Verwimp. 1991. A reassessment of *Schraderobryum* (Sematophyllaceae). Boletim do Museu Paraense “Emilio Goeldi”, Botânica 7: 645–654 [keys, illustrations, maps].

Allioniellopsis (Fig. 204) - A rare monotypic genus, with *A. cryphaeoides* (Broth.) Ochyra only known from the eastern Andean slopes of Ecuador and Peru.

HABITAT. On tree trunks and branches; lower montane forests, 1400 m.

DESCRIPTION. **Plants** rather small, forming dense mats. **Stems** to 4 cm long, few branched, creeping to subascending distally. **Leaves** crowded, homomallous, erect-spreading, narrowly oblong-lanceolate, 1.9–2.4 mm long, concave, weakly plicate, acuminate; margins strongly recurved below acumen, entire; costa absent; apical cells oblong-oval, weakly porose; median and lower cells oblong- to fusiform linear, strongly porose; alar region differentiated, 1 row of inflated cells, oblong to oval, thick-walled, porose; supra-alar cells subquadrate to short rectangular. **Autoicous**. **Perichaetia** rather numerously distributed along one side of stem; leaves lanceolate-subulate. **Seta** short, ca. 1 mm long, smooth. **Capsule** erect, urn ovoid, ca. 1 mm long; stomata at urn base; annulus absent. **Operculum** conic-short rostrate. **Peristome** single, exostome somewhat reduced, teeth set apart at base, margins with a faint, rather broad hyaline border, smooth below, tips papillose. **Calyptra** cucullate, smooth or somewhat roughened, naked. **Spores** spherical, finely papillose.

DISCUSSION. The numerous, homomallous, small sporophytes and the peristome represented only by somewhat reduced hyaline bordered exostome teeth is distinctive to this petite sematophyllacous genus. It is only known from three collections, in Ecuador from the original (type collection) made by Allioni in 1909, and a more recent collection in 1985; and a single collection from Peru. The generic name honors l’abbé Michel Allioni who made excellent collections along the slopes of the Ecuadoran Oriente. He died of yellow fever in 1911.

LITERATURE. Brotherus, V. F. 1911. *Allioniella*, eine neue Laubmoosgattung aus Ecuador. Ofversigt af Förhandlingar, Finska Vetenskaps-Societeten 53: 1–4 [illustrations]. - Ochyra, R. 1982. New names for genera of mosses. Journal of Bryology 12: 31–32.

Aptychella (Fig. 204) - Possibly a single species in the Neotropics, *Aptychella proligera* (Broth.) Herzog, in Mexico, Central America, Greater Antilles, tropical Andes, and southeastern Brazil. A genus of about seven species apparently with a pantropical distribution.

HABITAT. Epiphytic, on branches of shrubs and small trees, occasionally in somewhat exposed sites; lower to upper montane forests, extending into shrubby zacatonal, páramo and puna, 1600–3800.

DESCRIPTION. **Plants** small and rather delicate, forming tufts, occasionally mats that are occasionally pendent, pale to dark green, yellowish-green or golden-brown. **Stems** creeping, spreading or more commonly suberect; flagellate branches occasional, often pendent. **Leaves** distant, erect-spreading when dry, spreading when wet, somewhat plicate, linear- to oblong-lanceolate, 1.3–2 mm long, to 0.4 mm wide, apex short to long acuminate; margins recurved throughout or from base to midleaf and distally plane, smooth to distally serrulate, rarely serrate; costa none or more commonly single with some leaves doubly costate, 1/5–1/3(–1/2) lamina length; median cells long linear, firm-walled, weakly porose or not; basal cells porose; insertion cells often golden-brown; alar cells few, not inflated, subquadrate to quadrate, golden-brown or not. **Flagellate branch leaves** linear-lanceolate, 1.2–1.7 mm long, to 0.2 mm wide. **Gemmae** produced on terminal branches, in dense spherical or subspherical clusters, gemma long cylindrical, to 0.4 mm long or more. **Sporophytes** unknown.

DISCUSSION. The genus is characterized by the short tufts (commonly 2–3 cm) or occasional mats that often become long pendent, when erect stems terminating in a subspherical-cluster of gemmae, distant, oblong- to linear-lanceolate leaves, recurved margins, variable costa, mostly single, sometimes double or absent, and well differentiated, non-inflated, subquadrate alar cells. Reproduction is asexual, facilitated by both the production of gemmae and propagula in the form of fragile, flagellate branches. Given the amount of gametophytic variation in the Neotropics, a more critical study may be warranted than that presented by Tixier (1977).

LITERATURE. Tixier, P. 1977. Clastobryoidées et taxa apparentés. Revue Bryologique et Lichénologique 43: 397–464 [keys, illustrations].

Aptychopsis (Fig. 204) - A neotropical genus of four species, a single species in Colombia (*A. pycnodonta* Herzog), the remaining three species in southeastern Brazil (*A. pungifolia* (Hampe) Broth., *A. pyrrhophylla* (Müll. Hal.) Wijk & Margad., *A. subpungifolia* (Broth.) Broth.).

HABITAT. Montane forests, and the Colombian species at 3500 m, the Brazilian species probably at 1000–2000 m.

DESCRIPTION. **Plants** rather large, forming dense mats, golden brown or red. **Stems** creeping, distally stem and branches subascending, curved; in cross-section outer 2–4 rows of cells small, thick-walled, reddish-brown, inner cells larger, rather thick-walled, golden-yellow, central strand absent. **Leaves** subsecund, oblong, 1.7–2.4 mm long, 0.5–0.6 mm wide, concave, short acuminate or apiculate, flexed; margins reflexed below, distally involute, entire; costa none; laminal cells elongate and porose, median cells linear; alar cells strongly differentiated, 2–3 rows of oblong or oblong-oval cells, very thick-walled, dark rusty-red, somewhat inflated, supra-alar cells in 2–3 rows, quadrate- to short rectangular-rounded. **Autoicous**. **Perigonia** lateral; bud-like, leaves broadly ovate, to ca. 1 mm long. **Perichaetial** leaves elongate, 2.2 mm long. **Seta** elongate, 2–3.5 cm long, suberect, flexuose, smooth. **Capsule** suberect to subinclined, urn oblong-elliptical, 2 mm long, 0.6 mm wide; exothecial cells collenchymatous. **Operculum** conic-long rostrate. **Peristome** double, exostome narrowly lanceolate with apices obtuse, cross-striate; endostome basal membrane high, segments short, cilia absent. **Calyptra** not observed. **Spores** minutely punctate.

DISCUSSION. Distinguishing features of *Aptychopsis* include the oblong to oblong-lanceolate leaves that are abruptly short to rather long acuminate and often flexed in combination with the dark, reddish colored thick-walled oblong alar cells in 2–3 rows; and enlarged, colored and thickened supra-alar cells.

Colobodontium (= *Maguireella*) (Fig. 205) - A monotypic genus, with *C. vulpinum* (Mont.) S. P. Churchill & W. R. Buck confined to the neotropical lowlands, primarily the northern and western Amazon Basin.

HABITAT. On tree trunks and branches; wet lowland Amazonian forests, 100–500 m.

DESCRIPTION. **Plants** forming mats, irregularly pinnately branched; rhizoids numerous in clusters below. **Leaves** oval-ovate or semi-circular, to 1.4 mm long, to 0.8 mm wide, acute to broadly acuminate or obtuse-rounded; margins crenulate distally; costae short and double, indistinct; laminal cells smooth, apex cells rhombic or oval, median cells elongate-rhomboidal; alar cells oblong to rectangular-rounded, inflated, supra-alar cells quadrate. **Autoicous**. **Perichaetial** leaves lanceolate, acute. **Seta** usually elongate (2–9 mm long), smooth. **Capsule** erect or suberect, urn short-

cylindrical; exothecial cells rectangular, incrassate, not collenchymatous. **Operculum** conic-rostrate. **Peristome** double, exostome teeth slender distally from a broad base, separated at base, smooth to papillose, ± abruptly narrowed papillose above (often broken or appearing rudimentary); endostome basal membrane low or appearing absent, segments filiform or rudimentary, papillose. **Calyptra** cucullate, naked and smooth. **Spores** faintly to distinctly papillose.

DISCUSSION. The broadly oval to obovate leaves, erect to suberect capsules, broad based and abruptly narrowed and distally papillose exostome teeth, nearly absent basal membrane with rudimentary or filiform segments are useful in distinguishing the genus. *Colobodontium aciculare* was originally described as new by Herzog based on a collection from Caquetá, Río Orteguaza, Colombia. *Maguireella vulpina* (Mont.) W. R. Buck, *Meiothecium negrense* Spruce ex Mitt., *Potamium deceptivum* Mitt., and *P. leucodontaceum* (Müll. Hal.) Broth. are synonyms. Florschütz-de Waard (1992) presented a different interpretation and illegitimate typification of *Potamium* which recognized two species, that given above as *P. vulpinum* (Mont.) Mitt. and *P. deceptivum* Mitt.; both exhibit such overlap in the gametophytic and sporophytic features that supposedly separate the two that a single species concept is warranted.

LITERATURE. Churchill, S. P. & E. Linares C. 1995 (see general ref.). - Florschütz-de Waard, J. 1992. A revision of the genus *Potamium* (Musci: Sematophyllaceae). Tropical Bryology 5: 109–121 [keys, illustrations].

Donnellia (Fig. 205) - Three species in the Neotropics, *D. commutata* (Müll. Hal.) W. R. Buck locally common and the remaining two species, *D. lagenifera* (Mitt.) W. R. Buck and *D. lageniformis* (Müll. Hal.) W. R. Buck, confined to southeastern Brazil. A genus of six species of tropical America and Africa.

HABITAT. Epiphytic, on tree trunks and branches (including canopy), bamboo nodes, or on logs; lower montane forests, 200–2200 m.

DESCRIPTION. **Plants** small, forming tufts or mats, glossy green to yellowish. **Stems** creeping to subascending distally, radiculose below; central strand absent;, rhizoids clustered. **Leaves** often homomallous, erect-spreading, ovate- to oblong-lanceolate, 0.6–2 mm long, to 0.6 mm wide, concave, weakly biplicate at base, apex gradually acuminate, bluntly rounded; margins plane above, at base reflexed on one or both sides, entire; costa absent; median cells rhomboidal-rounded, smooth, thick-walled; basal cells weakly porose; insertion cells golden; alar cells subquadrate to short oblong, little inflated, in 1–2 rows, golden-yellow. **Autoicous**. **Perigonia** bud-like; leaves ovate, acute. **Perichaetial** leaves similar. **Seta** rather short to elongate, ca. 2.5–8 mm long, erect to somewhat flexuose, smooth. **Capsule** erect to suberect, urn obloid to ovoid-cylindrical, 1–2 mm long, constricted below mouth when dry and deoperculate; exothecial cells collenchymatous; stomata several at urn base, superficial. **Operculum** conic long rostrate. **Peristome** double, exostome teeth 16, hyaline, blunt, trabeculate, plate walls prominent on both surfaces; endostome basal membrane short, segments very slender, weakly keeled, lightly papillose, fragile and readily deciduous. **Calyptra** cucullate, naked and smooth. **Spores** spherical to ovoid, lightly papillose.

DISCUSSION. *Donnellia* and *Meiothecium* are rather similar. The former exhibits an exostome that is closely spaced, smooth and trabeculate with a fragile endostome, and the latter has a widely spaced, papillose exostome, and lacks an endostome. Buck (1982) demonstrated that *Donnellia* is an earlier name for *Meiotheciopsis*.

LITERATURE. Buck, W. R. 1982. On *Meiothecium* (Sematophyllaceae). Contributions to the University Michigan Herbarium 15: 137–140. - Buck, W. R. 1988. *Donnellia* (Sematophyllaceae) resurrected and refound in Florida after 110 years. The Bryologist 91: 134–135. - Buck, W. R. 1994. A synopsis of the American species of *Donnellia* (Sematophyllaceae). Hikobia 11: 377–385 [keys, maps].

Heterophyllium (Fig. 205) - A single species in the Neotropics, *H. affine* (Hook.) M. Fleisch. occurs from Mexico, Central America, Greater Antilles, northern Andes (also southeastern United States, Central Europe to Central Asia). About 15 species distributed in the temperate and montane tropical regions.

HABITAT. Epiphytic, usually at base of tree or on branches, also frequent on logs, in full or partial shade; montane forests, occasionally associated with somewhat drier sites, e.g., *Quercus* forests in Colombia, 500–3000 m.

DESCRIPTION. **Plants** rather large, forming dense mats, glossy green to yellowish- or brownish-green. **Stems** creeping, irregularly pinnately branched, spreading; in cross-section outer 2–3 rows of cells small, thick-walled, inner cells larger, thick-walled, central strand absent; pseudoparaphyllia foliose, linear-lanceolate; rhizoids dark brown, appearing finely papillose. **Stem leaves** spreading, decurved and secund, somewhat broadly oblong- to ovate-lanceolate, 2–3 mm long, 0.5–1 mm wide,

concave, apex abruptly long acuminate, base somewhat rounded; margins plane to recurved below, entire below, distal 1/3–1/2 sharply serrate; costa none or short and double; laminal cells porose, median cells linear, somewhat flexuose; insertion cells golden-yellow, strongly porose; alar cells quadrate-rounded to short oblong-rectangular, thick-walled, golden-yellow or hyaline, porose. **Branch leaves** differentiated, smaller, narrowly lanceolate, to 2 mm long, ca. 0.5 mm wide, usually falcate-secund. **Autoicous**. **Perichaetial** leaves lanceolate, to 2.4 mm long, serrulate distally. **Seta** elongate, 25–40 mm long, smooth. **Capsule** inclined to suberect, urn cylindrical, 1.2–3 mm long, curved; exothecial cells irregularly oblong or subquadrate-rounded, not collenchymatous; stomata at urn base, superficial. **Operculum** conic-apiculate to short rostrate. **Peristome** double, exostome teeth finely cross-striate, distally lightly papillose, bordered, with zig-zag median line, trabeculate on back; endostome basal membrane high, segments keeled and perforate, lightly papillose, cilia 2–3. **Calyptra** cucullate. **Spores** spherical, faintly papillose.

DISCUSSION. The genus is distinguished by the differentiated stem and branch leaves, coarsely serrated distal leaf margins, subquadrate to short oblong alar cells, short rostrate to conic-apiculate operculum, and well developed peristome.

Horridohypnum (Fig. 206) - A monotypic genus, with *H. mexicanum* (Thér.) W. R. Buck only known from Mexico and Guatemala.

HABITAT. On soil, rock, and base of trees; montane forests, 2100–3500 m.

DESCRIPTION. **Plants** rather small, forming mats. **Stems** creeping, rather rigid, irregularly pinnately branched, branches often curled; in cross-section outer 3–5 rows of cells small, thick-walled, inner cells large, thin-walled, central strand absent; pseudoparaphyllia foliose. **Leaves** crowded, ± homomallous, ovate-short lanceolate to oblong-elliptical, 0.7–0.9 mm long, concave, apex acute, rather bluntly so at times, base short decurrent; margins plane or weakly recurved at base, distally serrulate; costae short to rather elongate and forked, ca. 1/3–1/2 lamina length, diverging, united at base; laminal cells rather thick-walled, apical cells rhombic to oblong-fusiform or -linear, somewhat flexuose, usually papillose on back, papillae projecting at distal cell angle; lower and basal cells short to long oblong-rectangular; alar region weakly differentiated, cells subquadrate to short rectangular. **Dioicous**. **Perichaetial** leaves clasping at base, narrowly long acuminate. **Seta** elongate, to 2 cm long, slender, smooth. **Capsule** horizontal, urn cylindrical to obloid, to 3 mm long; exothecial cells collenchymatous; annulus in 1–2 rows. **Operculum** conic. **Peristome** double, exostome teeth finely cross-striate below, tips papillose or smooth; endostome basal membrane relatively high, segments broad, keeled, perforate, cilia 1–2. **Calyptra** unknown. **Spores** spherical, finely papillose.

DISCUSSION. The genus is distinguished by the rather rigid habit with branches curled or curved, foliose pseudoparaphyllia, homomallous short ovate-lanceolate leaves, distinct and rather strong forked costa, projecting papillae at distal angle of laminal cells, and little differentiated alar cells. *Horridohypnum* does not fit well with the Sematophyllaceae and requires further investigation as to its systematic position. Previously the genus was placed in the Hypnaceae (*Taxiphyllum mexicanum* (Thér.) H. Rob.) and Pterigynandriaceae (as *Pterigynandrum filiforme* var. *mexicanum* Thér.).

LITERATURE. Buck, W. R. 1980. Animadversions on *Pterigynandrum* with special commentary on *Forsstroemia* and *Leptopterigynandrum*. The Bryologist 83: 451–465.

Meiothecium (Fig. 206) - Two species are known in the Neotropics, *M. boryanum* (Müll. Hal.) Mitt. and *M. revolubile* Mitt.; about 30 species with a pantropical distribution

HABITAT. On tree trunks; lowland wet to semi-dry submontane forest, 280–1370 m.

