Guide to the Genera of Liverworts and Hornworts of Malaysia

Gaik Ee Lee
S. Robbert Gradstein

HATTORI BOTANICAL LABORATORY

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2021

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Front and back cover photographs: Background, *Hung Yung Tang*; Inset, *Gaik Ee Lee*. From left to right: *Marchantia emarginata* from Cameron Highlands, *Anthoceros angustus* from Gunung Raya, Langkawi, *Schistochila blumei* from Cameron Highlands, *Pleurozia gigantea* from Genting Highlands. Back: *Schistochila sciurea* from Gunung Jasar, Cameron Highlands.

Print ISBN: 978-4-902590-99-9 **Online ISBN: 978-4-910603-00-1**

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Date of publication: 20 December 2021
Published by Hattori Botanical Laboratory

Printed by the Kokusai Bunkensha
Yamabuki-cho 332–6, Shinjuku City, Tokyo 162–0801, Japan

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Publications supported by Grant-in-Aid for Scientific Research (Specially Designated Research Promotion) of Japan Society for the Promotion of Science.

Foreword

Schiffner once said that "No language in the world is rich enough to describe 800 different leaf forms" (Roth G. 1910; Allg. Bot. Z. Syst. 16: 123). To this could also be added: A picture saves a thousand words.

The simple, elegant and highly informative illustrations by Lee in this book are indeed welcome, whether as a beginner discovering the fascinating world of bryophytes or a professional bryologist familiar with the group, giving all a chance to determine to generic level the beautiful Malaysian bryophytes. The clarity of the drawings will be most useful, particularly to careful students, and open a new door to discovering the hidden biodiversity of East Asia. It is our pleasure to publish this book in the occasion of the 75th anniversary of the Hattori Botanical Laboratory, showing the efforts of the authors and of the scientific cooperation among worldwide bryologists.

October 2021

Tomoyuki Katagiri, Director of Hattori Botanical Laboratory

Acknowledgments

We express our gratitude to Prof. Rui-Liang Zhu (Shanghai) for sending critical literature, to Prof. Tamás Pócs (Eger) and Dr. Monica Suleiman (Sabah) for their constructive comments and corrections, to Dr. Vadim Bakalin (Vladivostok) for his help with the identification of *Solenostoma* species, and to Dr. Tomoyuki Katagiri for making it possible to publish the book with the Hattori Botanical Laboratory. Part of this work was supported by the Ministry of Education (MOE) Malaysia through Fundamental Research Grant Scheme (FRGS/1/2018/WAB13/UMT/03/1) awarded to Gaik Ee Lee.

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Preface

Malaysia has a very rich flora of liverworts and hornworts. Almost 800 species and infraspecific taxa have been reported (Pócs & Lee 2016; Lee *et al.* 2013, 2018a), representing about 15% of the world's liverwort species. The vascular flora of Malaysia has been well-studied but non-vascular plants, including liverworts and hornworts, have received much less attention. Although they are easy to collect, liverworts and hornworts of Malaysia are not easy to identify due to the lack of a good identification tool and this has been an impediment for their study. To fill part of this gap in the literature, we have prepared an illustrated generic guide to the liverworts and hornworts of Malaysia.

The present book provides keys, descriptions and illustrations for the 124 genera and 43 families of liverworts and hornworts recorded from Malaysia. A few additional genera, found in neighboring countries but not yet in Malaysia, have also been included in the keys. The generic and family descriptions include a brief morphological diagnosis of the group, a discussion of the most important features for identification, data on the diversity, distribution and habitats of the group, and references to the main literature. Illustrations are redrawn from the *Guide to the Liverworts and Hornworts of Java* or other sources mentioned in the figure legends. The drawings emphasize important characters for identification and are not exhaustive. Since qualitative characters are more important than quantitative characters for identification of the genera, we have omitted indications of magnification (Buck 1998). The introductory section of the book provides a brief history of the knowledge of the liverwort flora of Malaysia, a discussion of the main morphological features of liverworts and hornworts, a brief introduction on their ecology, and information how to collect and study liverworts and hornworts.

A glossary of technical terms, a bibliography and an index to scientific names are also provided. The following four new names are proposed in this book:

Heteroscyphus integerrimus (Schiffn.) Gradst. & G.E.Lee, comb. nov. (= *Chiloscyphus integerrimus* Schiffn.)
Syzygiella contracta (Reinw. *et al.*) Gradst. & G.E.Lee, comb. nov. (= *Cuspidatula contracta* (Reinw. *et al.*) Steph.)
Syzygiella flaccida (Steph.) Gradst. & G.E.Lee, comb. nov. (= *Anomacaulis flaccidus* (Steph.) Grolle)
Syzygiella flexicaulis (Nees) Gradst. & G.E.Lee, comb. nov. (= *Jamesoniella flexicaulis* (Reinw. *et al.*) Schiffn.)

History of the knowledge of the liverworts of Malaysia[1]

The first collections of liverworts were probably made on Penang Island in the early 19th century by Nathaniel Wallich, a surgeon and botanist of Danish origin who carried out major explorations in India and Southeast Asia based on Calcutta. Wallich gathered 12 liverwort species on Penang Island, including *Jungermannia ligulata* Lehm. & Lindenb. (= *Mastigolejeunea ligulata* (Lehm. & Lindenb.) Schiffn.) described by the German botanists Johann Georg Christian Lehmann and Johann Bernhard Lindenberg (Lehmann 1834), and *Ptychanthus tumidus* Nees (= *Schiffneriolejeunea tumida* (Nees) Gradst.) described by the German botanist Christian Gottfried Nees von Esenbeck (Nees 1838). During 1865–1867 the Italian naturalist Odoardo Beccari collected liverworts in Sarawak. His specimens were studied by the Guiseppe De Notaris in Rome (De Notaris 1874, 1876) who recorded 51 species, including 28 new to science and one new genus, i.e., *Diploscyphus* de Not. (= *Conoscyphus* Mitt.). The German hepaticologist Franz Stephani subsequently published 62 species, many of them new to science, in his *Species Hepaticarum* (1898–1924), based on collections made in various localities in Malaysia by Beccari, Henry Nicholas Ridley and Alfred Hart Everett. Stephani's work was critically revised by later authors, first of all Verdoorn (e.g., 1930, 1934), and many of the species newly described in *Species Hepaticarum* could not be substantiated.

During the first half of the 20th century, little liverwort exploration work was done in Malaysia. The most important collections were made by the distinguished British forest ecologist and bryologist Paul W. Richards in the framework of Oxford University Expedition to Sarawak in 1932 (Richards 1950). This material was worked up by Herzog (1950, 1951), who reported 141 liverwort taxa including 35 new species including two unusual new rheophytic genera from Gunung Dulit, *Stenorrhipis* Herzog (= *Kymatocalyx*) and *Aphanotropis* Herzog (= *Colura*). The Dutch bryologist Willem Meijer did extensive liverwort collecting in Sabah in the 1950s and published a few short papers based on this material (Meijer 1954, 1957, 1958). Further records based on Meijer's collections are found scattered in the taxonomic literature dealing with Asiatic liverworts.

In the second half of the 20th century major contributions to Malaysian liverworts were made by Japanese bryologists. In 1963 a bryological expedition to Mt. Kinabalu was carried out by the Japanese bryologists Zennoske Iwatsuki and Masami Mizutani. About 6000 liverwort specimens were collected and numerous new records and new taxa were published based on these collections (e.g., Hattori 1964, 1966; Hattori & Kamimura 1971; Kuwahara 1965; Kitagawa 1964, 1967a, 1970; Mizutani 1966, 1969, 1970, 1973, 1974). The two collectors were honored by new liverwort genera named after them, *Iwatsukia* N.Kitag. from Mt. Kinabalu (now a synonym of *Odontoschisma*; Aranda *et al.* 2014), and the unusual thalloid genus *Mizutania* Furuki & Z.Iwats., first discovered on Mt. Kinabalu and later found elsewhere in Borneo and in the Cameron Highlands (Furuki & Iwatsuki 1989). The minute thalloid plant was initially placed in a family of its own, Mizutaniaceae, in the thalloid Metzgeriales, but was recently, unexpectedly, shown to be a member of the

[1] Text adapted from Lee *et al.* (2018a). Since hornworts of Malaysia are little known and include only five recorded species, this chapter focuses on liverworts.

leafy liverwort family Calypogeiaceae (Jungermanniales) based on molecular evidence (Masuzaki *et al.* 2010). Several other Japanese bryologists collected on Mt. Kinabalu as well as in Peninsular Malaysia (Penang Island, Cameron Highlands), and additional new species were reported (e.g., Inoue 1967a, 1967b; Kitagawa 1969b, 1971; Kitagawa & Kodama 1974, 1975; Kodama 1976). Meanwhile, Johnson (1958, 1972) published an account of the thallose liverworts found in Peninsular Malaysia and a short report on bryophytes, including liverworts, from Gunung Benom, Pahang, whereas Tixier (1971, 1974, 1980) recorded liverworts from Fraser Hill, Kedah Peak (Gunung Jerai) and the Cameron Highlands.

A second major bryological expedition to Mt. Kinabalu took place in 1986 in the framework of the German BRYOTROP project, resulting in a series of papers on taxonomy, ecology and altitudinal zonation (e.g., Frahm 1990a, 1990b; Frahm *et al.* 1990; Kürschner 1990; Váňa 1991a, 1991b, 1992, 1993). In the framework of this project, a catalogue was prepared of the liverwort species recorded from Sabah and Sarawak (Menzel 1988). Chuah-Petiot (2011) provided the first comprehensive checklist of the liverworts for the whole of Malaysia and reported a total of 758 species and infraspecific taxa, in 122 genera and 38 families. An updated list of the Lejeuneaceae of Malaysia, the largest family of liverworts, was published by Lee *et al.* (2013), enumerating 274 species and 10 infraspecific taxa, in 30 genera. The information contained in these two catalogues has been an essential basis for this book.

Recent papers on Malaysian liverworts include a taxonomic revision of *Lejeunea* (Lee 2013; Lee & Gradstein 2013), leading to the recognition of 30 species and two varieties for the area, including various new records and description of some new species. Other recent work on Malaysian liverworts include the study on the large genus *Bazzania* with the report of 11 species new to the country and a key to 26 species from Peninsular Malaysia (Cheah & Yong 2016), descriptions of new Malaysian species of *Eotrichocolea*, *Mastigolejeunea* and *Riccardia* (Katagiri *et al.* 2012; Furuki *et al.* 2013; Sukkharak 2014), integrative morphological, molecular and/or ultrastructural studies of the peculiar genera *Metzgeriopsis* (Gradstein *et al.* 2006) and *Mizutania* (Masuzaki *et al.* 2010; Pressel 2016) as well as on *Trocholejeunea* (Wang *et al.* 2014), *Odontoschisma* (Gradstein & Ilkiu-Borges 2015), *Cheilolejeunea* (Ye *et al.* 2015), *Spruceanthus* (Shi *et al.* 2015), *Chiastocaulon* (Patzak *et al.* 2016), *Allorgella* (Bechteler *et al.* 2016a), *Thiersianthus* (Zhu *et al.* 2017), *Leptolejeunea* (Bechteler *et al.* 2017; Shu *et al.* 2021), *Mohamedia* (Zhu *et al.* 2019), and several chemical studies (e.g., Nagashima *et al.* 1991; Ng *et al.* 2016a, 2016b; for more complete list of titles see Lee *et al.* 2018a). Finally, results of new floristic liverwort explorations were published by Pócs *et al.* (2014a, 2020), Pócs & Lee (2016), Cheah (2017), Lee *et al.* (2019), Pesiu *et al.* (2021) and Sarimi *et al.* (2021).

Morphology and ecology of liverworts and hornworts[2]

Liverworts (Marchantiophyta) include about 5000–6000 species worldwide (Gradstein 2021; some authors suggest more than 7000 species worldwide but those figures are exaggerations), and are the basal group of the extant land plants, followed by mosses, hornworts and vascular plants. Together with mosses (Bryophyta s.str.) and hornworts (Anthocerotophyta) they belong to the bryophytes (Bryophyta s.l.). Differences between the three groups are shown in Table 1 (p. 156). Unique characters of liverworts, separating them from mosses and hornworts, are the great variety of **branch types**, the presence of **oil bodies** in the cells, and the **maturation of the spores before the elongation of the seta**. Moreover, growth (by a 2–3 sided apical cell) gives rise to a **thallus** or to **leaves in 2–3 straight rows**, not in a spiral. Like in other bryophytes, the life cycle of liverworts is characterized by an alternation of two generations, a haploid **gametophyte** (= the generation that produces gametes for sexual reproduction) and a diploid **sporophyte** (= the generation that produces spores for dispersal). The gametophyte of liverworts is the free-living green plant whereas the sporophyte is a "parasite", deriving nutrients for its growth from the gametophyte to which it is **permanently attached**. The gametophyte is attached to the substrate by **unicellular rhizoids**, consisting of only one single cell. Liverworts like other bryophytes do not have roots. The sporophyte of the liverworts consists of a foot, a seta, and a capsule which contains **spores** as well as **elaters** (see below). The spores germinate into a tiny **protonema** from which the new gametophyte develops. In liverworts the protonema is usually thalloid, and gives rise to only **one gametophyte**.

Liverworts were traditionally divided in **thalloid liverworts** and **leafy liverworts**. Modern studies based on molecular analysis have shown that liverworts comprise three major lineages or classes, **Haplomitriopsida**, **Marchantiopsida** and **Jungermanniopsida**. The Jungermanniopsida are further subdivided in at least four subclasses. A thallus occurs in Marchantiopsida and two subclasses (Metzgeriidae, Pelliidae) of Jungermanniopsida, whereas leaves and stems are seen in Haplomitriopsida and most of the Jungermanniopsida. In subclass Pelliidae, some families are leafy and other families are thalloid.

An outline of the classification of the liverworts of Malaysia is given in the chapter "Classification"; brief morphological descriptions and discussions of the classes and subclasses, as well as families and genera, are provided in the chapter "Keys and descriptions". Here, we will discuss the general morphology of liverworts, separately for leafy and thalloid plants.

Morphology of leafy liverworts

Leafy liverworts include Jungermanniopsida subclasses Jungermaniidae and Pleuroziidae, and the Haplomitriopsida (*Haplomitrium*, *Treubia*). The leaves of all leafy liverworts lack a midrib (= costa) and are arranged in 2–3 rows, two lateral rows of leaves and one ventral row (= underleaves). The underleaves are usually smaller than the leaves and are sometimes absent. The position of the lateral leaves may be **incubous**, **succubous** or **transverse**. In incubous leaves the dorsal leaf margin lies on top of the ventral margin of the adjacent

[2] Text adapted from Gradstein (2011).

younger leaf, in succubous leaves it is just the other way around. Another characteristic of liverwort leaves is that they are sometimes divided into two or more lobes or filaments. The lobes may be unequal in size, the dorsal lobe usually being larger than the ventral one (sometimes, however, the dorsal lobe is smaller). A small ventral lobe or **lobule** is found in the order Porellales which includes the main epiphytic liverwort groups such as Frullaniaceae, Lejeuneaceae, Porellaceae and Radulaceae.

The leaves and underleaves in Jungermanniopsida subclasses Jungermaniidae and Pleuroziidae are generally only one cell-layer thick (exceptionally more than one cell-layer, e.g., in *Schiffneria*). Moreover, they originate from 2 leaf-initial cells (in Porellales there is even a third initial cell, forming the stylus), and for this reason the leaf can be divided into lobes. In Haplomitriopsida and leafy members of subclass Pelliidae, in contrast, the leaves originate from only one leaf-initial cell, therefore they are always undivided; moreover, they are always more than one cell-layer thick in the lower half.

The stems of leafy liverworts are thin and fragile or thick and rigid, and can be variously branched. In cross section, the stem is made up of an outer layer of cells called **epidermis**, the inner part is called **medulla**. An epidermis consisting of large, thin-walled cells is called a **hyalodermis** and is commonly found in Cephaloziaceae and Lejeuneaceae. Other groups such as Herbertaceae and Plagiochilaceae have rigid stems with a thick-walled, brown epidermis and a **subepidermis** in several layers; such a differentiated thick-walled outer layer of the stem is called a **cortex**.

Leafy liverworts have many different types of branches in terms of their origin, and this sharply separates them from mosses which have only one branch type. There are two basic types, **intercalary branches** and **terminal branches**. Intercalary branches originate from inner stem cells, they have a small collar around the base, and usually originate at right angles (90º) with the stem. Terminal branches, in contrast, originate from a leaf-initial cell or juvenile epidermis cell, they lack a collar, and usually are at oblique angles (45–60º) with the stem. When originating from a leaf-initial cell, the leaf associated with the branch in Jungermanniidae and Pleuroziidae is a **half-leaf** because leaves and underleaves in these groups originate from 2 initials cells.

There are four types of **intercalary** branches:

Bazzania-type: branch originating from ventral side of stem, from underleaf axil. Its base is surrounded by a collar. Present in many families.

Plagiochila-type: branch originating from lateral side of stem, from leaf axil. Its base is surrounded by a collar. Present in many families.

Anomoclada-type: branch originating from the dorso-lateral side of stem. Its base is surrounded by a collar. Found in *Andrewsianthus*.

Lejeunea-type: branch originating from lateral side of stem, from behind the leaf. Its base is surrounded by a collar. Found in Lejeuneaceae and Jubulaceae.

In addition, at least three **terminal** branch types are distinguished:

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. Its base lacks a collar. Present in many families.

Acromastigum-type: branch originating from an initial cell of an underleaf so that it replaces half of the underleaf. The branch is therefore associated with a half-underleaf. Its

base lacks a collar. Found in *Acromastigum*.

Radula-type: branch originating from a juvenile epidermis cell just behind the apical cell, and therefore associated with an unmodified leaf. Its base lacks a collar. Found in *Radula* and Lejeuneaceae. In Lejeuneaceae, *Radula*-type branches are mostly restricted to **innovations** (= branches originating just below the perianth).

The basal liverwort *Haplomitrium* differs from all other leafy liverworts in possessing collarless branches originating from the (mature) stem epidermis. The branches of *Haplomitrium* are similar in origin to those found in mosses.

The leaf cells vary in shape and often have collenchymatous thickenings called **trigones**. The cells usually have chloroplasts and oil bodies when fresh. The **oil bodies** are cell organelles unique to liverworts and contain terpenoids. Their number per cell, size, and structure varies and is taxonomically important. In some liverworts they are finely or coarsely segmented, in others they are quite homogeneous. Oil bodies can only be observed in fresh material. In the leaves of Frullaniaceae and some members of Lejeuneaceae specialized cells occur that have one very large oil body and lack chloroplasts; these cells are called **ocelli**. The distribution of ocelli within the plants is an important taxonomic character.

Reproductive organs or gametangia are produced on stems or branches and are surrounded by bracts (= specialized leaves) and bracteoles (= specialized underleaves). The male gametangia or **antheridia** are developed in the axils of bracts (rarely in the axils of bracteoles), each bract holding one or more antheridia. The antheridia are usually spherical in shape and attached to the stem by a thin stalk. The female gametangia or **archegonia** are produced at the tip of long or short shoots, from the apical cell, exceptionally from the stem epidermis away from the apical cell (in Haplomitriopsida). They are surrounded by one or more series of bracts and bracteoles (bracteoles sometimes absent), and are frequently enclosed by a thin tubular organ, the **perianth**. The perianth is of foliar origin and develops by fusion of the inner pair of bracts and bracteoles (when present). It is very small before fertilization and becomes greatly enlarged after fertilization, emerging beyond the bracts. The function of the perianth is to protect the young, developing sporophyte. The perianth varies considerably in shape and structure and provides important taxonomic characters. In some taxa, the perianth is replaced by a fleshy, tubular structure, a pendent **marsupium** or an erect **perigynium**, which develops from stem tissue or from the calyptra (= wall of the modified, fertilized archegonium). A marsupium is seen in, e.g., Acrobolbaceae, *Balantiopsis*, Calypogeiaceae, Geocalycaceae and Jackiellaceae, a perigynium in, e.g., Haplomitriopsida, *Isotachis*, Lepicoleaceae, Schistochilaceae, Solenostomataceae and Trichocoleaceae. Like the perianth, the function of the marsupium or perigynium is the protection of the developing sporophyte.

The sporophyte of liverworts is composed of a small foot, anchoring the sporophyte into the gametophyte, a stalk or seta, and a capsule containing the spores. The sporophyte is enveloped within the calyptra until spores are mature. The seta remains very short until the spores are ripe; thereafter it elongates quickly, within one or a few days, by rapid elongation of its cells. The elongated seta is colorless and usually very delicate. The mature capsule is spherical or cylindrical and dehisces usually by four valves. Within the mature capsules, there are spores and **elaters**. The latter are narrowly elongate, unicellular organs provided

with one or more spirally thickened bands in their walls, that may become compressed upon dehiscence of the capsule, causing rotation and movement of the elaters (hygroscopic movement). The function of the elaters is to help release the spores from the capsule. In most leafy liverworts the elaters are free inside the capsule but in Lejeuneaceae and Frullaniaceae 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 ejecting the spores.

The spores of the liverworts germinate into a tiny, thalloid **protonema**. Each protonema gives rise to only one new gametophyte, different from mosses which have protonemata that may give rise to more than one gametophyte.

Vegetative reproduction is very common in liverworts and may take place by simple regeneration from leaf or stem cells, by special organs or gemmae produced on the surface or margins of leaves, by caducous or fragmenting leaves, or by caducous branches.

Morphology of thalloid liverworts

Thalloid liverworts have a flattened gametophyte or thallus, more or less resembling a green ribbon, which is not divided into stem and leaves. The thallus is usually dichotomously branched, occasionally pinnate (*Riccardia*), and variable in its internal structure. Two main groups of thalloid liverworts are recognized: **simple thalloid liverworts** (Jungermanniopsida subclasses Metzgeriidae and Pelliidae) and **complex thalloid liverworts** (Marchantiopsida). In the simple thalloid liverworts all cells of the thallus are green and filled with chlorophyll and oil bodies. In the complex thalloid liverworts, however, the thallus is internally differentiated, having green tissue on the dorsal side and colorless tissue on the ventral side. The green tissue usually contains air chambers that open by pores to the upper thallus surface, and the green cells lack oil bodies. The colorless ventral tissue is for storage of metabolites and often contains specialized oil cells or ocelli filled with a large oil body. Simple and complex thalloid liverworts also differ in the rhizoids and scales. The walls of the rhizoids are always smooth in the simple thalloid liverworts and there are no scales on the ventral surface. In the complex thalloid liverworts, however, the rhizoid walls are mostly densely papillose (= **pegged rhizoids**), with numerous papilla-like projections on the inner walls, and the ventral surface of the thallus is usually covered by **scales**, in two or more rows, which are often deeply purple in color.

The antheridia and archegonia of the thalloid liverworts are produced on the thallus surface, inside the thallus, or on swollen organs called receptacles. Receptacles are only found in the complex thalloid liverworts and may become stalked after fertilization. The stalked female receptacle is called **archegoniophore** and the stalked male receptacle is the **antheridiophore.** Antheridiophores are rare and only found in the families Dumortieraceae and Marchantiaceae, in all other complex thalloid liverworts the male receptacles have no stalk. The archegonia are produced from epidermis cells away from the growing tip of the thallus, not from the apical cell of the thallus like in most leafy liverworts, and the archegonia and the young sporophyte are often enclosed by an involucre called the **pseudoperianth**. The pseudoperianth resembles the perianth of the leafy liverworts but the latter originates from leaves whereas the pseudoperianth is of thallus origin.

The sporophyte of thalloid liverworts is similar to that of the leafy liverworts but the mode of opening of the capsule is more variable, and is by 1–4 valves, by an operculum or simply by decay of the capsule wall (Ricciaceae). In the complex thalloid liverworts, moreover, the seta is usually very short or lacking, and elaters are sometimes absent (Ricciaceae). During its development, the sporophyte is fully enveloped by the calyptra as usual in liverworts. The mature spores vary in size and in Marchantiales they are often very large and with a richly ornamented outer surface. These large spores are very resistant against drought and frost and retain their ability to germinate for many years. The elaters are free within the capsule except in Metzgeriidae (Aneuraceae, Metzgeriaceae), in which the elaters are attached like a brush to special capsule wall tissue, the **elaterophore**.

Vegetative reproduction in thalloid liverworts may be by simple regeneration from thallus cells or by gemmae produced on the thallus surface (Metzgeriales) or in specialized, cup-like structures (*Marchantia*, *Lunularia*).

Morphology of hornworts

The hornworts (Anthocerotophyta or Anthocerotae) contain probably no more than 150 species worldwide (many more species have been described, but many of them are probably synonyms). In the past, hornworts have often been treated as an order of the liverworts because of their superficial resemblance to the thalloid liverworts. The numerous unique morphological features of hornworts, however, indicate that hornworts should be treated separately from liverworts. Their separate position has been fully supported by molecular studies and some modern studies divide the bryophytes into two groups, hornworts without seta and **setaphytes** (mosses, liverworts) with a seta (Puttick *et al.* 2018). Differences between hornworts and the rest of the bryophytes are shown in Table 1. Some hornwort species, including members of the genera *Anthoceros*, *Folioceros*, *Notothylas* and *Phaeoceros*, grow on soil in rather open places (not inside forests), along rivers and creeks, and on road banks. Others, including members of *Dendroceros* and *Megaceros*, grow inside humid montane forests, on bark, rotten logs, rock or even living leaves.

Like other bryophytes, hornworts possess a gametophyte and a sporophyte, with the sporophyte remaining attached to the gametyphyte all its life. The structure of the gametophyte and sporophyte of hornworts differs fundamentally from that of mosses and liverworts. First, the thallus cells of hornworts are always thin-walled and have only one **large chloroplast** per cell (2–3 in *Megaceros*). Each chloroplast is usually provided with one or more **pyrenoids**, a specialized organelle involved in the synthesis of starch found only in the hornworts and the algae. The cells have no oil bodies. The thallus margins are entire, lobed, sinuous to strongly crispate, and the rhizoids have quite thin and smooth walls.

The thallus of hornworts is usually several layers of cells thick up to the margins. In *Dendroceros*, the middle portion of the thallus is considerable thicker than the rest and differentiated into a discrete midrib. On the ventral side of the thallus there are small air **chambers** that 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. The colonies are usually visible from the dorsal side as blackish dots in the thallus. In some genera (*Anthoceros*, *Folioceros*, *Dendroceros* p.p.) there are large

cavities inside the thallus, formed by destruction of cells, additional to the small ventral chambers containing *Nostoc* colonies.

Unlike mosses and liverworts, the gametangia of the hornworts originate from subepidermal cells of the thallus, not from epidermal cells. In this respect, hornworts resemble ferns. The antheridia are spherical and stalked, and are located in groups or solitary in small dorsal cavities of the thallus. The archegonia are immersed in the dorsal side of the thallus, and their necks usually just emerge beyond the thallus surface.

The sporophyte of the hornworts consists of a foot that anchores the sporophyte into the thallus, and a capsule. A seta, characteristic of liverworts and mosses, is fully absent in the hornworts. Unique characters of the hornwort sporophyte are furthermore the **narrowly linear capsule** (but shorter, egg-shaped in *Notothylas*), the growth of the capsule from a meristematic tissue at the base (**basal meristem**), and the **gradual spore maturation and capsule dehiscence**, that takes place step-by-step from the apex to the base of the capsule, during days or weeks. Dehiscence of the capsule is by **two valves**. Like in mosses, **stomata** are frequently present in the epidermis of the capsule wall.

When young, the capsule is protected by a sheet of cells produced by the gametophyte, the **involucre**. 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 surrounds almost the entire capsule until the spores are mature. Internally, the hornwort capsule has a central axis of sterile tissue, the **columella** (like in mosses), which is surrounded by sporogenous tissue. The sporogenous tissue produces **spores** and **elaters**; sometimes, however, elaters are lacking. The spores of the hornworts are usually richly ornamented on the outer surface. They are small and unicellular, or large and multicellular in *Dendroceros* due to germination of the protonema inside the spore wall. The elaters are quite variable in shape and may be unicellular or multicellular, rounded (*Notothylas*) or elongate (other genera), thick-walled (*Folioceros*) or thin-walled, and with or without one or more spiral bands. The peculiar multicellular elaters of *Anthoceros* and *Phaeoceros* with reduced spiral bands are sometimes called **pseudo-elaters**.

Vegetative reproduction is uncommon in hornworts and may occur by caducous thallus segments (*Megaceros*) or by subterraneous, bud-like organs, the **tubers** (*Phaeoceros*). The production of these tubers is apparently an adaptation to a rather dry tropical or subtropical climate, where vegetative thalli, with the exception of the tubers, die back during dry periods.

Ecology of tropical liverworts and hornworts

Liverworts and hornworts may grow on many different substrates: on soil, rock, bark of trees, rotten wood, and also as epiphylls on the living leaves of evergreen trees. They usually prefer moist habitats, and are good indicators of humidity. Liverworts and hornworts, like the mosses, are among the first colonizers of bare substrates and may play an important part in the development of soil. In cool and moist habitats such as tropical montane cloud forests, they may produce considerable amounts of biomass. Thick layers of liverworts on trees and soil may absorb large quantities of rain water and play an important role in the water balance and nutrient cycles of the forest. Up to 20–40% of rainfall is captured by the liverworts in these tropical cloud forests. 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, the bryophyte layer serves as a water reservoir, preventing water from running off immediately down to rivers and streams and thus limiting or even impeding erosion (Pócs 1980; Frahm *et al.* 1990).

Dense layers of liverworts may also serve as a substrate for other plants, such as tiny orchids or ferns, and offer shelter to small animals (frogs, lizards, snails, arthropods, etc.). The moist environment created by the liverworts is also favorable to the establishment and growth of many microorganisms, such as the nitrogen-fixing cyanobacteria. It has been shown that the amount of nitrogen fixed on living leaves by cyanobacteria is proportional to the density of the cover of the epiphyllous liverworts growing on these leaves (Bentley & Carpenter 1984).

Liverworts and hornworts, and also mosses, can be used as bio-indicators. Since they do not have a protective cuticle like flowering plants, liverworts and hornworts are quite sensitive to changes in the humidity of the environment and are efficient indicators of small changes or disturbances in the ecosystem. By mapping the distribution of sensitive liverwort and hornworts species, an assessment can be made of habitat quality. Liverworts and hornworts can also absorb pollutants through the surfaces of leaves or thallus, and accumulate these in the cells. By measuring and mapping their accumulation, the presence and concentration of these pollutants in the environment can be determined (e.g., Frahm 1998).

The bryophyte flora of tropical rain forests changes significantly with elevation. Different taxa often occur in the different forest belts. The floristic changes reflect the elevational changes in the climate, as has first been shown by the famous German scientist Alexander von Humboldt in the early 19th century. 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 excellent dispersal capacity, and the great variation in biomass, bryophytes are very useful indicators of life zones and forest types in tropical mountain regions (Gradstein & Pócs 1989; Frahm & Gradstein 1991). An excellent, richly illustrated description of bryophyte diversity along the elevational gradient is provided in the handsome booklet "Mosses and Liverworts of Mt. Kinabalu" by Frahm *et al.* (1990).

The majority of the tropical liverworts occur as epiphytes in the rain forests and cloud forests. Within the forest, epiphytic bryophytes are not randomly distributed but show distinctive distribution patterns, which can be related to the microclimatic preferences of individual species (Sillett & Antoine 2004; Léon-Vargas *et al.* 2006). Some species occur exclusively in the moist, shaded understory of the forest, others are found only in the drier, outer portions of the tree crowns high above the ground; some species occur in both habitats. These ecological types are called "shade epiphytes", "sun epiphytes" and "generalists", respectively. Shade epiphytes can often be recognized by their exposed habit (e.g., growing in loose tufts, or hanging), maximising exposure to light in the relatively poorly illuminated forest understory, while sun epiphytes usually grow in compact and prostrate mats, to reduce water loss in the relatively dry, exposed outer canopy of the forest. It has been shown that shade epiphytes are more sensitive to forest disturbance than sun epiphytes (e.g., Gradstein 1992; Gradstein & Sporn 2010). Therefore, shade epiphytes can

be used as indicators of forest quality and disturbance. Climate change also has its impact on bryphytes and an excellent overview of climate change effects on bryophytes is given in Zotz & Bader (2009) and Tuba *et al.* (2011).

Because of their specific ecological preferences, epiphytic liverworts of the tropical rain forest together with mosses occur in discrete communities (Kürschner & Parolly 1998). The composition of these epiphytic bryophyte communities is, again, predominantly influenced by micro-environmental conditions, due to the excellent dispersal ability of the bryophyte species (Mota de Oliveira *et al.* 2009). The processes governing the species composition of epiphytic bryophyte communities are thus quite different from those of the seed plants, which are mostly driven by dispersal. For excellent introductions into bryophyte biogeography and ecology see Vanderpoorten & Goffinet (2009) and the online handbook of bryophyte ecology of Glime (2018). The work provides a large, richly illustrated chapter on ecology of tropical bryophytes that is highly recommended.

How to collect and study bryophytes[3]

Collecting. Tools needed in the field are a 10(–20)× hand-lens, small and sturdy paper bags, some plastic bags (for use when it is raining), a sharp collecting knife, water proof markers, field notebook, and GPS for recording the elevation and coordinates of the collecting site. When field trips are long, it is recommended to bring a plant press with newspaper for drying thalloid liverworts and living leaves with epiphylls, to keep them flat and avoid that the leaves shrivel up. When collecting, it is very important to put each species in a separate bag as much as possible (unless they are too small to allow separation). Characteristics of the living plant such as color, growth form, fertility, habitat, elevation and substrate should be noted.

Forest inventory. Within humid tropical forests, more than half of the liverwort species may occur only in the forest canopy. Tree climbing using the single rope technique has proven to be a very effective and safe method for access to the forest canopy (ter Steege & Cornelissen 1988). A standard protocol for representative sampling of the epiphytic bryophyte diversity of tropical forests was published by Gradstein *et al.* (2003). Minimally five whole trees should be sampled per hectare. Trees should be standing well apart and differ in bark structure (smooth, rough) to optimize sampling results. For a more precise ecological study, small plots of minimally 6 dm^2 should be inventoried at different height zones on the trees: trunk base, lower trunk, upper trunk, lower canopy, middle canopy and outer canopy. In addition, treelets in the forest understory, which may harbor a different bryophyte flora, should be sampled. This is the layer, where most of the epiphylls occur. To describe the epiphyllous communities of a tropical forest habitat at least 30 leaves inhabited by epiphylls should be collected from each locality. It has been observed that after sampling more than 50 leaves with epiphylls in one locality, the number of epiphyllous species does hardly increase anymore. Special attention should be devoted to filmy ferns and hairy leaves, as they usually possess different epiphyllous assemblages.

Drying. The samples should be air-dried by placing the collecting bags open in an air-conditioned room or in a dry place. Do not heat the specimens, do not use a stove, this may damage the plants and destroy the oil bodies, which otherwise may be well-observable for 2–3 days after collecting. Keeping the plants moist in a refrigerator at 5–8°C, the oil bodies of many species may survive even up to 10 days with little or no deterioration (but in some species they may deterioriate very rapidly, therefore caution should be taken here). Thalloid species and epiphylls should be pressed lightly between filter paper or newspaper, in a plant press, and the paper should be replaced daily.

Storage. Once dried, samples can be stored in their original packet or, preferably, transferred to paper envelopes with labels. Very small samples, or fertile plants when they are few, should be put in tiny paper envelopes within the standard size envelope, to avoid that they get lost. Bryophytes are not usually eaten by insects and use of chemicals for

[3] Text adapted from Gradstein (2011).

storage is therefore not necessary. However, it is essential that the samples remain dry, to avoid that they get rotten or attacked by fungi. Storage in an air-conditioned room is therefore absolutely necessary in the humid tropics.

Microscopic examination and measurement. For species identification, microscopic examination of the material and measurement is normally required. Tools needed are a binocular dissecting microscope (magnification 20–30×), a compound microscope (magnification minimally to 400×), 2 watch-maker steel forceps with very fine tips, glass microscope slides and coverslips, a few petri dishes, and a packet of razor-blades for making cross sections.

The binocular dissecting microscope is used for examining the habit of the plants, the branching patterns, leaf insertion, thallus characteristics, reproductive organs, sexuality, and for making slides or cross sections. Material is always examined moistened in water after careful removal of the substrate. Epiphyllous specimens should be moistened before the removal from the leaf surface, as they are very fragile in the dry state and often tightly glued to the leaf surface by a viscous exudate. A few clean plants are placed in a little bit of cold or warm water (not too much water!) in a petri-dish or on a slide.

Microscopic slides of leafy liverworts should always contain several shoots with their ventral side upwards, to allow for examination of the underleaves. Several detached leaves should be added for the study of leaf and cell characters. For examination of the ventral stem surface and lobules of liverworts, or the decurrent bases of moss leaves, some leaves and underleaves must usually be removed. By adding a drop of glycerine under the cover slip, drying out is avoided and slides can be kept moist for days or weeks. Alternatively, tiny shoots of whole plants or the leaves of larger liverworts may be left in water under the coverslip, sealed at two corners by nail varnish and then left to dry. These "microslides" can subsequently be reexamined by putting a drop of water under the coverslip, remoistening the specimen.

Cross-sections of stems are made with the dissecting microscope, using a sharp razor- or surgical-blade. Place the shoot or thallus on a slide or on a wooden slab or cardboard sheet, hold it down with a dissecting-needle or finger-nail, and cut it vertically several times.

After identification of the material, the pieces examined are placed in a small paper envelope and returned to the herbarium packet. The presence of reproductive organs and the sexuality of the plants should be noted on the label.

The size of the plants is usually measured with the dissecting microscope, using a small, transparent ruler. Since stems are frequently broken, plant size is usually expressed as the width of mature stems with leaves in the moist state. Measurements of leaves, stems, cells, spores, etc. are done with a compound microscope, using a calibrated micrometer placed in the eye piece of the microscope.

Classification

The classification of the genera recorded from Malaysia into families follows the World Checklist of Hornworts and Liverworts (Söderström *et al.* 2016) with some modifications; that of families into orders and (sub)classes follows Crandall-Stotler *et al.* (2009) except for Pleuroziaceae, which are placed in a separate subclass Pleuroziidae (following Frey 2009). Arrangement of families and genera within higher groups is alphabetical.

MARCHANTIOPHYTA
(liverworts)

HAPLOMITRIOPSIDA

Haplomitriaceae
Haplomitrium Nees
Treubiaceae
Treubia K.I.Goebel

MARCHANTIOPSIDA

Aytoniaceae
Asterella P.Beauv.
Reboulia Raddi
Cyathodiaceae
Cyathodium Kunze
Dumortieraceae
Dumortiera Nees
Marchantiaceae
Marchantia L.
Ricciaceae
Riccia L.
Ricciocarpos Corda
Wiesnerellaceae
Wiesnerella Schiffn.

JUNGERMANNIOPSIDA

PELLIIDAE
Pallaviciniaceae
Jensenia Lindb.
Pallavicinia Gray
Podomitrium Mitt.
Symphyogynopsis Grolle
Sandeothallaceae

Sandeothallus R.M.Schust.

METZGERIIDAE
Aneuraceae
Aneura Dumort.
Lobatiriccardia (Mizut. & S.Hatt.) Furuki
Riccardia Gray
Metzgeriaceae
Metzgeria Raddi

PLEUROZIIDAE
Pleuroziaceae
Pleurozia Dumort.

JUNGERMANIIDAE
1. JUNGERMANNIALES
Acrobolbaceae
Acrobolbus Nees
Conoscyphus Mitt.
Saccogynidium Grolle
Adelanthaceae
Denotarisia Grolle
Pseudomarsupidium Herzog
Syzygiella Spruce
Balantiopsidaceae
Acroscyphella Kitag. & Grolle
Balantiopsis Mitt.
Isotachis Mitt.
Calypogeiaceae
Calypogeia Raddi
Mizutania Furuki & Z.Iwats.
Mnioloma Herzog
Cephaloziaceae
Cephalozia (Dumort.) Dumort.
Nowellia Mitt.
Odontoschisma (Dumort.) Dumort.
Schiffneria Steph.
Cephaloziellaceae
Cephaloziella (Spruce) Schiffn.
Cylindrocolea R.M.Schust.
Kymatocalyx Herzog
Gymnomitriaceae
Gymnomitrion Corda
Marsupella Dumort.

Nardia Gray

Herbertaceae

Herbertus Gray

Triandrophyllum Fulford & Hatcher

Jackiellaceae

Jackiella Steph.

Jungermanniaceae

Mesoptychia (Lindb.) A.Evans

Lepicoleaceae

Lepicolea Dumort.

Lepidoziaceae

Acromastigum A.Evans

Bazzania Gray

Hygrolembidium R.M.Schust.

Kurzia G.Martens

Lepidozia (Dumort.) Dumort.

Mastigopelma Mitt

Neolepidozia Fulford & J.Taylor

Psiloclada Mitt.

Telaranea Schiffn.

Tricholepidozia (R.M.Schust.) E.D.Cooper *et al.*

Zoopsis Gottsche *et al.*

Lophocoleaceae

Cryptolophocolea L.Söderstr.

Heteroscyphus Schiffn.

Lophocolea (Dumort.) Dumort.

Mastigophoraceae

Mastigophora Nees

Notoscyphaceae

Notoscyphus Mitt.

Plagiochilaceae

Chiastocaulon Carl

Plagiochila (Dumort.) Dumort.

Pseudolepicoleaceae

Blepharostoma (Dumort.) Dumort.

Pseudolepicolea Fulford & J.Taylor

Temnoma Mitt.

Scapaniaceae

Anastrophyllum (Spruce) Steph.

Andrewsianthus R.M.Schust.

Diplophyllum (Dumort.) Dumort.

Gottschelia Grolle

Plicanthus R.M.Schust.

Scapania (Dumort.) Dumort.

Sphenolobopsis R.M.Schust. & N.Kitag.
Sphenolobus (Lindb.) Berggr.
Tetralophozia (R.M.Schust.) Schljakov
Tritomaria Loeske

Schistochilaceae
Schistochila Dumort.

Solenostomataceae
Solenostoma Mitt.

Southbyaceae
Southbya Spruce

Trichocoleaceae
Eotrichocolea R.M.Schust.
Leiomitra Lindb.
Trichocolea Dumort.

2. PORELLALES

Frullaniaceae
Frullania Raddi

Jubulaceae
Jubula Dumort.

Lejeuneaceae
Acrolejeunea (Spruce) Steph.
Allorgella Tixier
Caudalejeunea Schiffn.
Cephalolejeunea Mizut.
Ceratolejeunea (Spruce) J.B.Jack & Steph.
Cheilolejeunea (Spruce) Steph.
Cololejeunea (Spruce) Steph.
Colura (Dumort.) Dumort.
Dactylophorella R.M.Schust.
Diplasiolejeunea (Spruce) Schiffn.
Drepanolejeunea (Spruce) Steph.
Lejeunea Lib.
Lepidolejeunea R.M.Schust.
Leptolejeunea (Spruce) Steph.
Lopholejeunea (Spruce) Steph.
Metalejeunea Grolle
Microlejeunea (Spruce) Steph.
Mohamedia R.L.Zhu & L.Shu
Myriocoleopsis Schiffn.
Pictolejeunea Grolle
Ptychanthus Nees
Pycnolejeunea (Spruce) Schiffn.
Schiffneriolejeunea Verd.

Soella R.L.Zhu *et al.*
Spruceanthus Verd.
Stictolejeunea (Spruce) Schiffn.
Thiersianthus R.L.Zhu & L.Shu
Thysananthus Lindenb.
Tuyamaella S.Hatt.

Porellaceae
Porella L.

Radulaceae
Radula Dumort.

ANTHOCEROTOPHYTA
(hornworts)

Anthocerotaceae
Anthoceros L.
Folioceros Bharadwaj

Dendrocerotaceae
Dendroceros Nees
Megaceros Campb.

Notothyladaceae
Phaeoceros Prosk.

Keys and descriptions

Introductory key

1. Plants with stem and leaves ····· 2
1. Plants thalloid ····· 4
2. Leaves with a midrib (sometimes very short or double and restricted to the leaf base only) ····· **Bryophyta** (mosses)
2. Midrib lacking ····· 3
3. Leaves in 2–3 rows ····· **Marchantiophyta** (liverworts)
3. Leaves not in 2–3 rows (except *Fissidens*, *Rhizogonium*)·····**Bryophyta** (mosses)
4. Thallus unistratose, only one cell-layer thick ····· 5
4. Thallus more than one cell-layer thick ····· 8
5. Thallus with a midrib, gametoecia on the ventral surface of the midrib. Cuticle of thallus cells smooth. ····· **Marchantiophyta:** Metzgeriaceae
5. Thallus without midrib. Cuticle smooth or papillose ····· 6
6. Thallus margins without cilia or rhizoids. Gametoecia on the ventral thallus surface, without protective structures····· **Fern prothallium**
6. Thallus margins with cilia or rhizoids. Gametoecia at the thallus margin or on short leafy branches, with protective structures ····· **Marchantiophyta** (liverworts) 7
7. Plant growing on living leaves in montane rainforest, very small and pale-colored, ± pinnate, thallus margin with cilia. Cuticle smooth. Gametangia produced on short leafy branches. ····· **Lejeuneaceae:** *Cololejeunea metzgeriopsis*
7. Plant growing on shaded soil, greenish, simple or irregularly branched, thallus margin with rhizoids. Cuticle densely striate-papillose. Gametangia produced at the thallus margin, leafy branches lacking····· **Calypogeiaceae:** *Mizutania riccardioides*
8. Thallus cells with 1–2 large chloroplasts. Capsule long-linear or ellipsoid (*Notothylas*), green, becoming black only after dehiscence, opening gradually (over a period of weeks or month) by 2 valves, from the apex downwards ····· **Anthocerotophyta** (hornworts)
8. Thallus cells with numerous small chloroplasts. Capsule black, globose, ellipsoidal or cylindrical, black, opening at once (not gradually), usually by 4 valves ····· ····· **Marchantiophyta** (liverworts)

Marchantiophyta (liverworts)

Plants (= gametophytes) leafy or thalloid, growing by means of a 2–3(–4)-sided apical cell. Leaves, when present, in 2–3 rows, the third row of leaves (= underleaves) ventral and usually smaller in size or absent; leaves usually composed of only one layer of cells, without midrib, undivided or divided into lobes. Thallus, when present, several cells thick at least in the middle, with or without midrib, inner tissue homogeneously green or differentiated into a green upper layer and a colorless lower layer. Cells usually with numerous small chloroplasts and with oil bodies, pyrenoids lacking, cell walls often with trigones. Rhizoids unicellular. 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 bracts (leafy liverworts) or an involucre. Sporophyte normally consisting of foot, seta and capsule, enveloped until maturity in a calyptra and usually enclosed by additional protective structures: a perianth, perigynium or marsupium in leafy liverworts, an involucre or pseudoperianth in thalloid liverworts. Seta colorless and rather fragile, elongating after spore maturation. Capsule globose to cylindrical, containing spores and elaters (elaters lacking in *Riccia*), capsule wall without stomata, columella and peristome absent; dehiscence of capsule usually by means of (1–)4 valves, rarely irregular or with an operculum. Protonema very small, thalloid, normally giving rise to only one gametophyte.

Contains 5000–6000 species worldwide (some authors suggest more than 7000 species worldwide but those figures are exaggerations); about 800 species in Malaysia, in 124 genera and 43 families.

Key to classes of liverworts

1. Plants with stem and leaves ····· 2
1. Plants thalloid ····· 5
2. Leaves divided into segments or lobes ····· **Jungermanniopsida** (p. 34)
2. Leaves undivided ····· 3
3. Leaves in 3 ± equal rows, leaf insertion transverse (Plants growing erect from a leafless rhizome. Rhizoids absent) ····· **Haplomitriopsida:** *Haplomitrium*
3. Leaves not in 3 equal rows, leaf insertion incubous or succubous (rarely transverse) ··· 4
4. Plants very large, 1–2 cm wide and 5–15 cm long, creeping on rotten wood near rivulets in montane forest, with a flat, thalloid appearance. Leaves tongue-shaped (longer than wide), laterally attached to the stem, underleaves absent. Dorsal stem surface with 2 rows of small, leaf-like scales, the scales alternating with the leaves ····· **Haplomitriopsida:** *Treubia*
4. Plants different, dorsal stem surface not with 2 rows of leaf-like scales alternating with the leaves ····· **Jungermanniopsida** (p. 34)
5. Thallus with pores and air chambers (cross section), thallus underside with scales (sometimes without scales). Rhizoids usually papillose (sometimes smooth in *Cyathodium*) ····· **Marchantiopsida** (p. 28)
5. Pores and air chambers lacking, thallus underside without scales. Rhizoids smooth or papillose ····· 6
6. Upper surface of the thallus with a median groove. Capsule embedded in the thallus, without elaters ····· **Marchantiopsida**: Ricciaceae (p. 33)
6. Upper surface of the thallus without median groove. Capsule not embedded in the thallus, with elaters ····· 7
7. Rhizoids papillose. Thallus large, 1–3 cm wide. Gametangia produced in receptacles with black hairs ····· **Marchantiopsida**: Dumortieraceae (p. 31)
7. Rhizoids smooth. Thallus small or large. Gametangia not produced in receptacles with black hairs ····· **Jungermanniopsida** (p. 34)

Class HAPLOMITRIOPSIDA (basal liverworts)

Plants with leaves, creeping or erect. Stems with a central strand. Leaves transverse or succubous, originating from one initial cell, in 2 or 3 rows, usually undivided. Cells thin-walled, without trigones, with or without oil bodies, cuticle smooth. Rhizoids present or lacking. Antheridia and archegonia produced in leaf axils, archegonia positioned laterally (anacrogynous), not terminally. Spermatozoid body massive. Sporophyte enclosed by a fleshy calyptra; perianth lacking. Seta long, thick. Capsule opening with (2–)4 valves, capsule wall 1–5-layered. Spores small, spore surface not ornamented.

Contains 2 genera, in 2 families.

Key to families of Haplomitriopsida

1. Plants growing upright, ca. 2 mm wide, stem base stoloniform. Leaves in 3 ± equal rows, underleaves similar to leaves. Stem surface without scales. Rhizoids absent ····· ····· **Haplomitriaceae**: *Haplomitrium*
1. Plants creeping, very large, 1–2 cm wide, stem base not stoloniform. Leaves in 2 rows, underleaves lacking. Dorsal stem surface with 2 rows of small, leaf-like scales, the scales alternating with the leaves. Rhizoids present, abundant ····· **Treubiaceae**: *Treubia*

HAPLOMITRIACEAE

A monotypic family.

Haplomitrium Nees Fig. 1A–D
(*Calobryum* Nees)

Plants 1–5 cm high, green, growing upright from a whitish leafless rhizome, rhizoids lacking. Branches lateral, without collar, originating from the epidermis. Leaves transverse, in 3 ± equal rows, undivided, ovate-orbicular to broadly reniform, insertion very narrow, margins ± entire, basal part of leaves 2–4-stratose. Cells very large, ca. 50–100 µm long, quadrate to rectangular, uniformly thin-walled, without trigones; oil bodies small, homogeneous, many per cell. Underleaves similar to leaves or slightly smaller. Dioicous. Antheridia and archegonia borne in discs terminal on the stem, surrounded by bracts and bracteoles in one or a few series. Capsule cylindrical, opening by (2–)4 valves, wall one cell-layer thick.

Contains 7 species worldwide; 1 species in Malaysia (Genting Highlands), *Haplomitrium blumei* (Nees) R.M.Schust. (often misspelled "*blumii*"), usually found on rotten wood or tree stumps, occasionally on the trunks of tree ferns, humic soil or rock (Bartholomew-Began 1991).

Note: *Haplomitrium blumei* can be easily recognized by the upright stems with a stoloniform base and 3 ± equal rows of undivided, transverse leaves with large, thin-walled cells. Rhizoids are completely lacking. The capsule of *H. blumei* is unusual for its dehiscence by means of only 2 valves.

Literature: Bartholomew-Began (1991); Higuchi (2005).

TREUBIACEAE

A small circumpacific family of 2 genera; 1 in Malaysia.

Treubia K.I.Goebel Fig. 1E–G

Plants large, 1–2 cm wide and 5–10(–15) cm long, glossy green, flat and fleshy, creeping. Branches lateral-intercalary. Leaves succubous, tongue-shaped, more than 1 cell-layer thick in the lower half, apex rounded, margins entire. Dorsal side of the stem with small, transversely oriented scales in 2 rows, the scales alternating with the leaves. Leaf cells large, ca. 50–60 µm in mid-leaf, of two types, either with chloroplasts and without oil

bodies, or with one large oil body and without chloroplasts. Rhizoids abundant, colorless, with smooth walls. Underleaves lacking. Capsule opening by 4 valves, wall 3–5 cell-layers thick.

Contains 7 species, mostly in Australasia; 1 species in Malaysia, *Treubia insignis* K.I.Goebel, recorded from Sabah; on wet rotten wood near rivulets in humid montane forests.

Note: *Treubia insignis* is easily recognized by the very large, fleshy, glossy-green plants with tongue-shaped, succubous leaves and two rows of small, leaf-like scales on the dorsal side of the stem.

Literature: Schuster & Scott (1969); Piippo (1988b).

Class MARCHANTIOPSIDA (complex thalloid liverworts)

Plants thalloid, with or without a midrib, dorsal surface often reticulate and with small pores; in cross section usually with a green upper layer composed of air chambers and photosynthetic tissue, and a colorless, non-photosynthetic lower layer lacking chlorophyll, without air chambers and with scattered oil cells containing one large oil body. Green cells without oil bodies. Ventral thallus surface with scales. Rhizoids frequently with papillose (= pegged) walls. Antheridia and archegonia in cavities or on receptacles, female receptacles often stalked after fertilization, male receptacles sessile or stalked. Spermatozoid body thin. Seta usually short or lacking. Capsule spherical to cylindrical, opening with an operculum, with valves or irregularly, capsule wall 1-layered. Spores often large and with a richly ornamented surface (small and not ornamented in *Marchantia*). Elaters present or lacking. Vegetative reproduction rare, by multicellular gemmae (*Lunularia*, *Marchantia*).

About 350 species worldwide.

Key to families of Marchantiopsida

1. Upper surface of the thallus with distinct pores, appearing as tiny, colorless or whitish dots. Air chambers present (thallus cross section) ····· 2
1. Pores lacking or indistinct. Air chambers present or absent ····· 9
2. Gemma receptacles present on dorsal surface of thallus ····· 3
2. Gemma receptacles absent ····· 4
3. Gemma receptacles cup-shaped ····· **Marchantiaceae**
3. Gemma receptacles moon-shaped. Not yet reported from Malaysia but to be expected (see Schuster 1992b) ····· Lunulariaceae: *Lunularia cruciata*
4. Thallus usually with a median groove and often growing in (partial) rosettes on bare soil, sometimes floating on water. Capsule embedded in the thallus, without elaters ····· ····· **Ricciaceae**
4. Thallus without median groove, usually not growing in rosettes. Capsule not embedded in the thallus, with elaters ····· 5

5. Thallus very thin, 2–3-layered, bright green, obcuneate. Ventral scales lacking (sometimes present at the thallus apex). Sporophyte on the ventral thallus surface ····· **Cyathodiaceae**
5. Thallus thicker, not translucent and not iridescent. Ventral scales present. Sporophyte not on the ventral thallus surface ····· 6
6. Thallus completely black when dry, margins and underside dark purplish-black. Sporophyte in a dark, swollen, mussel-like involucre below the thallus apex. Not yet reported from Malaysia but to be expected (see Hattori & Mizutani 1969; Schuster 1992b) ····· **Targioniaceae**: *Targionia hypophylla*
6. Thallus not completely black when dry, margins and underside green or tinged with purple. Sporophyte not in a mussel-like involucre below the thallus apex····· 7
7. Pores compound, made up of several layers of cells (cross section). Air chambers with green filaments. Male receptacle stalked ····· **Marchantiaceae**
7. Pores simple, of only one layer of cells. Air chambers with or without filaments. Male receptacle sessile, without stalk ····· 8
8. Thallus light green, very large, ca. 1–2 cm wide (or more). Pores somewhat elevated above the thallus surface. Ventral scales with a broad, rounded to reniform appendage. Air chambers in one layer. Pseudoperianths absent. Capsule opening irregularly by 4–6 valves ····· **Wiesnerellaceae**
8. Thallus dark green to light green, smaller. Pores not elevated above the thallus surface. Ventral scales with 1–3 linear or ovate-lanceolate appendages. Air chambers in 2–3 layers. Underside of female receptacle with or without large, conical pseudoperianths. Capsule opening by an operculum ····· **Aytoniaceae**
9. Plants small, thallus segments less than 0.5 cm wide, often growing in (partial) rosettes on bare soil. Thallus surface often with a median groove. Sporophyte embedded inside the thallus, receptacles absent····· **Ricciaceae**
9. Plants larger, thallus segments (0.5–)1–3 cm wide, not growing in rosettes. Thallus surface without median groove. Sporophyte not embedded in the thallus, receptacles frequently present, with black hairs on the margin····· **Dumortieraceae**

AYTONIACEAE

Thallus simple or dichotomously branched (forked), with simple pores (pore wall one cell-layer thick), the pores surrounded by 1–several rings of differentiated cells. Air chambers usually in 2–3 layers, walls green, filaments lacking. Ventral scales large, purple, in 2 rows, each scale with one or more small appendages. Antheridia in irregular groups embedded in the dorsal surface of the thallus, or in sessile receptacles; archegonia in receptacles. Female receptacles stalked after fertilization, stalk with or without a furrow, receptacle ± lobed, each lobe with 1(–several) archegonia in a cavity surrounded by a 2-lipped involucre. Fertilized archegonium and sporophyte sometimes enclosed by a large pseudoperianth (*Asterella*). Sporophyte with a very short seta. Capsule opening by an operculum. Spores usually large (ca. 50–150 µm). Vegetative reproduction lacking.

About 5 genera worldwide; 2 genera in Malaysia. The main characters of Aytoniaceae are: 1) thallus firm, with simple pores; 2) ventral scales large, purple, in 2 rows, with 1–4

narrow appendages; 3) air chambers in 2–3 layers, without filaments; 4) female receptacle stalked, male receptacle sessile; 5) capsule opening by an operculum. In *Asterella* and *Reboulia* (both known from Malaysia) the female receptacle arises from apex of the main thallus, but in the genus *Plagiochasma* (not yet recorded from Malaysia, but to be expected) the female receptacle arises from the thallus surface, away from the apex, and on a very short stalk.

1. Archegoniophore arising from the thallus surface (not at the apex), on a very short, 1–5 mm long stalk without furrow. Involucre large, globose, opening to the side of the receptacle. Thallus green to blue-green. Not yet reported from Malaysia but to be expected (see Chantanaorrapint & Sridith 2014) ····· *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, not blue-green ····· 2
2. Dorsal surface of thallus reticulate. Ventral scales with 1 ovate-lanceolate appendage, the appendage 5–9 cells wide at the base. Mature female receptacle shallowly 3–6-lobed, underside with large conical, colorless pseudoperianths ····· *Asterella*
2. Dorsal surface of thallus not reticulate. Ventral scales with 2–3 linear appendages, the appendages 2–3 cells wide at the base. Mature female receptacle deeply 4–7-lobed, underside without pseudoperianths ····· *Reboulia*

Asterella P.Beauv. Fig. 2J

Thallus 1.5–9 mm wide, green to purplish, dorsal surface of thallus distinctly reticulate; epidermis cells with or without trigones; thallus underside with large violet scales in 2 rows, each scale with 1–2 ovate-lanceolate appendages. Monoicous or dioicous. Antheridia in small receptacles on the main thallus or on short lateral branches. Female receptacles arising from apex of the main thallus or from small branches, stalk with one furrow; receptacle smooth or papillose, shallowly to deeply lobed, each lobe underneath with a small group of archegonia surrounded by a cup-shaped involucre. Fertilized archegonium (and sporophyte) enclosed by a large pseudoperianth, splitting longitudinally into 8–16 narrow segments and looking like a small basket.

A large genus (ca. 50 spp.); 1 species in Malaysia (Sabah), *Asterella limbata* D.G.Long & Grolle, on shaded soil or rock.

Note: *Asterella* is immediately recognized by the large, conical, whitish pseudoperianths hanging down from the underside of the female receptacle. When the sporophyte is mature, the pseudoperianth splits along its length into numerous narrow, ribbon-like segments, which usually remain connected at the tip. The dorsal surface of the female receptacle is normally papillose (covered by small to large turbercles).

Literature: Long & Grolle (1994); Long (2006).

Reboulia Raddi Fig. 2A–G

Thallus 3–12 mm wide, dull green above, purplish below, dorsal surface not distinctly reticulate; epidermal cells with distinct trigones; thallus underside with large purplish scales in 2 rows, each scale with 2–3 filiform appendages. Monoicous. Antheridia in small

receptacles near the base of the female receptacle. Female receptacles arising from the thallus apex, stalk with one furrow; receptacle distinctly 4–7-lobed, surface weakly papillose, archegonia in small groups in cavities underneath, each group surrounded by a large, 2-valved involucre. Pseudoperianth lacking.

A widespread monotypic genus; contains *Reboulia hemisphaerica* (L.) Raddi, recorded from Sabah; on soil over rock at high elevation.

Note: The main features of *Reboulia* are the dull green thalli without distinct reticulate pattern, the epidermal cells with distinct trigones, the ventral scales with several filiform appendages which may break away very easily, and the deeply 4–7-lobed female receptacles arising from the thallus apex, with swollen involucres opening along a narrow slit. Large pseudoperianths, as seen in *Asterella*, are absent.

Literature: Schuster (1992b); Paton (1999).

CYATHODIACEAE

A monotypic family.

Cyathodium Kunze Figs. 2H, I; 61A

Thallus very delicate, to 1.5 cm long and 1–4 mm wide, bright light green to yellowish-green or glaucous-green and sometimes iridescent, obcuneate with a narrow base and a broadly truncate apex, consisting of only 2–3-layers of cells; thallus usually growing in dense, flat mats on soil and sometimes with a bad smell. Dorsal surface of thallus reticulate and with large whitish pores surrounded by a few rings of cells (rings sometimes absent), epidermal cells thin-walled. Ventral scales present near thallus apex (in 2 rows) or absent. Air chambers in one layer, without filaments. Rhizoids smooth or papillose. Monoicous or dioicous. Antheridia on very small lateral branches. Archegonia on the ventral thallus surface. Sporophytes in a short row on the thallus underside, each sporophyte surrounded by a thin involucrum. Seta reduced. Capsule opening by an operculum. Spores ca. 30–55 µm, variously ornamented. Elaters few to many, with 2–4 spirals. Vegetative reproduction by tubers.

A pantropical genus (ca. 12 spp.); 2 species in Malaysia, *Cyathodium foetidissimum* Schiffn., recorded from Maxwell Hill (Bukit Larut), Perak and *C. cavernarum* Kunze from Gunung Reng, Kelantan (*G.E. Lee 13002,* UMTP); on damp rocks and soil in the deep shade of the forest or limestone outcrop.

Note: *Cyathodium* is recognized by: 1) thallus delicate, 2–3-layered, obcuneate, bright green-luminescent, sometimes with a bad smell; 2) ventral scales ± absent; 3) rhizoids smooth or papillose; 4) sporophytes on the underside of the thallus, surrounded by a thin involucrum.

Literature: Lang (1905); Srivastava & Dixit (1996).

DUMORTIERACEAE

A monotypic family.

Dumortiera Nees Figs. 2K, L; 61B–D

Thallus robust, 1–3 cm wide and 5–20 cm long, uniformly deep green, forked, sometimes with a narrow, colorless "midrib" made by rhizoids. Dorsal surface of thallus not reticulate, without pores and without distinct epidermis, sometimes with papilliform cells in groups on the surface. Thallus margins often with black hairs. Thallus underside green, with small, colorless scales in 2 rows and with papillose and smooth rhizoids forming a narrow, false midrib and often radiating to the thallus margins. Air chambers lacking or vestigial. Monoicous. Male receptacle on a short stalk, circular and ± unlobed, margins with stiff, bristle-like hairs. Female receptacles on an elongate, 3–6 cm long stalk with 2 furrows, becoming 8–10-lobed after fertilization, margins of receptacles with stiff, black hairs. Archegonia in groups on the ventral side of the segments, each group surrounded by a tubular involucre. Pseudoperianths lacking. Seta short. Capsule opening irregularly by valves. Spores small, 20–35 µm. Sporophyte otherwise as in the family. Vegetative reproduction lacking.

A tropical and warm-temperate genus, contains the polymorphic *Dumortiera hirsuta* (Sw.) Nees, distributed throughout Malaysia, on wet soil and rock.

Note: Characteristics of *D. hirsuta* are the smooth, green thalli without any pores or air chambers, and the receptacles with black, bristle-like hairs. The male and female receptacles are both elevated on stalks upon maturity, like in *Marchantia*. *Dumortiera hirsuta* contains two varieties, var. *hirsuta* and var. *nepalensis* (Tayl.) Frye & L.Clark, both of which have been reported from Malaysia. Recent molecular studies indicate the existence of several cryptic species in *D. hirsuta* (Forrest *et al.* 2011).

Literature: Schuster (1992b); Paton (1999); Forrest *et al.* (2011).

MARCHANTIACEAE

Contains 2 genera worldwide; 1 in Malaysia.

Marchantia L. Figs. 3; 62A–D

Thallus usually large, 0.3–2 cm wide, forked, with or without midrib, light green to rather dark green to glaucous, underside often purplish. Dorsal thallus surface reticulate and with numerous pores, the pores barrel-shaped, consisting of 4–7 layers of cells (cross section), each pore connected with a small air chamber. Thallus margins smooth or with small scales protruding beyond the margin. Thallus underside green or purple, with large colorless to violet scales in 4–10 rows, median scales with an elongate appendage. Air chambers in one narrow layer, with green filaments. Dioicous. Male and female receptacles on long stalks with 2 furrows, shallowly or deeply lobed, the lobes flat or terete, margin of receptacles without hairs. Archegonia in rows on the ventral side of the female receptacle, each row of archegonia surrounded by an involucre, fertilized archegonium (and young sporophyte) enclosed by a pseudoperianth. Seta short. Capsule opening irregularly by valves. Spores small, 10–35 µm, surface not sculptured. Vegetative reproduction by discoid gemmae born in rounded, cup-shaped receptacles on the dorsal thallus surface.

About 50 species worldwide; 7 species in Malaysia, common, on soil and rock.

Note: The main characters of *Marchantia* are: 1) gemmae produced in cup-shaped

receptacles on the thallus; 2) pores barrel-shaped, made up of several layers of cells (cross section); 3) ventral scales in 4–10 rows, scales sometimes reaching the thallus margin; 4) air chambers in one layer, with filaments; 5) male and female receptacles stalked.

Literature: Johnson (1958); Bischler (1989).

RICCIACEAE

Thallus growing in rosettes or gregarious patches, forked. Dorsal surface of thallus frequently with a median groove, usually not reticulate; pores present or absent, when present inconspicuous and simple, surrounded by a ring of cells or not. 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 disintegrating at the time of spore maturation. Spores large, 50–200 µm, surface variously ornamented. Elaters lacking. Vegetative reproduction usually lacking, occasionally by tubers.

Contains 2 genera worldwide; both in Malaysia. The main characters of Ricciaceae are: 1) thallus small, forked, often growing in rosettes on bare soil, dorsal thallus surface usually with a median groove; 2) air chambers and pores mostly absent or rudimentary; 3) gametoecia and sporophyte embedded inside the thallus; 4) seta and elaters lacking; 5) capsule cleistocarpous, dehiscing by disintegration of the capsule wall; 6) spores large, richly ornamented.

1. Plants floating on water (rarely on wet soil). Pores present, surrounded by a ring of cells. Ventral scales large, long-ligulate, with oil cells. Dorsal thallus surface ± dark-green, reticulate ····· *Ricciocarpos*
1. Plants on soil, rarely in water. Pores absent or present, when present without ring of cells. Ventral scales absent or small, not ligulate, without oil cells. Dorsal thallus surface pale green to glaucous green, not or slightly reticulate ····· *Riccia*

Riccia L. Fig. 4A–G

Thallus 0.5–4 mm wide, pale green to glaucous green, often tinged with red or purple, forked, often forming rosettes. Dorsal surface of thallus usually with a median groove, not or slightly reticulate; pores lacking or very small and inconspicuous; dorsal epidermis without oil cells, sometimes decayed 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. Air chambers in 1–3 layers or ± lacking, when lacking the upper tissue of the thallus forming dense vertical rows. Ventral scales small or large, when large sometimes projecting beyond the thallus margin, variously colored, in 1–2 rows, without oil cells. Monoicous or dioicous. Gametoecia and sporophyte as in the family.

About 150 species worldwide; 2 species recorded from Malaysia (Peninsular Malaysia, Sabah), *Riccia fluitans* L. and *R. treubiana* Steph., on moist soil. The genus *Riccia* has been neglected in Malaysia and needs study. Further *Riccia* species are to be expected from the

country.

Note: For main characters of *Riccia* see under the family. The species are typical pioneers of open, disturbed moist soil.

Literature: Meijer (1958); Cargill *et al.* (2016).

Ricciocarpos Corda Fig. 4J–L

Thallus to 1 cm long, 3–6 mm wide, yellow-green to dark green, often with purple margins, 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, violet, 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.

A monotypic subcosmopolitic genus; contains *Ricciocarpos natans* (L.) Corda, recorded from Sabah, growing floating on water.

Note: This aquatic plant is unmistakable.

Literature: Schuster (1992b); Paton (1999).

WIESNERELLACEAE

A monotypic family.

Wiesnerella Schiffn. Fig. 4H, I

Thallus robust, ca. 1–2 cm wide, light green to dark green, with simple pores, pore wall 1 cell-layer thick, pores very conspicuous, somewhat evelated above the thallus surface. Air chambers in one layer, with rudimentary photosynthetic filaments. Ventral scales in 2 rows, very delicate, broadly lunate, each scale with a large rounded appendage. Monoicous. Archegonia and antheridia in terminal cushion-like receptacles surrounded by scales. Female receptacles stalked after fertilization, 5–8-lobed; male receptacle not stalked. Sporophyte surrounded by a simple involucre. Capsule opening irregularly by 4–6 valves. Vegetative reproduction lacking.

A monotypic, widespread SE Asian genus; contains *Wiesnerella denudata* (Mitt.) Steph., recorded from Sabah; on soil.

Note: *Wiesnerella denudata* may be confused with *Marchantia*, but differs from *Marchantia* in: 1) pores simple, elevated; 2) ventral scales in only 2 rows, each scale with a large, reniform appendage; 3) male receptacles not stalked; 4) gemma cups lacking.

Literature: Johnson (1958); Piippo (1988a); Huang *et al.* (2012).

Class JUNGERMANNIOPSIDA
(leafy liverworts and simple thalloid liverworts)

Plants leafy or thalloid, creeping, ascending or erect rhizomes present or absent. Stems or thallus with or without central strand. Branches lateral or ventral, originating from leaf-initial cells or from stem- or thallus-cells, when from stem originating from inner stem cells,

not from the epidermis; collar at the base of branches present or lacking. Leaves (when present) in 2–3 rows: 2 lateral rows and 0–1 ventral row (= underleaves), each leaf originating from 1–3 initial cells, undivided or divided. Thallus (when present) homogeneous in cross section, air chambers and pores lacking; ventral scales absent. Cells with or without trigones, usually with oil bodies. Underleaves present or absent, when present usually smaller than the lateral leaves. Rhizoids usually present on the ventral side of the plant, always with smooth walls. Antheridia in leaf axils or on dorsal surface of thallus. Archegonia terminal on long or short shoots, in leafy plants surrounded by bracts and often by bracteoles, in thalloid plants protected by an involucre or scale, rarely naked. Sporophyte enclosed by the calyptra and a perianth or fleshy perigynium. Seta 1–10 cm long, thin to very thick. Capsule globose to cylindrical, opening by (2–)4 valves, rarely irregularly, capsule wall 2–10-layered. Elaters present.

