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Hymenophyllaceae

Series II – Ferns and Fern Allies

Cover: *Hymenophyllum pallidum* (Blume) Ebihara & K.Iwats.
Photo: A. Ebihara.

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HYMENOPHYLLACEAE

(K. Iwatsuki, Tokyo & A. Ebihara, Tsukuba, Japan)

Hymenophyllaceae [Link, Handbuch 3 (1833) 36 ('*Hymenophylleae*');] Mart., Consp. Regn. Veg. (1835) 3; Sadeb. in Engl. & Prantl, Nat. Pflanzenfam. 1, 4 (1899) 91, 112; C.Chr., Index Filic. (1906) xiii; Copel., Philipp. J. Sci. 67 (1938) 1, Gen. Fil. (1947) 31; Ching et al. in Ching, Fl. Reipubl. Popularis Sin. 2 (1959) 132; Holttum, Rev. Fl. Malaya 2 (1955) 72; C.V.Morton, Contr. U.S. Natl. Herb. 38 (1968) 153; R.M.Tryon & A.F.Tryon, Ferns All. Pl. Trop. Amer. (1982) 97; K.Iwats., Acta Phytotax. Geobot. 35 (1984) 165, J. Fac. Sci. Univ. Tokyo, Sect. 3, Bot. 13 (1985) 501, in Kubitzki, Fam. Gen. Vasc. Pl. 1 (1990) 157; Ebihara et al., Blumea 51 (2006) 221; PPG I, J. Syst. Evol. 54 (2016) 573. — Type: *Hymenophyllum* Sm.

Trichomanaceae Burmeist., Handb. Naturgesch. 12 (1837) 196; G.Kunkel, Feddes Repert. Spec. Nov. Regni Veg. 70 (1965) 155. — Type: *Trichomanes* L.

Perennial ferns of usually small size. *Rhizome* long- or short-creeping, less often ascending or erect, bearing hairs and lacking scales, with a so-called Hymenophyllaceae-protostele. *Fronds* simple to pinnately decompound, or simple dichotomous or seemingly digitate; stipes not joined to rhizome, terete, with a single leaf trace, hairy or glabrescent; laminae unistratose except on veins and sori, or bi- to quadri-stratose without intercellular spaces and stomata; veins pinnate or simple, often uninervate in ultimate segments, all free; pseudoveins often present, continuous to true veins or not, sometimes forming irregular networks. *Sori* terminal on veinlets, solitary at apex of ultimate segments, or marginal on simple to pinnatifid leaves; *involucre* cup-shaped to deeply 2-cleft nearly to base; receptacles terminating a vein, capitate, clavate, or elongate, maturation of sori gradate or maturing basipetally; *sporangia* short-stalked to nearly sessile, with oblique complete annulus; *spores* globose-trilete, tetrahedral, containing chloroplasts and soon dying after dehiscence. *Gametophytes* filamentous or ribbon-like, irregularly branched; archegonia on marginal cushions; antheridia at margin of ribbons or on lateral stalks of filaments.

DISTRIBUTION

Hymenophyllaceae are distributed worldwide, with the greatest diversity in tropical areas (Iwatsuki 1979). Circa 430–600 species are known. They occur mostly in wet or moist areas from the tropics and southern hemisphere throughout both the Old and New Worlds. A great diversity of species is in the southern hemisphere (45 species in Australia, Bostock & Spokes 1998; 27 spp. in New Zealand, Allan 1961).

Because most of the primitive forms of filmy ferns are in the southern hemisphere, and based on their diversity there, Copeland (1938: 85–89) speculated that the filmy ferns originated and diversified in Antarctica and then spread northward. He extended this idea to include most ferns, hypothesizing an Antarctic origin for them (Copeland 1939), but no evidence has been found to support his ideas.

There are a good number of species growing in warm temperate areas in the northern hemisphere, such as in China (50 species; Liu et al. 2013) and Japan (30 species;

Iwatsuki 1992, 1995). Only a few species extend into cold temperate areas and into alpine regions, although particular species grow far to the north where other ferns occur. Examples of some of the northernmost distributions of Hymenophyllaceae are *Hymenophyllum tunbrigense* (L.) Sm. in Baltasound, Shetland, Scotland at N60.7° and *Hymenophyllum wilsonii* Hook. in Iceland at N64°; several species are in Siberia, Sachalin and the Kuriles, and *Hymenophyllum wrightii* Bosch is in the Queen Charlotte Islands, Canada at N52°.