DESCRIPTION. **Plants** rather small, forming thin mats, green to yellowish-green or brown. **Stems** creeping, subpinnately branched, distal portion of branches subascending and curved, radiculose; central strand absent. **Leaves** erect to homomallous, oblong-elliptic, 0.8–1.3 mm long, to 0.5 mm wide, plicate and concave, apex abruptly short acute to acute-rounded or gradually acuminate; margins reflexed throughout except at apex or plane, entire or weakly serrulate at apex; costa none; laminal cells thick-walled, apical cells short; upper median cells oval-oblong; mid and lower cells oblong-linear; basal cells shorter, porose; insertion cells golden; alar cells inflated, oblong-oval, thick-walled, golden. **Autoicous**. **Perichaetial** leaves differentiated, oblong-lanceolate, to 1.5 mm long, distal margins sharply serrate. **Seta** somewhat elongate and slightly curved, 3.5–5 mm long, smooth. **Capsule** suberect, urn ovoid-cylindrical, ca. 1 mm long; exothecial cells short rectangular, collenchymatous; stomata few at urn base, superficial; annulus absent. **Operculum** conic short to long rostrate. **Peristome** single, exostome set below mouth, teeth widely spaced, narrow, finely papillose-spiculose to smooth. **Calyptra** cucullate, smooth to slightly roughened at apex. **Spores** large, coarsely papillose-spiculose.

DISCUSSION. The genus is characterized by smooth to papillose, narrow, widely spaced exostome teeth with endostome absent.

LITERATURE: Buck, W. R. 1982 (see ref. under *Donnellia*.).

Paranapiacabaea (Fig. 206) - A monotypic genus, with *P. paulista* W. R. Buck & Vital only known from southeastern Brazil (São Paulo).

HABITAT. Epiphytic, on tree branches and particularly on bamboo (nodes?), associated with *Acroporium*, *Donnellia* and *Sematophyllum;* lower montane forests, 500–1500 m.

DESCRIPTION. **Plants** medium sized, forming mats, bright-green to golden. **Stems** creeping, irregularly branched, branches often ascending and curved; in cross-section outer 2–4 rows of cells small, thick-walled, inner cells larger, central strand absent; pseudoparaphyllia broadly foliose. **Leaves** rather crowded, somewhat homomallous, erect-spreading, broadly oblong-lanceolate to oblong-ovate, 1.1–1.4 mm long, abruptly short acuminate, concave; margins recurved throughout, entire to weakly serrulate at apex; costae short and forked or absent; laminal cells smooth, firm-walled, faintly porose, apical cells short oblong-rhomboidal; median cells oblong-fusiform; alar cells in a single row of inflated oblong yellowish cells supra-alar cells in 2–4 rows, subquadrate. **Perichaetial** leaves oblong-lanceolate. **Seta** elongate, 6–14 mm long, smooth, twisted. **Capsule** erect, urn somewhat ovoid-long cylindrical, constricted below flared mouth; annulus undifferentiated. **Operculum** conic-long rostrate. **Peristome** double, exostome teeth incurved when dry, erect when wet, separated at base, obtuse at apex, with a zig-zag median line, finely papillose; endostome ca. 1/3 longer than exostome, papillose, basal membrane medium height, segments narrow, keeled and narrowly perforate, cilia absent. **Calyptra** cucullate, smooth and naked. **Spores** spherical, finely papillose.

DISCUSSION. The genus is distinguished by the absent or short and forked costa, single row of inflated, oblong alar cells, few (2–4) rows of quadrate supra-alar cells, ovoid-cylindrical capsule that is strongly constricted below the mouth, and papillose, exostome teeth separated at the base with obtuse apices. Buck and Vital (1992) provide a discussion and summary of the character differences between *Paranapiacabaea* and similar genera with reduced peristome, including: *Donnellia*, *Pterogoniopsis*, and *Maguireella* (= *Colobodontium*).

LITERATURE. Buck, W. R. & D. M. Vital. 1992. *Paranapiacabaea paulista*, a new genus and species of Sematophyllaceae from southeastern Brazil. Brittonia 44: 339–343 [table comparing similar genera; illustrations, map].

Potamium (Fig. 207) - As defined here a monotypic genus with *P. lonchophyllum* (Mont.) Mitt. distributed in the northern tributaries of the Amazon Basin.

HABITAT. Submerged on rock in streams; wet to semi-dry lowland forests, 120 m.

DESCRIPTION. **Plants** dark green to blackish-green, medium sized, forming loose mats. **Stems** and branches long and slender, radiculose at base of attachment; central strand absent. **Leaves** rather flaccid, distant, erect-spreading, narrowly oblong to ligulate, 1.6–2 mm long, 0.3 mm wide, 4–5:1, bluntly acute; margins plane or folded on one side, reflexed at base, denticulate from about mid leaf, distally serrulate; costa none; laminal cells smooth, median cells linear, apical cells shorter, rhomboidal to fusiform; basal cells oblong-rectangular, weakly porose, yellowish to golden; alar cells inflated, oblong or rectangular-rounded, 2–4 rows. **Seta** elongate. **Capsule** pendent, urn ovoid. **Peristome** double, exostome teeth distinctly furrowed.

DISCUSSION. The genus is characterized by the habitat and the spreading, elongate, dark green plants, ligulate leaves, distally serrate margins, smooth laminal cells, and furrowed exostome teeth. Transferred by Florschütz-de Waard (1990) to *Sematophyllum*, as *S. lonchophyllum* (Mont.) J. Florsch. (see ref. under *Colobodontium*). Other members of this genus, as treated by Brotherus (1923–1924, see general ref.), have either been transferred to *Sematophyllum* or transferred or synonymized under *Colobodontium*.

Pterogonidium (Fig. 207) - A neotropical genus of one or two species. The common widespread species is *P. pulchellum* (Hook.) Müll. Hal. ex Broth.

HABITAT. Epiphytic, on tree trunks and branches, also bamboo, occasionally on logs; in wet or moist submontane to lower montane forests, 150–1940 m.

DESCRIPTION. **Plants** small, forming soft somewhat delicate mats, glossy light green to yellowish-green. **Stems** and branches spreading to subascending; pseudoparaphyllia filamentous; rhizoids clustered beneath. **Leaves** erect-spreading to spreading, lanceolate to ovate-short lanceolate, 0.5–0.7 mm long, to 0.3 mm wide, slightly concave below, apex acuminate; margins plane, entire or distal 1/3–2/3 serrulate; costa none or short and forked; median cells fusiform, smooth; alar cells differentiated, 3–4 rows of quadrate to short rectangular cells (oblate or not), extending up to 6–8 cells along margin. **Autoicous**. **Perigonia** bud-like. **Perichaetial** leaves similar, outer series smaller. **Seta** elongate, ca. 3 mm long, smooth, reddish-orange to yellow. **Capsule** exserted, erect, urn short-cylindrical, slightly asymmetric, 0.7–0.8 mm long, smooth; exothecial cells irregularly short to long

rectangular, thin-walled; stomata few at urn base, superficial. **Operculum** short-rostrate, 0.4 mm long. **Peristome** single, exostome teeth brown, reduced, tips bluntly rounded, papillose. **Calyptra** cucullate, 0.7–0.8 mm long, smooth and naked. **Spores** spherical, lightly papillose.

DISCUSSION. The gametophyte of *Pterogonidium* is similar to that of various members of the Hypnaceae, and may be confused with *Isopterygium*, but the triangular group of alar cells, relatively short seta, and peristome consisting of a brown, papillose exostome assist in recognition. First collected by Humboldt and Bonpland in Colombia, this species is probably more common than the few existing collections would indicate. It is readily overlooked due to its small size.

Pterogoniopsis - A monotypic neotropical genus, with *P. cylindrica* Müll. Hal. known from northern Argentina, Paraguay, and southeastern Brazil.

HABITAT. Epiphytic, on trunk and branches of trees; in semi-dry to moist lowland forests, 15–200 m.

DESCRIPTION. **Plants** small, forming low mats, light green to yellowish-green. **Stems** creeping, rather inconspicuous, somewhat irregularly 1-pinnately branched, branches ascending and curled, ca. 3–4 mm long; in cross-section lacking a central strand; rhizoids clustered beneath. **Leaves** erect to erect-spreading, those of branches homomallous, lanceolate to ovate-short lanceolate, 0.8–1 mm long, slightly concave below, somewhat biplicate, apex gradually acuminate; margins plane, entire; costa none; median cells rhomboidal to rhomboidal-fusiform, smooth; alar cells differentiated, 1 row of short oblong or rectangular-rounded cells, supra-alar cells rather numerous, quadrate, extending along the margin. **Autoicous**. **Perigonia** bud-like. **Perichaetial** leaves similar, outer series smaller. **Seta** elongate, 3–4 mm long, smooth, reddish-orange. **Capsule** exserted, suberect, urn ovoid-cylindrical, slightly asymmetric and curved, 1–1.4 mm long, smooth; exothecial cells collenchymatous, thin-walled; stomata several at urn base, superficial. **Operculum** moderately rostrate, 0.4 mm long, slightly oblique. **Peristome** double, exostome teeth reduced and truncate (to ca. 110 µm long), tips bluntly rounded, smooth or nearly so, broadly bordered, trabeculate, hyaline, not furrowed; endostome hyaline and coarsely papillose, basal membrane moderately high, segments reduced, nearly equal to exostome teeth or slightly longer, tips blunt. **Calyptra** cucullate, smooth and naked. **Spores** spherical, lightly papillose.

DISCUSSION. The genus is characterized by rather numerous, short, ascending and curled branches, small, narrowly ovate-short lanceolate, ecostate leaves (to ca. 1 mm long), gradually acuminate apex, entire margins, upper cells smooth rhomboidal, alar cells short oblong-rectangular below and quadrate above, and a peristome of smooth or nearly so, short and truncate exostome teeth, coarsely papillose endostome equal to exostome with short, truncate segments and a moderately high basal membrane.

Schroeterella (Fig. 207) - A monotypic genus, with *S. zygodonta* Herzog known from Bolivia.

HABITAT. On lianas, probably to be expected on tree branches; montane forest, at 2200 m.

DESCRIPTION. **Plants** small, forming lax tufts, yellowish-green. **Stems** and branches ascending from short creeping stems, 5–8 mm long; rhizoids numerous beneath creeping stems. **Leaves** rather rigid, spirally arranged, lanceolate to oblong-lanceolate, gradually acuminate; margins reflexed, entire; costa absent; laminal cells linear-fusiform, rather thick-walled, apical cells shorter; alar cells oblong-oval, hyaline to yellowish, rather thick-walled, supra-alar cells few, in ca. 2 rows, subquadrate . **Autoicous**. **Seta** rather short, 2–3 mm long, smooth. **Capsule** erect, urn narrowly pyriform, to 0.6 mm long; exothecial cells irregularly collenchymatous. **Operculum** rostrate, oblique. **Peristome** double, exostome inflexed when dry, teeth in 8 pairs, broadly lanceolate with tips acute-rounded, finely papillose; endostome consisting of linear or narrowly lanceolate cilia, shorter than exostome teeth, ca. 2/3 the length. **Calyptra** cucullate, naked and smooth. **Spores** not observed.

DISCUSSION. The sporophyte features that characterize the genus and appear to be unique to the family are: short seta (2–3 mm long), exostomial teeth 8-paired with acute rounded tips, and endostome represented solely by narrow cilia about 2/3 the length of the exostome. The illustration provided by Herzog (1916; plate VII) suggests that the alar cells are obliquely arranged. *Schroeterella* is only known from the original collection made by Herzog from Río Tocorani valley, Bolivia. The generic name honors, according to Herzog, “Dr. C. Schröter, Professor de Botanik an der Eidgenöss. Technischen Hochschule in Zürich.”

LITERATURE. Herzog, T. 1916 (see general ref.).

Sematophyllum (Fig. 208) - About 125 species recorded for the Neotropics, probably closer to 40–50; primarily a pantropical genus (including *Rhaphidostichum*) reported to contain 150 or more species.

HABITAT. Epiphytic, on branches, trunks, bases of trees and shrubs, also on rocks and logs, occasionally on soil; wet to semi-dry lowland to upper montane forests, infrequent in páramo and puna, from near sea level to 4000 m.

DESCRIPTION. **Plants** small to large or robust, forming mats, glossy green to yellowish-green or golden-brown. **Stems** creeping to ascending and often secund distally, mostly irregularly pinnately branched. **Leaves** broadly to narrowly ovate, lanceolate, ovate- or oblong-lanceolate, erect or falcate, apex acute to broadly or narrowly acuminate, often abruptly so; margins plane to recurved, entire or serrulate to serrate distally; costa none; median cells rhomboidal, fusiform or linear, smooth, thin- to thick-walled, weakly porose or not; alar region well differentiated, cells inflated, oval to oblong-oval, in few to several rows, usually 1–2(3) cells high, often golden-brown, supra-alar cells often differentiated, mostly subquadrate- to rectangular-rounded; insertion cells usually golden-brown, often porose. **Autoicous** or dioicous. **Perigonia** lateral, bud-like. **Perichaetial** leaves usually differentiated. **Seta** elongate, smooth. **Capsule** erect to more often suberect or inclined, urn ovoid to ovoid-short cylindrical. **Operculum** conic-long rostrate, oblique. **Peristome** double, exostome teeth striate below, distally papillose, with median zig-zag line or furrow, bordered, trabeculate on back; endostome basal membrane high, segments hyaline, keeled, perforate or not, lightly papillose, cilia 1–2. **Calyptra** cucullate, smooth and naked. **Spores** spherical, smooth to lightly papillose.

DISCUSSION. The genus is characterized by distal portion of stems and branches often subascending to erect and curled, homomallous or falcate-secund, entire to occasionally weakly serrulate margins, smooth laminal cells, inflated, usually thick-walled, oval to oblong alar cells, often differentiated, subquadrate to rectangular supra-alar cells, finely cross-striate below and distally papillose exostomial teeth with median zig-zag line, and well developed endostome.

A species-rich genus in the Neotropics, Mitten (1869) recognized no fewer than 52 species (excluding *Acroporium* and *Trichosteleum*). The history of *Sematophyllum* is nearly as complex as is our present understanding of its constituent species. *Rhaphidorrhynchium* M. Fleisch. is sometimes segregated from *Sematophyllum* based on the falcate-secund leaves, a feature that is not always obvious is several neotropical species. *Trichosteleum*, as generally recognized, is usually defined by the unipapillose laminal cells that supposedly separate this genus from *Sematophyllum* (laminal cells smooth); however, there are a few species in which the papillae are very difficult to detect. *Rhaphidostegium* (Bruch, Schimp. & W. Gümbel) De Not., nom. illeg. incl. gen. prior, is a name previously used for some of the neotropical *Sematophyllum* species. *Rhaphidostichum* M. Fleisch., recognized by some authors (cf. Buck, 1998; see general ref.), is also included here; it is distinguished by the upper leaf margins serrate, large alar cells, and exostome teeth sometimes furrowed. A careful study of *Sematophyllum* is needed, with particular attention given to the gametophytic variation within and between species. Not unexpectedly, the aquatic or semi-aquatic species appear to pose the greatest problems in variation. Dixon (1920), possibly in a prolonged moment of despair, synonymized many names of what appear to be distinct species under the name *S. caespitosum* (= *S. subpinnatum* (Brid.) E. Britton), including a number of neotropical taxa.

LITERATURE. Buck, W. R. 1983. Nomenclatural and taxonomic notes on West Indian Sematophyllaceae. Brittonia 35: 309–311. - Buck, W. R. 1989. Miscellaneous notes on Antillean mosses, 2. *Rhapidostichum* (Sematophyllaceae) in the New World. Moscosoa 5: 189–193. - Dixon, H. N. 1920. *Rhaphidostegium caespitosum* (Sw.) and its affinities. Journal of Botany 58: 81–89.

Taxithelium (Fig. 208) - About six species in the Neotropics; a pantropical genus reported to contain over 100 species (many are synonyms), confined primarily in tropical Asia.

HABITAT. On logs and tree trunks; frequent in humid lowland and submontane forests, from near sea level to 1200 m.

DESCRIPTION. **Plants** rather small, forming thin to rather dense mats, pale olive green. **Stems** and branches spreading, regular to irregular pinnately branched. **Leaves** weakly to strongly complanate, lateral leaves somewhat larger and slightly asymmetric, broadly oblong-ovate to ovate-lanceolate, 0.7–1.2 mm long, to 0.6 mm wide, concave, apex broadly to narrowly acute; margins plane, serrulate throughout by projecting papillae; costa none; median cells linear, pluripapillose, papillae ca. 3–7 in a row over cell lumen; alar region usually differentiated, cells quadrate to short rectangular or oval. **Autoicous**. **Perichaetial** leaves sheathing seta, lanceolate, ca. 2 mm long, acuminate, cells papillose. **Seta** 8–22 mm long, slender, smooth. **Capsule** inclined to suberect, urn broadly short-ovoid to ovoid-cylindrical, ca. 0.5–1.2 mm long, asymmetric, contracted below mouth when deoperculate; exothecial cells thick-walled, weakly collenchymatous or not; stomata at urn base, superficial. **Operculum** conic-short rostrate. **Peristome** double, exostome teeth cross-striate below, papillose distally, with a median zig-zag line, bordered, trabeculate on back; endostome basal membrane high, segments keeled, papillose, cilia 1. **Calyptra** cucullate, smooth and naked. **Spores** spherical, appearing smooth to lightly papillose.

DISCUSSION. The genus is characterized principally by the pluripapillose laminal cells with the papillae arranged in a single row; the alar cells are not as strongly differentiated as in, for example, *Sematophyllum*. *Taxithelium planum* (Brid.) Mitt. is the most common and widespread species in the Neotropics.