About 5000 species worldwide. The class is subdivided into four subclasses, Pelliidae (= simple thalloid liverworts I), Metzgeriidae (= simple thalloid liverworts II), Pleuroziidae (leafy liverworts I) and Jungermanniidae (leafy liverworts II).

Key to subclasses of Jungermanniopsida

1. Plants with leaves ····· 2
1. Plants thalloid ····· 4
2. Rhizoids deep purple. Leaves irregularly undulate-crispate (plant looking like salad), more than 1 cell-layer thick in the lower half, cells fully thin-walled, without trigones. Antheridia naked on the stem surface, not enveloped by bracts. Spores large, surface coarsely sculptured by a lamellate or reticulate pattern. On soil in gardens, nurseries, disturbed waste places, etc. ····· **Pelliidae**: Fossombroniaceae (p. 36)
2. Rhizoids colorless, pale brown or reddish (not purple), or absent. Leaves not irregularly undulate-crispate, only 1 cell-layer thick (more than 1 cell-layer thick: *Schiffneria*, Cephaloziaceae). Antheridia in the axils of bracts. Spore surface not coarsely sculptured by a lamellate or reticulate pattern. On bark, rock or soil ····· 3
3. Plants usually robust, 4–7 mm wide, reddish or purplish. Leaves deeply concave, strongly clasping the stem, divided into two strongly swollen, sac-like lobes of different size, the large lobes imbricate. Underleaves absent. Perianth large, cylindrical, mostly terete, sometimes plicate ····· **Pleuroziidae** (p. 42)
3. Plants different ····· **Jungermanniidae** (p. 43)
4. Thallus unistratose (except for the narrow midrib, when present) ····· 5
4. Thallus mostly more than one cell-layer thick ····· 8
5. Thallus with a narrow midrib, gametoecia on the ventral surface of the midrib. Thallus margins with hairs ····· **Marchantiophyta:** Metzgeriaceae (p. 42)
5. Thallus without midrib. Thallus margins with or without hairs ····· 6
6. Thallus margins without cilia or rhizoids. Gametoecia on the ventral thallus surface, without protective structures ····· **Fern prothallium**
6. Thallus margins with cilia or rhizoids. Gametoecia at the thallus margin or on short leafy branches, with protective structures ····· (**Jungermanniidae)** 7
7. Plant growing on living leaves in montane rainforest, very small and pale-colored,

± pinnate, thallus margin with cilia. Cuticle smooth. Gametangia produced on short leafy branches . ····· **Lejeuneaceae:** *Cololejeunea metzgeriopsis*

7. Plant growing on shaded soil, greenish, simple or irregularly branched, thallus margin with rhizoids. Cuticle densely striate-papillose. Gametangia produced at the thallus margin, leafy branches lacking ····· **Calypogeiaceae:** *Mizutania riccardioides*
8. Rhizoids reddish or brown. Midrib present ····· **Pelliidae**
8. Rhizoids colorless. Midrib present or absent ····· 9
9. Midrib present, with a central strand. Gametoecia on the dorsal side of the midrib or on short branches at the base of the thallus ····· **Pelliidae**
9. Midrib present or absent, central strand absent. Gametoecia at the thallus margin ····· ····· **Metzgeriidae:** Aneuraceae (p. 40)

Subclass PELLIIDAE (simple thalloid liverworts I)

Plants thalloid or leafy, growing with a 2-sided apical cell, divided into 2 lateral merophytes, ventral merophyte absent. Thallus (when present) differentiated into a midrib and thinner lateral wings, midrib frequently with a central strand, wings undivided or divided into lobes. Leaves (when present) undivided, originating from one initial cell, succubous, several layers of cells thick toward the base; underleaves lacking. Cells thin-walled, usually without trigones; oil bodies usually present. Rhizoids with smooth walls. Antheridia and archegonia usually on the surface of the axis, naked or surrounded by an involucre or scales; archegonia not arising from the apical cell of thallus (plants anacrogynous). Sporophyte surrounded by a calyptra and, usually, by an involucre. Capsule globose to cylindrical, opening by 2–4 valves or irregularly, wall 2–6-layered.

Key to families of Pellidae

1. Plants with leaves usually growing in pale-green rosettes (leaf margins undulate, usually sinuate or toothed). Rhizoids violet. Capsule globose. Monoicous or dioicous. On soil in gardens, nurseries, disturbed waste places, etc. Not recorded from Malaysia but to be expected (see Krayesky *et al.* 2005) ····· **Fossombroniaceae**: *Fossombronia*
1. Plants thalloid, not growing in pale-green rosettes. Rhizoids colorless or deep reddish. Capsule elongate. Dioicous ····· 2
2. Rhizoids deep reddish-purple. Thallus very large, 1–2 cm wide. Midrib very narrow, less than 1/8 of thallus width, without central strand. Rare plants of wet soil near springs ····· ····· **Sandeothallaceae**
2. Rhizoids colorless or pale brown. Thallus less than 1 cm wide. Midrib broader, with or without central strand ····· 3
3. Thallus prostrate. Thallus margins strongly undulate to crispate, forming lobe-like structures. Midrib without central strand. Ventral scales present, small (visible near the thallus apex). Capsule globose. Not recorded from Malaysia but to be expected (see Printarakul *et al.* 2019) ····· **Calyculariaceae**: *Calycularia crispula*

3. Thallus prostrate or erect. Thallus margins not strongly undulate to crispate. Midrib with central strand (but strand sometimes indistinct in *Symphyogynopsis*). Ventral scales absent. Capsule linear. Common plants ····· **Pallaviciniaceae**

PALLAVICINIACEAE

Plants thalloid, 2–9 mm wide, green to reddish, with a distinct, swollen midrib and a unistratose lamina, creeping or erect, simple or forked, sometimes with ventral branches. Midrib ca. 1/8–1/2 of thallus width, with 1(–3) central strands of narrow, thick-walled cells. Oil bodies finely granular. Dioicous. Gametoecia on the dorsal surface of the midrib or on short lateral branches, usually protected by scales or an involucre. Sporophyte surrounded by a deeply laciniate pseudoperianth or covered by a scale. Capsule cylindrical, opening by (1–)2(–4) valves. Spores small, unicellular. Elaters with 2–3 spirals, free.

About 8 genera worldwide; 4 genera in Malaysia. The main characters of Pallaviciniaceae are: 1) thallus dioicous, 2–9 mm wide, simple or dichotomously branched, with a distinct, swollen midrib; 2) midrib with a central strand; 3) capsule elongate, usually opening by 2 valves.

1. Thallus growing erect from a creeping rhizome. Thallus margins sharply toothed ····· ····· *Jensenia*
1. Thallus prostrate. Thallus margins entire, sometimes with slime hairs ····· 2
2. Gametangia on very short branches at the base of the thallus. Midrib often somewhat assymetrical····· *Podomitrium*
2. Gametangia occurring on the main thallus, not on short branches. Lamina equal on either side of midrib ····· 3
3. Midrib with a distinct central strand (= dark line inside the midrib), shortly ciliate, without slime hairs. Sporophyte enclosed by a long tubular pseudoperianth····· ····· *Pallavicinia*
3. Midrib without distinct central strand, always with bicellular slime hairs. Sporophyte covered by a scale, long tubular pseudoperianth absent ····· *Symphyogynopsis*

Jensenia Lindb. Fig. 5A

Thallus green to reddish, dendroid, differentiated into an upright stipe and frond arising from a prostrate, stolon-like base, the frond 2–4 times forked, the branches in one plane, flat or deeply concave, winged. Midrib of the branches very broad and thick, to 1/2× branch width, with one central strand of narrow, thick-walled cells. Thallus margins usually toothed. Rhizoids colorless. Archegonia in clusters at the lower furcations of the thallus, each cluster of archegonia surrounded by a cup-like involucre with a fringed mouth. Sporophyte enclosed by a long-tubular pseudoperianth several times longer than the involucre.

A tropical and southern-temperate genus (7 spp.); 1 species in Malaysia (Sarawak, Sabah), *Jensenia decipiens* (Mitt.) Grolle (= *Makednothallus obtusidens* Herzog), on moist soil and rock above 1000 m.

Note: *Jensenia* is readily separated from all other thalloid liverworts of Malaysia by

its dendroid habit.

Literature: Miller & Inoue (1966); Grolle & Piippo (1986).

Pallavicinia Gray Figs. 5D–H; 63A

Thallus green, creeping to ascending, usually simple, sometimes with ventral branches; rhizome-like wingless base absent or present, short. Midrib ca. 1/8–1/6× thallus width, with one central strand of narrow, thick-walled cells. Thallus wings slightly bordered by somewhat narrower cells, margins with 2–3 cell long slime hairs, otherwise entire. Rhizoids colorless or brown. Gametoecia on the dorsal surface of the midrib. Antheridia in long bands along the midrib, each antheridium covered by a laciniate scale. Archegonia in clusters on the midrib, each cluster surrounded by a circle of free or slightly connate, ciliate-laciniate scales. After fertilization, a long, tubular pseudoperianth develops surrounding the sporophyte.

About 12 species worldwide; 3 species in Malaysia, on rotten wood, tree bases and soil.

Note: Characteristics of *Pallavicinia* are the prostrate to ascending, unlobed thalli with a distinct central strand and with scattered, stalked slime hairs on the margins. The gynoecia are scattered on the dorsal midrib and covered by ciliate-laciniate scales; after fertilization, a tubular pseudoperianth develops surrounding the sporophyte.

Literature: Johnson (1958); Grolle & Piippo (1986).

Podomitrium Mitt. Fig. 5B

Thallus green, creeping, usually simple, sometimes with ventral branches; rhizome-like wingless base present, short. Midrib as in *Pallavicinia*, ca. 1/8–1/6× thallus width, with a conspicuous central strand of narrow, thick-walled cells. Thallus margins unbordered, entire, sometimes with a few 2-celled slime hairs near the apex. Rhizoids colorless. Gametoecia on very short, ventral branches sprouting from the base of the thallus. Antheridia spicate, not covered by scales. Archegonia in clusters surrounded by an involucre. After fertilization, a long, tubular pseudoperianth develops surrounding the sporophyte.

A small Asian-Australasian genus (3 spp.); 1 species widespread in Malaysia, *Podomitrium malaccense* (Steph.) Campb., on tree trunks, rotten wood or soil.

Note: *Podomitrium* is readily recognized by the prostrate thalli with entire margins and with gametangia on very short branches at the base of the thallus.

Literature: Johnson (1958 as *Hymenophytum malaccense*); Grolle & Piippo (1986); Piippo *et al.* (2002).

Symphyogynopsis Grolle Fig. 5C

Thallus green, creeping to ascending, usually with a single bifurcation; rhizome-like base usually absent. Midrib fleshy, ca. 1/8–1/6× thallus width, with an inconspicuous central strand of narrow, thin-walled cells. Thallus wings slightly bordered by somewhat narrower cells, margins with 2–3 cell long slime hairs, otherwise entire. Gametoecia on the dorsal surface of the midrib. Antheridia in long bands along the midrib, each antheridium covered by a laciniate scale. Archegonia in clusters on the midrib, each cluster surrounded by a

circle of free or slightly connate, ciliate-laciniate scales. After fertilization, a long, tubular pseudoperianth develops surrounding the sporophyte.

A monotypic Southeast Asian genus; contains *Symphyogynopsis gottscheana* (Mont. & Nees) Grolle, in Malaysia recorded from Perak (Grolle & Piippo 1986); on sheltered soil and rotten wood.

Note: *Symphyogynopsis* closely resembles *Pallavicinia*, but clearly differs from *Pallavicinia* by the characters given in the key.

Literature: Grolle & Piippo (1986).

SANDEOTHALLACEAE

A monotypic family.

Sandeothallus R.M.Schust. Fig. 7F–J

Plants thalloid, large, 1–2 cm wide, 3–6 cm long, unbranched or dichotomous. Thallus with a narrow midrib and broad wings, the wings mostly 2–4 cells thick, becoming unistratose towards the margin, the margins entire, without hairs. Midrib without central strand. Oil bodies homogeneous. Rhizoids deep reddish-purple. Dioicous; male plants smaller than female plants. Antheridia and archegonia on the dorsal surface of the midrib, covered by scales. Seta long. Sporophyte surrounded by a long involucre. Capsule ovoid, opening by two valves which remain attached to each other at the tip, capsule wall 2–6-layered. Spores small, coarsely papillose. Elaters free.

A monotypic Southeast Asian genus, contains *Sandeothallus radiculosus* (Schiffn.) R.M.Schust., recorded from Sarawak. In montane forest areas, on humid soil and on tree bases near springs, sometimes growing submerged.

Note: *Sandeothallus radiculosus* resembles *Pallavicinia* in producing gametangia on the dorsal side of the midrib and covered by scales, but differs from *Pallavicinia* in the deeply reddish-purple color of the rhizoids, the absence of a central strand in the midrib, and the ovoid capsule which opens irregularly by two valves. The capsule valves may remain attached to each other at the tip after dehiscence.

Literature: Campbell (1913 as *Calycularia radiculosa*); Schuster (1982).

Subclass METZGERIIDAE (simple thalloid liverworts II)

Plants thalloid, growing with a 2-sided apical cell, divided into 2 lateral merophytes, ventral merophyte absent. Thallus often differentiated into a midrib and thin wings. Cells with or without trigones; oil bodies usually present. Rhizoids with smooth walls. Antheridia and archegonia on abbreviated branches at the thallus margin or on the ventral surface of the midrib; archegonia not arising from the apical cell of thallus (plants anacrogynous). Sporophyte enclosed by a fleshy calyptra. Seta well developed, 1–3 cm long, thin to very thick. Capsule ellipsoid, opening by 4 valves.

Key to families of Metzgeriidae

1. Thallus margins usually with hairs. Thallus dichotomous (rarely pinnate), with a very narrow midrib and broad, unistratose wings. Gametoecia on the ventral side of the midrib ····· **Metzgeriaceae**
1. Thallus margins without hairs. Thallus unbranched or pinnate to palmate, with a broad, indistinct midrib or with a distinct midrib on branches; unistratose wings present or absent. Gametoecia on short lateral branches or on the underside of the thallus margin ··· ····· **Aneuraceae**

ANEURACEAE

Plants thalloid, 0.3–10 mm wide, green to brown to black, creeping to erect, unbranched or pinnate to palmate, without midrib or with a distinct midrib on branches; thallus apex and ventral surface with slime papillae. Oil bodies finely to coarsely granular, sometimes absent. Monoicous or dioicous. Gametoecia in cavities on short lateral branches or on small receptacles on the underside of the thallus margin. Sporophyte enclosed by a fleshy calyptra; pseudoperianth lacking. Seta 4–15 cells thick. Capsule ellipsoidal, opening by 4 valves, wall 2-layered. Spores small, unicellular. Elaters with 1(–2) spirals, attached to the tips of the capsule valves. Vegetative reproduction by multicellular gemmae.

About 5 genera worldwide; 3 genera in Malaysia. The most important characteristics of Aneuraceae are: 1) thallus pinnate or unbranched; 2) midrib usually indistinct; 3) gametoecia at thallus margins or on short lateral branches; 4) sporophyte in a fleshy calyptra; 5) elaters attached to the tips of the valves.

1. Thallus 2–4-pinnate, main axis 0.3–1.5(–2) mm wide. Midrib present or absent. Male branches with antheridia in 2 rows. Archegonia on short branches. Seta 4 cells thick. Vegetative reproduction by gemmae ····· *Riccardia*
1. Thallus unbranched or irregularly 1-pinnate, main axis 2–10 mm wide. Midrib absent. Male branches with antheridia in 2–6 rows. Archegonia on small receptacles hidden under the thallus margin, not on short branches. Seta 8–15 cells thick. Gemmae absent ····· 2
2. Thallus irregularly pinnately branched. Male branches with antheridia in 2 rows ····· ····· *Lobatiriccardia*
2. Thallus branches absent or very scarce. Male branches with antheridia in 2–4(–6) rows ··· ····· *Aneura*

Aneura Dumort. Fig. 6A

Thallus 3–10 mm wide, fleshy, bright green to dark green, creeping, flat or convex, sometimes crisped, ± simple, branches lacking or very scarce, thallus thickened to near the margins, without midrib, wings lacking or narrow, margins entire or lobed. Oil bodies numerous per cell (usually more than 10, fewer in thallus margin cells), small, finely granular. Dioicous. Antheridia in 2–4(–6) transverse rows on short or long branches. Archegonia in clusters in incisions of the thallus margin, hidden under small thallus flaps. Seta thick, in cross section 8–16 cells in diameter. Vegetative reproduction lacking.

About 20 species worldwide; 2 species in Malaysia, *Aneura maxima* (Schiffn.) Steph. and *A. pinguis* (L.) Dumort., on rotten wood, earth banks and rock in lowland and montane rainforests.

Note: Characteristic of *Aneura* is the fleshy and rather broad (3–10 mm wide), scarcely branched thallus without midrib and with entire to somewhat crisped margins.

Literature: Furuki (1991).

Lobatiriccardia (Mizut. & S.Hatt.) Furuki Fig. 6B, C, J

Thallus 2–8 mm wide, fleshy, glistening green to darkish-green to bluish-green, creeping, concave, pinnate, without a midrib, margins with a 2–4 cell wide unistratose wing. Oil bodies 1–8 per cell, brownish, finely granular, sometimes lacking in the epidermis. Dioicous. Antheridia in 2 rows on short branches. Archegonia in clusters on small receptacles at incisions of the thallus margins, surrounded by multicellular paraphyses and thick-walled unicellular rhizoids. Seta thick, in cross section 8–15 cells in diameter. Vegetative reproduction lacking.

Contains 7 species, mostly in Southeast Asia and New Zealand; only 1 species in Malaysia, *Lobatiriccardia coronopus* (Steph.) Furuki (= *L. lobata* (Schiffn.) Furuki), recorded from Pahang, Sarawak and Sabah, same habitat as *Aneura* and *Riccardia*.

Note: *Lobatiriccardia* resembles *Riccardia* in the pinately branched thallus, but differs from *Riccardia* in the broader thallus (2–8 mm mm wide), the thicker seta and presence of the archegonia on small receptacles hidden under the thallus margins, not on short branches.

Literature: Furuki (1991, 1996); Preußing *et al.* (2010).

Riccardia Gray Figs. 6D–I; 63B

Thallus 0.3–2 mm wide, green to brown to black, with or without midrib, creeping, ascending or erect, sometimes dendroid, irregularly to regularly (1–)2–4-pinnate to palmate, the branches suberect (branching palmate) to widely spreading (branching pinnate), sometimes with a distinct midrib; sometimes with short stolons at the base. Main axis ca. 3–20(–40) cells in diameter, concave-convex, plano-convex, bi-convex or rounded in diameter, sometimes with a subepidermis of cells with thick-walled, brownish walls; axis and branches with or without unistratose lateral wings, thallus margins entire or toothed. Oil bodies finely to coarsely granular (vermiculate in *R. deguchii*), 1–10(–25) per cell, of regular or very irregular shape, sometimes absent or scarce in the epidermis. Monoicous or dioicous. Gametoecia in 2 rows on short lateral branches. Archegonia surrounded by unicellular and thick-walled rhizoids or by multicellular paraphyses. Seta thin, in cross section 4 cells in diameter. Vegetative reproduction by gemmae from the apex and surface of narrow thallus branches.

About 100 species worldwide; 19 species in Malaysia, on rotten wood, earth banks and rock in lowland and montane rainforests.

Note: *Riccardia* is easily recognized by the 2–4-pinnate to palmate thalli.

Literature: Furuki (1991, 1994, 1995, 1998); Furuki *et al.* (2013).

METZGERIACEAE

A family of 2–3 genera worldwide; 1 in Malaysia.

Metzgeria Raddi Figs. 7A–E; 63C
(*Apometzgeria* Kuwah.)

Plants thalloid, thin and with a narrow midrib, to 2(–3) mm wide, pale green to yellowish, sometimes becoming blue when dry, creeping to erect or pendent, forked (very rarely pinnate), usually with hairs (= rhizoids) on the margins, on the underside of the midrib and, sometimes, on the ventral surface of the thallus, rarely on the dorsal surface (*M. pubescens*). Hairs unicellular, arising singly or in pairs, sometimes in groups of 3–5. Thallus surface plane to strongly convex with reflexed margins. Midrib 2–8(–12) cells wide, epidermis cells smooth or papillose, larger than the inner cells; central strand absent. Thallus wings unbordered or with a narrow border of elongate cells. Oil bodies absent or very small, homogeneous. Monoicous or dioicous. Gametoecia on very short branchlets scattered along the ventral side of the midrib, the antheridia in a globose sac, the archegonia hidden under a flap (= female branchlet or involucre). Sporophyte enclosed by a fleshy calyptra, the calyptra often densely hairy; pseudoperianth lacking. Capsule spherical to ovoid, opening by 4 valves, wall 1–2-layered. Spores small, unicellular. Elaters 1-spiralled, attached to valve apices. Vegetative reproduction by gemmae or caducous branches.

About 75 species worldwide; 9 species in Malaysia, on bark of trees and shrubs and on living leaves in lowland and montane rain forests; occasionally on rotten wood or rock.

Note: Characteristics of *Metzgeria* are the dichotomously branched thallus with a unistratose lamina, a very narrow midrib, thallus margins (and sometimes the surface) with numerous hairs, and gametoecia produced on the underside of the midrib. The species usually grow epiphytic.

Literature: Johnson (1958); Kuwahara (1965, 1966), So (2003b), Sukkharak & Chantanaorrapint (2020).

Subclass PLEUROZIIDAE
(leafy liverworts I)

Plants with leaves, growing with a 2-sided apical cell and made up of 2 merophytes, ventral merophyte absent. Stems without central strand. Leaves originating from 2 initial cells, one layer of cells thick, undivided or bifid. Underleaves absent. Antheridia in leaf axils. Archegonia terminal on long or short shoots, surrounded by bracts. Sporophyte enclosed by a perianth and a thin calyptra. Seta thick. Capsule ovoid, opening by 4 valves, wall 6–8-layered. Vegetative reproduction not observed.

Contains only the genus *Pleurozia* (family Pleuroziaceae). *Pleurozia* was traditionally classified with the Jungermanniidae but molecular data show that the genus is closer to the simple thalloid liverworts. The genus shares with the simple thalloid liverworts a 2-sided apical cell and the complete lack of a ventral merophyte.

PLEUROZIACEAE

A monotypic family.

Pleurozia Dumort. Figs. 7K, L; 64A, B
(*Eopleurozia* R.M.Schust.)

Plants usually robust, 2–10 cm long, 4–7 mm wide, olive-green to deep wine-red to purplish, creeping to ascending with leafy shoots sometimes arising from a rhizome-like base, loosely branched or in dense tufts. Stems rigid, with a thick-walled cortex. Branches lateral-intercalary. Leaves deeply concave and imbricate, strongly enveloping the stem, succubous, undivided or divided into 2 lobes, the dorsal lobe usually smaller and sac-like (sometimes explanate), sac opening with a valve, leaf tips acute or short-bifid, margins entire or toothed. Cells 40–100 µm long, with large trigones, cuticle smooth; oil bodies finely granular. Rhizoids scarce, scattered. Underleaves absent. Perianths cylindrical, terete and sterile or plicate and fertile.

Contains 12 species, mostly in the tropics; 4 species in Malaysia, on tree trunks and branches and on rock in montane and subalpine forests.

Note: *Pleurozia* is readily recognized by the robust, often wine-red to purple plants with deeply concave leaves strongly enveloping the stem and two types of perianths, plicate fertile ones and terete sterile ones. The leaves are usually divided into a dorsal and a ventral lobe, with the dorsal lobe smaller in size and modified into a closed sac. In some phenotypes of *P. gigantea* (F.Weber) Lindb., the sac is very small or even lacking. Plants without sacs have been described as *P. simplicissima* Herzog (= *Eopleurozia simplicissima* (Herzog) R.M.Schust.), which is a synonym of *P. gigantea* (Thiers 1993).

Literature: Thiers (1993); Sukkharak (2017a).

Subclass JUNGERMANNIIDAE (leafy liverworts II)

Plants leafy (very rarely thalloid: *Cololejeunea metzgerioides*, *Mizutania riccardioides*), growing with a 3-sided apical cell and divided into 3 merophytes (two lateral, one ventral). Stems without central strand. Branches lateral or ventral, with or without collar, originating from a leaf initial cell or from the stem. Leaves originating from 2 or 3 initial cells, usually one layer of cells thick, divided or undivided, in 2–3 rows, underleaves usually smaller than leaves or lacking. Cells with or without trigones. Antheridia in leaf axils. Archegonia terminal on long or short shoots (acrogynous), surrounded by bracts and often by bracteoles. Sporophyte enclosed by a perianth and a calyptra, or by a fleshy perigynium. Capsule globose to cylindrical, opening by four valves, wall 2–10-layered.

The subclass Jungermanniidae is the largest subclass of the liverworts and contains about 80% of the species worldwide. The subclass is subdivided into two major orders, Jungermanniales and Porellales. All Malaysian members of the subclass are leafy with exceptions, *Mizutania riccardioides* (Jungermanniales: Calypogeiaceae) and *Cololejeunea*

metzgerioides (Porellales: Lejeuneaceae).

Key to orders of Jungermanniidae

1. Leaves without ventral lobule ····· **Jungermanniales**
1. Leaves with a ventral lobule (= small or large fold or sac on the ventral side of the leaf) ····· **Porellales** (p. 87)

JUNGERMANNIALES

Plants terrestrial, saxicolous or epiphytic. Branching lateral and/or ventral. Leaves transverse, succubous or incubous, originating from 2 initial cells; ventral lobule lacking. Seta long, thin or thick. Capsule globose to cylindric, wall 2–9-layered. Spores normally small and unicellular, germination exosporic.

Key to families of Jungermanniales

1. Leaves deeply dissected into hair-like segments ····· 2
1. Leaves not deeply dissected into hair-like segments ····· 4
2. Leaves divided to the base into 1–4 filaments, margins entire. Plants very small, alga-like ····· 3
2. Leaves divided into (2–)4–9 segments, margins strongly hairy. Plants larger, not alga-like ····· **Trichocoleaceae**
3. Underleaves ± as large as lateral leaves. Cuticle of leaf cells with narrowly elongate papillae. Perianth at stem apex ····· **Pseudolepicoleaceae**
3. Underleaves smaller than lateral leaves or absent. Cuticle of leaf cells smooth or with small, rounded papillae. Perianth on a short ventral branch ····· **Lepidoziaceae**
4. Plants filamentose, with rudimentary leaves (1 cell long, 2 cells wide), leaf cells at the tip with a sausage-like slime papilla or a stiff bristle ····· **Lepidoziaceae**: *Zoopsis*
4. Plants different ····· 5
5. Underleaves almost as large as leaves ····· 6
5. Underleaves much smaller than leaves (when in doubt try both leads) ····· 9
6. Leaves 4-lobed, margins ciliate ····· **Lepicoleaceae**
6. Leaves 2–3-lobed ····· 7
7. Plants (bi)pinnate ····· **Mastigophoraceae**
7. Plants not pinnate ····· 8
8. Leaf margins toothed. Leaves ovate ····· **Balantiopsidaceae**: *Isotachis*
8. Leaf margins entire. Leaves narrowly elongate ····· **Herbertaceae**
9. Leaves divided into a large ventral lobe and a smaller dorsal lobe, the two lobes usually connected by a keel ····· 10
9. Leaves not divided into a large ventral lobe and a smaller dorsal lobe ····· 12
10. Keel winged ····· **Schistochilaceae**
10. Keel not winged ····· 11
11. Underleaves present. Leaf margins densely ciliate by long cilia. Sporophyte enclosed by

a pendent marsupium ····· **Balantiopsidaceae**: *Balantiopsis*
11. Underleaves absent. Leaf margins toothed or entire, not longly ciliate. Sporophyte enclosed by a flat perianth ····· **Scapaniaceae**: *Scapania*
12. Leaves incubous ····· **Key A**
12. Leaves succubous or transverse ····· 13
13. Underleaves present ····· **Key B**
13. Underleaves absent (or very small) (when in doubt try both leads) ····· **Key C**

Key A. Leaves incubous

1. Underleaves present ····· 2
1. Underleaves absent ····· **Lejeuneaceae**: *Cololejeunea*
2. Leaves with 3 or more lobes or teeth ····· **Lepidoziaceae**
2. Leaves with 0–2 lobes or teeth ····· 3
3. Vestigial lobule (consisting of a few cells) present at ventral base of leaf. Stems fragile, ventral stem surface only 2–4 cells wide, hyalodermis often present. Ventral branches absent ····· **Lejeuneaceae** (with reduced lobules)
3. Lobule lacking. Stems rigid, ventral stem surface more than 4 cells wide, hyalodermis absent. Ventral branches frequently present. ····· 4
4. Plants dichotomously branched. Flagelliform ventral branches present. Leaf apex bifid or trifid with sharp teeth (rarely entire) ····· **Lepidoziaceae**
4. Plants unbranched or irregularly branched. Flagelliform ventral branches lacking. Leaf apex entire or short-bifid ····· **Calypogeiaceae**

Key B. Leaves succubous or transverse, underleaves present

1. Leaved undivided or shallowly retuse ····· 2
1. Leaves distinctly divided into 2 or more lobes (when in doubt try both leads) ····· 7
2. Leaf margins toothed in the upper half or throughout. (Dorsal leaf base decurrent. Leaves asymmetrical, ventral margin arched, dorsal margin ± straight) ····· **Plagiochilaceae**
2. Leaf margins entire or with a few teeth in the lower half ····· 3
3. Underleaves large, about half the length of the leaves, underleaf margins usually toothed ····· 4
3. Underleaves smaller, underleaf margins entire ····· 5
4. Rhizoids wine red, in long tufts at underleaf bases. Dorsal leaf base decurrent. Leaf cells with many small papillae and with small trigones (not bulging) ····· **Balantiopsidaceae**: *Acroscyphella*
4. Rhizoids colorless, in short tufts. Dorsal leaf base not decurrent. Leaf cells with one large papilla and with large bulging trigones ····· **Acrobolbaceae**: *Conoscyphus*
5. Leaves deeply concave-canaliculate. Leaf cells fully thin-walled, without trigones. Underleaves broadly ovate ····· **Lepidoziaceae**: *Hygrolembidium*
5. Leaves flat or weakly concave. Leaf cells with trigones. Underleaves lanceolate ····· 6
6. Plants pale green. Leaves almost longitudinally inserted, flat. Underleaves bifid ····· **Notoscyphaceae**

6. Plants brownish-green to violet to black. Leaves subtransverse, concave. Underleaves undivided ····· **Gymnomitriaceae**: *Nardia*
7. Leaves divided into 3 or more lobes ····· **Lepidoziaceae**
7. Leaves bifid ····· 8
8. Plants very small, 0.3–0.5 mm wide. Cells uniformly thick-walled, densely striped. Stolons present ····· **Cephaloziaceae**: *Odontoschisma exigua*
8. Plants larger. Cell walls with trigones, not densely striped. Stolons absent ····· 9
9. Leaves deeply 2–4-lobed to more than 1/2 of leaf length. Leaf margins often densely toothed-ciliate, rarely entire ····· **Scapaniaceae**
9. Leaves 2-lobed to maximally 1/3 of leaf length. Leaf margins entire or toothed ····· 10
10. Leaves ± transverse. Branches flagelliform. Rhizoids scattered, scarce ····· **Scapaniaceae**: *Andrewsianthus recurvifolius*
10. Leaves succubous, often almost longitudinally inserted. Branches not flagelliform. Rhizoids in tufts at underleaf bases ····· 11
11. Stem cells densely papillose. Leaves opposite, ca. 2× longer than wide, ligulate ····· **Acrobolbaceae**: *Saccogynidium*
11. Stem cells smooth. Leaves alternate, less than 2× longer than wide ··· **Lophocoleaceae**

Key C. Leaves succubous or transverse, underleaves absent (or very small)

1. Leaves 2–3-lobed ····· 2
1. Leaves undivided or shallowly emarginate (when in doubt try both leads) ····· 11
2. Plants minute, 0.2–0.4 mm wide, shoot tips usually with gemmae. Leaf cells very small, ca. 8–20 µm, thin or thick-walled, without trigones. Leaves bifid ····· **Cephaloziellaceae**
2. Plants larger. Leaf cells larger, often with trigones. Leaves undivided or bifid ····· 3
3. Stem with hyalodermis, very transparent, of thin-walled cells ····· **Cephaloziaceae**
3. Stem without hyalodermis, rigid, of thick-walled cells ····· 4
4. Leaf tips longly piliferous ····· **Adelanthaceae**: *Pseudomarsupidium*
4. Leaf tips not longly piliferous ····· 5
5. Very small rheophilous plant. Dorsal leaf insertion not reaching the stem midline. Plants arising from a leafless, rhizome-like shoot ····· **Cephaloziellaceae**: *Kymatocalyx*
5. Plants not rheophilous. Dorsal leaf insertion reaching the stem midline. Plants with or without rhizome-like shoot ····· 6
6. Leaf margins often with hair-like cilia. Oil bodies brown. Cuticle papillose. Plants without secondary pigmentation, pale green. Sporophyte in a pendent marsupium at the shoot apex ····· **Acrobolbaceae**: *Acrobolbus* p.p.
6. Leaf margins without hair-like cilia. Oil bodies colorless or grayish. Cuticle papillose or smooth. Plants with or without secondary pigmentation. Sporophyte enveloped by a perianth or by bracts, not in a marsupium ····· 7
7. Leaves transverse. Dorsal leaf insertion crossing beyond the stem midline. Sporophyte enveloped by bracts, perianth ± lacking ····· **Gymnomitriaceae**
7. Leaves succubous. Dorsal leaf insertion ending at the stem midline, not crossing beyond.

Sporophyte enveloped by a long perianth ····· 8
8. Leaf margins usually toothed (rarely entire), dorsal leaf margin recurved, leaf bases decurrent ····· **Plagiochilaceae**
8. Leaf margins usually entire (rarely toothed), dorsal margin not recurved, leaf bases not or very shortly decurrent ····· 9
9. Leaves truncate to very shallowly and broadly 2-lobed (to 1/10(–1/6) of leaf length), apex with 1–2 teeth ····· **Adelanthaceae**: *Syzygiella* (= *Anomacaulis) flaccida*
9. Leaves more deeply 2-lobed ····· 10
10. Plants frequently with reddish or purple secondary pigmentation. Gemmae usually present. Trigones often large. Perianth plicate ····· **Scapaniaceae**
10. Plants without secondary pigmentation, green to pale brown. Gemmae absent. Trigones small. Perianth smooth, terete ····· **Jungermanniaceae:** *Mesoptychia*
11. Leaves opposite, dorsal leaf bases united ····· 12
11. Leaves alternate, dorsal leaf bases not united ····· 14
12. Plant very small, worm-like, 0.3–0.6 mm wide, strongly attached to soil, green to brown, growing at high elevation. Trigones very small or lacking ····· **Southbyaceae**
12. Plants larger, usually epiphytic. Trigones small or large ····· 13
13. Plants with reddish or purple pigmentation. Perianth plicate ····· **Adelanthaceae**: *Syzygiella*
13. Plants without reddish or purple pigmentation. Perianth not plicate ····· **Plagiochilaceae**: *Chiastocaulon*
14. Leaf margin toothed ····· 15
14. Leaf margin entire ····· 17
15. Dorsal leaf margin incurved. Not yet reported from Malaysia but to be expected (see Grolle 1965a; Menzel 1988; *Wettsteinia inversa* (Sande Lac.) Schiffn. occurs in Kalimantan) ····· **Adelanthaceae**: *Wettsteinia*
15. Dorsal leaf margin recurved or plane ····· 16
16. Leaf apex obliquely truncate-emarginate. Stems pale-colored. Plants pale green to yellowish-green when fresh (grayish or yellow-brown when dry). Oil bodies pale brown, numerous per cell. Sporophyte in a marsupium ··· **Acrobolbaceae**: *Acrobolbus*
16. Leaf apex not obliquely truncate-emarginate. Stems brown, darker-colored than leaves. Plants green or brown. Oil bodies colorless or gray. Sporophyte in a flattened perianth ··· **Plagiochilaceae**: *Plagiochila*
17. Robust, reddish (or green) plants with dorsal leaf bases strongly overlapping and closely enveloping the stem ····· 18
17. Dorsal leaf bases not closely enveloping the stem ····· 19
18. Trigones inside with dark, star-like markings. Dorsal leaf insertion not crossing the dorsal stem midline. Leaf margin without gemmae ····· **Adelanthaceae**: *Denotarisia*
18. Trigones without dark, star-like markings. Dorsal leaf insertion crossing the dorsal stem midline. Leaf margin often with gemmae ····· **Scapaniaceae**: *Gottschelia*
19. Small green to reddish-purple plants with ventral stolons. Gemmae produced in whitish clusters on the tips of upright flagelliform branches. Trigones very large, cell-lumen star-shaped. Gynoecia on a short ventral branch ····· **Cephaloziaceae**: *Odontoschisma*
19. Plants small or large, without ventral stolons. Flagelliform branches without gemmae.

Trigones small or large. Gynoecia terminal on a long shoot ·····20
20. Dorsal leaf insertion line frequently not reaching the dorsal midline of stem. Branches (when present) always ventral, lateral branching absent. Plants brown. Leaf margins often with gemmae. Rhizoids in tufts, colorless. Sporophyte in a marsupium····· ·····**Jackiellaceae**
20. Dorsal leaf insertion line reaching the dorsal midline of stem. Branches (when present) usually lateral. Gemmae absent. Rhizoids scattered (rarely in tufts), colorless or reddish. Sporophyte not in a marsupium ·····21
21. Leaf insertion transverse. Rare, reddish brown to blackish plants from rock above 3000 m on Mt. Kinabalu ····· 22
21. Leaf insertion succubous ····· 23
22. Flagelliform branches present. Stem base not stoloniform. Sporophyte enveloped by a plicate perianth ····· **Scapaniaceae**: *Andrewsianthus mizutanii*
22. Flagelliform branches absent. Stem base stoloniform. Sporophyte enveloped by bracts (perianth lacking) ····· **Gymnomitriaceae**: *Marsupella subintegra*
23. Rhizoids few, scattered, colorless. Plants frequently growing upright. Leaf apex acute or rounded ····· **Adelanthaceae**: *Syzygiella*
23. Rhizoids numerous, scattered or in long tufts, colorless or reddish. Plants creeping or ascending. Leaf apex rounded ····· **Solenostomataceae**

ACROBOLBACEAE

Plants yellowish-green to bluish-green or brown, creeping, upright or pendent, sometimes with a stoloniferous base. Stems with or without thick-walled cortex. Branches intercalary (lateral or ventral), terminal branching lacking; stolons present or absent. Leaves succubous, undivided or 2-lobed (rarely 3–4-lobed), margins sometimes with long rhizoids. Cells usually with a papillose cuticle; oil bodies finely granular, usually brown. Underleaves present or absent. Rhizoids usually scattered, rarely in tufts (*Conoscyphus*). Dioicous. Gametoecia terminal on the stem or on very short branches. Sporophytes usually enclosed by a marsupium, rarely by a perianth and a short perigynium (*Conoscyphus*). Setae thick. Capsule ellipsoid, wall 4–10-layered. Vegetative reproduction scarce, by gemmae or caducous leaves.

About 8 genera worldwide; 3 genera in Malaysia. The main characters of Acrobolbaceae are: 1) plants yellowish-green to blue-green to brown; 2) leaves succubous, undivided or bifid; 3) cuticle papillose; 4) underleaves present or absent; 4) oil bodies brown, finely granular; 5) sporophyte in a marsupium.

1. Underleaves absent ····· *Acrobolbus*
1. Underleaves present ····· 2
2. Underleaves ± undivided. Plants worm-like, swollen. Leaves alternate, asymmetrically ovate. Leaf cells with a large papilla ····· *Conoscyphus*
2. Underleaves deeply bifid. Plants not worm-like. Leaves opposite, ligulate. Leaf cells with numerous small papillae ····· *Saccogynidium*

Acrobolbus Nees Fig. 8A–C
(*Tylimanthus* Mitt.)

Plants small to robust, 1.5–5 mm wide, glossy pale green to yellowish-green, creeping or ascending, with or without stoloniform base. Stems pale-colored, with a cortex of (1–)2–4 cell-layers. Branches lateral- or ventral-intercalary. Leaves succubous, ovate-oblong or subrectangular, bifid or obliquely truncate to emarginate, tips rounded to acute to acuminate, margins entire or toothed. Cells with trigones, cuticle papillose; oil bodies 5–40 per cell, granular, brown. Underleaves absent. Dioicous; male plants frequently smaller than female plants. Antheridia 1–10 per bract. Archegonia terminal on long shoots or on a short ventral branch, often surrounded by large bracts forming a flower-like involucre, margins toothed-ciliate or entire; female bracteoles absent. Marsupium short or long. Capsule tip acute or rounded. Vegetative reproduction sometimes by caducous leaves.

About 30 species worldwide; 2 species in Malaysia (Sabah), *Acrobolbus ciliatus* (Mitt.) Schiffn. and *A. saccatus* (Hook.) Briscoe (= *Tylimanthus saccatus* (Hook.) Schiffn.), on bark of trees (mostly trunk bases) or rotten wood in montane forests.

Note: *Acrobolbus* is recognized by the pale green to yellowish-green plants without underleaves and with succubous leaves with a bifid or obliquely truncate to emarginate apex, papillose cuticle and brown oil bodies. The sporophyte is produced in a pendent marsupium at the apex of a long shoot, with a large, frequently dentate, flower-like involucre. The genus *Tylimanthus* was long accepted as a separate genus, but has been placed in the synonymy of *Acrobolbus* based on molecular evidence (Briscoe *et al.* 2017).

Literature: Piippo (1985a); Briscoe *et al.* (2015, 2017).

Conoscyphus Mitt. Fig. 8D

Plants 2–3 mm wide, worm-like, brown to reddish-brown, creeping or ascending, or pendent (plants growing upside down when pendent), without stoloniform base. Stems blackish-brown, with a thick-walled cortex of several cell-layers. Branches intercalary. Leaves succubous, strongly convex, densely imbricate, ovate-falcate and strongly asymmetric, apex rounded, dorsal margin ± straight-undulate and entire, ventral margin broadly arched and often with a few teeth in the lower half, bases not decurrent. Cells with large bulging trigones and a broad dorsal papilla; oil bodies granular, brown. Rhizoids colorless, in short tufts at underleaves, often absent. Underleaves present, large, ± undivided, margins irregularly toothed. Dioicous. Sporophyte enclosed by a long tube consisting of a perianth and a short perigynium.

A small paleotropical genus (2 spp.); 1 species in Malaysia (Pahang, Malacca, Sabah), *Conoscyphus trapezoides* (Sande Lac.) Schiffn., on tree bark in montane forest.

Note: Characteristics of *Conoscyphus* are the rather robust, reddish-brown, wormlike plants with densely imbricate and highly asymmetric leaves, rounded leaf apex, subentire leaf margins, leaf cells with large bulging trigones and with a broad papilla, and large imbricate underleaves. The genus was long considered a member of Lophocoleaceae or Geocalycaceae, but molecular evidence shows that it belongs in Acrobolbaceae.

Literature: Piippo (1985b); Dimon *et al.* (2018).

Saccogynidium Grolle Fig. 8E, F

Plants ca. 3–4 mm wide, green to brown, creeping, without stoloniform base. Stems fragile or rigid, cells thin-walled or thick-walled; cuticle of stem densely papillose. Branches only ventral-intercalary. Leaves succubous, opposite, the dorsal bases often connate, ligulate-oblong, apex rounded or short-bifid, margins entire or crenulate. Cells with rather trigones, cuticle densely papillose; oil bodies up to 20 per cell, granular. Dioicous. Gametoecia on very short ventral branches; male branches tiny, catkin-like. Marsupium long. Capsule tip rounded. Vegetative reproduction sometimes by caducous leaves.

A mainly Malesian-Australasian genus (7 spp.); 3 species in Malaysia, on soil, rotten logs or tree trunks in montane environments.

Note: *Saccogynidium* was considered a member of Geocalycaceae but molecular study has shown that it belongs in Acrobolbaceae (Shaw *et al.* 2015). The elongate, opposite leaves with entire or crenulate margins and a rounded to bidentate apex, densely papillose cuticle, and gametoecia on very short ventral branches, are the main characters of *Saccogynidium*. The stem is often somewhat bluish-green in fresh material.

Literature: Grolle (1960); Hattori (1964); Piippo (1985b); Gao & Cao (2001); Shaw *et al.* (2015).

ADELANTHACEAE (Jamesoniellaceae)

Plants small to large, green, yellowish, reddish, purplish, brown or black, creeping or upright, sometimes with a stoloniferous base. Stems rigid, usually with a thick-walled cortex. Branches terminal or ventral-intercalary. Leaves succubous or transverse, alternate or opposite (leaf bases free or connected), ± undivided, apex rounded to acute to shortly bifid, margins entire or toothed, dorsal margin plane or incurved, sometimes recurved, dorsal base frequently decurrent. Cells with or without trigones, cuticle smooth or papillose, papillae rounded or elongate; oil bodies finely granular. Underleaves lacking or very small. Rhizoids scattered, scarce. Dioicous. Gametoecia terminal on the stem or on short basal branches. Sporophyte in an inflated, plicate perianth or a fleshy calyptra. Seta thick. Capsule ellipsoid, wall 4–6-layered. Vegetative reproduction rare, by caducous leaves or gemmae.

About 10 genera, mostly in tropical mountains and the Southern Hemisphere; 5 genera in Malaysia. The main characters of Adelanthaceae are: 1) stems rigid, with a thick-walled cortex; 2) leaves undivided or short-bifid, succubous or transverse, alternate or opposite; 3) underleaves absent or very small; 4) rhizoids scattered; 5) sporophyte in an inflated, plicate perianth or a fleshy shoot calyptra; 6) capsule wall 4–6-layered. Adelanthaceae are divided into two distinct subfamilies, Adelanthoideae (genera *Pseudomarsupidium* and *Wettsteinia*) and Jamesonielloideae (genera *Cuspidatula*, *Denotarisia* and *Syzygiella*), which can also be treated as separate families. The record of *Wettsteinia inversa* in Sabah (Chuah-Petiot 2011) was actually from Kalimantan Selatan (see Grolle 1965a; Menzel 1988), but its occurrence in Sabah is also to be expected.

1. Leafy shoots arising from a stoloniform base. Gynoecia produced on short basal branches; sporophyte in a fleshy shoot calyptra. Leaf margins ± toothed. Leaves alternate, transverse or succubous ····· (Adelanthoideae) 2
1. Leafy shoots not arising from a stoloniform base (except in *Syzygiella sonderi*). Gynoecia produced produced terminal on the stem; sporophyte in an inflated, plicate perianth. Leaf margins entire, rarely with a few small teeth near the apex. Leaves alternate or opposite, succubous ····· (Jamesonielloideae) 3
2. Plants dark green to brown. Leaf apex bifid, with longly piliferous tips. Leaves with a few teeth on the ventral margin. Dorsal leaf margin flat. Epidermis cells of stem thick-walled ····· *Pseudomarsupidium*
2. Plants light green. Leaf apex rounded to truncate to shallowly emarginate, with rounded to acute tips. Leaves finely toothed almost all around. Dorsal leaf margin curved upwards. Epidermis cells of stem thin-walled. Reported in Kalimantan (Menzel 1988), expected to occur in Sabah or Sarawak ····· *Wettsteinia*
3. Trigones large and bulging, with conspicuous, dark star-like markings inside. Ventral side of the stem with stolon-like branches (Robust brown or reddish plants with dorsal leaf bases strongly overlapping and closely enveloping the stem, on rock or soil) ··· *Denotarisia*
3. Trigones small or large, without star-like markings inside. Ventral side of the stem without stolon-like branches ····· *Syzygiella*

Denotarisia Grolle Fig. 9A–C

Plants 1.5–2.5 mm wide, green, brown or reddish, ascending but not arising from a stoloniform base. Branches ventral-intercalary, often with reduced leaves, stolon-like. Leaves succubous, alternate, densely imbricate, strongly concave, insertion line very long, extending to the dorsal midline of the stem (but not beyond), leaf apex rounded, margins entire, dorsal base decurrent, ventral base broad and not decurrent, bases not connected to leaf bases. Cells with large bulging trigones, the trigones inside with conspicuous, dark, star-like markings, cuticle weakly papillose; oil bodies not yet observed. Underleaves reduced. Perianths on elongate stems, inflated, plicate, the folds straight. Gemmae lacking.

A monotypic paleotropical genus; contains *Denotarisia linguifolia* (De Not.) Grolle, recorded from Pahang, Malacca, Sarawak and Sabah, on rock and soil in montane environments.

Note: Characteristics of *Denotaria* are the robust, brownish or reddish plants with stolon-like ventral branches, dorsal leaf bases strongly overlapping and enveloping the stem, and, especially, trigones of leaf cells with dark, star-like markings (inside the trigones).

Literature: Grolle (1971); Schuster (2002).

Pseudomarsupidium Herzog Fig. 9D–F

Plants 1–2 mm wide, dark green to brown, ascending, arising from a stoloniform base. Stems rigid, with a 1-layered cortex of thick-walled cells. Branches ventral-intercalary. Leaves transverse, distant, apex shallowly bilobed and with piliferous tips, ventral margin entire or with a few teeth, dorsal margin entire and plane or incurved, dorsal base decurrent. Cells ± quadrate, 12–35 µm, with trigones, often thicker-walled along the leaf margin and

forming a border, vitta lacking, cuticle smooth. Underleaves lacking. Gametoecia on very short branches at the stoloniform stem base; sporophyte in a fleshy shoot calyptra. Gemmae lacking.

A small tropical and warm-temperate genus (4 spp.); 1 species in Malaysia (Mt. Kinabalu), *Pseudomarsupidium borneensis* (Grolle) Váňa *et al.* (= *Adelanthus borneensis* Grolle), found on soil over rock and on rotten wood near Paka Cave. The species is only known from Mt. Kinabalu.

Note: *Pseudomarsupidium* is recognized by: 1) leaf shoots dark green to brownish, with a stolon-like base; 2) ventral branching; 3) leaves transverse, bifid with piliferous tips, margins ± flat, entire or with a few teeth; 4) leaf cells small, quadrate, with trigones; 5) underleaves absent.

Literature: Grolle (1972 as *Adelanthus borneensis*).

Syzygiella Spruce Fig. 10

(*Anomacaulis* (R.M.Schust.) Grolle, *Cuspidatula* Steph., *Cryptochila* R.M.Schust., *Jamesoniella* (Spruce) F.Lees)

Plants small to large, 1–10 cm long and 1–6 mm wide, green, yellowish, reddish, purplish, brown or black, creeping to erect, little branched, shoot apex often decurved, stolons usually absent (present in *S. sonderi*). Branches terminal and ventral-intercalary. Leaves succubous, alternate or opposite, apex rounded to acute, undivided (rarely shallowly bifid), margins entire or with a few teeth near apex, bases symmetrical or asymmetrical, free or connected to leaf bases. Cells usually with trigones, occasionally uniformly thick-walled, cuticle smooth or papillose. Underleaves lacking or very small (very rarely large). Rhizoids usually scarce and scattered. Dioicous. Perianths on elongate stems, inflated, usually plicate (terete in *S. flaccida*), perianth folds straight, rarely spirally twisted above (*S. sonderi*). Capsule walls 4–6-layered. Gemmae lacking.

About 40 species worldwide; 8 species in Malaysia, on bark, rotten wood, soil or rock in montane forest environments.

Note: *Syzygiella* is recognized by: 1) leaves alternate or opposite, succubous, leaf apex rounded, obtuse or acute and sometimes toothed, leaf margins (sub)entire; 2) leaf cells with well-developed trigones; 3) underleaves ± absent; 4) rhizoids scattered; 5) perianth large, plicate, terminal on a long shoot; 6) capsule wall thick, 4–6-layered. A molecular study (Feldberg *et al.* 2010a) found that *Jamesoniella* and *Cryptochila* were nested in *Syzygiella* and placed these two genera in synonymy. However, *Cuspidatula* (= *Anomacaulis*) – a genus very similar to *Jamesoniella* and frequently considered a synonym of the latter (Kitagawa 1970; Váňa & Piippo 1989b) – was sister to *Syzygiella* and therefore retained as a separate genus, in spite of the lack of differentiating characters. Since *Cuspidatula* cannot be separated from *Syzygiella* based on morphology, we include this genus in *Syzygiella*. This requires new combinations for three Malaysian taxa:

Syzygiella contracta (Reinw. *et al.*) Gradst. & G.E.Lee, **comb. nov.** (= *Jungermannia contracta* Reinw. *et al.*, Nova Acta Phys.-Med. Acad. Caes. Leop.-Carol. Nat. Cur. 12: 233, 1824; *Cuspidatula contracta* (Reinw. *et al.*) Steph.; *Jamesoniella contracta* (Reinw. *et al.*) N.Kitag.). Fig. 11I–S.

Syzygiella flaccida (Steph.) Gradst. & G.E.Lee, **comb. nov.** (= *Anastrophyllum*

flaccidum Steph., Sp. Hepat. 6: 105, 1917; *Anomacaulis flaccidus* (Steph.) Grolle; *Cuspidatula flaccida* (Steph.) K.Feldberg *et al.*). Fig. 11A–H.

Syzygiella flexicaulis (Nees) Gradst. & G.E.Lee, **comb. nov.** (= *Jungermannia flexicaulis* Nees, Linnaea 6: 604, 1831; *Jamesoniella flexicaulis* (Reinw. *et al.*) Schiffn.; *Cuspidatula flexicaulis* (Reinw. *et al.*) Váňa & L.Söderstr.). Fig. 10B, F, J.

Literature: Inoue (1966); Kitagawa (1970); Grolle (1971 as *Cryptochila, Jamesoniella*); Váňa & Piippo (1989b); Schuster (2002 as *Anomacaulis, Cryptochila, Cuspidatula, Jamesoniella*); Feldberg *et al.* (2010a, 2010b).

BALANTIOPSIDACEAE

Plants green, red, purple, brown or black, creeping or erect. Stems usually with a thick-walled cortex. Branches ventral-intercalary, occasionally terminal, *Frullania*-type; stolons mostly lacking. Leaves transverse or succubous, undivided, bifid or trifid, margins entire or toothed. Cells rounded to rectangular, rather thin-walled, with or without trigones, cuticle smooth or papillose; oil bodies finely granular, colorless, 2–3(–5) per cell. Underleaves well developed, similar to leaves but smaller. Rhizoids in tufts from underleaf bases. Dioicous. Gametoecia on long shoots. Sporophyte enclosed by a perigynium, a marsupium or a fleshy perianth. Seta thick. Capsule cylindrical, wall 3–4-layered, valves linear and spirally twisted. Vegetative reproduction unknown.

About 7–8 genera worldwide; 3 genera in Malaysia. The main characters of the family are: 1) leaves transverse or succubous, bifid or undivided; 2) underleaves large, bifid; 3) rhizoids in bundles; 4) sporophyte in a fleshy structure (fleshy perianth, perigynium or marsupium); 5) capsule valves spirally twisted.

1. Leaves complicate-bilobed with a small dorsal lobe and a large ventral lobe. Leaf margins with numerous long cilia, the cilia terminating in a row of 4–5 cells. Sporophyte in a pendent marsupium ····· *Balantiopsis*
1. Leaves not complicate-bilobed. Leaf margins entire or toothed, not with numerous long cilia. Sporophyte in an upright perigynium ····· 2
2. Leaves transverse, shallowly bifid or trifid, upper margins strongly toothed. Rhizoids colorless (or absent). Leaf cells rectangular, thin-walled ····· *Isotachis*
2. Leaves succubous, undivided, margins ± entire. Rhizoids wine red. Leaf cells rounded, with trigones ····· *Acroscyphella*

Acroscyphella Kitag. & Grolle Fig. 12A

Plants delicate, green to yellowish-brown, sometimes tinged with red, creeping, little branched. Branches ventral-intercalary. Leaves standing upwards and usually densely imbricate, succubous, concave, undivided, wider than long, apex broadly rounded, margins entire or with 1–2 teeth in the lower half, dorsal base decurrent. Cells rounded, with trigones, cuticle with small, rounded to oblong papillae, each cell with numerous papillae. Underleaves much smaller than leaves and more flat, bifid, margins entire or somewhat toothed. Rhizoids wine red. Sporophyte in a conical, fleshy perigynium at the tip of long shoots. Gemmae absent.

A small Asia-Australasian genus (3 spp.): 1 species in Malaysia, *Acroscyphella tjiwideiensis* (Sande Lac.) N.Kitag. & Grolle (= *Clasmatocolea tjiwideiensis* (Sande Lac.) Grolle), recorded from Genting Highlands (Cheah 2017) where it grows on bark or soil at 1675–1755 m.

Note: *Acroscyphella tjiwideiensis* is a rare species that is recognized by the very broad, upright, concave, succubous leaves with a broadly rounded apex, subentire margins and a decurrent dorsal base, bifid underleaves, and wine-red rhizoids produced in tufts at underleaf bases.

Literature: Engel (1980 as *Clasmatocolea*); Piippo (1985b as *Clasmatocolea*).

Balantiopsis Mitt. Fig. 12C, D

Plants large, to 7 cm long, light-green to rose-tinted or purple. Branches mostly terminal, *Frullania*-type, ventral branches scarce. Leaves succubous, complicate-bilobed with a large ventral lobe and a smaller dorsal lobe connected to each other by a short keel without wing, margins strongly ciliate. Cells rectangular, rather large and thin-walled, cuticle finely papillose to almost smooth. Underleaves slightly smaller, more clearly bifid, not complicate-bilobed. Sporophyte in a pendent marsupium at the stem tip. Gemmae absent.

A southern-temperate genus (11 spp.); 1 species in Malaysia (Sabah), *Balantiopsis ciliaris* S.Hatt., on moist, shaded soil.

Note: *Balantiopsis* is readily recognized by the characters mentioned in the key. By the complicate-bilobed, succubous leaves with toothed margins and the presence of underleaves, *Balantiopsis* resembles *Schistochila*, but *Schistochila* differs in having a winged keel, leaf cells with trigones, sporophytes in a fleshy, upright perigynium (not in a marsupium) and straight capsule valves.

Literature: Hattori (1966); Engel (1968); Engel & Smith-Merrill (1997).

Isotachis Mitt. Fig. 12B

Plants green, brown to reddish, creeping or usually erect growing. Branches ventral-intercalary. Leaves transverse, bifid, occasionally trifid, about as long as wide, concave, leaf tips acute, margins toothed, especially towards the apex. Cells rectangular, thin-walled, cuticle striate-papillose. Underleaves similar to leaves but slightly smaller and more flat. Sporophyte in a conical, fleshy perigynium at the tip of long shoots. Gemmae absent.

A southern hemispheric genus (15 spp.); 1 species in Malaysia (Pahang), *Isotachis japonica* Steph.; on moist soil.

Note: *Isotachis* is readily recognized by the transverse, bifid to trifid leaves with toothed margins, and the large underleaves, which are similar to leaves but slightly smaller.

Literature: Singh & Singh (2009).

CALYPOGEIACEAE

Plants small, 0.5–2 mm wide, leafy, rarely thalloid, translucent, whitish-green to deep-green to brownish, creeping. Branches ventral-intercalary, usually sparse; stolons lacking. Leaves incubous, undivided or short-bifid, margins entire or crenulate. Cells thin-walled,

cuticle smooth or finely papillose; oil bodies granular, colorless, blue, brown or violet. Underleaves small, undivided or (bis)bifid. Rhizoids in tufts from underleaf bases. Monoicous or dioicous. Gametoecia on very short ventral branches. Sporophyte in a fleshy, subterranean marsupium. Seta thick. Capsule cylindrical, wall 2-layered, valves spirally twisted. Vegetative reproduction by gemmae or caducous leaves.

About 4 genera worldwide; 3 in Malaysia. The main characters of the family are: 1) plants leafy, rarely thalloid (*Mizutania*), leafy plants with incubous leaves with an entire to short-bifid apex, and with distinct underleaves; 2) rhizoids in tufts; 3) gametoecia on very short ventral branches; 4) sporophyte produced in a subterranean marsupium. The species usually grow on soil or rotten wood in shaded environments.

Herzog (1950) recorded *Metacalypogeia alternifolia* (Nees) Grolle from Sarawak but according to Grolle (1964, p. 186) this record is erroneous; the identity of the specimen from Sarawak remains unclear. *Metacalypogeia* is a small genus restricted to temperate regions of East Asia and North America, and its occurrence in Malaysia was therefore highly unlikely. The record of *M. alternifolia* from Java is also erroneous (Söderström *et al.* 2010).

1. Plants thalloid ····· *Mizutania*
1. Plants leafy ····· 2
2. Plants brown. Leaf apex and underleaves undivided. Cuticle of leaf cells coarsely papillose. Underleaf cells different from leaf cells, elongate, fully hyaline, without chlorophyll ····· *Mnioloma*
2. Plants pale green. Leaf apex and underleaves bifid. Cuticle of leaf cells smooth or finely punctate-papillose. Underleaf cells similar to leaf cells, with chlorophyll, not hyaline····· ····· *Calypogeia*

Calypogeia Raddi Fig. 13A

Plants ca. 1–2.5 mm wide, pale green. Leaves short-ovate to oblong, apex usually shallowly bifid. Cells thin-walled, trigones small to medium-sized, cuticle smooth or finely papillose; oil bodies colorless, sepia or bluish, coarsely granular. Underleaves variable in size and shape, bilobed to at least 1/4 of their length, not bordered, cells chlorophyllose, similar to leaf cells. Vegetative reproduction by gemmae produced on upright, flagelliform branches.

About 30 species worldwide; 2 species in Malaysia, *Calypogeia apiculata* (Steph.) Steph. and *C. arguta* Nees & Mont., on shaded soil or rotten wood.

Note: *Calypogeia* is recognized by: 1) plants small, pale green, creeping, 2) leaves incubous, apex shallowly bifid; 3) underleaves small, bifid; 4) leaf cells with small trigones, cuticle smooth or very finely papillose; 5) vegetative reproduction by gemmae produced at the tips of upright flagelliform branches.

Literature: Schuster (2002).

Mizutania Furuki & Z.Iwats. Fig. 13C–G

Plants thalloid, ribbon-like, 0.5–1.5 mm wide, bluish-green, unistratose, without costa, little branched, margins with rhizoids, straight or undulate. Cells very large, subrectangular,

80–150×30–70 μm, walls with elongate trigones. Cuticle densely striate-papillose. Oil bodies finely granular, numerous, 10–30 per cell, filling the cell-lumen, Gynoecia sessile at the thallus margins. Sporophyte in a long, bluish marsupium (R.L. Zhu pers. com.).

A monotypic Malesian genus, contains *Mizutania riccardioides* Furuki & Z.Iwats., distributed in montane areas, on shaded soil.

Note: *Mizutania* is recognized by the small, ribbon-like, unistratose thalloid plants without costa and with large, subrectangular cells with a densely striate-papillose cuticle and with numerous finely granular oil bodies. *Mizutania* was long classified in the Metzgeriidae but molecular evidence and the presence of a marsupium show that *Mizutania* is a member of Calypogeiaceae, in spite of its thalloid habit.

Literature: Furuki & Iwatsuki (1989); Masuzaki *et al.* (2010); Pressel *et al.* (2011).

Mnioloma Herzog Fig. 13B

Plants 1–2 mm wide, brown (in the Malaysian species). Leaves ovate-oblong, apex rounded or emarginate, margins frequently bordered by transversely rectangular or obliquely elongate cells, entire or crenulate. Cells thin-walled, trigones small, cuticle coarsely papillose; oil bodies brownish, finely granular. Underleaves suborbicular, undivided or retuse, margins entire or irregularly crenate, cells elongate and hyaline, without chlorophyll and with a smooth cuticle. Vegetative reproduction by caducous leaves.

A pantropical genus of about 10 species; 1 species in Malaysia, *Mnioloma fuscum* (Lehm.) R.M.Schust., recorded from Sarawak; on soil, tree bases or rock in humid forests.

Note: *Mnioloma* is easily recogized by the brown plants with incubous leaves, rounded leaf apex, cuticle of leaf cells coarsely papillose, and underleaf cells fully hyaline, without chlorophyll.

Literature: Schuster (2002); Gao *et al.* (2002).

CEPHALOZIACEAE

Plants usually small, pale green to brown, red or purplish, creeping to ascending. Stems with or without hyalodermis. Branches ventral-intercalary or lateral-terminal, *Frullania*-type; ventral stolons sometimes present. Leaves succubous or transverse, bifid or undivided, inserted laterally on the stem, dorsal side of the stem often leaf-free, leaf margins usually entire. Cells thin-walled or thickened, often large, cuticle smooth or papillose; oil bodies present or absent, when present finely granular. Underleaves lacking or small. Rhizoids scattered. Monoicous or dioicous. Gametoecia on leading shoots or on short ventral branches. Sporophyte enclosed by a perianth. Seta of 12 rows of cells: 8 outer rows and 4 inner rows. Capsule ellipsoid, wall 2-layered. Vegetative reproduction frequently by 1–2-celled gemmae produced on ascending flagelliform shoots.

About 15 genera worldwide; 4 in Malaysia. The main characters of Cephaloziaceae are: 1) leaves succubous, frequently laterally inserted with the leaf insertion not reaching the dorsal stem midline; 2) underleaves usually absent; 3) rhizoids scattered; 4) seta thin (only 12 cell rows); 5) capsule elongate, surrounded by a perianth, capsule wall 2-layered.

1. Leaves undivided ····· 2
1. Leaves bifid ····· 3
2. Plants fleshy, almost thalloid, stem very broad, wider than the leaves. Leaves more than one cell-layer thick in the lower half. Leaf cells very large, ca. 50–100 µm in midleaf, fully thin-walled. On shaded, rotten wood in humid montane forest ····· *Schiffneria*
2. Plants not fleshy, stem not wider than leaves. Leaves one cell-layer thick throughout. Leaf cells smaller, 15–30(–40) µm in midleaf, with trigones ····· *Odontoschisma*
3. Leaf cells uniformly thick-walled, cuticle densely papillose, cell walls densely striped by plasmodesmata. Stems rigid, without hyalodermis. Underleaves present ····· *Odontoschisma jishibae*
3. Leaf cells thin-walled, cuticle smooth, cell walls not densely striped by plasmodesmata. Stems fragile, transparent, with a hyalodermis. Underleaves absent ····· 4
4. Leaves with a ventral sac, formed by the infolded ventral leaf margin. Leaves tips acuminate to longly piliferous. Leaf margins entire or with long cilia. Leaf insertion very narrow ····· *Nowellia*
4. Leaves without ventral sac. Leaf tips acute. Leaf margins usually entire, rarely with small, 1-celled teeth. Leaf insertion broad ····· *Cephalozia*

Cephalozia (Dumort.) Dumort. Fig. 12G–O
(*Metahygrobiella* R.M.Schust.)

Plants 0.5–3 mm wide, pale green to yellowish-green creeping, stolons absent or present. Stems fragile, with a hyalodermis. Leaves succubous or transverse, concave to canaliculate-conduplicate, without sac, insertion line reaching the dorsal midline of stem or not, orbicular to ovate, deeply bifid, tips acute (to acuminate), margins entire, rarely with small, 1-celled teeth, bases not decurrent. Cells thin-walled, 25–50(–60) µm, cuticle smooth, oil bodies lacking. Underleaves absent.

About 25 species worldwide; 5 species in Malaysia (including 4 species previously attributed to *Metahygrobiella*), on moist soil, rotten logs, tree bases and on sandstone rock near water.

Note: *Cephalozia* is readily recognized by the small, pale green to yellowish-green plants with fragile stems with a distinct hyalodermis and bifid, succubous to transverse leaves.

Literature: Váňa (1984, 1993); Schuster (2002); Váňa *et al.* (2013).

Nowellia Mitt. Fig. 14

Plants 0.5–1.5 mm wide, whitish-green to red, rose or purplish, creeping, without stolons. Stems fragile, with a hyalodermis. Leaves subtransverse, with very narrow insertion, standing upwards away from the stem, bifid (rarely undivided), deeply concave and saccate in the lower half due to inrolling of the ventral margin; leaf tips acuminate to longly piliferous, leaf margins entire or toothed. Cells fully thin-walled, without trigones, cuticle smooth; oil bodies lacking. Underleaves absent. Gemmae not observed.

A tropical-holarctic genus (10 spp.); 3 species in Malaysia, on rotten and dead wood.

Note: *Nowellia* is readily recognized by the deeply concave, bifid leaves with the lower half of the leaf modified into a sac.

Literature: Grolle (1968); Schertler (1977); Váňa (1993).

Odontoschisma (Dumort.) Dumort. Fig. 15
(*Iwatsukia* N.Kitag.)

Plants 0.5–2 mm wide, glistening green to yellowish-brown to reddish or deep purplish, little-branched, creeping, with stolons. Stems rigid, of thick-walled cells, without hyalodermis. Leaves succubous, undivided or bifid, flat to strongly concave, orbicular to elongate, apex rounded, margins sometimes bordered by thick-walled cells, leaf insertion line extending to the dorsal midline of stem or not. Cells ± isodiametric, 15–30(–40) µm in midleaf, with trigones or uniformly thick-walled, cuticle smooth or papillose; oil bodies rather large, 2–5 per cell, finely granular. Underleaves absent or present. Gametoecia on short ventral branches. Vegetative reproduction by gemmae produced on upright flagelliform shoots.

A tropical-holarctic genus (21 spp.); 3 species in Malaysia, on rotten wood, trunk bases, shaded soil and rock in montane environments.

Note: *Odontoschisma* is recognized by: 1) stems rigid, without hyalodermis, with ventral stolons; 2) leaves succubous, ovate-orbicular, undivided, occasionally bifid; 3) leaf cells with large trigones or uniformly thick-walled; 4) underleaves absent or present (but small); 5) gynoecia on short ventral branches; 6) gemmae produced on upright, flagelliform shoots. *Odontoschisma* may be confused with *Solenostoma* but the latter genus lacks stolons and gemmae, the trigones of leaf cells are smaller, and the gynoecia in *Solenostoma* are terminal on the stem, not on short ventral branches.

Literature: Aranda *et al.* (2014); Gradstein & Ilkiu-Borges (2015).

Schiffneria Steph. Fig. 12E, F

Plants ca. 2 mm wide, very fleshy and somewhat thallus-like, pale green, creeping, without stolons. Stems very broad, wider than leaves, with a weak hyalodermis. Leaves succubous, imbricate, ovate-orbicular with entire margins, laterally inserted, dorsal stem surface completely leaf-free. Cells thin-walled, very large, ca. 50–100 µm in midleaf, cuticle smooth; oil bodies absent. Underleaves lacking. Dioicous.

A monotypic Southeast Asian genus; contains *Schiffneria hyalina* Steph., recorded from Pahang and Sabah; on shaded rotten wood in humid montane forests.

Note: *Schiffneria* is readily recognized by the characters given in the key.

Literature: Schuster (1984, 2002).