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HABITAT AND ECOLOGY

Hymenophyllaceae occupy a variety of habitats in Malesia. They are obligately or facultatively epipetric, or terrestrial on the forest floor or on earth banks (Copeland 1933, 1937, Taton 1946, Morton 1947, Holttum 1955, Lellinger 1984). Filmy ferns are most abundant in mossy forests, usually at elevations of 1000–2500 m in tropical areas. Most of the species are epiphytes, usually immersed or intermingled in mats of mosses on tree trunks. There are a few terrestrial species of *Abrodictyum* C.Presl in the summit zone in the tropics. Outside the mossy forests, most filmy ferns are epiphytic on tree trunks or epipetric on moist, moss-covered rocks. A number of terrestrial species often occur near streams in dense gloomy forests. Most species of *Cephalomanes* C.Presl and some of *Abrodictyum*, *Callistopteris* Copel., *Crepidomanes* C.Presl and *Vandenboschia* Copel. are terrestrial. *Cephalomanes* is distinct in its mostly rheophytic habitat; no species of filmy ferns in other genera usually grow on muddy rocks along streams. Rheophytic features are indistinct in Hymenophyllaceae, except in some species of *Cephalomanes*.

Although the filmy ferns are abundant at mid to high elevations in moist zones, they are also diverse in moist places in the lowlands. The unistratose construction of the laminae (one cell layer thick) makes them susceptible to drought. When the air becomes dry, the fronds of filmy ferns curl, as if they appear dead, but soon revive and the leaves unfold once they become wet (Kornaś 1977). In this way, filmy ferns with unistratose leaves can survive in the same manner as bryophytes. However, despite this adaptation to drought, there are no xerophytic species of Hymenophyllaceae in open or very dry places.

One particular habitat for the family is seen in several species of *Abrodictyum* subg. *Abrodictyum*, which are restricted to the trunks of tree ferns. Outside Malesia, *Polyphlebium venosum* (R.Br.) Copel. is known to be epiphytic on the tree fern trunks.

Detailed descriptions of the ecology and habitat of constituent species are described in many worldwide monographs and revisions. Some examples are: Mueller 1854, Holttum 1955, Diem & De Lichtenstein 1959, Sledge 1968, Stolze 1976, Proctor 1985, Parris 1992.

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FOSSILS

Relatively few records of fossils of Hymenophyllaceae exist, as nearly all species are generally fragile, as reflected in their colloquial name, filmy ferns. Most of the Palaeozoic and Mesozoic fossil records of filmy ferns were critically reviewed by Seward (1910). Iwatsuki (1990) suggested that it was hardly possible for plants in such a family as the filmy ferns to be preserved as fossils. Most of the earlier records of fossils in the family lacked sufficient information and they were usually described under such generic names as *Hymenophyllitis* Göpp., *Trichomanides* Ten.-Woods or *Trichomanites* Göpp. Most new records are based on well-preserved materials.

There are detailed studies of fossils of possible filmy ferns. Deng (1997) described *Eogonocormus* Deng from the early Cretaceous of China and Axsmith et al. (2001) observed fossils of *Hopetedia* Axsmith, Krings & Taylor from the Upper Triassic of the United States. *Hopetedia* was noted as being a member of Trichomanoideae and has more primitive features still not completely differentiated from Hymenophylloideae. These scientific reports confirm the presence of the family already in the Triassic. The origin and diversification of the family is still to be elucidated with much more information needed from both fossils and extant plants.

Herrera et al. (2017) dared to assign the well-preserved Mongolian fossils from the early Cretaceous to the extant genus *Hymenophyllum*. They noted that the fossil species was an epiphyte and distinctly different from Trichomanoideae. Diversification in the Hymenophyllaceae is traceable by such fossil evidence and coincides well with recent research that uses molecular methods to reconstruct phylogenies.