LITERATURE. Buck, W. R. 1985. A review of *Taxithelium* (Sematophyllaceae) in Brazil. Acta Amazonica 15 (Suplemento): 43–53. - Damanhuri, A. & R. E. Longton. 1996. Towards a revision of the moss genus *Taxithelium*. Anales del Instituto de Biologia, Universidad Nacional Autónoma de México, Serie Botánica 67: 35–58.

Timotimius - A monotypic genus, with *T. titanotus* W. R. Buck known only from the province of Pichincha, Ecuador.

HABITAT. Montane cloud forest; substrate unknown, at 2350 m elevation.

DESCRIPTION. **Plants** medium sized, forming tufts, golden. **Stems** ascending, to 2 cm long, irregularly branched; central strand absent. **Leaves** of stem and branch undifferentiated, erect-spreading, oblong-lanceolate, 2.5–3 mm long, gradually long acuminate, somewhat flexuose or not, deeply concave; margins entire, narrowly recurved throughout; ecostate; laminal cells smooth, median cells subflexuose, thick-walled, weakly porose; alar cells enlarged but not conspicuously inflated, 3–4(5) celled, thick-walled, yellow, mostly with a single supra-alar cell. **Propagula** absent. **Autoicous**. **Perichaetial** leaves inconspicous, similar to stem leaves. **Seta** to 2 cm long, slender, flexuose. **Capsule** erect to suberect, urn short-cylindrical, 0.8–1 mm long; exothecial cells subquadrate to short-rectangular, collenchymatous; annulus undifferentiated. **Opercula** long-rostrate, oblique (as long or longer than urn). **Peristome** double, white and incurved when dry, hyaline and erect when wet, exostome teeth unpaired, to 440 µm long, outer surface with a zig-zag median line, papillose, horizontal plates thickened and projecting, inner surface weakly trabeculate, appearing unornamented; endostome finely papillose throughout, basal membrane high, segments 16, slightly shorter than exostome teeth, keeled, not or weakly perforate, cilia absent or rudimentary. **Calyptra** cucullate, naked and smooth. **Spores** subspherical, papillose

DISCUSSION. The outer exostome surface with projecting thick-walled plates is the unique feature of this otherwise typically *Sematophyllum*.

LITERATURE. Buck, W. R. 1999. *Timotimius*, a new genus of Sematophyllaceae (Bryopsida) from Ecuador. Bryobrothera 5: 77–79.

Trichosteleum (Fig. 208) - About 23 species in the Neotropics, possibly only 10–15 that are valid; a pantropical genus of 130 species with the greatest diversity in tropical Asia.

HABITAT. On logs, humus and soil; humid lowland to lower montane forests, from near sea level to 1800 m.

DESCRIPTION. **Plants** forming loose to dense mats, light green to yellowish-green or golden. **Stems** and branches spreading to short ascending, radiculose; central strand absent. **Leaves** erect to erect-spreading, often homomallous, occasionally falcate, oblong to oblong-lanceolate, 0.8–1.2 mm long, apex acute to short or long acuminate, often abruptly so; margins usually reflexed or at base recurved, dentate to more commonly serrate or serrulate; costa none; median cells linear and often vermicular or fusiform to rhomboidal, strongly to weakly unipapillose, papillae over cell lumen; alar region differentiated, cells inflated, oval to oblong, often golden red. **Propagula** absent. **Autoicous**. **Perichaetial** leaves differentiated. **Seta** elongate, 6–10 mm long or more, slender and wiry, often twisted, smooth or weakly papillose distally. **Capsule** inclined to horizontal, urn obovoid, 0.5–1 mm long, constricted below urn mouth when dry; exothecial cells collenchymatous. **Operculum** conic-rostrate. **Peristome** double, exostome teeth cross-striate below, distally papillose, furrowed; endostome segments keeled, lightly papillose. **Calyptra** cucullate, naked and smooth. **Spores** spherical, lightly papillose.

DISCUSSION. Except for the unipapillose laminal cells, *Trichosteleum* is very similar to *Sematophyllum*, although in this genus there is considerable more variation. The papillae are occasionally so faint in some *Trichosteleum* species that such species are readily misidentified as *Sematophyllum*. *Acroporium* occasionally exhibits unipapillose laminal cells, but the leaves are deeply concave and alar cells are distinctly obliquely arranged. *Trichosteleum* is much in need of definition and revision; see comments under *Sematophyllum*.

LITERATURE. Buck, W. R. 1983. A revision of the Antillean species of *Trichosteleum* (Musci: Sematophyllaceae). Moscosoa 2: 54–60 [keys to the six Antillean species].

Wijkia (Fig. 209) - Four species in the Neotropics; a pantropical genus of some 50 species with the greatest diversity in the Paleotropics.

HABITAT. On logs and base of trees, occasionally on rocks; montane forests, 200–2900 m.

DESCRIPTION. **Plants** medium sized, forming rather coarse mats, dark green to yellowish-green, or golden. **Stems** creeping or stems and branches ascending, sub- to bipinnately branched, radiculose below, flagellate branches present or absent; central strand absent; pseudoparaphyllia foliose. **Leaves** differentiated between stem and branches, **stem leaves** spreading to erect, oblong to ovate short-lanceolate, to 1.6 mm long, concave, apex short to abruptly long acuminate, base subauriculate or not; margins plane to slightly recurved below, entire to weakly serrulate distally; costa none or short and forked; median laminal cells linear and often vermicular, smooth or unipapillose, papillae over lumen, thick-walled; basal cells weakly porose or not, reddish-orange; alar region differentiated, cells inflated, 2-several rows, oblong-rectangular; **branch leaves** erect-spreading, distinctly smaller, lanceolate, oblong-lanceolate to ovate; margins entire to distinctly serrate; flagellate branches, when present, with reduced, appressed scale-like leaves, oblong-acute, rather coarsely serrate. **Sporophytes** not observed in the Neotropics.

DISCUSSION. *Wijkia*, similar to *Heterophyllium* in exhibiting differentiated stem and branch leaves, is distinguished from the latter by the smaller stem leaves (to 1.2 mm long), absence of porose cells or with faintly porose cells, and the oblong-oval alar cells. The genus appears to be rather uncommon, which may only reflect the lack of intensive collecting efforts. The name *Acanthocladium* was previously used for our species.

LITERATURE. Buck, W. R 1986. *Wijkia* (Sematophyllaceae) in the New World. Hikobia 9: 297–303 [keys, illustrations].

SORAPILLACEAE

A monotypic family placed in the Leucodontales.

Sorapilla (Fig. 209) - A single species in the Neotropics, *S. sprucei* Mitt. is known only from Ecuador. The second of the two species in this genus is known from Australasia.

HABITAT. Epiphytic, on base of trees; lower montane forests, possibly at ca. 1850 m.

DESCRIPTION. **Plants** medium sized, forming mats, dark reddish-brown. **Stems** appearing prostrate, to 4.5 cm long, rather stiff, irregularly pinnate branched; pseudoparaphyllia foliose; rhizoids cluster beneath stems. **Leaves** complanate, in 2 ranks, ovate-oblong, to ca. 1.8 mm long (branch leaves similar but smaller), differentiated between a vaginant lamina, ca. 4/5–5/6 total lamina length, and dorsal and ventral laminae (as in *Fissidens*), apex acute; margins plane, dorsal and ventral laminae appearing crenulate by projecting papillae, vaginant laminae limbate and entire; costa single, subpercurrent, appearing to end somewhat diffusely; laminal cells above base isodiametric and stellate, pluripapillose, papillae over cell lumen, simple or weakly branched; basal cells elongate, appearing sinuose; marginal cells of vaginant lamina forming a border of 3–5 rows of enlarged, subrectanulgar, hyaline, smooth, thin-walled cells, ending near base and apex of vaginant lamina. **Autoicous**. **Perichaetia** lateral, along both stems and branches, leaves elongate, lanceolate, to 2.4 mm long. **Seta** short, ca. 1.4 mm long, smooth. **Capsule** immersed, ovoid-short cylindrical or short cylindrical, ca. 1.4 mm long. **Operculum** rather long rostrate. **Peristome** double and reduced, exostome teeth 16, ca. 1/2 length of endostome, smooth; endostome basal membrane absent (or low?), segments narrowly linear, smooth, cilia absent . **Calyptra** mitrate, sparsely hairy. **Spores** not observed.

DISCUSSION. The leaves of *Sorapilla* and *Fissidens* represent a truly remarkable example of parallel evolution. The prostrate habit, hyaline bordered leaves, immersed capsules and reduced double peristome readily differentiate *Sorapilla* from *Fissidens*. *Sorapilla sprucei* is apparently quite rare, only known from the original collection made by Richard Spruce from Abitagua, Ecuador, probably in 1857. Early relationships of this genus were thought to be with the Fissidentaceae, and later the Rhizogoniaceae; however, features of both the gametophyte, particularly the pseudoparaphyllia, and sporophyte with the double, reduced peristome, support a placement near the Neckeraceae and related taxa (cf. Allen, 1981).

LITERATURE. Allen, B. H. 1981. A reevaluation of the Sorapillaceae. The Bryologist 84: 335–338.

SPHAGNACEAE

A monotypic family, assigned to a separate order, Sphagnales, and class, Sphagnopsida.

Sphagnum (Fig. 210) - About 160 species in nine sections recorded for the Neotropics; a genus approaching 300 species, widespread but primarily from moist temperate, montane and boreal regions.

HABITAT. Typically found in wet sites such as bogs, marshes, swamps and seeps, rarely aquatic or epiphytic; particularly common in open montane to zacatonal, páramo, and puna. A few species are found infrequently in swampy sites in lowland savannas and wet tropical forests, from about 100 to more commonly 2000–4400 m.

DESCRIPTION. **Plants** medium sized to rather robust, forming dense cushions or tufts, white or pale green to yellow or brown, occasionally tinged pink or red. **Stems** erect to suberect, solitary or sparsely forked, terminating in a compact tuft or capitulum of very short branches, branches fasciculate; stems in cross-section with 2 or more layers of large, thin-walled, hyaline cortical cells, spirally fibrillose and porose on outer walls or not, pores when present retort or not, wood cylinder cells small and thick-walled, often pigmented. **Stem leaves** appressed, broadly oblong- or ovate-acute, -rounded or -truncate; costa none. **Branches** single or more commonly in fascicles of 2–6, spirally arranged, distant or somewhat crowded along stem. **Branch leaves** frequently differentiated from stem leaves in shape, commonly larger, rarely smaller, broadly elliptic to ovate or ovate-lanceolate, concave or tubulose below, apex narrowly to broadly acuminate, acute to obtuse; margins often channeled or inrolled, entire or serrulate, erose or fimbriate; costa none; laminal cells differentiated and alternating between large leucocysts (hyaline cells) and linear chlorocysts (green cells), the former enclosed in a network of the latter; leucocysts oblong to rhomboidal, vermiculate with pores present on outer or inner or both leaf surfaces, fibrils present or absent, in cross-section plane or convex; chlorocysts exposed equally on both surfaces, or exclusively or partially on either the outer or inner leaf surface, or completely included, in cross-sectional shape typically elliptical, triangular or trapezoid. **Dioicous** or monoicous. **Perichaetial** branches short, near apex, leaves enlarged. **Pseudopodium** (seta-like) elongating at maturity. **Capsule** immersed in early development, at maturity mostly exserted, urn globose, when deoperculate ovoid-cylindrical; annulus and peristome absent. **Operculum** flat to slightly convex. **Calyptra** a fragile hyaline membrane. **Spores** tetrahedral.

DISCUSSION. The genus, possibly the most diverse in the Neotropics, is characterized by pale green or whitish gametophytes that are occasionally reddish or pink tinged, a terminal capitulum, fasciculate branches, often differentiated stem and branch leaves, ecostate, unistratose lamina, two alternating cell types, hyaline cells and green cells, and globose eperistomate capsule on a short to elongate pseudopodium.

Sphagnum is one of the most important genera in terms of the role it plays in tropical highland ecosystems, both in terms of maintaining the landscape and water conservation due to its holding capacity. Dried plants of *Sphagnum* are estimated to absorb up to 20 times their weight in water. The genus is also well know to influence the surrounding environment, inhibiting or enhancing colonization by other plants; e.g., decomposers are excluded due to the low oxygen availability and high levels of acidity, thus leading to an increase of organic matter. Increased acidity is accomplished by *Sphagnum* through its ability to selectively absorb basic ions and at the same time releasing hydrogen ions. Extensive or local bogs are frequent in the highlands, e.g., the páramos of the northern Andes. Howard Crum's *A Focus on Peatlands and Peat Mosses* (1988, University of Michigan Press) is an excellent introduction to the morphology, biology, and habitats of *Sphagnum* and should be useful in developing research programs to study *Sphagnum* communities in the Neotropics, particularly high elevational bogs.

The Neotropics likely represents one of the richest regions of the world, if not the richest, with regard to *Sphagnum* diversity. Much of the diversity is contributed from the regions of southeastern Brazil and the tropical Andes. Four of the nine sections of neotropical *Sphagnum* account for 97% of the total number of species: *Subsecunda* (45%), *Sphagnum* (25%), *Acutifolia* (16%), and *Cuspidata* (11%).

The recent contributions by Crum for Mexico (in Sharp *et al*., 1994, see general ref.) and Central America (in Allen, 1994, see general ref.) provide the only modern regional treatments available for the Neotropics. Unfortunately, no such treatment, with the exception of the dated worldwide treatment by Warnstorf (1911), exist for South America where numerous new species have been recently described. The naming of South American sphagna is presently inadvisable without reference to Crum's recent publications (see below); about half of the species recognized for the Neotropics, including two new sections, have been described in just the last 10 years. Keys provided below to the sections are adapted from the various publications of Crum (pers. comm.).

Study guide. To properly identify *Sphagnum* it is best to obtain both stem and branch leaves in order to observe the abaxial and adaxial surfaces, and a cross-section of both leaf types. Further features to note include the surface of the stem and branches, as well as a cross-section of both. Attention should also be given to the habit, noting the orientation and number of branches per fascicle.

A stain will enhance microscopic features - either crystal violet in a saturated solution with water, or methylene blue mixed in a 1–2% solution of water, or substituting water for 50% alcohol.

LITERATURE. Crum, H. 1980. A guide to the identification of Mexican Sphagna. Contributions from the University of Michigan Herbarium 14: 25–52 [keys, illustrations]. - Crum, H. 1984a. Sphagnopsida. Sphagnaceae. North American Flora Series II, part 11: 1–180 [keys to species of North America, north of Mexico, illustrations]. - Crum, H. 1985. New Sphagna from Brazil. Cryptogamie: Bryologie, Lichénologie 6: 181–184 [2 spp. nov.]. - Crum, H. 1987. New species of *Sphagnum* from South America. Journal of the Hattori Botanical Laboratory 63: 77–97 [13 spp. nov.]. - Crum, H. 1989a. Notes on South American species of *Sphagnum*. Journal of Bryology 15: 531–536 [2 spp. nov.]. - Crum, H. 1989b. New tropical American species of *Sphagnum*. The Bryologist 92: 98–104 [5 spp. nov.]. - Crum, H. 1991. Two new species of *Sphagnum* from Brazil. The Bryologist 94: 301–303 [2 spp. nov.]. - Crum, H. 1992. Miscellaneous notes on the genus *Sphagnum*. 3. New species from Brazil. The Bryologist 95: 419–429 [7 spp. nov.]. - Crum, H. 1993a. New species of *Sphagnum* from South America. Journal of the Hattori Botanical Laboratory 74: 145–154 [5 spp. nov.]. - Crum, H. 1993b. Miscellaneous notes on the genus *Sphagnum*. 3[4]. The Bryologist 96: 455–462. - Crum, H. 1994. Miscellaneous notes on the genus *Sphagnum*. 5. New and notable species of South America. Journal of the Hattori Botanical Laboratory 77: 233–253 [12 spp., 1 var. nov.]. - Crum, H. 1995a. Miscellaneous notes on the genus *Sphagnum*. 6. Contributions from the University of Michigan Herbarium 20: 126–140 [8 spp. nov.]. - Crum, H. 1995b. Miscellaneous notes on the genus *Sphagnum* 8. Additional species from South America. The Bryologist 98: 265–268 [2 spp. nov.]. - Crum, H. 1995c. Miscellaneous notes on *Sphagnum*: 9. South American species. The Bryologist 98: 578–589 [5 spp. nov.]. - Crum, H. 1995d. Miscellaneous notes on the genus *Sphagnum* (Musci, Sphagnaceae). 7. Fragmenta Floristica et Geobotanica 40: 167–176 [1 sp. nov.] - Crum, H. 1997. Miscellaneous notes on *Sphagnum* 10. Contributions from the University of Michigan Herbarium 21: 147–159 [8 spp. nov.]. - Crum, H. & W. R. Buck. 1988. A contribution to the *Sphagnum* (Sphagnaceae) flora of Paraguay. Brittonia 40: 188–194 [1 spp. nov.]. - Crum, H. & W. R. Buck. 1992. Sphagna of the 1979 Projecto Flora Amazônica expedition. Brittonia 44: 448–460 [5 spp. nov.]. - Griffin, D. III. 1981. El género *Sphagnum* en los Andes de Colombia y Venezuela. Cryptogamie: Bryologie, Lichénologie 2: 201–211 [keys, illustrations]. - Warnstorf, C. 1911. Sphagnales-Sphagnaceae (Sphagnologia Universalis), 1–546. *In* A. Engler, Das Pflanzenreich. Heft 51. W. Engelmann, Leipzig [keys, illustrations].