CEPHALOZIELLACEAE

Plants usually less than 1 mm wide, creeping or ascending, with or without stoloniform base. Stems without hyalodermis. Branches intercalary and terminal, *Frullania*-type. Leaves transverse or succubous, bifid or entire, insertion line extending to dorsal midline of stem or not. Cells small, less than 25 µm in diameter, with thin or uniformly thickened walls, trigones absent, cuticle smooth or papillose; oil bodies finely granular. Underleaves lacking or very small. Rhizoids scattered. Monoicous or dioicous. Gametoecia on leading shoots or very short branches. Sporophyte enclosed by a long-cylindrical perianth, mouth of the

perianth often crenate and bordered by elongate, thick-walled cells. Seta very thin, usually of only 8 rows of cells: 4 large outer rows of cells and 4 very small inner rows. Capsule ellipsoid, wall 2-layered. Vegetative reproduction by gemmae produced on upright flagelliform shoots.

About 7–8 genera worldwide; 3 in Malaysia. The main characters of Cephaloziellaceae are: 1) seta very thin, in cross section usually of 4 large outer cells and 4 tiny inner cells; 2) very small plants; 3) leaves bifid or undivided, transverse or succubous; 4) leaf cells small, thin-walled or uniformly thick-walled, without trigones; 5) hyalodermis absent; 6) underleaves absent or very small. In the World Checklist, several genera of Scapaniaceae were transferred to Cephaloziellaceae but morphological and molecular support for this transfer was lacking. Here we follow the traditional circumscription of the family (e.g., Gradstein *et al.* 2001; Crandall-Stotler *et al.* 2009).

1. Leafy stems arising from a creeping stolon. Leaves shallowly bifid to maximally 1/5. Plants rheophytic ····· *Kymatocalyx*
1. Leafy stems not arising from a creeping stolon. Leaves shallowly to deeply bifid (to 1/6–1/2). Plants not rheophytic ····· 2
2. Leaves retuse or shortly bifid, to 1/6 of leaf length ····· *Cylindrocola*
2. Leaves more deeply bifid, to 1/3–2/3 of leaf length ····· *Cephaloziella*

Cephaloziella (Spruce) Schiffn. Fig. 16A–D, F, H, J

Plants very small, thread-like, 0.2–0.4 mm wide, dull green to brown or red; stolons lacking. Stems without hyalodermis, cells thin-walled or thick-walled. Leaves suberect to spreading, subtransverse, usually inserted to the dorsal midline of the stem, rarely ending shortly before the dorsal midline (*C. kiaeri*), bifid to 1/3–2/3 of leaf length, lobe tips acute, margins entire or toothed. Cells very small, ca. 8–16 µm long in midleaf, thin-walled or uniformly thick-walled, without trigones, cuticle smooth or papillose; oil bodies as in the family. Underleaves lacking or very small (absent in Malaysian species). Gemmae sometimes present, produced on upright flagelliform shoots, green to brown to reddish.

A large genus, ca. 50 species worldwide; 3 species in Malaysia, *Cephaloziella capillaris* (Steph.) Douin, *C. kiaeri* (Austin) Douin (= *Cylindrocolea kiaeri* (Austin) Váňa) and *C. microphylla* (Steph.) Douin, on soil and rock.

Note: *Cephaloziella* is closely similar to *Cylindrocolea* and one species, *C. kiaeri*, is sometimes placed in *Cylindrocolea*. The main difference between the two genera is that in *Cephaloziella* the leaves are almost transverse, deeply bifid, and the insertion line normally extends up to the dorsal midline of the stem (ending shortly before the midline in *C. kiaeri*), whereas in *Cylindrocolea* the leaves are more obliquely inserted, often only shallowly bifid, and the leaf insertion line ends well before the dorsal midline, leaving a broad, 3–6 cells wide "leaf-free" strip on the stem. A further difference is the presence of gemmae in *Cephaloziella* (absent in *Cylindrocolea*). *Cephaloziella kiaeri* (Austin) Douin is here treated as a member of *Cephaloziella* (instead of *Cylindrocolea* as in World Checklist), because it has gemmae and transverse, deeply bifid leaves.

The species of *Cephaloziella* are sometimes confused with *Cephalozia*, but *Cephalozia* is a larger plant with a large-celled stem epidermis (= hyalodermis) and with larger leaf

cells, more than 20 µm in midleaf, with very thin cell walls and no oil bodies. Moreover, the leaf margins in *Cephalozia* are always entire.

Literature: Kitagawa (1969a); Schuster (2002).

Cylindrocolea R.M.Schust. Fig. 16E, G, I

Plants minute, sometimes flagelliform, 0.2–0.3 mm wide, green to brown; stolons lacking. Stems without hyalodermis, cells thin-walled or thick-walled. Leaves succubous, insertion line ending far before the dorsal midline of the stem, leaving a 3–6 cells wide dorsal leaf-free strip, apex retuse or shortly bifid to 1/6, lobe tips obtuse or acute, margins entire. Cells in the Malaysian species only 8–11 µm long and thick-walled (in other species larger and thin-walled). Cuticle smooth or finely papillose; oil bodies as in the family. Underleaves and gemmae absent.

About 15 species in tropical and warm-temperate regions; 1 species in Malaysia, *Cylindrocolea tagawae* (N.Kitag.) R.M.Schust., on soil and rock ar rather low elevations. A second species recorded from Malaysia, *C. kiaeri* (Austin) Váňa, is treated here as a member of *Cephaloziella*.

Note: Close to *Cephaloziella*; for differences see under the latter genus.

Literature: Kitagawa (1969a as *Cephaloziella*); Váňa (1992 as *Cephaloziella*); Schuster (2002).

Kymatocalyx Herzog Fig. 16K–M

(*Stenorrhipis* Herzog)

Plants dark green to brown, with upright leafy shoots arising from creeping stolons, forming small mats. Branching purely ventral-intercalary. Leaves succubous or almost transverse, inserted to the dorsal midline of the stem or not, orbicular to elongate, apex rounded to shortly bifid (to maximally 1/5). Cells 12–22 µm long, walls slightly thickened, cuticle smooth. Underleaves lacking. Gemmae not observed.

A small pantropical genus (4 spp.); 1 species in Malaysia (Sarawak, Sabah), *Kymatocalyx rhizomatica* (Herzog) Gradst. & Váňa, found on soil or rock along river at low elevation (under 300 m), rheophilous.

Note: *Kymatocalyx* is recognized by the very small, rheophilous plants with upright leafy shoots arising from a creeping stolon, succubous leaves with a short-bifid apex, and absence of underleaves.

Literature: Gradstein & Váňa (1999).

GYMNOMITRIACEAE

Plants very small to medium-sized, 0.2–2 mm wide, green to brownish or purplish or black, sometimes silver-white, creeping to erect, forming small mats or dense cushions, little branched, stem base frequently with stolons. Stems with or without thick-walled cortex. Branches lateral-intercalary, occasionally terminal, *Frullania*-type (*Nardia*). Leaves transverse or succubous, alternate, imbricate, bifid or undivided, sometimes scale-like (*Marsupella stoloniformis*), leaf margins entire or crenulate, leaf insertion line extending beyond the dorsal midline of the stem (but not in *Nardia*). Cells rather small, ca.

12–25(–35) µm in midleaf, with trigones, cuticle smooth or papillose; oil bodies usually 2–3 per cell, finely granular. Underleaves usually lacking. Rhizoids scattered. Dioicous or monoicous. Gametoecia on leading shoots. Sporophyte enclosed by tubular bracts and a short perigynium, perianth lacking or small, rarely well-developed (*Nardia*). Seta thick. Capsule globose or ellipsoid, wall 2-layered. Vegetative reproduction unknown.

About 10 genera mainly in cold regions of the world; 3 genera at high elevation on Mt. Kinabalu. The main characters of Gymnomitriaceae are: 1) plants frequently with basal stolons; 2) leaves imbricate, transverse or succubous, dorsal insertion line usually extending beyond the dorsal stem midline; 3) underleaves usually absent (present in *Nardia*); 4) rhizoids scattered; 5) sporophyte in a short perigynium, perianth present or absent.

1. Leaces succubous, apex rounded. Underleaves present. Stem base without stolons ····· ····· *Nardia*
1. Leaves transverse, apex bifid. Underleaves absent. Stem base with stolons ····· 2
2. Plants whitish to brown. Leaves loosely to very densely imbricate. Leaf margin cells usually without oil bodies. Perianth lacking ····· *Gymnomitrion*
2. Plants green to brown to reddish, not whitish. Leaves loosely imbricate. Leaf margin cells with oil bodies. Perianth present but small, hidden between the bracts ····· *Marsupella*

Gymnomitrion Corda Fig. 17A–C
(*Apomarsupella* R.M.Schust.)

Plants 0.5–1.5 mm wide, ascending from stoloniform base, silver-white or grayish, rarely purplish or brown, often forming dense cushions. Leaves transverse, loosely to very densely imbricate, bifid or emarginate, leaf tips rounded to acute-acuminate, margins often white (sometimes the entire leaf), leaf insertion extending beyond the dorsal midline of the stem. Leaf margin cells without oil bodies (present in *G. revolutum*). Underleaves absent. Perianth absent.

About 25 species worldwide; 3 species in Malaysia (Sabah); on soil and rock at high elevation on Mt. Kinabalu.

Note: *Gymnomitrion* is recognized by the whitish to grayish plants growing in dense cushions, with mostly densely imbricate leaves, absence of oil bodies in leaf margin cells, and lack of a perianth. *Gymnomitrion revolutum* (= *Apomarsupella revoluta* (Nees) R.M.Schust.) is similar to *Marsupella* in the rather robust plants with laxly imbricate leaves and oil bodies present in all leaf cells (also in margin cells), but the species lacks a perianth. Molecular evidence has confirmed that the species is a member of *Gymnomitrion*.

Literature: Váňa (1991a); Schuster (2002); Váňa *et al.* (2010).

Marsupella Dumort. Fig. 17E–F

Plants 0.3–1.5 mm wide, ascending from stoloniform base, green, brown, black, reddish-purple, never whitish. Leaves transverse, loosely imbricate or distant, appressed to the stem or erect-spreading, bifid or emarginate, leaf tips rounded or acute, leaf insertion often extending beyond the dorsal midline of the stem. All leaf cells (including margin cells) with oil bodies. Underleaves absent. Perianth present, small, hidden between the bracts.

About 20 species worldwide; 2 species in Malaysia (Sabah), *Marsupella emarginata*

(Ehrh.) Dumort. and *M. stoloniformis* N.Kitag., on soil and rock at high elevation on Mt. Kinabalu.

Note: *Marsupella* is recognized by the upright plants with a stoloniform base growing in small mats, transverse leaves with a bifid or emarginate apex, and absence of underleaves.

Literature: Váňa (1991a); Schuster (2002); Váňa *et al.* (2010).

Nardia Gray Fig. 17D, H, I

Plants 0.5–2 mm wide, green to brown to reddish-brown, creeping, not arising from a stoloniform base. Branches absent or scarce, terminal, *Frullania*-type. Leaves succubous to subtransverse, weakly concave, ovate or reniform, apex rounded to emarginate, margins entire, bases short-decurrent, leaf insertion not extending beyond the dorsal midline of stem. Leaf cells with small trigones, all cells with oil bodies. Underleaves rather large, broadly lanceolate. Dioicous, often fertile. Perianths fusiform, the lower half united with the bracts and fleshy, forming a perigynium. Gemmae lacking.

About 15 species wordwide; 1 species in Malaysia (Sabah), *Nardia assamica* (Mitt.) Amakawa, found on soil around Paka Cave on Mt. Kinabalu, at about 3000 m.

Note: *Nardia* is recognized by the small, creeping plants with ovate to reniform leaves with a rounded apex, leaf cells with small trigones, and large, broadly lanceolate underleaves. The genus resembles *Solenostoma* and *Jungermannia* – and was long classified in Jungermanniaceae or Solenostomataceae – but differs from *Solenostoma* and *Jungermannia* in the presence of underleaves. Recent molecular evidence (Shaw *et al.* 2015) shows that *Nardia* belongs in Gymnomitriaceae.

Literature: Váňa (1976, 1991b); Váňa *et al.* (2005); Shaw *et al.* (2015).

HERBERTACEAE

Plants medium-sized to robust, green to brown or reddish-purple, ascending to erect or pendent, sometimes with a rhizome-like creeping base, irregularly branched. 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 broader, margins entire or toothed. Cells with small or large trigones; vitta present or absent; oil bodies granular or homogeneous. Underleaves similar to the leaves but more symmetrical. Rhizoids absent or very scarce, in tufts from underleaf bases. Dioicous. Gametoecia on elongate shoots. Antheridia in the axils of bracts and bracteoles. Sporophyte enclosed by a strongly plicate perianth and a fleshy calyptra. Seta thick. Capsule globose, wall 4–7-layered. Vegetative reproduction unknown.

Three genera worldwide; 2 in Malaysia. The main characteristics of the family are: 1) leaves and underleaves 2–3-lobed, underleaves as long as the leaves; 2) leaves transverse or incubous; 3) stems rigid, with a thick-walled, brown cortex; 4) sporophyte enclosed by plicate perianth and a fleshy calyptra; 5) antheridia present in axils of bracts and bracteoles.

1. Leaves deeply bifid to 1/2–3/4 of leaf length, with a distinct vitta of elongate cells. Leaf cells with large trigones ····· *Herbertus*
1. Leaves bifid to 1/3, without vitta. Leaf cells thin-walled with very small trigones ····· ····· *Triandrophyllum*

Herbertus Gray Figs. 18A–C; 65A, B

Plants usually robust, to 10–30 cm long, sometimes small, green to brown to reddish-brown or purple, ascending to erect or pendent. Leaves transversely inserted but often incubous in position, spreading or falcate-secund, 1.5–7× longer than wide, deeply bifid with lanceolate to linear lobes, the dorsal leaf-lobe usually broader than the ventral lobe, leaf tips acute to long-piliferous, sometimes ending in a whitish hairpoint, leaf margins entire or toothed. Cells short along the margins, elongate toward the middle and forming a distinct and often very broad vitta from leaf base to apex; cell walls with large trigones and intermediate thickenings, cuticle papillose; oil bodies faintly granular or homogeneous, often numerous.

A genus of about 10–15 species worldwide; 4 species in Malaysia (Pahang, Sabah), *Herbertus aduncus* (= *H. dicranus, H. longifissus*), *H. ceylanicus*, *H. pilifer* and *H. sendtneri* (= *H. armitanus*, *H. circinatus*), on bark and rock in humid montane forests.

Note: *Herbertus* is easily recognized by the robust plants with three almost equal rows of narrowly elongate, deeply bifid leaves (including underleaves), the leaf cells with large trigones and the presence in the leaves of a long vitta from base ot apex.

Literature: Juslén (2006); He & Sun (2017); Sun & He (2019).

Triandrophyllum Fulford & Hatcher Fig. 18D, E

Plants medium-sized, to 6 cm long, green to yellowish-brown, occasionally reddish, creeping or ascending, irregularly branched. Leaves incubous, spreading and somewhat reflexed, asymmetrical, often somewhat falcate-secund, shallowly bifid or trifid to maximally 1/3 of leaf length with elongate-triangular lobes and obtuse to acute-acuminate tips, margins entire. Cells small, quadrate to subrectangular, rather thin-walled with very small trigones, vitta lacking, cuticle smooth or finely striate-papillose; oil bodies finely granular.

A southern-temperate and tropical-montane genus (4 spp.); 1 species in Malaysia, *Triandrophyllum heterophyllum* (Steph.) Grolle, collected in the Genting Highlands by Cheah (2017), growing on bark of tree at 1550 m elevation.

Note: Characteristics of *Triandrophyllum* are the slender plants, to 6 cm long plants with three almost equal rows of narrowly elongate shallowly bifid leaves (including underleaves), and quadrate to subrectangular leaf cells with small trigones. A vitta is lacking in *Triandrophyllum*.

Literature: Grolle (1964); Schuster (2000).

JACKIELLACEAE

A monotypic family.

Jackiella Steph. Fig. 19A–D

Plants 1–2 mm wide, brown or black, creeping, stolons absent. Stems rigid, cells thick-walled. Branches mostly ventral-intercalary, occasionally ventro-lateral. Leaves succubous, alternate, concave, undivided, apex rounded, margins entire, insertion line usually not reaching dorsal midline of stem, bases shortly decurrent. Cells ca. 30–40 µm in diameter, trigones small or large, cuticle smooth; oil bodies large, 1–4 per cell, brown, finely granular. Underleaves absent or very small. Rhizoids in tufts, hyaline. Dioicous. Gametoecia usually on short ventral branches. Sporophyte in a pendent marsupium, bracts reduced. Sporophyte foot with a conspicuous haustorial collar of long, sheathing filaments. Seta rather thin, of ca. 20 rows of cells: 8 large outer cells and ca. 12 smaller cells. Capsule ellipsoid, wall 2-layered. Vegetative reproduction common, by 1–2-celled gemmae.

A small genus restricted to Southeast Asia and New Zealand (4 spp.); 3 species in Malaysia, *Jackiella angustifolia* Herzog, *J. javanica* Schiffn. and *J. singapurensis* Schiffn., usually on soil.

Note: *Jackiella* is recognized by the brownish plants with rigid stems and ventral branching, undivided succubous leaves, underleaves reduced, rhizoids in long tufts, gametoecia on very short ventral branches, a pendent marsupium, and frequent presence of gemmae.

Literature: Herzog (1950); Piippo (1985a); Váňa (1992); Piippo *et al.* (2002); Schuster (2002).

JUNGERMANNIACEAE

Plants small to medium-sized, usually green to brown. Stems without hyalodermis, cortex weakly differentiated. Leaves succubous, undivided or bifid, alternate, insertion line reaching the dorsal stem-midline, leaf margins usually entire. Oil bodies finely granular, grayish. Underleaves lacking or very small. Rhizoids scattered, mostly colorless. Gametoecia on long shoots. Sporophyte surrounded by an inflated, ± smooth perianth (sometimes plicate towards the mouth), bracts not connected to the perianth. Seta thick, of numerous rows of cells. Capsule wall 2–3-layered. Gemmae usually absent.

A small family of 5 genera; 1 in Malaysia (*Mesoptychia*). The circumscription of the family Jungermanniaceae has undergone many modifications in the course of time and has considerably been reduced in size based on molecular evidence (see Crandall-Stotler *et al.* 2009; Váňa & Long 2009). All species of *Jungermannia* recorded from Malaysia (see Chuah-Petiot 2011) are now placed in *Solenostoma* (Solenostomataceae) and the genus *Jungermannia* is excluded from the flora of Malaysia. The main characters of the family are: 1) leaves succubous, entire or shallowly bifid, inserted to the dorsal midline of stem; 2) underleaves absent or very small; 3) rhizoids scattered; 4) gametoecia on long shoots; 5) sporophyte in an inflated, ± terete perianth; 6) gemmae usually absent.

Mesoptychia (Lindb.) A.Evans Fig. 19E–H

(*Hattoriella* (Inoue) Inoue)

Plants 0.7–2(–4) mm wide, pale green to brown to black, little branched, branches usually lateral-intercalary. Leaves succubous, sometimes almost longitudinally inserted, not

or slightly decurrent, bifid to 1/3, rarely undivided. Leaf cells rather thin-walled, ca. 20–40 µm wide in midleaf, trigones small or large, cuticle papillose or smooth. Underleave very small, ± lanceolate, hidden among the rhizoids, sometimes reduced. Rhizoids sparse to abundant. Dioicous or paroicous. Perianth pyriform and ± terete, smooth, suddenly contracted to the mouth, the mouth crenulate and frequently terminating in a short beak. Gemmae usually absent (present in *M. heterocolpa*).

A mostly northern-temperate genus (ca. 15 spp.); 1 species in Malaysia, *Mesoptychia subcrispa* (Herzog) L.Söderstr. & Váňa (= *Hattoriella subcrispa* (Herzog) Bakalin), recorded from Genting Highlands (Cheah 2017) where it was found growing epiphytically at 1675 m.

Note: *Mesoptychia subcrispa* is the only tropical species in the genus *Mesoptychia* and a rare taxon, that has been recorded from Indonesia (Sumatra, Java) and Malaysia. The species is recognized by the ca. 1.5 mm wide, green to pale brownish plants with imbricate, succubous, concave leaves that are bifid to ca. 1/3, with obtuse to shortly apiculate leaf tips and slightly undulate margins. The leaf cells have small trigones and an almost smooth cuticle, the underleaves are absent or very small, the female bracts and bracteole are highly connate and somewhat crisped-undulate, and the perianth is terete, without a beak.

Literature: Herzog (1942a as *Lophozia subcrispa*); Bakalin (2003 as *Hattoriella subcrispa*); Cailliau *et al.* (2013).

LEPICOLEACEAE

Contains 2 genera; 1 in Malaysia.

Lepicolea Dumort. Figs. 20A–K; 65D

Plants robust, to 10 cm long, pale green to grayish or brownish, ascending to erect or pendent, forming large mats, (bi)pinnate. Branches *Frullania*-type, often flagelliform toward the tips, occasionally lateral-intercalary. Stems rigid, with a thick-walled cortex in 2–4 layers, stem surface with or without paraphyllia. Leaves transverse, deeply 4-lobed, segments lanceolate, margins densely ciliate-laciniate. Cells with large trigones, cuticle papillose; oil bodies small, few per cell, faintly and finely granular. Underleaves similar to the leaves but more symmetrical. Rhizoids in tufts on flagelliform branches. Dioicous. Gametoecia on elongate shoots. Sporophyte enclosed by a fleshy perigynium covered by paraphyllia; perianth lacking. Seta thick. Capsule ellipsoid, wall 5-layered. Vegetative reproduction unknown.

A mostly southern-temperate genus (10 spp.); 2 species in Malaysia (Pahang, Sabah), *Lepicolea rara* (Steph.) Grolle (= *L. loriana* Steph.) and *L. yakusimensis* (S.Hatt.) S.Hatt., on bark of trees and shrubs and on rotten logs in mossy forests (Frahm *et al.* 1990).

Note: *Lepicolea* is readily recognized by the robust, bipinnate plants with deeply 4-lobed leaves and underleaves with densely ciliate-laciniate margins. The genus somewhat resembles *Mastigophora*; for differences see under the latter.

Literature: Hattori (1953); Kitagawa (1978); Piippo (1984a).

LEPIDOZIACEAE

Plants leafy, rarely thalloid, pale green to brown, creeping to ascending, rarely pendent, pinnate, dichotomous or irregularly branched, leafy stems sometimes arising from a stoloniferous base. Branching terminal or intercalary; flagella frequently present. Stems with or without hyalodermis. Leaves incubous, succubous or transverse, alternate, usually divided into several lobes or teeth, rarely undivided, leaf insertion extending to dorsal midline of stem or not, leaf margins mostly entire, sometimes toothed. Cells variable; oil bodies present or absent. Underleaves usually well developed, rarely reduced. Rhizoids in tufts from underleaf bases. Dioicous, rarely monoicous. Gametoecia on short ventral branches, the androecia occasionally on long shoots. Sporophyte enclosed by a 3-keeled perianth. Seta thin, of 8 or 16 outer rows of cells surrounding 4, 8 or more smaller inner rows. Capsule ellipsoid, wall 2–5-layered. Vegetative reproduction rare, by caducous leaves; gemmae absent.

About 28 genera worldwide; 11 in Malaysia. The main characters of the family are: 1) leaves usually divided into lobes; 2) underleaves present, rhizoids in tufts from underleaf bases; 3) gynoecia on very short ventral branches; 4) seta thin; 5) sporophyte in a 3-keeled perianth; 6) gemmae absent. Branching and leaf insertion in Lepidoziaceae are quite variable, branching may pinnate, dichotomous or irregular, and leaves may be incubous, succubous or transverse.

1. Plants filamentose, with rudimentary leaves (1 cell long, 2 cells wide), leaf cells at the tip with a sausage-like slime papilla or a stiff bristle ····· *Zoopsis*
1. Plants different ····· 2
2. Plants pinnate or irregularly branched. Leaves usually deeply lobed (sometimes only shallowly lobed), incubous or transverse ····· 3
2. Plants dichotomous or unbranched (except for presence of ventral flagellae). Leaves unlobed or with 2–3 coarse teeth at the apex ····· 8
3. Leaves split to the base into 1–2 hair-like filaments. Underleaves ± absent. Leaf cells very thin-walled, smooth, narrowly rectangular ····· *Telaranea* (= *Arachniopsis*)
3. Leaves not split to the base into 1–2 hair-like filaments. Underleaves present. Leaf cells thin-walled or thick-walled, smooth or papillose ····· 4
4. Leaf lobes ending in a long-linear, hyaline bristle (= finger-like cell) that stands stiffly upwards. Leaves and underleaves deeply split into 4–8 lobes of small thick-walled cells ····· *Psiloclada*
4. Leaf lobes not terminating in a long-linear, hyaline bristle. Leaves and underleaves 2–6-lobed ····· 5
5. Leaf cells thick-walled. Stems without hyalodermis ····· 6
5. Leaf cells thin-walled. Stem with a hyalodermis ····· 7
6. Leaves incubous, lobed to 1/10–1/2 of leaf length. Cuticle smooth ····· *Lepidozia*
6. Leaves transverse, lobed to near the base. Cuticle papillose ····· *Kurzia*
7. Leaf cells smooth. Leaves clearly incubous ····· *Neolepidozia*
7. Leaf cells densely papillose. Leaves transverse ····· *Tricholepidozia*

8. Plants dichotomous. Leaves incubous ····· 9
8. Plants not dichotomous. Leaves incubous or succubous ····· 10
9. Epidermis cells larger than inner cells (stem cross section). Plants rather small, 0.5–1.5 mm wide. Leaf apex undivided or short-bifid with two unequal teeth, the dorsal tooth larger ····· *Acromastigum*
9. Epidermis cells not larger than inner cells. Plants larger, 2–6 mm wide. Leaf apex usually trifid ····· *Bazzania*
10. Leaves succubous, deeply concave, ovate-orbicular, undivided or short-bifid····· *Hygrolembidium*
10. Leaves incubous, ± plane, oblong, short-bifid ····· *Mastigopelma*

Acromastigum A.Evans Fig. 21

Plants small, 0.4–1.5 mm wide, pale green to brown, creeping or ascending, forming rough mats, dichotomously branched, with long ventral flagella. Stems rigid, of thick-walled cells, hyalodermis lacking, epidermis cells larger than inner cells. Branching lateral-terminal (*Frullania*-type) and ventral-intercalary (*Bazzania*-type and *Acromastigum*-type). Leaves incubous, convex, wide-spreading, ovate to clearly elongate, apex undivided or divided into 2(–3) coarse teeth, margins entire or finely toothed. Cells with small or large trigones, cuticle smooth or papillose, a vitta-like region of larger cells frequently present but true vitta absent (?); oil bodies as in *Bazzania*. Underleaves much smaller than leaves, distant or imbricate, undivided or 2–3-toothed or lobed, margins usually entire, bases cuneate. Dioicous. Vegetative reproduction by caducous leaves.

An tropical and southern-temperate, amphi-Pacific genus (ca. 35 spp.); 16 species recorded from Malaysia, on tree trunks, rotten wood and rock.

Note: *Acromastigum* resembles *Bazzania* but the plants are smaller, the stem epidermis is enlarged and leaf apex is mostly undivided or short-bifid with unequal lobes. Moreover, ventral branches in *Acromastigum* are of two different types: *Bazzania*-type (intercalary, associated with an unmodified underleaf) and *Acromastigum*-type (terminal, associated with a half-underleaf).

Literature: Evans (1934); Piippo (1991); Schuster (2000).

Bazzania Gray Figs. 22; 66A–D

Plants 1–6 mm wide, deep green to brown or reddish-brown, creeping or ascending, forming rough mats, dichotomously branched, with long ventral flagella. Stems rigid, of thick-walled cells, hyalodermis lacking, epidermis cells not larger than inner cells. Branching lateral-terminal (*Frullania*-type) and ventral-intercalary (*Bazzania*-type only). Leaves incubous, wide-spreading, straight to falcate, elongate, apex divided into 2–3(–4) coarse teeth, rarely undivided, margins entire or finely toothed. Cells with small or large trigones, cuticle smooth or papillose, cells in the lower half of the leaf middle frequently larger, resembling a vitta, sometimes with a true vitta of 4–6 rows of larger and longer cells sharply separate from the rest of the leaf cells; oil bodies large, few-segmented, almost homogeneous. Underleaves well developed, distant or imbricate, apex and lateral margins entire to shallowly lobed to toothed, bases cuneate to auriculate, free or connate to the leaf bases on one or both sides; underleaf cells sometimes in part without chlorophyll. Dioicous.

Vegetative reproduction by caducous leaves.

A large genus of over 100 species worldwide; 54 species recorded from lowland and montane forests throughout Malaysia, on various substrates but most commonly on trunk bases and logs, usually abundant in mossy forests.

Note: *Bazzania* is easily recognized by the dichotomously branched plants, incubous leaves with a 2–3-toothed apex (rarely entire), well developed underleaves, and long flagelliform branches sprouting from the axils of the underleaves. The Malaysian species of *Bazzania* remain incompletely known in spite of the detailed studies by N.Kitagawa, Y.H. Cheah & K.T.Yong, and others. A useful key to 26 species known from Peninsular Malaysia was provided by Cheah & Yong (2016).

Literature: Kitagawa (1967b, 1977, 1979, 1980); Cheah & Yong (2016).

Hygrolembidium R.M.Schust. Fig. 23A

Plants 1–1.5 mm wide, pale green to pale brown, creeping or ascending. Stems fleshy, cells ± thin-walled, hyalodermis lacking. Branches mostly ventral-intercalary (terminal branching lacking), stolons present at stem base. Leaves succubous, obliquely spreading, ovate-orbicular, deeply concave-canaliculate with upcurved margins and ± flat apex, apex rounded, univided to short-bifid, entire or somewhat toothed, margins entire. Cells thin-walled, without trigones, cuticle smooth or finely striate-papillose; oil bodies lacking in most cells. Underleaves very small, distant, undivided, broadly ovate, apex ± toothed. Dioicous.

A mostly southern-hemispheric genus (8 spp.): 1 species in Malaysia, *Hygrolembidium boschianum* (Sande Lac.) R.M.Schust., on humic humic soil at high elevation.

Note: *Hygrolembidium boschianum* is recognized by the pale green (to pale brown) plants with mostly ventral-intercalary branching, basal stolons, undivided to short-bifid canaliculate leaves with very thin-walled cells, and very small underleaves.

Literature: Piippo (1991); Schuster (2000).

Kurzia G.Martens Fig. 20L–Y

Plants very small, 0.3–0.5 mm wide, pale green to olive green to brown, creeping, irregularly pinnate. Branching terminal, lateral and ventral. Stems thin, without or with a weak hyalodermis. Leaves very small, usually transverse, deeply divided into 4(–6) subulate (rarely narrow-triangular) lobes, the lobes straight or incurved, 2–3(–4) cells wide at the base, margins entire. Cells thick-walled, without trigones, cuticle usually papillose; oil bodies finely granular. Underleaves about half the size of the leaves, deeply 3–4-lobed, the segments often unequal in length. Dioicous.

About 40 species worldwide; 6 species recorded from Malaysia, on shaded soil, rock and rotten wood in humid montane forest environments.

Note: *Kurzia* is closely related to *Lepidozia* but differs by: 1) plants very small, less than 0.5 mm wide, usually brown; 2) leaves transverse or succubous, deeply divided into 4 subulate (or triangular) lobes; 3) cuticle of leaf cells frequently papillose. A further peculiarity of *Kurzia* is the occurrence of *Frullania*-type branches on one side of the stem and *Microlepidozia*-type branches on the other side.

Literature: Mizutani (1974); Piippo (1985c).

Lepidozia (Dumort.) Dumort. Figs. 24; 65C

Plants small to large, 0.5–2 mm wide, pale green to brown, creeping or ascending, sometimes long pendent, often forming large mats, 1–3-pinnate. Branches lateral-terminal (*Frullania*-type) and ventral-intercalary, often flagelliform. Leaves incubous, usually convex, shallowly to deeply divided into 4(–6) equal or unequal lobes, the lobes plane or incurved, margins entire or with teeth. Cells uniformly thick-walled, trigones ± lacking, cuticle usually smooth; oil bodies finely granular. Underleaves about half the size of the leaves, 3–4-lobed. Usually dioicous.

About 75 species worldwide (or less); 19 species recorded from Malaysia, mostly from Sarawak and Sabah, on tree trunks, soil, rock or rotten wood in montane forests and alpine grasslands, abundant in mossy forests.

Note: *Lepidozia* is recognized by the small to robust, whitish-green to greenish-brown, 1–3-pinnate plants with incubous, convex leaves divided into 4–6 short or long lobes. The leaf cells are small and uniformly thick-walled with a smooth cuticle and finely granular oil bodies. The branches become progressively narrower toward the tips and often end in a flagellum.

Literature: Mizutani (1968, 1974); Piippo (1984c).

Mastigopelma Mitt. Fig. 25G–N

Plants 1–1.5 mm wide, green to brown, creeping, with long ventral flagella, otherwise unbranched. Stems rigid, of thick-walled cells, hyalodermis lacking, epidermis cells not larger than inner cells. Branching purely ventral-intercalary. Leaves incubous, wide-spreading, elongate, apex short-bifid, apical and dorsal margin toothed, ventral margin entire. Cells with well-developed trigones, cuticle sligthly papillose, vitta absent. Underleaves well developed, undivided or shallowly 2-lobed. Dioicous.

A small Malesian-Oceanic genus (3 spp.); 1 species recorded from Malaysia (Sarawak: Mt. Dulit), *Mastigopelma pulvinatum* (De Not.) Grolle (= *M. bilobum* Herzog), found in crevices of sandstone boulders near waterfall at ca. 1100 m.

Note: The genus *Mastigopelma* resembles *Bazzania* but lacks dichotomous branching.

Literature: Herzog (1950 as *Mastigopelma bilobum*).

Neolepidozia Fulford & J.Taylor Figs. 24B, J; 25A–E

(*Telaranea* sect. *Neolepidozia* (Fulford & J.Taylor) J.J.Engel & G.L.Merr., *Telaranea* subg. *Neolepidozia* (Fulford & J.Taylor) R.M.Schust.)

Plants 0.4–0.8 mm wide, pale green, 1–3-pinnate. Branches lateral-terminal (*Frullania*-type) and ventral-intercalary. Stems with a distinct hyalodermis. Leaves clearly incubous, partially divided into 3–4 lobes. Cells usually large, longer than wide, walls uniformly thin, cuticle smooth; oil bodies finely granular. Underleaves similar to leaves but smaller and with one lobe less. Dioicous or monoicous. Perianths longly cylindrical, mouth short-toothed or with long lacinia.

A mostly southern-temperate genus (ca. 30 spp.); 3 species in Malaysia, *Neolepidozia longitudinalis* (Herzog) E.D.Cooper, *N. ophiria* (Steph.) E.D.Cooper (= *Lepidozia ophiria*), and *N. wallichiana* (Gottsche) Fulford & J.Taylor (= *Telaranea wallichiana* and *Lepidozia variifolia*), in Peninsular Malaysia (Penang, Negeri Sembilan), Sarawak (Mt. Dulit) and

Sabah (Mt. Kinabalu). The species are usually found on soil, humus, tree bases or rock at 1400–2850 m, exceptionally at lower elevation.

Note: *Neolepidozia* is recognized by stems with a distinct hyalodermis and incubous leaves split to about half into 3–4 lobes of very thin-walled, smooth cells. The genus has often been considered a subgenus or section of *Telaranea* but was reinstated based on molecular evidence. It clearly differs in having incubous instead of transverse leaves and leaves not lobed to the base. *Neolepidozia* is close to *Tricholepidozia* (see there). The Malaysian species of *Neolepidozia*, *N. longitudinalis*, stands out by dimorphic foliation, the main stems having reduced leaves whereas the branches have normally developed leaves.

Literature: Herzog (1950 as *Lepidozia longitiudinalis*); Mizutani (1974 as *Lepidozia ophiria*); Schuster (2000 as *Telaranea* subg. *Neolepidozia*); Engel & Smith-Merrill (2004 as *Telaranea* sect. *Neolepidozia*); Cooper (2013).

Psiloclada Mitt. Fig. 25F

Plants small, less than 1 mm wide, dull green, creeping or ascending, 1–2-pinnate. Branches lateral-terminal (*Frullania*-type) and occasionally ventral-intercalary, often flagelliform. Leaves ± transverse, deeply divided into 4–8 equal or unequal lobes, the lobes incurved, margins entire, lobe tips terminating in a long-linear, hyaline, stiffly upwards pointing bristle (= finger-like cell). Cells quadrate to subrectangular, small, uniformly thick-walled, trigones ± lacking, cuticle smooth; oil bodies finely granular. Underleaves smaller than the leaves, 3–6-lobed, lobe tips terminating in a long-linear, hyaline, stiffly upwards pointing bristle (like leaves). Usually dioicous.

A monotypic, eastern Malesian-Australasian genus; contains *Psiloclada clandestina* Mitt., in Malaysia recorded from Pahang, Sarawak and Sabah, where it is a characteristic element of montane forest on humus and rotten wood.

Note: *Psiloclada* is easily recognized by the 4–8-lobed leaves and underleaves with the lobes terminating in a long-linear, hyaline, stiffly upwards pointing bristle (= finger-like cell).

Literature: Fulford & Taylor (1959); Schuster (2000).

Telaranea Schiffn. Fig. 23E

(*Arachniopsis* Spruce)

Plants filamentous, less than 1 mm wide, pale green, 1–3-pinnate or irregularly branched. Branches lateral-terminal (*Frullania*-type) and ventral-intercalary. Stems with a distinct hyalodermis. Leaves transverse, divided to the base into 1–2 hair-like, uniseriate lobes (in Malaysian species). Cells large, rectangular, walls thin, cuticle smooth; oil bodies finely granular. Underleaves reduced (in Malaysian species). Perianths longly cylindrical, mouth usually with long, bristle-like lacinia.

Contains about 30 species worldwide; 3 species in Malaysia, *Telaranea major* (Herzog) J.J.Engel & G.L.Merrill, *T. monocera* (R.M.Schust. & Grolle) J.J.Engel & G.L.Merrill, *T. papulosa* (Steph.) J.J.Engel & G.L.Merr., on tree bases and rotten wood.

Note: *Telaranea* is recognized by the leaves divided to the base into 1–2 hair-like filaments made up of rectangular cells with thin, smooth walls, and stems with a distinct hyalodermis. The underleaves are reduced in the Malaysian species. Species of *Telaranea*

with leaves only partly divided into lobes are currently placed in *Neolepidozia* or *Tricholepidozia.*

Literature: Piippo (1985c as *Arachniopsis*); Engel & Smith-Merrill (2004).

Tricholepidozia (R.M.Schust.) E.D.Cooper *et al.* Fig. 23B, C

(*Telaranea* subg. *Tricholepidozia* R.M.Schust.)

Plants delicate, to ca. 1 mm wide, pale green, 1–3-pinnate. Branches lateral-terminal (*Frullania*-type) and ventral-intercalary. Stems with a hyalodermis. Leaves transverse, partially divided into 3–4 or more lobes. Cells thin-walled, cuticle smooth; oil bodies finely granular. Underleaves similar to leaves but smaller and with one lobe less.

A mostly southern-temperate genus (ca. 30 spp.); 5 species in Malaysia, on bark, roots and rotten wood in humid forests.

Note: *Tricholepidozia* is recognized by the stems with a distinct hyalodermis, the transverse leaves split to 1/2–3/4 into 4–7 or more lobes, and the densely papillose cells. The group was part of *Telaranea* but has been raised to generic level based on molecular evidence. Morphologically, *Tricholepidozia* differs from *Telaranea* in the leaves not split to the base into lobes, the greater number of leaf lobes, and the densely papillose cuticle. *Tricholepidozia* can be confused with *Kurzia*, which also has a papillose cuticle, but *Kurzia* has ± evenly thick-walled cells and stems without a hyalodermis.

Literature: Engel & Smith-Merrill (2004).

Zoopsis Gottsche *et al.* Fig. 23D, F

Plants minute, 0.25–0.4 wide, filamentose, glossy light green, creeping, irregularly branched. Branches lateral-terminal and ventral-intercalary, ventral branches flagelliform. Stems thin, asymmetric, dorsal side of two rows of large cells, ventral side of smaller cells, hyalodermis present. Leaves rudimentary, 1 cell long and 2 cells wide, apex of each cell with a large, sausage-shaped hyaline papilla with smooth walls (*Z. liukiuensis* Horik.) or a stiff bristle with papillose walls (*Z. setigera* K.I.Goebel). Leaf cells large, thin-walled, without trigones, oil bodies small, finely granular. Underleaves reduced, consisting of 2 small cells tipped by a slime papillas. Dioicous or monoicous. Perianths long-cylindrical, mouth with bristle-like lacinia or cilia. Seta thin, of 8 outer cell rows and 8–12 (or more) smaller inner rows.

An Asian-Australasian genus (8 spp.); 2 species in Malaysia (Pahang, Sarawak, Sabah), *Zoopsis liukiuensis* Horik. and *Z. setigera* K.I.Goebel, on rotten wood and trunk bases in montane forest.

Note: *Zoopsis* is immediately recognized by the minute, filamentose, glossy light green plants with rudimentary leaves consisting of two large cells, each capped by a sausage-shaped slime papilla or a stiff bristle.

Literature: Piippo (1984b); Schuster (2000).

LOPHOCOLEACEAE

Plants green to brown or reddish-brown, creeping to ascending. Branches *Frullania*-type and intercalary; stolons absent. Stems without hyalodermis, without differentiated

cortex. Leaves succubous, usually almost horizontal in position, bifid or undivided, leaf margins entire or toothed, insertion reaching dorsal stem-midline. Cells with or without trigones, cuticle smooth or finely papilose; oil bodies finely granular. Underleaves present, attached to leaves or free. Rhizoids in tufts from underleaf bases. Dioicous or monoicous. Gametoecia on leading shoots or on short branches. Sporophyte enclosed by a 0–3-keeled perianth. Seta thick. Capsule ellipsoid, wall 3–8-layered. Vegetative reproduction rare, by gemmae or caducous leaves.

About 20 genera worldwide; 3 genera in Malaysia. The principal characters of Lophocoleaceae are: 1) leaves succubous, usually almost horizontally inserted, undivided or bifid; 2) underleaves well developed, often connected to leaf bases; 3) rhizoids in tufts at underleaf bases; 4) sporophyte enclosed by a 0–3-keeled perianth. The family was previously included in Geocalycaceae but molecular analysis has shown that these two families are not closely related. They differ in the presence of a perianth in Lophocoleaceae and a marsupium in Geocalycaceae.

1. Underleaves free from the leaves or narrowly attached to leaves on one side. Perianth with 3 sharp keels, terminal on a long shoot ····· *Lophocolea*
1. Underleaves broadly attached to leaves on both sides. Perianth without keels or with 3 sharp keels ····· 2
2. Leaf margins entire. Leaf apex entire or bifid (rarely apex with up to 10 small teeth in the common *H. argutus*). Gametangia on very short ventral branches, hidden under the leaves. Perianth without keels ····· *Heteroscyphus*
2. Leaf margins entire or toothed. Leaf apex not entire (bifid or toothed). Gametangia on long branches, not hidden under the leaves. Perianth sharply 3-keeled ····· ····· *Cryptolophocolea*

Cryptolophocolea L.Söderstr. Fig. 26A–C

Plants 2–4 mm wide, green to brown, creeping, irregularly branched. Branches lateral, *Frullania*-type or intercalary. Leaves succubous, alternate, ovate-rectangular to narrow-rectangular, apex bifid, margins toothed (in Malaysian species), leaf surface smooth. Cells with small or large trigones, cuticle smooth; oil bodies usually finely granular. Underleaves broadly attached to leaves on both sides, bifid or undivided, margins toothed. Gametoecia on elongate shoots. Perianths 3-keeled, long-exserted beyond the bracts.

About 23 species, mostly in the Tropics; 4 species in Malaysia (Kedah, Pahang, Sabah), *Cryptolophocolea ciliolata* (Nees) L.Söderstr. *et al.*, *C. costata* (Nees) L.Söderstr., *C. fleischeri* (Steph.) L.Söderstr., and *C. levieri* (Schiffn.) L.Söderstr., typically growing on rotten wood, occasionally on tree bases, twigs or rock.

Note: *Cryptolophocolea* was traditionally included in *Lophocolea* but molecular studies showed that the group merits recognition as a separate genus. Morphologically, the two genera differ in underleaves connected to the leaves on both sides (*Cryptolophocolea*) or ± free from the leaves (*Lophocolea*). *Cryptolophocolea* is close to *Heteroscyphus* and sterile material may be difficult to distinguish (see key).

Literature: Piippo (1985b as *Lophocolea*); Söderström *et al.* (2013).

Heteroscyphus Schiffn. Figs. 26D–F; 67A–C

Plants 1–5 mm wide, green to brown, creeping, irregularly branched. Branches usually ventral-intercalary. Leaves succubous, ± flat, alternate to opposite, ovate-subrectangular to lingulate, apex undivided, short-bifid or with 3 or more teeth or cilia, dorsal margin usually entire, ventral margin entire or toothed or ciliate, plane or undulate. Cells thin-walled or with distinct trigones, cuticle smooth or weakly papillose; oil bodies unknown. Underleaves bifid, margins entire or toothed, bases broadly attached to leaves on both sides. Gametoecia on very short ventral or lateral branches hidden behind the stem leaves. Male branches tiny, catkin-like. Perianths inflated, smooth, without keels, the mouth 3-lobed-ciliate.

About 65 species, mostly in Southeast Asia; about 14 species in Malaysia, on logs, soil, tree trunks and rock.

Note: *Heteroscyphus* is recognized by: 1) underleaves connected to leaf bases on both sides; 2) gametoecia on very short sexual branches, originating from the axils of the underleaves and usually hidden behind the leaves; 3) perianths without keels.

Pócs *et al.* (2014) reported *Chiloscyphus integerrimus* Schiffn. new to Malaysia. This species, originally described from Java, resembles the common *Heteroscyphus argutus* (Reinw. *et al.*) Schiffn. but differs from the latter in the subopposite lingulate leaves with mostly entire leaf margins and perhaps in smaller leaf cells (Schiffner 1900). Although known only from sterile plants, *C. integerrimus* is more similar to *Heteroscyphus* than to *Chiloscyphus* Corda as currently circumscribed (Söderström *et al.* 2013, 2016), and the species is therefore transferred to *Heteroscyphus*, as ***Heteroscyphus integerrimus*** (Schiffn.) Gradst. & G.E.Lee, **comb. nov.** (= *Chiloscyphus integerrimus* Schiffn., Die Hepaticae der Flora von Buitenzorg, p. 197. 1900).

Literature: Piippo (1985b, 1992).

Lophocolea (Dumort.) Dumort. Fig. 26G

Plants (0.6–)1–5 mm wide, (pale) green, creeping, irregularly branched. Branches *Frullania*-type or intercalary, mostly lateral, rarely ventral. Leaves succubous, alternate, ovate-orbicular to rectangular, apex bifid or with a few teeth or cilia, margins entire or toothed to ciliate, leaf surface smooth or roughened by tooth-like papillae in *L. muricata*. Cells usually thin-walled, hexagonal-subisodiametrical, trigones lacking or small, cuticle smooth or papillose; oil bodies usually finely granular. Underleaves free from the leaves or narrowly attached to leaves on one side, bifid, often toothed. Gametoecia on elongate shoots. Perianths 3-keeled.

About 90 species worldwide; 6 species in Malaysia, on logs, soil, rock and tree trunks.

Note: *Lophocolea* is recognized by the underleaves free from the leaves or narrowly connected to the leaf base on one side only. The genus has sometimes been placed in *Chiloscyphus* Corda, but molecular study shows that these two groups should be kept apart as separate genera. *Chiloscyphus* does not occur in Malaysia and the Malaysian species previously assigned to *Chiloscyphus* (Chuah-Petiot 2011) belong to *Cryptolophocolea* (*C. ciliolatus, C. costatus*), *Heteroscyphus* (*C. acutangulus, C. argutus, C. iwatsukii, C. succulentus*), *Lophocolea* (*L. bidentata, L. kurzii, L. muricata, L. sikkimensis, L. steetziae*), or are synonyms.

Literature: Piippo (1985b, 1992); Söderström *et al.* (2013).

MASTIGOPHORACEAE

A family of 2 genera; 1 in Malaysia.

Mastigophora Nees Figs. 27A–D; 64C, D

Plants robust, greenish-brown to reddish brown, 1–3-pinnate. Branches *Frullania*-type. Stems rigid, with a thick-walled brown cortex. Leaves transverse to slightly incubous, asymmetrically 2–3(–4)-lobed, dorsal lobe largest, segments lanceolate, margins entire or with a few lacinia in the lower half. Cells with large trigones, cuticle smooth, oil bodies small, granular. Underleaves large, bifid, symmetrical. Rhizoids scarce. Dioicous. Gametoecia on short lateral branches. Antheridia in axils of bracts and bracteoles. Sporophyte enclosed by a perianth. Seta thick. Capsule globose, wall 4–6-layered. Vegetative reproduction absent.

A small genus of 2 well-defined species, the variable *Mastigophora diclados* (F.Weber) Nees widespread in the Paleotropics including Malaysia and *M. woodsii* (Hook.) Nees in western Europe. Several further species are listed in World Checklist but their status is doubtful. *Mastigophora diclados* is a very characteristic and common bryophyte of moist montane forests and elfin forests in Malaysia, growing on tree trunks, roots and rock (Frahm *et al.* 1990).

Note: *Mastigophora* is readily recognized by the robust, often reddish-brown, pinnate plants with 2–3-lobed leaves and large bifid underleaves. The leaf lobes are lanceolate and the margins are entire or slightly laciniate in the lower half. *Mastigophora* somewhat resembles *Lepicolea* but the latter genus has purely 4-lobed leaves and underleaves with densely ciliate margins and a papillose cuticle, the sporophyte of *Lepicolea* is enclosed by a fleshy perigynium, not by a perianth, and the plants vary in color but are not reddish-brown.

Literature: Piippo (1984a); Schuster (2000).

NOTOSCYPHACEAE

A monotypic family.

Notoscyphus Mitt. Fig. 27E

Plants small, 1–2 mm wide, pale green, creeping. Stems rigid, cells thick-walled. Branching ventral-intercalary. Leaves succubous, alternate, rather flat and ovate, apex rounded, margins entire, insertion line usually not reaching dorsal midline of stem, bases shortly decurrent. Cells ca. 30–40 µm in diameter, trigones small or large, cuticle minutely papillose; oil bodies large, 2(–3) per cell, finely granular, persistent, can be seen also in dry herbarium samples. Underleaves present, small, bifid. Rhizoids most in small tufts at underleaf bases, hyaline. Dioicous or paroicous. Gametoecia on short ventral branches. Sporophyte in a short, bulbous marsupium with one series of large bracts and bracteole. Sporophyte foot without collar of long filaments. Seta thick, of numerous cell rows (?). Capsule ellipsoid, wall 2-layered, outer wall cells ± tiered, with nodular thickenings. Vegetative reproduction not observed.

A monotypic, paleotropical genus; contains the variable *Notoscyphus lutescens* (Lehm.

& Lindenb.) Mitt. (= *N. paroicus* Schiffn.), rather widely distributed in Malaysia, on shaded soil.

Note: Characteristics of *Notoscyphus* are the small pale green plants with small bifid underleaves and rather flat and almost longitudinally inserted, undivided ovate leaves with rounded apex, entire margins and a finely punctate-papillose cuticle. The gametoecia are produced on short ventral branches and the sporophyte is enclosed by a short marsupium and a series of long bracts and bracteole. The genus was recovered as sister to *Jackiella* in a recent molecular analysis and these two genera have many characters in common (e.g., rigid stems, ventral-intercalary branching, succubous undivided leaves with insertion line not reaching the dorsal midline, large and finely granular oil bodies, gametoecia on short ventral branches, a marsupium, a thin seta and ellipsoid capsules with a 2-layered wall with nodular thickenings on the outer walls). However, *Jackiella* differs in brownish plant color, lack of well-developed underleaves and female bracts, a much longer marsupium and thinner seta, presence of a collar of filaments on the sporophyte foot, and presence of gemmae.

Literature: Váňa & Piippo (1989a); Váňa (1991b); Schuster (2002); Shaw *et al.* (2015).

PLAGIOCHILACEAE

Plants small or large, green to brown, often with a rhizome-like creeping base. Stems usually with a thick-walled, brown cortex of several cell-layers. Branching terminal and intercalary. Leaves succubous, alternate or opposite, leaf bases decurrent, dorsal margin usually recurved, leaf apex and margins (especially the ventral margin) usually sharply toothed. Cells usually with trigones, cuticle smooth or papillose; oil bodies usually finely granular. Underleaves lacking or very small. Rhizoids few, scattered. Dioicous, rarely monoicous (*Pedinophyllum*). Gametoecia on elongate shoots. Androecia in long, terminal spikes. Sporophyte enclosed by a perianth, perianths laterally compressed, with a wide, truncate mouth, often with innovations. Seta thick. Capsule ellipsoid, wall 4–9-layered. Vegetative reproduction by cladia, caducous leaves or leaf fragmentation, rarely by gemmae.

Contains 7–8 genera worldwide; 2 in Malaysia. The main characters of Plagiochilaceae are: 1) leaves succubous, with a decurrent dorsal base and a recurved dorsal margin, leaf margin frequently toothed; 2) underleaves absent or very small; 3) stems rigid, brown, with a thick-walled cortex; 4) male spikes very long; 5) perianths flattened, with a wide, truncate and often ciliate mouth.

1. Leaves opposite, leaf bases connected, ventral flagelliform branches present…… ……*Chiastocaulon*
1. Leaves not opposite, leaf bases free, ventral flagelliform branches lacking…… ……*Plagiochila*

Chiastocaulon Carl Fig. 27F–L
(*Acrochila* Inoue, *Plagiochilion* S.Hatt.)
Plants 2–3 mm wide, green to brown, ascending from a rhizom-like base, sometimes

clearly dendroid. Branches ventral-intercalary or terminal, *Frullania*-type, rarely lateral-intercalary; the ventral branches usually flagelliform, with scale-like leaves. Leaves opposite or alternate, reniform to orbicular to ovate to oblong to ligulate, usually asymmetrical, with plane or reflexed dorsal margin and decurrent bases, margins frequently toothed to ciliate, especially along the apical and ventral margins, rarely entire; the apical teeth often larger. Leaf cells with small or large trigones, cuticle smooth. Underleaves absent. Dioicous.

An Asian-Australasian genus (ca. 15 spp.); 5 species in Malaysia (including the members of the former genus *Plagiochilion*), habitat as in *Plagiochila*.

Note: *Chiastocaulon* was previously included in *Plagiochila* but molecular study showed that it is a good genus, with *Plagiochilion* (a group characterized by opposite leaves) as a synonym. *Chiastocaulon* differs from *Plagiochila* in the presence of ventral branches; the ventral branches are usually flagelliform.

Literature: Inoue (1964, 1984 as *Plagiochila* and *Plagiochilion*); Groth & Heinrichs (2003); Patzak *et al.* (2016).

Plagiochila (Dumort.) Dumort. Figs. 28; 68A–C

Plants small to very robust, (0.5–)1–10 mm wide, green to brown, creeping to ascending or pendent, often with a rhizome-like creeping base. Branches *Frullania*-type or lateral-intercalary. Leaves alternate, rarely opposite, reniform to orbicular to ovate to oblong to almost linear, usually 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, rarely entire. Leaf cells usually with trigones, cuticle smooth or papillose. Underleaves lacking or small. Dioicous.

The largest genus of liverworts with about 400–450 species worldwide, in several sections; 36 species recorded from Malaysia, on various substrates including bark, rock and soil, usually abundant in montane and mossy forests.

literature: Inoue (1984); So (2000, 2001); Söderström *et al.* (2015).

PSEUDOLEPICOLEACEAE (Blepharostomataceae)

Plants green to brown, creeping to ascending, irregularly branched, stolons lacking. Stems rigid, without hyalodermis. Branches terminal and intercalary. Leaves transverse, shallowly or deeply divided into 3–4(–5) stiff, hair-like or lanceolate lobes, margins entire or ciliate. Cells with uniformly thickened walls and a striate-papillose cuticle; oil bodies granular. Underleaves similar to the leaves but often a bit smaller. Rhizoids in tufts from underleaf bases. Dioicous or monoicous. Gametoecia on long shoots. Sporophyte enclosed by a plicate perianth, perianth surface smooth, perianth mouth with long cilia. Seta rather thin, with 8–20 outer rows of cells. Capsule ellipsoid, wall 2–5-layered. Vegetative reproduction rare.

Contains 8 or 9 genera worldwide; 3 genera in Malaysia. The main characters of Pseudolepicoleaceae are the small plants with mostly transverse, 3–4-fid leaves and

underleaves with stiff lobes, and uniformly thick-walled cells with a striate-papillose cuticle. The family shares many characters with Lepidoziaceae but the gametoecia of Pseudolepicoleaceae are produced terminal on the main stem, not on short ventral branches, and the leaves and underleaves almost similar in size.

1. Leaves divided to the base into 3–4 hair-like filaments. Underleaves similar to leaves····· ····· *Blepharostoma*
1. Leaves not divided to the base, with an undivided lamina and 4–5 hair-like lobes, each lobe terminating in a long cilium ····· 2
2. Leaves regularly 4-lobed, lobe margins entire or with a short cilium ··· *Pseudolepicolea*
2. Leaves irregularly 4–5-lobed, lobe margins with several short or long cilia ····· *Temnoma*

Blepharostoma Dumort. Fig. 29A, B

Plants very small, less than 1 mm wide, pale green to brown, little branched. Branches mostly *Frullania*-type. Leaves transverse, divided to the base into 3–4(–5) hair-like filaments. Underleaves similar to the leaves but with one filament less. Monoicous or dioicous. Vegetative reproduction (rare) by gemmae.

A mainly northern-temperate genus of 4 species, including the widespread *Blepharostoma trichophyllum* (L.) Dumort., which has been recorded from Sabah (Mt. Kinabalu), growing on bark, rotten wood, rock or soil.

Note: Characteristic of *Blepharostoma* is the alga-like habit of the plants, with leaves and underleaves of equal length and divided to the base into 3–4 hair-like lobes. The genus may be confused with *Telaranea,* but in the latter genus the underleaves are shorter than the leaves or absent, the stem has a distinct hyalodermis (lacking in *Blepharostoma*), the leaf cells are thin-walled and smooth (thick-walled and ± striate-papillose in *Blepharostoma*), and the gametoecia are situated on a very short lateral branch (on a long shoot in *Blepharostoma*). Due to the thickened cell walls, the leaves in *Blepharostoma* are rather stiff and dull in color while those of *Telaranea* are flexible and glistening. *Blepharostoma* is sometimes placed in a separate family, Blepharostomataceae, but is kept here in Pseudolepicoleaceae following Crandall-Stotler *et al.* (2009).

Literature: Schuster (2000); Asthana *et al.* (2013); Singh *et al.* (2014).

Pseudolepicolea Fulford & J.Taylor Fig. 29C, E, F

(*Lophochaete* R.M.Schust.)

Plants 1–2 mm wide, deep green to brown, little branched. Branching terminal and ventral-intercalary. Leaves transverse, obcuneate, 4-lobed, each lobe terminating in a 5–9 cell long, hair-like cilium; lobe margins entire or with one short cilium. Underleaves similar to the leaves but smaller, 3-lobed.

A mainly southern-hemispheric genus of 6–7 species; 2 species in Malaysia (Sabah), *Pseudolepicolea trollii* (Herzog) Grolle & Ando (= *Lophochaete trollii* (Herzog) R.M.Schust.) and *P. andoi* (R.M.Schuster) S.Hatt. & Mizut. (= *P. trolii* subsp. *andoi* (R.M.Schuster) S.Hatt. & Mizut.), on bark or rock in humid montane forest on Mt. Kinabalu.

Note: *Pseudolepicolea* is closely similar to *Temnoma* but differs from the latter by the

characters given in the key.

Literature: Hattori & Mizutani (1968); Piippo (1984a); Singh *et al.* (2014).

Temnoma Mitt. Fig. D, G

Plants 1–2 mm wide, deep green to brown, little branched. Branching terminal and ventral-intercalary. Leaves transverse, rounded to reniform, shallowly divided into 4–5 lobes, each lobe terminating in a 6–9 cell long cilium, lobe margins with 2 or more shorter cilia. Underleaves similar to leaves but slightly smaller, with fewer cilia.

A southern-hemispheric genus (ca. 10 spp.); 1 species in Malaysia (Sabah), *Temnoma setigerum* (Lindenb.) R.M.Schust., on rotten wood or bark in humid montane forest on Mt. Kinabalu.

Note: *Temnoma* is recognized by the small, green to brownish plants with three almost equal rows of transverse, 4–5-lobed leaves and underleaves, each lobe terminating in a long cilium.

Literature: Piippo (1984a); Singh *et al.* (2014).

SCAPANIACEAE
(Anastrophyllaceae, Lophoziaceae)

Plants green to brown to red or purple, creeping or erect, simple or irregularly branched, sometimes arising from a stoloniform base (*Gottschelia*). Stems usually rigid and with a thick-walled cortex. Branches usually lateral-intercalary, sometimes *Frullania*-type; stolons lacking. Leaves succubous or transverse, alternate, insertion line reaching the dorsal stem midline, 2–4-lobed to complicate-bilobed, or undivided (*Gottschelia*), the lobes equal or unequal, leaf margins entire or toothed. Cells usually with trigones, occasionally uniformly thick-walled; oil bodies finely granular. Underleaves present or lacking. Rhizoids scattered, scarce. Dioicous. Gametoecia on long shoots. Sporophyte enclosed by a perianth, the perianth inflated with a narrow mouth or dorsiventrally flattened and with a wide mouth, perianth surface plicate or smooth. Seta usually thick. Capsule ellipsoid to cylindrical, wall 2–8-layered. Vegetative reproduction common by 1–2-celled gemmae from leaf margins, gemmae smooth or angular, pale green to red or brown.

About 10–20 genera worldwide; 10 in Malaysia, mostly at high elevation on Mt. Kinabalu. The circumscription of the family is controversial and varies among authors; here it is defined in a broad sense and includes the genera of the former family Lophoziaceae as well as the Anastrophyllaceae, which is a molecular lineage without distinctive morphological features. The main features of Scapaniaceae are: 1) plants frequently with secondary pigmentation (brown, reddish, purple), stems rigid, 2) leaves succubous, 2(–4)-lobed, sometimes differentiated into a small dorsal lobe and a large ventral lobe; 3) underleaves usually absent; 4) rhizoids scattered; 5) gametoecia on long shoots; 6) sporophyte in a perianth; 7) gemmae commonly present, rounded or angular-stellate.

1. Leaves undivided ····· 2
1. Leaves divided into lobes ····· 3

2. Plants robust, 2–4 mm wide, reddish. Leaves densely enveloping the stem ··· *Gottschelia*
2. Plants smaller, ca. 1 mm wide, brown. Leaves not densely enveloping the stem. On rock above 3500 m on Mt. Kinabalu ····· *Andrewsianthus mizutanii*
3. Leaves conduplicate-bilobed, with a small dorsal lobe and a large ventral lobe, the lobes connected by a sharp keel ····· 4
3. Leaves not conduplicate-bilobed ····· 5
4. Leaves ovate, ventral lobe 1–1.5× longer than wide ····· *Scapania*
4. Leaves more elongate, ventral lobe 2–4× longer than wide ····· *Diplophyllum*
5. Leaves divided to near the base into 3–4 lobes. Underleaves present, large ····· 6
5. Leaves divided to about 1/3–2/3 of leaf length into 2–3 lobes. Underleaves usually absent ····· 7
6. Plants robust, 3–4 mm wide. Leaf margins densely ciliate-laciniate ····· *Plicanthus*
6. Plants much smaller, less than 1 mm wide. Leaf margins with a few cilia near the base, otherwise entire ····· *Tetralophozia*
7. Leaves trifid, the lobes very unequal in size, the dorsal lobe very small ····· *Tritomaria*
7. Leaves bifid ····· 8
8. Leaf cells uniformly thick-walled, trigones absent ····· 9
8. Leaf cells with trigones (often very large) ····· 10
9. Plants minute, less than 0.5 mm wide. Leaves distant, lobes spreading, not deeply concave-canaliculate. Gemmae absent ····· *Sphenolobopsis*
9. Plants larger, 0.5–1 mm wide. Leaves imbricate, lobes deeply concave-canaliculate. Gemmae present ····· *Sphenolobus*
10. Flagelliform branches present ····· *Andrewsianthus*
10. Flagelliform branches absent ····· *Anastrophyllum*

Anastrophyllum (Spruce) Steph. Fig. 30

(*Anastrophyllopsis* (R.M.Schust.) Váňa & L.Söderstr., *Schizophyllopsis* Váňa & L.Söderstr., *Zantenia* (S.Hatt.) Váňa & J.J.Engel)

Plants 0.5–3 mm wide, brownish-green or purple, creeping or ascending, little branched. Branches terminal and intercalary; flagelliform branches absent. Stems rigid. Leaves succubous to almost transverse, bifid with the lobes usually unequal in size, dorsal lobe transversely inserted and ventral lobe obliquely inserted, strongly concave to canaliculate with the tips often somewhat incurved, apices acute to acuminate, rarely obtuse, margins entire, rarely toothed (subg. *Zantenia*). Cells with large trigones, cuticle smooth or papillose. Underleaves absent. Perianths inflated, plicate, sometimes with a white mouth. Gemmae present or absent.

About 25 species worldwide; 10 species at high elevations in Malaysia, on soil, rock and tree trunks.

Note: *Anastrophyllum* is readily recognized by the green to brown or purplish plants with deeply concave, bilobed, subtransverse leaves, cells with large trigones, no underleaves and the frequently white mouth of the perianth. Schuster (2002) divided *Anastrophyllum* into several subgenera and sections, which were treated as separate genera in the World Checklist (*Anastrophyllum* s.str., *Anastrophyllopsis, Schizophyllopsis, Sphenolobus,*

Zantenia) even though differences with *Anastrophyllum* are usually rather subtle and hardly warrant generic status. Here, these segregate genera are maintained in *Anastrophyllum* with the exception of *Sphenolobus*, which is well separated from *Anastrophyllum* by the uniformly thick-walled leaf cells and fragile stem without thick-walled cortex, and is widely accepted as a good genus (e.g., Crandall-Stotler *et al.* 2009).

Literature: Kitagawa (1970); Váňa (1991c); Schuster (2002).

Andrewsianthus R.M.Schust. Fig. 29H–Q

Plants ca. 1–1.5 mm wide, green to brown or reddish-brown, creeping or ascending, little branched. Branches lateral-intercalary (frequently dorso-lateral, *Anomoclada*-type), flagelliform branches normally present. Stems rigid. Leaves succubous to almost transverse, bifid, rarely entire (*A. mizutanii*), concave to canaliculate, apices rounded to acute to acuminate, margins entire. Cells with trigones, cuticle smooth or papillose; oil bodies finely granular. Underleaves usually absent (present in *A. recurvifolium*). Perianths inflated, plicate, mouth longly ciliate-laciniate. Capsule walls (2–)3–8-layered. Gemmae present or absent.

A tropical Asian and southern temperate genus (15–20 spp.); 7 species at high elevations on Mt. Kinabalu (mostly in the summit region), on soil and rock.

Note: *Andrewsianthus* is recognized by the green to brownish, dioicous plants with succubous to transverse, bifid leaves (entire in *A. mizutanii*), no underleaves, flagelliform branches and frequent presence of *Anomoclada*-type branches developing from leaf axils on the dorsal side of the stem.

Literature: Kitagawa (1970); Váňa (1974, 1991c); Schuster (2002).

Diplophyllum (Dumort.) Dumort. Fig. 31A–D

Plants delicate, 0.5–1.5 mm wide, less than 1 cm long, pale green to reddish-brown, creeping, irregularly branched. Stems rigid. Leaves complicate-bilobed with a small dorsal lobe and a large ventral lobe, the ventral lobe lingulate to lanceolate, ca. 2–4× longer than wide, apex rounded or acute, margins entire to crenulate to toothed, dorsal lobe much smaller than the ventral lobe, connected over its whole length to the ventral lobe by a keel. Cells uniformly thick-walled or with trigones, cuticle papillose, a vitta sometimes present; oil bodies finely granular. Underleaves absent. Perianths inflated, not plicate. Gemmae sometimes present, papillose-stellate.

A mainly cool-temperate genus (ca. 20 spp.); 1 species in Malaysia (Sabah), *Diplophyllum kinabaluense* Furuki & M.Suleiman, known only from Mt. Kinabalu where it has been collected twice on cut earth banks along trails in montane forest, at 1500–1650 m. A further species, *D. nanum* Herzog, occurs scattered at high elevations in Southeast Asia and may be expected to occur in Malaysia.

Note: Characteristics of *Diplophyllum* are the narrowly elongate leaves (2–4× longer than wide) divided in a ventral lobe and a much smaller dorsal lobe connected by an unwinged keel, absence of underleaves, an inflated-plicate perianth, and papillose-stellate gemmae. The species recorded from Malaysia, *D. kinabaluense*, stands out by acute ventral leaf lobes; the other Southeast Asian species, *D. nanum*, has rounded lobes. According to Furuki & Suleiman (2016) the two species also differ in sexuality, *D. kinabaluense* being

autoicous and *D. nanum* dioicous, but according to Schuster (2002) *D. nanum* is often autoicous.

Literature: Herzog (1951); Schuster (2002); Furuki & Suleiman (2016).

Gottschelia Grolle Figs. 31E–M; 68D

Plants rather robust, 2–4 mm wide, reddish, ascending from a stoloniform base, stem base with numerous stolons. Branches lateral-intercalary. Stems rigid. Leaves succubous to transverse, undivided, deeply concave-canaliculate and strongly enveloping the stem, dorsal leaf insertion extending beyond the stem midline, margins entire. Cells with trigones, cuticle lightly striate-papillose (almost smooth); oil bodies finely granular. Underleaves absent. Perianths inflated, plicate, mouth of thin-walled cells. Capsule cylindrical. Gemmae present, angular-stellate, red, produced in large reddish clusters on leaf tips.

A small paleotropical genus (2 spp.); 1 species in Malaysia (Pahang, Sabah), *Gottschelia schizopleura* (Spruce) Grolle, common in montane forest areas on bark, rock and soil.

Note: Characteristics of *Gottschelia* are 1) plants robust, reddish, with stolons at the base; 2) leaves succubous to transverse, deeply concave-canaliculate, undivided, strongly enveloping the stem, margins entire; 3) dorsal leaf insertions strongly interlocking, extending beyond the dorsal stem midline; 4) underleaves absent; 5) gemmae present, reddish.

Literature: Grolle (1968); Váňa & Piippo (1989b); Schuster (2002).

Plicanthus R.M.Schust. Fig. 32A–J

Plants robust, 3–4 mm wide, yellowish to golden brown, ascending, little branched. Stems rigid, with paraphyllia. Leaves imbricate, almost transverse, deeply bifid to near the base into 3–4 lobes, apices acute-acuminate, margins densely ciliate-laciniate. Cells with large bulging trigones, cuticle smooth or striate-papillose; oil bodies finely granular. Underleaves large, deeply bifid, margins densely ciliate. Perianths inflated, plicate. Gemmae absent.

A small genus of 3 species disjunctly distributed in the Paleotropics and in eastern Asia-western North America; 1 species in Malaysia (Pahang, Sarawak, Sabah), *Plicanthus hirtellus* (F.Weber) Mitt. (= *Chandonanthus hirtellus* (F.Weber) Mitt.), on bark of trees in humid montane and subalpine forests.

Note: *Plicanthus* is readily recognized by the robust, yellowish to golden-brown plants with 3–4-lobed falcate leaves with densely ciliate-laciniate margins, and large, toothed underleaves.

Literature: Horikawa (1930 as *Mastigophora spinosa*); Kitagawa (1965a as *Chandonanthus hirtellus*); Váňa (1991c); Schuster (2002).