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TAXONOMIC CHARACTERISTICS

The circumscription of the Hymenophyllaceae is stable, and the family is treated here based on traditional concepts.

Vegetative features

In many species, the *rhizomes* are long-creeping, but some species have short, erect or ascending rhizomes. The rhizomes are protostelic in construction, although the protostelic condition is not necessarily primitive and is often called a Hymenophyllaceae protostele. The surfaces of the rhizomes are covered with hairs, at least at their apex, although older portions are often glabrescent.

The rhizomes of most species of *Hymenophyllum* Sm., *Didymoglossum* Desv., *Crepidomanes* C.Presl subg. *Crepidomanes*, *Polyphlebium* Copel. and *Vandenboschia* are long-creeping, slender, and usually branch irregularly. Those of *Hymenophyllum* are usually wiry, glabrous or very sparsely hairy in the older portion, or glabrescent. These genera are usually epiphytic.

The rhizomes of *Didymoglossum*, *Crepidomanes* subg. *Crepidomanes*, *Polyphlebium* and *Vandenboschia* are thicker and tender and usually densely covered with dark brown or blackish hairs. Most of the species in these genera are epipetric, terrestrial, or sometimes epiphytic. Most species of *Abrodictyum* subg. *Pachychaetum* (C.Presl) K.Iwats., *Crepidomanes* subg. *Nesoptertis* (Copel.) Ebihara & K.Iwats., *Cephalomanes* and *Callistopteris* have a caudex with thicker, wiry roots, and are epipetric or terrestrial.

Roots

Usually adventitious, and obsolete in some species of *Crepidomanes* and *Didymoglossum*. Species without roots have hairs on the rhizomes and appear to also absorb moisture from the surface of the leaves. Although it is not clearly observed, it is suspected that the rootless species have roots during their first developmental stages and loose them when adventitious roots develop. Ascending and erect rhizomes often have very stout, wiry roots. Schneider (2000) made critical observations of the roots of Trichomanoideae, paying particular attention to their ecology and habitat.

Leaves

Differentiated into two portions: a stipe and a frond (or blade). *Stipes* are either terete or variously winged, at least in their upper portion. Leaves with winged stipes are sometimes difficult to distinguish from fronds, especially in cases of simple fronds. Stipes are often hairy, and the nature of the hairs is variable according to the group or to the species. Hairs are simple, stellate, unicellular, multicellular, articulated, thick bristles, downy multicellular, and so on. The hairs are sometimes valuable systematic indicators especially in their position and nature.

Fronds

Simple to pinnately decompound, or irregularly dissected. The smallest fronds are only several millimeters long; larger ones may be more than 50 cm long. Some species have simple and entire fronds, and many simple-fronded species have irregularly lobed fronds.

The fronds are attached basipetally, even when they are simple. Development is principally on the apical margin, as is usual in megaphyllous leaves. Only in *Didymoglossum tahitense* (Nadeaud) Ebihara & K.Iwats. in the Asian tropics do the orbicular fronds centrifugally develop along the entire margin; the attachment of the stipe in *D. tahitense* is in the center of the blade, thereby forming peltate fronds. The marginal growth is unlimited so that the largest fronds can exceed 10 cm diam. The African *D. hildebrandtii* (Kuhn) Ebihara & Dubuisson also has peltate fronds and marginal growth, resulting in fronds up to 12 cm diam.

The American *Lecanium*, or *Didymoglossum membranaceum* (L.) Vareschi, is similar in its continuous marginal growth, but the fronds are larger and strap-like, not peltate or circular in form. The unlimited marginal growth occurs on the distal and lateral margins and not on the basal margin.

Larger fronds are compound and pinnate. Branching patterns in frond construction appear variable, but in fact most species have a principally pinnate branching plan. In some species of *Hymenophyllum*, especially in extremely moist habitats, one or a few lower pinnae abnormally enlarge to form structures called side leaves. In such cases, the fronds are seemingly composite, and often cubic in construction, having many segments in small spaces.