1. Cortical cells of branch stems lacking epidermal pores; Bolivia ..... sect. **Inretorta**
1. Cortical cells of branch stems with epidermal pores 2
2. Resorption furrows present on stem and branch leaves; branch leaves rather similar to stem leaves but narrower, both with apex cucullate-concave; elliptical chlorocysts centrally included ..... sect. **Cuculliformes**
2. Resorption furrows absent or if present only on stem leaves or on branch leaves (not both); branch leaves similar or more commonly differentiated from stem leaves; apices cucullate or not; chlorocysts variously shaped including elliptical, included (centrally) or not 3
3. Cortical cells of stems and branches reinforced by delicate spiral fibrils; branch leaves broad, broadly pointed, and cucullate-concave, rough at back of apex, margins denticulate and bordered by a resorption furrow ..... sect. **Sphagnum**
3. Cortical cells of stems and branches not reinforced by spiral fibrils; branch leaves generally narrower and usually tapered to a slender, truncate apex, involute-concave, not cucullate or rough at the apex, only rarely denticulate at the margins 4
4. Cortical cells of branches uniform, each with a single pore at the upper end; stem leaves very small; branch leaves broadly truncate, denticulate at the margins and bordered by a resorption furrow ..... sect. **Rigida**
4. Cortical cells of branches of 2 kinds, some without pores, others enlarged and apically porose (retort-shaped); stem leaves usually not particularly small; branch leaves usually tapered to a narrow, truncate apex (rarely rounded or broadly truncate at the apex), nearly always entire except across the apex, bordered by linear cells 5
5. Plants aquatic; branch leaves with hyaline cells very long, scarcely broader than the green cells, without fibrils but with numerous to many pores on the outer surface (ca. 8–20 in 1 row or 15–60 in 2 rows) ..... sect. **Isocladus**
5. Plants mostly not aquatic, associated with boggy or seepy sites; branch leaves with hyaline cells distinctly broader than green cells, with fibrils, pores usually no more than ca. 8 on the outer surface ..... 6.
6. Stems simple or with 1–3 branches per fascicle 7
6. Stems with 3 or more branches per fascicle 8

7. Stems simple or with 1–3 short branch per fascicle; hyaline cells of branch leaves with thick annular fibrils almost completely dividing the cells into squarish segments, without pores on the outer surface (but rarely with 1–4 rounded, irregular membrane gaps), with short membrane pleats oriented in various directions in each segment ..... sect. **Hemitheca**
7. Stems simple or sparsely and irregularly fasciculate; hyaline cells with narrow fibrils, on the outer surface with few to numerous pores, with membrane pleats none or longer and oriented lengthwise ..... sect. **Subsecunda** p.p.
8. Plants often tinged with orange-yellow; branches of the capitulum sometimes curved; branch leaves often ± secund; hyaline cells of branch leaves usually with numerous pores crowded in bead-like rows along the commissures on 1 or both surfaces ..... sect. **Subsecunda** p.p
8. Plants green, yellowish, brownish, or reddish; branches not or very rarely curved; branch leaves erect or variously spreading, not or rarely subsecund; hyaline cells with pores not particularly numerous, not crowded in commissural rows 9
9. Plants commonly red or red-tinged; green cells of branch leaves triangular to trapezoidal, usually exposed exclusively or more broadly on the inner surface ..... sect. **Acutifolia**
9. Plants not reddish; green cells exposed more broadly on the outer surface ..... sect. **Cuspidata**

Sect. **Acutifolia**

DISCUSSION. A widespread section, in the Neotropics containing about 25 species, including the rather common *S. limbatum* Mitt. (Fig. 210, A-E), *S. meridense* (Hampe), and *S. sparsum* Hampe. *Acutifolia* is characterized by slender, often reddish tinged plants, marginal border of stem leaves often abruptly dilated at base of leaf, chlorocysts triangular to trapezoidal and exposed only or more broadly on the inner leaf surface with leucocysts bulging on the outer surface, leucocysts of stem leaves commonly resorbed on the inner surface, and leucocysts of branch leaves typically exhibiting elliptic pores that are ringed along the commissures.

LITERATURE. Crum, H. 1990b. A new look at *Sphagnum* sect. *Acutifolia* in South America. Contributions to the University of Michigan Herbarium 17: 83–91. - Crum, H. & D. Pinheiro da Costa. 1994. *Sphagnum costae*, a new Brazilian species related to *S. molle* Sull. Cryptogamie: Bryologie, Lichénologie 15: 111–115.

Sect. **Cuculliformes**

DISCUSSION. This new section, described by Crum (1987), contains a single species, *S. cuculliforme* H. A. Crum and is known only from the type collection in Ecuador at 2200–2250 m. *Cuculliformes* is characterized by the small, slender habit, ascending branches in fascicles of 2, epidermal stem cells uniporose, fibrils lacking, leaves broadly elliptic or oblong-ovate, apex cucullate-obtuse, denticulate-bordered due to marginal resorption furrow, adjacent cell angles with 3 small pores on the outer stem leaf surface, branch leaves oblong-ovate, concave, with obtuse-cucullate apex likewise denticulate due to a marginal resorption furrow, and chlorocysts central and included.

LITERATURE. Crum, H. 1987. A new section and species of *Sphagnum* from Ecuador. Contributions to the University of Michigan Herbarium 16: 141–143.

Sect. **Cuspidata**

DISCUSSION. A widespread section, in the Neotropics containing 17 species, a few rather common, including *S. cuspidatum* Ehrh. ex Hoffm. and *S. recurvum* P. Beauv. *Cuspidata* is characterized by the cortical stem cells lacking both pores and fibrils, stem leaves typically shorter than branch leaves, the former extensively resorbed on the inner surface, occasionally on both surfaces across or down from the apex, cortical cells of branches lacking fibrils, occasionally distally porose, retort-shaped, branch leaves ovate to short or narrowly long lanceolate, occasionally with margins somewhat flat or wavy, bordered by a few rows of linear cells, leucocysts convex on the inner surface, plane on the outer, fibrillose, porose on 1 or both surfaces, and chlorocysts exposed more extensively or only on the outer leaf surface.

LITERATURE. Crum, H. 1984a (see family ref.).

Sect. **Hemitheca**

DISCUSSION. This section is represented by a single species, *S. pylaesii* Brid., recorded from a few localities in the tropical Andes; widespread in eastern North America and western Europe. *Hemitheca* is characterized by simple branches or with 1–3 short branches per fascicle, similar stem and branch leaves, the latter somewhat smaller, fibrils strong, short membrane pleats oriented in various directions within each fibril subdivision, pores few or none, and chlorocysts elliptical, central and included.

LITERATURE. Crum, H. 1984a (see family ref.).

Sect. **Inretorta**

DISCUSSION. A new section described by Crum (1990) and containing a single species, *S. inretortum* H. A. Crum, which came from a moist montane forest in Bolivia at 3100 m. The species and section are characterized by cortical cells of branches uniform in shape and size, and of particular importance, the absence of pores, the branch leaves with apex entire and obtuse-rounded, not truncate, margins with a resorption furrow, and chlorocysts elliptical, central and included.

LITERATURE. Crum, H. 1990. *Sphagnum inretortum*, a new species in a new section from Bolivia. The Bryologist 93: 283–285.

Sect. **Isocladus**

DISCUSSION. A monotypic section, *S. macrophyllum* Brid. is known from coastal eastern North America and from a single locality in Honduras at 150 m. The section is distinguished by large plants, typically aquatic, short, wide-spreading to rarely deflexed branches in 2 fascicles, stem leaves small, triangular, branch leaves larger, elliptical to oblong-ovate, tubulose below, narrowed distally and inrolled, leucocysts of branch leaves conspicuously elongate, narrow, pores on outer leaf surface, rather numerous, single rowed and lacking pores on the inner surface, and chlorocysts broadly exposed on both surfaces.

LITERATURE. Crum, H. 1984a (see family ref.). - Crum, H. in B. Allen. 1994 (see general ref.).

Sect. **Rigida**

DISCUSSION. A section containing three species, represented in the Neotropics by two, both also widespread in the Northern Hemisphere, *S. compactum* DC. and *S. strictum* Sull. Section *Rigida* is characterized by cortical stem cells lacking spiral fibrils and pores, cortical branch cells uniporose, distally positioned, conspicuously smaller-sized stem than branch leaves, the latter elliptical or broadly ovate, broadly truncate, bordered by a resorption furrow and denticulate at margins, chlorocysts either elliptical and included, or triangular and exposed to the outer leaf surface, and leucocysts with pores grouped in threes at adjacent cell angles on the inner leaf surface.

LITERATURE. Crum, H. 1984a (see family ref.).

Sect. **Sphagnum**

DISCUSSION. A widespread section, in the Neotropics containing about 40 species including a few that are common and widespread within and beyond the Neotropics, e.g., *S. magellanicum* Brid. (Fig. 210, F-L) and *S. palustre* L., the majority, however, are regionally or locally restricted within tropical America. The section is characterized by rather large, stout plants, typically in compact tufts, branches tumid, often in fascicles of 4–6, cortical stem and branch cells with delicate spiral fibrils, stem leaves flat, lingulate, finely fringed, branch leaf apex extensively resorbed, resulting in a roughened appearance, resorption furrow along margin, and branch leaf leucocysts with pores ringed, elliptic, with 2–3 pores at adjacent angles.

LITERATURE. Buck, W. R. & H. Crum. 1993. Notes on Guayana mosses with new information on *Sphagnum ornatum*. Brittonia 45: 17–20. - Crum, H. 1990. Comments on *Sphagnum* sect. *Sphagnum* in South America. Contributions to the University of Michigan Herbarium 17: 71–81. - Crum, H. 1993. Progress toward understanding *Sphagnum* section *Sphagnum* in Brazil. Advances in Bryology 5: 9–29.

Sect. **Subsecunda**

DISCUSSION. The most diverse section in the Neotropics with about 71 species; only *S. subsecundum* Nees & Sturm (Fig. 210, M-Q) with two varieties, var. *platyphyllum* (Lindb. & Braithw.) Cardot and var. *rufescens* (Nees & Hornsch.) Hüb. are found in the Northern Hemisphere, the remaining species represent regional or local endemics within the Neotropics. *Subsecunda* is characterized by stem cortical cells lacking fibrils or pores, or the latter weakly present and occurring singly, stem leaves conspicuously smaller or larger than branch leaves, branches often curved, cortical cells of branches lacking fibrils, some distally porose, enlarged as retort cells, branch leaves somewhat secund, broadly ovate to elliptical below, distally narrowly truncate and toothed at apex, bordered by linear cells, leucocysts ± convex on both surfaces, outer surface with numerous ringed and crowded, elliptic pores, often arranged in commissural rows, inner surface with none, few or rather numerous pores, and chlorocysts exposed equally or somewhat more so on the outer surface, elliptic to rectangular or somewhat trapezoidal.

LITERATURE. Crum, H. 1990. Preliminary notes on *Sphagnum* sect. *Subsecunda* in South America. Contributions to the University of Michigan Herbarium 17: 93–97.

SPLACHNACEAE

Plants somewhat small to medium sized, gregarious or forming loose to dense tufts, often lustrous green or reddish-brown. **Stems** erect, few to several branched by innovations, radiculose below, occasionally tomentose; central strand present. **Leaves** distant to crowded, often comose distally, rather lax, occasionally crispate when dry, ovate-lanceolate, oblong or obovate to spathulate, apex acuminate, acute or obtuse, base occasionally decurrent; margins entire or bluntly to sharply serrate or ciliate, limbate or elimbate; costa single, subpercurrent to long excurrent; laminal cells rather large, smooth, median cells rhomboidal, hexagonal or irregularly rectangular; lower and basal cells laxly oblong or rectangular; alar region undifferentiated. **Propagula** apparently absent. **Autoicous** or dioicous. **Perigonia** on lateral short branches; paraphyses clavate. **Perichaetia** terminal, leaves little differentiated. **Seta** somewhat short to more commonly elongate, rather stout, smooth to scabrous or papillose. **Capsule** erect, urn mostly short or long cylindrical; hypophysis lacking or when present inflated and elongate or obovoid, often as long or longer than urn; annulus mostly appearing absent. **Operculum** conic. **Peristome** single, double with endostome adhering to exostome and appearing single, or absent, teeth 16 and united in 8 pairs or initially 4 pairs at base and distally divided, erect or reflexed, mostly variously papillose. **Calyptra** mitrate and lobed at base, or cucullate, naked to roughened-papillose or sparsely hairy. **Spores** spherical, smooth or variously papillose.

DISCUSSION. The Splachnaceae contain seven genera and about 70 species, widely distributed in boreal and temperate regions, and in the tropics confined to the highlands; in the Neotropics six genera and 17 species. The Splachnaceae are the only family of mosses known to exhibit entomophily, usually involving those plants found growing on dung or carrion. The studies summarized by Koponen (1990) have shown that various species in several genera produce volatile compounds, emitting an odor from the stomata that attracts flies and assists in the dispersal of spores (not unlike that of many members of the family Araceae). Most of the studies involve taxa from the Northern Hemisphere, and it is apparently unknown if any of the neotropical Splachnaceae are also entomophilous, although at least *Splachnum weberbaueri* and *Tayloria scabriseta* are typically found on dung.

LITERATURE. Koponen, A. 1982. On the structure and function of the peristome in Splachnaceae. Journal of the Hattori Botanical Laboratory 53: 73–98. - Koponen, A. 1983. Studies on the generic concept in the classification of the moss family Splachnaceae. Academic Dissertation, University of Helsinki. - Koponen, A. 1990. Entomophily in the Splachnaceae. Botanical Journal of the Linnean Society 104: 115–127. - Koponen, A., T. Koponen, H. Pyysalo, K. Himberg & P. Mansikkamäki. 1990. Composition of volatile compounds in Splachnaceae. Pages 449–460. *In*: H. D. Zinsmeister & R. Mues, Bryophytes: Their Chemistry and Chemical Taxonomy. Clarendon Press, Oxford.

1. Leaf margins ciliate or distinctly bordered; peristome teeth 16, united in pairs at the apex .... **Brachymitrion**
1. Leaf margins not or weakly bordered or ciliate; peristome teeth in pairs of 8 or initially 4 and divided distally, erect or reflexed, or absent 2
2. Leaf apices bluntly acute or obtuse to acuminate 3
2. Leaf apices narrowly acuminate 4
3. Capsules cupulate, flared when deoperculate, hypophysis and peristome absent; southeastern Brazil ..... **Moseniella**
3. Capsules cylindrical, not flared when deoperculate, hypophysis and peristome present; montane or páramo and puna..... **Tayloria**
4. Leaf margins weakly bordered; hypophysis noticeably inflated, often greatly so; peristome of 8 pairs of fused teeth ..... **Splachnum**
4. Leaf margins not differentiated; hypophysis slightly expanded or absent; peristome absent or when present fused initially in 4 pairs distally divided 5
5. Leaves oblong-lanceolate to oblanceolate; leaf costa percurrent; peristome present .... **Tetraplodon**
5. Leaves ovate to ovate-lanceolate; costa short excurrent; peristome absent ..... **Voitia**

Brachymitrion (Fig. 211) - Four species in the Neotropics (Mexico to the Andes); a genus of six species, *B. jamesonii* Taylor and *B. moritzianum* (Müll. Hal.) A. K. Kop. are present in the montane tropics of Africa and America.

HABITAT. On humus, soil or rocks, less often epiphytic on trunks and branches, or occasionally on decaying logs; submontane to upper montane forests, extending into forested galleries in páramo and puna, 900–4200 m.

DESCRIPTION. **Plants** medium sized to rather large, forming loose tufts, glossy or somewhat lustrous green, yellowish-green or golden. **Stems** erect, few branched, densely tomentose; in cross-section angular (5-sided), hyalodermis present, central strand present; rhizoids reddish-brown, smooth or papillose. **Leaves** crispate or contorted when dry, erect-spreading when wet, obovate to spathulate, 4–6 mm long, apex broadly acute or obtuse and apiculate, base short to long decurrent; margins plane, bluntly serrate or ciliate, limbate or not; costa subpercurrent to ending well below apex; laminal cells smooth, median cells short hexagonal to rhomboidal; lower and basal cells long rectangular; marginal cells forming a weak border with a single row of cells or distinct golden colored border of 4–6 rows, cells fusiform to rhomboidal. **Autoicous**. **Seta** short to elongate, 2–20 mm long, smooth, twisted or not. **Capsule** immersed to exserted, erect, urn cylindrical, 1.5–4.5 mm long, mouth somewhat flared when deoperculate, hypophysis absent; neck short; exothecial cells thick-walled; stomata at base of urn, superficial. **Operculum** short rostrate. **Peristome** single, teeth 16, united at apex, reticulate or reticulate-striate, occasionally with few perforations along median line. **Calyptra** mitrate, ciliate or scabrous. **Spores** reticulate.

DISCUSSION. The genus is characterized by ciliate or distinctly bordered leaf margins, apices of peristome teeth united in pairs, and a ciliate or scabrous mitrate calyptra.

LITERATURE. Goffinet, B. 1999. *Brachymitrion immersum* (Splachnaceae, Musci), a new species from Cameroon. The Bryologist 102: 108-111 [keys].