Scapania (Dumort.) Dumort. Fig. 32K–Q

Plants 1–5 mm wide, pale green to reddish or brown, usually creeping, sparsely branched. Stems rigid. Leaves complicate-bilobed with a small dorsal lobe and a large ventral lobe (sometimes the two lobes subequal), lobes ovate, 1–1.5× longer than wide, connected by a short or long keel, lobe margins entire or toothed, sometimes brown-colored.

Cells usually with trigones, cuticle smooth or papillose; oil bodies finely granular. Underleaves absent. Perianths dorsiventrally flattened, not plicate. Gemmae frequently present, usually brownish and smooth.

A large, mainly holarctic genus (ca. 90 spp.); 2 species in Malaysia (Sabah), *Scapania lepida* Mitt. and *S. ornithopodioides* (With.) Waddell, on earth banks, rock, rotten logs or tree bases in montane and subalpine forests.

Note: Characteristics of *Scapania* are the ovate leaves (1–1.5 × longer than wide) divided in a ventral lobe and a smaller dorsal lobe connected by an unwinged keel, the usually brown gemmae on leaf margins, absence of underleaves and the flat perianth. *Scapania lepida* is a characteristic liverwort seen along the summit trail in subalpine forest on Mt. Kinabalu, characterized by leaves with brown margins (Frahm *et al.* 1990, Fig. 59).

Literature: Amakawa & Hattori (1954); Schuster (2002).

Sphenolobopsis R.M.Schust. & N.Kitag. Fig. 33A–D

Plants minute, 0.3–0.4 mm wide, green to reddish-brown, creeping, little branched. Stems fragile, without thick-walled cortex. Leaves distant, transverse, bifid to 1/2, lobes broadly ovate-triangular, apices acute, margins entire. Cells very small, 12–16 µm in midleaf, subquadrate, uniformly thick-walled, trigones absent, cuticle smooth; oil bodies minute, faintly granular. Underleaves absent. Seta thin, of 7–8 outer rows of cells and 2–3 inner cell rows of similar size. Capsule wall thin, 2-layered. Perianths plicate above, mouth denticulate. Gemmae absent.

A monotypic genus, containing *Sphenolobopsis pearsonii* (Spruce) R.M.Schust. & N.Kitag. (= *S. kitagawae* R.M.Schust.) distributed scattered in the Holarctic and on high mountains of Malesia. In Malaysia found on Mt. Kinabalu, above 3000 m, growing in thin mats on shaded rock.

Note: *Sphenolobopsis* is recognized by the minute, *Cephaloziella*-like plants with fragile stems (epidermis thin-walled), deeply bifid transverse leaves with spreading lobes and entire margins, and very small, subquadrate leaf cells with uniformly thickened walls. Underleaves are absent.

Literature: Kitagawa (1965b as *Cephaloziopsis pearsonii*); Váňa (1991c); Schuster (2002).

Sphenolobus (Lindb.) Berggr. Fig. 33H–L

(*Anastrophyllum* subg. *Crossocalyx* (Meylan) R.M.Schust.)

Plants 0.5–1 mm wide, greenish-brown to reddish-brown, creeping, little branched. Stems fragile, without thick-walled cortex. Leaves transverse, subsymmetrically bifid to 1/4–1/2, strongly concave-canaliculate, apices acute, margins entire. Cells very small, 12–20 µm in midleaf, with ± uniformly thickened walls, trigones inconspicuous, cuticle smooth or faintly papillose; oil bodies finely granular. Underleaves absent. Perianths inflated, plicate, usually with a white mouth. Gemmae yellow-brown to wine-red to purplish, angular, on apices of upper leaves.

A small, mainly holarctic genus (3 spp.); 1 species in Malaysia (Sabah), *Sphenolobus minutus* (Schreb.) Berggr., on rock at high elevation on Mt. Kinabalu, above 3500 m.

Note: *Sphenolobus* is sometimes included in *Anastrophyllum* but differs in the

uniformly thick-walled cells without trigones, and the fragile stems without a thick-walled cortex.

Literature: Váňa (1991c); Schuster (2002 as *Anastrophyllum* subg. *Crossocalyx*).

Tetralophozia (R.M.Schust.) Schljakov Fig. 33E–G
(*Chandonanthus* subg. *Tetralophozia* R.M.Schust.)

Plants small, ca. 1 mm wide, brown, creeping, little branched. Stems rigid, without paraphyllia. Leaves imbricate, almost transverse, deeply divided into 4 narrowly lanceolate lobes, apices filiform, margins mostly entire, with a few teeth at the base. Cells with large but ill-defined trigones, the trigones mostly coalesced, cuticle smooth; oil bodies finely granular. Underleaves large, deeply bifid, margins toothed. Perianths inflated, plicate. Gemmae very rare.

A small mainly holarctic genus of 4 species; 1 in Malaysia (Sabah), *Tetralophozia filiformis* (Steph.) Urmi (= *Chandonanthus filiformis* Steph.), found on Mt. Kinabalu, at 3400–4100 m, usually growing on rock.

Note: *Tetralophozia* is closely related to *Plicanthus* but differs from the latter in the much smaller plants with deeply 4-lobed leaves with subentire margins.

Literature: Urmi (1983); Váňa (1991c); Schuster (2002).

Tritomaria Loeske Fig. 34A–E
(*Heterogemma* (Jörg.) Konstant. & Vilnet)

Plants 1–2 mm wide, pale green to brown, creeping. Stems rigid. Leaves succubous (dorsal part of leaf transversely inserted, ventral part obliquely inserted), strongly concave, asymmetrically 3-lobed, the dorsal lobe much smaller, apices acute to acuminate, margins entire. Cells with trigones, these often elongate and confluent, cuticle smooth or papillose; oil bodies granular. Perianths inflated, plicate. Gemmae abundant in the Malesian material, reddish, angular, forming red clusters on shoot tips.

About 8 species worldwide; 1 species in Malaysia (Sabah), *Tritomaria exsecta* (Schrad.) Loeske, on rock in the summit area of Mt. Kinabalu, at 4050–4100 m.

Note: *Tritomaria exsecta* is recognized by the creeping plants with strongly concave, asymmetrically 3-lobed leaves (dorsal lobe very small) with acute tips, and conspicuous, reddish clusters of gemmae at the shoots tips.

Literature: Kitagawa (1970); Váňa (1991c); Schuster (2002).

SCHISTOCHILACEAE

A monotypic family.

Schistochila Dumort. Figs. 34F–K; 70A–C

Plants usually large, green to red, without stolons. Stems rigid, without hyalodermis. Branches lateral, intercalary and terminal. Leaves transverse, incubous or succubous, complicate-bilobed with a dorsal lobe and a larger ventral lobe (sometimes the two lobes almost equal in size), dorsal lobe attached to the surface of the ventral lobe, keel winged, margins usually toothed to ciliate. Cells with small trigones, cuticle smooth; oil bodies

finely granular. Underleaves present or lacking. Rhizoids either scattered and red or in tufts and colorless. Gametoecia on long shoots. Sporophyte in a fleshy perigynium. Seta thick, sometimes with a massive haustorial collar. Capsule ellipsoid, wall 2–5-layered. Gemmae lacking.

A mainly southern-hemispheric genus (ca. 75 spp.); 7 species widely distributed in Malaysia where they are a common and characteristic element of humid montane forests, on tree trunks, rock and rotten wood.

Note: *Schistochila* is readily recognized by the robust plants with conduplicate, elongate leaves (at least 2 × longer than wide) divided into a small dorsal lobe and large ventral lobe, the two lobes being connected along a winged keel, and with toothed to ciliate leaf margins. Underleaves may be present or absent and the sporophyte is enclosed by a fleshy perigynium. The genus may be confused with *Balantiopsis* and *Scapania* but the leaves in the latter are less elongate, the keel is not winged, and the sporophyte is enclosed in a marsupium in *Balantiopsis* and in a perianth in *Scapania*. The latter genus, moreover, has gemmae.

Literature: So (2003a); He & Glenny (2010); He *et al.* (2014); Juengprayoon *et al.* (2015).

SOLENOSTOMATACEAE

Contains 4 genera; 1 in Malaysia.

Solenostoma Mitt. Figs. 35; 69A, B
(*Jungermannia* p.p.)

Plants small to medium-sized, 0.6–4 mm wide, pale green to reddish or brown, creeping or ascending, little branched, stolons lacking. Branches lateral-intercalary. Stems fragile, without hyalodermis, cortex weakly differentiated. Leaves succubous, usually somewhat spreading, concave and clasping the stem in the lower half, undivided, ovate-orbicular, rarely lingulate, apex rounded, margins entire, bases not or short-decurrent, insertion line reaching the dorsal stem-midline. Cells with usually rather small trigones, cuticle smooth or papillose; oil bodies finely granular. Underleaves absent. Rhizoids numerous, colorless or reddish or brown, usually scattered, occasionally in tufts. Dioicous or paroicous. Gametoecia on long shoots. Perianths plicate, long-exserted or short and hidden between the bracts, perianth base united with the bracts and forming a short perigynium. Perianth mouth narrowed into a short beak. Seta thick. Capsule ellipsoid, wall 2-layered. Gemmae lacking.

About 120 species wordwide; 15 species in Malaysia, on humid soil and rock.

Note: Diagnostic characters of *Solenostoma* are the beaked, plicate perianth and the presence of a short stem perigynium at the base of the perianth. The presence of a perigynium can be ascertained by the bracts being attached to the base of the perianth. *Solenostoma* was long considered a subgenus of *Jungermannia* (Jungermanniaceae), but molecular evidence showed that *Solenostoma* and *Jungermannia* are not closely related and belong to different families. All Malaysian species of *Jungermannia* listed in Chuah-Petiot (2011) belong to *Solenostoma*.

Literature: Váňa (1974 as *Jungermannia*); Váňa (1991b as *Jungermannia*); Váňa & Long (2009).

SOUTHBYACEAE

Contains 2 genera worldwide; 1 in Malaysia.

Southbya Spruce Fig. 36A–H

Plants less than 1 mm wide, greenish to brown, creeping. Stems without hyalodermis; stolons lacking. 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 smooth or papillose; oil bodies finely granular. Underleaves absent. Rhizoids scattered, colorless. Dioicous or monoicous. Gametoecia on long shoots. Sporophyte enclosed by a perianth with a fleshy base. Seta thick. Capsule ellipsoid, wall 2-layered. Gemmae absent.

A small genus with scattered distribution in warm-temperate and tropical regions (4 spp.); 1 species in Malaysia (Sabah), *Southbya organensis* Herzog (= *S. grollei* N.Kitag.), found on Mt. Kinabalu on moist soil over rock at about 3000 m.

Note: The main characters of *Southbya* are the small, creeping, terrestrial plants with densely imbricate opposite leaves. The leaf cells are very large and with a papillose cuticle in *S. grollei*, and the sporophyte (rarely seen in *S. grollei*) is produced in a perianth.

Literature: Kitagawa (1973); Váňa *et al.* (2012; Malaysian record not mentioned); Shaw *et al.* (2015).

TRICHOCOLEACEAE

Plants small to large, whitish-green to pale brown, creeping to pendent. Plants irregularly to regularly 1–3-pinnate. Branches mostly terminal, *Frullania*-type. Stems without cortex or with a 1–5-layered thick-walled cortex; paraphyllia present or absent. Leaves succubous, rarely incubous, densely hairy, deeply divided into (2–)4–8 strongly ciliate lobes, insertion line oblique to sublongitudinal. Cells narrowly elongate, with uniformly thickened walls, cuticle striate-papillose; oil bodies small, homogeneous to coarsely granular. Underleaves similar to the leaves but slightly smaller. Rhizoids scarce, in tufts from underleaf bases. Dioicous. Gametoecia on long or short shoots. Sporophyte enclosed by a fleshy, hairy perigynium with or without a short perianth on top. Seta thick. Capsule globose or ellipsoid, wall 6–8-layered. Vegetative reproduction lacking.

A family of 4 genera worldwide; 3 genera in Malaysia. Trichocoleaceae are easily recognized by the woolly plants with leaves split into numerous hair-like cilia. The plants are usually light green to whitish-green when fresh, pinnately branched, the leaves are normally succubous, the leaf cells are narrowly elongate with striate-papillose walls, and the underleaves are similar to the leaves but slightly smaller. The below generic key is adapted from Katagiri & Deguchi (2012).

1. Leaves incubous ····· *Eotrichocolea*
1. Leaves succubous ····· 2
2. Plants irregularly to regularly 1-pinnate. Stem without cortex or with a 1-layered thick-walled cortex. Perigynium with a short perianth at the tip. Capsule globose ··· *Leiomitra*
2. Plants regularly 2–3-pinnnate. Stem with a 1–7-layered, thick-walled cortex. Perigynium without perianth. Capsule ellipsoid ····· *Trichocolea*

Eotrichocolea R.M.Schust. Fig. 37A–D

Plants yellow-green to yellow-brown, 2–6 cm long. ca. 1–1.5 mm wide, 1–2-pinnate. Stems (in *E. furukii*), with a 3–4-layered thick-walled cortex and without paraphyllia. Leaves incubous, deeply 4–8-lobed, undivided lamina only 1–3 cells high, lobes with numerous long cilia. Perigynium without perianth. Capsule ellipsoid.

A small Asian-Australasian genus (2 spp.); 1 species in Malaysia (Mt. Kinabalu), *Eotrichocolea furukii* T.Katag., on soil in montane forest.

Note: *Eotrichocolea* is similar to *Trichocolea* in branching, stem structure, absence of a perianth and shape of the capsule, but differs from *Trichocolea* in having incubous instead of succubous leaves.

Literature: Katagiri *et al.* (2012).

Leiomitra Lindb. Fig. 37E–H

Plants irregularly to regularly 1-pinnate. Stem without cortex or with a 1-layered thick-walled cortex, with or without paraphyllia. Leaves succubous, 2–8-lobed, undivided lamina 2–8 cells high, lobes with numerous long cilia. Perigynium with a short perianth at the tip. Capsule globose.

An tropical amphi-Pacific genus of about 10 species, mainly in tropical America (Katagiri 2019); 1 species in Malaysia, *Leiomitra merrillana* (Steph.) T.Katag. (= *Trichocolea obconica* Steph.), recorded from Pahang and Sabah, on tree trunks, rock and humic soil in humid montane forests.

Note: *Leiomitra* resembles *Trichocolea* but differs in plants 1-pinnate (2–3-pinnate in *Trichocolea*), thick-walled cortex absent or 1-layered only, presence of a perianth and capsules globose (ellipsoid in *Trichocolea*).

Literature: Katagiri & Deguchi (2012).

Trichocolea Dumort. Figs. 38; 69C

Plants regularly (1–)2–3-pinnnate. Stems with a 1–7-layered thick-walled cortex, without or with paraphyllia. Leaves succubous, 4–6-lobed, undivided lamina 3–5 cells high, lobes with numerous long cilia, the cilia sometimes fragile. Perigynium without perianth. Capsule ellipsoid.

About 15 species worldwide, mainly in Southeast Asia; 5 species in Malaysia (Katagiri *et al.* 2013), common in humid montane forests on bark, rock, humic soil and rotten wood.

Note: Characteristics of *Trichocolea* are the whitish-green, 2–3-pinnate plants with densely hairy-lobed leaves and underleaves, succubous leaves, stems with a thick-walled cortex, and capsule ellipsoid, developed in a fleshy perigynium without perianth.

Literature: Katagiri *et al.* (2013).

PORELLALES

Plants mostly epiphytic. Branching lateral, not ventral. Leaves incubous, originating from 2 or 3 initial cells; ventral lobule and sometimes a stylus present. Underleaves present or absent. Seta very short, thin or thick. Capsule usually globose, rarely cylindric, wall 2–4(–6)-layered. Spores usually large and multicellular, germination endosporic (occasionally unicellular and germination exosporic in *Radula*).

Key to families of Porellales

1. Underleaves present ····· 2
1. Underleaves absent ····· 5
2. Lobule for most of its length attached to the lobe along a keel. Keel and lobule obliquely to widely spreading, away from stem. Plants variously colored but not reddish or purple ····· **Lejeuneaceae**
2. Lobule not for most its length attached to the lobe, keel lacking or short. Lobule parallel to the stem or obliquely spreading. Plants green, brown, reddish or purple ····· 3
3. Plants robust, 3–7 mm wide, green to brown. Underleaves undivided. Lobule flat, with rounded apex ····· **Porellaceae**
3. Plants smaller, 0.5–2.5 mm wide, green to reddish or purple. Underleaves bifid (very rarely undivided in *Frullania*). Lobule sac-like or concave (occasionally plane, then with acute apex) ····· 4
4. Plants green, without any reddish pigmentation. Leaf margins toothed (rarely entire). Lobules rounded (or flat), very small, attached to the ventral margin of the lobe at some distance from the stem. Stylus absent ····· **Jubulaceae**
4. Plants usually with reddish pigmentation, rarely purely green. Leaf margins entire (rarely toothed). Lobules rounded or elongate, usually very close to the stem (at some distance from stem in subg. *Diastaloba*: small reddish plants). Stylus present ··· **Frullaniaceae**
5. Stems rigid, epidermis of numerous rows of cells. Rhizoids in tufts from the surface of the lobule. Lobules broadly attached to stem. Plants usually more than 1 mm wide. Oil bodies brown. Perianth cylindrical, truncate, without beak ····· **Radulaceae**
5. Stems fragile, epidermis of only 5–10 rows of cells. Rhizoids in tufts from the ventral stem surface. Lobules very narrowly attached to stem (by only 1–3 cells). Plants usually less than 1 mm wide, occasionally larger. Oil bodies colorless. Perianth shorter and broader, with a beak ····· **Lejeuneaceae** (*Cololejeunea*, *Myriocoleopsis*)

FRULLANIACEAE

A monotypic family.

Frullania Raddi Figs. 39; 71A, B
(*Steerea* S.Hatt.)

Plants small to large, usually reddish to purplish to blackish, sometimes green, creeping, ascending or pendent, pinnate. Stems rigid, made up of thick-walled cells.

Branches *Frullania*-type, base with a hemiphyll. Leaves incubous, insertion line very short; lobes usually ovate-orbicular, apex rounded to acute to acuminate, margins entire, rarely toothed; lobules almost free from the dorsal lobe, rounded to elongate, normally forming a sac, sometimes flattened; stylus linear and minute, rarely large. Cells usually elongate (sometimes isodiametric), with trigones and intermediate thickenings, the trigones often confluent and cell walls often irregularly undulate-sinuose, cuticle smooth; oil bodies finely granular; ocelli sometimes present. Underleaves small or large, bifid, rarely undivided. Rhizoids in tufts from underleaf bases. Dioicous or monoicous. Gynoecia on short or long shoots, with 2–5 archegonia; without innovations. Perianths flattened or inflated, with 0–14 keels, mouth contracted into a beak. Foot of the sporophyte not penetrating into the stem. Seta thick. Capsule globose, wall 2-layered. Elaters attached to the capsule valves, with 2–3 spirals. Spores large, multicellular, germination endosporic, spore suface with rosettes. Vegetative reproduction rare, by caducous leaves or by regeneration (buds) from leaf margins, exceptionally by gemmae (seen in *F. gemmipara* S.Hatt. & R.M.Schust.).

A large genus of at least 300 species worldwide, in several subgenera and sections; 51 species recorded from Malaysia, mostly epiphytic but also on rock or living leaves.

Note: *Frullania* is the third largest genus of liverworts in Malaysia, after *Cololejeunea* and *Bazzania*. It is recognized by: 1) plants pinnate, reddish, purplish or brown to blackish, branches *Frullania*-type, with a hemiphyll at the base; 2) leaves incubous, apex undivided and margins usually entire; 3) lobule mostly sac-like, almost free from the dorsal lobe; 4) stylus present; 5) underleaves usually bifid, rhizoids in tufts at the underleaf base; 6) gynoecia with 2–5 archegonia, without innovations; 7) perianth with a beak; 8) sporophyte foot not penetrating into the stem; 9) seta thick; 10) capsule globose, wall 2-layered; 11) spores large, multicellular, spore surface with rosettes; 12) elaters attached to capsule valves.

Literature: Hattori (e.g., 1972–1981, 1980); Hattori & Piippo (1986); Yuzawa (1991); Hentschel *et al.* (2015); Sukkharak (2017b).

JUBULACEAE

Contains 3 genera; 1 in Malaysia. A second genus of Jubulaceae, *Neohattoria* Kamim., has been recorded from Malaysia (Tixier 1974) but the species, *N. perversa* (Steph.) R.M.Schust., does not belong in *Neohattoria* and is a synonym of *Frullania junghuhniana* Gottsche var. *tenella* (Sande Lac.) Grolle & S.Hatt. (Larrain *et al.* 2015).

Jubula Dumort. Fig. 36I, J

Plants glossy deep green, not reddish, creeping, regularly pinnate. Branches *Frullania*-type or *Lejeunea*-type. Leaves incubous, insertion line short; lobe ovate, apex mucronate to long-piliferous, margins sharply toothed or entire; lobule small, rounded and saccate (sometimes ± flat), almost free from the lobe, attached to the lobe at some distance from the stem; stylus absent. Cells thin-walled, with minute trigones. Underleaves bifid, with longly decurrent bases and deeply arched insertion. Monoicous. Androecia on tiny, elongate branches. Gynoecia on elongate shoots, with 1–2 *Radula*-type innovations and 2–3 archegonia. Perianth flattened, with 3 sharp keels (2 lateral, 1 ventral), perianth mouth

beaked. Seta thin, of only 20 rows of cells: 4 inner rows and 16 outer rows. Capsule as in *Frullania*. Spores without rosettes. Vegetative reproduction absent.

About 5 species wordwide; 1 species in Malaysia, *Jubula javanica* Steph. (= *J. hutchinsiae* subsp. *javanica* (Steph.) Verd.), on bark, rock and rotten wood in the understory of shaded, moist forests.

Note: *Jubula* is close to *Frullania* but differs in the complete lack of reddish pigmentation, the absence of a stylus, gynoecia with innovations, seta thin, of only 20 rows of cells, and spore surface without rosettes.

Literature: Guerke (1978); Katagiri *et al.* (2010).

LEJEUNEACEAE

Plants leafy (very rarely thalloid: *Cololejeunea metzgeriopsis*), green, yellowish, brown, black or whitish, not reddish; creeping to ascending or pendent, pinnate, forked or irregularly pinnate. Branches usually *Lejeunea*-type, sometimes *Frullania*-type; innovations of the *Radula*-type; stolons lacking. Stems with or without hyalodermis. Leaves incubous, insertion line long or short; lobe and lobule highly variable, lobule broadly attached to the dorsal lobe along a keel, sometimes reduced; stylus reduced. Cells with homogeneous or granular oil bodies; ocelli sometimes present. Underleaves undivided or bifid, rarely lacking. Rhizoids in tufts from underleaf bases, producing an ashesive disc in epiphyllous plants. Dioicous or monoicous. Gametoecia on leading shoots or on short branches. Androecia with 1–2 antheridia per bract, antheridium globose, on a long 1-seriate stalk. Gynoecia with only one archegonium. Perianth mouth beaked. Sporophyte foot reduced, not penetrating the stem. Seta thin, usually of 16 or 20 rows of cells: 4 inner rows and 12 or 16 outer rows. Capsule globose, wall 2-layered. Elaters attached to the capsule valves, arranged vertically inside capsule, spirals well developed or reduced. Spores large, germination endosporic, spore surface with or without rosettes. Vegetative reproduction by multicellular gemmae and caducous leaves or branches.

The largest family of the liverworts with more than a thousand species worldwide in about 70 genera; more than 300 species in 29 genera have been recorded from Malaysia (Lee *et al.* 2013, with update). Lejeuneaceae is close to Frullaniaceae but differs in: 1) plants without reddish pigmentation; 2) branches mostly *Lejeunea*-type; 3) lobe and lobule connected along a long keel, stylus reduced; 4) perianth with only one archegonium; 5) seta thin, of only 16 or 20 rows of cells. The species of Lejeuneaceae frequently grow on living leaves and almost all typically epiphyllous bryophyte species are members of Lejeuneaceae. An adaptation to growth on living leaves is the large, adhesive rhizoid disc at the base of the underleaves seen in epiphyllous Lejeuneaceae. The family is subdivided into two subfamilies, Lejeuneoideae and Ptychanthoideae, which are separated as follows (see Gradstein 2013):

Ptychanthoideae. Underleaves undivided. Branches *Lejeunea*-type and *Frullania* type. Ventral merophyte 4 or more cells wide. Ocelli absent. Sporophyte “ptychanthoid”: spores isodiametric; upper ends of elaters attached to valve surface and margins, spiral bands well developed, brown; inner wall of capsule valves brownish, covered by a

fenestrate thickening layer; capsule dehiscence "explosive". Seta with 16 outer rows of cells. Genera: *Acrolejeunea*, *Caudalejeunea*, *Cephalolejeunea, Lopholejeunea*, *Ptychanthus, Schiffneriolejeunea*, *Spruceanthus*, *Thysananthus.*

Lejeuneoideae. Underleaves bifid or absent, occasionally undivided. Branches *Lejeunea*-type (*Frullania*-type branches very rare). Ventral merophyte mostly 2 cells wide, occasionally wider. Ocelli present or absent. Sporophyte "lejeuneoid": spores elongate-rectangular; upper ends of elaters attached to valve margins only, spiral bands usually rudimentary, pale-colored; inner wall of capsule valves pale, usually lacking a thickening layer; capsule dehiscence gentle (not "explosive"). Seta with 12 outer rows of cells (16 in *Stictolejeunea*). Genera: *Allorgella*, *Ceratolejeunea*, *Cheilolejeunea*, *Cololejeunea, Colura*, *Dactylophorella, Diplasiolejeunea*, *Drepanolejeunea*, *Lejeunea*, *Lepidolejeunea*, *Leptolejeunea*, *Metalejeunea*, *Microlejeunea*, *Mohamedia, Pictolejeunea*, *Pycnolejeunea, Soella, Stictolejeunea, Thiersianthus, Tuyamaella.*

Key to the genera of Lejeuneaceae of Malaysia

1. Plants thalloid, growing epiphyllous in montane rainforest. Thallus very small and pale-colored, ± pinnate, margins with cilia. Gametangia produced on short leafy branches ····· *Cololejeunea metzgeriopsis*
1. Plants leafy ····· 2
2. Leaves highly specialized, distal part forming an inflated sac (extension of the lobule) ··· *Colura*
2. Leaves less specialized, distal part not forming an inflated sac ····· 3
3. Underleaves absent ····· 4
3. Underleaves present (but sometimes very small) ····· 5
4. Plants growing on bark in dry, open environments or epiphyllous. Leaves convex to squarrose, obovate, margins and apex entire, without hyaline cells, vitta lacking. Leaf cells smooth. Lobule large, 1/2–2/3× leaf length, without a sharp keel, with 2 teeth, but sometimes reduced to a long, flat fold along the ventral leaf margin. Perianth inflated, with 5 smooth keels, perianth base often stalk-like elongated ····· *Myriocoleopsis minutissima*
4. Plants different ····· *Cololejeunea*
5. Underleaves undivided to weakly emarginate ····· **Key A**
5. Underleaves bifid ····· **Key B**

Key A. Underleaves undivided to weakly emarginate

1. Leaves with a long vitta, extending over at least 1/2 of leaf length ····· *Thysananthus*
1. Leaves without long vitta ····· 2
2. Trigones cordate, with 2 convex sides and one concave side. Midleaf cells ± longer than wide ····· 3
2. Trigones not cordate. Midleaf cells almost isodiametric ····· 9
3. Branches predominantly *Frullania*-type ····· 4

3. Branches predominantly *Lejeunea*-type ····· 5
4. Plants regularly (bi-)pinnate, robust, to 10 cm long, frequently pendent. Leaf apex acute. Margins of leaves and underleaves toothed or entire. Stems with a thick-walled subepidermis ····· *Ptychanthus*
4. Plants irregularly branched, smaller, 1–3 cm long, creeping. Leaf apex rounded. Margins of leaves and underleaves entire. Stems without thick-walled subepidermis ····· *Acrolejeunea*
5. Cells of the ventral epidermis in cross section distinctly higher than medullary cells. Gynoecia without innovations. Oil bodies homogeneous, more than 10 per cell ····· 6
5. Cells of the ventral epidermis not distinctly higher than medullary cells (but higher in *Thysananthus reconditus*). Gynoecia with innovations. Oil bodies granular, less than 10 per cell ····· 7
6. Intermediate thickenings in leaves 1–3 per cell wall. Leaves when dry more or less spreading or weakly convoluted. Perianth 3-keeled. Male bracts hypostatic, conspicuous. Plants sometimes with disciform gemmae ····· *Caudalejeunea*
6. Intermediate thickenings in leaves 0–1 per cell wall. Leaves when dry strongly convolute. Perianth 3–10-keeled. Male bracts epistatic, inconspicuous. Plants not with disciform gemmae ····· *Acrolejeunea*
7. Leaf margins toothed, at least near apex ····· *Thysananthus*
7. Leaf margins entire ····· 8
8. Plants green to glossy brown, ± julaceous (= smoothly cylindrical) when dry. Lobules with 2–4 teeth. Gynoecial innovations absent. Perianth with 4–6 rounded keels ····· *Schiffneriolejeunea*
8. Plants olive green to brown to blackish, not julaceous when dry. Lobule with 1–2 teeth (3–4 in *Thysananthus indicus*). Gynoecial innovations present. Perianth with 3 sharp keels ····· *Thysananthus*
9. Leaf lobes with scattered ocelli. Green leaf cells without oil bodies ····· 10
9. Leaf lobes without ocelli. Green leaf cells with oil bodies ····· 11
10. Ventral merophyte 4 cells wide. Plants dark green. Stems without hyalodermis, rigid. Perianth keels extended above into large auricles ····· *Stictolejeunea*
10. Ventral merophyte 2 cells wide. Plants pale olive green. Stems with hyalodermis, fragile. Perianth keels extended into auricles ····· *Lepidolejeunea*
11. Plants usually with blackish pigmentation in cell walls. Gynoecial innovations absent (but sometimes with pseudo-innovations) ····· *Lopholejeunea*
11. Plants without blackish pigmentation. Gynoecial innovations present ····· 12
12. Plants usually more than 2 mm wide. Epidermis cells not or scarcely larger than inner cells. Ventral merophyte 4–14 cells wide. Stem bases often with small microphyllous branches. Oil bodies homogeneous ····· *Spruceanthus*
12. Plants smaller, less than 2 mm wide. Epidermis cells distinctly larger than inner cells. Ventral merophyte 2–4 cells wide. Oil bodies granular ····· 13
13. *Frullania*-type branches present. Leaf apex toothed or entire. Well-developed lobules with 2 teeth. Perianth keels ciliate-laciniate. Not yet reported from Malaysia but to be expected (see Kruijt 1987) ····· *Acanthocoleus*
13. *Frullania*-type branches absent. Leaf apex entire. Well-developed lobules with 1 tooth.

Perianth keels smooth or crenate ·····14
14. Ventral merophyte 4 cells wide. Perianth subterete, with up to 10 very short crenate keels near the apex ····· *Cephalolejeunea*
14. Ventral merophyte 2 cells wide. Perianth with 5 keels ····· *Lejeunea*

Key B. Underleaves bifid

1. Leaves highly specialized, upper part forming an inflated sac ····· *Colura*
1. Leaves less specialized, upper part not forming an inflated sac ····· 2
2. Leaf lobes split into two large segments with densely spinose-crispate margins ····· *Dactylophorella*
2. Leaf lobes not split into two large segments with densely spinose-crispate margins ····· 3
3. Underleaf lobes diverging (spreading outwards) ····· 4
3. Underleaf lobes not diverging ····· 7
4. One underleaf to each leaf, the underleaves usually imbricate, with broad lobes. Leaf apex rounded ····· *Diplasiolejeunea*
4. One underleaf to each pair of leaves, the underleaves usually distant, with narrow lobes. Leaf apex acute-acuminate to rounded ····· 5
5. Attachment of leaf lobe and lobule to the stem very short, by only 1–2 cells, leaf insertion tranverse ····· 6
5. Attachment longer, leaf insertion J-shaped ····· 9
6. Leaf lobule ovate, with 2 teeth. Underleaves obcordate; lobes ovate to oblong, 5–12 cells wide ····· *Tuyamaella*
6. Leaf lobule long and slender, without teeth. Underleaves divergent; lobes linear, 1–2 cells wide ····· *Colura corynophora* (non-saccate lobules)
7. Leaf lobes with a very large ocellus near leaf base, 2.5–4× longer than surrounding leaf cells, or with 2–5 basal ocelli in a continuous row. Lobule tooth short and blunt, not falcate. Leaf apex mostly rounded ····· 8
7. Ocellus at leaf base smaller, 1–2× longer than surrounding leaf cells, or lacking. Lobule with a long, falcate tooth (rarely short and blunt). Leaf apex acute-acuminate or rounded.... ····· *Drepanolejeunea*
8. Leaf lobes with 2–4(–6) basal ocelli in a continuous row (horizontally arranged). Underleaf usually with a long 1–2-celled tooth on the outer margins. Gynoecia with one pycnolejeuneoid innovation ····· *Soella*
8. Leaf lobes with a large basal ocellus. Underleaf entire, without tooth. Gynoecia innovation absent ····· *Leptolejeunea*
9. Plants minute, 0.2–0.6 mm wide. Lobules very large, 3/5–4/5 of lobe length. Leaves mostly suberect, almost parallel to the stem ·····10
9. Plants small or large. Lobules smaller. Leaves spreading ·····11
10. Leaf base with one or more ocelli. Innovations lejeuneoid. Plants usually dioicous ····· *Microlejeunea*
10. Leaf base without ocelli. Innovations pycnolejeuneoid. Plants monoicous ····· *Metalejeunea*
11. Ocelli present ·····12

11. Ocelli lacking ……19
12. Ocelli present in leaves and underleaves ……13
12. Ocelli present in leaves only ……15
13. Ocelli in dried plants reddish or brown. Leaf cells often papillose …… *Pictolejeunea*
13. Ocelli colorless or gray. Leaf cells smooth .……14
14. Basalmost ocellus in leaf lobes positioned directly adjacent to stem cells … *Mohamedia*
14. Basalmost ocellus in leaf lobes not positioned directly adjacent to stem cells ("suprabasal"), separated from stem cells by at least one leaf cell …… *Lepidolejeunea*
15. Ocelli in leaf lobes in a long unbroken row (and scattered) … *Cheilolejeunea falsinervis*
15. Ocelli in leaf lobes in a broken row, scattered or restricted to the leaf base……16
16. Leaves with a very large ocellus at the base, the basal ocellus 2.5–4× larger than adjacent leaf cells. Underleaf lobes subulate (1–2 cells wide), inserted at the outer edges of the underleaf. Underleaf margins bordered by 6 large cells …… *Leptolejeunea*
16. Basal ocellus absent or smaller, maximally 2× larger than adjacent leaf cells. Underleaf lobes wider, not inserted at outer edges of underleaf. Underleaf margins not bordered by 6 large cells ……17
17. Plants brown or brownish-green. Walls of leaf cells ± yellowish brown, trigones radiate (or lacking). Branch bases sometimes with a huge, strongly inflated lobule ("utricle"). Perianth usually with inflated horns …… *Ceratolejeunea*
17. Plants pale green or yellowish green (rarely brown). Walls of leaf cells colorless, trigones not radiate. Utricles lacking. Perianth without inflated horns ……18
18. Green leaf cells fully thin-walled, without oil bodies. Underleaves small, distant, 1.5–2× stem width. Cuticle smooth. [Plants very delicate, less than 1 mm wide] …. *Thiersianthus*
18. Green leaf cells with trigones and oil bodies. Underleaves larger, contiguous to imbricate. Cuticle smooth or papillose …… *Pycnolejeunea*
19. Leaves with a very short insertion, attached to the stem by only 2–3 cells. Vegetative reproduction by discoid gemmae …… *Tuyamaella*
19. Leaves with a longer insertion. Vegetative reproduction not by discoid gemmae ……20
20. Leaf margins with *Allorgella*-type denticulations. Perianths flattened, 2-keeled, keels expanded into large auricles …… *Allorgella*
20. Leaf margins without *Allorgella*-type denticulations. Perianths usually different ……21
21. Plants opaque or dull. Oil bodies usually large (more than 1/2× the cell lumen in length), coarsely segmented. Hyaline papilla distal to the largest lobule tooth. …… *Cheilolejeunea*
21. Plants usually not opaque. Oil bodies smaller (less than 1/4 the cell lumen in length), finely segmented or smooth. Hyaline papilla proximal to the lobule tooth …… *Lejeunea*

Acrolejeunea (Spruce) Steph. Figs. 40; 72A
(*Trocholejeunea* Schiffn.)

Plants 1–2 mm wide, yellow-green to yellow-brown, creeping. Branches *Lejeunea*-type and *Frullania*-type. Stems fragile, 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; ocelli lacking. Lobules 2/5–1/2× leaf length, not reduced, with (2–)3–8 teeth.

Underleaves undivided, margins entire, insertion line shallowly curved. Male bracts rather similar to leaves, with epistatic lobules and only one antheridium per bract. Gynoecia without innovations (or with *Frullania*-type innovations). Perianths with (5–)8–10 smooth keels. Sporophyte ptychanthoid. Vegetative reproduction sometimes by caducous leaves produced on upright flagelliform shoots.

A pantropical genus (21 spp.); 5 species in Malaysia (including the rare *Acrolejeunea crassicaulis* (Mizut.) J.Wang bis & Gradst., which was previously placed in *Trocholejeunea*). The record of *A. sandvicensis* from Malaysia (Tixier 1975 as *Brachiolejeunea sandvicensis*) is erroneous and belongs to *Thysananthus reconditus* (Steph.) Sukkharak & Gradst. (Sun *et al.* 2018). The species mostly on bark of trees in rather open, well-illuminated places.

Note: *Acrolejeunea* is readily recognized by the small, glossy green to yellowish-brown plants growing on bark in rather open environments with densely imbricate leaves that are strongly convolute when dry. The underleaves are undivided, the stems are fragile (with a hyalodermis), the lobules have (2–)3–8 teeth, the leaf cells have cordate trigones and small, homogeneous oil bodies, the gynoecia usually lack innovations (*Frullania*-type innovations in some members of the former genus *Trocholejeunea*), and the perianth is pluriplicate. *Acrolejeunea* can be confused with *Schiffneriolejeunea* but the latter genus has more rigid stems without hyalodermis, granular oil bodies, lobules with only 1–3 teeth, hypostatic male bracts, and 0–5-keeled perianths.

Literature: Gradstein (1975); Wang *et al.* (2014, 2016).

Allorgella Tixier Fig. 41A–D

(*Otolejeunea* Grolle & Tixier subg. *Allorgella* (Tixier) Grolle)

Plants small, 1–1.5 mm wide, yellowish green when dry, creeping, frequently epiphyllous. Stems with hyalodermis; ventral merophyte 2 cells wide. Leaf lobes obliquely to widely spreading, oblong, ca. 2× longer than wide, apex rounded, margins entire or slightly denticulate, plane, dorsal margin curved, ventral margin straight. Midleaf cells subisodiametrical, thin-walled, trigones small, cuticle smooth; oil bodies granular; ocelli lacking. Lobules small, 1/5 of leaf length, inflated, narrow-rectangular, tooth reduced. Underleaves small, distant, 1.5–2.5× stem width, bifid with upright lobes, tips acute, margins entire or with a blunt tooth, insertion line straight. Monoicous. Gynoecia on a very short branch without or with a pycnolejeuneoid innovation. Perianths ± flattened with 2 broad lateral keels expanded above into a large auricle. Sporophyte lejeuneoid. Vegetative reproduction not observed.

A pantropical genus (10 spp.); 1 species in Malaysia, *Allorgella semperiana* (Steph.) Bechteler *et al.* (= *O. semperiana* (Steph.) Grolle), on living leaves.

Note: *Allorgella* was usually considered a subgenus of *Otolejeunea* but molecular analysis showed that it is a separate genus. Its main characters are the ovate-oblong, entire-margined leaves with a small inflated lobules, small bifid underleaves with upright lobes, gynoecia on a very short branch without or with a pycnolejeuneoid innovation, and flat, 2-keeled perianths with lateral keels expanded above in a large auricle.

Literature: Grolle (1985); Zhu & So (1997, 2001); Bechteler *et al.* (2016a).

Caudalejeunea Schiffn. Figs. 42; 72B

Plants 1.5–2.5 mm wide, yellow green to brown, creeping to ascending. Branches mostly *Lejeunea*-type, rarely *Frullania*-type. Stems with a hyalodermis; ventral merophyte 4 cells wide. Leaf lobes obliquely spreading, somewhat falcate, apex obtuse to acute, margins entire or toothed. Cells with small cordate trigones and frequent intermediate thickenings, 1–2 per wall; oil bodies homogeneous; ocelli lacking. Lobules inflated with inflexed free margin, 1/3–2/5× leaf length, with 2–20 teeth. Underleaves emarginate, margins entire, bases decurrent, insertion line curved. Male bracts hypostatic, with 2 antheridia. Gynoecia without innovations. Perianths with 4–5 sharp keels, keels smooth or dentate. Sporophyte ptychanthoid. Vegetative reproduction by disciform gemmae produced on strongly toothed leaves on specialized, upright or circinate shoots.

A pantropical genus (ca. 13 spp.); 2 species in Malaysia, *Caudalejeunea cristiloba* (Steph.) Gradst. and *C. reniloba* (Gottsche) Steph., on bark (especially branches or twigs), rock and living leaves.

Note: The main features of *Caudalejeunea* are the stem with a hyalodermis, a 4-cell wide ventral merophyte, small cordate trigones, homogeneous oil bodies, emarginate underleaves, gynoecia without innovations and a 3–5-keeled perianth, and asexual reproduction by disciform gemmae from leaves on specialized, upright or circinnate shoots. *Caudalejeunea cristiloba* is an unusual species with lobules with up to 20 teeth.

Literature: Mizutani (1988); Gradstein (1974); Gradstein *et al.* (2002).

Cephalolejeunea Mizut. Fig. 41H–Q

Plants ca. 1 mm wide, olive-green to brown when dry, creeping and densely branched with numerous flagelliform branches. Branches *Lejeunea*-type. Stems with hyalodermis; ventral merophyte 4 cells wide. Leaf lobes wide-spreading, when dry not appressed or convolute, apex rounded, margins entire. Cells (sub)isodiametric, trigones simple-triangular, intermediate thickenings frequently present; oil bodies 7–12 per cell, finely granular but becoming homogeneous upon desintegration (Bi *et al.* 2019). Lobules to 1/3× leaf length, sometimes reduced, with one tooth. Underleaves undivided, distant to subimbricate, with entire margins and slightly curved insertion line. Monoicous. Gynoecia with 1–2 lejeunoid innovations. Perianths inflated, subterete, with up to 10 very short and weakly developed keels near the apex, otherwise smooth, the keels ± crenate. Vegetative reproduction not observed.

A monotypic genus known only from Malaysia and Brunei (Bi *et al.* 2019); contains *Cephalolejeunea parvilobula* Mizut., a rare species from tree trunks in lowland rainforest.

Note: *Cephalolejeunea* is characterized by fragile stems with a hyalodermis, 4-cell wide ventral merophyte, isodiametric leaf cells with simple-triangular trigones and granular oil bodies, gynoecia with lejeuneoid innovations, and subterete perianths with up to 10 weak keels at the apex. Bi *et al.* (2019) found that *Cephalolejeunea* is very similar to the Afro-American genus *Dibrachiella* (Spruce) X.Q.Shi *et al.*; the two genera seem to differ only in the shape of the perianth, which is longly 4–5-keeled in *Dibrachiella*. When congeneric, *Dibrachiella* becomes a synonym of *Cephalolejeunea*. A critical study of *Cephalolejeunea* is currently being undertaken in the laboratory of Prof. R.L. Zhu in Shanghai.

Literature: Mizutani (1979); Bi *et al.* (2019).

Ceratolejeunea (Spruce) J.B.Jack & Steph. Fig. 43
(*Acantholejeunea* (R.M.Schust.) R.M.Schust)

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 mostly with a hyalodermis; ventral merophyte 2 cells wide. Leaf lobes wide-spreading, apex rounded to acute, margins entire or toothed. Cells with elongate, triradiate trigones or uniformly thick-walled, the walls pale brown and usually with a darker brown middle lamellae, cuticle smooth; oil bodies finely granular; ocelli present or absent, when present 1–10 near the base or in the lower half of the leaf, sometimes in a short row. Lobules 1/6–1/3× leaf length, sometimes reduced, inflated, ovate to globose, at the base of branches sometimes much enlarged and forming an "utricle", with one 1-celled tooth. Underleaves usually bifid (rarely undivided), small or large, insertion line straight to arched. Gynoecia on long or short branches, with 1–2 pycnolejeuneoid innovations. Perianths 4-keeled, the keels extended above into narrow, horn-like (rarely bulbous) projections. Sporophyte lejeuneoid. Vegetative reproduction rare, by caducous leaf lobes.

A pantropical genus (ca. 37 spp.); 7 species in Malaysia, on bark, rock and living leaves.

Note: *Ceratolejeunea* is readily recognized by the glossy greenish-brown plants with a 2-cell wide ventral merophyte, bifid underleaves, pale brownish cell walls with a darker colored middle lamella and triradiate trigones, leaf lobes often with ocelli and with entire to toothed margins, frequent presence at the branch bases of “utricles” (= huge, inflated lobule with reduced lobe), and perianth keels extended above into horn-like projections.

Two Malaysian species are very widespread and exibit intercontinental ranges, *C. belangeriana* (Gottsche) Steph. and *C. cornuta* (Lindenb.) Steph. Both are very closely related and Pócs (2011) suggested that they might be conspecific. Nevertheless, the distributions of the two species, in spite of being very large, are quite different. While *C. belangeriana* is widely distributed in the Paleotropics, *C. cornuta* commonly occurs in tropical America and Africa but is extremely rare in Asia where it has been reported once from Malaysia (Inoue 1967a), from the Philippines and from Tahiti, each time under the name *C. tahitensis* Steph. (= *C. cornuta*, fide Pócs & Chantanaorrapint 2015). The very limited and scattered occurrence of *C. cornuta* in Asia and its close similarity to the common *C. belangeriana* casts doubt about the identity of the two species in Asia (and elsewhere). This needs further study.

Literature: Mizutani (1981); Zhu *et al.* (2005); Pócs (2011); Scheben *et al.* (2016); Sarimi *et al.* (2021).

Cheilolejeunea (Spruce) Steph. Figs. 44; 73A, B
(*Leucolejeunea* A.Evans)

Plants small to large, 0.4–2.5 mm wide, usually rather dull pale green to olive-green to brown, sometimes whitish, creeping to ascending, occasionally pendent. Stems with or without hyalodermis; ventral merophyte 2–12 cells wide. Leaf lobes usually wide-spreading, apex rounded to acute, margins entire or crenulate. Cells plane or mammillose,

sometimes with a broad, lenticular papilla, trigones small to large, intermediate thickenings scarce; oil bodies usually large, 1–3(–5) per cell, coarsely granular; ocelli mostly lacking; vitta sometimes present. Lobules 1/6–1/2(–3/4)× leaf length, not reduced, ovate to narrowly rectangular, strongly inflated, usually with one tooth (= the second tooth; the first tooth is reduced) bearing the hyaline papilla on its distal side, sometimes with 2 teeth. Underleaves small or large, bifid or undivided, margins entire, insertion line straight to deeply arched. Gynoecia on long or short shoots, with 1(–2) lejeuneoid or pycnolejeuneoid innovations, ocasionally without innovations. Perianths usually inflated and with 3–5(–10) smooth keels. Sporophyte lejeuneoid. Vegetative reproduction rare, by caducous leaf lobes.

A large pantropical genus of ca. 100 species in at least eight sections; 24 species recorded from Malaysia, mosty epiphytic, also found on rock or living leaves.

Note: *Cheilolejeunea* is mainly recognized by the somewhat dull, pale-colored plants with entire-margined leaves, ventral merophyte 2–4 cells wide, leaf cells with small or large trigones, mostly without intermediate thickenings, 1–3 large and coarsely granular oil bodies per cell, no ocelli (present in *C. falsinervis*), inflated lobules that are not reduced and usually possess one tooth with a distal hyaline papilla (first tooth normally reduced), and underleaves bifid or undivided.

Literature: Mizutani (1967, 1970, 1972); Zhu *et al.* (2002); Ye *et al.* (2015); Pócs *et al.* (2019).

Cololejeunea (Spruce) Steph. Fig. 45

(*Aphanolejeunea* A.Evans, *Cryptolejeunea* Benedix, *Metzgeriopsis* Goebel)

Plants leafy, rarely thalloid (*Cololejeunea metzgeriopsis*), small, 0.25–1.5(–2) mm wide, pale green to brown, creeping, frequently epiphyllous. Stems with a hyalodermis, very thin, of only one row of medullary cells surrounded by 5–6 rows of epidermis cells (rarely more: *C. madothecoides*). Leaf lobes attached to stem by few cells only, wide-spreading, ovate-obovate to narrowly lanceolate, sometimes reduced, leaf surface smooth, papillose or mammillose, leaf apex rounded to acute-acuminate, margins entire to denticulate, sometimes bordered by hyaline cells. Cells thin-walled, with or without small trigones, cuticle smooth or finely papillose; oil bodies granular or smooth; ocelli lacking or present as a 1–2 cells wide vitta. Lobules small or large, attached to the stem by only one cell, inflated, sometimes reduced, with (0–)1–2 teeth. Underleaves absent. Rhizoids in small tufts on the ventral side of the stem, near each leaf base. Gynoecia with 0–2 innovations. Perianths inflated or flattened, 0–5-keeled, perianth surface smooth or papillose. Sporophyte lejeuneoid. Vegetative reproduction by disciform gemmae.

A large pantropical genus with about 300 species in several subgenera and sections; the largest genus of liverworts in Malaysia with about 87 recorded species, mostly epiphyllous but also on bark and rock.

Note: *Cololejeunea* is readily recognized by the tiny plants with very thin stems of only 5–6 rows (rarely more) and the absence of underleaves. Many species grow on living leaves or twigs and are very small and fragile. The genus has been subdivided into several subgenera (see e.g., Pócs & Piippo 2011) but this classification was not supported by DNA sequences (Yu *et al.* 2013). One subgenus, *C.* subg. *Protocolea* R.M.Schust., has been transferred to *Myriocoleopsis* (Yu *et al.* 2014).

Literature: Mizutani (1984, 1986); Pócs & Piippo (2011); Yu *et al.* (2013, 2014); Sarimi *et al.* (2021).

Colura (Dumort.) Dumort. Figs. 46; 73C, D

(*Aphanotropis* Herzog ?; fide R.L.Zhu, pers. com.)

Plants 0.5–2 mm wide, pale green, creeping, rarely growing upright from a prostrate base. Stems with or without hyalodermis, of 7 rows of epidermal cells surrounding 3 inner rows; ventral merophyte 2 cells wide. Leaf lobes attached to the stem by only few cells, usually standing upright, longer than wide, in the upper half usually with a closed sac formed by the lobule, sac occasionally absent, margins entire or toothed. Cells thin-walled, with or without small trigones, cuticle smooth or finely papillose; oil bodies granular or smooth; ocelli lacking. Lobules attached to the stem by only one cell, cylindrical, longer than the leaves (rarely reduced), from a narrow base usually widening above into a sac, the sac rounded, conical or cylindrical, sometimes with a linear beak, the opening of the sac (positioned at the base) with a small valve. Underleaves present near the base of each leaf, distant or overlapping, bifid, lobes often strongly diverging, margins entire, insertion line almost straight. Gynoecia on long or short shoots, with 1–2 innovations. Perianths with 3–5 smooth or horned keels. Sporophyte lejeuneoid. Vegetative reproduction by multicellular, disciform gemmae.

A large pantropical genus of about 70 species in several sections; 28 species recorded from Malaysia, on bark and living leaves.

Note: *Colura* stands out by its upright leaves with an apical sac (formed by the lobule). The sac varies greatly in shape and size, and can be absent (e.g., in *C. corynophora,* in which case one has to be careful not to mistake the species for a *Diplasiolejeunea*. *Colura corynophora*, however, has a very narrow, linear lobule, which is never seen in *Diplasiolejeunea*). The underleaves are deeply bifid, with widely diverging lobes, and are produced one to each leaf like in *Diplasiolejeunea*. The peculiar rheophytic genus *Aphanotropis* Herzog, described from Sarawak, is probably a synonym of *Colura*. A critical assessment of this peculiar plant is currently undertaken in the laboratory of Prof. R.L. Zhu in Shanghai.

Literature: Jovet-Ast (1953); Zhu & So (2001); Sangrattanaprasert *et al.* (2018, 2019); Sarimi *et al.* (2021).

Dactylophorella R.M.Schust. Fig. 41E–G

Plants ca. 1 mm wide, light green to pale brown, creeping. Stems with hyalodermis, of 7 rows of epidermal cells surrounding 5–8 inner rows; ventral merophyte 2 cells wide. Leaf lobes split into two ovate-triangular segments, the segments with densely spinose-crispate margins. Cells (?); ocelli absent. Lobules 1/3× leaf length, inflated, smooth, with one short tooth. Underleaves distant, bifid, lobes erect, margins recurved and strongly spinose-crispate. Dioicous. Gynoecia on short branches, with one lejeuneoid innovation. Perianths inflated, with 5 strongly winged-toothed keels. Sporophyte and vegetative reproduction not observed.

A monotypic Malesian genus, contains *Dactylophorella muricata* (Gottsche) R.M.Schust., recorded from Perak and Sabah, on tree trunks and rotten wood.

Note: *Dactylophorella* is a very peculiar genus, that is recognized by the densely spinose-crispate margins of leaves and underleaves, and the leaf lobes split into two large, ± pinnate segments.

Literature: Herzog (1934); Mizutani (1970); Grolle (1984); Yang & Lin (2013).

Diplasiolejeunea (Spruce) Schiffn. Fig. 47

Plants 0.7–3 mm wide, pale green to pale brown, creeping, often closely appressed to the substrate, frequently epiphyllous. Stems without hyalodermis, of 7 rows of epidermal cells surrounding 3 inner rows; ventral merophyte 2 cells wide. Leaf lobes attached to the stem by only few cells, wide-spreading, apex rounded, margins entire. Cells thin-walled or uniformly thick-walled, occasionally with trigones; oil bodies small, usually coarsely granular; ocelli frequently present scattered in leaf lobes, sometimes lacking. Lobules 1/3–3/4× leaf length, attached to the stem by only one cell, inflated, with two teeth, the second tooth usually smaller than the first one. Underleaves one to each lateral leaf, distant to subimbricate, deeply bifid with diverging lobes and a broad, V-shaped sinus. Gynoecia on long or short shoots, with one pycnolejeuneoid innovation. Perianths usually 4–5-keeled, keels sharp, smooth. Sporophyte lejeuneoid. Vegetative reproduction by disciform gemmae.

A pantropical genus (ca. 50 spp.); 6 species in Malaysia, mostly on living leaves but also on bark.

Note: *Diplasiolejeunea* is recognized by the leaves and lobules with a very short insertion and the presence of one underleaf per leaf (instead of one per leaf pair). The underleaves are deeply bifid and with widely diverging lobes, the stem cells are rather thick-walled (hyalodermis lacking), the hyaline papilla of the lobule is positioned at base of the first tooth on the inner side of the lobule, and ocelli are frequently present scattered in leaf lobes (but absent in underleaves).

Literature: Herzog (1950); Grolle (1966); Schäfer-Verwimp (2006); Dong *et al.* (2012).

Drepanolejeunea (Spruce) Steph. Figs. 48A–H; 74A–D

Plants 0.3–1(–1.5) mm wide, light green to pale brown, creeping, frequently epiphyllous. Stems without hyalodermis, of 7 rows of epidermal cells surrounding 3 inner rows; ventral merophyte 2 cells wide. Leaf lobes suberect to wide-spreading, asymmetrically ovate-triangular to lanceolate, rarely elliptical, often falcate, apex acute-acuminate or rounded, margin entire or toothed. Cells small, midleaf cells 10–25 µm, with trigones, cuticle smooth or coarsely papillose; oil bodies finely granular; ocelli colorless, 1–10 per leaf, scattered or in a short row, sometimes absent, basal ocellus not conspicuously enlarged. Lobules 1/3–3/4× leaf length, occasionally reduced, inflated, with one long, falcate tooth (occasionally short), a "preapical" tooth often present at the junction of lobule and lobe. Underleaves small, distant, bifid with very narrow, diverging lobes, the lobes 1–2 cells wide. Gynoecia on short branches, usually with one pycnolejeuneoid innovation. Perianths inflated, 5-keeled above, the keels extending into toothed, laminate or horn-like projections or auricles. Sporophyte lejeuneoid. Vegetative reproduction by caducous branchlets (= cladia).

A pantropical genus (ca. 60 spp.); 26 species in Malaysia, mostly growing on living

leaves but also found on bark or rock.

Note: *Drepanolejeunea* is readily recognized by the tiny, frequently epiphyllous plants with elongate, asymmetrically leaves with an acute-acuminate or rounded apex, entire or toothed margins and a narrow leaf base. Ocelli are usually present in leaf lobes, the lobules typically have a long-falcate or curved tooth (short-straight tooth in *D. levicornua* and *D. thwaitesiana*), and the underleaves are very small and deeply bifid, with very narrow (linear) diverging lobes without specialized marginal cells.

Literature: Herzog (1930–1939); Mizutani (1990); Zhu & So (2001); Pócs *et al.* (2019); Grolle & Zhu (2000).

Lejeunea Lib. Figs. 49; 75A–D

(*Hygrolejeunea* (Spruce) Schiffn., *Taxilejeunea* (Spruce) Steph.)

Plants small to rather large, 0.4–3 mm wide, pale to bright green or whitish, often glossy, creeping or hanging. Stems usually with a hyalodermis; ventral merophyte usually 2 cells wide. Leaf lobes obliquely to widely spreading, apex rounded to acute-acuminate or apiculate, margins entire or crenulate, occasionally toothed, leaf surface smooth, rarely rough by conically projecting cells. Cells plane, usually thin-walled without or with small trigones, intermediate thickenings present or absent; oil bodies small to large, finely to moderately granular or homogeneous; cuticle smooth or finely papillose, sometimes with wax crystals; ocelli lacking. Lobules often reduced, when well developed to maximally 1/2 × leaf length, oval, with 1(–2) teeth; hyaline papilla proximal. Underleaves usually bifid (undivided in *L. mimula* and *L. exilis*), small to very large. Gynoecia on long or short shoots, with (0–)1–2 lejeuneoid innovations, the innovations sterile or again fertile, bracts without winged. Perianths with 0–5 keels, the keels smooth, crenate, toothed or ornamented with lacinia and/or cilia, apex usually with a beak. Sporophyte lejeuneoid. Vegetative reproduction by caducous leaves, caducous branches or by elongate, ribbon-like gemmae from leaf margins.

A large, pantropical genus (ca. 200 spp.); 38 species in Malaysia, mostly epiphytic on bark, also on living leaves, rotten wood and rock, rarely on soil.

Note: *Lejeunea* is recognized by the usually pale-green, creeping or pendent plants with mostly bifid underleaves with upright lobes. The stems have a hyalodermis and a 2-cell wide ventral merophyte, the lobules are up to 1/2× leaf lobe in length, often less or reduced, with 1(–2) teeth and a proximal hyaline papilla, the leaf cells are thin-walled with small trigones and small to large, granular or homogeneous oil bodies, ocelli are lacking, and the gynoecia have lejeuneoid innovations.

Literature: Lee (2013, 2020); Lee & Gradstein (2013); Heinrichs *et al.* (2013); Lee *et al.* (2016, 2018b, 2020); Sarimi *et al.* (2021).

Lepidolejeunea R.M.Schust. Fig. 48I–P

Plants 1–2 mm wide, yellowish-green to olive green to pale brown, loosely creeping to pendent. Stems with a hyalodermis, of 7 rows of epidermal cells and 6–30 smaller inner rows; ventral merophyte 2 cells wide. Leaf lobes wide-spreading, often falcate, with scattered ocelli, apex rounded to acute-apiculate, margins entire to crenulate. Cells small, ca. 15–25(–30) µm in midleaf, walls thin or uniformly thickened, cuticle smooth or finely

papillose; oil bodies absent in green cells; ocelli numerous, colorless, scattered in leaves, underleaves, bracts, bracteoles and perianths, about as large as the green cells, the basalmost ocellus in the leaf lobe suprabasal, its position not directly adjacent to stem cells. Lobules ca. 1/10–1/3× leaf length, ovate, inflated, often decurved with the apex touching the ventral leaf margin, with one tooth, ocelli usually present. Underleaves bifid or undivided, 2.5–10× stem width, bases usually cordate, insertion line curved, ocelli present. Gynoecia on elongate shoots, with 1–2 pycnolejeuneoid innovations. Perianths inflated, 5-keeled, the keels swollen, smooth. Sporophyte lejeuneoid. Vegetative reproduction absent in Malaysian species.

A pantropical genus (12 spp.); 2 species in Malaysia, the common and widespread *Lepidolejeunea bidentula* (Steph.) R.M.Schust. and *L. integristipula* (J.B.Jack & Steph.) R.M.Schust., recorded from Sabah, on bark of trees and on living leaves. A third species, *L. borneensis* (Steph.) R.M.Schust., was recently moved to the new genus *Mohamedia* on molecular grounds (Zhu *et al.* 2019).

Note: *Lepidolejeunea* is recognized by the numerous scattered ocelli both in leaves and underleaves, and the small, uniformly thickened (or thin-walled) green cells without oil bodies. The stems are rather fragile, with a hyalodermis, the underleaves are bifid or undivided, and the gynoecia have pycnolejeuneoid innovations.

Literature: Piippo (1986); Zhu *et al.* (2019a).

Leptolejeunea (Spruce) Steph. Figs. 50; 76A, B

Plants 0.3–1(–1.5) mm wide, pale green to pale brown, creeping, frequently epiphyllous. Stems with a hyalodermis, of 7 rows of epidermial cells surrounding 3 rows of inner cells; ventral merophyte 2 cells wide. Leaf lobes obliquely spreading, often standing up when dry, obovate to elliptical from a narrow base, with ocelli, apex rounded or acute-apiculate, 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), one very large ocellus present at leaf base (ca. 2.5–4× larger than adjacent cells), smaller additional ocelli usually present, scattered and/or in a broken row in the lamina, becoming progressively smaller to the apex. Lobules 1/3–1/2× leaf length, not reduced, inflated, with one tooth. Underleaves small, remote, usually with a large adhesive rhizoid disc, bifid with very slender, upright or diverging lobes, the lobes 1(–3) cells wide, lamina usually with a border of 6 or more large outer cells surrounding smaller inner cells, insertion line almost straight. Gynoecia on short branches, without innovation. Perianths inflated, 5-keeled above, the keels extending into short, horn-like projections. Sporophyte lejeuneoid. Vegetative reproduction by caducous branchlets.

A pantropical genus (ca. 30 spp.).; about 13 species in Malaysia, mostly on living leaves.

Note: *Leptolejeunea* is recognized by the very small plants with obliquely spreading, obovate to elliptical leaf lobes with ocelli scattered or in a broken row, including a very large basal ocellus (more than 2× larger than adjacent green cells). The underleaves are small and bifid with two subulate, upright or diverging lobes and an undivided lamina bordered by large cells. In the field most species has a special odor from its volatile oil content in the oil bodies. The gynoecia of *Leptolejeunea* do not have innovations.

Literature: Herzog (1942b); Zhu & So (2001); Bechteler *et al.* (2017); Shu *et al.* (2021).

Lopholejeunea (Spruce) Steph. Figs. 51; 72C

Plants 1–2 mm wide, glossy green to black (or brown), usually creeping. Branches mostly *Lejeunea*-type, occasionally *Frullania*-type. Stems with a hyalodermis; ventral merophyte 4 cells wide. Leaf lobes ± wide-spreading both in the dry and the wet state, apex rounded to apiculate, margins entire. Cells (sub)isodiametric, walls often with blackish pigmentation, trigones simple-triangular or radiate; oil bodies homogeneous; ocelli lacking. 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. Male bracts hypostatic, with 2 antheridia. Gynoecia without true, *Radula*-type innovations. Perianths with 4–5 dentate-laciniate keels (rarely entire). Sporophyte ptychanthoid. Vegetative reproduction not observed.

A pantropical genus (ca. 35 spp.); 12 species in Malaysia, on bark, logs and rock, occasionally on living leaves.

Note: The main characters of *Lopholejeunea* are the dark-green to brown to blackish plants with undivided underleaves, 4 cells wide ventral merophytes, leaves spreading when dry (not convolute), isodiametric leaf cells with somewhat darkish colored walls and homogeneous oil bodies, gynoecia without innovations and toothed female bracts and perianths. Although *Radula*-type innovations (originating between inner bract and perianth, without collar at the base) are lacking, "pseudo-innovations" of the *Lejeunea*-type are frequently observed in *Lopholejeunea*. These resemble true innovations but originate below the inner female bract, away from the perianth, and possess a collar at the branch base.

Literature: Zhu & Gradstein (2005).

Metalejeunea Grolle Fig. 52A–F

Plants very small, 0.2–0.4 mm wide, whitish-green to dull yellowish, creeping. Stems without hyalodermis, of 7 rows of epidermal cells and 3 smaller inner rows, all cells thick-walled; ventral merophyte 2 cells wide. Leaf lobes distant, suberect, elongate, apex rounded, margins entire. Cells small, 12–17 µm long in midleaf, trigones usually small; oil bodies unknown; ocelli lacking. Lobules 1/2–2/3× leaf length, occasionally reduced, strongly swollen, with one long tooth, keel crenate. Underleaves bifid, distant, small, 1.5–2.5× stem width. Monoicous. Gynoecia on long or short shoots, with one pycnolejeuneoid innovation, the innovation sterile or with androecia; bracts ± winged. Perianths inflated, with (3–)5 smooth keels. Sporophyte lejeuneoid. Vegetative reproduction not observed.

A small pantropical genus (3 spp.); 1 species in Malaysia, the widespread pantropical *Metalejeunea cucullata* (Reinw. *et al.*) Grolle, on bark, logs and living leaves.

Note: *Metalejeunea* closely resembles *Microlejeunea* but differs in having pycnolejeuneoid innovations and lack of ocelli. Moreover, the plants are always monoicous.

Literature: Miller *et al.* (1963); Gradstein *et al.* (2001); Zhu & So (2001).

Microlejeunea (Spruce) Steph. Fig. 53

Plants minute, 0.2–0.5 mm wide, pale green to pale brown, usually somewhat dull-colored, creeping. Stems straight or zig-zag, with or without hyalodermis, of 7 epidermal rows of cells and 3 smaller inner rows; ventral merophyte 2 cells wide. Leaf lobes usually

distant, suberect and almost parallel to the stem or obliquely spreading, with large lobules (usually more than 1/2× the lobe), apex rounded to acute to finely acuminate (*M. filicuspis*), margins entire or crenulate. Cells small, 15–25 µm in midleaf, thin-walled or thick-walled, with or without trigones, cuticle smooth; oil bodies small, finely granular; ocelli 1–3 at leaf base, single or in a short row. Lobules 0.4–0.8× leaf length, sometimes reduced, swollen, with one tooth, keel smooth or strongly crenate, Underleaves bifid, distant. Dioicous, rarely monoicous. Gynoecia on long or short shoots, with 1–2 lejeuneoid innovations; bracts usually winged. Perianths inflated-pyriform, with 0–5 smooth keels. Sporophyte lejeuneoid. Vegetative reproduction very rare, by caducous branchlets.

A pantropical genus (ca. 25 spp.); 8 species in Malaysia (some of them were previously described in *Harpalejeunea*), mostly on bark and living leaves.

Note: *Microlejeunea* is recognized by the minute, usually dioicous plants with leaf lobes almost parallel to the stem or obliquely spreading and 1–3 ocelli, single or in a short row, large lobules usually more than half the size of the leaf, and distant bifid underleaves. The perianths are 5-keeled, the innovations are lejeuneoid and the bracts are usually winged. *Microlejeunea* is close to *Lejeunea* but differs in its minute size, very large lobules, presence of ocelli and winged female bracts. The genus was recently expanded on molecular grounds and several Malaysian species of *Harpalejeunea* were transferred to *Microlejeunea* (Dong *et al.* 2013).

Literature: Mizutani (1973 as *Harpalejeunea*); Zhu & So (2001); Dong *et al.* (2013).

Mohamedia R.L.Zhu & L.Shu Fig. 54N–P

Plants very small, 0.4–0.8 mm wide, yellow green, creeping. Stems thin, with a hyalodermis, of 7 epidermal rows of cells surrounding 3–4 smaller inner rows; ventral merophyte 2 cells wide. Leaf lobes obliquely to widely spreading, apex rounded to acute to apiculate, margins crenulate to denticulate. Cells small, ca. 15–25 µm in midleaf, thin-walled with or without trigones, cuticle smooth or roughened by wax crystals; oil bodies absent in green cells; ocelli ca. 5–15 per leaf lobe, usually scattered and about as large as non-ocellate cells, the basalmost ocellus adjacent to the stem. Lobules 1/3–1/2× leaf length, sometimes reduced, swollen, with one short or long tooth, with or without ocelli, keel smooth. Underleaves bifid, distant, with ocelli. Monoicous. Gynoecia on long or short shoots, with 1–2 pycnolejeuneoid innovations; bracts not winged. Perianths inflated-pyriform, with 4–5 crenulate to denticulate keels. Sporophyte lejeuneoid. Vegetative reproduction very rare, by caducous branchlets.

A small tropical Asian-Oceanic genus of 2 species, *Mohamedia borneensis* (Steph.) R.L.Zhu & L.Shu and *M. brunnea* (Mizut). R.L.Zhu & L.Shu, both occurring in Malaysia (Pahang, Sarawak, Sabah), on bark and rotten wood, occasionally on living leaves.

Note: *Mohamedia* is similar to *Lepidolejeunea* in the presence of ocelli in leaves and underleaves, absence of oil bodies in green cells, and pycnolejeuneoid innovations, but differs from *Lepidolejeunea* in the thinner stems with 3–4 rows of medullary cells, and the basalmost ocellus in leaf lobes positioned directly adjacent to the stem cells (not adjacent to stem cells in *Lepidolejeunea*). The genus was erected on molecular grounds, to achieve monophyly of *Lepidolejeunea* and *Drepanolejeunea*.

Literature: Zhu *et al.* (2019a); Piippo (1986 as *Lepidolejeunea borneensis*).

Myriocoleopsis Schiffn. Fig. 52G–I

Plants minute, 0.3–0.6 mm wide, yellowish-green, creeping. Stems with a hyalodermis, very thin, of only one row of medullary cells surrounded by 5–6 rows of epidermis cells. Leaf attached to stem by only few cells, leaf insertion very short, transverse. Leaf lobes obliquely spreading, sometimes squarrose, obovate, apex rounded, plane, margins crenulate, without hyaline border and without vitta. Cells thin-walled with small trigones; oil bodies finely granular; ocelli lacking. Lobules large, (1/2–2/3 of lobe length, with 2 teeth, but often reduced to a long, flat fold along the ventral margin of the lobe, sometimes large and inflated, with 2 teeth. Underleaves absent; rhizoids in small tufts from the ventral side of the stem, near the base of each leaf. Monoicous. Gynoecia on elongate branches, with one sterile innovation. Perianths inflated, with five smooth keels, base often stalk-like elongate. Sporophyte lejeuneoid. Vegetative reproduction by multicellular, disciform gemmae from leaf surfaces.