Several species are described as dichotomously or digitately branching, but most examples are only seemingly so, being caused by an extreme shortening of the rachis. The fronds of non-proliferous types of *Crepidomanes minutum* (Blume) K.Iwats. are nearly circular in outline, but they have serrated margins with one veinlet in each dentation, indicating that the dwarfed fronds of *C. minutum* are derived from pinnately dissected ones. The actual pattern of branching is the same as in pinnate fronds (Iwatsuki 1975). A few species have true dichotomous branching, as exhibited in *Crepidomanes vitiense*, though this species usually has only two, or at most four, segments.

Unistratose laminae are a distinctive feature of Hymenophyllaceae. This feature is suspected of having been derived through extreme reduction in a wet climate. Even in laminae with more than two cell layers, there are no intercellular spaces, and no stomata have been observed in any species of the family.

The ultimate segments of Hymenophyllaceae are typically uninervate, although they should not be considered to be homologous with telomes in primitive land plants. They may be referable to some species of *Asplenium*, such as *A. prolongatum* Hook., which has uninervate ultimate segments. The segments are usually thin, as is the leaf construction in general, membranous, and so-called filmy. The margin is entire or dentate, flat or more or less crisped.

When dried, the unistratose fronds usually curl, but can survive for long periods under such conditions and can easily and quickly become flat again once moisture is restored. This type of drought resistance is similar to that of bryophytes, and construction

of the filmy fern sporophyte is similar to that of bryophyte gametophytes, the feature of their dominant generation.

The structure of the unistratose leaves and uninervate ultimate segments has resulted in another interesting feature of filmy ferns comparable to the gametophytes of mosses. The dentation of the filmy fern lamina is similar to that of bryophytes and distinct from the serrations usually seen in the megaphyllous leaves of vascular plants. Generally, denticulations are in relation to veinlets in most megaphyllous plants, or each dentition is occupied by one veinlet. In the Hymenophyllaceae, in contrast, the ultimate segments are uninervate and a number of serrations are on the margin of the segments in some species of *Hymenophyllum*. Such dentition is formed by an irregular arrangement of the laminar cells, which are structurally quite similar to those of bryophytes and distinct from those of normal megaphyllous leaves.

Distinct dimorphism of leaves occurs in some species of *Trichomanes* subg. *Feea* but not in the members in our region. Heterophylly occurs in *Crepidomanes aphlebioides* (Christ) I.M.Turner, in which aphlebiae are present between adjacent leaves, which are short-stalked or subsessile, pinnately divided as minute leaves, tri- to quadripinnate, oblong, with acute apex and cuneate base, and c. 10 by 3 cm. The aphlebiae are usually variable in size and form, rachis and rachis of pinnae distinctly winged, up to 1.2 mm broad, pinnae short-stalked, ascending, ultimate segments often bending, spreading in various directions and resulting in a somewhat cubic construction of aphlebiae, often elongate to 3–5 mm, ultimate segments setaceous and usually with only one row of laminar cells on each side of the costa, 0.15–0.2 mm broad, entire and acute at the apex.

The colour of the lamina is variable; green to deep green in the wild and yellowish brown or reddish brown in dried specimens in many species of *Hymenophyllum*, but dark green in many species of *Crepidomanes*, *Vandenboschia* and *Abrodictyum*.

As in many other families of ferns, asexual reproduction occurs in some Hymenophyllaceae. Gemmae are on the leaves of *Crepidomanes minutum*. The form of the frond is variable in this species, from funnel-shaped to pinnately compound with gemmae borne on every leaf axis, on the stipes, on the rachis, on the rachis of the pinnae, the costa of the blade and the segments. In some cases, one or a few gemma(e) grow(s) on the frond, but in other cases the gemmae grow profusely, especially in very moist habitats, so that a frond often takes on the appearance of a composite of more than several fronds.

Many species of Hymenophyllaceae form mats on their substrate, on tree trunks and on rocks, resembling the habit of bryophytes. The rhizome develops very well and a mat of fronds is usually formed from a single or at most a few plant(s), somewhat like a bamboo thicket. It is a distinct way for pteridophytes to prosper through vegetative reproduction and an infinitely elongating rhizome. Vegetative reproduction through the formation of gemmae, however, is not common in the family.