Moseniella (Fig. 211) - An endemic neotropical genus of two species, *M. brasiliensis* Broth. and *M. ulei* (Müll. Hal. ex Broth.) A. K. Kop., both apparently rare and restricted to the Planalto and southeastern Brazil.

HABITAT. Apparently on soil; in primary forests, at low elevations.

DESCRIPTION. **Plants** small. **Stems** erect, to 10 mm tall, rather densely covered below by rhizoids; in cross-section hyalodermis present, outer few rows of cells rather small, thick-walled, inner cells larger, thin-walled, central strand well developed. **Leaves** laxly imbricate, erect-spreading when wet, obovate, apex acute; margins plane, recurved at base, distally irregularly serrate; costa rather strong below, percurrent; laminal cells smooth, firm-walled, upper and median cells rather short hexagonal; basal cells oblong-rectangular; marginal cells smaller. **Dioicous**. **Perichaetia** terminal. **Seta** short, ca. 3 mm long (ca. twice the capsule length), stout. **Capsule** erect, urn cupulate, ca. 1 mm long, mouth flared when deoperculate; neck short, hypophysis absent; stomata superficial on neck; annulus absent. **Operculum** low conic-rostrate. **Peristome** absent. **Calyptra** mitrate, hairy at base. **Spores** pitted.

DISCUSSION. The genus, in aspect similar to *Physcomitrium* as noted by Brotherus (1917), is characterized by the short seta, flared capsule mouth when old, absence of a hypophysis and peristome.

LITERATURE. Brotherus, V. F. 1917. *Moseniella*, un nouveau genre des mousses du Brésil. Arkiv för Botanik 15: 1–3.

Splachnum (Fig. 211) - Two species in the Neotropics, *S. pennsylvanicum* (Brid.) Grout ex H. A. Crum from the tepuis of Venezuela (also eastern North America) and *S. weberbaueri* Reimers from Costa Rica and the Andes; a genus of nine species associated with cool, moist temperate regions.

HABITAT. On dung or soil probably previously associated with dung; lower to upper open montane forests, 2300–3950 m.

DESCRIPTION. **Plants** forming dense tufts, glossy pellucid green. **Stems** to ca. 1 cm tall, few branched, tomentose below; central strand present. **Leaves** small below, distally crowded and larger, ± crispate or contorted when dry, erect-spreading when wet, elliptical-lanceolate or oblanceolate, 3–5.5 mm long, to 2 mm wide, distally folded, apex long acuminate; margins plane, entire to sharply serrate distally; costa short excurrent; median cells large, hexagonal to hexagonal-fusiform; lower and basal cells long rectangular; alar region undifferentiated; marginal cells oblong-rectangular. **Autoicous**. **Perigonia** on short branches; leaves with an oval base and distal wide-spreading, lanceolate limb. **Perichaetia** terminal; leaves similar. **Seta** elongate, 5–40 mm long, slender, flexuose or not, pale whitish-green to pink or dark bright red, smooth, twisted when dry. **Capsule** erect, short to long exserted, differentiated between a short urn and inflated neck (hypophysis), urn cylindrical, 0.6–1.4 mm long, brown; exothecial cells strongly collenchymatous, oblate-rectangular or subquadrate; hypophysis (neck) pyriform or only slightly inflated, 1.5–6 mm long, to 4 mm wide, pale pink or red; stomata on distal hypophysis, superficial; columella often shortly exserted when dry. **Operculum** convex- or conic-apiculate. **Peristome** teeth fused in 8 pairs, papillose, reflexed when dry. **Calyptra** mitrate-campanulate, ca. 1.2 mm long. **Spores** spherical or oval, smooth or lightly papillose.

DISCUSSION. The genus is readily recognized by the inflated, pale rose or whitish-green colored hypophysis, additional combined features include long-acuminate, elliptical-lanceolate or oblanceolate

leaves, often weakly bordered margins, and peristome teeth fused into 8 paired. The hypophysis of *S. pennsylvanicum* is equal to, or less than, the urn width, only slightly inflated, whereas *S. weberbaueri* the hypophysis is inflated, globose and tapered below, and several times broader than urn.

Tayloria (Fig. 212) - Six or seven species in the Neotropics (Mexico, Central America, Andes and southeastern Brazil); about 40 species rather widely distributed but concentrated in the highland tropics and subtemperate regions.

HABITAT. On soil and humus, occasionally on dung; open montane forests and páramo, (320)2000–4700 m.

DESCRIPTION. **Plants** small to medium sized, forming tufts, glossy green to reddish-brown. **Stems** erect, simple or few branched, usually tomentose below; in cross-section epidermis small, inner cells large and thin-walled, central strand present; rhizoids smooth to papillose. **Leaves** mostly crispate or contorted when dry, erect-spreading when wet, ovate-short lanceolate, elliptical to obovate or spathulate, apex broadly acuminate, acute or obtuse; margins plane to reflexed below, entire, bluntly serrate or crenulate distally, elimbate; costa 3/4–4/5 lamina length or subpercurrent; upper and median cells large and smooth, hexagonal to rhomboidal; basal cells rectangular, rather lax. **Autoicous**. **Perichaetia** terminal, leaves similar to stem leaves. **Seta** rather short to elongate, twisted or not, smooth or scabrous. **Capsule** emergent to long exserted, erect, dark red to reddish-black, urn short cylindrical; exothecial cells oblate, thick-walled; hypophysis short (usually equal to shorter than urn), cells elongate, thin-walled, stomata in distal half, superficial. **Operculum** not observed. **Peristome** single, teeth 8 or 16, papillose, reflexed when dry. **Calyptra** not observed. **Spores** spherical, appearing smooth to lightly papillose.

DISCUSSION. The genus is characterized by the obovate, spathulate to elliptical or broadly short lanceolate leaves, elimbate, entire to toothed margins, smooth to occasionally papillose seta, cylindrical capsule, rather narrow and short hypophysis, and papillose, 8 or 16 toothed peristome.

LITERATURE. Koponen, A. 1990. *Tayloria rubicaulis*, a new species of Splachnaceae (Musci) from the Venezuelan and Colombian Andes. Annales Botanici Fennici 27: 43–46.

Tetraplodon (Fig. 212) - Probably a single species in the Neotropics, *T. mnioides* (Hedw.) Bruch, Schimp. & W. Gümbel (tropical highlands of Central America and South American Andes, possibly southeastern Brazil); about nine species, primarily of the Northern Hemisphere.

HABITAT. On soil or humus in open moist or wet sites; páramo and possibly puna, (1800–) 3500–3800 m.

DESCRIPTION. **Plants** medium sized, forming dense compact tufts, pale green to yellowish-green. **Stems** erect, to 3 cm or more tall, few branched, densely tomentose; central strand well developed. **Leaves** crowded, erect to erect-spreading, oblong- to obovate-lanceolate, 4–5.5 mm long, to 1.8 mm wide, deeply concave, apex narrowly acuminate, ending in a long hyaline subula; margins entire; costa ending in subula; laminal cells smooth, median cells oblong, rectangular- to hexagonal-rounded; basal cells long rectangular, lax. **Autoicous**. **Perichaetia** terminal, leaves ± larger than stem leaves. **Seta** elongate, to 30 mm long or more, stout, smooth. **Capsule** erect, urn short cylindrical, to 1.5 mm long, hypophysis narrowly elliptical, ca. 2 times longer than urn. **Operculum** conic. **Peristome** single, teeth fused into 4 pairs at base, and distally becoming 2-paired, reflexed when dry, outer surface papillose, inner surface smooth. **Calyptra** mitrate, smooth and naked. **Spores** smooth, smooth.

DISCUSSION. The genus is distinguished by the densely compact tufted plants, oblong-lanceolate to oblanceolate leaves, percurrent costa ending in a subula, and 8 peristome teeth, papillose on the outer surface, smooth on the inner.

Voitia (Fig. 212) - A single species in the Neotropics, *V. nivalis* Hornsch., recorded from Peru and possibly Bolivia; a genus of three species of Arctic and boreal distribution in the Northern Hemisphere.

HABITAT. In boggy sites; puna, at elevations 4000–4800 m.

DESCRIPTION. **Plants** medium sized, forming dense tufts, light green to yellowish-green or golden-brown. **Stems** erect, to 3 cm or more tall, few branched, tomentose; in cross-section outer 1–2 rows of cells small, thick-walled, inner cells large, thin-walled, central strand well developed; rhizoids smooth. **Leaves** crowded, contorted when dry, erect-spreading when wet, ovate to ovate-lanceolate, to 3.5 mm long, concave, apex long acuminate; margins plane, slightly incurved, entire; costa somewhat long excurrent; laminal cells smooth, median cells hexagonal to short rectangular, thin-walled, lax; basal cells laxly rectangular. **Autoicous**. **Perichaetia** terminal on branches. **Seta** to 35 mm long, twisted, smooth. **Capsule** cleistocarpous, ovoid-cylindrical with a long rostrate beak, to 3 mm long, asymmetric; exothecial cells short to rather long oblong-rectangular, thick-walled; stomata at

base, superficial. **Operculum** and peristome absent. **Calyptra** cucullate, smooth and naked. **Spores** spherical, appearing smooth.

DISCUSSION. The genus, apparently rare in the Neotropics, is characterized by long acuminate, concave, ovate to ovate-lanceolate leaves; entire, elimbate margins; rather long excurrent costa, and long-rostrate beaked, ovoid-cylindrical, cleistocarpic capsules.

SPLACHNOBRYACEAE

A monotypic family, placed in the Pottiaceae by some authors; treated here as a member of the order Funariales.

Splachnobryum (Fig. 213) - Two species recorded for the Neotropics, *S. obtusum* (Brid.) Müll. Hal. common and widespread, and *S. spruceanum* Müll. Hal. recorded for Peru (status unknown); a pantropical genus stated to contain some 25 species.

HABITAT. On rocks, especially limestone, less often on soil; from wet to semi-dry lowland forests, 50–750 m.

DESCRIPTION. **Plants** small, forming loose tufts, dark to blackish-green. **Stems** erect, 2–5(10) mm tall, reddish; in cross-section epidermal cells somewhat thin-walled, inner cells little larger, thin-walled, central strand weak. **Leaves** obovate to oblong-elliptical, occasionally subspathulate, 0.8–1(–1.5) mm long, 0.25–0.4 mm wide, apex broadly acute to rounded; margins plane, recurved below, entire to slightly crenulate distally; costa single, percurrent or ending several cells below apex; median cells rhomboidal to hexagonal, firm-walled and smooth; basal cells lax, rectangular; distal marginal cells quadrate. **Dioicous**. **Perichaetia** terminal, leaves similar to somewhat longer. **Seta** elongate, to 5 mm long, smooth. **Capsule** erect, urn short-cylindrical, 0.9–1.4 mm long; exothecial cells irregularly quadrate to rectangular, firm but thin-walled; stomata few at urn base, superficial; annulus persistent. **Operculum** conic, 0.2–2.25 mm long. **Peristome** single, endostome papillose. **Calyptra** cucullate, 1.2–1.4 mm long, smooth. **Spores** spherical, papillose.

DISCUSSION. The genus is characterized by small statured, erect plants, with stem epidermal cells somewhat thin-walled (as seen in cross-section), inner cells little larger, thin-walled, central strand weak, obovate to oblong-elliptical, occasionally subspathulate leaves, broadly acute to rounded apex, margins plane, recurved below, entire to distally crenulate, percurrent or subpercurrent costa, rhomboidal to hexagonal, smooth and firm-walled median cells, quadrate distal marginal cells, elongate seta, erect, and short cylindrical capsule with a peristome represented by a papillose endostome.

Splachnobryum has previously been placed in the Pottiaceae and Splachnaceae; however, Koponen (1981) established a new family for this genus, suggesting its placement in the Funariales based primarily on peristomial features. A revision would likely reduce significantly the number of species presently accepted in this genus, as initially demonstrated by Breen and Pursell (1959).

LITERATURE. Breen, R. S. & R. A. Pursell. 1959. The genus *Splachnobryum* in the United States, Mexico, Central America and the Caribbean. Revue Bryologique et Lichénologique 28: 280–289. - Koponen, A. 1981. Splachnobryaceae, a new moss family. Annales Botanici Fennici 18: 123–132.

STEREOPHYLLACEAE

Plants somewhat small to medium sized, forming loose to dense mats, mostly glossy light to dark green, or yellowish. **Stems** creeping and spreading, occasionally subascending, simple to few irregularly pinnately branched, radiculose below; central strand present or absent; rhizoids smooth or papillose. **Leaves** weakly to strongly complanate or terete, lanceolate, oblong or oblong-ovate, apex acute to acuminate; margins plane, occasionally reflexed at base, entire to serrulate distally; costa single, 1/2 to 2/3 lamina length, or both none and weak, short and forked or single; median cells rhombic, rhomboidal or linear, smooth or papillose, papillae over cell lumen or projecting at angles, angles tapering or obtuse-rounded; alar region differentiated, asymmetric with cells often more numerous on one side, alar cells often extending to or over costa, quadrate to short rectangular. **Autoicous**. **Perichaetia** lateral, leaves elongate, lanceolate. **Seta** elongate, smooth. **Capsule** inclined to subpendent, rarely erect, urn ovoid-short cylindrical to cylindrical, ± asymmetric; annulus present or absent. **Operculum** conic-short rostrate, usually oblique. **Peristome** double, exostome teeth 16, cross-striate or striate-papillose below, distally papillose; endostome slightly to distinctly shorter than the exostome, mostly finely papillose, basal membrane high to occasionally low, segments 16, keeled and perforate, cilia 1–3 or rudimentary to absent. **Calyptra** cucullate, naked and smooth. **Spores** spherical, finely to coarsely papillose.

DISCUSSION. The Stereophyllaceae contain eight genera and about 30 species largely confined to the tropics; in the Neotropics six genera and 13 species. A distinguishing feature of the family is the asymmetric development of alar cells on either side of the costa, more numerous on one side of the leaf and often extending over the costa on the ventral surface, a result of the lateral disposition of leaves.

Most of the genera were previously assigned to the Plagiotheciaceae; however, Buck and Ireland (1994) suggest a close relationship of the Stereophyllaceae with the Brachytheciaceae based on phenetic similarities that included a single costa, elongate median cells, and similar hypnoid peristome.

LITERATURE. Buck, W. R. & R. R. Ireland. 1985. A reclassification of the Plagiotheciaceae. Nova Hedwigia 41: 89–125. - Ireland, R. R. & W. R. Buck. 1994. Stereophyllaceae. Flora Neotropica Monograph 65: 1–50 [keys, illustrations, maps].

1. Costa absent on median leaves, costate on lateral leaves, forked or short and single; insertion cells porose ..... **Pilosium**
1. Costa single, mostly beyond midleaf, very rarely forked (occasionally spurred below); insertion cells porose or not 2
2. Laminal cells rhombic, low unipapillae present (sometimes indistinct) ..... **Stereophyllum**
2. Laminal cells fusiform to linear, smooth or papillose by projecting cell angles 3
3. Leaf apex bluntly acute to obtuse; margins distally dentate-serrate; laminal cells appearing papillose by projecting angles ..... **Eulacophyllum**
3. Leaf apex acute or acuminate (if obtuse then cells smooth); margins entire to weakly denticulate distally; laminal cells smooth 4
4. Pseudoparaphyllia foliose; rhizoids papillose; Chile (northern) ..... **Juratzkaea**
4. Pseudoparaphyllia filamentous; rhizoids smooth 5
5. Capsule inclined, rarely erect; annulus present; endostomial segments slightly shorter than exostome teeth; at elevations mostly below 1500 m, rather widespread ..... **Entodontopsis**
5. Capsule erect; annulus absent; endostomial segments ca. 2/3 the length of exostome teeth; at elevations from ca. 2000–3000 m, Ecuador and Peru ..... **Sciuroleskea**

Entodontopsis (Fig. 213) - Seven species widespread in the Neotropics; a pantropical genus of about 17 species.

HABITAT. On tree trunks or logs, occasionally on lianas, rocks and soil (sandy); semi-dry or somewhat moist open forests, from near sea level to 1500(–2900?) m.

DESCRIPTION. **Plants** forming loose and often thin mats, glossy light green. **Stems** creeping and spreading; central strand absent; pseudoparaphyllia filamentous; rhizoids clustered beneath stem, smooth. **Leaves** somewhat homomallous, lanceolate to ovate-lanceolate or -oblong, concave, 1–3 mm long, apex obtuse to broadly or narrowly acuminate; margins plane, reflexed at base or not, entire to more commonly serrulate or serrate distally; costa single, ca. 1/2 lamina length, slender; median laminal cells linear, smooth to weakly projecting at angles; basal cells (adjoining or above alar region) weakly porose; alar region differentiated, often stronger on one side, extending to costa, cells quadrate. **Perichaetial** leaves small. **Seta** 5–15 mm long, slender and wiry. **Capsule** horizontal to inclined, rarely erect, ovoid to ellipsoid, 0.8–3 mm long, asymmetric, often constricted below mouth when deoperculate; exothecial cells collenchymatous, irregularly quadrate-round or -short rectangular; stomata at base urn, superficial; annulus present. **Operculum** conic-short rostrate. **Peristome** with exostome cross-striate, distally hyaline and papillose, weakly to strongly trabeculate on back; endostome smooth to papillose, basal membrane low to high, segments slightly shorter than exostome teeth, keeled and perforate, cilia 1. **Spores** lightly papillose.