A small pantropical genus (5 spp.); 1 species in Malaysia, *Myriocoleopsis minutissima* (Sm.) R.L.Zhu *et al.*, on bark or epiphyllous in rather dry, open or shaded environments.

Note: *Myriocoleopsis minutissima* is very similar to *Cololejeunea* and was usually considered a species of *Cololejeunea*, but was found nested in *Myriocoleopsis* in molecular analysis. The members of *Myriocoleopsis* are usually rheophilous plants with leaf stems upright from a stoloniform base and rigid stems of thick-walled cells. *Myriocoleopsis minutissima* contains two subspecies in Malaysia, *M. minutissima* subsp. *minutissima* with leaves not squarrose and with well-developed lobules, and *M. minutissima* subsp. *myriocarpa* (Nees & Mont.) R.M.Schust. with squarrose leaves and lobules reduced to a long, flat fold along the ventral leaf margin.

Literature: Schuster (1992a as *Cololejeunea minutissima*); Yu *et al.* (2014); Pócs *et al.* 2014b.

Pictolejeunea Grolle Fig. 54A–M

Plants 0.5–1 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, margins entire or finely denticulate due to papillae. Cells thin-walled, trigones lacking, cuticle with or without large, lens-shaped papilla; oil bodies absent in green cells (Bi *et al.* 2019, Lee pers. obs.); ocelli in dried plants dark reddish to pale brown, in fresh plants at least in part grayish, scattered in leaves and underleaves, bracts and perianths, protruding from the leaf surface. Lobules ca. 1/3× leaf length, ovate-inflated, with one long second tooth, hyaline papilla on the inner side of the first, obselete tooth. Underleaves small, 1–2× stem width, bifid, with ocelli, margins entire, insertion line curved. Monoicous. Gynoecia on short branches, without innovations. Perianths ± flattened, with 2 broad lateral keels expanded above into short auricles. Sporophyte lejeuneoid. Vegetative reproduction by linear gemmae from leaf margins.

A predominantly neotropical genus (6 spp.); 1 species in Malaysia (Sabah), *Pictolejeunea mizutanii* Grolle, found on roots of trees in submontane rainforest at the foot of Mt. Kinabalu.

Note: The main characters of *Pictolejeunea* are the numerous reddish or brown ocelli in leaves and underleaves (grayish in fresh plants), the leaf cells with a large papilla, the

green cells without oil bodies, the gynoecia without innovations, and the 2-keeled perianths with lateral keels expanded above into short auricles.

Literature: Mizutani (1970 as *Cheilolejeunea picta*); Grolle (1977); Bechteler *et al.* (2016b); Bi *et al.* (2019).

Ptychanthus Nees Fig. 54Q, R

Plants 2–4 mm wide, dark green to brown, ascending or pendent, regularly (2-)pinnate. Branches mostly *Frullania*-type. Stems with a thick-walled, brown epidermis and subepidermis (1–2-layered) surrounding a thinner-walled, colorless medulla, epidermis cells not larger than subepidermis cells; ventral merophyte 12–18 cells wide. Leaf lobes wide-spreading, elongate, when dry convolute, apex acute-acuminate, margins entire or toothed. Cells longer than wide, trigones cordate; oil bodies coarsely granular to almost homogeneous; ocelli lacking. Lobules small, sometimes reduced, with 1–2 teeth. Underleaves undivided, apex rounded to emarginate, margins entire or toothed, insertion line ± straight. Male bracts hypostatic, with 2 antheridia. Gynoecia with one repeatedly fertile, lejeuneoid innovatios. Perianths pluriplicate, the keels entire. Sporophyte ptychanthoid. Vegetative reproduction not observed.

A paleotropical genus of 2 species; 1 species in Malaysia, the common *Ptychanthus striatus* (Lehm. & Lindenb.) Nees, on bark of trees and shrubs, also on rock or rotten wood.

Note: *Ptychanthus* is a very distinct genus that is immediately recognized by the robust, pendent, bipinnate plants with *Frullania*-type branches, rigid stems with a brown, thick-walled epidermis and subepidermis (epidermis cells similar to subepidermis cells), a very broad ventral merophyte, elongate-acute leaves with entire or toothed margins, and elongate leaf cells with small cordate trigones and coarsely granular to almost homogeneous oil bodies. The lobules are small, with 0–2 teeth, the underleaves are undivided and toothed, the gynoecia are positioned on elongate branches with one, repeatedly fertile innovation, and the perianth is pluriplicate.

Literature: Gradstein *et al.* (2002); Ahonen *et al.* (2005).

Pycnolejeunea (Spruce) Schiffn. Figs. 55A–H; 76C, D

Plants small to rather robust, 0.6–2.5 mm wide, dull green to brownish, creeping. Stems of thick-walled cells, hyalodermis lacking; ventral merophyte 2–8 cells wide. Leaf lobes wide-spreading, with scattered ocelli, apex rounded to obtuse, entire or crenulate. Cells with small to large trigones, cuticle smooth or papillose; oil bodies large, 1–3 per cell, coarsely granular; ocelli present or absent, when present large, scattered in the leaf lobe or, more often, restricted to the base of the lobe, usually larger than surrounding green cells, lacking in underleaves. Lobules 0.1–0.5× leaf length, with one short tooth, hyaline papilla proximal. Underleaves orbicular to reniform, bifid, imbricate, insertion line arched or almost straight, ocelli absent. Gynoecia on elongate shoots, with 1–2 pycnolejeuneoid innovations. Perianths inflated, with five smooth or crenulate keels. Sporophyte lejeuneoid. Vegetative reproduction by caducous leaf lobes.

A pantropical genus (ca. 17 spp.); 4 species in Malaysia, mostly on bark and frequently growig in the forest canopy and in open, well-illuminated places.

Note: *Pycnolejeunea* is recognized by the dull green to brownish plants with rigid

stems without hyalodermis, the leaf lobes with scattered ocelli, a rounded to obtuse apex and entire to crenulate margins, cells with small or large trigones and large, coarsely granular oil bodies, imbricate or contiguous, bifid underleaves without ocelli, gynoecia with pycnolejeuneoid innovations, and 5-keeled perianths with smooth keels. The genus is close to *Cheilolejeunea* but differs from the latter genus in the proximal hyaline papilla and ocelli in leaf lobes. Many *Pycnolejeunea* species are sun epiphytes and grow in well-illuminated habitats.

Literature: Mizutani (1970); He (1999).

Schiffneriolejeunea Verd. Fig. 55I–P

Plants 1–2 mm wide, green to glossy brown, creeping or ascending. Branches *Lejeunea*-type and *Frullania*-type. Stems with enlarged dorsal epidermis cells (ventral epidermis cells not enlarged), epidermis brown; 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; ocelli lacking. Lobules 1/3–1/2× leaf length, sometimes reduced, with 1–2 teeth. Underleaves undivided, with entire margins and straight or weakly curved insertion line. Male bracts hypostatic, with 2 antheridia. Gynoecia without innovations. Perianths with (0–)4–5 smooth keels, the keels inflated-swollen or sharp. Sporophyte ptychanthoid. Vegetative reproduction by regeneration from leaf cells.

A pantropical genus (14 spp.); 4 species in Malaysia, mostly on bark of trees in rather open, well-illuminated sites, also on rock.

Note: The main features of *Schiffneriolejeunea* are the glossy green to brown plants with rigid stems rigid with an asymmetrical epidermis (dorsal epidermis with enlarged cells), elongate leaf cells with cordate trigones and granular oilbodies, undivided underleaves, and gynoecia without innovations and and (0-)4–5-keeled perianth with smooth keels. The genus may be confused with *Acrolejeunea* and *Thysananthus* (see there).

Literature: Gradstein *et al.* (2002); Gradstein (2015).

Soella R.L.Zhu *et al.*

Plants 0.3–1 mm wide, yellowish green to pale green, creeping. Stems with a hyalodermis, of 7 rows of epidermial cells surrounding 3–10 rows of inner cells; ventral merophyte 2 cells wide. Leaf lobes obliquely spreading, slightly falcate, oblong or asymmetrically ovate to triangular-ovate, with ocelli, apex obtuse to rounded, margins entire. Cells thin-walled, trigones minute, intermediate thickenings absent, cuticle smooth; oil bodies few per cell, granular, usually homogeneous; ocelli colorless (rarely yellowish to reddish), a row of 2–4(–6) large ocelli present at leaf base, smaller additional ocelli present scattered in the lamina. Lobules 1/4–1/2× leaf length, sometimes reduced, inflated, with one unicellular, slightly curved tooth. Underleaves small, remote, usually with a 1–2-celled tooth on the outer margins, bifid with narrowly triangular to lanceolate and erect lobes, the lobes 3–7 cells long, 2–4 cells wide at base, insertion line almost straight. Gynoecia on short or long branches, with one pycnolejeuneoid innovation. Perianths inflated, 5-keeled. Sporophyte lejeuneoid. Vegetative reproduction by means of ribbon-like marginal regenerants.

A small Southeast Asian genus of 2 species; 1 species in Malaysia (Sabah), *Soella spinistipula* (Mizut.) R.L.Zhu & L.Shu, collected on tree tree roots in lowland rainforest.

Note: *Soella spinistipula* was originally described in *Pycnolejeunea* (Mizutani 1970) and moved to *Leptolejeunea* by He (1997). A recent integrative analysis of *Leptolejeunea*, however, showed that the species is sister to *Soella obtusifolia* (T.Yamag.) R.L.Zhu *et al.* from China and Japan, and must be transferred to *Soella* R.L.Zhu *et al.* (Shu *et al.* 2021). The two *Soella* species share a stem with more than 4 medullary cell rows, leaf lobes with 2–4(–6) basal, horizontally arranged ocelli, thin-walled leaf cells without a trace of trigones and intermediate thickenings, oil bodies frequently homogeneous due to disintegration, a unicellular and slighly curved lobule tooth, and gynoecia innovated by a short male spike. The characters of the stem, ocelli and innovation most readily separate *Soella* from *Leptolejeunea*.

Literature: Mizutani (1970 as *Pycnolejeunea spinistipula*); Zhu *et al.* (2019b); Shu *et al.* (2021).

Spruceanthus Verd. Fig. 56A, B

Plants 1–4 mm wide, pale green to brownish to blackish, creeping or ascending or pendent, often forked when fertile. Branches *Lejeunea*-type only; small microphyllous branches at stem bases present or absent. Stems without hyalodermis, in robust species with a thick-walled, brown subepidermis, medulla colorless, thin-walled medulla; ventral merophyte 4–14 cells wide. Leaf lobes wide-spreading, when dry not convolute, apex rounded to acute to apiculate, margins entire or toothed near the apex. Cells 1–2× longer than wide, trigones radiate, intermediate thickenings 0–3 per wall; oil bodies homogeneous. Lobules 1/5–1/2× leaf length, sometimes reduced, with 1–3 teeth. Underleaves undivided, distant to imbricate, small or very large, margins entire or toothed, insertion line straight or deeply arched. Male bracts hypostatic, with 2 antheridia. Gynoecia with 1–2 lejeuneoid innovations; female bract apices acute. Perianths with 4–8 keels, the keels smooth or slightly toothed. Sporophyte ptychanthoid. Vegetative reproduction not observed.

A pantropical genus (ca. 16 spp.); 4 species in Malaysia, on bark, rock and rotten wood.

Note: Characteristics of *Spruceanthus* are the small to robust plants stems with rigid stems without a hyalodermis, microphyllous branches often present at stem bases, isodiametric or elongate leaf cells with simple-triangular to triradiate trigones (not cordate) and small homogenous oil bodies, and lejeuneoid innovations.

Literature: Gradstein *et al.* (2002); Shi *et al.* (2015); Wang *et al.* (2016).

Stictolejeunea (Spruce) Schiffn. Fig. 56C–I

Plants ca. 1 mm wide, dark green or brown, creeping. Branches *Lejeunea*-type, occasionally *Frullania*-type. Stems rigid, without hyalodermis; ventral merophyte 4 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, with one tooth. Underleaves undivided, distant, insertion line straight, ocelli present. Gametoecia on

very short branches. Monoicous. Gynoecia without innovations or with one short, pycnolejeuneoid innovation. Perianths flattened, 2-keeled, the keels expanded above into a large auricle. Sporophyte lejeuneoid. Vegetative reproduction not observed.

A small pantropical genus (3 spp.); 1 species in Malaysia (Sarawak, Sabah), *Stictolejeunea balfourii* (Mitt.) E.W.Jones, on tree bases and rock along creeks in lowland rainforest, in sheltered places.

Note: The main characters of *Stictolejeunea* are stems with the leaves and underleaves with numerous scattered ocelli and frequently with a whitish border, underleaves undivided, isodiametric small leaf cells with uniformly thickened walls and no oil bodies and 2-keeled perianths with 2 large auricles. The genus shares many character with *Lepidolejeunea* (scattered ocelli in leaves and underleaves, absence of oil bodies in green leaf cells) but differs from *Lepidolejeunea* in the dark green color, rigid stems without hyalodermis, presence of *Frullania*-type branching, gametoecia on very short branches, auriculate perianth, and seta with 16 outer rows of cells (12 in *Lepidolejeunea*).

Literature: Gradstein (1985); Haerida & Gradstein (2010).

Thiersianthus R.L.Zhu & L.Shu Fig. 57A

Plants 0.5–0.8 mm wide, yellowish-green, creeping. Stems with a hyalodermis, of 7 rows of epidermal cells and 6–8 smaller inner rows; ventral merophyte 2 cells wide. Leaf lobes imbricate, rather widely spreading, ovate-falcate, apex rounded, margins entire. Cells ca. 15–25 µm in midleaf, very thin-walled with minute trigones and without intermediate thickenings, cuticle smooth; oil bodies absent in green cells; ocelli present, up to 15 per leaf lobe, scattered, the basal ocelli slightly larger, basalmost ocellus suprabasal (not directly adjacent to stem cells). Lobules 1/2–2/3× leaf length, occasionally reduced, inflated, somewhat deflexed with the apex touching the ventral leaf margin, tooth short, ocelli absent. Underleaves bifid, distant, small, 1.5–2× stem width, outer margins frequently with a tooth, ocelli absent. Monoicous. Gynoecia on long or short shoots, with one pycnolejeuneoid innovation. Perianths inflated, with (3–)5 smooth keels. Sporophyte lejeuneoid. Vegetative reproduction not observed.

A monotypic genus endemic to Malaysia, contains *Thiersianthus silamensis* R.L.Zhu & L.Shu, known from a few collections of Mt. Silam, Sabah, on tree tree roots in lowland rainforest.

Note: *Thiersianthus silamensis* is very similar to *Lepidolejeunea bidentula* (Steph.) R.M.Schust., a species common in the type locality of *Thiersianthus* (see Piippo 1986). The latter genus differs from *L. bidentula* in smaller plant size, smaller underleaves without cordate base, and absence of ocelli in underleaves and leaf lobules. In a morphological analysis (Zhu *et al.* 2017) the two taxa were not closely related; apparently, their similarity is due to homoplasic evolution.

Literature: Piippo (1986); Zhu *et al.* (2017).

Thysananthus Lindenb. Figs. 57B–E; 72D

(*Mastigolejeunea* (Spruce) Steph.)

Plants 2–4 mm wide, glossy dark green to brown, creeping, ascending or pendent; stem bases frequently with small microphyllous branches. Branches *Lejeunea*-type. Stems

without enlarged epidermis or with enlarged dorsal epidermis cells (ventral epidermis cells not enlarged), the epidermis strongly thick-walled and brown; ventral merophyte 4–10 cells wide. Leaf lobes wide-spreading, when dry convolute, flatly appressed to the stem or spreading, apex rounded or acute, margins entire or toothed. Cells longer than wide or isodiametric, trigones cordate or not cordate; oil bodies coarsely granular; ocelli lacking; vitta of large elongate cells present or absent. Lobules 1/5–1/2× leaf length, not reduced, with 1–3 teeth. Underleaves undivided, apex rounded to emarginate, margins entire or toothed, insertion line ± straight, bases free or adnate to leaf bases on one side. Male bracts hypostatic, with 2 antheridia. Gynoecia with 1–2 lejeuneoid innovations. Perianths with 3–10 keels, the keels entire or toothed. Sporophyte ptychanthoid. Vegetative reproduction frequently by regeneration from leaf cells.

A pantropical genus of 30 species, in 2 subgenera, subg. *Mastigolejeunea* (Spruce) Sukkharak & Gradst. and subg. *Thysananthus* (Sukkharak & Gradstein 2017); 15 species in Malaysia, on bark, rotten wood and rock.

Note: *Thysananthus* is characterized by the rather robust, dark green plants with rigid stems, frequent presence of microphyllous branches at stem bases, leaves when dry suberect and appressed to the stem or convolute, leaf cells elongate with cordate trigones, and gynoecia with 1–2 lejeuneoid innovations and a 3–10-keeled perianth. Sterile plants can be confused with *Schiffneriolejeunea* but the latter plants are typically glossy brown in color, julaceous when dry, and frequently produce *Frullania*-type branches. Female plants of *Schiffneriolejeunea* are immediately recognized by the absence of innovations.

Literature: Sukkharak (2015); Sukkharak & Gradstein (2015, 2017).

Tuyamaella S.Hatt. Fig. 58

Plants ca. 1–2 mm wide, yellowish-green to pale brown, creeping, frequently epiphyllous. Stems fragile, thin-walled, with a hyalodermis, of 7 rows of epidermal cells surrounding 3 inner rows; ventral merophyte 2 cells wide. Leaf lobes attached to the stem by only few cells, wide-spreading, apex rounded, margins entire or slightly toothed, sometimes with a hyaline border. Cells thin-walled, trigones small, cuticle smooth; oil bodies rather small, 2–6 per cell, finely granular; ocelli absent. Lobules large, 1/2–3/4× leaf length, attached to the stem by only one cell, inflated, with two teeth, the second tooth usually smaller than the first one, hyaline papilla large, on the inner base of the first tooth (ental). Underleaves one per leaf pair, distant to imbricate, bifid (but sometimes only retuse), lobes upright, with a rounded apex. Monoicous. Gynoecia on long or short shoots, with one pycnolejeuneoid innovation. Perianths 4–5-keeled, keels rounded, smooth. Sporophyte lejeuneoid. Vegetative reproduction by disciform gemmae.

A small Asiatic genus (6 spp.); 4 species in Malaysia, usually epiphyllous.

Note: The main features of *Tuyamaella* are the medium-sized, frequently epiphyllous plants with fragile stems of thin-walled cells, leaves and lobules with a very short insertion, presence of one underleaf per leaf pair, underleaves bifid and with upright lobes, absence of ocelli, ental hyaline papilla, and pycnolejeuneoid innovations. The genus is morphologically close to some species of *Diplasiolejeunea* due to the hyaline margin of lobe, but the latter genus has one underleaf to each leaf, underleaf lobes usually diverging, a thick-walled stem epidermis (hyalodermis absent) and a perianth with 5 sharp keels.

Literature: Tixier (1973); Zhu & So (2001).

PORELLACEAE

A family of 2 genera; 1 genus in Malaysia.

Porella L. Fig. 57F–M

Plants robust, 5–20 cm long and 3–7 mm wide, green to brown, not reddish, creeping or pendent, (bi)pinnate. Branches *Frullania*-type. Stems brown, rigid, with a thick-walled cortex; paraphyllia sometimes present. Leaves incubous, with a short insertion; lobe apex rounded or mucronate, margins entire or toothed, bases sometimes ciliate-laciniate; lobule flat and usually distinctly elongate parallel to the stem (or slightly spreading) and almost free from the dorsal lobe, margins entire to dentate-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, apex broadly rounded, undivided, margins entire or dentate-ciliate. Rhizoids in tufts from underleaf bases. Dioicous. Gametoecia on short branches. Gynoecium with numerous archegonia (to 30). Perianth bluntly 3-keeled, without beak. Sporophyte foot not penetrating into the stem. Seta thick. Capsule globose, wall 3–6-layered. Elaters free, not attached to capsule valves. Spores large, multicellular, germination endosporous, spore surface without rosettes. Vegetative reproduction unknown.

About 50 species worldwide; 2 species in Malaysia, *Porella javanica* (Gottsche) Inoue and *P. caespitans* subsp. *latior* (S.Hatt.) S.Hatt., on bark or rock.

Note: *Porella* is recognized by: 1) plants robust, pinnate, dark green to brown; 2) lobule almost free from the lobe, elongate and ± parallel to the stem, flat; 3) gynoecium with numerous archegonia; 4) perianth without beak; 5) sporophyte foot not penetrating into the stem; 6) capsule globose, wall 3–6-layered; 7) elaters free, not attached to the capsule wall.

Literature: Hattori (1978); Hentschel *et al.* (2007); Sukkharak & Chantanaorrapint (2018).

RADULACEAE

A monotypic family.

Radula Dumort. Figs. 59; 71C, D

Plants small to medium-sized, 1–10 cm long, ca. 1–3 mm wide, dull pale green to bright green to brown, not reddish, creeping, sometimes pendent, (bi)pinnate or dichotomously branched. Branches *Radula*-type. Stems rigid, without hyalodermis. Leaves incubous, with a long insertion; lobe apex rounded, occasionally acute, margins usually entire; lobule 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, rarely verruculose; oil bodies large, brown, 1–2 per cell, rarely more. Underleaves lacking.

Rhizoids in tufts from the lobules. Dioicous, rarely monoicous. Gynoecium with 2–4 archegonia. Perianth narrowly elongate, flattened, 2-keeled, mouth broad, without beak, base thin or fleshy (when fleshy = perigynium). Sporophyte as in Porellaceae but foot penetrating into the stem and capsule cylindric. Spores unicellular or multicellular, germination exosporous or endosporous, spore surface without rosettes. Vegetative reproduction by multicellular gemmae or caducous leaf lobes.

About 200 species worldwide, in several subgenera (Devos *et al.* 2011); about 33 species in Malaysia, mostly on bark but also on rock or living leaves.

Note: The main characters of *Radula* are: 1) branches *Radula*-type; 2) lobule attached to leaf lobe and stem along a long keel; 3) oil bodies very large, brown, in most cases only 1–2 per cell, filling the cell-lumen; 4) underleaves absent; 5) rhizoids in tufts from the lobules; 6) perianth narrowly elongate, flattened above, with a broad, entire mouth; 7) sporophyte as in Porellaceae but foot penetrating into the stem and capsule cylindric or funnel-shaped, truncate.

Literature: Yamada (1979); Devos *et al.* (2011); Sarimi *et al.* (2021).

Anthocerotophyta (hornworts)

Plants thalloid, growing by a wedge-shaped, 4-sided apical cell, sporophyte growing by a basal meristem. Thallus several cells thick at least in the middle, with or without midrib, inner tissue ± undifferentiated, sometimes with large cavities. *Nostoc* colonies usually present inside the thallus, visible as darkish dots or blue lines. Epidermis cells with or without perforations, with 1(–4) large, plate-like chloroplasts, each sometimes containing a pyrenoid; oil bodies absent. Rhizoids unicellular, smooth. Gametangia immersed in the thallus, originating from an inner thallus cell; antheridia 1–several in cavities, ± spherical, stalked; archegonia borne single, flask-shaped. Sporophyte 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 (or up to the apex, in *Notothylas*) by a tubular involucre, capsule epidermis with or without stomata, spores unicellular or multicellular, with or without trilete mark, elaters ("pseudo-elaters") usually present, 1–4-celled, with or without spiral band, columella usually present (± absent in *Notothylas*); capsule dehiscence gradual, from apex downwards, by means of two valves, rarely by up to four valves, with an operculum or rupturing irregularly; spore maturation asynchronous; peristome absent. Protonema very small, thalloid, normally giving rise to only one gametophyte.

Contains about 220 species worldwide, in 5 families and 12 genera (Villarreal & Cargill 2016). Five species in 5 genera have been recorded from Malaysia, in the following three families:

Anthocerotaceae (*Anthoceros, Folioceros*). Sporophyte usually erect. Capsule with columella and stomata. Elaters without spiral band. On soil in open environments, not inside forests.

Dendrocerotaceae (*Dendroceros, Megaceros*). Sporophyte erect. Capsule with

columella, stomata usually absent. Elaters 1-celled, with spiral band. In montane forests, usually on bark, rotten wood, rock or living leaves.

Notothyladaceae (*Phaeoceros*). Sporophyte erect or subhorizontal and lying on the thallus. Capsule without or with a short columella, stomata lacking. Elaters without spiral band. On soil in open environments, not inside forests.

Key to genera of hornworts of Malaysia

1. Thallus cells frequently with 2 chloroplasts. Thallus dark green to blackish-green. Spores green. On moist rock, rotten wood or bark in montane forest ····· *Megaceros*
1. Thallus cells with only 1 chloroplast. Thallus more pale green. Spores yellow to brown or black ····· 2
2. Epiphyte. Thallus differentiated into a thick midrib and thin wings, the wings strongly crisped or almost flat. Spores large, multicellular ····· *Dendroceros*
2. On soil. Thallus not differentiated into a thick midrib and thin wings. Spores small, unicellular ····· 3
3. Sporophytes lying nearly horizontally on the thallus, ovoid-cylindrical, usally less than 2 mm long, wholly enclosed by involucres. Plants mainly in lowlands; not yet recorded from Malaysia but to be expected (see Hasegawa 1979; Piippo *et al.* 2002; *Notothylas javanica* (Sande Lac.) Gottsche occurs in Singapore) ····· *Notothylas*
3. Sporophytes erect, more than 5 mm long (mostly more than 1 cm long). Plants in lowland and montane ····· 4
4. Thallus with cavities (cross section), and with colonies of blue-green algae inside the thallus, visible as black dots. Spores brown or black. Elater thick-walled (cell-lumen hardly visible). ····· *Anthoceros* or *Folioceros* (see descriptions)
4. Cavities and algal colonies lacking. Spores yellow. Elater thin-walled ····· *Phaeoceros*

Anthoceros L. Figs. 60A; 77A

Thallus usually forming rosettes to 1.5 cm in diameter, light green, thin, rapidly decaying and becoming blackish in the herbarium, with scattered, globose *Nostoc* colonies (visible as black dots), without a midrib, margins irregularly dissected into small, often somewhat crispate segments, dorsal surface usually with a reticulate pattern, smooth or covered with crisped or toothed lamellae, cells with 1(–2) chloroplasts with or without pyrenoids; thallus with large internal cavities (cross section). Antheridial chambers with more than 4 antheridia, antheridial jacket of 4 tiers of cells. Sporophytess when mature erect, 1–5 cm long, linear, with stomata and a well developed columella. Spores brown to dark brown, rounded-tetrahedral, unicellular, outer surface with blunt papillae or sharp spines, inner surface with trilete mark. Elaters (= pseudo-elaters) (1–)2–4-celled, pale blackish-brown, flaccid, walls thin and with irregular bands of thickenings, without spiral band.

A subcosmopolitan genus of about 40 species; 1 species recorded from Malaysia, *Anthoceros angustus* Steph. (= *A. formosae* Steph.; see Peng & Zhu 2013), on soil in open, usually disturbed sites, along roads etc.

Note: The principal characters of *Anthoceros* are: 1) thallus light green, with internal

cavities, margins dissected, dorsal surface usually reticulate, smooth or with lamellae; 2) spores dark brown; 3) elaters (1–)2–4-celled, without spiral band.

Literature: Hasegawa (1984); Peng & Zhu (2013).

Dendroceros Nees Fig. 60E

Thallus 2–5 mm wide, yellowish- or bluish-green, with scattered, globose *Nostoc* colonies (visible as black dots), ± pinnately branched or forked, with a midrib and unistratose wings, the wings conspicuously undulate-crispate in neotropical plants and sometimes with large holes (perforations), cells with 1(–2) chloroplasts, epidermis cells with trigones; thallus solid or with cavities in the midrib (subg. *Apoceros*). Antheridial chambers with 1(–4) antheridia. Sporophyte when mature erect, 1–5 cm long, linear, without stomata, columella present. Spores green, large, ca. 40–80 µm long, rounded, multicellular, outer surface papillose. Elaters long and narrow (to ca. 300 µm long), with spiral band.

A pantropical genus of about 30 species; 1 species recorded from Malaysia (Sabah), *Dendroceros cavernosus* J.Haseg., on bark (twigs, branches) in montane forest.

Note: *Dendroceros* is recognized by: 1) thallus differentiated into midrib and unicellular wings, the wings strongly undulate-crispate or almost flat, midrib solid or with cavities; 2) capsule wall without stomata; 3) spores green, multicellular; 4) elaters long and narrow, with a spiral band. Contrary to most other hornwort taxa, the species of *Dendroceros* are typically epiphytic (or epiphyllous), not terrestrial.

Literature: Hasegawa (1980).

Folioceros Bharadwaj Fig. 60D

(*Anthoceros* subg. *Folioceros* (Bharadwaj) R.M.Schust.)

Similar to *Anthoceros* but differing in: 1) elaters strongly thick-walled, with a very narrow lumen visible as a narrow line within the elater; 2) spore surface with indistinct or poorly developed triradiate mark.

A genus of about 18 species, mostly in tropical Asia; 1 species recorded from Malaysia, *Folioceros glandulosus* (Lehm. & Lindenb.) D.C.Bharadwaj (= *Anthoceros glandulosus* Lehm. & Lindenb.), on moist sand or clay.

Note: *Folioceros glandulosus* is habitually recognized by the strap-shaped, dark-colored (often almost blackish) thalli with deeply lobed margins and with large, spongy gemmae on the surface and margins (Piippo *et al.* 2002).

Literature: Piippo (1993); Piippo *et al.* (2002).

Megaceros Campb. Figs. 60C; 77B

Thallus often large, 0.5–1.2 cm wide, dark green, usually with scattered, globose *Nostoc* colonies (visible as black dots), forked, pinnate or irregularly branched, usually without a midrib, margins crispate-undulate or finely ruffled and ± colorless, sometimes ± entire, cells with 1–2(–3) chloroplasts, pyrenoid present or lacking; thallus solid (cross section), without cavities. Antheridial chambers with 1(–2) antheridia. Sporophyte when mature erect, often very long (over 5 cm), linear, without stomata, columella present. Spores green to yellowish-brown, usually unicellular (multicellular in *Nothoceros renzagliensis*),

rounded to ovoid, outer surface papillose-tuberculate. Elaters long and narrow (to 450 µm long), with spiral band.

A paleotropical genus of about 8 species; 1 species in Malesia, the common and widespread *Megaceros flagellaris* (Mitt.) Steph., on wet rock, rotten wood and trunk bases in montane forests.

Note: Characteristics of *Megaceros* are the frequent presence of more than one chloroplast in the thallus cells, relatively long sporophytes without stomata, and long and narrow elaters with a spiral band. Also characteristic is its occurrence inside forests, as different from *Anthoceros, Folioceros* and *Phaeoceros*.

Literature: Hasegawa (1983); Villarreal *et al.* (2010).

Phaeoceros Prosk. Fig. 60B, F

Thallus usually forming rosettes to 2–3 cm in diameter, deep green, rather fleshy, with scattered, globose *Nostoc* colonies (visible as black dots), without a midrib, margins entire or crenate, flat or somewhat crispate, dorsal surface smooth, not reticulate, cells with 1(–2) chloroplasts and usually with pyrenoids inside the chloroplasts; thallus solid (cross section), without cavities. Antheridial chambers with 2–4 antheridia, antheridial jacket of irregularly arranged cells. Sporophyte when mature erect, 1–4(–9) cm long, linear, with epidermal stomata and a well developed columella. Spores yellow, rounded-tetrahedral, unicellular, outer surface variously ornamented by spines or papillae, inner surface with trilete mark. Elaters (1–)2–4-celled, pale brown, walls thin and with irregular thickenings, without spiral band.

A subcosmopolitan genus of about 30 species; 1 species in Malaysia, the widespread *Phaeoceros carolinianus* (Michx.) Prosk., on soil.

Note: The principal characters of *Phaeoceros* are: 1) thallus deep green, rather fleshy, solid, margins entire or somewhat dissected, dorsal surface smooth, not reticulate; 2) spores yellow; 3) elaters (1–)2–4-celled, without spiral band. *Phaeoceros carolinianus* is recognmized by the monoicous thallus and the presence of small papillae on the inner (proximal) surface of the spores (Hasegawa 1993).

Literature: Hasegawa (1984, 1993).

Glossary[4]

abaxial. The side of a leaf or branch away from the stem (opposed to **adaxial**).
acrogynous. Archegonia at the apex of a stem or branch (opposed to **anacrogynous**).
acuminate. From a broad apex gradually tapered toward a sharp point (Fig. 11S).
acute. Sharply pointed (Fig. 12N).
adaxial. The side of a leaf or branch toward the stem (opposed to **abaxial**).
air chamber. A cavity in the thallus of complex thalloid liverworts (Marchantiopsida) (Fig. 4K).
alpine. Upper vegetation belt on high mountains, above the upper forest line. Usually without trees.
amphigastria (sing. **amphigastrium**). Underleaves in leafy liverworts (Figs. 20H, I; 21F, G, H, I; 47F, G).
ampliate. In *Plagiochila*, ventral leaf base expanded, covering the stem.
amphitropical. Distributed in the Mediterranean and subtropical regions of the Northern and Southern Hemisphere; absent or very rare in the tropics.
anacrogynous. Archegonia in a lateral position on stem, branch or thallus, not at the apex (opposed to **acrogynous**).
androecium (plur. **androecia**). Antheridia and surrounding bracts; the male gametoecium (Figs. 42B; 51H; 52A).
angular. Shape or outline with angles, not rounded.
annular thickenings. Ring-like thickenings extending over both tangential and radial cell walls in liverwort capsules.
antheridiophore (= **male gametangiophore**). Stalked, antheridia-bearing receptacle on the thallus of the Marchantiaceae (Fig. 3B, D, F).
antheridium (plur. **antheridia**). Male sex organ or gametangium, producing antherozoids (= spermatozoids).
antherozoid (= **spermatozoid**). Male gamete.
antical. The leaf margin oriented toward the shoot apex (opposite of **postical**). Also used for the dorsal surface of a stem.
apical. At the tip.
apical cell. An embryonic cell at the growing tip that divides repeatedly to form new cells.
apiculate. Abruptly ending in a short point (**mucronate**, Fig. 30M, is shorter pointed; **cuspidate**, Fig. 30K, is longer and more stoutly pointed).
appendiculate. With short lacinia or auricles at leaf or underleaf bases.
appressed. Lying closely together; leaves lying close or flat against the stem or against each other; plants lying close to the substrate (Figs. 63C; 73A, B).
aquatic. Of plants, growing permanently submerged or floating, completing the life cycle in water (opposed to **rheophytic** or **terrestrial**).
archegoniophore (= **female gametangiophore**). Stalked, archegonia-bearing receptacle on the thallus of many Marchantiales (Figs. 2A, G, J, K; 3A, C, E; 61B).
archegonium (plur. **archegonia**). Female sex organ or gametangium, containing an egg.

[4] Based on Magill (1990) and Gradstein *et al.* (2001) with additions and modifications.

areolate (= reticulate). Surface with a network formed by areoles, e.g., of spores or thallus.
areole. Small angular surface area, the basic unit of a network formed by areoles.
ascending. Pointing or arising obliquely upward, away from the substrate.
athecal. Without a sheath of tissue at the base; said of collarless branches.
attenuate. Slenderly tapering.
auricle. A small, ear-like lobe, often present at leaf base.
auriculate. With **auricles**.
autoicous (= **autoecious**). With archegonia and antheridia on separate branches of the same plant (Figs. 16J; 29E; 52A).
axil. Angle between stem and leaf.
axillary. In the leaf axils.
axis. The main stem.

***Bazzania*-type branch.** Ventral-intercalary branch (with collar at the base), originating from the axil of underleaves.
beak (= **rostrum**). Elongate apex of a lobule, perianth or operculum (see also **lobule beak**) (Fig. 49R, S, T).
bifid. Divided into two segments or lobes.
bilobed. Bifid.
bipolar. Distributed in the temperate regions of the Northern and Southern Hemisphere; absent or very rare in the tropics.
biseriate. In two rows, of cells.
bipinnate. Twice pinnately branched.
bisbifid. Twice bifid with the subsequent parts more shallowly bifid.
blunt. Obtuse.
bordered. Having margins differentiated from the rest of the structure (leaf, underleaf, perianth, etc.) in cell shape, size, color or thickness (Fig. 58F, J).
bracteole. A modified underleaf associated with a gametangium (Figs. 20U; 53G; 54H).
bracts. Specialized leaves surrounding reproductive organs (Figs. 33J; 41P; 54G, I).

caducous (= **deciduous**). Detaching, falling off.
calyptra. A membrane covering the developing sporophyte, derived largely from the archegonial venter.
campanulate. Bell-shaped.
canaliculate. Channeled (lengthwise).
capsule (= **theca**). The sporangium or spore-bearing portion of the sporophyte (Fig. 67A).
caulocalyx. Protective structure surrounding the sporophyte in *Fossombronia*, resembling a perianth.
central strand. A small bundle of narrowly elongate cells forming a central axis in stems, thalli or midrib.
chlorophyllose. Containing chlorophyll (= green pigment), generally green unless masked by some other pigments.
cilia (sing. **cilium**). Hair-like or thread-like structures, mostly one cell wide and unbranched (Figs. 24I, 32C, D).

ciliate. With hair-like appendages.
circinate. Curved in a circle.
cladia (sing. **cladium**). Modified, small caducous branches for vegetative reproduction.
clasping. Closely surrounding or enveloping a structure.
cleistocarpous. Indehiscent; capsule without a regular mechanism for opening.
coalesced. Two or more structures becoming united and loosing their identity; e.g., of trigones (compare **confluent**).
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* and *Leiomitra* (Fig. 37A).
collar. Sheath of tissue around the base of branches in leafy liverworts.
collenchymatous. With cell walls more heavily thickened at the angles (**trigone**) (Fig. 9F).
columella. The central, sterile column of tissue in the capsule of mosses and hornworts.
complanate. Flattened or compressed; e.g., leaves flattened into one plane.
complicate. Folded together.
complicate-bilobed. Having 2 leaf lobes folded against one another (Figs. 31B; 40E–K).
concave. Hollow (opposed of **convex**).
conduplicate. Folded longitudinally along the middle.
confluent. Two structures becoming united without loosing their identity; e.g., of trigones or margins (compare **coalesced**).
conical. Cone-shaped
connate. Fused, e.g., the bases of opposite leaves, or underleaves with leaves (Fig. 26E, F).
connivent. Directed or pointing together; e.g., tips of leaf segments converging toward one another (Fig. 34D).
constricted. Abruptly narrowed.
contiguous. Adjacent.
contorted (= tortuose). Irregularly curved or twisted.
convex. Bulging outwards (opposed to **concave**).
convolute. Rolled together.
cordate. Heart-shaped. Of leaves with two large auricles at base, or of trigones with 2 convex sides and one concave side (Fig. 42I, M).
cortex. The differentiated outer cell layer(s) of the stem (Fig. 49P, Q).
cortical. Referring to the outer part of a stem, or cortex.
corticolous. Growing on bark of trees and shrubs (Figs. 67C; 68C).
cosmopolitan. Occurring in all major floristic zones of the world.
coprophilous. Growing on animal dung.
costa (= **midrib, nerve**). Mid-vein of a leaf or thallus, always more than one cell thick (Fig. 5A–C, E, H).
costate. With a costa.
crenate. With rounded teeth.
crenulate. With minute, rounded teeth (smaller than **crenate**).
crisped (= **crispate**). Strongly wavy; variously curled, twisted and contorted.
cristate. Crested; bearing a crest-like ridge.

cucullate. Hooded or hood-shaped; used to describe strongly concave leaves that are inflexed at the tips.
cuneate (= **cuneiform**). Wedge-shaped, narrowed to the base along straight, oblique lines (Fig. 58D).
cushion. Growth form with stems erect, tightly clustered and somewhat radiating at edges.
cuspidate. Ending abruptly in a stout, rigid point (more longly and stoutly pointed than **apiculate** or **mucronate**).
cuticle. A cutin layer combined with wax on the outside surface of the epidermis. In bryophytes it is usually very thin.
cylindrical. Narrowly elongate, circular in transverse section.

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. 9E).
decussate. Cross-shaped; of tetrads, spores arranged pair-wise, at a right angle to each other; characteristic of Lejeuneoideae.
dehiscent. Having a distinct opening mechanism.
dendroid. Tree-like; with erect stems that are branched in the upper part.
dentate. With sharp, coarse teeth (Figs. 21K; 46I).
denticulate. Finely toothed (Figs. 8E; 45G).
depauperate. Poorly developed.
diaspore. An agent of dispersal; any structure that becomes detached from the parent plant and gives rise to a new individual (spore, gemma, cladium, leaf, etc.)
dimorphic. Occurring in two forms; e.g., with two types of leaves.
dioicous (= dioecious). With archegonia and antheridia on separate plants.
diploid. Having a double set of chromosomes (2n).
disciform. Flat and circular.
discoid. Flat and rounded, shaped like a disc.
disc cell. Large margin cell of the lobule, distal to the apex of the lobule of some species of *Lejeunea*.
disjunct. Distribution discontinuous, with major gaps.
distal. Away from the base or point of attachment; toward the apex of a leaf or stem; the outer, convex face of a spore (opposed to **proximal**).
distal hyaline papilla. See: **hyaline papilla**.
distant. Well-spaced; e.g., leaves positioned with a space between adjacent leaves (Figs. 8A; 13A; 34A).
distichous. Leaves in two rows.
divergent. Turned in opposite directions.
dorsal. The upper surface, away from the substrate (opposed to **ventral**).
dorsal leaf-free strip. Portion of the dorsal stem surface that is not occupied by the leaf insertion. A leaf-free strip is present when the leaf insertion line does not extend to the dorsal stem-midline, as for example seen in several members of Cephaloziaceae and

Zoopsidella. The width of the leaf-free strip is measured as the approximate number of longitudinal stem cell rows between opposite leaf bases.

dorsiventral. Flattened, with distinct upper and lower surfaces.

edentate. Without teeth.

egg. The female gamete, produced in an archegonium.

elater. Long and narrow, diploid, hygroscopic cell with spiral thickenings, derived by mitotic division.

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*).

elliptical. Oblong with convex sides.

elobulate. Without lobule.

emarginate. Having a broad and shallow notch at the apex (opposed to **retuse**).

embryo. Young sporophyte, developing from a zygote.

emergent. Partially exposed, referring to capsules or perianths only partly projecting beyond the tips of the bracts (Figs. 40D; 56A).

endemic. Geographic distribution restricted; limited to a single country or floristic area.

endogenous. Originating from internal rather than superficial cells or tissues.

endosporic (= **endosporous**). Inside the spore; protonema germinating inside the spore wall, hence spores multicellular (opposed to **exosporic**).

entally. Toward the inner side, referring to the position of the hyaline papilla of the lobule in Lejeuneaceae (Figs. 52H, 55P, 58K, L).

entire. Without teeth (Fig. 51K).

epidermis. The outer cell layer of a stem, thallus, capsule or other structure.

epilithic (= **saxicolous**). Growing on rock (Fig. 77B).

epiphyllous (= **foliicolous**). Growing on living leaves of other plants (Figs. 74C, D; 76A, B).

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 (opposed to **hypostatic**).

eplicate. Without keels, referring to the perianth: see also **terete** (Fig. 19H).

erect. Upright; leaves directed toward stem apex (Fig. 15I).

erose. Irregularly notched or ragged.

exosporic (= **exosporous**). Outside the spore wall.

explanate (= **laminate**). In *Frullania*, lobule that is not rolled inwards forming a sac (opposed to **saccate**).

exserted. Protruding and largely exposed (opposed to **immersed**; compare also **emergent**) (Fig. 67A).

exsiccatae (sing. **exsiccata**). Dried plants; referring to widely distributed sets of herbarium specimens with printed labels, that are used as standards for comparison.

falcate. Curved like the blade of a sickle (Figs. 18C, D; 22M).

falcate-secund. Strongly curved and turned to one side

fenestrate. Pierced with openings or perforations.

fertile. In bryophytes, with gametangia or sporophytes (opposed to **sterile**).
fide. According to.
filamentous. Thread-like.
filiform. Very slender and elongate.
flabellate. Fan-shaped, with several branches spreading outwards from almost a single point.
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 or rudimentary leaves (compare **stolon**) (Figs. 22A, B, H; 66B, D).
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.
fragmentation. Breaking up; a method of vegetative reproduction in which an organ (or whole plant) is separated into parts capable of producing a new organism.
fringed. With a ciliate margin.
frond. The branched or foliose part of an erect stem, occurring in dendroid liverworts and mosses.
***Frullania*-type branch**. Terminal branch (without collar at the base) originating from a ventral leaf initial so that it replaces the ventral half of a leaf. The branch is therefore associated with a half-leaf on its dorsal side.
furcate. Forked.
furrowed. Grooved.
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 (**antheridiophore**, **archegoniophore**).
gametangium. Sex organ (**archegonium, antheridium**).
gamete. Sexual reproductive cell (**spermatozoid**, **egg**).
gametoecium. Gametangia and surrounding bracts (**androecium**, **gynoecium**).
gametophyte. The haploid, sexual generation producing gametes (spermatozoids and eggs). In bryophytes, the gametophyte is the actual plant.
gemmae (sing. **gemma**). Vegetative diaspores, can be produced on leaves, stems, thalli or rhizoids (Fig. 16B, C, gemmae at the shoot-apex; 34B, C, gemmae at the shoot and leaf apices).
gemma cup. Cup-shaped, gemma-containing structure, produced on the thallus of *Marchantia* (Fig. 62D, E).
gibbous. Swollen on one side.
glabrous. Smooth.
glaucous. Whitish-blue.

globose. Rounded, spherical.
granular. Composed of small globules, referring to oil bodies (= **segmented**) (Figs. 33C; 54Q).
granulose. Roughened with minute, blunt projections.
groove. With a narrow and shallow furrow in the middle.
gynoecium (plur. **gynoecia**). Archegonia and the surrounding bracts; the female gametoecium (Figs. 48D; 54R; 57M)

habit. The general appearance of a plant.
habitat. The local environment of a plant.
haploid. Having a single set of chromosomes (n).
hemiphyll. First leafy appendage at the ventral base of *Frullania*-type branches in *Frullania*. Hemiphylls may be bifid or undivided; bifid hemiphylls resemble an underleaf, undivided ones resemble a half-leaf.
heteroicous (= **polyoicous**). Used for species that can be monoicous or dioicous.
hexagonal. With 6 angles, usually of cells.
hispid. With short, stiff hairs; bristly.
humus. Decomposing organic material.
hyaline. Colorless or transparent.
hyaline papilla. 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 *Frullania*, at the tips of the leaves in *Telaranea* (Fig. 23E) and *Zoopsis* (Fig. 23F), and at the base and the apex of the lobule in the Lejeuneaceae. The papilla at the lobule apex is always positioned at the proximal base of the first lobule tooth (= the distalmost tooth) (Fig. 48E, K; 49I). Sometimes the first tooth is reduced (e.g., *Cheilolejeunea*); in the latter case the distalmost visible tooth is the second tooth and the papilla is positioned distal to the base of this tooth (Fig. 44J).
hyalodermis. Stem epidermis of enlarged cells with thin (not thickened) walls.
hygrophytic. Growing in wet places.
hygroscopic. Moving in response to changes in humidity; e.g., elaters.
hypostatic. In leafy liverworts, lobules of male bracts overlapping ventrally, imbricate (opposed to **epistatic**) (Fig. 51H).

idioblast. Uniquely differentiated cell, distinct from other cells of the same tissue in size, form and/or content; e.g., ocellus, oil-cell (Figs. 54E; 56G).
imbricate. Overlapping, like shingles on a roof.
immersed. Completely below the surface; e.g., said the perianth completed covered by bracts (compare **exserted**).
inclined. Bent down.
incubous. An oblique leaf insertion in which the dorsal leaf margin is oriented toward the apex of the stem (when viewed from above; each leaf overlaps the adjacent younger leaf above), e.g., in *Calypogeia*, *Bazzania* and members of Porellales (opposed to **succubous**).
incurved (= **involute**). Curved upward (adaxially) and inward (opposed to **recurved**).

indehiscent. Lacking a distinct opening mechanism (opposed to **dehiscent**).
inflexed. Bent abruptly upward (adaxially) at more than 90° and inwardly.
inflorescence (= **gametoecium)**. The term "inflorescence" refers to the flowers of angiosperms and should not be used for bryophytes.
innovation. A branch formed at the base of the perianth. In Lejeuneaceae, innovations can be lejeuneoid (first leafy appendage at the base of the branch is a lateral leaf, Fig. 53F) or pycnolejeuneoid (first leafy appendage is an underleaf, Fig. 52A).
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 inside the stem, away from the apex, usually having a collar at the base; the associated leaves are not modified by branch formation (opposed to **terminal branch**).
involucre. A thin structure surrounding the gametangia or the developing sporophyte; also, the bracts (and bracteoles) of the gynoecium (= **perichaetium**) (Fig. 7C, D, male involucres).
involute (= **incurved**). Rolled upward (adaxially) and inward (opposed to **revolute**).
isodiametric. About as broad as long, of cells.

keel. Fold.
keeled. Folded along the middle, like the keel of a boat.

laciniae (sing. **lacinia**). Appendages that are more than one cell wide (Figs. 24M; 29F).
laciniate. With lacinia.
lamella. Ridge, plate, or filament-like outgrowth of the surface
lamina. The undivided portion of the leaf; the thin wings on either side of the midrib of a thallose liverwort (Fig. 5D, E).
laminate (= **explanate**). In *Frullania*, lobule that is not rolled inwards, not forming a sac (opposed to **saccate**).
lanceolate. Lance-shaped, narrow and tapered from near the base.
lax. Loosely.
***Lejeunea*-type branch**. Intercalary branch (with a collar at the base) originating from the lateral side of the stem, from behind a leaf.
lejeuneoid innovation. Innovation in which the first leafy appendage arising at the base of the innovation is a lateral leaf, Fig. 53F (compare **pycnolejeuneoid innovation**, Fig. 52A).
lejeuneoid sporophyte. Sporophyte of members of Lejeuneaceae subfam. Lejeuneoideae, characterized by slow dehiscence of the capsule, decussate tetrads, elongate spores, and elaters with reduced spirals.
lignicolous. Occurring on dead, decorticated wood.
ligulate. Strap-shaped; long and narrow with parallel sides (sometimes used to mean tongue-shaped or **lingulate**).
linear. Very long and narrow, with parallel sides; narrower than lingulate.
lingulate. Tongue-shaped, oblong below, somewhat broader toward the apex (cf. **ligulate**).

lobe. A major segment of a leaf, larger than a tooth (cf. **lobule**)
lobule. A small lobe; e.g., the smaller segment of a complicate-bilobed leaf with unequal segments.
lobule beak. Downward extension of the sac along the adaxial margin of the laminate part of the lobule, in *Frullania* subg. *Chonanthelia*.
longitudinal. Lengthwise, parallel to the long axis; e.g., longitudinal leaf insertion.
lowland. Area between sea level and ca. 500 m elevation
lumen (plur. **lumina**). The cavity of a cell, enclosed by the cell wall.
lunulate. With a wide, shallow sinus; moon-shaped.

mamilla. Alternate spelling (British English, Latin) of mammilla.
mammilla (plur. **mammillae**; American English). Hollow projection from the cell surface, with the cell lumen extending into the protuberance (opposite of **papilla**) (Fig. 29P, Q).
mammillose. With **mammillae.**
marsupium. A fleshy, cylindrical structure that penetrates downward into the soil and contains the sporophyte. Usually derived from stem tissue. (Figs. 8F; 13B).
mat. Growth form with stems horizontal and densely interwoven.
median. Central, middle.
medulla. Internal tissue of stem and seta.
meristem. Embryonic tissue.
merophyte. A segment cut off from the apical cell and the tissues and organs derived from it. A mature merophyte consists of one leaf or underleaf and associated stem tissue.
***Microlepidozia*-type branch**. Terminal branch (without collar at the base) originating from a dorsal leaf initial so that it replaces the dorsal half of a leaf. The branch is therefore associated with a half-leaf on its ventral side.
micrometer (= **micron**). One thousandth of a millimeter (abbreviated µm).
microphyllous. Small-leaved (cf. **flagelliform**).
midleaf. Middle part of a leaf.
midrib = **costa**.
monochasial. An arrangement of gynoecia in a row, formed by repeatedly innovating branches (Fig. 59C).
monoicous (= **monoecious**). Bisexual, with antheridia and archegonia on the same plant; including **autoicous**, **synoicous** and **paroicous**.
monolete. In spores, having a single, linear scar on the proximal surface that marks the point of attachment in the tetrad (compare **trilete**).
montane. Pertaining to mountains; altitudinal belt between lowlands and upper forest line. In the tropics usually extending from about 500 to 3000(–4000) m. The upper forest line may be lowered due to local climate and human impact and is much lower on islands. The transitional belt between lowland and montane is called the **submontane** belt (500 to ca. 1000 m) and the belt above ca. 2500 m is called the **upper montane** belt.
mucro. A short, abrupt point.
mucronate. Ending in a short, abrupt point (**apiculate** is somewhat longer; **cuspidate** is even longer and stouter).
multi-. Many.

n. The haploid (gametophytic) chromosome number of an organism.
neotenic. Mature organism with juvenile characters.
neoteny. Occurrence of juvenile characters in mature organism.
nerve = **costa**.
nodulose. With knob-like wall thickenings.
notch. V-shaped indentation, e.g., at the tip of the thallus.

obcuneate. Wedge-shaped with apex broader than base.
oblique. Slanted; e.g., an oblique leaf insertion is one that is between transverse and longitudinal.
obliquely spreading. Spreading at an angle of 30º–60°.
oblong. Rectangular with rounded corners or ends.
obovate. Egg-shaped with apex broader than base.
obpyriform. Pear-shaped with apex narrower than base.
obtuse. Blunt, broadly pointed, at an angle greater than 90º.
ocellus (plur. **ocelli**). A specialized cell in the leaves (and perianth) of some members of *Frullania* and Lejeuneaceae, having one very large oil body and lacking chloroplasts. Ocelli may be translucent and shiny, light gray, brown or red in color (Figs. 43P; 48E; 53 L; 54O; 55H).
oil body. A membrane-bound organelle containing terpenoids, characteristic of liverwort cells. The content of oil bodies may be homogeneous (Figs. 40H; 46P; 51Q), or segmented (Figs. 13F; 54Q) and made up of numerous small or large granules (Fig. 59H). Upon degeneration, homogeneous oil bodies may become segmented while degenerated oil bodies may become homeogeneous. Therefore, it is necessary to study oil bodies on fresh material.
oil cell. Colorless cell in the thallus of complex thalloid liverworts (Marchantiopsida), containing a large oil body or oil droplets, and no chloroplasts.
opaque. Not transparent.
operculum. Lid covering the mouth of the capsule, falling away when the spores are mature; found in mosses, some complex thalloid liverworts (Marchantiopsida) and some hornworts (Anthocerotophyta).
orbicular. Rounded, circular.
oval. Widely elliptical
ovate. Egg-shaped, broader at the base than at the apex.
ovoid. Egg-shaped in 3 dimensions.
ovum. Egg.

paired (= **twinned**). Associated in groups of two; e.g., hairs, teeth.
palmate. Lobed or branched in a radiating fashion, resembling fingers spreading from the palm of a hand.
pantropical. Occurring throughout the tropics (America, Africa, Asia).
papilla (plur. **papillae**). A solid projection from the cell surface (opposed to **mammilla**); papillae can be rounded or elongate in circumference, and rather low and flat (lens-shaped) or highly swollen (**tuberculate**) (Figs. 45M; 54F).

papillose. Roughened by papillae (Fig. 8E).

paraphyllia (sing. **paraphyllium**). Small, green outgrowths of stems, much smaller than leaves and of various shapes, i.e., filiform, lanceolate, etc (Fig. 38J).

paraphyses (sing. **paraphysis**). Multicellular hairs associated with antheridia and archegonia.

parenchymatic. Isodiametric or rectangular cells with broad, truncate tips (opposite to **prosenchymatic**).

paroicous (= **paroecious)**. With antheridia in the axils of bracts just below the perichaetium, on the same shoot.

pegged rhizoids. Rhizoids with papilla-like projections on the inner wall surface.

pellucid. Clear, translucent, transparent, hyaline.

pendent (= **pendulous**). Hanging downward.

perianth. Organ of foliar origin enclosing the developing sporophyte in leafy liverworts (Figs. 39N, O; 41D, F,Q).

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 (in mosses).

perigynium. Fleshy structure surrounding and protecting the developing sporophyte, derived from stem cells; a perigynium may or may not be associated with a shoot calyptra.

piliferous. With hair point.

pilose. With long hairs.

pinnate. Branched in a feather-like fashion, with numerous branches on opposite sides of the stem.

plane. Flat.

***Plagiochila*-type branch.** Lateral-intercalary branch (with collar at the base), originating from the axil of lateral leaves.

plica (plur. **plicae**). Longitudinal furrow.

plicate. With longitudinal furrows.

plumose. Closely and regularly pinnate, feathery.

pluricellular. Made up of several cells (more than one; compare **unicellular**).

pluriplicate. With many keels or folds (more than 5), referring to the perianth.

polymorphic. Of more than one form, variable.

polyoicous = **heteroicous**.

pore. A small opening.

porose. Having pores.

postical. The leaf margin oriented toward the base of the shoot (opposite of **antical**). Also used for the ventral surface of a stem.

pre-apical tooth. Tooth arising from the sinus between keel and ventral leaf margin, beyond the first lobule tooth. Seen in *Drepanolejeunea* and some other genera of Lejeuneaceae.

propagule. Reduced bud, branch or leaf serving in vegetative reproduction (compare **diaspore**).

prosenchymatic. Elongate cells with narrow tips (opposite to **parenchymatic**).

prostrate. Laying flat on the surface; creeping.
protonema (plur. **protonemata**). A filamentous or thalloid structure resulting from spore germination and giving rise to one or more gametophytes.
proximal. Near the base or the point of attachment; the internal face of a spore (opposite of **distal**).
proximal hyaline papilla. (Fig. 49I). See: **hyaline papilla**
pseudo-elater. Unicellular or multicellular sterile cells in the hornwort capsule, lacking spirals.
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. 5H).
ptychanthoid sporophyte. Sporophyte of members of Lejeuneaceae subfam. Ptychanthoideae, characterized by explosive dehiscence of the capsule, tetrahedral tetrads, isodiametric spores, and elaters with well developed spirals.
pycnolejeuneoid innovation. Innovation in which the first leafy appendage arising at the base of the innovation is an underleaf (compare **lejeuneoid innovation**) (Fig. 52A).
pyrenoid. Colorless, rounded body in the chloroplasts of algae and hornworts that is involved in carbon fixation and starch formation and storage.
pyriform. Pear-shaped.

quadrate. Square or nearly so.
quadrifid. Divided into four lobes or segments.

radiate. Elongate at the angles, of trigones.
***Radula*-type branch**. Terminal branch (without collar at the base) originating from the stem epidermis and therefore associated with an unmodified leaf.
ramicolous. Growing on twig and branches.
receptacle. A rounded or elongate structure bearing antheridia or archegonia in thalloid liverworts; found on the thallus, inside the thallus or elevated on a stalk (**gametangiophore**) (Fig. 2C, E, female receptacles).
recessed. Sunken; perianth beak sunken in a hollow perianth apex, becoming invisible.
rectangular. Longer than wide with straight angles.
recurved (= **revolute**). Curved downward (abaxally) and inward (opposed to **incurved**).
reflexed. Bent abruptly down (abaxally) at more than 90° and inwardly.
reniform. Kidney-shaped, much wider than long.
reticulate (= areolate). Forming a network; surface covered by a network of areoles.
retuse. Having a narrow, shallow indentation in a broad, rounded apex (opposed to **emarginate**).
revolute (= **recurved**). Rolled downward (abaxally) and backward (opposed to **involute**).
rheophytic (= rheophilous). Growing partly or periodically submerged in running water (rivers, creeks) and producing reproductive organs on emerged shoots, above the water (opposed to **aquatic** or **terrestrial**).
rhizoid disc. A cushion-like swelling at the base of an underleaf, from which rhizoids originate.

rhizoid. A root-like hair that functions in anchorage; in liverworts and hornworts typically 1-celled, in mosses many-celled and with oblique end walls.
rhizome. A slender, creeping, often subterranean stem with reduced leaves, giving rise to erect leafy stems or fronds.
rhombic. Diamond-shaped, oblong-hexagonal.
rhomboidal = **rhombic**.
rosette. In thalloid liverworts, a rounded, segmented thallus with segments radiating from a central point; in leafy liverworts (*Frullania*, Lejeuneaceae), a small rounded area on the spore surface consisting of radially arranged spines.
rostrum = **beak**.
ruffled. Curled, irregulary crisped; refers to the thallus margin of some hornwort species.
rupicolous. Growing on rocks or concrete.

saccate. Sac-like.
saxicolous (= **epilithic**). Growing on rocks.
scale. A thin, membranous structure; usually present on the ventral surface of the thallus of complex thalloid liverworts (Marchantiopsida).
secondary rhizoid disc. Disc of fused rhizoids in epiphyllous liverworts, firmly fixing the plant to the leaf surface.
secund. Turned to one side
segmented. Divided in parts, e.g., lobed leaves, granular oil bodies.
seriate. In a row, e.g., uni-, bi-, tri-, multiseriate; applied to number of adjacent rows of cells.
serrulate. Finely toothed.
seta (plur. **setae**). Stalk-like portion of the sporophyte, between capsule and foot (Fig. 67A).
sheathing. Surrounding and clasping the stem or the perianth.
shoot calyptra. A somewhat fleshy calyptra derived from the archegonial venter and from axial or thalline tissue peripheral to the archegonium.
shouldered. In *Plagiochila*, leaf margin rather longly stretched upwards before curving outwards.
sinuate (= **sinuose**). Wavy.
sinus. The depression separating two segments or lobes.
slime hair. A hair-like, mucilage-secreting outgrowth of the epidermis (Fig. 5F).
slime papilla. A mucilage-secreting cell.
spathulate. Tapering to the base from a broad, rounded apex.
spermatozoid (= **antherozoid**). The male gamete, produced in an antheridium.
spinose. With long and sharp teeth.
spore. In bryophytes, a reproductive unit produced in the capsule as a result of meiosis, upon germination giving rise to a protonema.
sporeling. Protonema and juvenile gametophore arising from a spore.
sporophyte. The diploid, asexual generation producing (meio)spores, in bryophytes normally consisting of a foot, seta and capsule and permanently attached to the gametophyte.
spreading. Forming an angle of 30º–90º; e.g., leaves spreading from the stem.

squarrose. Spreading at almost right angles.
stellate. Star-shaped.
sterile. In bryophytes, without gametangia or sporophytes (opposed to **fertile**).
stipitate. Having a stalk-like base.
stolon. Slender branch or shoot without leaves.
stoloniferous. With stolons.
stoma (plur. **stomata**). Pore bordered by two guard cells, occurring in the capsule wall of many mosses and hornworts.
-stratose. In layers; e.g., uni-, bi-, multistratose.
striate. With fine ridges or lines.
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, especially *Frullania* (Figs. 39I, M; 45G, K, I).
sub-. Under, below; almost.
suberect. Almost upright; almost parallel to the stem; Spreading at an angle of less than 30°.
subfloral innovation. A branch that arises just below the perianth in leafy liverworts.
subspecies. Taxon characterized by one or two morphological characters and by a different geographic distribution (= geographic race, allopatric race).
subula. A long, slender point.
subulate. Slenderly long-acuminate.
succubous. Oblique leaf insertion in which the dorsal leaf margin is oriented toward the base of the stem (when viewed from above, each leaf overlaps the adjacent older leaf underneath), e.g., in *Lophocolea* and *Plagiochila* (opposed to **incubous**) (Figs. 10A, B; 28A–E, H).
synoicous (**= synoecious**). With antheridia and archegonia mixed in the same gametoecium.

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 -underleaf and has no collar at its base (opposed to **intercalary branch**).
terrestrial (= **terricolous**). Growing on soil, not submerged.
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. Tetrads in bryophytes are usually **tetrahedral** in shape, with three spores in one plane and one centrally over the other three. The presence of a **trilete scar** on the inner spore surface marks the tetrahedral position of the spores in the tetrad. Some bryophytes, e.g., members of the subfamily Lejeuneoideae, have **decussate** tetrads, characterized by the spores being arranged pair-wise in the tetrad, at a right angle to each other.
tetrahedral. Four-sided; e.g., shape of the spore tetrad of most bryophytes (see above); shape of the apical cell of leafy liverworts (Jungermanniidae).
thalloid (= thallose). Thallus-like; flat and ribbon- or rosette-like (Figs. 61A–D; 77A, B).
thallus (plur. **thalli**). A flattened plant body that is not differentiated into stems and leaves.
theca (plur. **thecae**) = **capsule**.

tomentose. Woolly.
tooth (plur. **teeth**). Sharp, projecting cells on the margin or surface of a leaf.
tortuose. Irregularly bent or twisted.
transverse. Across, perpendicular to the axis (opposed to **oblique** and **longitudinal**) (Fig. 18A, leaf insertion transerve).
trifid. Divided into three segments.
trigone. A 3-angled thickening at corners of cells (compare **collenchymatous**) (Figs. 9F; 11N; 15M).
trigonous. Three-angled; applied to a 3-keeled perianth.
trilete mark. Triradiate scar on the inner (= proximal) surface of spores, marking the tetrahedral position of the spores in the tetrad.
truncate. Abruptly cut off at the apex (Fig. 59C–E).
tubercle. Wart, large papilla.
tuberculate. With warts (coarser than papillae).
tubular. Cylindrical and hollow.
tuft. Small cushion; growth form with stems erect but radiating at the edges.
twinned (= **paired**). Associated in groups of two.

underleaves (= **amphigastria**). Leaves originating from the ventral surface of the stem (Fig. 47F, G; 52B, C; 56F).
undulate. Wavy
unicellular. Made up of only one cell (compare **pluricellular**).
uniseriate. In one row, of cells.
unistratose. One-layered, of a single layer of cells.
utricle. The strongly enlarged, bladder-like lobule on branch leaves of *Ceratolejeunea* (Fig. 43N).

valve. One of the segments into which the capsule separates upon dehiscence; small lamina regulating the opening of the lobule sac in *Colura* (Fig. 46 L, M) and *Pleurozia*.
variety. Taxon characterized by a single diagnostic morphological character but not differing in geographic distribution.
ventrad. Directed toward the ventral side of the plant.
ventral. The lower surface or side, next to the substrate (compare **dorsal**).
verrucose = **papillose**.
verruculose. Slightly roughened by small papillae.
vitta. In liverworts, a band of larger, elongate cells in a leaf (in Lejeuneaceae usually made up of ocelli), resembling a nerve but only one cell layer thick (Figs. 39G; 43 L).

wart. A solid projection from the surface; large **papilla**.
wide-spreading. Spreading at an angle of 60º–90º.
wing. A thin, flat expansion or appendage.

xerophytic. Growing in dry places.

Abbreviations

a.o. = among others
aff. = *affinity*, related to
alt. = *altitude*, elevation
auct. = *auctorum*, according to certain authors; used for misused names, that have been applied by certain authors to a different species than the type specimen
ca. = *circa*, approximately
cf. = *confer*, compare; used for a preliminary, tentative identification of a species
comb. = *combinatio*, combination; referring to the association of a species epithet with a particular genus name
c. andr. = *cum androeciis*, with male gametangia
c. gyn. = *cum gynoeciis*, with female gametangia
c. per. = *cum perianthiis*, with perianths.
c. spor. = *cum sporis*, with spores, with sporophytes
det. = *determinavit*, identified by
e.g., = *exempli gratia*, for example
et al. = *et alii*, and others
fo. = *forma*, form
herb. = herbarium
incl. = including
ICN = International Code of Nomenclature for Algae, Fungi and Plants
l.c. = *loco citato*, as cited above
leg. = *legit*, collected by
loc. = locality
nom. = *nomen* (plural *nomina*), name
nom. illeg. = illegitimate name
nom. inval. = invalid name; among them the most common one is **nom. nud.** = *nomen nudum*, "naked name", published without description, or without reference to a previously published valid name
nov. = *novum*, *nova*, new
nr. = *numero*, number
p.p. = *pro parte*; partly
s.d. = *sine dato*, without collecting date
s.l. = *sensu lato*, in a broad sense; or *sine loco*, without collecting locality
s.n. = *sine numero*, without number
s.str. = *sensu stricto*, in a narrow sense
sp. = species (singular)
spp. = species (plural)
subfam. = subfamily
subsp. = subspecies
subg. = subgenus
syn. = synonym
var. = variety

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Table 1. Differences between liverworts, mosses, and hornworts (adapted from Gradstein *et al.* 2001).

	Liverworts	Mosses	Hornworts
Plants	With stem and leaves in 2–3 rows, or thalloid.	With leaves usually in a spiral, not thalloid.	Thalloid.
Branches	From leaf initial cells, stem epidermis, or inner stem cells.	From stem epidermis.	Absent.
Leaves	Undivided or lobed. Midrib absent.	Undivided. Midrib present or absent.	Absent.
Cells	With numerous small chloroplasts. Oil bodies present. Trigones common.	With numerous small chloroplasts. Oil bodies absent. Trigones rare.	With 1–2 large chloroplasts. Oil bodies absent. Trigones rare.
Rhizoids	Unicellular.	Pluricellular.	Unicellular.
Sporophyte	Growth by one apical cell. Fully covered until maturity by the calyptra and by special protective organs (perianth, marsupium, involucre, etc.).	Growth by an apical cell. Upper part when young covered by the calyptra; further protective organs lacking.	Growth by a basal meristem. Basal part covered by an involucre; calyptra absent.
Seta	Fragile, elongates after spore maturation; elongated seta ephemeral, soon decaying after capsule dehiscence.	Rigid, elongates before spore maturation; elongated seta perennial, not decaying soon after capsule dehiscence.	Absent.
Capsule	Globose to cylindrical. Dehiscence at once by (1–)4 valves, rarely by an operculum. Elaters present. Columella and peristome absent.	Globose to cylindrical. Dehiscence at once by an operculum. Elaters absent. Columella and peristome usually present.	Filiform (or ellipsoid). Dehiscence gradually by 2 valves. Elaters and columella present, peristome absent.
Spore maturation	Synchronous (all at same time), before elongation of seta.	Synchronous (all at same time), after elongation of seta.	Asynchronous (gradual).
Protonema	Very small, thalloid, producing one gametophyte.	Filamentous, producing several gametophytes.	Very small, thalloid, producing one gametophyte.