The arrangement of laminar cells is diverse, and the morphology of the internal cell walls is a reliable key character for tracing relationships among species. The cells of the lamina exhibit a particular arrangement in *Abrodictyum* subg. *Abrodictyum*, and the marginal cells have a peculiar morphology in *Hymenophyllum* subg. *Pleuromanes* and *Crepidomanes* subg. *Crepidium*. The laminar cells are nearly obsolete in such species

as, e.g., *Abrodictyum idoneum* (C.V.Morton) Ebihara & K.Iwats., *A. pluma* (Hook.) Ebihara & K.Iwats., *A. setaceum* (Bosch) Ebihara & K.Iwats.

Another distinctive characteristic for tracing relationships among species is in the pseudoveins (false veinlets), which occur in *Crepidomanes* subg. *Crepidomanes* and *Didymoglossum*. Pseudoveins in the Hymenophyllaceae are veins without vascular tissues, as shown in anatomical features (Mettenius 1864, Wessels Boer 1962, Iwatsuki 1978). They are easily recognizable in *Didymoglossum*, as most of the pseudoveins continue from true veins. In some species of *Crepidomanes*, however, there are oblique false veinlets, independent from true veins. In such cases, it is necessary to explain that the false veinlets are veinlets without vascular bundles.

Trichomes

Scales do not occur in the Hymenophyllaceae. The scale-like structures of *Didymoglossum membranaceum* are in fact particular modifications of the margin of the lamina, and those of *Hymenophyllum mirificum* C.V.Morton and *H. odontophyllum* Copel. (a synonym of *H. brassii* C.Chr.) are particularly torn wings of the rachis (Iwatsuki 1977a, 1978).

Smaller hairs on all parts of the frond are usually unicellular, and often necessary to observe by microscope.

Simple hairs are various in their nature and distribution. In *Hymenophyllum digitatum* (Sw.) Fosberg and its allies, simple hairs are at the margin of the ultimate segments. They appear as bristles with thick cell walls, but are tender in *H. palmatifidum* (Müll.Berol.) Ebihara & K.Iwats.. Simple hairs of some species of *Hymenophyllum* are on the stipe and on the axis of the abaxial surface of the frond.

There are also multicellular hairs in many species and these are especially characteristic in *Hymenophyllum pallidum* (Blume) Ebihara & K.Iwats., species of *Callistopteris*, and in some species of *Abrodictyum*. The multicellular hairs are also variable in nature, articulated, downy, more or less appressed or bristle-like. Multicellular hairs coincide well with taxonomic groups, but provide no particular features to indicate interspecific relationships.

Stellate hairs have received special attention in regard to specific variation by Morton (1947) and Iwatsuki (1982).

Sori and sporangia

Sori are always at the apical margin of ultimate or axial segments. In simple fronds and those that are circular in outline the sori are on the frond margin and usually at the end of veinlets.

The receptacle of the sorus is at the very apical portion of a veinlet and is clavate, rounded or capitate. In some species, the receptacle portion is scarcely elongate and is included below the outer margin of the lips of the involucre, although some receptacles elongate beyond the lips of the involucre. In many cases, elongate receptacles occur in sori with a cup-shaped involucre, and short, capitate or clavate receptacles often occur in sori with a bivalvate involucre.

Actually, involucres have usually been described as bivalvate or cup-shaped, and this difference in construction of involucres was considered to be a valuable indicative feature to distinguish the two genera, *Trichomanes* s.lat. and *Hymenophyllum* s.lat.,

in a former bigeneric system of classification. The morphology of the involucre was observed in four representative species, especially with reference to development by Iwatsuki (1977b), with the conclusion that the involucre of Hymenophyllaceae was originally cup-shaped with a long-extruded receptacle and that bivalvate involucres evolved later as a derived feature. The construction of the sorus in the family is quite similar to that in the Dicksoniaceae. Most of the difference between them may be explained by the unistratose laminar construction of Hymenophyllaceae. Thus, the evolution of the soral construction appears to be due to parallelism in the two lines.