DISCUSSION. Distinguishing features include filamentous pseudoparaphyllia, smooth rhizoids, laminal cells mostly linear with tapered angles, smooth or weakly projecting, inclined capsule, rarely erect, presence of an annulus, and well developed peristome, with endostomial segments slightly shorter than the teeth. See comments under *Eulacophyllum* for differences between the two genera.

Eulacophyllum (Fig. 213) - A monotypic neotropical genus, with *E. cultelliforme* (Sull.) W. R. Buck & Ireland widespread in the Neotropics (absent from the eastern Amazon Basin).

HABITAT. On rocks and logs; moist to semi-dry lowland to submontane forests, from near sea level to 1030 m.

DESCRIPTION. **Plants** rather small, forming loose to dense mats, somewhat glossy yellowish-green to green. **Stems** creeping and spreading, loosely complanate foliate, irregularly pinnately branched, radiculose; central strand absent; pseudoparaphyllia filamentous; rhizoids clustered beneath, smooth. **Leaves** rather narrowly ovate-oblong, 0.7–1.5 mm long, to 0.3 mm wide, apex bluntly acute, lateral

leaves folded to midleaf on one side; margins plane, distal 2/3–1/3 serrulate; costa single, ca. 2/3 lamina length; median cells oblong-linear, angles rounded, smooth or angles projecting; alar region differentiated, asymmetric, one side better developed than other, cells quadrate to short rectangular. **Perigonia** to 1 mm long. **Perichaetial** leaves oblong-lanceolate, to 2 mm long, narrowly long acuminate. **Seta** to 11 mm long, smooth. **Capsule** horizontal, somewhat asymmetric, urn ovoid, to 1.5 mm long. **Operculum** conic-short rostrate. **Peristome** with exostome teeth cross-striate below, papillose distally; endostome lightly papillose, basal membrane high, segments keeled and perforate, cilia usually single. **Spores** papillose.

DISCUSSION. *Eulacophyllum* is distinguished by the obtuse to bluntly acute, narrowly ovate-oblong leaves, rather coarsely and irregularly dentate-serrate margins at apex, single costa ca. 2/3 the leaf length, oblong-linear median cells with rounded, weakly projecting cell angles. The genus may be confused with some members of *Entodontopsis*, but that genus differs in the gradually elongate and sharp angle of the median cells, neither rounded or projecting; and, when the leaf apices are bluntly acute or obtuse-rounded, then they are finely dentate or weakly serrulate, not irregularly and rather coarsely serrate as in *Eulacophyllum*.

Juratzkaea (Fig. 214) - A single species in the Neotropics, *J. seminervis* (Kunze ex Schwägr.) Lorentz, known from northern to central Chile. A genus of four species, the remaining species recorded from Argentina, South Africa and Australia.

HABITAT. On base of tree trunks or occasionally on rocks; coastal lowlands, from 20–700 m.

DESCRIPTION. **Plants** rather small to medium sized, forming loose mats, glossy green or yellowish-green. **Stems** creeping, irregularly few pinnately branched; in cross-section outer 1–2 rows of cells small, thick-walled, inner cells large, thin-walled, central strand weak; rhizoids clustered beneath, smooth or possibly papillose. **Leaves** terete-foliate, loosely erect dry or wet, lanceolate, to 1.5(–3) mm long, apex gradually long acuminate, straight or somewhat flexuose; margins plane, reflexed at base, entire; costa single, to mid leaf or slightly less or more, slender; median cells linear, smooth, thin-walled; basal cells or those above alar region long hexagonal; alar region differentiated, unequally distributed on either side, one or both sides reaching or extending over costa, cells quadrate, walls somewhat irregular, thin-walled; branch leaves slenderly lanceolate, costa absent to ca. 1/3 lamina length. **Perichaetial** leaves oblong-lanceolate, costate or ecostate. **Seta** to 12 mm or more long, twisted, smooth. **Capsule** erect to suberect, short cylindrical, to ca. 1.5 mm long, slightly constricted below mouth when deoperculate; exothecial cells thick-walled; stomata at urn base, superficial; annulus absent. **Operculum** short-conic, apiculate. **Peristome** with exostome teeth weakly cross-striate-papillose below, distally smooth with few scattered papillae, weakly projecting on back; endostome shorter than exostome, finely papillose, basal membrane rather low, segments narrow, keeled, perforate, cilia absent. **Spores** rather coarsely papillose.

DISCUSSION. The genus is characterized by the glossy, terete-foliate plants; foliose pseudoparaphyllia; papillose rhizoids; gradually long acuminate apex; long linear median cells; erect capsule; and endostome slightly shorter than exostome with smooth to finely papillose narrow segments. *Juratzkaea* barely extends into the neotropical range, possibly to be found in Bolivia, more common further south in Chile. The name honors the botanist Jakob Juratzka (1821–1878).

LITERATURE. Buck, W. R. 1977. A taxonomic investigation of *Juratzkaea* Lor. and *Juratzkaella* gen. nov. Revue Bryologique et Lichénologique 43: 309–325.

Pilosium (Fig. 214) - A monotypic genus, with *P. chlorophyllum* (Hornsch.) Müll. Hal. confined to and rather widespread in the Neotropics. It is one of the more common species encountered in moist or wet lowlands.

HABITAT. On logs, occasionally on tree bases or on soil, rarely on rocks; wet lowland and submontane forests, from near sea level to 1000 m.

DESCRIPTION. **Plants** forming mats, glossy green to yellowish-green. **Stems** creeping and spreading, radiculose beneath; central strand absent; rhizoids cluster beneath, rusty-red, smooth to faintly papillose. **Leaves** loosely complanate, wide-spreading, median leaves symmetric, lateral leaves asymmetric, oblong to oblong-short lanceolate, 1.5–2 mm long, to 0.7 mm wide, apex broadly acuminate or acute, margins folded at base, distally plane, smooth to faintly serrulate; costa none or present on lateral leaves, short and forked, or rarely weakly single; median cells linear, smooth, alar cells often differentiated on one side, cells quadrate to rectangular, walls firm, entire to porose, often golden-brown, alternate side with cells elongate, strongly porose; **median leaves** symmetric. **Perigonial** leaves lanceolate, to 1 mm long. **Perichaetial** leaves lanceolate-acuminate, to 1.3 mm long. **Seta** 10–18 mm long, smooth. **Capsule** inclined to subpendent, urn ovoid or short cylindrical, 1–1.2 mm long; exothecial cells collenchymatous; neck distinct; annulus undifferentiated. **Operculum** short rostrate. **Peristome** with exostome teeth cross-striate below, papillose distally; endostome

papillose, basal membrane high, segments shorter than exostome teeth, keeled and perforate, cilia 1. **Spores** papillose.

DISCUSSION. *Pilosium* is characterized by the glossy loosely complanate plants, differentiated leaves, with ecostate, symmetric median leaves and costate, asymmetric lateral leaves with costa either forked or short and single, linear median cells, porose insertion cells, subpendent to inclined capsules, and endostome shorter than exostome.

Sciuroleskea (Fig. 214) - An endemic Andean genus (Ecuador and Peru) with two rare species, *S. xanthophylla* (Hampe & Lorentz) Broth. and *S. mittenii* (Spruce *ex* Mitt.) M. Fleisch. *ex* Broth.

HABITAT. Epiphytic, on trees; montane forests, 1300–3160 m.

DESCRIPTION. **Plants** medium sized, forming thin mats, glossy green or yellow. **Stems** creeping, to 3.5 cm long, simple to few irregularly pinnately branched; in cross-section outer 1–2 rows of cells small, thick-walled, inner cells large, thin-walled, central strand absent; pseudoparaphyllia filamentous; rhizoids clustered beneath stems. **Leaves** crowded to distant, imbricate when dry, erect- to wide-spreading when wet, somewhat narrowly lanceolate to ovate-lanceolate, to 3 mm long, apex gradually long acuminate; margins plane, entire to weakly denticulate distally; costa single, ca. 2/3 lamina length, strong below; laminal cells thin-walled, smooth, apical cells oblong-fusiform; median cells linear, somewhat flexuose; alar region differentiated, asymmetric, cells subquadrate to oblate short rectangular, extending over costa. **Perichaetial** leaves oblong-lanceolate. **Seta** to 20 mm long, straight to ± flexuose, smooth. **Capsule** erect to suberect, urn cylindrical, to 2.2 mm long, smooth; annulus undifferentiated. **Operculum** short rostrate, oblique. **Peristome** with exostome teeth cross-striate below, papillose distally; endostome lightly papillose, basal membrane moderately high, segments ca. 2/3 exostome height, keeled and perforate, cilia rudimentary or absent. **Spores** finely papillose.

DISCUSSION. The genus is characterized by filamentous pseudoparaphyllia, gradually long acuminate, ovate-lanceolate to lanceolate leaves, somewhat flexuose linear median laminal cells, erect capsules, undifferentiated annulus, and exostome teeth 1/3 longer than endostomial segments. The two species differ in the following characteristics: *S. xanthophylla* — leaves lanceolate, to 0.7 mm wide; and *S. mittenii* — leaves ovate-lanceolate, to 1.5 mm wide.

Stereophyllum (Fig. 215) - A single species in the Neotropics, *S. radiculosum* (Hook.) Mitt., widespread in the region but absent from the wet Amazon Basin and highlands. Apparently a monotypic genus distributed in tropical America and Africa, also India and Australia.

HABITAT. On rock, logs and tree trunks; lowland to lower montane semi-dry forests, from near sea level to 1500 m.

DESCRIPTION. **Plants** somewhat small to medium sized, forming mats, dull to glossy yellowish-green to dark green. **Stems** creeping to erect-spreading to spreading, irregularly branched, radiculose beneath; in cross-section outer 2–4 rows of cells small, thick-walled, inner cells large, thin-walled, central strand weak; pseudoparaphyllia filamentous; rhizoids clustered. **Leaves** loosely to strongly complanate, differentiated with median symmetric and lateral asymmetric leaves, ovate-oblong, 1.5–2.4 mm long, to 1 mm wide, apex acute to subobtuse; margins weakly serrulate distally; costa single, ca. 2/3 lamina length; median cells rhombic to rhomboidal, smooth to weakly unipapillose (best viewed along folded margin), papillae over cell lumen, thick-walled; alar region differentiated, usually more abundant on one side, cells subquadrate to short rectangular and oblate. **Perigonial** leaves ca. 0.5 mm long. **Perichaetial** leaves ovate-lanceolate, abruptly short to long acuminate, to 2 mm long. **Seta** 8–15 mm long, smooth. **Capsule** inclined to horizontal, urn ovoid-short cylindrical, ca. 1.5 mm long; exothecial cells collenchymatous; stomata few at urn base, superficial. **Operculum** conic-short rostrate. **Peristome** with exostome teeth cross-striate below, distally papillose; endostome papillose, basal membrane high, segments keeled and perforate, cilia 1–3. **Spores** coarsely papillose.

DISCUSSION. The genus is characterized by loosely to strongly complanate-foliate stems, broadly acute to obtuse, ovate-oblong leaves, a strong, single costa projecting on dorsal side, and unipapillose, rhombic laminal cells.

SYMPHYODONTACEAE

The Symphyodontaceae are monotypic, placed in the order Hypnales.

Symphyodon (Fig. 215) - A single species in the Neotropics, *S. imbricatifolius* (Mitt.) S. P. Churchill (Mexico, Central America, northern Andes, planalto, and southeastern Brazil). A genus of 15 species concentrated in eastern India to the Malay Peninsula.

HABITAT. Epiphytic, on branches and trunks of trees and shrubs, rarely on logs or rocks; submontane to montane in relatively undisturbed forests, 700–2925 m.

DESCRIPTION. **Plants** small, forming loose and thin mats, often pendent, glossy yellowish-green or golden-brown. **Stems** and branches spreading and pendulous, to 8 cm long, often complanate-foliate. **Leaves** ovate to short ovate-lanceolate, 0.7–1.5 mm long, ± asymmetric, apex acute to broadly and short acuminate, base short decurrent; margins plane, serrulate to serrate distally; costae short and forked; median cells oblong-linear, vermicular, smooth or slightly projecting at cell angles; alar cells somewhat differentiated, ca. 6–10 cells, quadrate to short oblong; marginal cells narrow and longer. **Dioicous**. **Perichaetia** lateral, leaves longer and narrower than stem leaves. **Seta** elongate, to 20 mm long, slender, smooth below, distally roughened or papillose. **Capsule** erect, urn ovoid, 1.5–2 mm long, symmetric, surface with short spines. **Operculum** conic-rostrate, ca. 0.8 mm long. **Peristome** double, exostome teeth 16, smooth and slightly furrowed at base, distally lightly papillose, not projecting on back; endostome basal membrane very low, segments 16, shorter than exostome, linear, papillose, keeled and narrowly perforate, cilia absent. **Calyptra** not observed. **Spores** spherical, finely papillose.

DISCUSSION. When fertile, the spines present on the urn are a unique character among neotropical pleurocarpic mosses; gametophytic features include the soft, glossy ovate to ovate-lanceolate leaves (to 1 mm long) with short decurrent bases, short and forked costa, and few quadrate to oblong alar cells.

Sporophytes are relatively uncommon, and the assumed mode of reproduction is via propagula in the form of fragile and deciduous stem and branch tips. An overview of our species is presented by Buck and Ireland (1992). This is an excellent example of one of a few moss genera that represent an Asian element in the neotropical moss flora (cf. He & Snider, 2000).

LITERATURE. Buck, W. R. & R. R. Ireland. 1992. *Symphyodon* (Symphyodontaceae) in the Americas. The Bryologist 95: 433–435 [illustrations, map]. - He, S. & J. Snider. 2000. A revision of *Symphyodon* (Musci: Symphyodontaceae). The Bryologist 103: 52–81[keys, illustrations, maps].

THAMNOBRYACEAE

Plants mostly medium sized to large and robust, forming loose to dense tufts or mats. **Primary stems** creeping, leaves mostly scale-like. **Secondary stems** usually stiffly erect and frondose; stipitate or indistinctly so, leaves of stipe triangular to ovate-triangular; secondary stems irregularly to regularly pinnately branched, distal branch tips often flagelliform. **Leaves** of secondary stems ovate-oblong to oblong-lanceolate or -ligulate, concave, smooth to weakly plicate, apex acute to obtuse, base weakly auriculate or not; margins plane to recurved (usually below), serrate distally, often coarsely and irregularly so at apex; costa single, occasionally forked below, 1/2–4/5 lamina length, usually strong; apical cells short, median cells linear to fusiform or rhomboidal, walls entire or weakly porose, smooth to occasionally papillose by projecting cell angles, alar region differentiated or not. **Branch leaves** often differentiated, usually narrower, oblong-ligulate; flagelliform leaves reduced, scale-like. **Dioicous**. **Perichaetia** lateral. **Seta** elongate, smooth. **Capsule** erect to horizontal, cylindrical to ovoid or obloid, stomata at urn base. **Operculum** short to long rostrate. **Peristome** double, exostome teeth 16, cross-striate or striate-papillose below, distally papillose; endostome basal membrane high, segments 16, perforate and keeled, cilia well developed or rudimentary. **Calyptra** cucullate, smooth and naked. **Spores** spherical, papillose.

DISCUSSION. The Thamnobryaceae contain six or seven genera and over 150 species, primarily distributed in the tropics; in the Neotropics, seven genera and about 18 species. The family is characterized by the dendroid or frondose habit, frequently producing flagellate branches, leaves of secondary stems oblong-ovate or -lanceolate with branch leaves commonly narrower, apical cells shorter than those of mid lamina, the elongate seta, and moderately well developed double peristome.

The treatment presented here is adopted largely from Sastre-De Jesús (1987), with the exception of the inclusion of *Porotrichodendron*. Flagellate branches are produced by most species in the Neotropics. These branches serve as asexual propagulae and probably promote local dispersion. The Thamnobryaceae is placed in the Neckeraceae by various authors; see discussion under the Neckeraceae.

Study guide. Leaves of the stipe (and their orientation both when dry and wet), secondary stem and branches are required for identification; a sample of each of the three types of leaves should be obtained to observe variation.

LITERATURE. Enroth, J. 1994. On the evolution and circumscription of the Neckeraceae (Musci). Journal of the Hattori Botanical Laboratory 76: 13–20. - Sastre-De Jesús, I. 1987. A revision of the Neckeraceae Schimp. and Thamnobryaceae Marg. & Dur. in the Neotropics. Ph. D. dissertation, City University of New York.