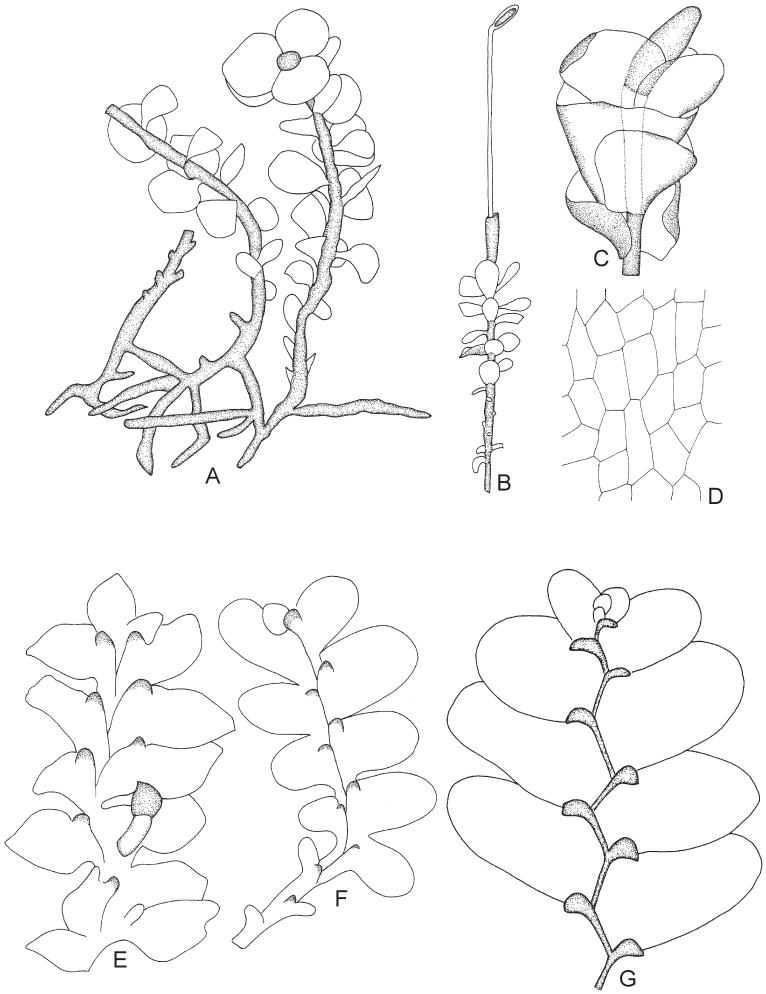


Figure 1. *Haplomitrium blumei* (Nees) R.M.Schust. A: Habit of male plant, ventral view. B: Part of plant with sporophyte. C: Apex of plant with gynoecium and sporophyte. D. Median leaf cells. *Treubia insignis* K.I.Goebel. E,F: Habit, ventral view. G: Habit, dorsal view. (A,B redrawn from Verdoorn 1931 as *Calobryum blumei*; C,D redrawn from Gradstein *et al.* 2001; E,F redrawn from Verdoorn 1931; G redrawn from Gradstein 2011).

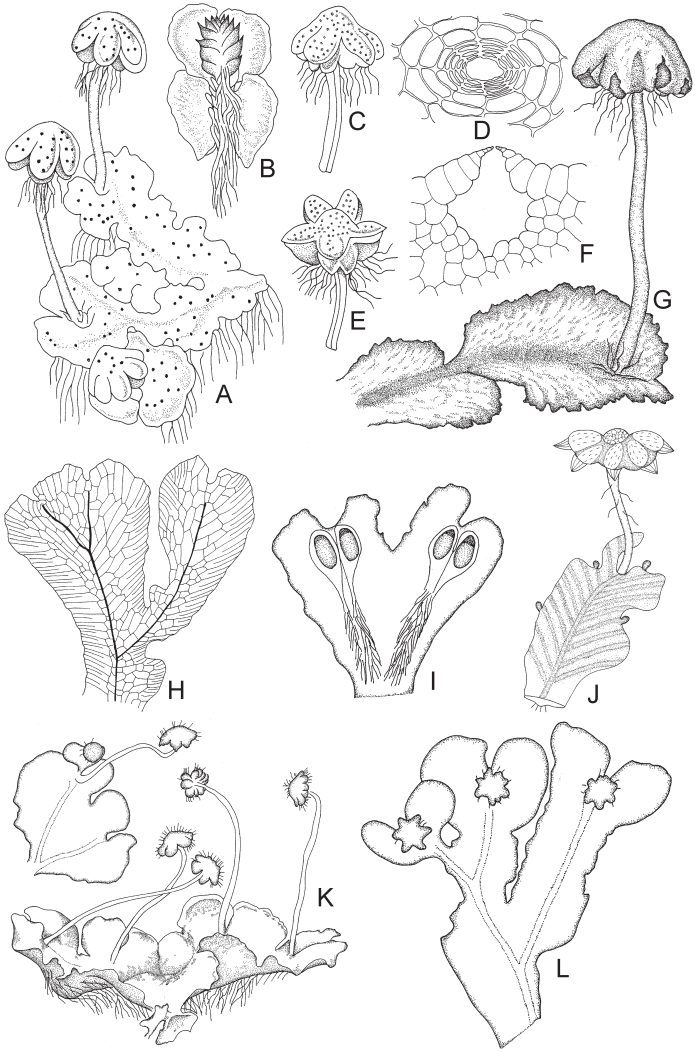


Figure 2. *Reboulia hemisphaerica* (L.) Raddi. A,G: Habit with archegoniophore, dorsal view. B: Frond, ventral view. C,E: Female receptacles. D: Pore. F. Section through pore. *Cyathodium foetidissimum* Schiffn. H: Vegetative thallus. I: Female thallus. *Asterella limbata* D.G.Long & Grolle. J: Habit with androecia and archegoniophore. *Dumortiera hirsuta* (Sw.) Nees. K: Female thallus with mature archegoniophores. L: Female thallus with young archegoniophores. (A–D redrawn from Pearson 1902; E–G redrawn from Macvicar 1926; J redrawn from Long & Grolle 1994; K,L redrawn from Campbell 1918).

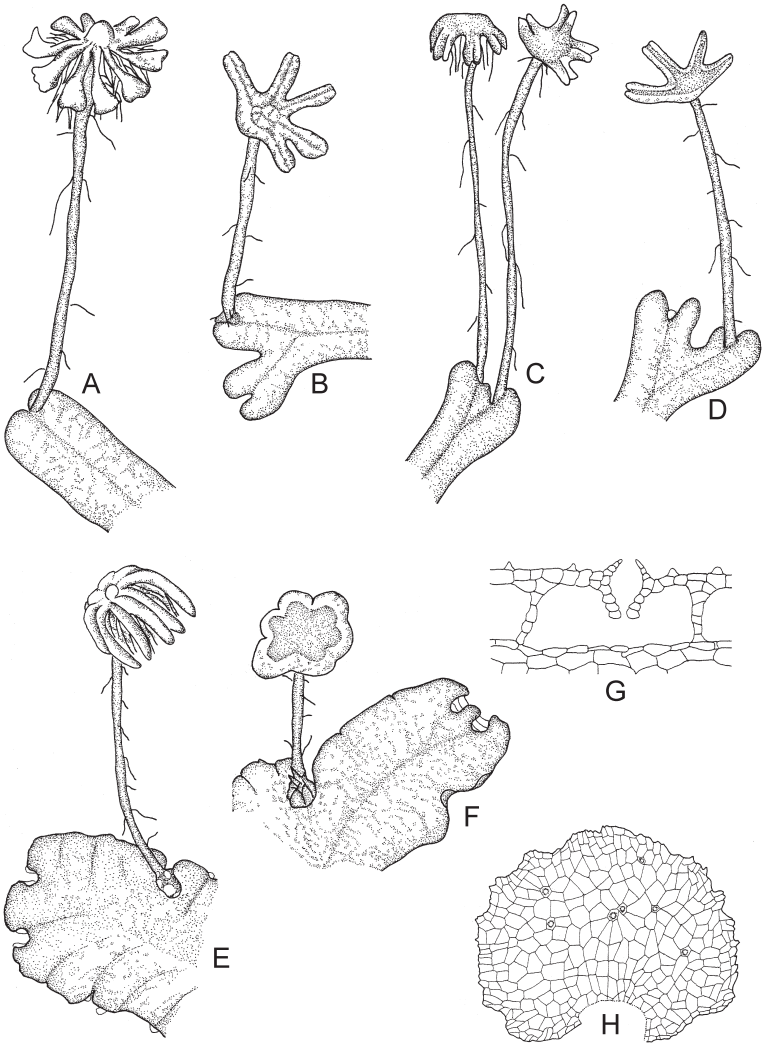


Figure 3. *Marchantia emarginata* Reinw. *et al.* A: Female thallus. B: Male thallus. G: Section of epidermal pore. *Marchantia germinata* Reinw. *et al.* C: Female thallus. D: Male thallus. *Marchantia polymorpha* L. E: Female thallus. F: Male thallus. H: Appendage of median scale. (All redrawn from Gradstein 2011).

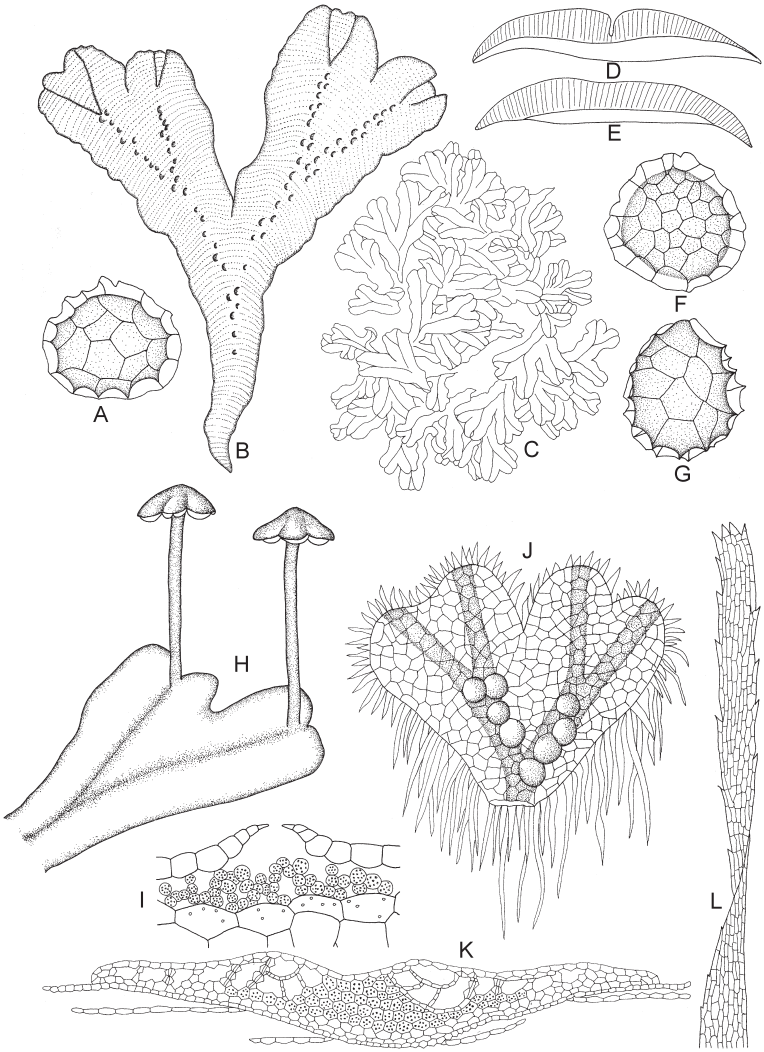


Figure 4. *Riccia treubiana* Steph. A,F,G: Spores. B,C: Habit. D,E: Section of thallus. *Wiesnerella denudata* (Mitt.) Steph. H: Female thallus. I: Cross section of thallus. *Ricciocarpos natans* (L.) Corda. J: Habit. K: Cross section of thallus. L: Portion of scale. (A–E redrawn from Meijer 1958; H,I redrawn from Gradstein 2011; J redrawn from Hooker 1830; K,L redrawn from Pearson 1902).

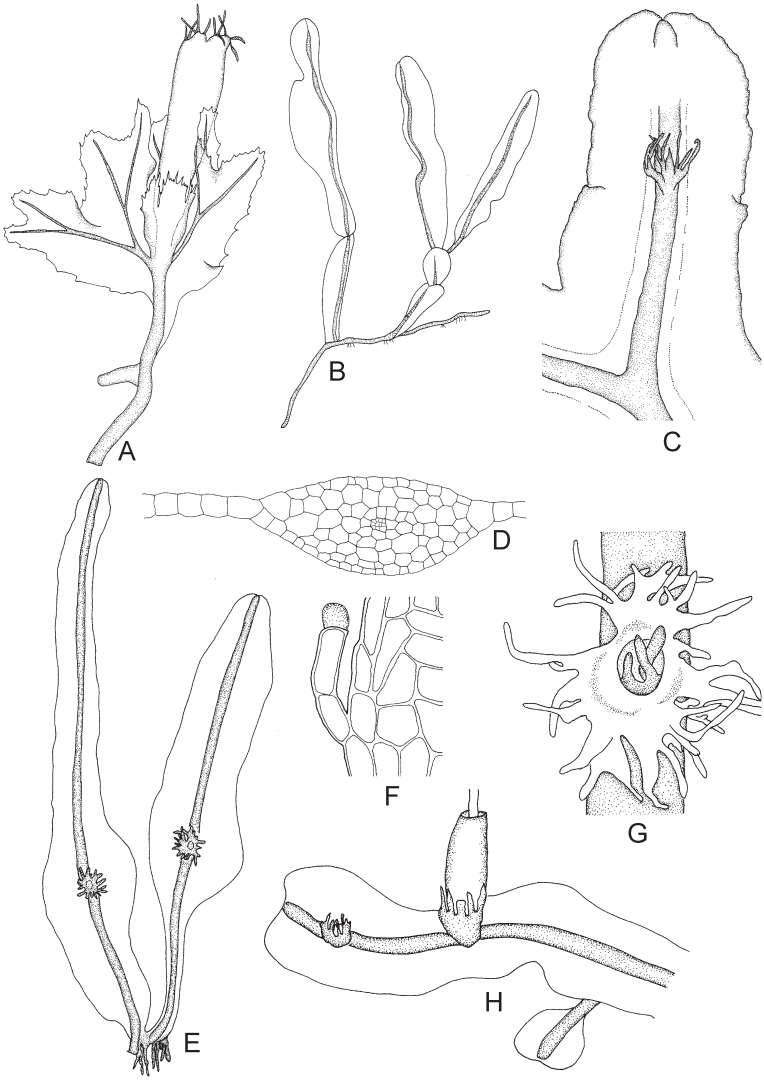


Figure 5. *Jensenia decipiens* (Mitt.) Grolle. A: Female thallus. *Podomitrium malaccense* (Steph.) Campb. B: Habit. *Symphyogynopsis gottscheana* (Mont. & Nees) Grolle. C: Part of thallus with gynoecium. *Pallavicinia lyellii* (Hook.) Gray. D: Cross section through thallus middle. E: Part of thallus with gynoecia. F: Thallus margin with slime hair. G: Gynoecium. H: Portion of thallus with gynoecium and pseudoperianth. (A redrawn from Miller & Inoue 1966 as *J. macrogyna*; B redrawn from Johnson 1958 as *Hymenophytum malaccense*; C redrawn from Grolle & Piippo 1986 as *S. filicum*; others redrawn from Gradstein 2011).

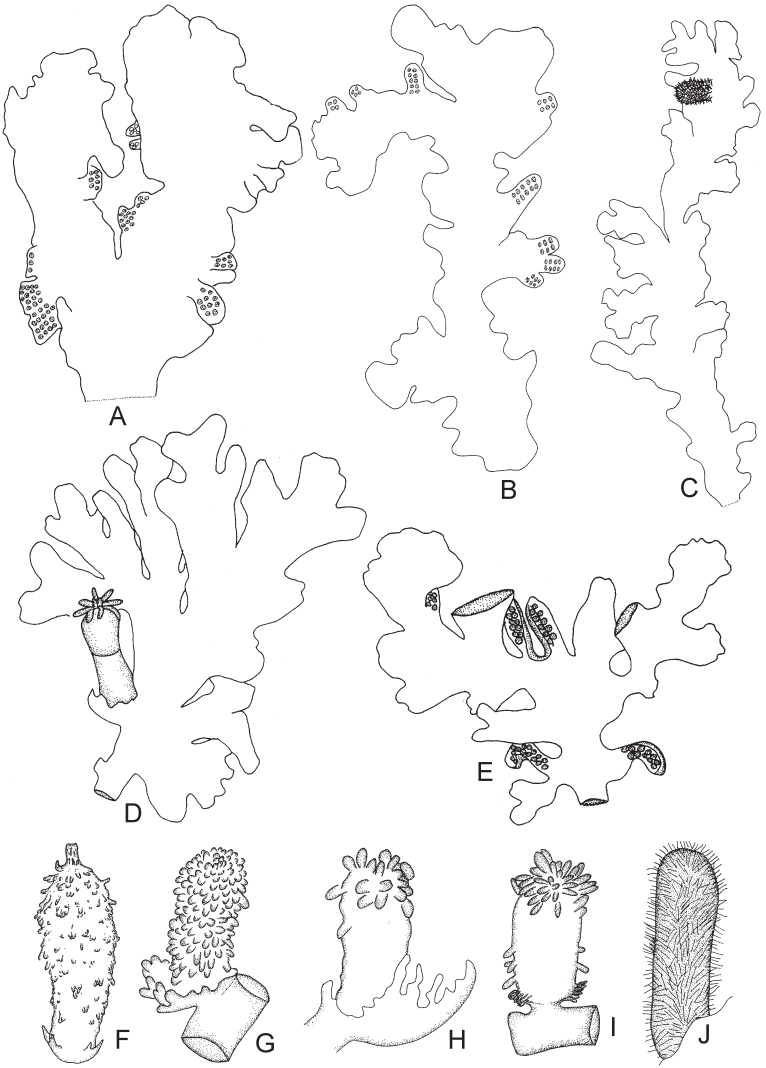


Figure 6. *Aneura pinguis* (L.) Dumort. A: Male thallus. *Lobatiriccardia lobata* (Schiffn.) Furuki. B: Male thallus. C: Female thallus. J: Calyptra. *Riccardia deguchii* Furuki & K.T.Yong. D: Female thallus. E: Male thallus. *Riccardia heteroclada* Schiffn. F: Calyptra. *Riccardia planiflora* var. *aequatorialis* Furuki. G: Calyptra. *Riccardia tenuicostata* Schiffn. H: Calyptra. *Riccardia grossitexta* (Steph.) Furuki. I: Calyptra. (A redrawn from Gradstein 2011; B,C,J redrawn from Furuki 1996; D,E redrawn from Furuki *et al.* 2013; F redrawn from Furuki 1998; G redrawn from Furuki 1997; H,I redrawn from Furuki 1994).

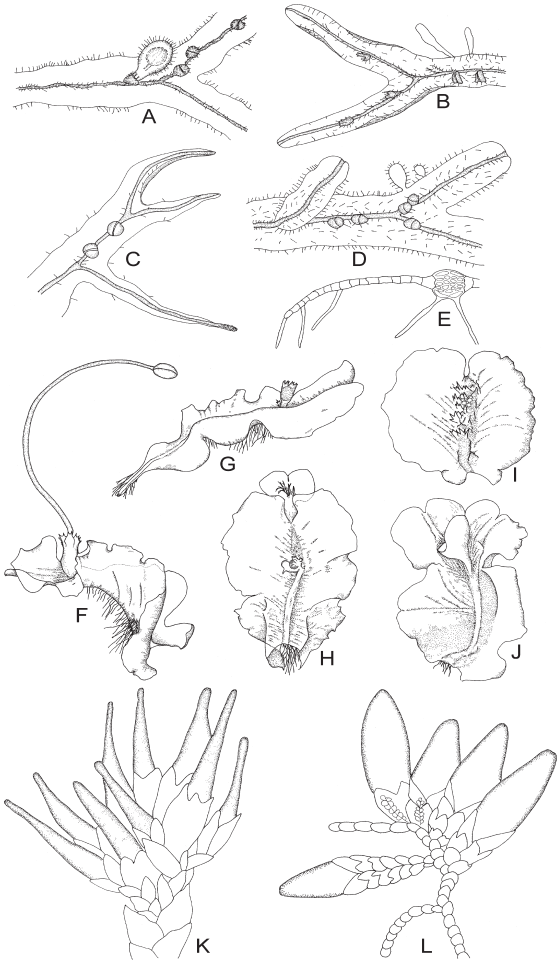


Figure 7. *Metzgeria lindbergii* Schiffn. A: Part of thallus, with a calyptra and antheridial branches, ventral view. *Metzgeria consanguinea* Schiffn. B: Part of thallus with antheridial branches, ventral view. *Metzgeria furcata* (L.) Corda. C: Part of thallus, with involucres and marginal gemmae, ventral view. D: Part of thallus, with antheridial branches, marginal gemmae and an adventitious shoot. E: Cross section of thallus. *Sandeothallus radiculosus* (Schiffn.) R.M.Schust. F: Plant with mature sporophyte. G: Female plant bearing a young sporophyte. H: Female plant. I,J: Male plants. *Pleurozia gigantea* (F.Weber) Lindb. K: Part of plant, ventral view. *Pleurozia acinosa* (Mitt.) Trevis. L: Part of plant. (A redrawn from Kuwahara 1966 as *M. pectinata*; B,C redrawn from Kuwahara 1966; D,E redrawn from Kuwahara 1960 as *M. molokaiensis*; F–J redrawn from Campbell 1913 as *Calycularia radiculosa;* K,L redrawn from Thiers 1933).

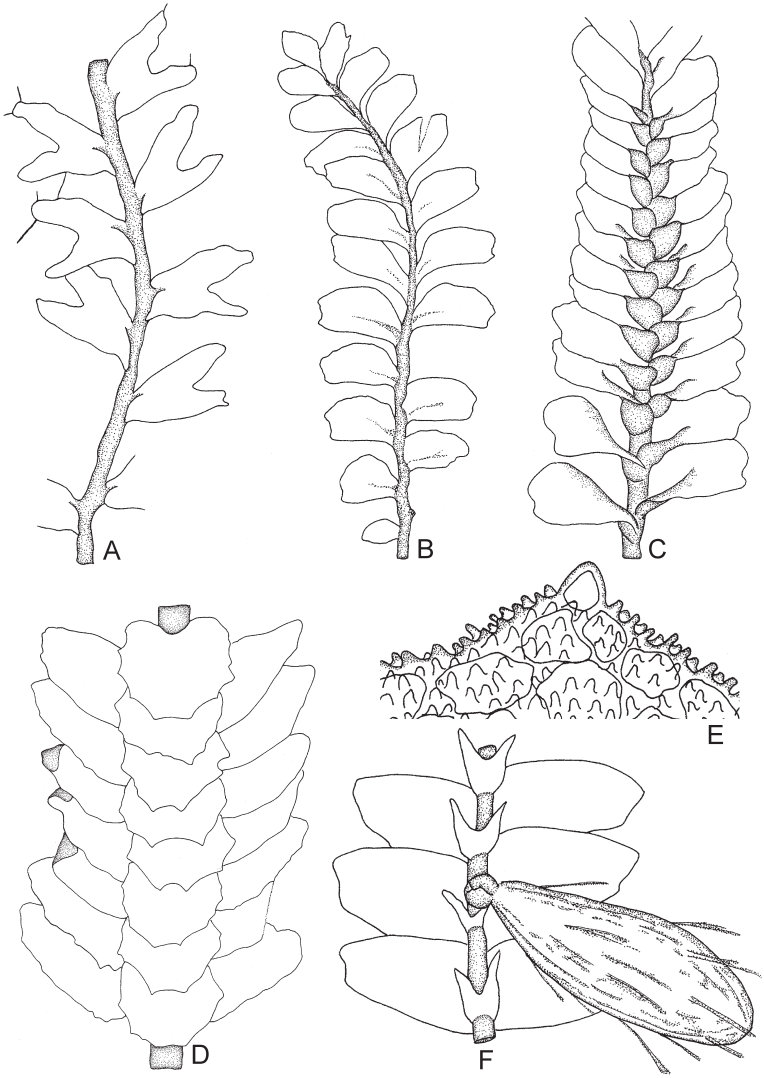


Figure 8. *Acrobolbus ciliatus* (Mitt.) Schiffn. A: Shoot, dorsal view. *Acrobolbus saccatus* (Hook.) Trevis. B: Shoot, ventral view. C: Male shoot, dorsal view. *Conoscyphus trapezioides* (Sande Lac.) Schiffn. D: Shoot, ventral view. *Saccogynidium rigidulum* (Nees) Grolle. E: Apical leaf cells. F: Part of plant with marsupium. (A–C redrawn from Piippo 1985a B,C as *Tylimanthus saccatus*; D redrawn from Piippo 1985b; E,F redrawn from Gao & Cao 2001).

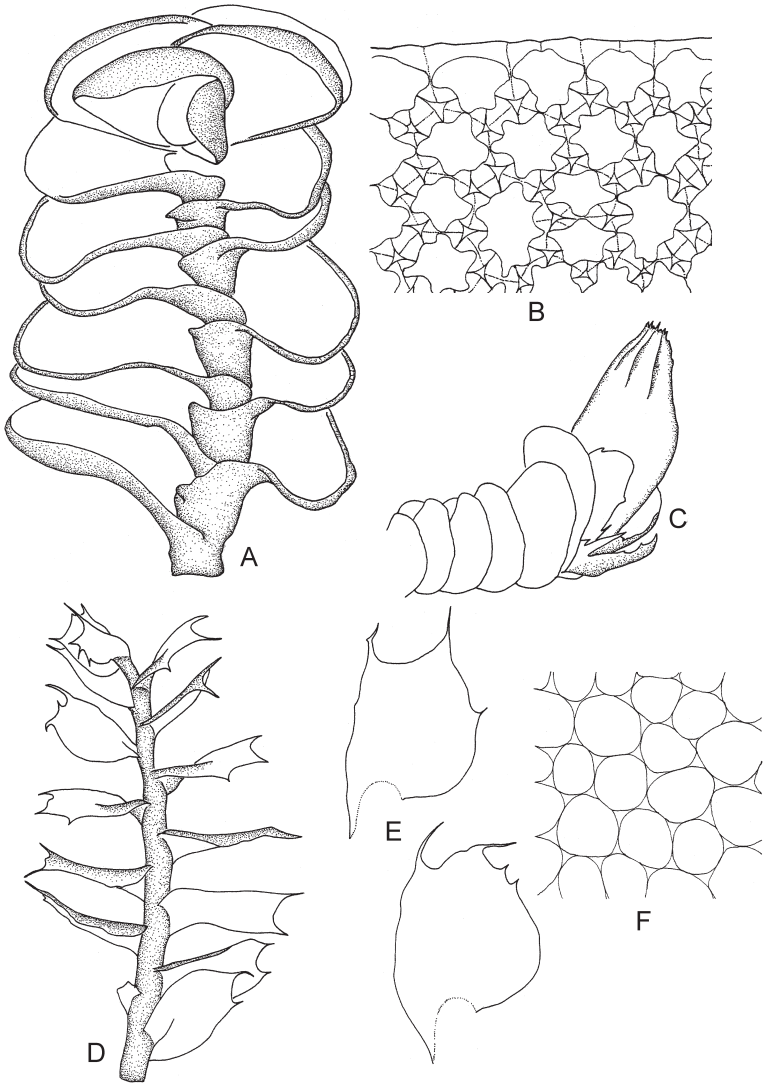


Figure 9. *Denotarisia linguifolia* (De Not.) Grolle. A: Part of plant, dorsal view. B: Marginal leaf cells, showing stellate markings inside the trigones. C: Part of female shoot with perianth. *Pseudomarsupidium borneensis* (Grolle) Váňa. D: Part of plant, ventral view. E: Leaves. F: Apical leaf cells. (A,B redrawn from Gradstein 2011; C redrawn from Grolle 1971; D–F redrawn from Grolle 1972 as *Adelanthus borneensis*).

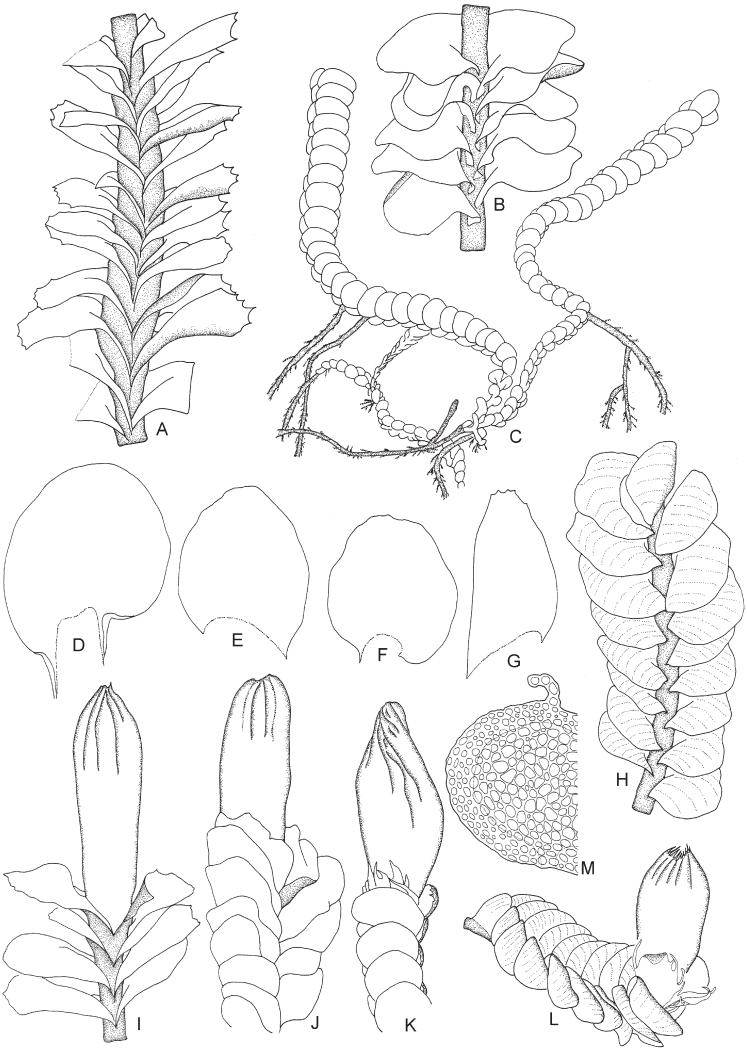


Figure 10. *Syzygiella subintegerrima* (Reinw. *et al.*) Spruce. A: Male plant, dorsal view. G: Leaf. I: Part of plant with perianth, dorsal view. *Syzygiella flexicaulis* (Nees) Gradst. & G.E.Lee. B: Part of plant. F: Leaf. J: Part of plant with perianth. *Syzygiella sonderi* (Gottsche) K.Feldberg *et al.* C: Part of plant. D: Leaf. K: Part of plant with perianth, dorsal view. M: Cross section of stem. *Syzygiella autumnalis* (DC.) Feldberg *et al.* E: Leaf, H: Habit, L: Part of plant with perianth. (A,G,I redrawn from Inoue 1966; others redrawn from Grolle 1971, B,F,J as *Jamesoniella flexicaulis*, C,D,K,M as *Cryptochila grandiflora*, E,H,L as *J. autumnalis*).

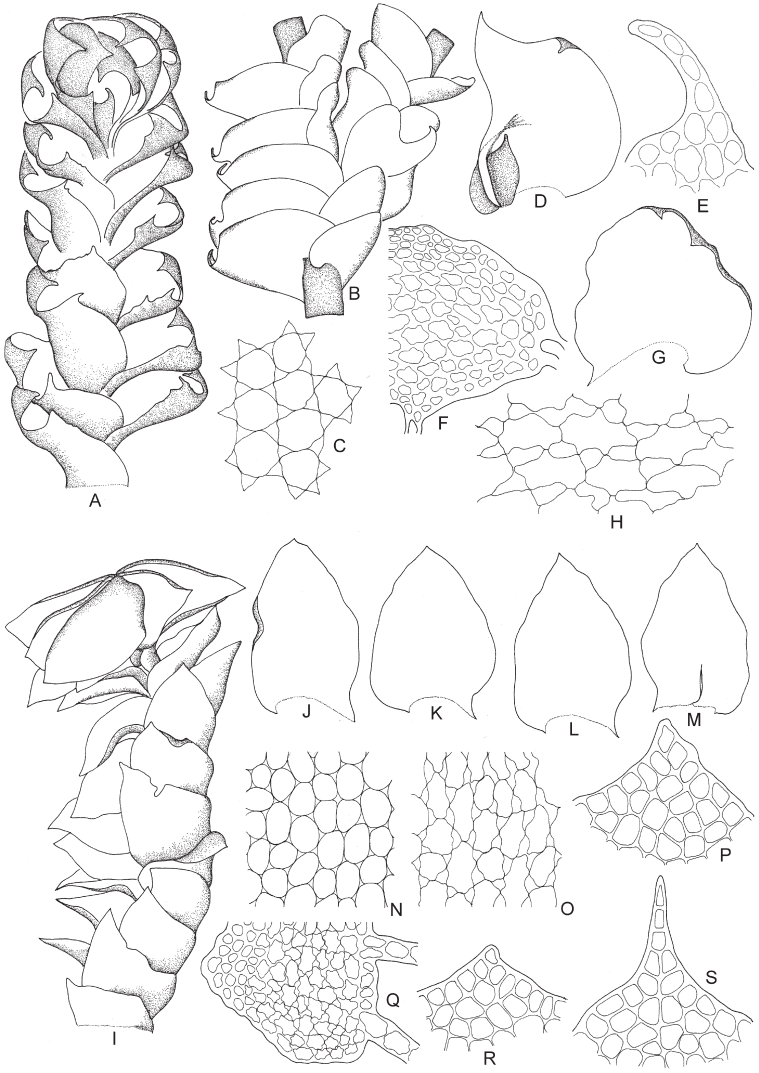


Figure 11. *Syzygiella flaccida* (Steph.) Gradst. & G.E.Lee. A: Part of plant, dorsal view. B: Part of plant ventral view. C: Median leaf cells. D,G: Leaf. E: Apical leaf cells. F: Part of cross section of stem. H: Basal leaf cells. *Syzygiella contracta* (Reinw. *et al.*) Gradst. & G.E.Lee. I: Portion of shoot. J–M: Leaves. N: Median leaf cells. O: Basal leaf cells. P,R,S: Apical leaf cells. Q: Cross section of stem. (A–H redrawn from Grolle 1965b as *Lophozia hamatifolia*; I–S redrawn from Kitagawa 1981 as *Jamesoniella contracta*).

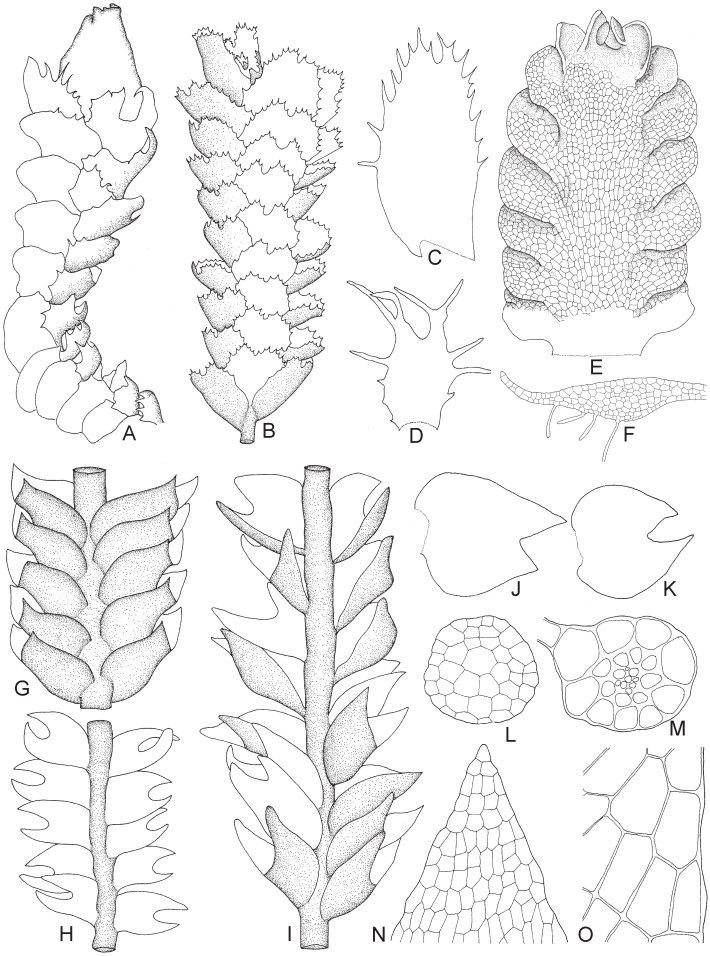


Figure 12. *Acroscyphella tjiwideiensis* (Sande Lac.) N.Kitag. & Grolle. A: Female shoot, lateral view. *Isotachis japonica* Steph. B: Part of plant, ventral view. *Balantiopsis ciliaris* S.Hatt. C: Ventral leaf lobe. D: Underleaf. *Schiffneria hyalina* Steph. E: Dorsal aspect of shoot. F: Cross section through axis and rhizoids. *Cephalozia acutiloba* (Inoue) Váňa. G: Part of plant, ventral view. J: Leaf. L: Cross section of stem. N: Postical lobe of leaf. O: Marginal leaf cells. *Cephalozia hamatiloba* Steph. H: Part of plants, dorsal view. I: Part of plant, ventral view. K: Leaf. M: Cross section of stem. (A redrawn from Piippo 1985b as *Clasmatocolea tjiwideiensis*; B redrawn from Singh & Singh 2009; C,D redrawn from Hattori 1966; E,F redrawn from Schuster 1984; G,J,L,N,O redrawn from Inoue 1967b as *Metahygrobiella acutiloba*; H,I,K,M redrawn from Amakawa 1952 as *Cephalozia otaruensis*).

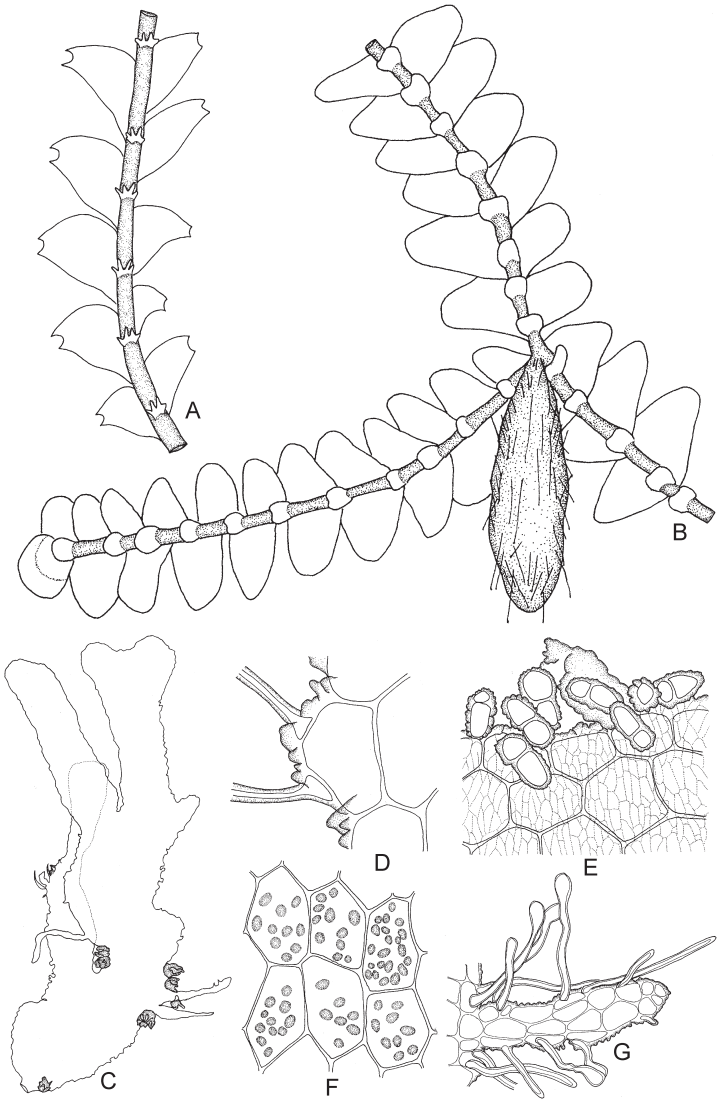


Figure 13. *Calypogeia arguta* Nees & Mont. A: Part of plant. *Mnioloma fuscum* (Lehm.) R.M.Schust. B: Part of female plant with marsupium. *Mizutania riccardioides* Furuki & Z.Iwats. C: Part of plant. D: Marginal cells of thallus with rhizoids. E: Marginal cells of thallus with gemmae. F: Median cells of thallus with oil bodies. G: Young, narrow, subterranean regenerated branch, ventral view. (A redrawn from Gradstein 2011; B redrawn from Gao *et al.* 2002; others redrawn from Furuki & Iwatsuki 1989).

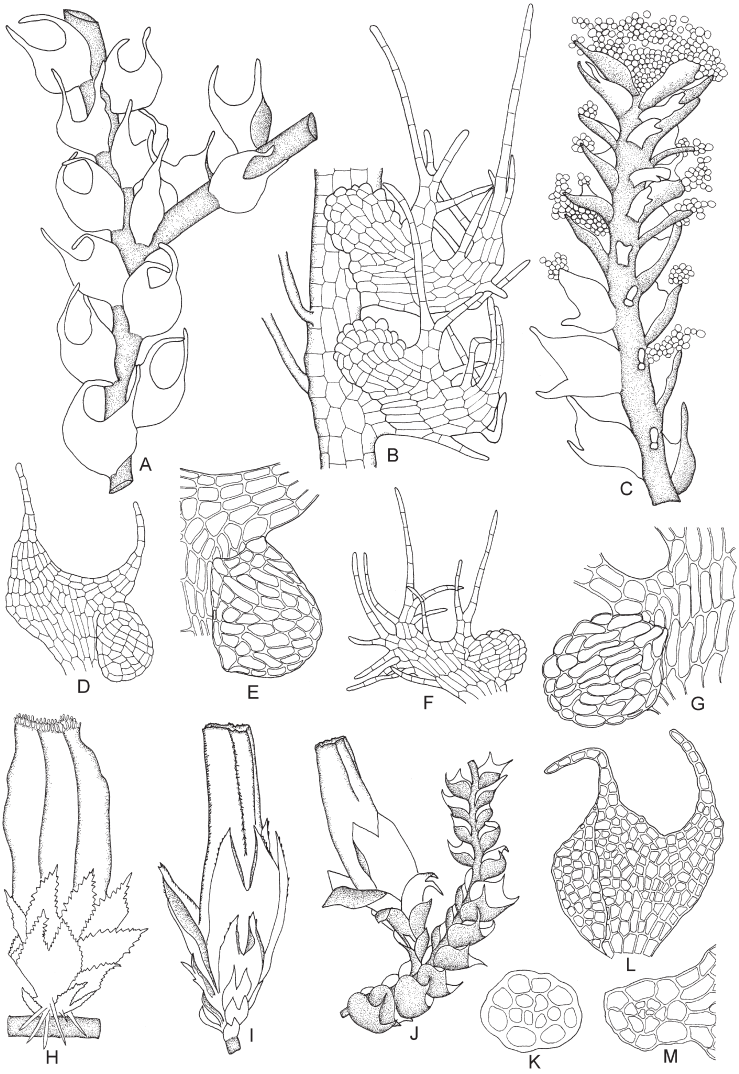


Figure 14. *Nowellia curvifolia* (Dicks.) Mitt. A: Part of plant, dorsal view. C: Tips of gemmiparous leaf showing gemmae formation. H,J: Part of plant with perianth, ventral view. L: Mature leaf. M: Cross section of stem. *Nowellia borneensis* (De Not.) Schiffn. D: Leaf. E: Part of leaf showing leaf lobule. K: Cross section of leaf. *Nowellia langii* Pearson. B: Part of plant. F: Leaf. G: Part of leaf showing leaf lobule. I: Part of plant with perianth. (A,C,H,L,M redrawn from Schertler 1977; others redrawn from Grolle 1968).

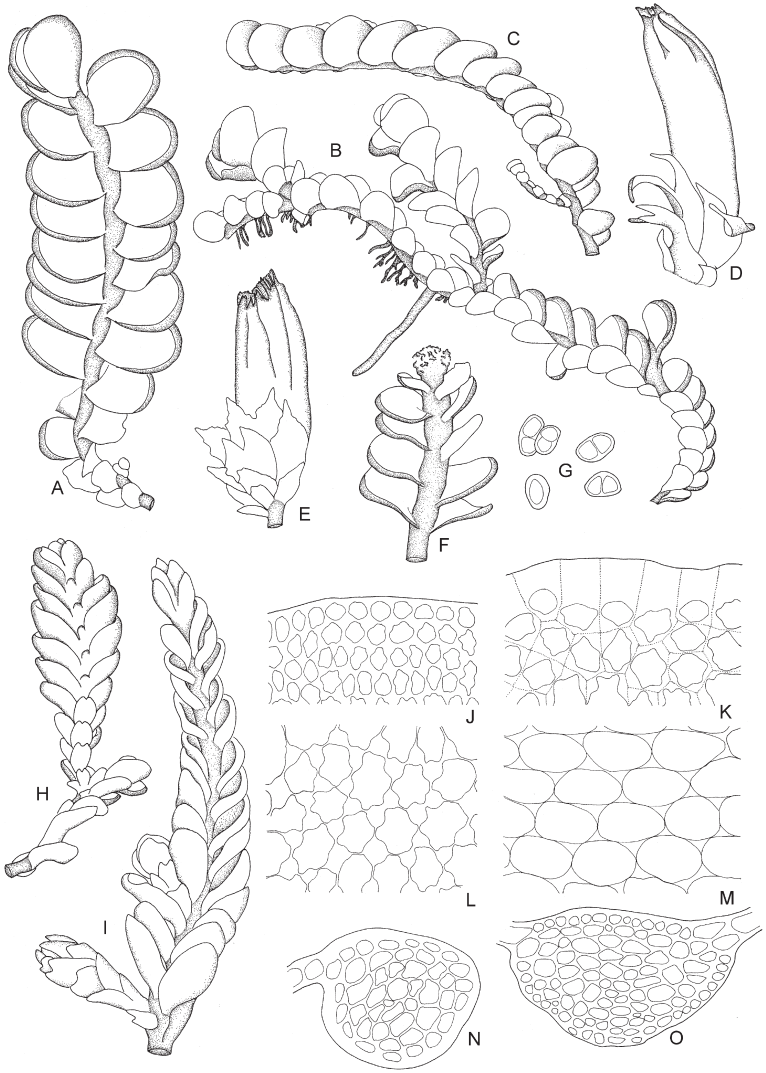


Figure 15. *Odontoschisma sphagi* (Dicks.) Dumort. A: Part of plant, dorsal view. C: Part of plant, lateral view. D: Gynoecium with mature perianth. M: Median leaf cells. O: Cross section of stem. *Odontoschisma denudatum* (Mark.) Dumort. B: Part of plant, lateral view. E: Gynoecium and perianth. F: Part of plant, ventral view showing gemmae. G: Gemmae. J: Leaf margin. L: Median leaf cells. *Odontoschisma purpuratum* Herzog. H: Part of plant, dorsal view. I: Plant of plant with gynoecial branch, ventral view. K: Marginal leaf cells. N: Cross section of stem. (All redrawn from Gradstein & Ilkiu-Borges 2015).

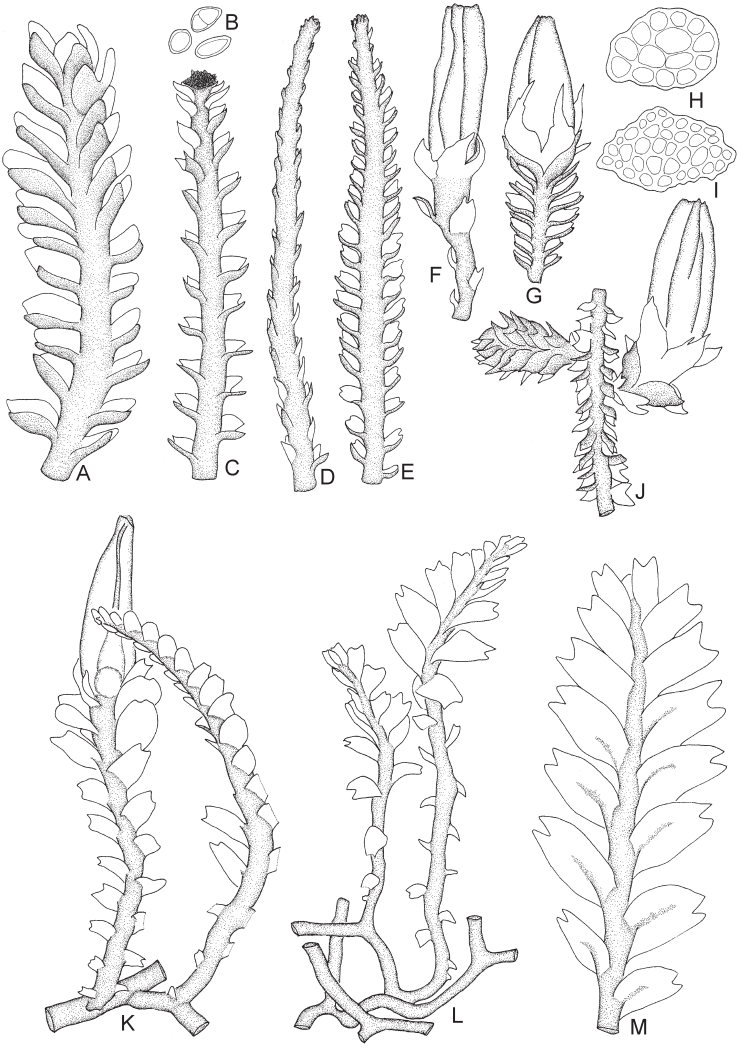


Figure 16. *Cephaloziella capillaris* (Steph.) Douin. A: Shoot, ventral view. F: Gynoecium and perianth. H: Cross section of stem. *Cephaloziella kiaeri* (Austin) Douin. B: Gemmae. C: Part of plant with gemmae at the shoot-apex. D: Flagelliform shoot. J: Male and female plants. *Cylindrocolea tagawae* (N.Kitag.) R.M.Schust. E: Part of plant. G: Gynoecium and perianth. I: Cross section of stem. *Kymatocalyx rhizomatica* (Herzog) Gradst. & Váňa. K: Portion of fertile plant, ventral view. L: Portion of sterile plant, dorsal view. M: Portion of leafy shoot, ventral view. (A–J redrawn from Kitagawa 1969a B–D as *Cephaloziella willisana*, E,G,I as *Cephaloziella tagawae*; K–M redrawn from Gradstein & Váňa 1999).

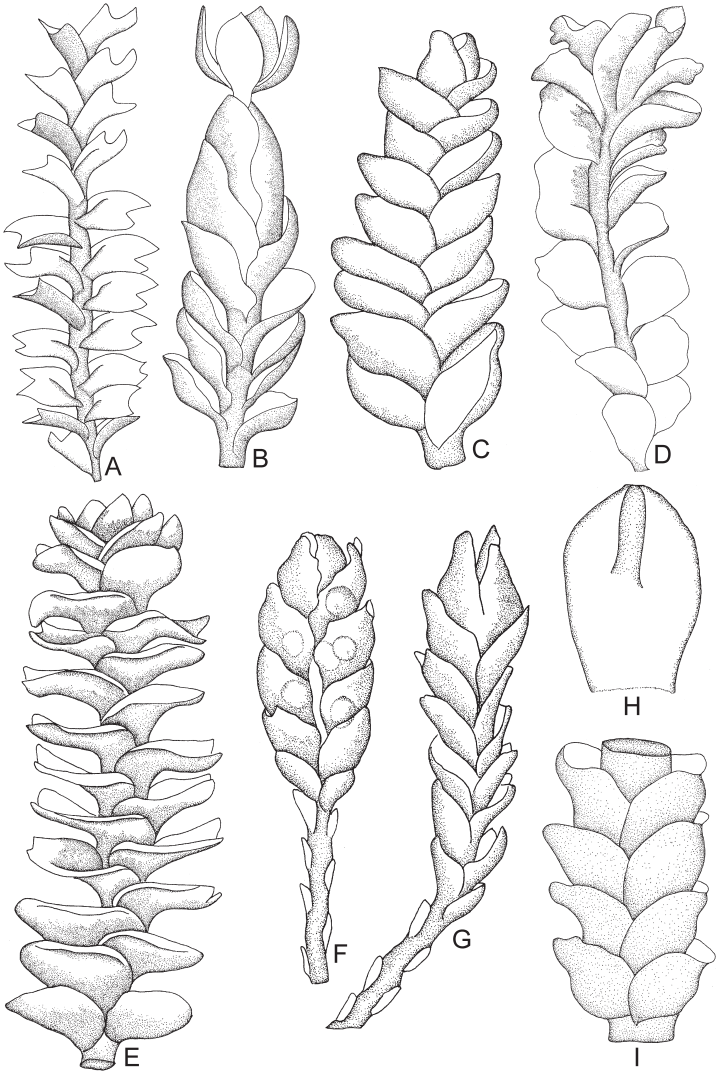


Figure 17. *Gymnomitrion revolutum* (Nees) H.Philib. A: Part of plant. *Gymnomitrion subintegrum* (S.W.Arnell) Váňa. B: Female plant. C: Male plant. *Marsupella emarginata* (Ehrh.) Dumort. E: Part of plant. *Marsupella stoloniformis* N.Kitag. F: Male plant. G: Female plant. *Nardia assamica* (Mitt.) Amakawa. D: Part of plant, dorsal view. H: Perianth. I: Male plant. (A redrawn from Váňa & Piippo 1989a as *Marsupella revoluta*; B,C,F,G redrawn from Kitagawa 1967 B,C as *M. integra*; D redrawn from Váňa *et al.* 2005; H,I redrawn from Váňa 1976; E redrawn from Schuster 1974).

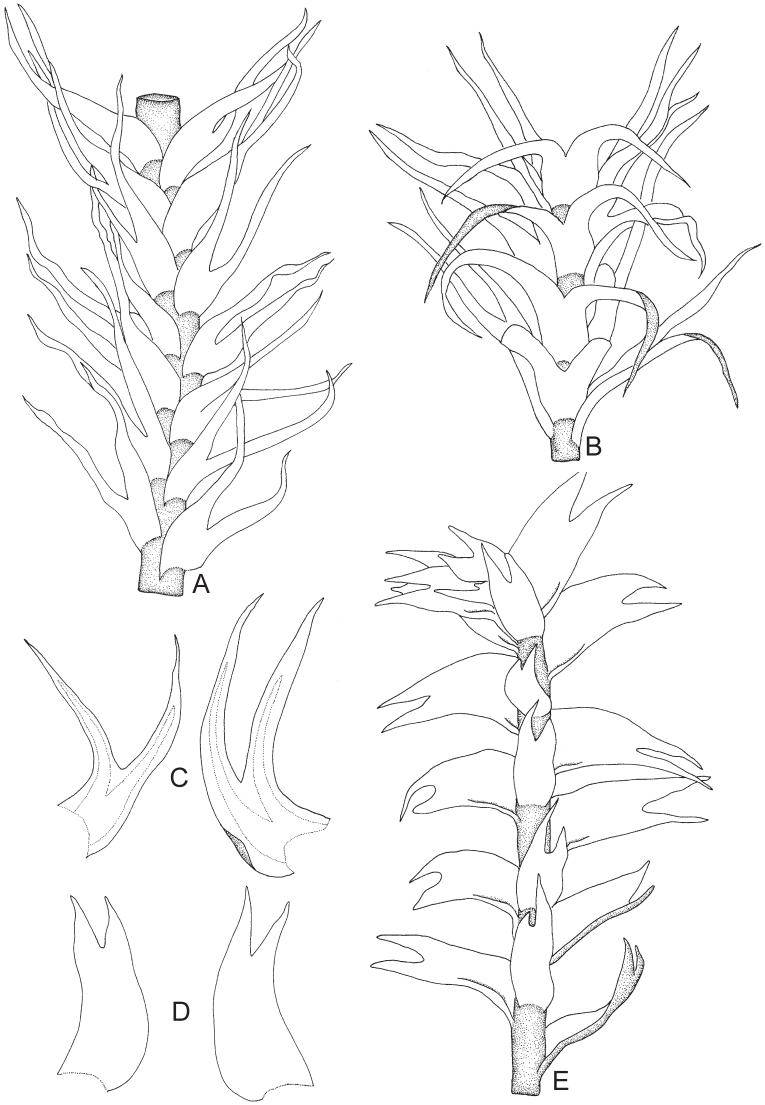


Figure 18. *Herbertus pilifer* Schiffn. A: Part of plant, dorsal view. *Herbertus armitanus* (Steph.) H.A.Mill. B: Part of plant, dorsal view. C: Leaves. *Triandrophyllum heterophyllum* (Steph.) Grolle. D: Leaves. E: Part of plant, ventral view. (A,B redrawn from Juslén 2006; C redrawn from Gradstein 2011; D,E redrawn from Grolle 1964).

Figure 19. *Jackiella angustifolia* Herzog. A: Part of plant, dorsal view with marsupium. B: Marsupium. C,D: Leaves. *Mesoptychia subcrispa* (Herzog) L.Söderstr. & Váňa. E: Leaf. F: Median leaf cells. G: Habit. H: Perianth. (A–D redrawn from Herzog 1950; E–H redrawn from Herzog 1942a as *Lophozia subcrispa*).

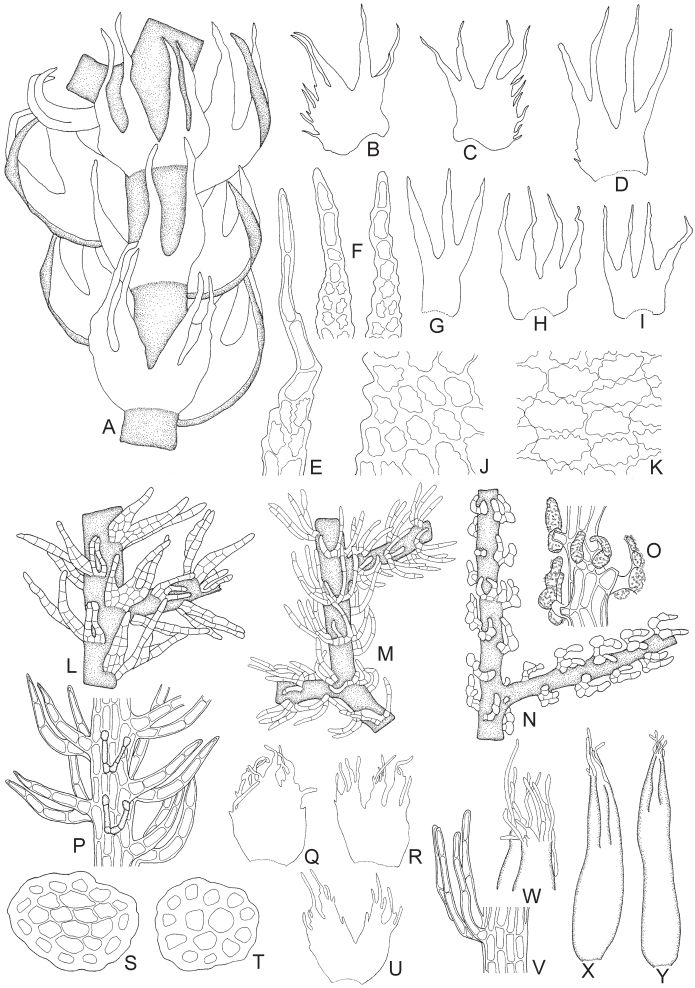


Figure 20. *Lepicolea yakusimensis* (S.Hatt.) S.Hatt. A: Part of plant, ventral view. B,C: Leaves. E: Underleaf apex. H,I: Underleaves. J: Marginal underleaf cells. K: Basal leaf cells. *Lepicolea rara* (Steph.) Grolle. D,G: Leaves. F: Leaf apices. *Kurzia abietinella* (Herzog) Grolle. L: Part of stem, ventral view. *Kurzia lineariloba* Mizut. M: Part of stem, ventral view. T: Cross section of stem. V: Stem leaf. *Kurzia geniculata* Mizut. N: Part of stem. O: Part of branch, ventral view. *Kurzia gonyotricha* (Sande Lac.) Grolle. P: Part of stem. *Kurzia abbreviata* Mizut. Q,R: Female bracts. U: Female bracteole. S: Cross section of stem. Y: Perianth. *Kurzia borneensis* Mizut. W: Apex of perianth. X: Perianth. (A–C,E,H–J redrawn from Hattori 1953; D,G,F redrawn from Kitagawa 1978 as *L. loriana*; L–Y redrawn from Mizutani 1974).

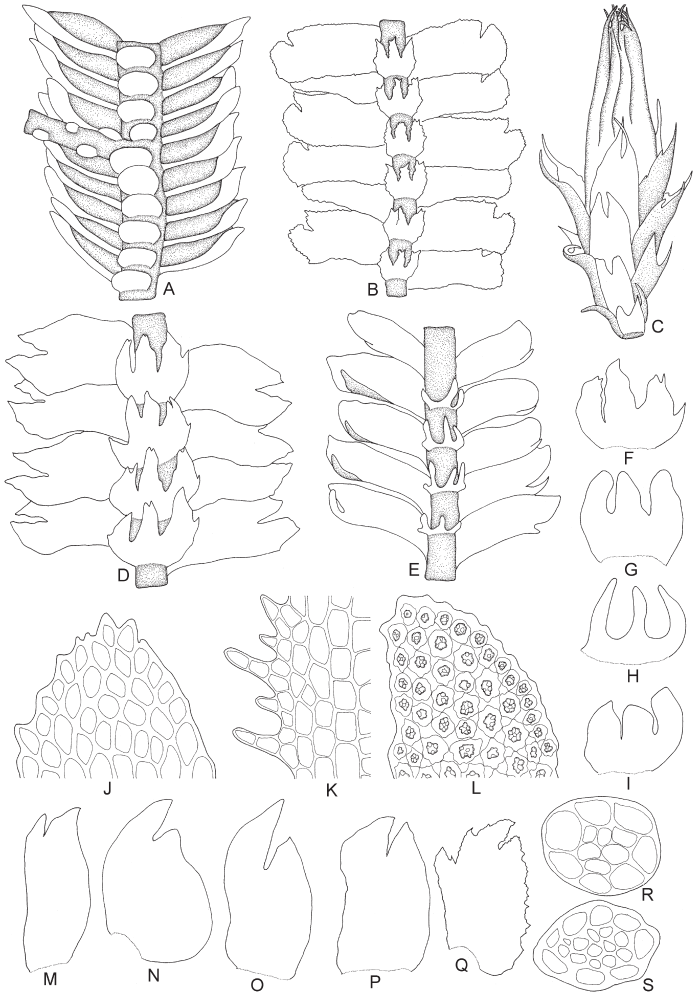


Figure 21. *Acromastigum bancanum* (Sande Lac.) A.Evans. A: Part of plant, ventral view. *Acromastigum inaequilaterum* (Lehm. & Lindenb.) A.Evans. B,D: Part of plants, ventral view. J: Dorsal division of leaf. F: Underleaf. P: Leaf. S: Cross section of stem. *Acromastigum laevigatum* A.Evans. C: Gynoecium and perianth. *Acromastigum echinatum* (Gottsche) A.Evans. I: Underleaf. L: Ventral division of leaf. N: Leaf. *Acromastigum obliquatum* (Mitt.) A.Evans. E: Part of plant, ventral view. H: Underleaf. M: Leaf. R: Cross section of stem. *Acromastigum echinatiforme* (De Not.) A.Evans. G: Underleaf. O: Leaf. *Acromastigum fimbriatum* (Steph.) A.Evans. K: Cells from leaf base. *Acromastigum lobuliferum* A.Evans. Q: Leaf. (D,E redrawn from Piippo 1991; others redrawn from Evans 1934 A as *A. bidenticulatum*).

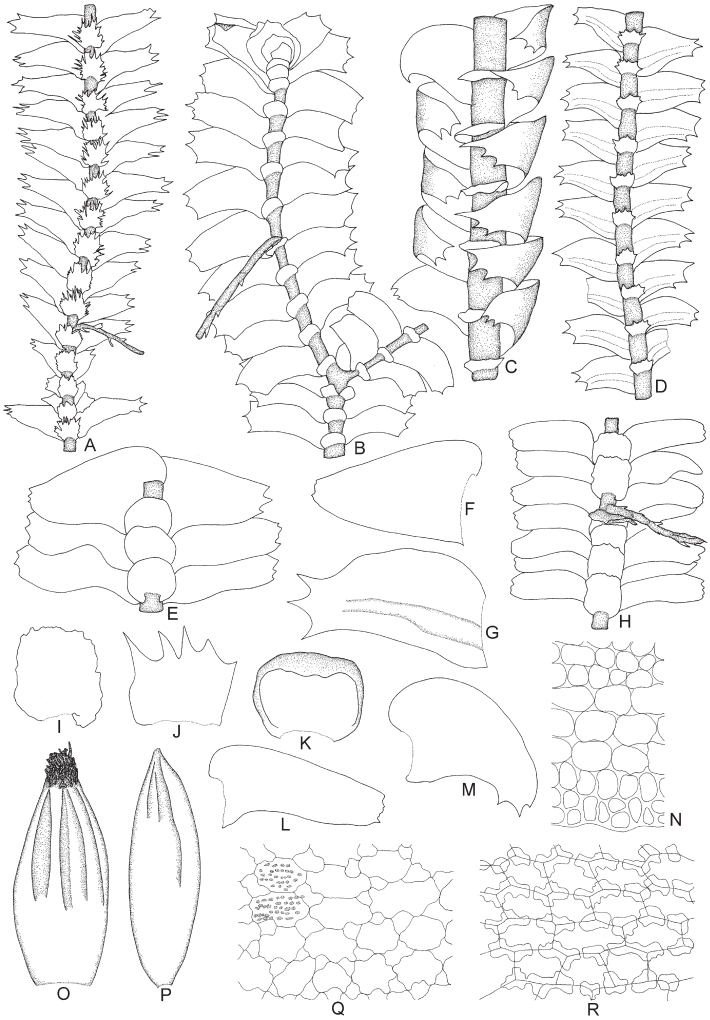


Figure 22. *Bazzania calcarata* (Sande Lac.) Schiffn. A: Part of plant, ventral view. R: Median leaf cells. *Bazzania parvitexta* Steph. B: Part of plant, ventral view. Q: Median leaf cells. *Bazzania serpentina* (Nees) Trevis. C: Part of plant, ventral view. K: Underleaf. M: Leaf. P: Perianth. *Bazzania subtilis* (Sande Lac.) Trevis. D: Part of plant, ventral view. G: Leaf. J: Underleaf. N: Median leaf cells, showing three rows of cells forming a vitta. *Bazzania erosa* (Reinw. *et al.*) Trevis. E: Part of plant, ventral view. F: Leaf. *Bazzania longicaulis* (Sande Lac.) Schiffn. H: Part of plant, ventral view. I: Leaf. L. Leaf. O: Perianth. (A,B,Q,R redrawn from Kitagawa 1979; others redrawn from Kitagawa 1977).

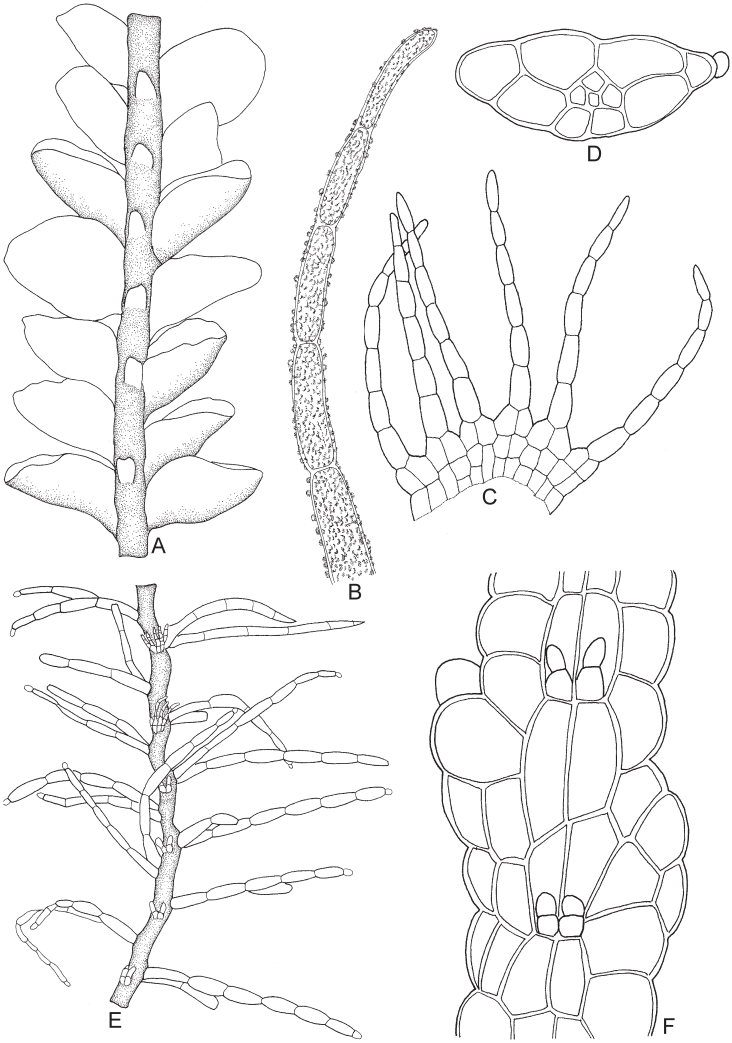


Figure 23. *Hygrolembidium boschianum* (Sande Lac.) R.M.Schust. A: Part of plant, ventral view. *Tricholepidozia trichocoleoides* (Herzog) E.D.Cooper. B: Part of leaf lobe showing papillae. *Tricholepidozia neesii* (Lindenb.) E.D.Cooper. C: Leaf. *Zoopsis liukiuensis* Horik. D: Cross section of stem. F: Part of plant, ventral view. *Telaranea major* (Herzog) J.J.Engel & G.L.Merr. E: Part of plant, ventral view. (A redrawn from Piippo 1991; C,D,F redrawn from Gradstein 2011 C as *Telaranea neesii*; E redrawn from Piippo 1985c as *Arachniopsis major*; B redrawn from Engel & Smith-Merrill 2004 as *Telaranea trichocoleoides*).

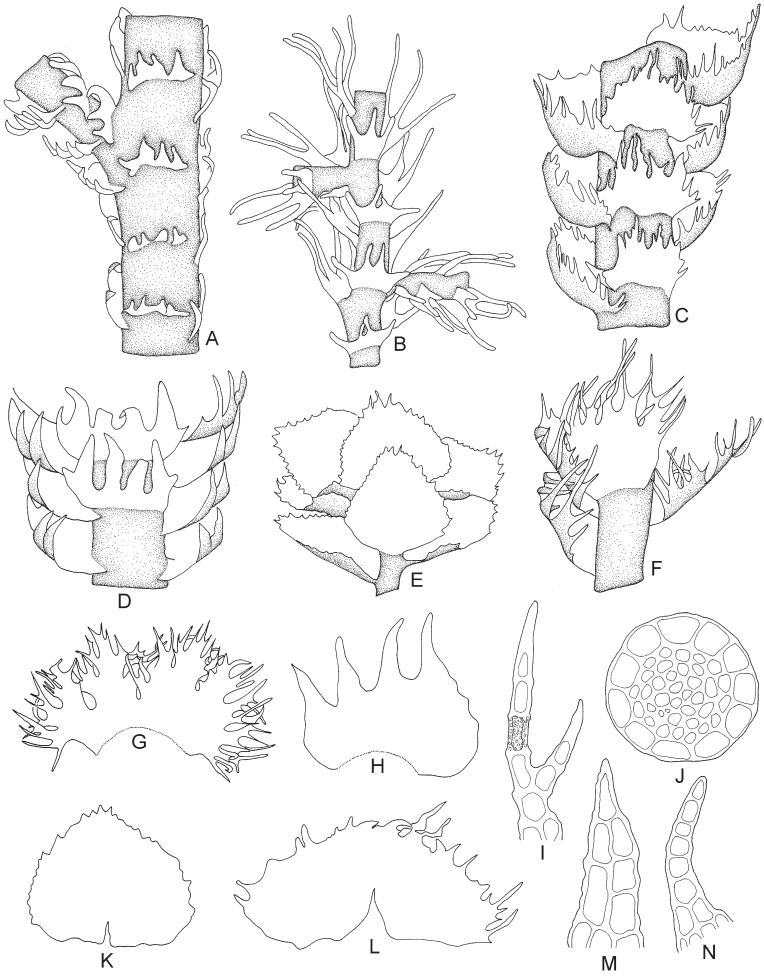


Figure 24. *Lepidozia kinabaluensis* Mizut. A: Part of plant, ventral view. N: Lobe of stem leaf. *Neolepidozia ophiria* (Gottsche) E.D.Cooper. B: Part of plant, ventral view. J: Cross section of stem. *Lepidozia holorhiza* (Reinw. *et al.*) Nees. C: Part of plant, ventral view. L: Leaf. *Lepidozia everettii* Steph. D: Part of plant, ventral view. H: Underleaf. *Lepidozia ferdinandi-muelleri* Steph. E: Part of plant, ventral view. K: Leaf. M: Lobe of branch leaf. *Lepidozia borneensis* Steph. F: Part of plant, ventral view. *Lepidozia miqueliana* Sande Lac. G: Leaf. I: Cilia of lobe of stem leaf. (A,B,J,N,O redrawn from Mizutani 1974 B,J as *Lepidozia ophiria*; others redrawn from Mizutani 1968).