1. Apical leaf cells usually rounded with angles projecting or not; secondary stem leaves small, to 1.4 mm long ..... **Pinnatella**
1. Apical leaf cells rhombic to fusiform, smooth or if papillose by projecting angles; secondary stem leaves mostly longer than 1.5 mm 2
2. Costa short, 1/4–1/3 lamina length, single or forked ..... **Homalia**
2. Costa usually elongate, 1/2 or more the lamina length, single 3
3. Marginal teeth at apex of stem leaves deeply serrate; cells of teeth often with 5 or more oblong cells ..... **Homaliodendron**
3. Marginal teeth at apex of stem leaves not deeply serrate; cells of teeth 1–3 4
4. Plants usually dull or dark green to blackish; costa strong, mostly subpercurrent; apical cells mostly short-rhombic ..... **Thamnobryum**
4. Plants usually glossy light yellowish-green to somewhat dark green; costa slender, mostly 1/2–3/4 lamina length; apical cells fusiform to long-rhomboidal 5
5. Plants lax and somewhat soft, often subpendent; branches terete-foliate .. **Porotrichodendron**
5. Plants often rather stiffly erect, or if lax then leaves distant; branches mostly complanate-foliate ..... 6.
6. Leaf alar region differentiated, cells subquadrate, ± thick-walled, golden-brown; rather rare, lower to upper montane of Colombia and Bolivia ..... **Porotrichopsis**
6. Leaf alar region weakly or not differentiated, cells gradually differentiated, concolorous; common and widespread ..... **Porotrichum**

Homalia (Fig. 215) - Two species in the Neotropics, *H. glabella* (Hedw.) Bruch, Schimp. & W. Gümbel found in Mexico, Central America, Caribbean, Venezuela and southeastern Brazil, and *H. trichomanoides* (Hedw.) Brid. var. *trichomanoides* known only from Jalisco, Mexico (widespread in the Northern Hemisphere). A genus of five species primarily from the Northern Hemisphere.

HABITAT. Moist or wet shaded sites on rock (limestone boulders), exposed tree roots or trunks; lowland to (lower) montane forests, at elevations from 20–2500 m.

DESCRIPTION. **Plants** medium sized to large, forming tufts, iridescent green. **Primary stems** creeping; leaves oblong-ligulate; costae single or double. **Secondary stems** frondose, perpendicular to substrate, to 15 cm tall, complanate-foliate, simple to irregularly pinnately branched; pseudoparaphyllia filamentous. **Leaves** erect-spreading, oblong-ligulate or -lingulate, 1.2–3.5 mm long, to 1.5 mm wide, asymmetric, apex obtuse-rounded to broadly acute; margins plane, occasionally folded, serrulate to serrate distally; costae single or forked or mixed with a few leaf costa short and single, 1/4–2/3 lamina length; apical cells rhomboidal to irregularly rhombic; median cells long fusiform or long hexagonal, porose or not; basal cells hexagonal to linear, weakly porose. **Perichaetia** lateral. **Seta** elongate, 10–20 mm long, smooth. **Capsule** erect, urn cylindrical, to 2.2 mm long; stomata superficial. **Operculum** conic. **Peristome** with exostome teeth finely cross-striate below, distally papillose; endostome basal membrane high, segments keeled and perforate, papillose, cilia 1–4. **Calyptra** cucullate. **Spores** spherical, faintly papillose.

DISCUSSION. The genus is readily distinguished by the short, forked or occasional single costa. Additional features include the glossy, asymmetric broadly oblong-ligulate or lingulate leaves, distally finely serrulate to weakly serrulate, broadly acute to obtuse-rounded leaf apex, and rhomboidal to rhombic apical cells. *Homalia* may be confused with the Neckeraceae, particularly *Neckera*, but in the latter genus the leaf apex is gradually short acuminate to acute (if obtuse then stem paraphyllia abundant), the capsules are immersed to shortly exserted. In addition, in Neckera the sparse to abundant paraphyllia (not present in all species) and undulate leaf surface all aid in distinguishing this genus from Homalia.

LITERATURE. He, S. 1997. A revision of *Homalia* (Musci: Neckeraceae). Journal of the Hattori Botanical Laboratory 81: 1–52 [keys, illustrations, maps].

Homaliodendron (Fig. 216) - A single species in the Neotropics, *H. flabellatum* (Sm.) M. Fleisch. known from Mexico, Central America, and the Greater Antilles (also Central and East Asia, Pacific); about 25 species primarily from Southeast Asia.

HABITAT. Montane forests, at elevations from 1000–3000 m.

DESCRIPTION. **Plants** rather large, forming tufts. **Primary stems** creeping. **Secondary stems** frondose, perpendicular to substrate, to 15 cm tall, irregularly pinnately branched, flagellate branches

frequent; in cross-section outer rows of cells small, thick-walled, inner cells larger, central strand absent; pseudoparaphyllia foliose. **Stipte leaves** erect-appressed, triangular to lanceolate. **Stem leaves** erect-spreading to spreading, oblong-ligulate to obovate, 3–4 mm long, to 1.5 mm wide, apex obtuse to round; margins plane, folded at base or not, coarsely and sharply toothed, teeth multicellular; costa single, 1/2–3/4 lamina length, rather slender; apical cells rhombic; median cells rhomboidal; basal cells oblong-rectangular, porose; branch leaves similar, 2–3 times smaller. **Dioicous**. **Perichaetia** lateral. **Seta** rather short. **Capsule** erect, urn ovoid to cylindrical; stomata superficial; annulus absent. **Operculum** conic. **Peristome** with exostome teeth lanceolate, faintly striate-papillose below, distally papillose; endostome basal membrane moderately high, segments narrow, keeled and narrowly perforate, papillose, cilia absent. **Calyptra** cucullate, hairy. **Spores** spherical, papillose.

DISCUSSION. *Homaliodendron* is distinguished by the frequently flagellate, frondose plants, obtuse to rounded, short oblong-ligulate to obovate leaves, single costa, coarse and sharp teeth along the upper margin, with teeth composed of several cells, and rhombic median cells. Sporophytes are unknown for the Neotropics; reproduction is by propagula in the form of flagellate branches. Enroth (1990) transferred *Porotrichum piniforme* (Brid.) Mitt. to *Homaliodendron* on the basis of sporophytes discovered from the Paleotropics.

LITERATURE. Enroth, J. 1989. *Homaliodendron decompositum* (Brid.) Wagn. reduced to synonymy with *H. flabellatum* (Sm.) Fleisch. Journal of Bryology 15: 805–806. - Enroth, J. 1990. Notes on the Neckeraceae (Musci) 3–7. *Homaliodendron piniforme* comb. nov. and new synonyms in *Porotrichum*, *Himantocladium* and *Neolindbergia*. Nova Hedwigia 51: 551–559.

Pinnatella (Fig. 216) - A single species in the Neotropics, *P. minuta* (Mitt.) Broth. (also found in Africa and southern India); a pantropical genus of 15 species.

HABITAT. On tree trunks and rocks; moist lowland to submontane forests, from near sea level to 800(–1200) m.

DESCRIPTION. **Plants** small, forming inconspicuous short tufts. **Primary stems** creeping; leaves ovate-lanceolate, acute, margins crenulate. **Secondary stems** erect to somewhat curved, frondose, 1–2(–4) cm tall, regularly pinnately branched, flagellate branches slender. **Secondary stem leaves** erect-spreading, ovate-short ligulate, 1–1.4 mm long, slightly concave, apex obtuse to broadly acute; margins plane, crenulate; costa single, ca. 3/4 lamina length, strong, notched at the tip; apical and median cells oval to irregularly rounded, mostly isodiametric; uni- to pluripapillose, rather inconspicuous, thick-walled; basal cells oblong-rectangular, smooth. **Branch leaves** ligulate, smaller. **Dioicous**. **Perichaetia** lateral. **Seta** short, roughened above. **Capsule** erect, urn ovoid; stomata superficial; annulus somewhat differentiated. **Operculum** conic-short rostrate. **Peristome** with exostome teeth papillose; endostome basal membrane low, segments papillose, cilia absent. **Calyptra** type unknown. **Spores** spherical, papillose.

DISCUSSION. The genus is readily distinguished by the small habit, obtuse to broadly acute-rounded, ovate short-ligulate leaves, and unipapillose, rounded upper laminal cells. In the Neotropics sporophytes are unknown and apparently only female plants are present (Enroth, 1994). Reproduction is likely asexual by flagellate branches.

LITERATURE. Enroth, J. 1994. A taxonomic monograph of the genus *Pinnatella* (Neckeraceae, Bryopsida). Acta Botanica Fennica 151: 1–90 [keys, illustrations, maps]. - Hyvönen, J. & J. Enroth. 1994. Cladistic analysis of the genus *Pinnatella* (Neckeraceae, Musci). The Bryologist 97: 305–312.

Porotrichodendron (Fig. 216) - A neotropical genus of possibly only 3-4 species; *P. lindigii* (Hampe) W. R. Buck and *P. superbum* (Taylor) Broth. are two common species known from the Greater Antilles, Mexico, Central America, tropical Andes.

HABITAT. Epiphytic on treelets and shrubs, occasionally on leaf litter and humus; most frequent in upper montane forests, 1050–3750 m.

DESCRIPTION. **Plants** medium to large, often pendulous, forming soft mats or wefts, mostly brown to golden-brown. **Primary stems** creeping. **Secondary stems** stipitate or substipitate -often appearing absent, distinctly to weakly frondose, erect to subpendent, irregularly 1–2-pinnately terete-foliate branched; flagellate branches frequent. **Leaves** broadly to somewhat narrowly ovate-short lanceolate, to 1.5 mm long, concave, apex acute to acute-obtuse and apiculate, base subauriculate or not; margins plane to more commonly somewhat enrolled or incurved, distal half serrulate, apex often serrate; costa single, 2/3–3/4 lamina length, occasionally costa branched or spurred below; laminal cells firm-walled and smooth; apical cells rhombic to rhombic-oblong; median cells linear to fusiform or rhomboidal, smooth, porose; alar cells differentiated or not. **Branch leaves** smaller, narrowly ovate to oblong, acuminate, auriculate or not. **Dioicous**. **Seta** elongate, to 20 mm long, smooth. **Capsule** erect to suberect, symmetric, urn ovoid to obloid, to 2 mm long, neck short; annulus persistent.

Operculum conspicuously long rostrate. **Peristome** with exostome teeth cross-striate at base, papillose distally; endostome densely papillose, basal membrane high, segments narrow, keeled and perforate, cilia absent or rudimentary. **Calyptra** cucullate, naked, slightly roughened above. **Spores** not observed.

DISCUSSION. The genus is characterized by the rather densely-foliate, erect to subpendent, frondose, secondary stems, terete-foliate branches, concave leaves, moderately long costa, 2/3–3/4 the length of leaf, and very long rostrate operculum. Previously placed in the Lembophyllaceae, and recently in the Neckeraceae. *Porotrichodendron* is in need of revision. The species are poorly circumscribed, and the highly polymorphic habit certainly suggests that some of the described species are simply variations in growth form. Recently Buck (1998) transferred *Porotrichum lindigii* (Hampe) Mitt. to *Porotrichodendron*; *Pireella cavifolia* (Cardot & Herzog) Cardot is a synonym.

LITERATURE. Buck, W. R. 1998 (see general ref.).

Porotrichopsis (Fig. 217) - A monotypic genus, with *P. flacca* Herzog confined to the tropical Andes (Colombia and Bolivia).

HABITAT. On decaying logs and shrubs (associated in part with *Streptopogon*); upper montane forests, 2000–3575 m.

DESCRIPTION. **Plants** forming lax, soft tufts, light green to yellowish-green. **Primary stems** creeping, rusty red, rhizoids clustered beneath, leaves scale-like, triangular-acuminate, ca. 0.25 mm long. **Secondary stems** rather compressed, dark red, few branched; in cross-section outer 2–3 rows of cells small and thick-walled, inner cells large and thin-walled, central strand weak; pseudoparaphyllia foliose. **Stem and branch leaves** distant, deciduous, distally with terminal cluster of young leaves persisting, **stem leaves** oblong-ligulate, 1.9–2.1 mm long, to 0.65 mm wide, apex acute to short acuminate; margins plane, reflexed at base; costa single, to just below or beyond midleaf, weak, occasionally spurred below; laminal cells smooth, median cells rhomboidal to rhomboidal-fusiform; insertion cells golden-brown; alar region differentiated, cells subquadrate, inner cells somewhat inflated, thick-walled, golden-brown; **branch leaves** slender, 1.2–1.5 mm long, to 0.3 mm wide, costa ending below midleaf. **Dioicous**. **Seta** 15–28 mm long, smooth. **Capsule** inclined to horizontal, urn ovoid-cylindrical, to 1.8 mm long, asymmetric. **Operculum** unknown. **Peristome** inserted slightly below mouth, exostome bordered, finely cross-striate papillose; endostome finely papillose, basal membrane relatively high, segments keeled and perforate, cilia absent. **Calyptra** unknown. **Spores** verrucose or papillose.

DISCUSSION. *Porotrichopsis* appears in aspect as a rather depauperate *Porotrichum*. The differentiated subquadrate alar cells that are golden-brown or somewhat reddish help in separating this species from members of that genus. The alar cells are rather suggestive of *Porotrichodendron*. Although yet not recorded for Ecuador or Peru, this inconspicuous species will certainly be found there.

LITERATURE. Enroth, J. 1995. Notes on the Neckeraceae (Musci), 21–22. A taxonomic study on *Porotrichopsis flacca* and *Neckeriopsis inundata*. Fragmenta Floristica et Geobotanica 40: 181–188.

Porotrichum (Fig. 217) - About nine species rather widespread in the Neotropics; *Porotrichum*, including *Porothamnium*, contains far fewer than the reported 70 or more tropical species.

HABITAT. Epiphytic, on trunks and branches of trees and treelets, occasionally on rocks or logs, in moist shaded sites; essentially montane, rarely extending into lowlands except adjacent to the highlands, from near sea level to 3500 m.

DESCRIPTION. **Plants** medium sized to large, forming loose, rarely dense, tufts, glossy to dull green, yellowish-green or golden. **Primary stems** creeping, leaves scale-like or eroded, radiculose. **Secondary stems** frondose, 2–12 cm tall, regularly to irregularly pinnately branched, flagelliform branches common; **stipe** short to long, leaves clasping to squarrose. **Secondary stem leaves** erect to erect-spreading, mostly ovate-oblong or -ligulate, 1–4 mm long, apex mostly broadly acute to obtuse; margins plane to recurved, serrate in distal 3/4 or less, serration often irregular, coarse; costa single, 1/2–3/4 lamina length; median cells fusiform-rhomboidal to oblong-linear, smooth to papillose, papillae projecting at cell angles, variously porose throughout, or only at base, basal cells linear to rectangular, alar region undifferentiated or differentiated, cells short-rectangular or subquadrate. **Branch leaves** often differentiated, or progressively so, smaller and often narrower. **Dioicous**. **Perichaetial** leaves oblong- or ovate-subulate. **Seta** elongate, 10–30(–40) mm long, smooth. **Capsule** erect to horizontal, urn cylindrical, 1–3 mm long, stomata at urn base. **Operculum** short to long rostrate. **Peristome** with exostome teeth papillose to striate or striate-papillose below, distally papillose; endostome basal membrane high, segments papillose, perforate, cilia well developed to rudimentary. **Calyptra** cucullate, smooth and naked. **Spores** spherical, papillose.

DISCUSSION. The genus is characterized by the frondose habit, short to long stipes bearing scale-like leaves, mostly irregularly pinnate with complanate-foliate branches, mostly symmetric leaves, marginal serrations of 1(–2) cells, slender costa 1/2–3/4 leaf length, and elongate rhomboidal to fusiform apical cells. Sporophytes have only been occasionally observed among herbarium collections or in the field. Undoubtedly the primary means of reproduction and dispersal is by the rather fragile flagellate branches that are usually present. The separation of *Porothamnium* from *Porotrichum* is based primarily on peristome features, the former with the exostome cross-striate or striate-papillose below, and cilia rudimentary, the latter with papillose exostome and well developed cilia.

Thamnobryum (Fig. 217) - Two species in the Neotropics, *T. fasciculatum* (Hedw.) I. Sastre (Central America, West Indies, tropical Andes, and southeastern Brazil) and *T. tumidicaule* (K. A. Wagner) F. D. Bowers (Central America, Jamaica); about 40 species, distributed in both the tropics and moist temperate regions.

HABITAT. On rocks along or in inclined stream beds, rarely epiphytic, usually shaded sites; rare in lowland, more commonly montane forests, 200–2700 m.

DESCRIPTION. **Plants** small to rather robust, 5–15(–20) cm tall, forming loose tufts, glossy dark green to blackish. **Primary stems** creeping, leaves scale-like, ovate-triangular, to ca. 1.5 mm long, often eroded from stem, radiculose. **Secondary stems** frondose, stipes mostly elongate, leaves ovate-subulate. **Stem leaves** loosely complanate, erect-spreading, ovate to ovate-lanceolate or oblong-ligulate, 2.5–4 mm long, to 1.2 mm wide, ± plicate when dry, ± concave, lateral leaves folded below, apex broadly acute, base undifferentiated to weakly auriculate; margins plane or slightly recurved at base, irregularly strong serrate in distal 1/4–1/3; costa single, subpercurrent strong; apical cells rhomboidal-fusiform or short-hexagonal, thick-walled, smooth; median cells linear to oblong-rectangular; lower and basal cells irregularly long-rectangular. **Branch leaves** small, flagellate branches usually present, leaves reduced, ligulate-acute, 1 mm long or less. **Dioicous**. **Perichaetia** leaves ovate-subulate. **Seta** elongate, to 20 mm long, smooth. **Capsule** horizontal, urn cylindrical, ca. 3 mm long, stomata base. **Operculum** conic-long rostrate. **Peristome** with exostome teeth cross-striate at base, becoming striate-papillose, distal 1/4 papillose; endostome papillose, basal membrane high, keeled and perforate, cilia present. **Calyptra** unknown. **Spores** possibly papillose.

DISCUSSION. The genus is characterized by the dull, dark green to blackish green plants, subpercurrent costa, and rhombic apical cells. The two neotropical species can be separated as follows: *T. fasciculatum* — leaves oblong-ligulate to ligulate, somewhat plicate when dry, flat, and *T. tumidicaule* — leaves ovate to ovate-lanceolate, smooth when dry, weakly concave.