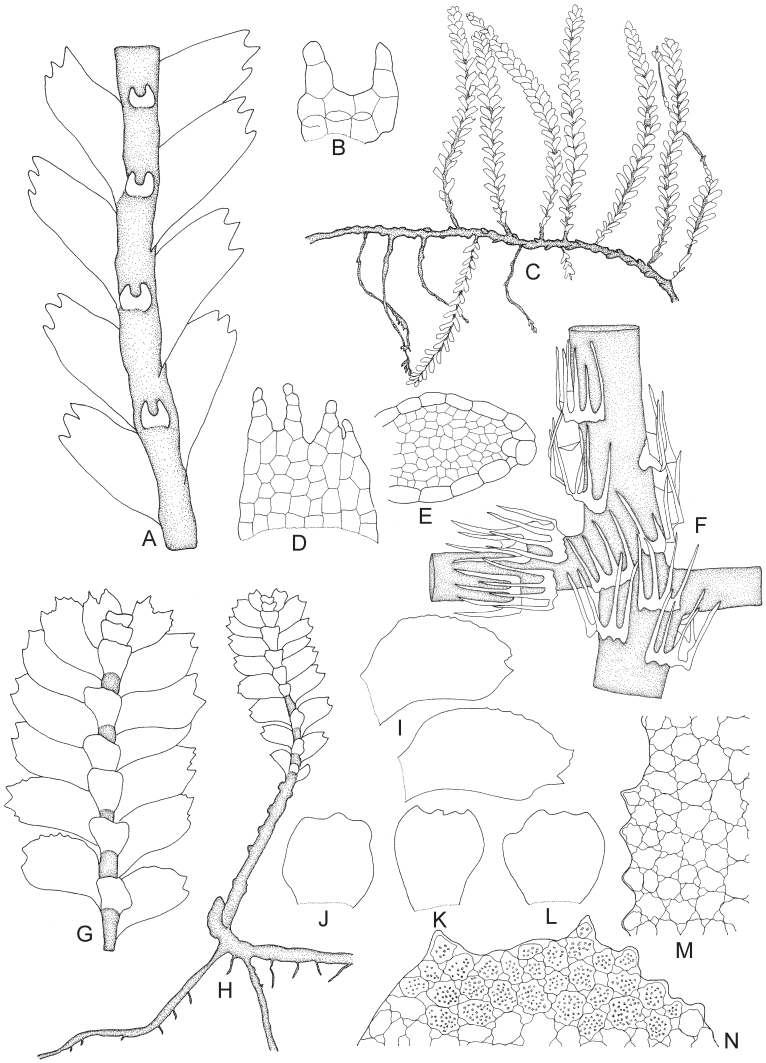


Figure 25. *Neolepidozia longitudinalis* (Herzog) E.D.Cooper. A: Part of plant, ventral view. B: Underleaf. C: Habit. D: Leaf. E: Cross section of stem. *Psiloclada clandestina* Mitt. F: Part of plant. *Mastigopelma pulvinulatum* (De Not.) Grolle. G: Part of plant. H: Habit. I: Leaves. J–L: Underleaves. M: Marginal leaf cell. N: Apical leaf cells. (A–E redrawn from Herzog 1950 as *Lepidozia longitudinalis*; F redrawn from Fulford & Taylor 1959; G–N redrawn from Herzog 1950 as *Mastigopelma bilobum*).

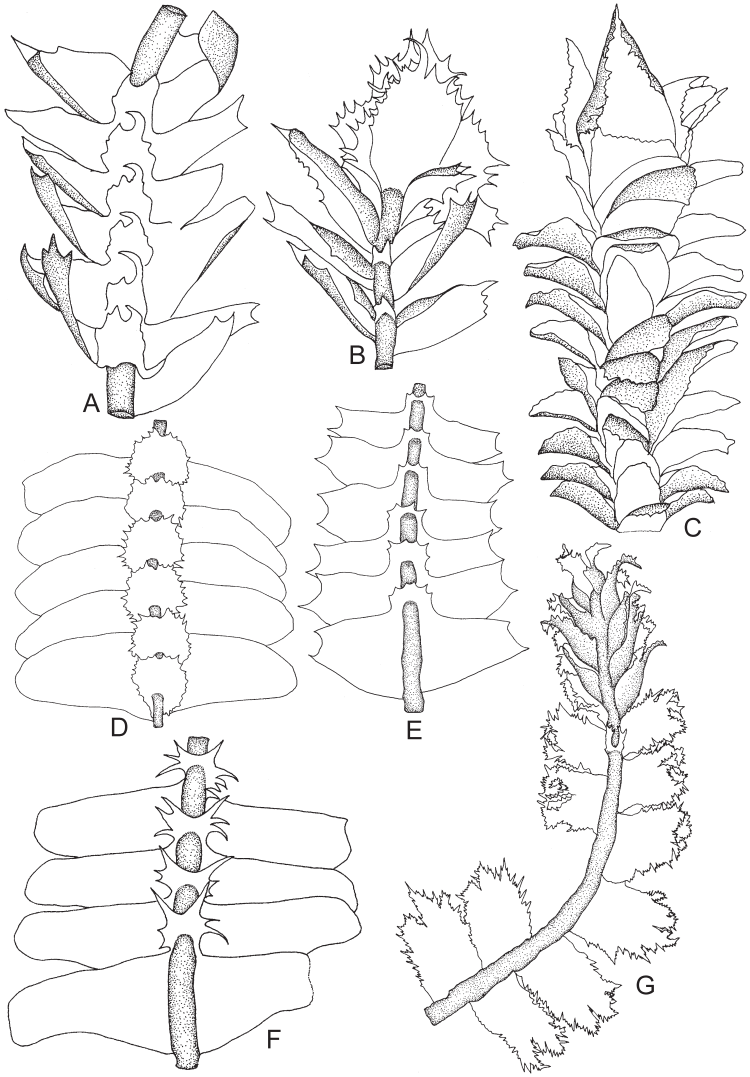


Figure 26. *Cryptolophocolea ciliolata* (Nees) L.Söderstr. A: Part of plant, ventral view. B: Female plant. *Cryptolophocolea costata* (Nees) L.Söderstr. C: Female plant. *Heteroscyphus splendens* (Lehm. & Lindenb.) Grolle. D: Part of plant, ventral view. *Heteroscyphus coalitus* (Hook.) Schiffn. E: Part of plant. *Heteroscyphus succulentus* (Gottsche) Schiffn. F: Part of plant. *Lophocolea muricata* (Lehm.) Nees. G: Part of plant. (A–C redrawn from Piippo 1985b A,B as *Lophocolea ciliolata,* C as *L. costata*; D–F redrawn from Gradstein 2011; G redrawn from Piippo 1985a as *Lophocolea bidentula*).

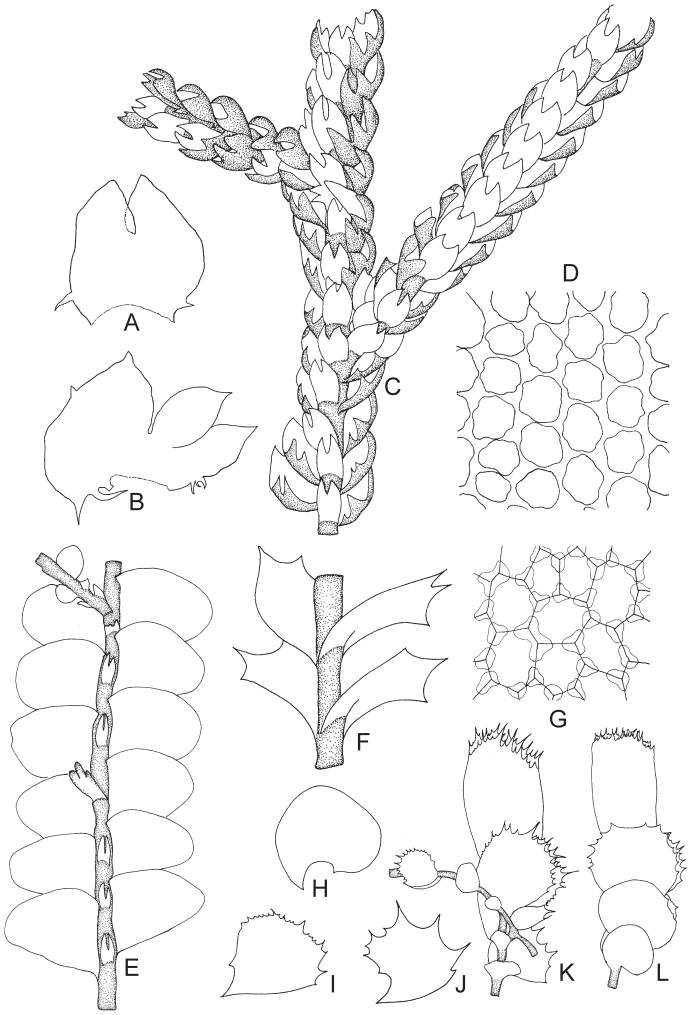


Figure 27. *Mastigophora diclados* (F.Weber) Nees. A: Underleaf. B: Leaf. C: Part of plant, ventral view. D: Median leaf cells. *Notoscyphus lutescens* (Lehm. & Lindenb.) Mitt. E: Part of plant, ventral view. *Chiastocaulon pachycephalum* (De Not.) Herzog. F: Part of plant, dorsal view. G: Median leaf cells. *Chiastocaulon braunianum* (Nees) S.D.F.Patzak *et al.* H: Leaf. L: Part of plant with perianth, *Chiastocaulon oppositum* (Reinw. *et al.*) S.D.F.Patzak *et al.* I,J: Leaves. K: Part of plant with perianth, lateral view. (A,B redrawn from Gradstein 2011; C,D redrawn from Daniels & Kariyappa 2012; E redrawn from Váňa & Piippo 1989a; F–L redrawn from Inoue 1964 F,G as *Plagiochilion pachycephalum*).

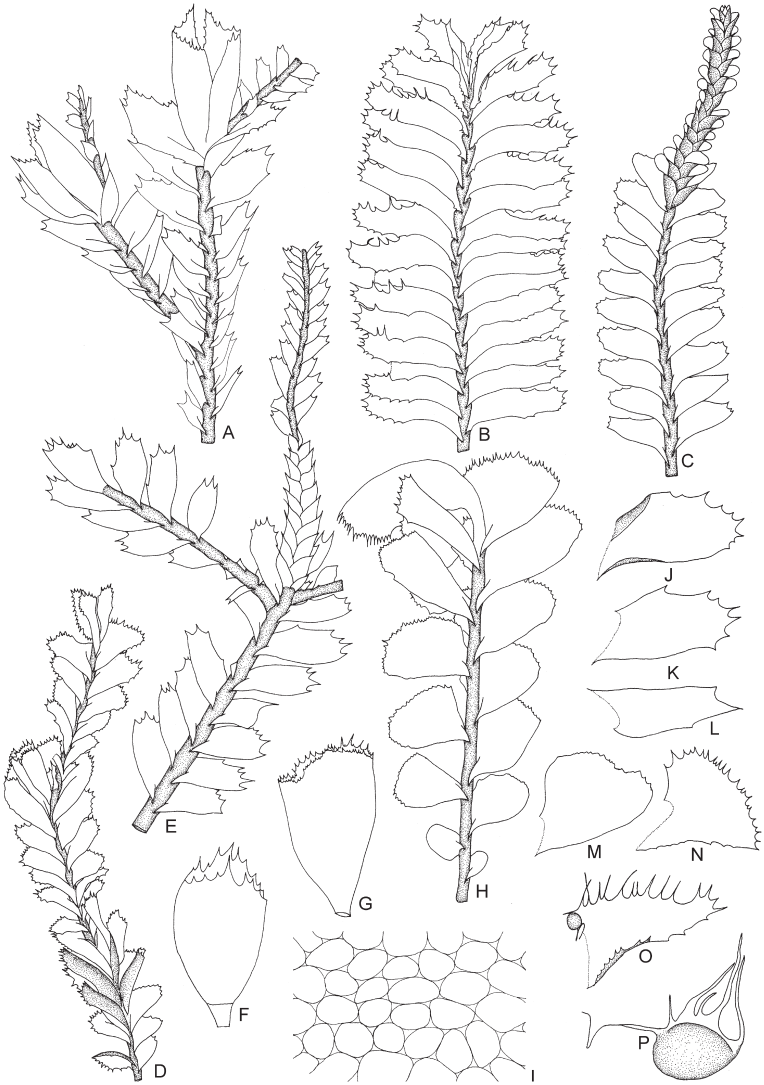


Figure 28. *Chiastocaulon dendroides* (Nees) Carl. A: Female plant, dorsal view. F: Perianth. L: Leaf. *Plagiochila bantamensis* (Reinw. *et al.*) Mont. B: Part of plant. O: Leaf. P: Ventral sac. *Plagiochila kurzii* Steph. C: Male plant. I: Basal leaf cells. J: Leaf. *Plagiochila peculiaris* Schiffn. D: Part of plant. G: Perianth. N: Leaf. *Plagiochila singularis* Schiffn. E: Male plant. K: Leaf. *Plagiochila sumatrana* Schiffn. H: Part of plant and perianth. M: Leaf. (H,M redrawn from So 2000; others redrawn from So 2001).

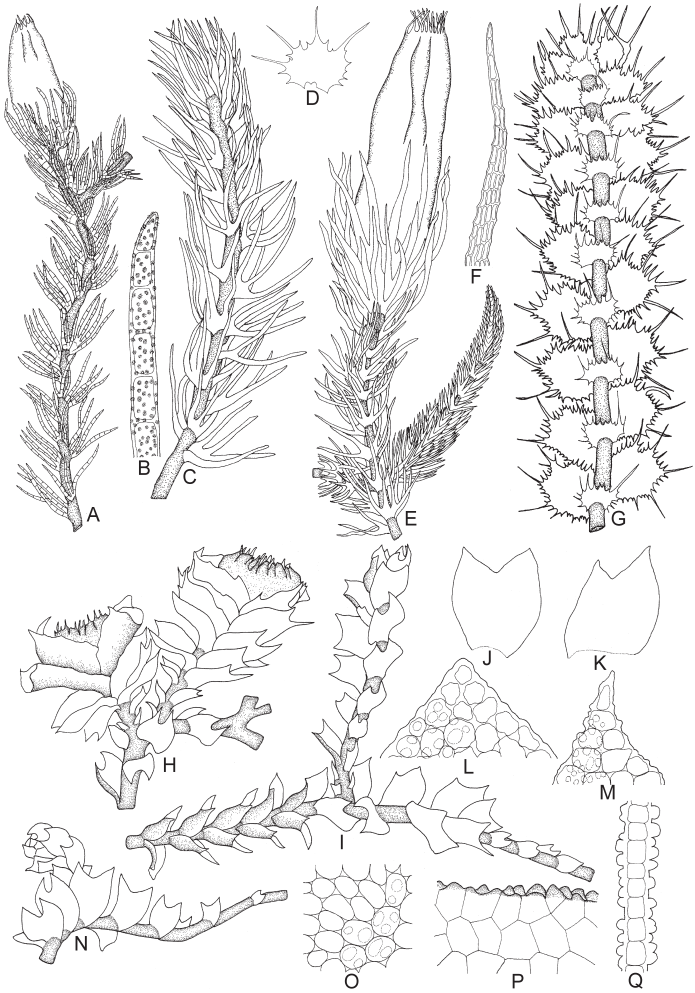


Figure 29. *Blepharostoma trichophyllum* (L.) Dumort. A: Female plant, ventral view. B: Part of leaf lobe showing papillose cuticle. *Pseudolepicolea trollii* (Herzog) Grolle & Ando. C: Part of plant, dorsal view. E: Part of plant with gynoecial and androecial branches, ventral view. F: Apical leaf cell. *Temnoma setigerum* (Lindenb.) R.M.Schust. D: Leaf. G: Part of plant, ventral view. *Andrewsianthus kinabaluensis* N.Kitag. H: Part of plant with gynoecia and perianths. J: Leaf. L: Apical leaf cells. N: Part of plant. O: Median leaf cells. *Andrewsianthus papillosus* N.Kitag. I: Part of plant. K: Leaf. M: Apical leaf cells. P: Marginal leaf cells. Q: Cross section of leaf. (B redrawn from Asthana *et al.* 2013; D redrawn from Gradstein 2011; A,C,E–G redrawn from Singh *et al.* 2014; H–Q redrawn from Kitagawa 1970).

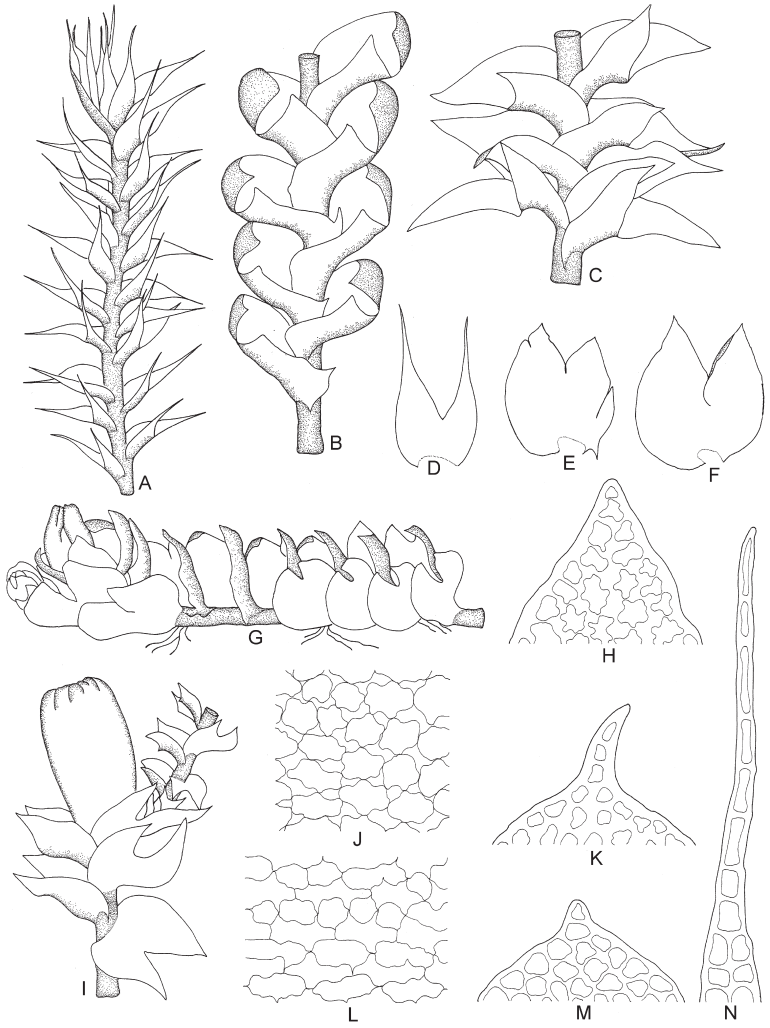


Figure 30. *Anastrophyllum aristatum* (N.Kitag.) A.E.D.Daniels *et al.* A: Part of plant, ventral view. D: Leaf. N: Apical leaf cells. *Anastrophyllum auritum* (Lehm.) Steph. B: Part of plant. E: Leaf. G: Part of plant with gynoecium and perianth. J: Median leaf cells. M: Apical leaf cells. *Anastrophyllum squarrosum* Herzog. C: Part of plant. I: Gynoecium and perianth. L: Median leaf cells. *Anastrophyllum piligerum* (Nees) Steph. F: Leaf. K: Apical leaf cells. *Anastrophyllum revolutum* Steph. H: Apical leaf cells. (All redrawn from Kitagawa 1970 B as *A. appendiculatum*).

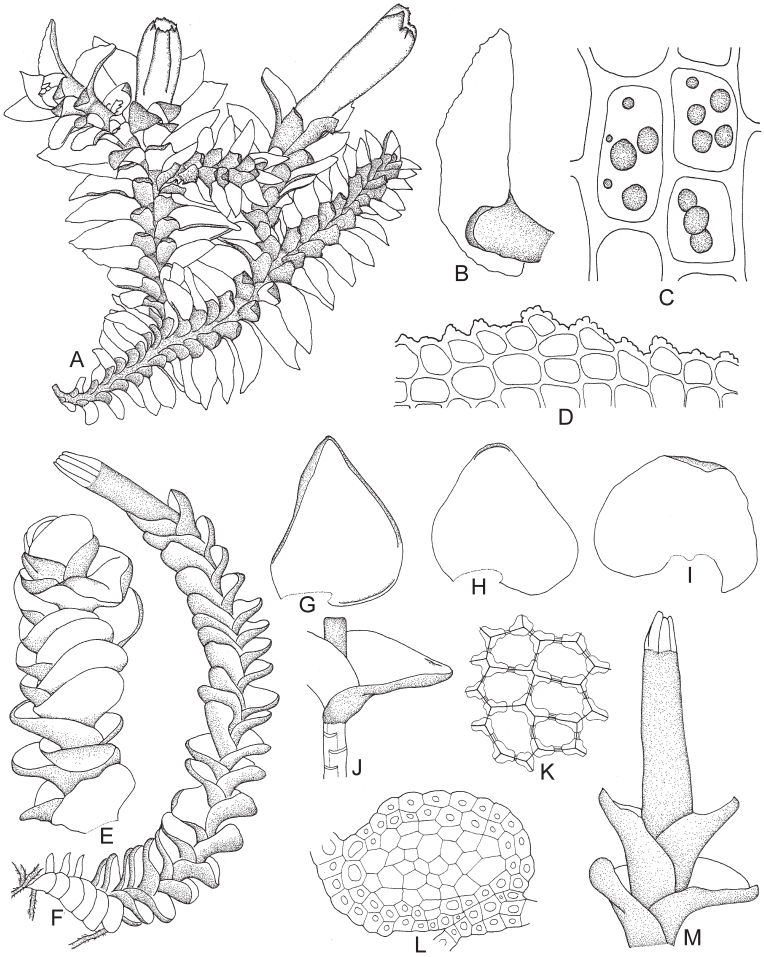


Figure 31. *Diplophyllum kinabaluense* Furuki & M.Suleiman. A: Part of plant with gynoecia and perianths. B: Leaf. C: Apical leaf cells showing oil bodies. D: Marginal leaf cells. *Gottschelia schizopleura* (Spruce) Grolle. E: Part of plant. F: Part of plant with gynoecium and perianth. G–I: Leaves. J: Part of plant showing dorsal insertion of leaves. K: Median leaf cells. L: Cross section of stem. M: Gynoecium and perianth. (A–D redrawn from Furuki & Suleiman 2016; E,I redrawn from Váňa & Piippo 1989b; F–H,J–M redrawn from Grolle 1968).

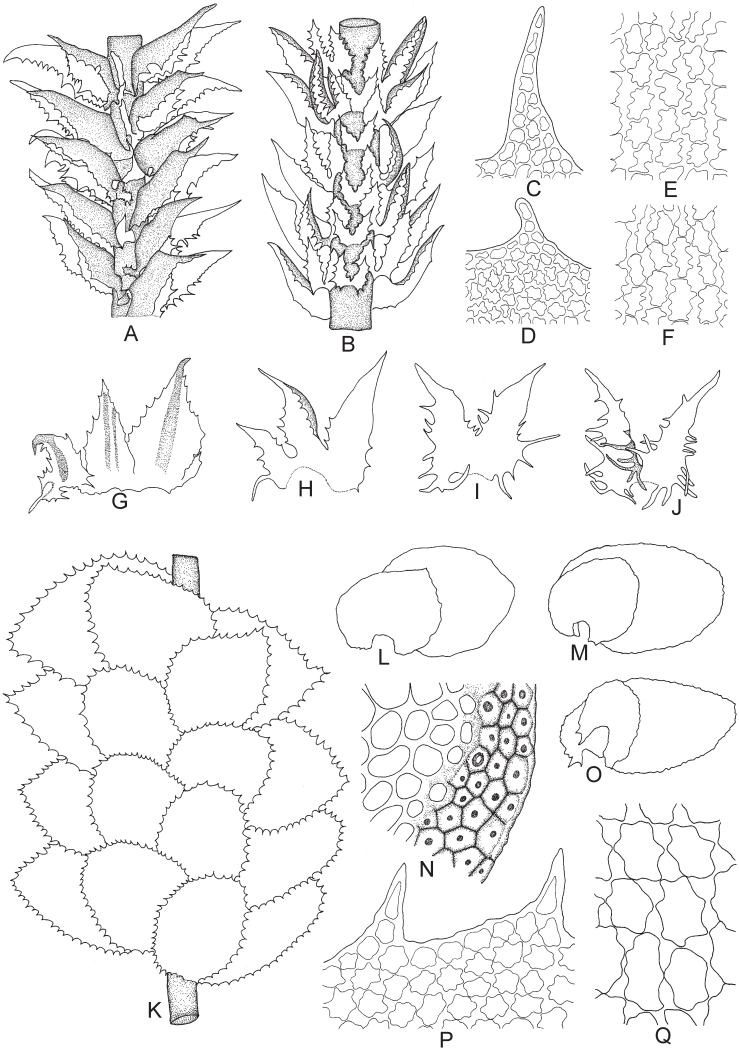


Figure 32. *Plicanthus hirtellus* (F.Weber) R.M.Schust. A: Part of plant, dorsal view. B: Part of plant, ventral view. C,D: Marginal leaf cells with cilia or tooth. E: Median leaf cells. F: Basal leaf cells. G,H: Leaves. I,J: Underleaves. *Scapania ornithopodioides* (With.) Waddell. K: Part of plant, ventral view. L,M,O: Leaves. N: Part of cross section of stem. P: Marginal leaf cells. Q: Basal leaf cells. (A,D,G redrawn from Horikawa 1930 as *Mastigophora spinosa*; B–E,F, H–J redrawn from Kitagawa 1965a as *Chandonanthus hirtellus*; K redrawn from Pearson 1902; L–Q redrawn from Amakawa & Hattori 1954).

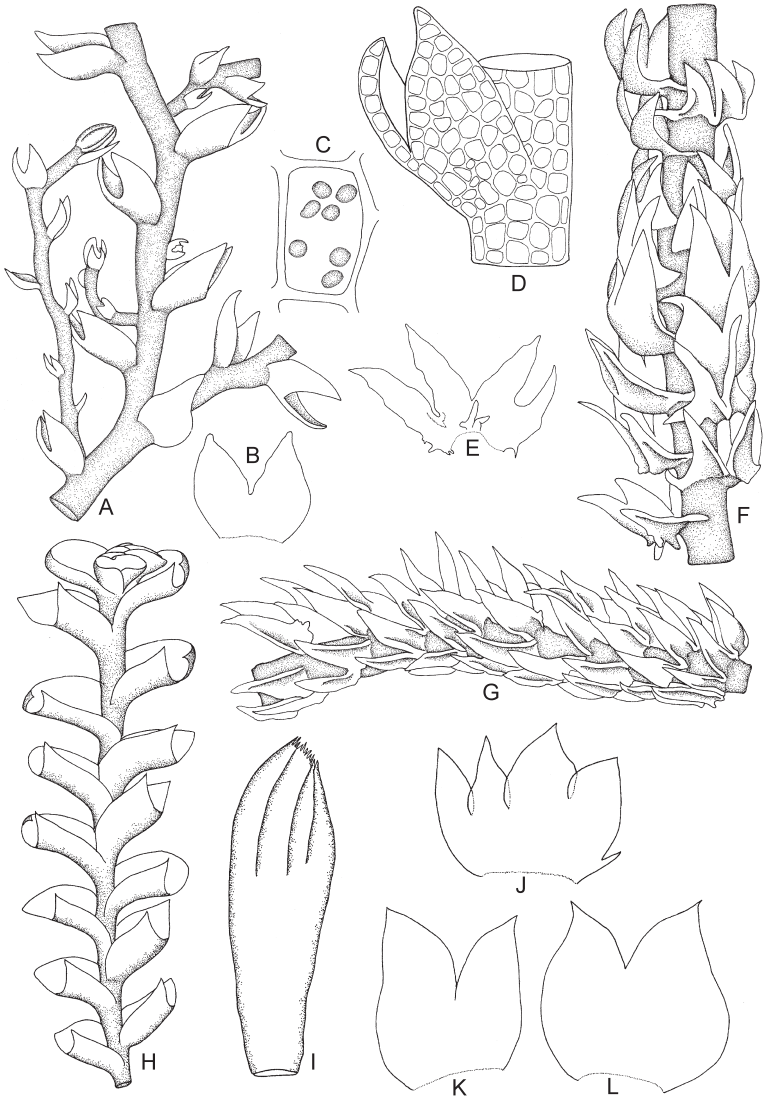


Figure 33. *Sphenolobopsis pearsonii* (Spruce) R.M.Schust. A: Part of plant. B: Leaf. C: Median leaf cells with oil bodies. D: Part of stem and leaf. *Tetralophozia filiformis* (Steph.) Urmi. F,G: Part of plant. E: Leaf. *Sphenolobus minutus* (D.Crantz) Berggr. H: Part of plant. I: Perianth. J: Female bracts. K,L: Leaves. (A,C redrawn from Schuster 1962 *Cephaloziopsis pearsoni*; B,D redrawn from Kitagawa 1965b as *C. pearsonii*; F,G redrawn from Urmi 1983; H–L redrawn from Pearson 1902 as *Jungermannia minuta*).

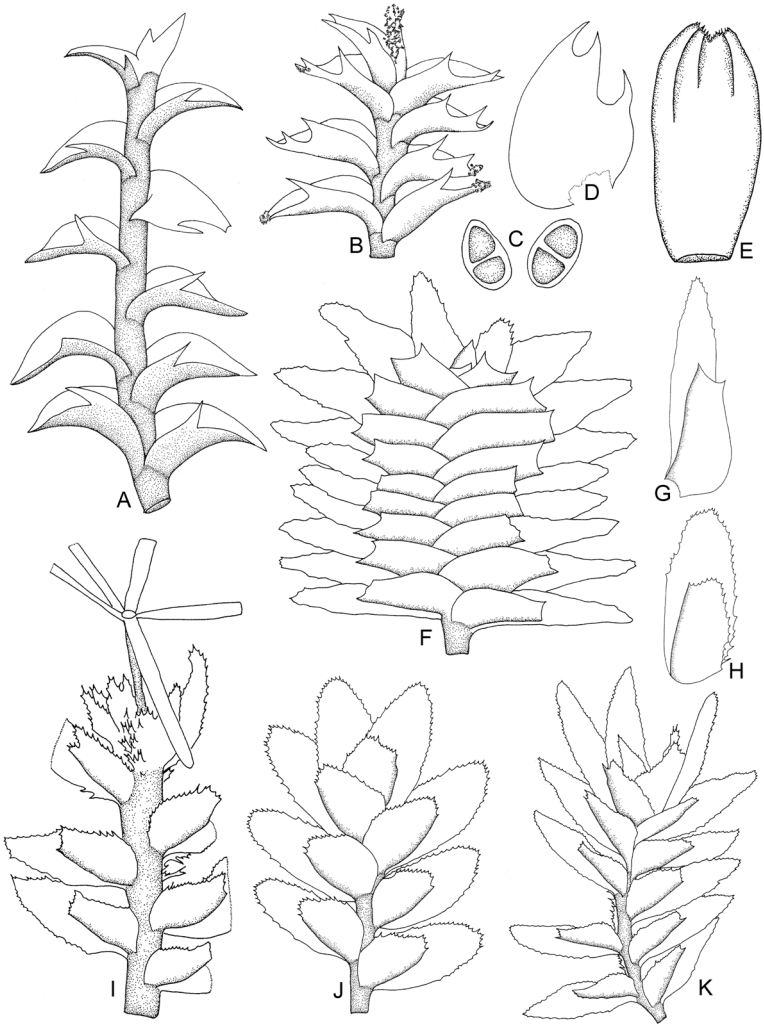


Figure 34. *Tritomaria exsecta* (Schmidel) Loeske. A: Part of plant. B: Part of plant with gemmae. C: Gemmae. D: Leaf. E: Perianth. *Schistochila aligera* (Nees & Blume) J.B.Jack & Steph. F: Part of plant, dorsal view. G: Leaf. *Schistochila beccariana* (De Not.) Trevis. H: Leaf. J: Part of plant. *Schistochila doriae* (De Not.) Trevis. I: Female plant. K: Part of plant. (A,E redrawn from Pearson 1902 as *Jungermannia exsecta*; B–D redrawn from Macvicar 1926; F–K redrawn from So 2003a).

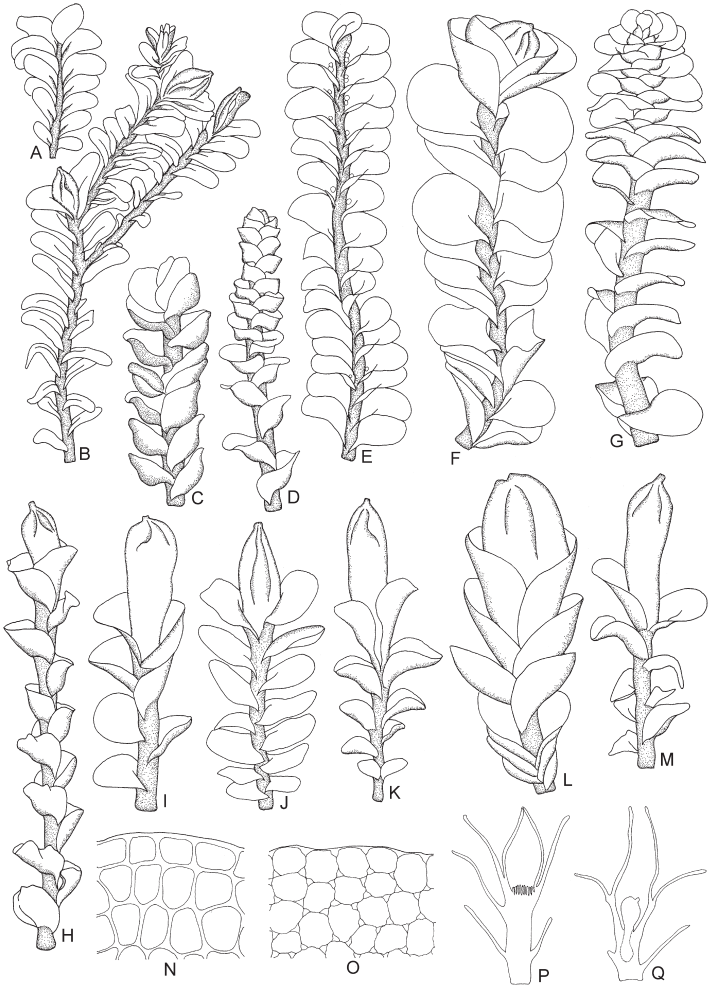


Figure 35. *Solenostoma comatum* (Nees) C.Gao. A: Part of plant. B: Female plant. P: Longitidunal section of perianth. *Solenostoma javanicum* (Schiffn.) Steph. C: Male plant. K: Female plant. *Solenostoma clavellatum* Steph. D: Male plant. H,I: Female plant. *Solenostoma borneense* (Amakawa) Váňa *et al.* E: Male plant. *Solenostoma stephanii* (Schiffn.) Steph. F,L: Female plant. O: Marginal leaf cells. *Solenostoma virgatum* (Mitt.) Váňa & D.G.Long. G: Male plant. J: Female plant. N: Marginal leaf cells. Q: Longitidunal section of perianth. *Solenostoma strictum* (Schiffn.) Váňa *et al.* M: Female plant. (A,B,P,E redrawn from Amakawa 1970 as *Jungermannia comata* and *J. borneensis*; C,F,K–M,O redrawn from Amakawa 1968 as *J. javanica*, *J. stricta* and *J. stephanii*; D,G–J,N,Q redrawn from Amakawa 1960 as *J. clavellata* and *J. virgata*).

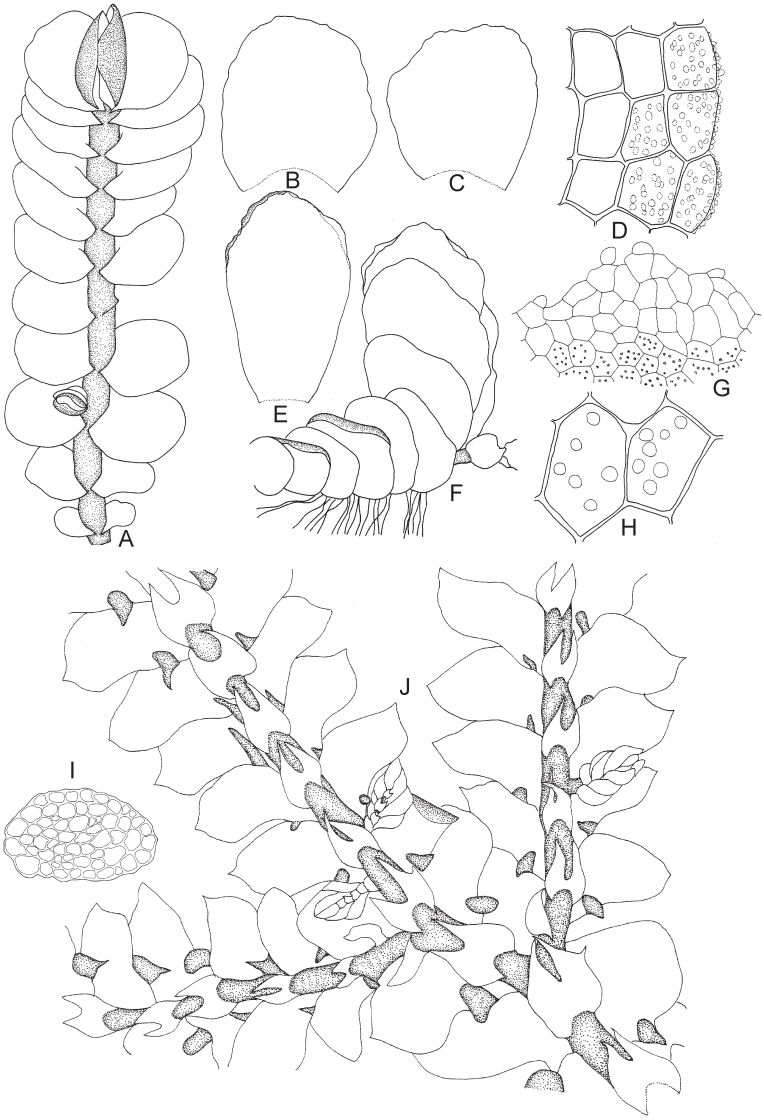


Figure 36. *Southbya organensis* Herzog. A: Part of plant. B,C: Leaves. D: Marginal leaf cells. E: Perianth. F: Female plant. G: Part of perianth-mouth. H: Median leaf cells with oil bodies. *Jubula javanica* Steph. I: Cross section of stem. J: Male plant, ventral view. (A–H redrawn from Kitagawa 1973 as *S. grollei*; I,J redrawn from Katagiri *et al.* 2010).

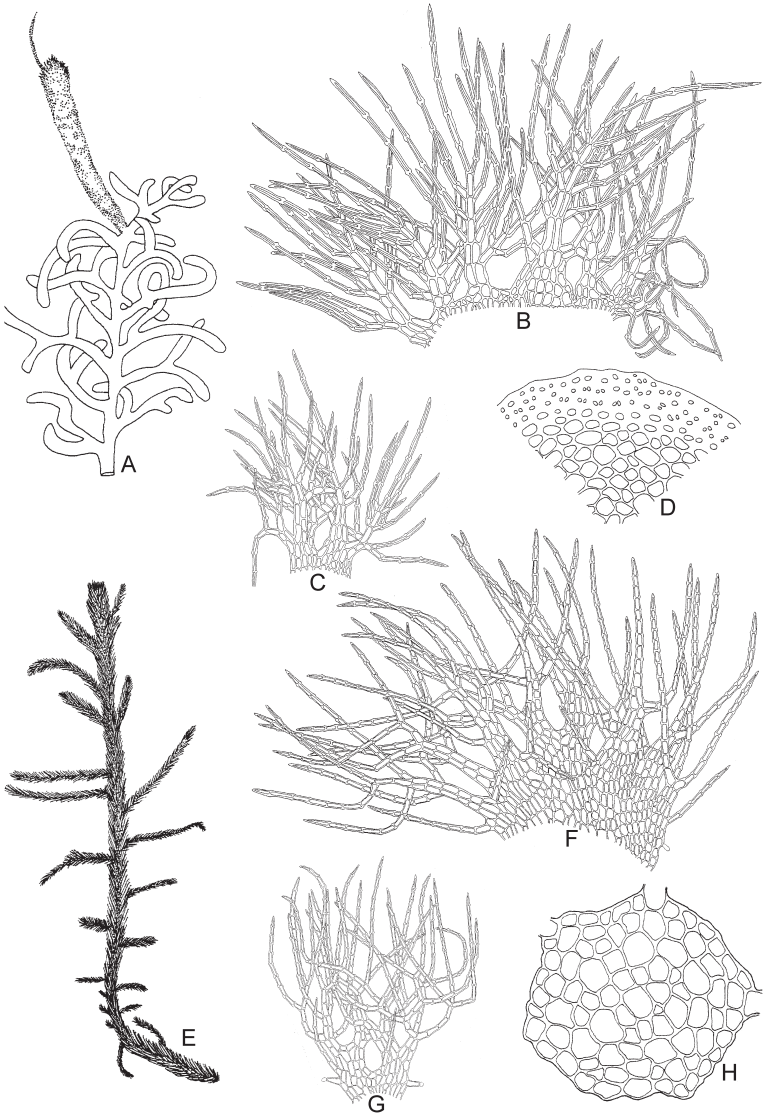


Figure 37. *Eotrichocolea furukii* T.Katag. A: Female plant. B: Lateral leaf. C: Underleaf. D: Part of cross section of stem. *Leiomitra merillana* (Steph.) T.Katag. E: Habit. F: Lateral leaf. G: Underleaf. H: Cross section of stem. (A–D redrawn from Katagiri *et al.* 2012; E–H redrawn from Katagiri & Deguchi 2012).

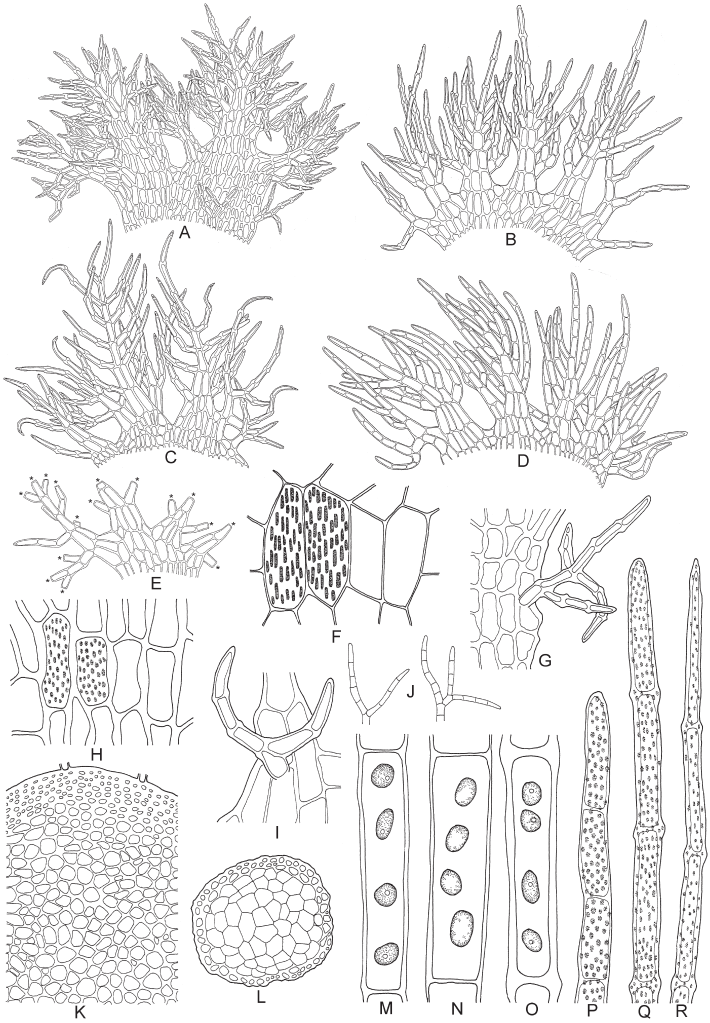


Figure 38. *Trichocolea magna* T.Katag. A: Lateral leaf. G: Superficial cilium on basal part of disc. H: Median leaf cells showing surface ornamentation. K: Part of cross section of stem. *Trichocolea mollissima* (Hook.f. & Taylor) Gottsche. B: Lateral leaf. I: Superficial cilium on marginal part of disc. R: Apex of cilia. *Trichocolea pluma* (Reinw. *et al.*) Mont. C: Lateral leaf. O: Cilium cells with oil bodies. Q: Apex of cilia. *Trichocolea tomentella* (Ehrh.) Dumort. D: Lateral leaf. F: Median disc cells showing surface ornamentation. J: Paraphyllia from stem. N: Cilium cells with oil bodies. *Trichocolea rudimentaris* Steph. E: Lateral leaf. L: Cross section of stem. M: Cilium cells with oil bodies. P: Apex of cilia. (All redrawn from Katagiri *et al.* 2013).

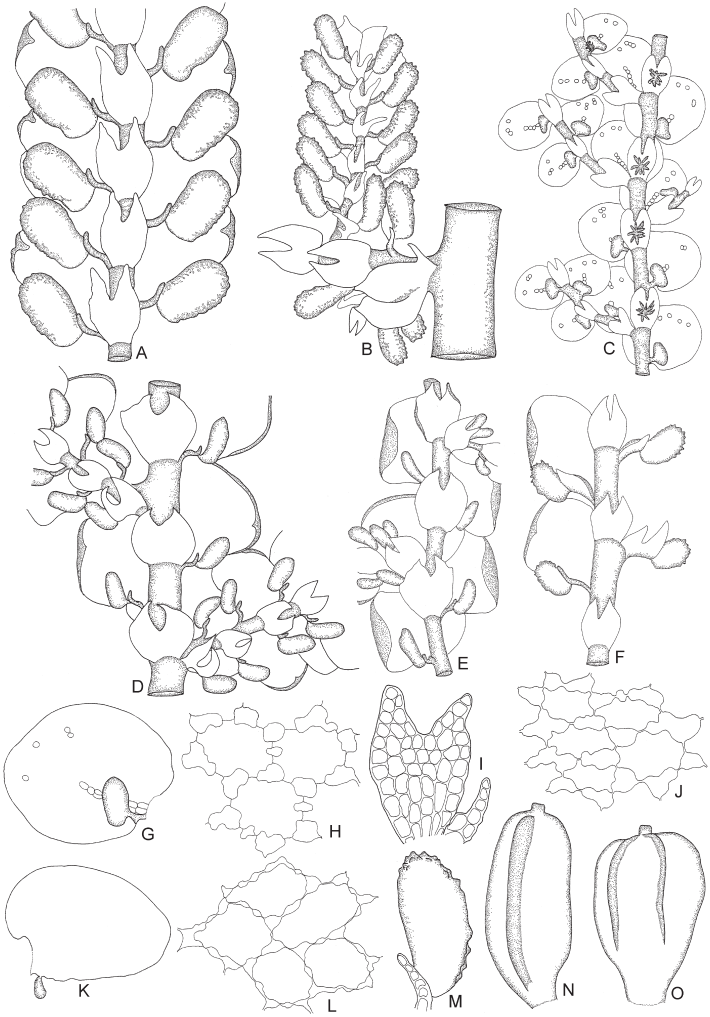


Figure 39. *Frullania meijeri* S.Hatt. A: Part of plant. I: Underleaves. L: Stem-leaf cells. *Frullania repandistipula* subsp. *spinibractea* S.Hatt. B: Part of plant. M: Lobule and stylus of stem-leaf. O: Perianth. *Frullania alstonii* Verd. C: Part of plant. G: Leaf. *Frullania apiculata* (Reinw. *et al.*) Nees. D: Part of plant. *Frullania pulogensis* Steph. E: Part of plant. *Frullania junghuhniana* Gottsche. F: Part of plant. *Frullania sabahana* S.Hatt. H: Stem-leaf cells. K: Leaf. *Frullania claviloba* Steph. J: Stem-leaf cells. N: Perianth. (A,I,L redrawn from Hattori 1974a; C,G redrawn from Hattori 1974b; H,K redrawn from Hattori 1976; others redrawn from Hattori 1975 F as *F. junghuhniana* var. *minutissima*).

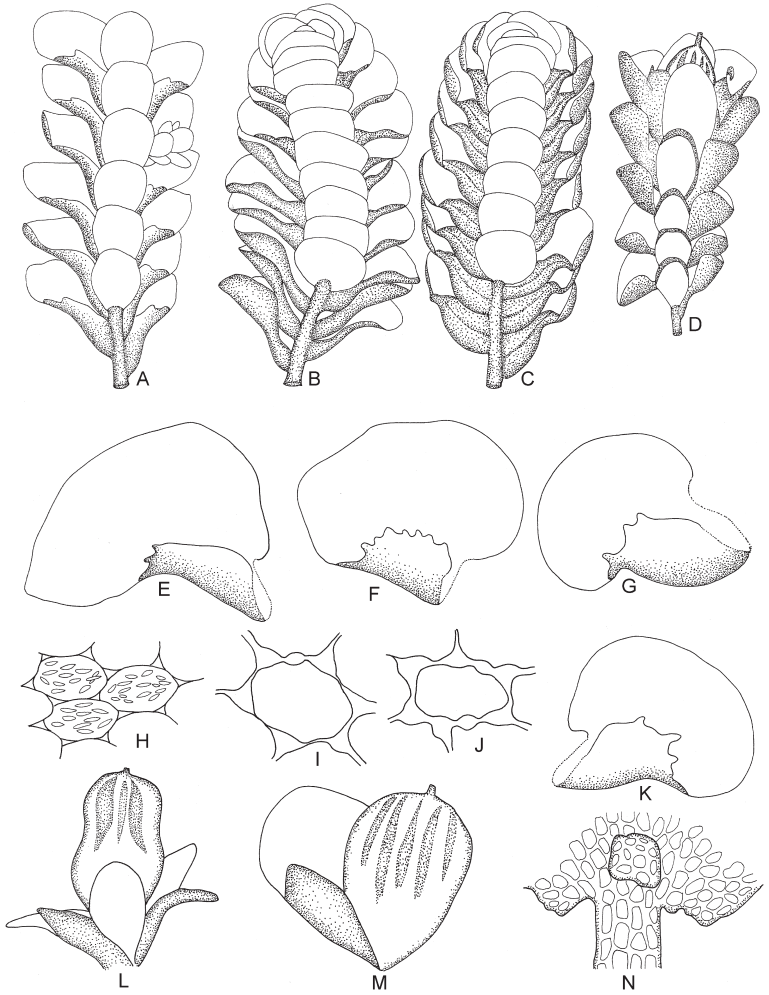


Figure 40. *Acrolejeunea arcuata* (Nees) Grolle & Gradst. A: Part of plant. E: Leaf. L: Gynoecium and perianth. N: Base of underleaf. *Acrolejeunea fertilis* (Reinw. *et al.*) Schiffn. B: Part of plant. F: Leaf. H: Median leaf cells with oil bodies. H: Median leaf cell. M: Female bract and perianth. *Acrolejeunea pycnoclada* (Taylor) Schiffn. C: Part of plant. G: Leaf. *Acrolejeunea tjibodensis* (Verd.) Grolle & Gradst. D: Part of female branch. K: Leaf. (A–C redrawn from Gradstein *et al.* 2002; others redrawn from Gradstein 1975).

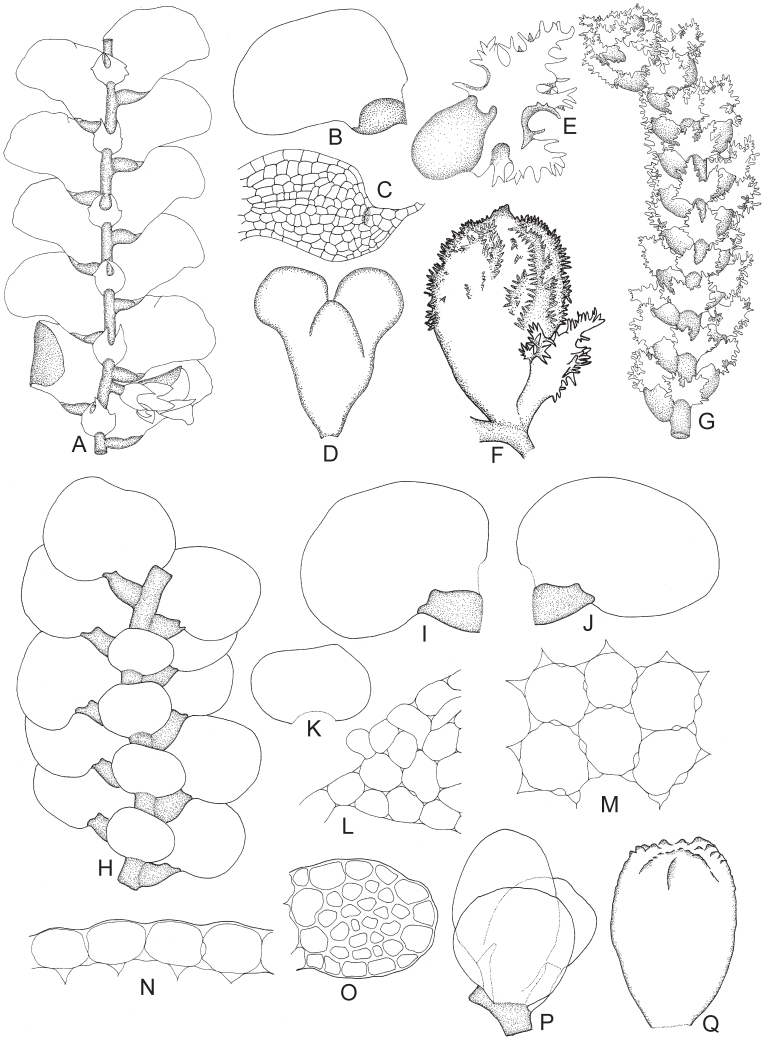


Figure 41. *Allorgella semperiana* (Steph.) Bechteler *et al.* A: Part of plant. B: Leaf. C: Leaf lobule. D: Perianth. *Dactylophorella muricata* (Gottsche) R.M.Schust. E: Leaf. F: Female bract and perianth. G: Part of plant, ventral view. *Cephalolejeunea parvilobula* Mizut. H: Part of plant, ventral view. I,J: Leaves. K: Underleaf. L: Upper part of leaf lobule. M: Median leaf cells. N: Marginal leaf cells. O: Cross section of stem. P: Female bracts and bracteole. Q: Perianth. (A,C redrawn from Zhu & So 1997 as *Otolejeunea semperiana*; B,D redrawn from Bechteler *et al.* 2016a; E,F redrawn from Herzog 1934; G redrawn from Yang & Lin 2013; H–Q redrawn from Mizutani 1979).

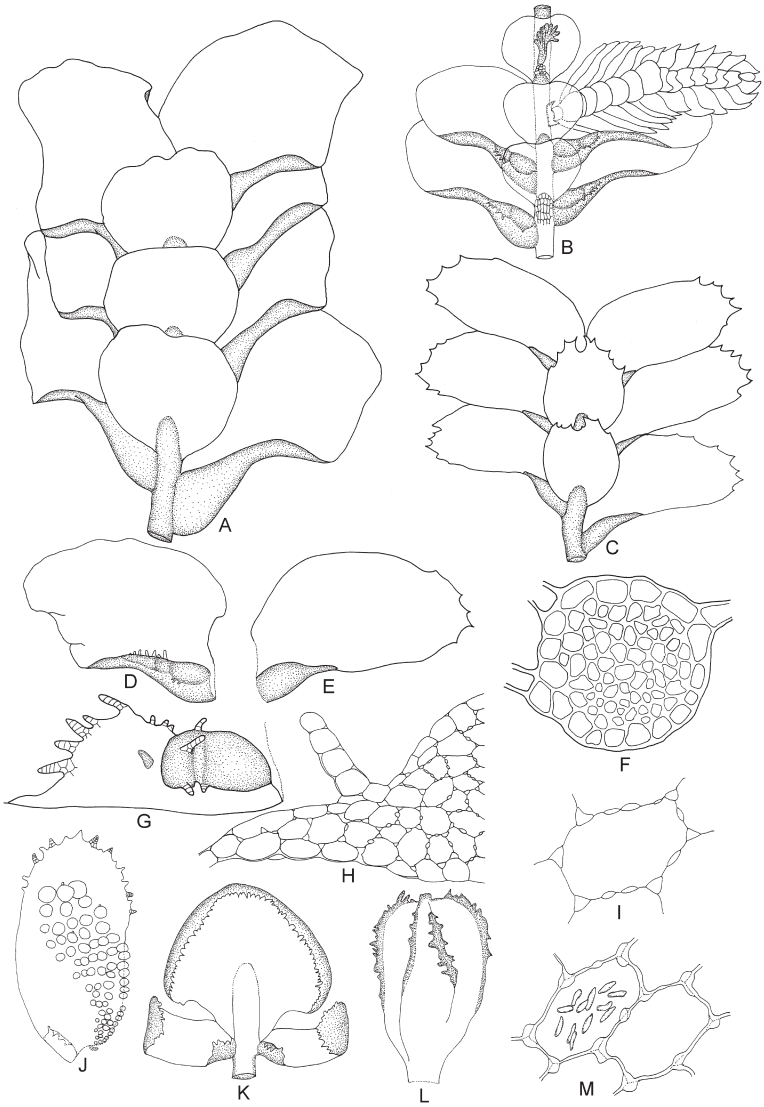


Figure 42. *Caudalejeunea cristiloba* (Steph.) Gradst. A: Part of plant, ventral view. B: Part of male plant. D: Leaf. F: Cross section of stem. G: Leaf lobule. I: Leaf cell. J: Apical leaf showing gemmae. K: Gemmiparous shoot. M: Median leaf cells with oil bodies. *Caudalejeunea reniloba* (Gottsche) Steph. C: Part of plant. E: Leaf. H: Upper part of leaf lobule. (A,C–E,H,I,L redrawn from Mizutani 1988; others redrawn from Gradstein 1974).

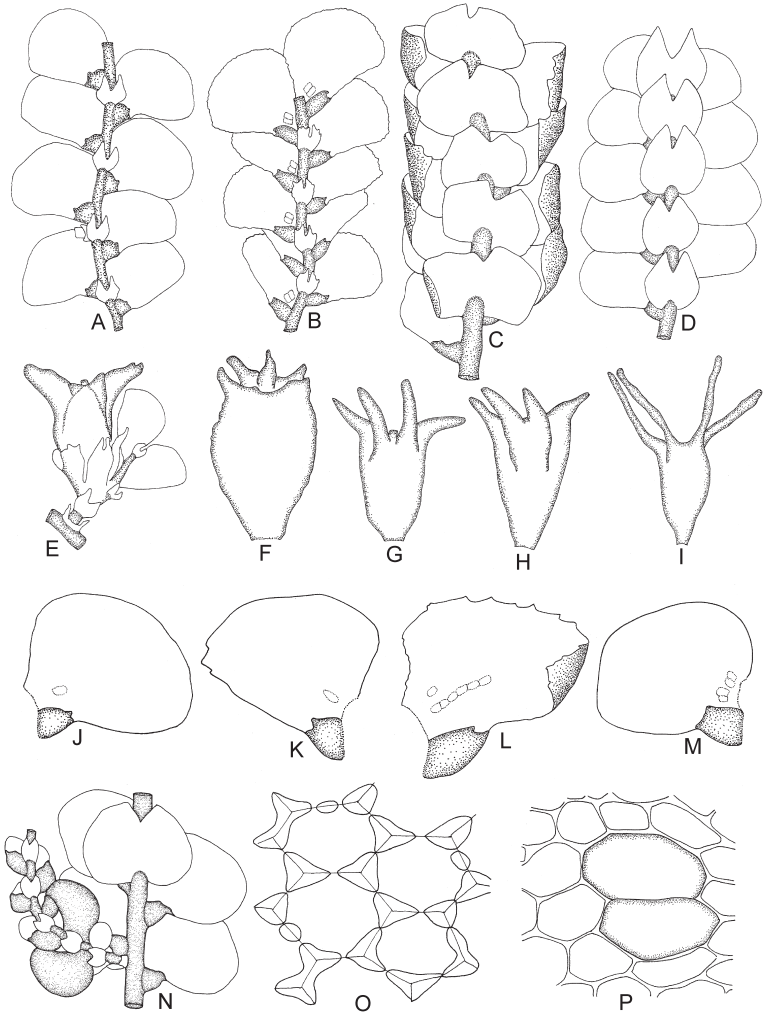


Figure 43. *Ceratolejeunea aliena* Herzog. A: Part of plant, ventral view. E: Gynoecium and perianth. *Ceratolejeunea minor* Mizut. B: Part of plant. P: Basal leaf cells and ocelli. *Ceratolejeunea belangeriana* (Gottsche) Steph. C: Part of plant. G,H: Perianths. J,K: Leaf. O: Median leaf cells. *Ceratolejeunea singapurensis* (Lindenb.) Schiffn. D: Part of plant. F: Perianth. M: Leaf. *Ceratolejeunea moniliata* Herzog. I: Perianth. L: Leaf. *Ceratolejeunea cornuta* (Lindenb.) Schiffn. N: Portion of shoot and utricle. (N redrawn from Gradstein *et al.* 2001; others redrawn from Mizutani 1981 C,G,H,J,K,O as *C. oceania*).

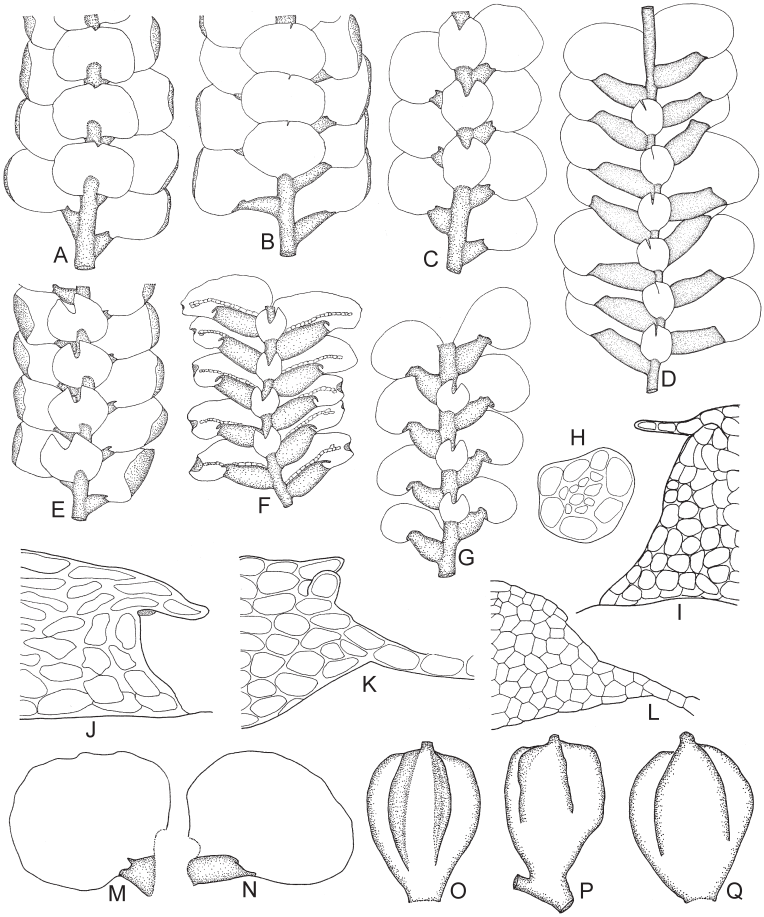


Figure 44. *Cheilolejeunea lindenbergii* (Gottsche) Mizut. A: Part of plant, ventral view. *Cheilolejeunea incisa* (Gottsche) R.M.Schust. & Kachroo. B: Part of plant. L: Upper part of leaf lobule. N: Leaf. *Cheilolejeunea intertexta* (Lindenb.) Steph. C: Part of plant. K: Upper part of leaf lobule. P: Perianth. *Cheilolejeunea trapezia* (Nees) Kachroo & R.M.Schust. D: Part of plant. H: Cross section of stem. I: Upper part of leaf lobule. Q: Perianth. *Cheilolejeunea orientalis* (Gottsche) Mizut. E: Part of plant. J: Upper part of leaf lobule. *Cheilolejeunea falsinervis* (Sande Lac.) R.M.Schust. & Kachroo. F: Part of plant. *Cheilolejeunea decursiva* (Sande Lac.) R.M.Schust. G: Part of plant. O: Perianth. *Cheilolejeunea trifaria* (Reinw. *et al.*) Mizut. M: Leaf. (A–C,K,L,N,P redrawn from Mizutani 1967; D,H,I,Q drawn from *J. Havasi & T. Pócs 1811/BF* (UMTP); G,O redrawn from Mizutani 1970 as *C. spathulata*; E,J,M redrawn from Mizutani 1972; F redrawn from Mizutani 1978).

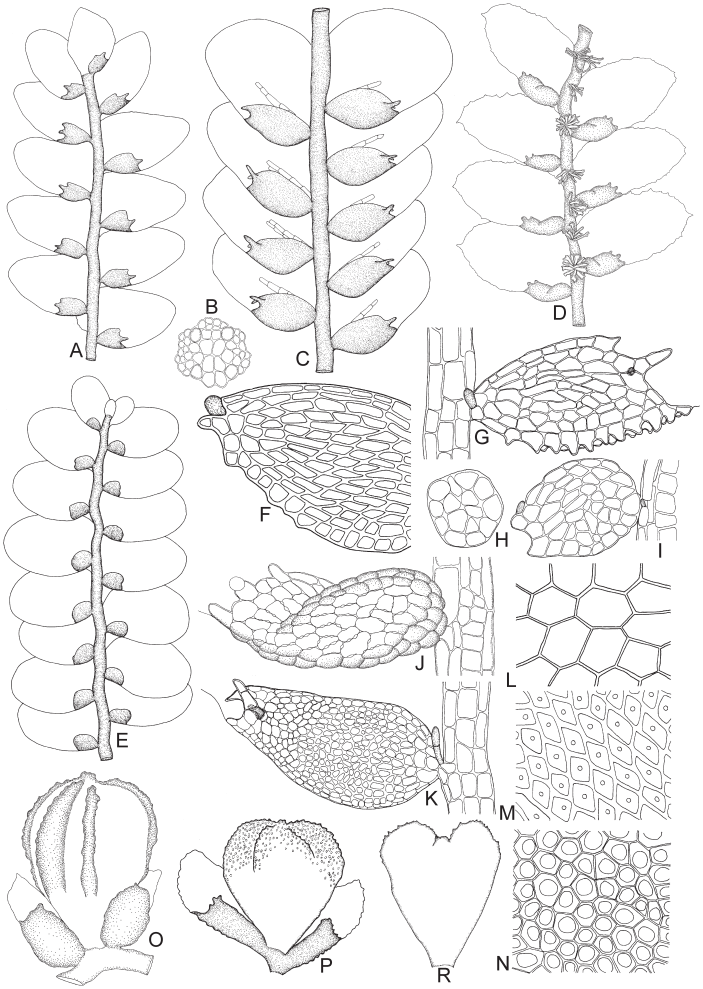


Figure 45. *Cololejeunea schmidtii* Steph. A: Part of plant, ventral view. H: Gemma. N: Median leaf cells. P: Female bracts and perianth. *Cololejeunea gottschei* (Steph.) Pandé *et al.* B: Gemma. D: Part of plant. J: Part of stem and leaf lobule. O: Female bracts and perianth. *Cololejeunea ensifera* L.Söderstr. *et al.* C: Part of plant. K: Part of stem and leaf lobule. R: Perianth. *Cololejeunea equialbi* Tixier. E: Part of plant. I: Part of stem and leaf lobule. L: Median leaf cells. *Cololejeunea appressa* (A.Evans) Benedix. F: Upper part of leaf lobule. M: Median leaf cells. (A,H,N drawn from *G. E. Lee et al. 19015*; B,D,J,O from *S. & T. Pócs et al. 13180/R*; C,K,R from *J. Havasi & T. Pócs 1823/AL*; E,I,L from *E. Pesiu et al. 19955*; F,M from *G. E. Lee et al. 19011.* All specimens deposited in UMTP).

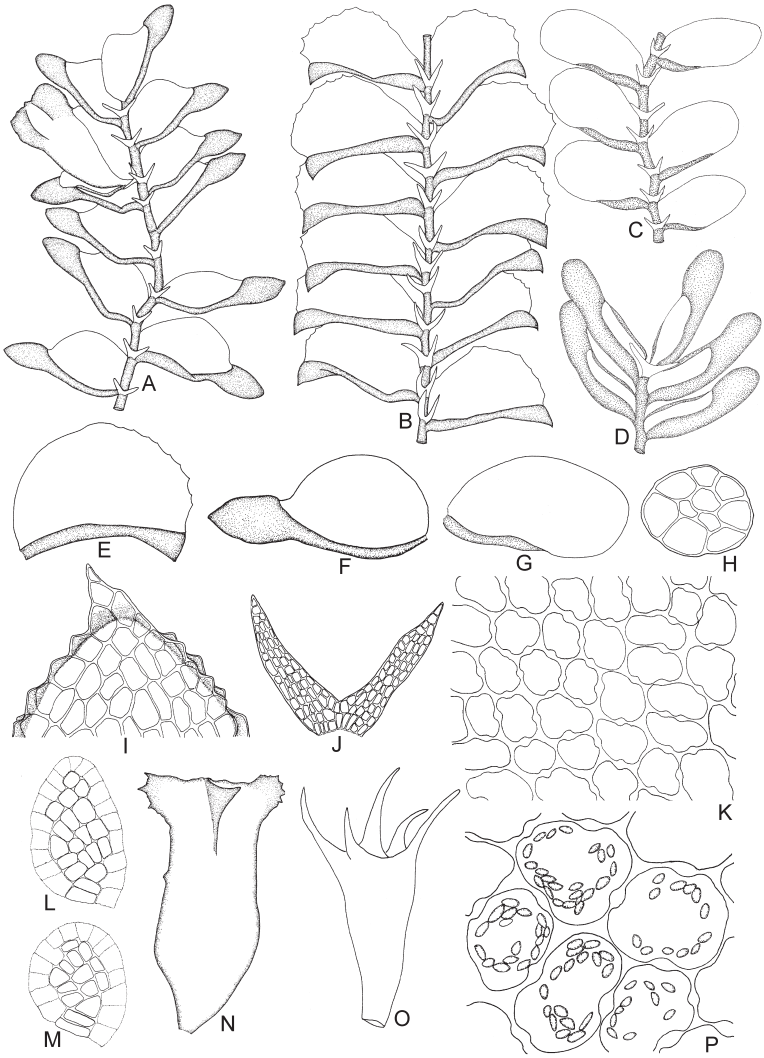


Figure 46. *Colura inuii* Horik. A: Part of plant, ventral view. F: Leaf. H: Cross section of stem. P: Median leaf cells and ocelli. L: Valve. *Colura ari* (Steph.) Steph. B: Part of plant. E: Leaf. I: Apex of lobule sac. J: Underleaf. K: Median leaf cells. M: Valve. N: Perianth. *Colura corynophora* (Nees *et al.*) Trevis. C: Part of plant. G: Leaf. *Colura karstenii* K.I.Goebel. D: Part of plant. *Colura tenuicornis* (A.Evans) Steph. O: Perianth. (A,H drawn from *G. E. Lee 19019*; F,P,L from *G. E. Lee et al. 21011*; B,E,I–K,M,N from *G. E. Lee et al. 19020*; C,D,G,O redrawn from Zhu & So 2001).