THUIDIACEAE

Plants small to large and rather robust, forming loose to somewhat dense mats or wefts, dull light to dark green, yellowish-green to -brown, or golden. **Stems** 1–3 pinnately branched, often rather densely tomentose; central strand present; paraphyllia scattered or dense, simple to more commonly branched, papillose. **Leaves** usually weakly to strongly dimorphic. **Stem leaves** appressed to erect-spreading, ovate- or cordate (triangular)-lanceolate or -subulate, apex short to long acuminate; margins plane distally, recurved or reflexed below, entire to serrulate- or crenulate-papillose; costa single, usually strong and projecting on back, percurrent to excurrent; median cells oval to isodiametric, uni- or pluripapillose on back or both surfaces, papillae low or long and often curved. **Branch leaves** broadly to somewhat narrowly ovate or ovate-short lanceolate, apex acute to obtuse, costa often ending below apex. **Asexual structures** apparently absent. **Autoicous** or dioicous. **Perigonia** lateral, leaves ovate to short ovate-lanceolate. **Perichaetia** lateral, leaves usually differentiated, long ovate-lanceolate to lanceolate, margins ciliate or not. **Seta** elongate, smooth to papillose. **Capsule** suberect to horizontal, urn cylindrical, usually curved. **Operculum** short to long rostrate, oblique. **Peristome** double, exostome teeth 16, cross-striate below, distally papillose, endostome lightly papillose, basal membrane high, segments 16, keeled and perforate?, cilia 2–3(4). **Calyptra** cucullate, naked and smooth. **Spores** spherical, smooth to more commonly papillose.

DISCUSSION. The Thuidiaceae contain about seven genera, as defined here (Buck & Crum, 1990), and 150 or more species widely distributed in temperate and tropical regions; in the Neotropics three genera and about 30 species. Recently, Buck and Crum (1990) have segregated *Cyrto-hypnum* (Hampe) Hampe & Lorentz from *Thuidium*; however, Touw (1993) has noted that at least for tropical Asia members, the distinction between these two genera is not clear. Obviously, this needs to be reexamined in greater detail in the Neotropics. The treatment provided by Gier (1980) of the Thuidiaceae for Latin America is minimally useful, but does little to resolve numerous taxonomic problems. All genera are in need of critical study in the Neotropics.

Study guide. Attention must be given to branching pattern, i.e., 1-, 2-, 3-pinnately branched. Paraphyllia need to be observed, both on stems with some of the leaves removed and separated from the stem in order to examine the surface ornamentation. Stem and branch leaves are required with particular attention paid to papillae which, together with paraphyllia allow many of the neotropical species can be identified. In a few cases, seta ornamentation and the inclination of the capsule are required.

LITERATURE. Buck, W. R. & H. Crum. 1990. An evaluation of familial limits among the genera traditionally aligned with the Thuidiaceae and Leskeaceae. Contributions to the University of Michigan Herbarium 17: 55–69. - Gier, L. J. 1980. A preliminary study of the Thuidiaceae (Musci) of Latin America. Journal of Bryology 11: 253–309 [poor keys and illustrations]. - Touw, A. 1976. A taxonomic revision of *Thuidium*, *Pelekium*, and *Rauiella* (Musci: Thuidiaceae) in Africa south of the Sahara. Lindbergia 3: 135–195. - Touw, A. 1993. Notes on tropical Asian Thuidiaceae, with two new Malesian species of *Thuidium* s.l. Journal of the Hattori Botanical Laboratory 74: 193–204. - Watanabe, R. & I. Kawai. 1975. Systematic studies on the conducting tissue of the gametophyte in Musci (5). What is expected of systematics regarding the inner structure of the stem in some species of Thuidiaceae. The Science Reports of Kamazawa University 20: 21–76.

1. Stem and branch leaf apices ending in a single short or blunt point; plants irregular- or 1-pinnate; paraphyllia smooth or papillose; seta smooth 2
1. Stem and branch leaf apices bifid or notched; plants mostly 2–3 pinnately branched; paraphyllia typically papillose; seta smooth or papillose 3
2. Paraphyllia smooth; laminal cells not bulging, unipapillose ... **Haplocladium** (see Leskeaceae)
2. Paraphyllia papillose; laminal cells strongly bulging, uni- or pluripapillose ..... **Rauiella**
3. Leaf cells papillose on both surfaces; paraphyllia few, unbranched or weakly so; plants mostly small, autoicous; seta smooth or papillose ..... **Cyrto-hypnum**

3 Leaf cells papillose only on back; paraphyllia numerous, branched; plants medium sized to large, dioicous; seta smooth ..... **Thuidium**

Cyrto-hypnum (Fig. 218) - About 30 species recorded for the Neotropics, probably 15 or less are valid.

HABITAT. On soil, logs, tree bases and rocks; moist to semi-dry lowland to lower montane forests, rarely higher, from near sea level to 3000 m.

DESCRIPTION. **Plants** small, forming loose to ± dense mats, light to dark green. **Stems** and branches loosely spreading, 1–3 pinnately branched; central strand present; paraphyllia few and scattered along stems, often absent on branches, unbranched or little-branched, mostly 2–7 celled, weakly papillose. **Leaves** of stems and branches differentiated. **Leaves of stem and primary branches** somewhat similar in size and shape, ovate to cordate- or triangular-short to long acuminate, 0.4–0.7 mm long, often biplicate and short decurrent; margins recurved to reflexed; costa ending below the apex; laminal cells subhexagonal- to subquadrate-rounded, thick-walled, pluripapillose on both surfaces. **Leaves of secondary or tertiary branches** often smaller, mostly ovate to oblong-ovate, 0.15–0.5 mm long, concave, apex acute to acute-rounded or obtuse, mostly bifid or notched; margins plane to erect, entire; costa mostly ending well below the acumen. **Autoicous**. **Perichaetial** leaves elongate, ovate-triangular to -lanceolate, costa single, extending into acumen, apex short to more commonly long acuminate, margins entire to ciliate. **Seta** 8–20 mm long, papillose, occasionally smooth. **Capsule** inclined or pendent, rarely erect or suberect, urn short to ± long ovoid or ovoid-cylindrical, 0.7–2.5 mm long, slightly curved or not; annulus in 2–3 rows. **Operculum** conic to conic short to long rostrate, oblique. **Peristome** with exostome teeth cross-striate, papillose distally; endostome basal membrane high, segments keeled, cilia 1–3(4). **Calyptra** cucullate, naked and smooth. **Spores** spherical, appearing smooth to lightly papillose.

DISCUSSION. The genus is distinguished by small, 1–3 pinnately branched plants, simple or weakly branched paraphyllia of few cells, bifid or notched secondary branch leaf apex, both surfaces of leaf papillose, sexual condition autoicous, and a frequently papillose seta. *Cyrto-hypnum* is typical of tropical lowland forests whereas *Thuidium* is rare or absent in these habitats but becomes relatively common in the highlands where *Cyrto-hypnum* is rare.

Rauiella (Fig. 218) About 4–6 species confined to the neotropical highlands, the two most common species include *R. lagoensis* (Hampe) W. R. Buck (Mexico, Central America, Brazil), and *R. praelonga* (Schimp. ex Besch.) Wijk & Margad. (Mexico, Central America, Greater Antilles, Andes; also SW United States and Africa). There are a few additional species in Africa and Asia.

HABITAT. On rocks and soil, also logs and base of tree trunks, often in somewhat exposed sites; submontane to lower montane forests, occasionally extending into lowlands adjoining montane regions, 330–2350 m.

DESCRIPTION. **Plants** small, forming coarse thin to dense mats, dull olive green, yellowish, or golden to reddish-brown. **Stems** creeping and spreading, pinnately branched; central strand weak; rhizoids beneath, often produced on terminal branch tips; pseudoparaphyllia foliose; paraphyllia rather abundant on stems, few to absent on branches, simple or weakly branched, papillose. **Leaves** erect when dry, spreading when wet, stem and branch leaves dimorphic. **Stem leaves** short to long lanceolate from an ovate base, 0.5–0.9 mm long, to 0.5 mm wide, plicate, apex usually abruptly long acuminate, base weakly decurrent; margins reflexed, crenulate; costa strong, percurrent to short excurrent; laminal cells similar throughout, oval to quadrate-rounded, strongly bulging, uni- or pluripapillose. **Branch leaves** ovate, ca. 0.5 mm long, apex acute to bluntly short acuminate. **Autoicous**. **Perichaetial** leaves glossy pale yellow, setaceous from an ovate base, to 2.3 mm long. **Seta** to 10–15 mm or more long, slightly twisted, smooth. **Capsule** inclined, urn ovoid-short cylindrical, ca. 1.5–2 mm long; annulus present. **Operculum** rostrate, oblique. **Peristome** with exostome teeth finely cross-striate below, distally papillose; endostome basal membrane high, cilia 1–2. **Calyptra** cucullate, naked and smooth. **Spores** spherical, lightly papillose.

DISCUSSION. The genus is characterized by 1-pinnate stems; paraphyllia papillose, leaf apices ending in a single short or blunt point, both surfaces of leaf lamina papillose with cells strongly bulging, and a smooth seta. A few species, previously transferred to *Rauiella* (cf. Gier, 1980), have been retained in *Leskea*, e.g., *L. plumaria* Mitt. and *L. teretiuscula* Mitt. (Buck & Crum, 1990). The species were previously placed in *Rauia* Austin, *hom. illeg*.

LITERATURE. Buck, W. R. & H. Crum 1990 (see family ref.). - Gier, L. J. 1980 (see family ref.).

Thuidium (Fig. 218) - Sixteen species in the Neotropics, probably 5–10 that are valid; a genus widespread in temperate and cool tropical regions.

HABITAT. On soil, humus, logs, and tree bases; submontane to upper montane forests and associated open sites, to páramo or puna.

DESCRIPTION. **Plants** medium sized to large, forming loose to dense coarse mats, olive to dark green, yellowish-brown or golden. **Stems** and branches spreading, 1–3 pinnately branched; central strand well developed; paraphyllia numerous, branched and usually strongly papillose. **Leaves** of stems and branches usually strongly dimorphic. **Stem leaves** broadly ovate-short to long lanceolate, 0.5–2 mm long, biplicate, apex broadly to narrowly short to long acuminate, occasionally ending in a long hyaline capillary hair point; margins often strongly incurved at base, partially inflexed or erect above, serrate or serrulate in distal 2/3; costa strong, ending below acumen or long excurrent; median cells oval-rhombic to ± elongate, unipapillose, rarely pluripapillose, papillae projecting only on lamina back, somewhat erect to curved, basal cells ± elongate. **Branch leaves** ovate-short lanceolate, 0.1–0.5 mm long, 1–3 papillae projecting at back. **Dioicous**. **Perichaetial** leaves elongate, lanceolate to oblong-lanceolate, apex mostly gradual to abruptly long acuminate, margins ciliate or not. **Seta** 15–45 mm long, smooth, rather stout and wiry. **Capsule** inclined to horizontal, urn cylindrical, 1.8–4 mm long, asymmetric. **Operculum** conic-short rostrate. **Peristome** with exostome teeth cross-striate below, distally papillose, with a median zig-zag line, bordered, back trabeculate; endostome basal membrane high, segments keeled, narrowly perforate, finely papillose, cilia 3. **Calyptra** cucullate, naked and smooth. **Spores** spherical, papillose.

DISCUSSION. Features distinguishing this genus include medium to large-sized habit, strongly differentiated stem and branch leaves, numerous, branched paraphyllia, dorsal surface of lamina uni- or pluripapillose, the dioicous sexual condition, and the smooth seta. *Thuidium* is a typical and common component of the open and forested montane, and páramo.

TRACHYPODACEAE

Plants medium sized to rather large, forming loose to dense mats. **Primary stems** creeping. **Secondary stems** spreading or subascending, regularly to irregularly pinnately branched. **Leaves** crowded, spreading to wide-spreading, narrowly lanceolate from an ovate base or triangular-lanceolate, weakly to strongly plicate, apex broadly or long acuminate, base distinctly although not strongly auriculate; margins rather coarsely serrate to finely papillose and serrulate; costa single, strong below, ending in or well below acumen; laminal cells rhombic to oblong-rhomboidal or -hexagonal, unipapillose or pluripapillose, papillae over cell lumen or along walls or both; auricle region with cells subquadrate to short rectangular, mostly smooth; marginal cells forming a border of more elongate, smooth cells or marginal cells similar or slightly smaller and pluripapillose. **Dioicous**. **Sporophytes** not known from the Neotropics. **Perichaetia** lateral. **Seta** elongate, papillose.

Capsule erect, urn subglobose to ovoid. **Operculum** conic long-rostrate, oblique. **Peristome** double, exostome teeth 16, narrow, papillose, with a median zig-zag line; endostome basal membrane low, segments 16, shorter than exostome, papillose, keeled or not, cilia absent. **Calyptra** cucullate, apparently naked, or mitrate and hairy. **Spores** subspherical, papillose.

DISCUSSION. The Trachypodaceae contain six genera and about 20 species, exhibiting a pantropical distribution, primarily of the Paleotropics; in the Neotropics, two genera and two species. The family is placed in the Leucodontales. Recently, Buck (1994) transferred the neotropical taxa of the Trachypodaceae to the Meteoriaceae. There appears to be a good case for this decision, although it was based on traditional phenetic reasoning. Sporophytes are unknown in the Neotropics for both genera, and the descriptions are based on specimens from the Paleotropics. It is assumed that these mosses reproduce asexually, although no specialized structures have been described.

LITERATURE. Buck, W. R. 1994. A new attempt at understanding the Meteoriaceae. Journal of the Hattori Botanical Laboratory 75: 51–72. - Zanten, van B. O. 1959. Trachypodaceae. A critical revision. Blumea 9: 477–575.

1. Leaf cells unipapillose, papillae centrally located over cell lumen; leaves strongly plicate; costa ending in acumen ..... **Trachypodopsis**
1. Leaf cells pluripapillose, papillae appearing numerous over cell lumen and along and between walls; leaves weakly plicate; costa ca. 2/3 lamina length ..... **Trachypus**

Trachypodopsis (Fig. 219) - A single species in the Neotropics, *T. serrulata* var. *crispatula* (Hook.) Zanten known from Mexico and Guatemala (also Southeast Asia).

HABITAT. At the base of trees, on logs and rocks; mostly associated with montane forests, reported from moderate elevations.

DESCRIPTION. **Plants** rather large, mostly glossy green, yellow or golden. **Secondary stems** spreading, irregularly pinnately branched. **Leaves** narrowly lanceolate from an ovate base or triangular-lanceolate, to 4 mm long, strongly plicate, apex long acuminate, often crispate-undulate when dry, base usually auriculate; margins coarsely serrate; costa strong below, ending in acumen; laminal cells rhombic to oblong-rhombic, unipapillose, papillae over cell lumen; auricle region with cells subquadrate to short rectangular; marginal cells forming a border of more elongate, smooth cells, not papillose. **Capsule** with urn subglobose to ovoid. **Peristome** with endostome segments often keeled. **Calyptra** cucullate, apparently naked. **Spores** subspherical, strongly papillose.

DISCUSSION. The genus is characterized by the spreading secondary stems, strongly plicate, triangular-lanceolate leaves, elongate, smooth, rather sharply serrate cells at margins, costa ending in the acumen, and unipapillose laminal cells. *Trachypodopsis otiophylla* (Cardot) Cardot is a synonym used by some authors.

Trachypus (Fig. 219) - A single species and two varieties in the Neotropics, *T. bicolor* Reinw. & Hornsch. var. *viridulus* (Mitt.) Zanten known from Mexico, Central America, Greater Antilles, and the northern Andes (also the Paleotropics), and var. *hispidus* (Müll. Hal.) Cardot known from southeastern Brazil (also the Paleotropics); about five species with a pantropical distribution.

HABITAT. On soil, humus, logs, base trunk of trees or rocks; montane forests, 1050–3100 m.

DESCRIPTION. **Plants** medium sized, dull olive to dark green, usually blackish or brownish tinged. **Secondary stems** spreading to occasionally subpendent, pinnately branched; in cross-section central strand weak; pseudoparaphyllia foliose. **Leaves** somewhat appressed to spreading, broadly lanceolate above from an ovate base to broadly triangular-lanceolate, to 3 mm long, to 0.9 mm wide, weakly plicate, becoming narrowly acuminate, tips capillary or not, base short decurrent and auriculate; margins plane to recurved above base, bluntly serrulate and finely papillose; costa ca. 3/4–4/5 lamina length; median cells oblong-linear, thick-walled, finely pluripapillose, papillae over cell lumen and along cell walls; basal cells smooth, porose; auricle cells rounded, smooth. **Capsule** with urn ovoid. **Peristome** with endostome segments not keeled. **Calyptra** mitrate, with long nodose hairs.

DISCUSSION. The genus is distinguished by the partially blackish- or brownish-tinged plants, the weakly plicate leaves that are narrowly long lanceolate above from a rather distinctly expanded base, the serrulate margins of finely pluripapillose-serrulate cells, costa ca. 2/3 lamina length, and the finely pluripapillose laminal cells with papillae extending over and between the cell lumens. The var. *viridulus* (Mitt.) Zanten, has been recognized by some authors at the species level.