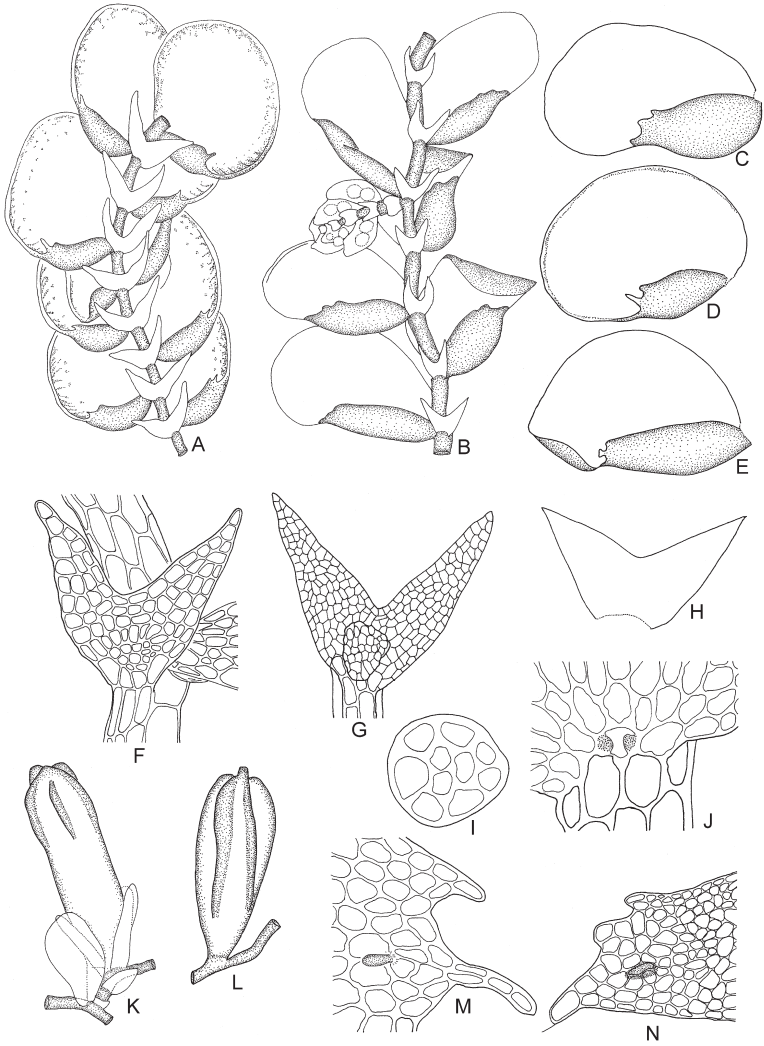


Figure 47. *Diplasiolejeunea patelligera* Herzog. A: Part of plant, ventral view. D: Leaf. G: Underleaf. I: Cross section of stem. J: Base of underleaf. L: Gynoecium and perianth. M: Upper part of leaf lobule. *Diplasiolejeunea jovet-astiae* Grolle. B: Part of plant and androecial shoot. C: Leaf. F: Underleaf. K: Gynoecium and perianth. N: Upper part of leaf lobule. *Diplasiolejeunea longilobula* Herzog. E: Leaf. H: Underleaf. (E,H redrawn from Herzog 1950; others redrawn from Grolle 1966 A,D,G,I,J,L,M as *D. neobrachyclada*).

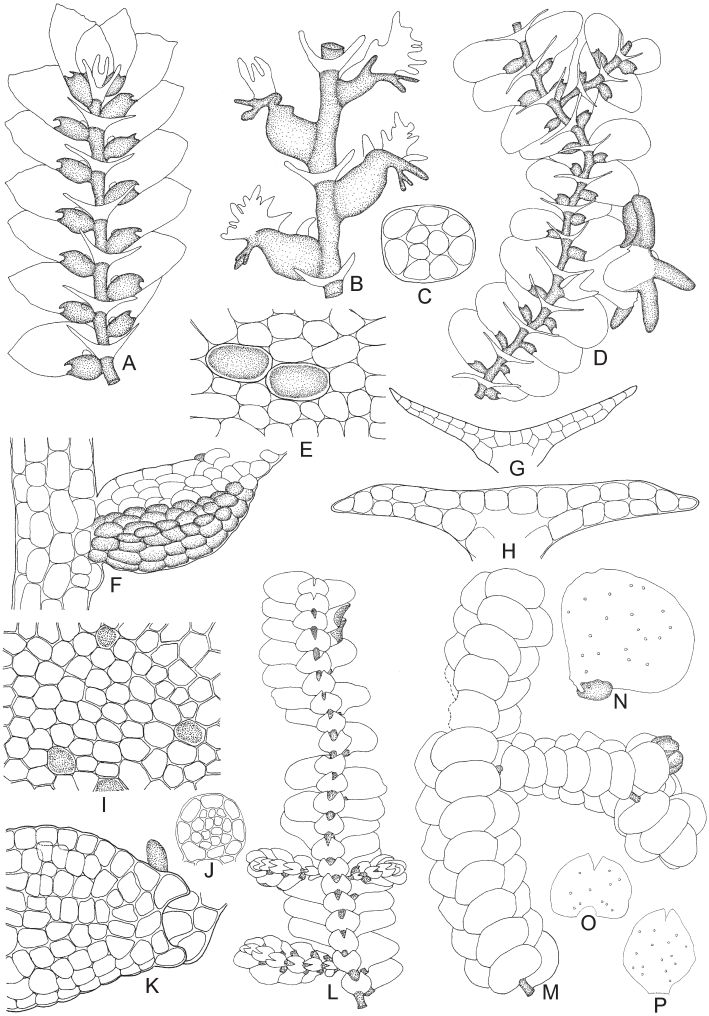


Figure 48. *Drepanolejeunea foliicola* Horik. A: Part of plant, ventral view. G: Underleaf. *Drepanolejeunea dactylophora* (Nees *et al.*) J.B.Jack & Steph. B: Part of plant. *Drepanolejeunea spicata* (Steph.) Grolle & R.L.Zhu. C: Cross section of stem. D: Part of plant and perianth. E: Basal leaf cells and ocelli. *Drepanolejeunea angustifolia* (Mitt.) Grolle. F: Part of stem and leaf lobule. *Drepanolejeunea levicornua* Steph. H: Underleaf. *Lepidolejeunea bidentula* (Steph.) R.M.Schust. I: Median leaf cells and ocelli. K: Upper part of leaf lobule. L: Part of plant. P: Underleaf. *Lepidolejeunea integristipula* (J.B.Jack & Steph.) R.M.Schust. J: Cross section of stem. N: Part of plant. O: Leaf. (A,C–E,G redrawn from Grolle & Zhu 2000; B,F,H redrawn from Zhu & So 2001; I–P redrawn from Piippo 1986).

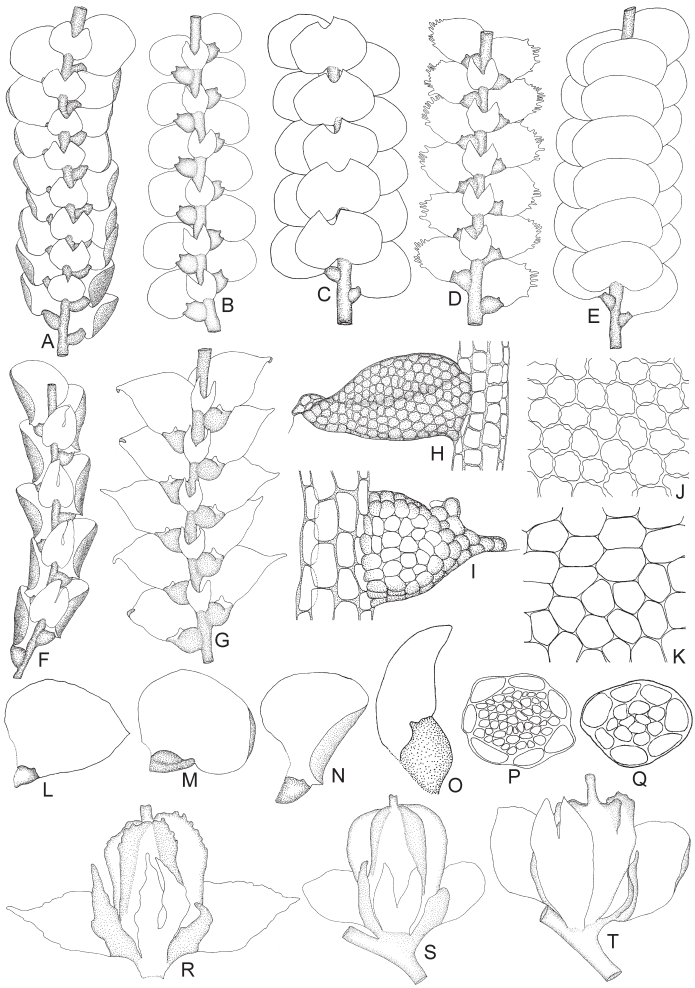


Figure 49. *Lejeunea umbilicata* (Nees) Nees. A; Part of plant, ventral view. J: Median leaf cells. Q: Cross section of stem. *Lejeunea tuberculosa* Steph. B: Part of plant. *Lejeunea sordida* (Nees) Nees. C: Part of plant. *Lejeunea patriciae* Schäf.-Verw. D: Part of plant. S: Female bracts, bracteole and perianth. E: *Lejeunea mimula* Hürl. E: Part of plant. *Lejeunea lumbricoides* (Nees) Nees. F: Part of plant. N: Leaf. P: Cross section of stem. T: Female bracts, bracteole and perianth. *Lejeunea apiculata* Sande Lac. G: Part of plant. R: Female bracts, bracteole and perianth. *Lejeunea pectinella* Mizut. H: Part of stem and leaf lobule. M: Leaf. *Lejeunea micholitzii* Mizut. I: Part of stem and leaf lobule. *Lejeunea eifrigii* Mizut. K: Median leaf cells. L: Leaf. *Lejeunea exilis* (Reinw. *et al.*) Grolle. O: Leaf. (S drawn from *G. E. Lee 2204* (UKMB); others redrawn from Lee 2013).

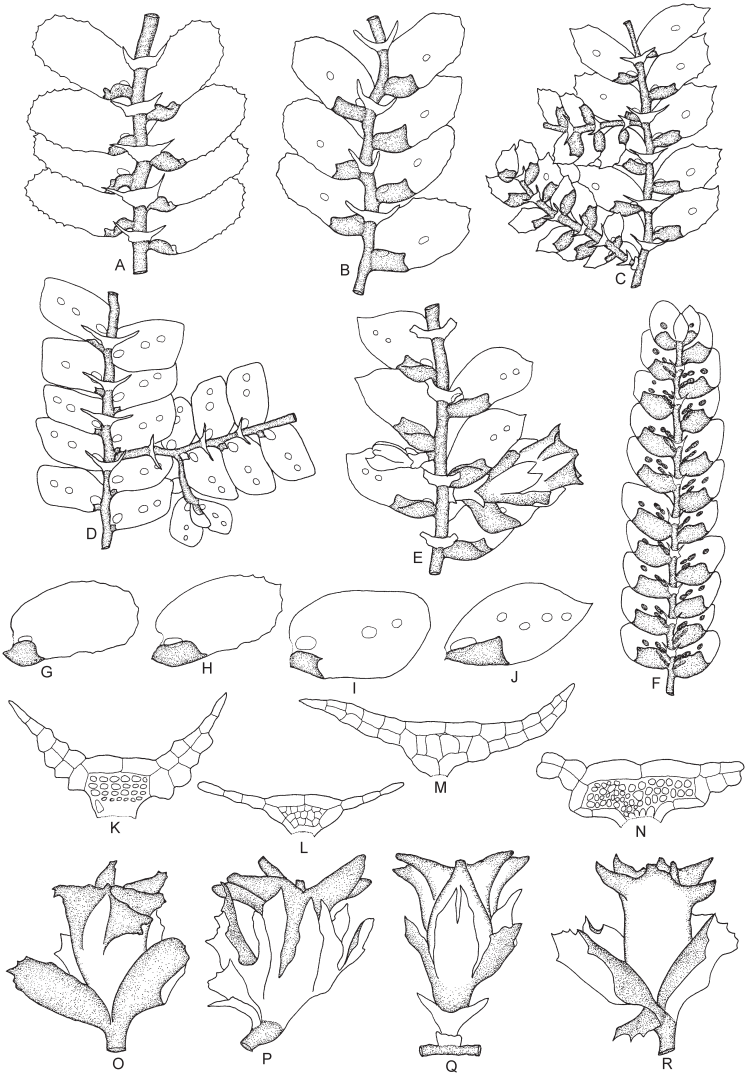


Figure 50. *Leptolejeunea vitrea* (Nees) Schiffn. A: part of plant, ventral view. G: Leaf. K: Underleaf. P,R: Female bracts, bracteoles and perianths. *Leptolejeunea borneensis* Herzog. B: Part of plant. H: Leaf. M: Underleaf. O: Female bracts, bracteole and perianth. *Leptolejeunea tripuncta* (Mitt.) Steph. C: Part of plant. Q: Female bracts, bracteole and perianth. *Leptolejeunea epiphylla* (Mitt.) Steph. D: Part of plant. I: Leaf. L: Underleaf. *Leptolejeunea foliicola* Steph. E: Part of plant. J: Leaf. N: Underleaf. *Leptolejeunea amphiophthalma* Zwickel F: Part of plant. (All redrawn from Herzog 1930 C,Q as *L. serrulata*).

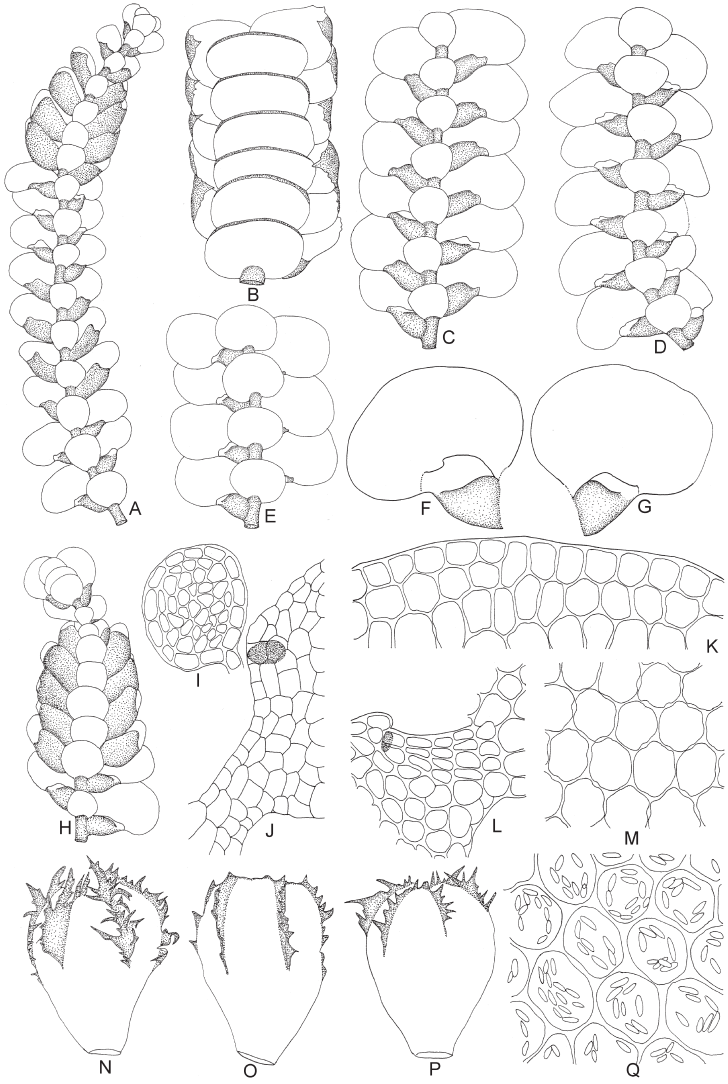


Figure 51. *Lopholejeunea horticola* Schiffn. A: Part of plant, ventral view. *Lopholejeunea applanata* (Reinw. *et al.*) Schiffn. B: Part of plant. *Lopholejeunea ceylanica* Steph. C,D: Part of plant. F: Leaf. L: Upper part of leaf lobule. O: Perianth. Q: Median leaf cells and oil bodies. *Lopholejeunea subfusca* (Nees) Schiffn. E: Part of plant. G: Leaf. H: Androecial shoot. J: Upper part of leaf lobule. K: Marginal leaf cell. M: Median leaf cells. *Lopholejeunea wiltensii* Steph. I: Cross section of stem. N: Perianth. *Lopholejeunea zollingeri* (Steph.) Schiffn. P: Perianth. (All redrawn from Zhu & Gradstein 2005).

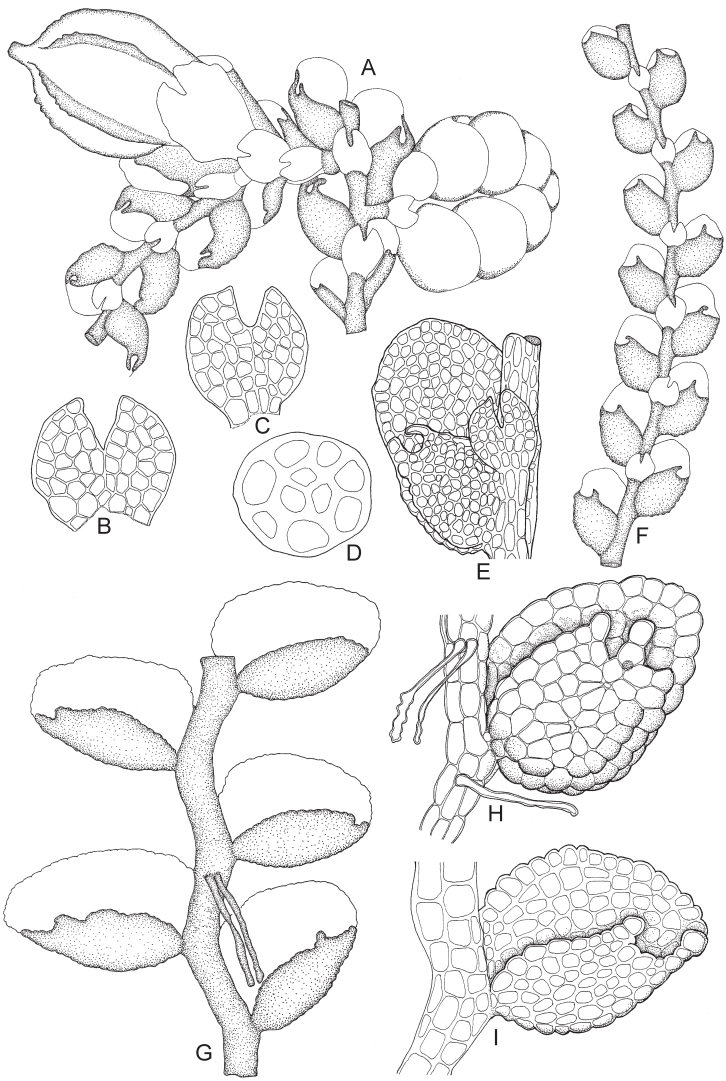


Figure 52. *Metalejeunea cucullata* (Reinw. *et al.*) Grolle. A: Part of plant with perianth and androecial shoot, ventral view. B,C: Underleaves. D: Cross section of stem. E,F: Part of plant. *Myriocoleopsis minutissima* subsp. *myriocarpa* (Nees & Mont.) R.L.Zhu *et al.* G,I: Part of plant, ventral view. *Myriocoleopsis minutissima* (Sm.) R.L.Zhu *et al.* H: Part of plant. (A–F redrawn from Miller *et al.* 1963 as *Microlejeunea cucullata*; G,H,I redrawn from Pócs *et al.* 2014b G,I as *Cololejeunea minutissima* subsp. *myriocarpa*; H as *C. minutissima*).

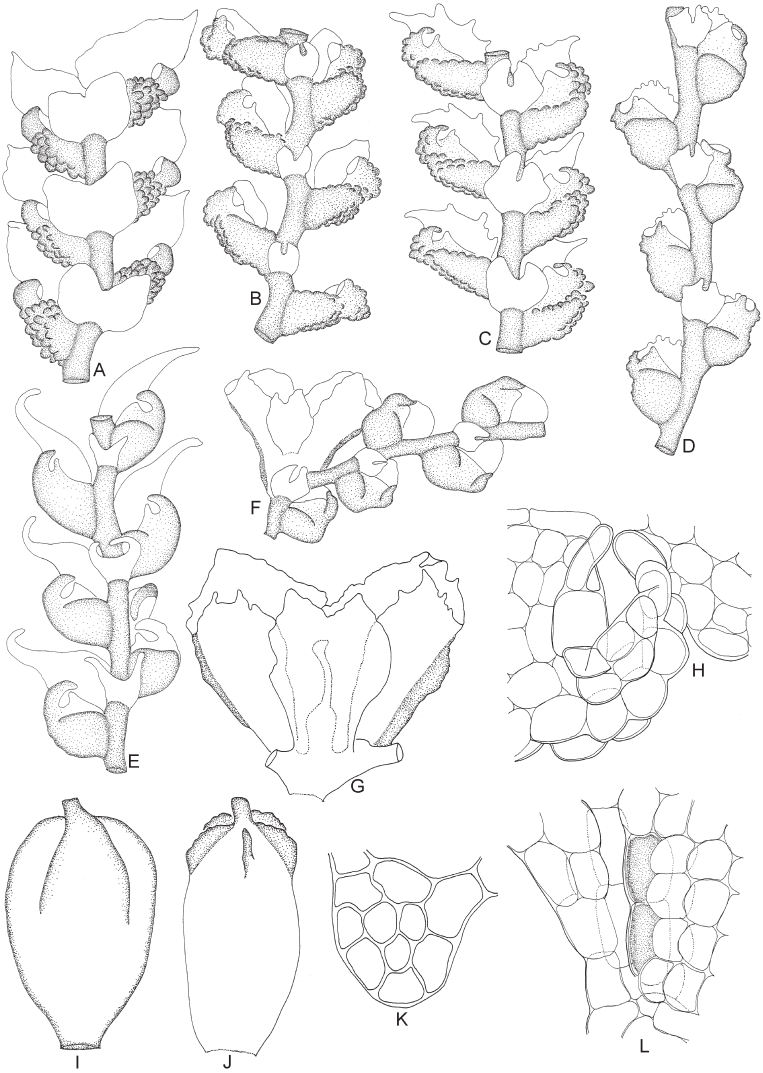


Figure 53. *Microlejeunea mammillosa* (Mizut.) Grolle. A: Part of plant, ventral view. G: Female bracts and bracteole. J: Perianth. K: Cross section of stem. *Microlejeunea constricta* (Grolle) Grolle. B: Part of plant. L: Basal leaf cells and ocelli. *Microlejeunea spinosa* (Mizut.) Grolle. C: Part of plant. H: Upper part of leaf lobule. *Microlejeunea minutissima* (Mizut.) Grolle. D: Pasrt of plant. *Microlejeunea filicuspis* (Steph.) Heinrichs *et al.* E: Part of plant. I: Perianth. *Microlejeunea kinabaluensis* (Mizut.) Grolle. F: Part of plant. (All redrawn from Mizutani 1973 as *Harpalejeunea*).

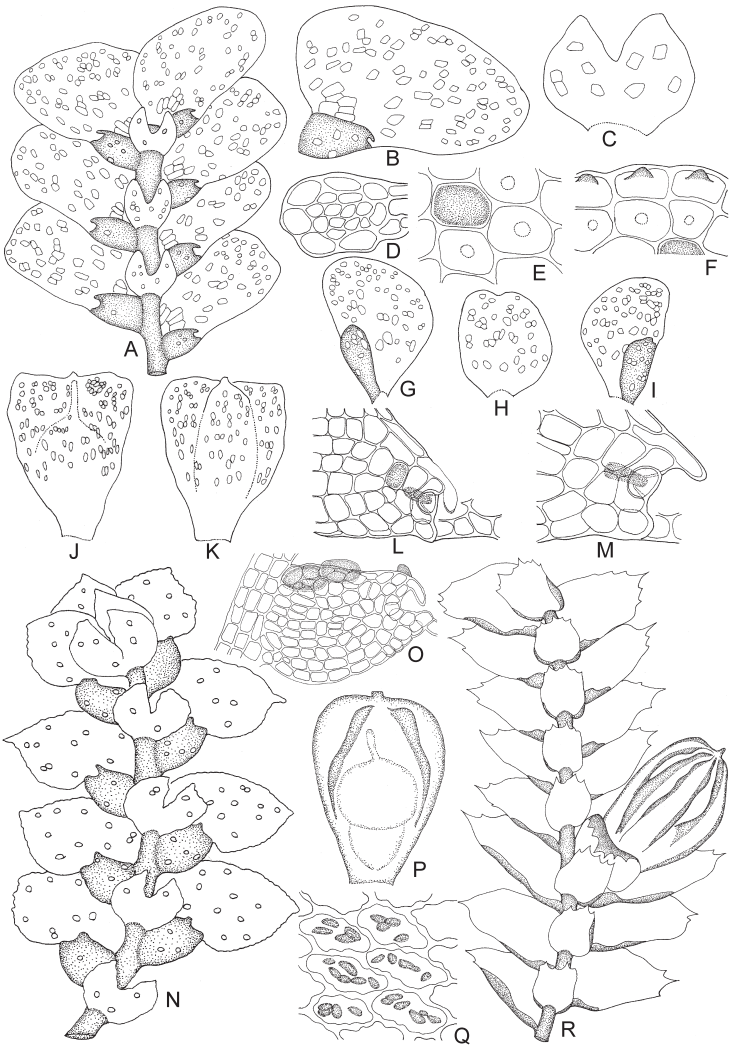


Figure 54. *Pictolejeunea mizutanii* Grolle. A: Part of plant, ventral view. B: Leaf. C: Underleaf. D: Cross section of stem. E: Median leaf cells and ocelli. F: Marginal leaf cells. G,I: Female bracts. H: Female bracteole. J,K: Perianths. L,M: Upper part of leaf lobules. *Mohamedia borneensis* (Steph.) R.L.Zhu & L.Shu. N: Part of plant. P: Perianth. *Mohamedia brunnea* (Mizut.) O: Leaf lobule and ocelli. *Ptychanthus striatus* (Lehm. & Lindenb.) Nees. Q: Median leaf cells and oil bodies. R: Part of plant and perianth. (A–M redrawn from Mizutani 1970 as *Cheilolejeunea picta*; N,O,P redrawn from Zhu *et al.* 2019; Q,R redrawn from Wang *et al.* 2016).

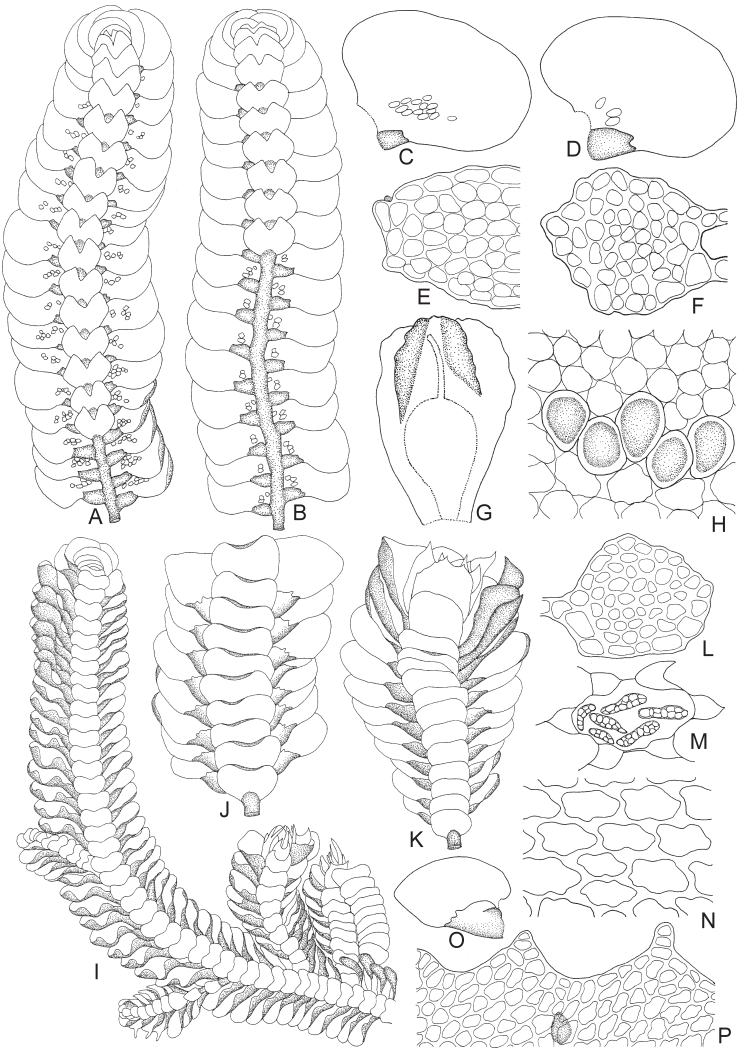


Figure 55. *Pycnolejeunea grandiocellata* Steph. A: Part of plant, ventral view. C: Leaf. E: Upper part of leaf lobule. *Pycnolejeunea contigua* (Nees) Grolle. B: Part of plant. D: Leaf. H: Basal leaf cells and ocelli. *Pycnolejeunea sphaeroides* (Sande Lac.) J.B.Jack & Steph. F: Cross section of stem. G: Perianth. *Schiffneriolejeunea tumida* (Nees) Gradst. I: Part of plant. M: Median leaf cell and oil bodies. *Schiffneriolejeunea pulopenangensis* (Gottsche) Gradst. J,K: Part of plant. L: Cross section of stem. N: Median leaf cells. O: Leaf. P: Upper part of leaf lobule and hyaline papillae. (A–H redrawn from He 1999; I,M redrawn from Gradstein & Terken 1981; J,K,L,N–P redrawn from Wang *et al.* 2016).

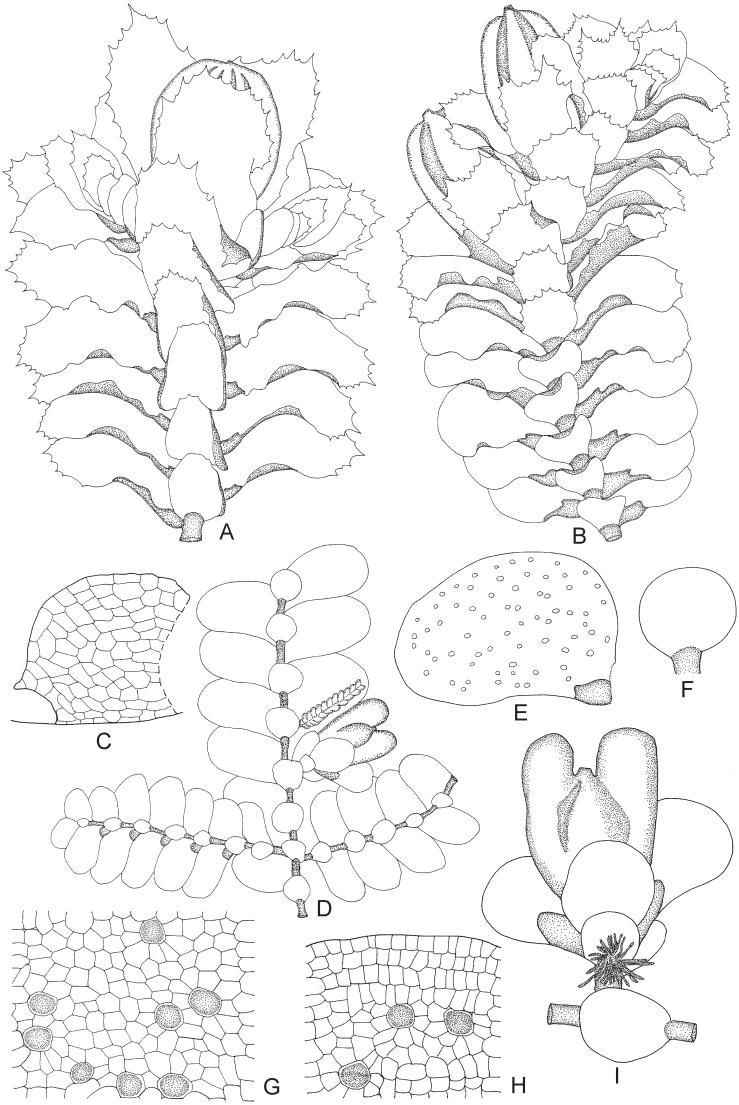


Figure 56. *Spruceanthus semirepandus* (Nees) Verd. A: Part of plant and perianth, ventral view. *Spruceanthus polymorphus* (Sande Lac.) Verd. B: Part of plant and perianths. *Stictolejeunea balfourii* (Mitt.) E.W.Jones. C: Leaf lobule. D: Part of plant, androecial shoot and perianth, ventral view. E: Leaf. F: Underleaf. G: Median leaf cells and ocelli. H: Marginal leaf cells. I: Part of stem, gynoecium and perianth. (A,B redrawn from Wang *et al.* 2016; C–I redrawn from Herzog 1950).

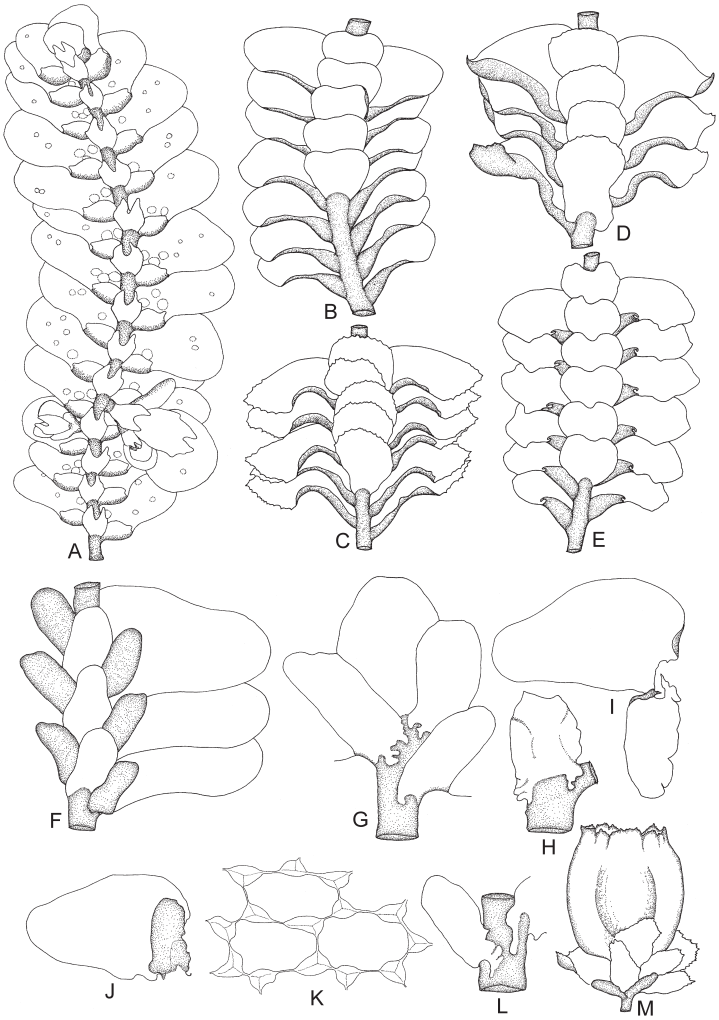


Figure 57. *Thiersianthus silamensis* R.L.Zhu & L.Shu. A: Part of plant, ventral view. *Thysananthus virens* Ångstr. B: part of plant. *Thysananthus spathulistipus* (Reinw. *et al.*) Lindenb. C: Part of plant. *Thysananthus convolutus* Lindenb. D: Part of plant. *Thysananthus retusus* (Reinw. *et al.*) B.M.Thiers & Gradst. E: Part of plant. *Porella javanica* (Gottsche) Inoue. F,G: Part of plant, ventral view. I,J: Leaves. K: Median leaf cells. *Porella acutifolia* subsp. *latior* S.Hatt. H: Underleaf showing insertion to the stem. L: Ventral leaf lobe showing insertion to the stem. M: Gynoecium and perianth. (A redrawn from Zhu *et al.* 2017; B–E redrawn from Gradstein *et al.* 2002; F,G,J,K redrawn from Hattori 1971; I redrawn from Hattori 1970 as *P. integrifolia*; H,L,M redrawn from Hattori 1969).

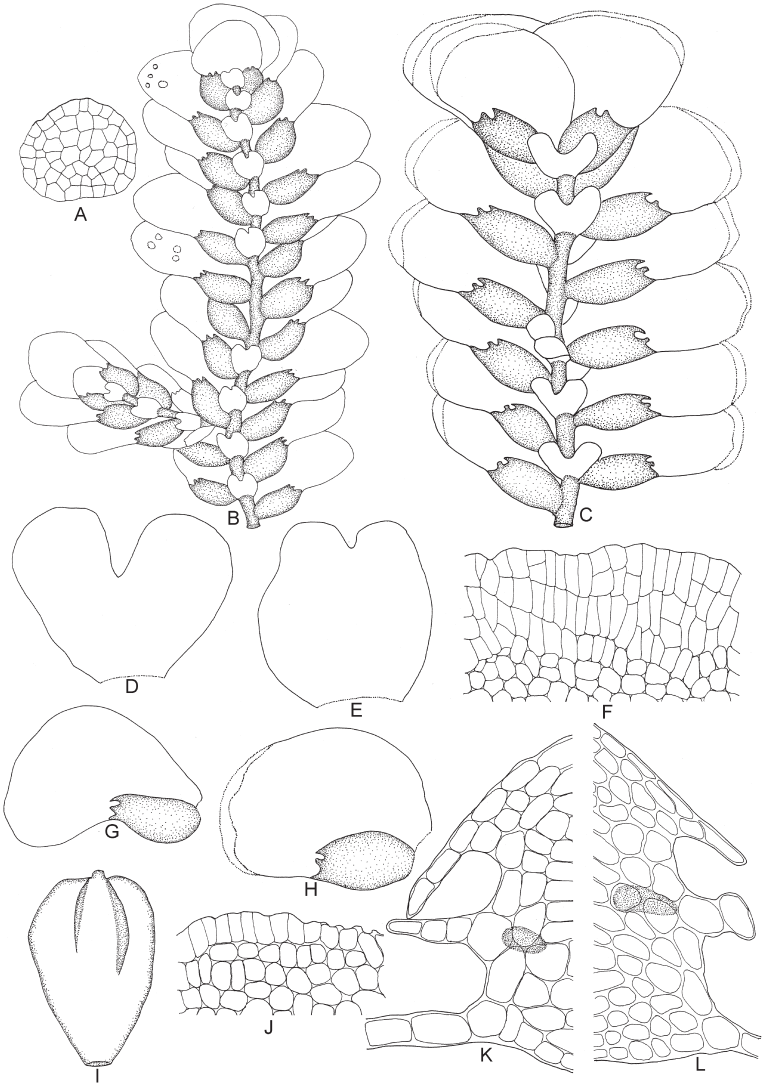


Figure 58. *Tuyamaella serratistipa* S.Hatt. A: Cross section of stem. B: Part of plant, ventral view. E: Underleaf. G: Leaf. I: Perianth. J: Marginal leaf cells. K: Upper part of leaf lobule and hyaline papillae (in gray). *Tuyamaella molischii* (Schiffn.) S.Hatt. C: Part of plant. D: Underleaf. F: Marginal leaf cells. H: Leaf. L: Upper part of leaf lobule and hyaline papillae (in gray). (A,B,E,G,I–K redrawn from Zhu & So 1998; others redrawn from Zhu & So 2001).

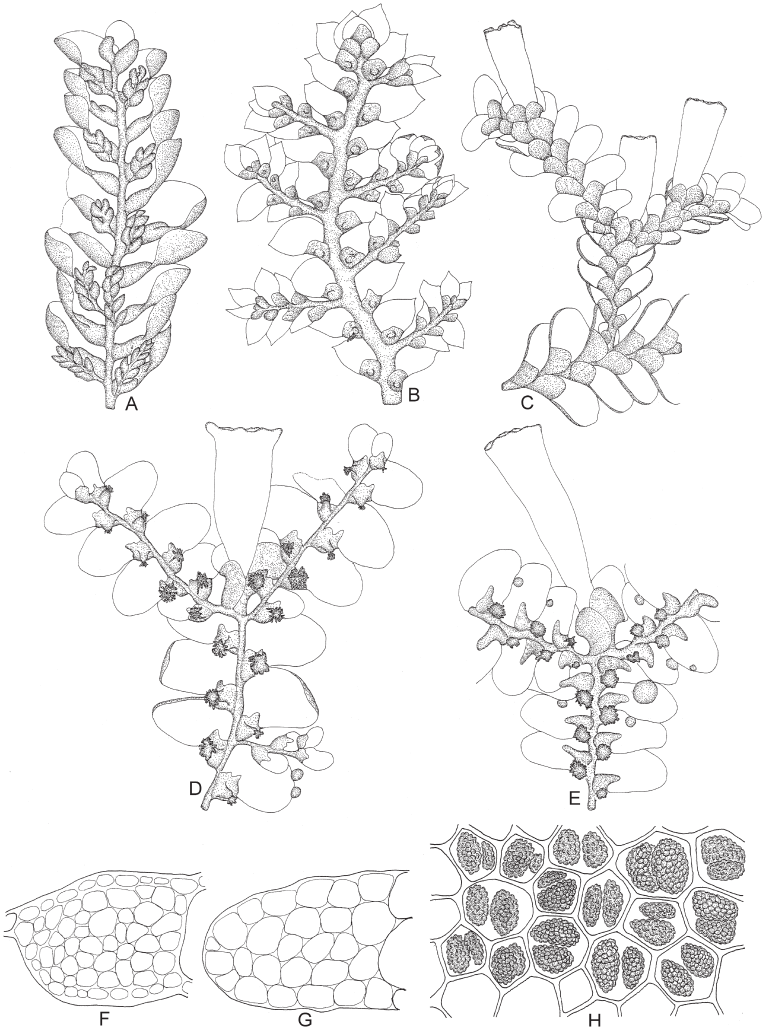


Figure 59. *Radula iwatsukii* K.Yamada. A: Part of plant, ventral view. *Radula acuta* Mitt. B: Part of plant. *Radula vrieseana* Sande Lac. C: Part of plant and perianths. *Radula tjibodensis* K.I.Goebel. D: Part of plant and perianth. *Radula nymannii* Steph. E: Part of plant and perianth. G: Cross section of stem. *Radula philippinensis* K.Yamada. F: Cross section of stem. *Radula* sp. H: Median leaf cells and oil bodies. (All redrawn from Yamada 1979 B as *R. apiculata*).

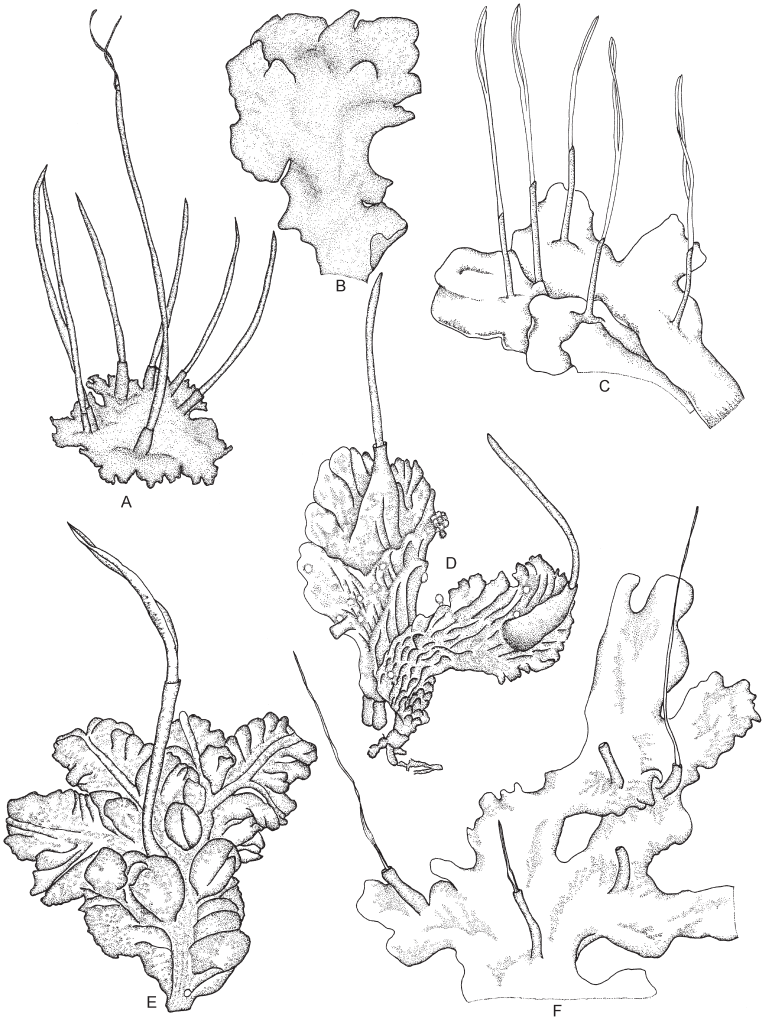


Figure 60. *Anthoceros angustus* Steph. A: Habit. *Phaeoceros carolinianus* (Michx.) Prosk. B,F: Habit. *Megaceros flagellaris* (Mitt.) Steph. C: Habit. *Folioceros glandulosus* (Lehm. & Lindenb.) D.C.Bharadwaj. D: Habit. *Dendroceros cavernosus* J.Haseg. E: Habit. (A drawn from *G. E. Lee 19023* (UMTP); B redrawn from Meijer 1954 as *A. laevis*; F redrawn from Piippo 1993 as *P. laevis* subsp. *carolinianus*; C redrawn from Gradstein 2011; D redrawn from Meijer 1957 as *A. glandulosus*; E redrawn from Hasegawa 1980).

Figure 61. A: *Cyathodium cavernarum* Kunze, on soil in limestone cave, growing in deep shade. B–D: *Dumortiera hirsuta* (Sw.) Nees, on wet soil and rock. B: Female thallus with young archegoniophores. C,D: Male thallus.

Figure 62. A,B,E: *Marchantia polymorpha* L. A: Female thallus. B: Male thallus. E: Thallus with gemmae cups. C,D: *Marchantia emarginata* Reinw. *et al.* C: Male thallus. D: Thallus with gemmae cups. All in open places in montane forest areas, above 1000 m alt.

Figure 63. A: *Pallavicinia lyellii* (Hook.) Gray, thallus with gynoecia, on soil near stream at waterfall. B: *Riccardia crassiretis* Schiffn., on earth bank. C: *Metzgeria foliicola* Schiffn., on leaf.

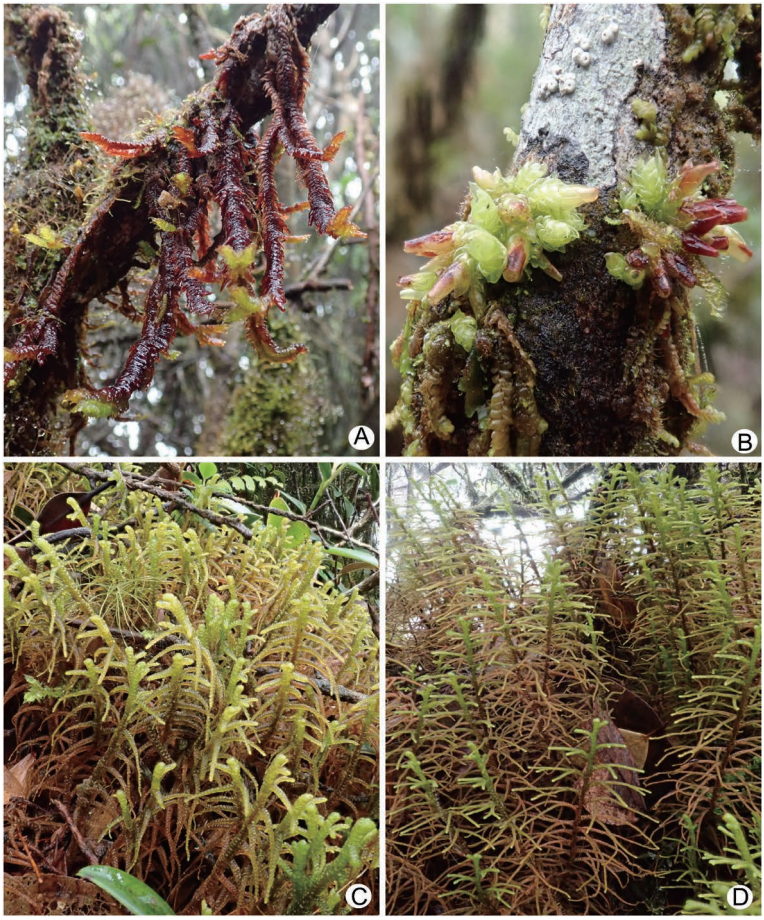


Figure 64. A: *Pleurozia gigantea* (F.Weber) Lindb. B: *Pleurozia acinosa* (Mitt.) Trevis. C,D: *Mastigophora diclados* (F.Weber) Nees. All inside the montane forest, above 1500 m alt.

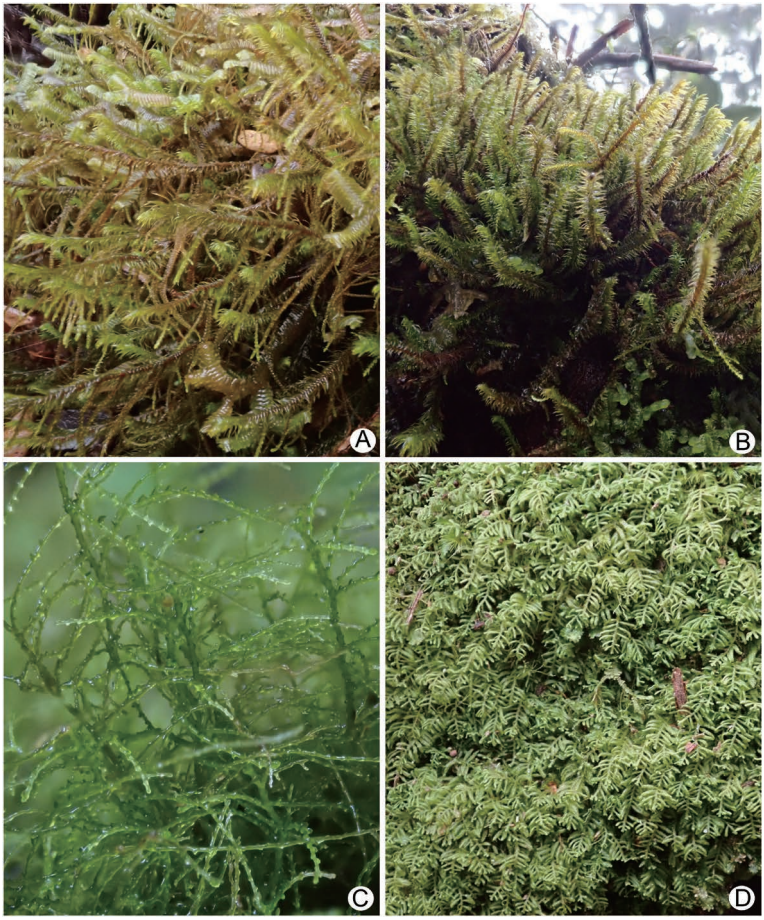


Figure 65. A,B: *Herbertus sendtneri* (Nees) Lindb. C: *Lepidozia trichodes* (Reinw. *et al.*) Nees. D: *Lepicolea rara* (Steph.) Grolle. All inside the montane forest, above 1500 m alt.

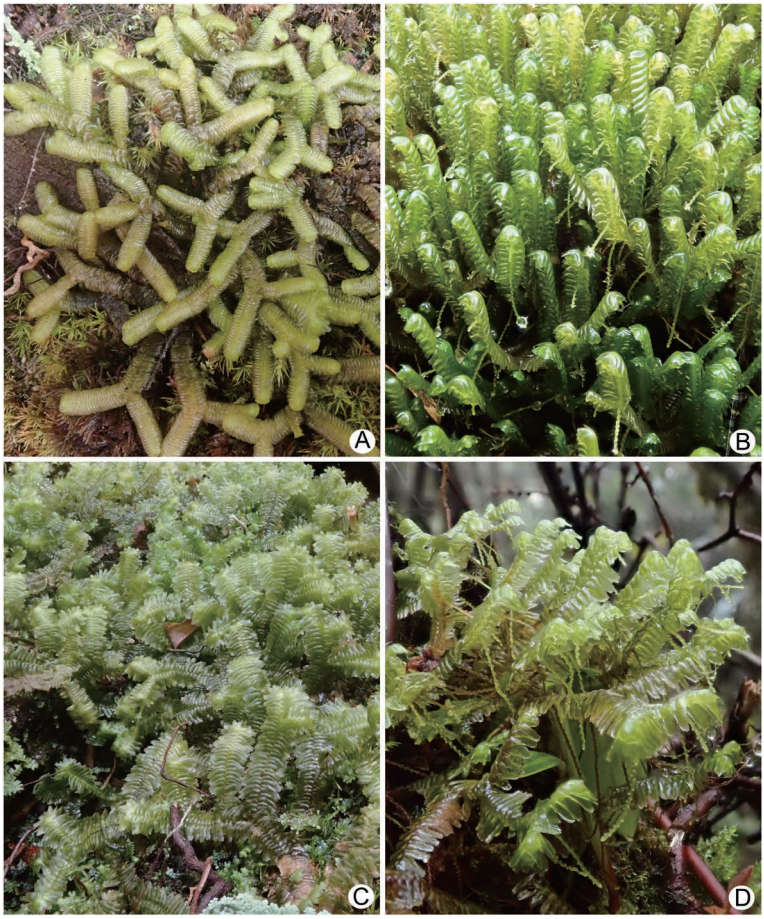


Figure 66. A: *Bazzania spiralis* (Reinw. *et al.*) Meijer. B,D: *Bazzania erosa* (Reinw. *et al.*) Trevis. C: *Bazzania uncigera* (Reinw. *et al.*) Trevis. A,C: Plants showing dichotomous branching. B,D: Plants showing flagelliform branches sprouting from the axils of the underleaves. Very common on tree trunks, rotten wood and rock in montane forest.

Figure 67. A: *Heteroscyphus coalitus* (Hook.) Schiffn., plants with sporophytes. B: *Heteroscyphus argutus* (Reinw. *et al.*) Schiffn. C: *Heteroscyphus aselliformis* (Reinw. *et al.*) Schiffn. On tree trunks and branches in the montane forest.

Figure 68. A: *Chiastocaulon dendroides* (Nees) Carl. B,C: *Plagiochila bantamensis* (Reinw. *et al.*) Mont., very common on tree trunks and branches in lowland and montane forests. D: *Gottschelia schizopleura* (Spruce) Grolle, on tree trunk in montane forest, above 1500 m alt.

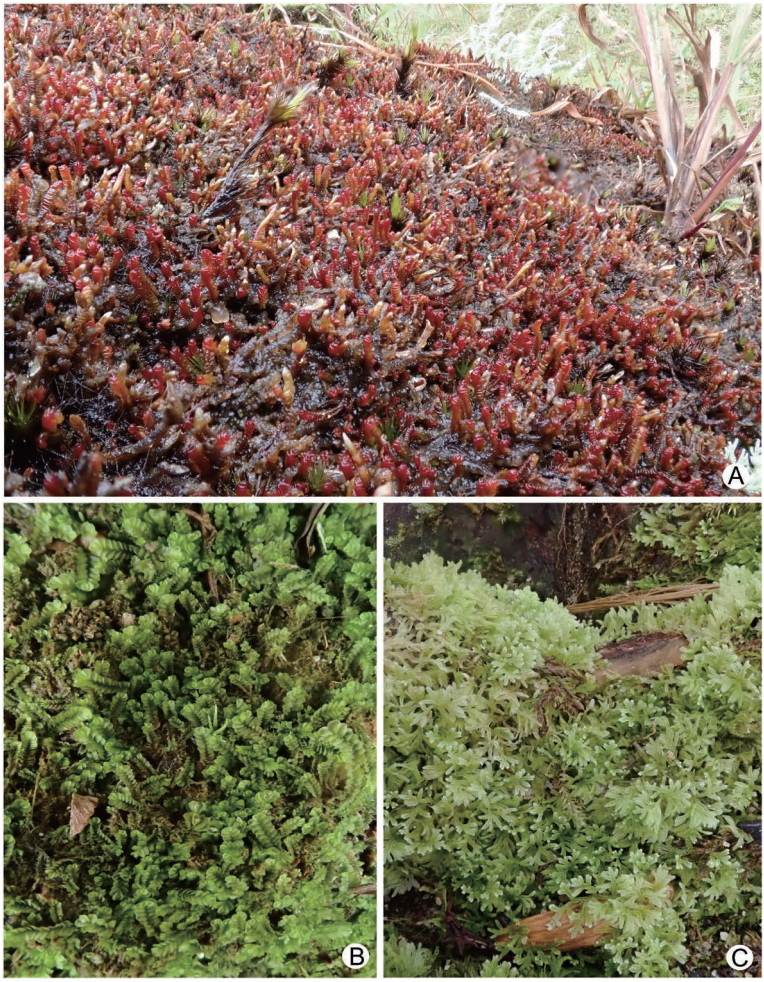


Figure 69. A: *Solenostoma javanicum* (Schiffn.) Steph. B: *Solenostoma comatum* (Nees) C.Gao, on soil and rock in montane forest. C: *Trichocolea pluma* (Reinw. *et al.*) Mont., on rotten log in montane forest.

Figure 70. A: *Schistochila sciurea* (Nees) Schiffn. B: *Schistochila blumei* (Nees) Trevis. C: *Schistochila aligera* (Nees & Blume) J.B.Jack & Steph., on tree trunks and rotten logs in montane forest, above 1500 m alt.

Figure 71. A: *Frullania apiculata* (Reinw. *et al.*) Nees. B: *Frullania grandistipula* Lindenb. C: *Radula assamica* Steph. D: *Radula javanica* Gottsche. On tree trunks in lowland and montane forests.

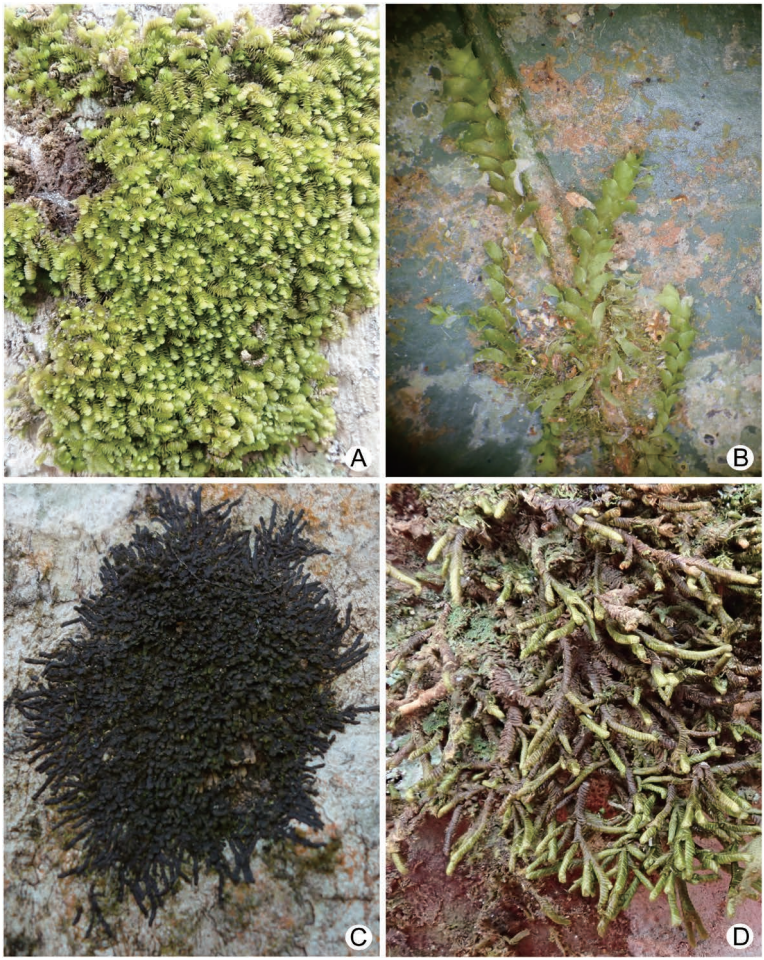


Figure 72. A: *Acrolejeunea pycnoclada* (Taylor) Schiffn. B: *Caudalejeunea reniloba* (Gottsche) Steph. C: *Lopholejeunea nigricans* (Lindenb.) Schiffn. D: *Thysananthus gottschei* (J.B.Jack & Steph.) Steph. On tree trunks or leaves in lowland forest.

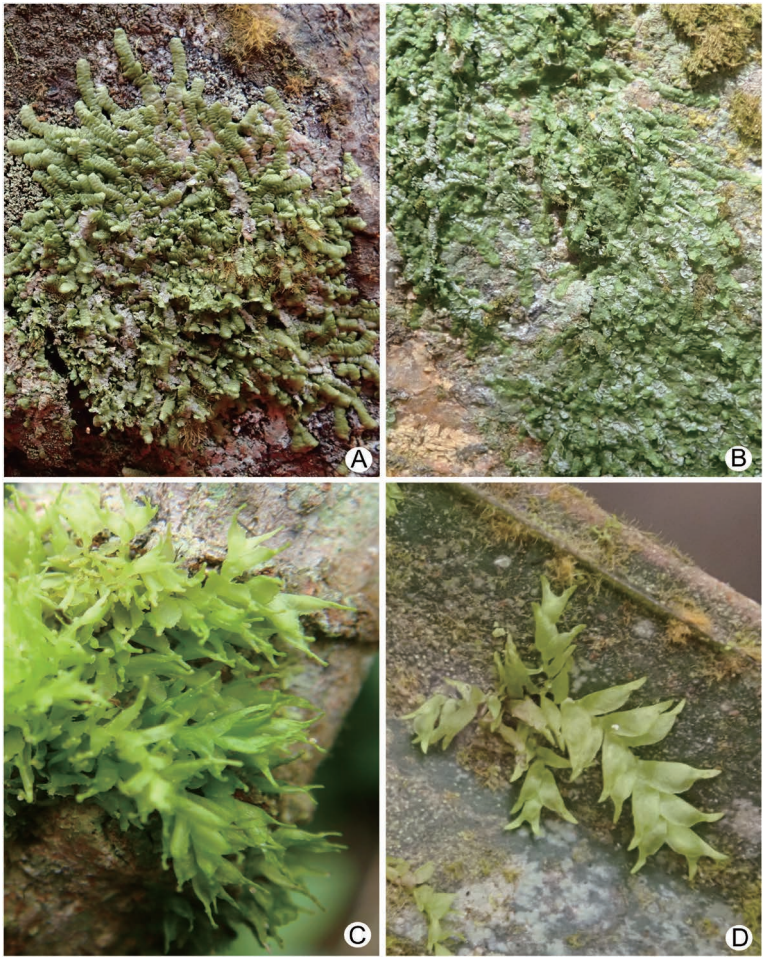


Figure 73. A: *Cheilolejeunea ceylanica* (Gottsche) R.M.Schust. & Kachroo. B: *Cheilolejeunea intertexta* (Lindenb.) Steph., on tree trunks in open places. C: *Colura ari* (Steph.) Steph., on tree trunk in lowland forest. D: *Colura conica* (Sande Lac.) K.I.Goebel, on leaf in montane forest.

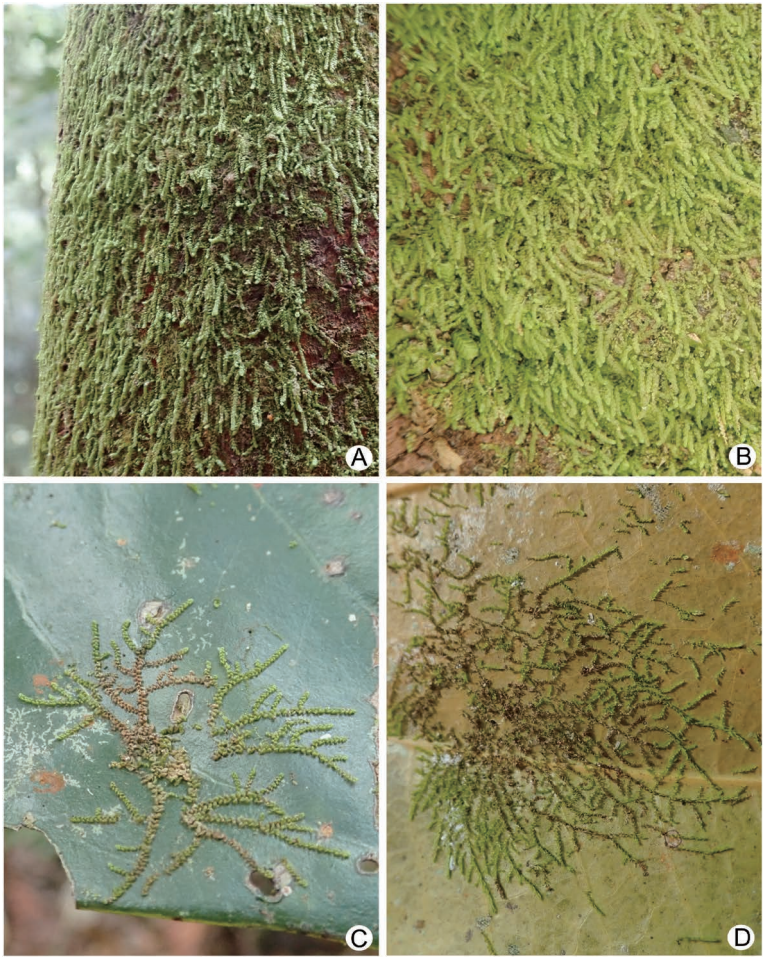


Figure 74. A: *Drepanolejeunea pentadactyla* (Mont.) Steph. B: *Drepanolejeunea vesiculosa* (Mitt.) Steph. C: *Drepanolejeunea levicornua* Steph. D: *Drepanolejeunea dactylophora* (Nees *et al.*) J.B.Jack & Steph. On tree trunks or leaves in lowland forest.

Figure 75. A: *Lejeunea albescens* (Steph.) Mizut. B: *Lejeunea discreta* Lindenb. C: *Lejeunea flava* (Sw.) Nees. D: *Lejeunea tuberculosa* Steph. On litter, branches and leaves in montane forest.

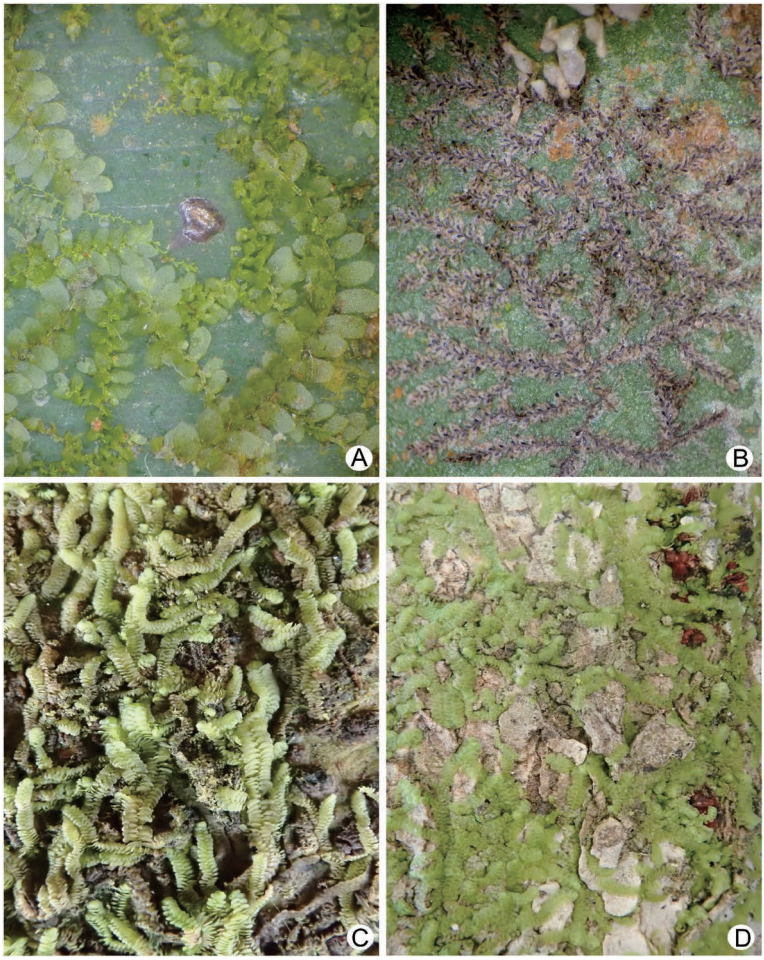
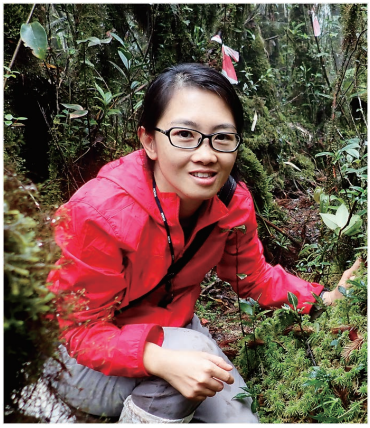


Figure 76. A: *Leptolejeunea vitrea* (Nees) Schiffn. B: *Leptolejeunea amphiophthalma* Zwickel. C: *Pycnolejeunea grandiocellata* Steph. D: *Pycnolejeunea contigua* (Nees) Grolle. On tree trunks and leaves in lowland forest.

Figure 77. A: *Anthoceros angustus* Steph., on soil in open place. B: *Megaceros flagellaris* (Mitt.) Steph., on wet rock in running water, montane forest.



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Guide to the Genera of Liverworts and Hornworts of Malaysia

This book is the first illustrated guide to the genera of liverworts and hornworts recorded from Malaysia. The work provides keys, descriptions, illustrations, distribution, habitats, and literature references for 124 genera in 43 families.

The introductory section includes a brief history of the knowledge of the liverwort flora of Malaysia, a discussion on morphological features and ecology of liverworts and hornworts, and instructions for collecting, storing, and studying the plants. This book has been written for use by advanced undergraduate and postgraduate students as well as all those interested in the rich liverwort and hornwort flora of tropical Asia.