As soral construction is not sustainable as a vital key character to distinguish the classical *Trichomanes* and *Hymenophyllum*, it has been necessary to find other features to distinguish phylogenetic groups in the family. It is therefore natural to make use of a variety of features. The present classification (Ebihara et al. 2006) shows that soral construction, either bivalvate or cup-shaped, is not a good key character by itself to define genera, but remains as one of the key characters (see section on Systematics below).

Spores

The spores of Hymenophyllaceae are globose and tetrahedral and contain green chloroplasts while they are alive. As they are rather soft on the surface and short-lived, it is hardly possible to observe surface sculpturing patterns in spores removed from herbarium specimens.

Spores in the family usually germinate within the sporangium and can die soon after dehiscence. It is noted that the spores lose their viability usually within a week. It is sometimes reasoned that such a feature is an adaptation for species in the family to germinate quickly and become fixed to such unstable substrates as the mossy tree trunks and rock surface in moist forests where they grow. Even at such an early stage, the spores have chloroplasts and are autotrophic.

Gametophytes

The morphology of the gametophytic generation is interesting because of its unique structure among vascular plants and various features have been described from a biological standpoint. Holloway (1930, 1944) described the distinct morphology of filmy fern gametophytes. Stokey (1930) compared the diversity of the gametophyte generation in ferns, first in her study of the prothalia of Cyatheaceae, then germination in the gametophytes of Hymenophyllaceae (Stokey 1940) and finally in their reproductive structures (Stokey 1948). Based on a comparison of gametophyte morphology in various families, she commented on the phylogeny of the ferns during this stage of their life cycle (Stokey 1951). Her successor, Atkinson (1960) also studied the germination patterns of spores of Hymenophyllaceae and collaborated with Stokey in comparing the morphology of this particular generation (Atkinson & Stokey 1964).

Observations on 12 species of Hymenophyllaceae were reported by Yoroi (1972) in her study of Japanese species. She commented on the phylogeny of the Hymenophyllaceae based on her own observations as well as those from preceding studies (Yoroi 1976) and distinguished 8 patterns based on the mode of germination and on features of the mature prothallus that bears the reproductive organs.

Since then, a variety of observations on the morphology and reproductive mode in gametophytes of Hymenophyllaceae have contributed toward elucidating the systematics of ferns, although the number of such observations is limited when compared with number of studies of the sporophyte generation.

Farrar (1967, 1985, Farrar et al. 1983) made interesting observations on fern gametophytes in nature. Those on Hymenophyllaceae are comprehensive because of the distinct features of the gametophytes. Based on a gametophyte specimen, Farrar (1992) described a new species, *Trichomanes intricatum*, which was elucidated to be the gametophyte of the Asian *Crepidomanes schmidtianum* (Ebihara et al. 2008).

Chromosomes and reproductive pattern

Chromosome numbers have been reported for some species of Hymenophyllaceae since the time of Manton in 1950 (Mehra & Singh 1957, Tatuno & Takei 1969, Braithwaite 1969, 1975, Löve et al. 1977, Tilquin 1978, Takamiya 1996), although the number of species examined is still limited. Haploid chromosome number in many cases ranges from 11 to 36 (for *Hymenophyllum*), 32 (for *Cephaolomanes*), 33 (for *Abrodictyum*), 34 (for *Didymoglossum*) and 36 (for *Crepidomanes*, *Polyphlebium*, *Vandenboschia* and *Callistopteris*), although a variety of other numbers have also been reported (Hennequin et al. 2010). Since chromosome numbers are known for only a restricted number of species in this large family, more fundamental data and observations of chromosome numbers are still badly needed. Even with the limited number of reports, however, differences in basic chromosome numbers have been evaluated as highly reliable in tracing the phylogeny of species, species groups and the family itself.

A special pattern of reproductive cell formation is reported for *Trichomanes proliferum* Blume (a synonym of *Crepidomanes minutum* (Blume) K.Iwats.; Bell 1960). Agamospory (apospory) in relation to a wide range of phenetic variation in this species complex has also been observed by Yoroi & Iwatsuki (1977). According to our observations of the *C. minutum* complex, agamospory appears to be independent of the division pattern of the leaves, or from the occurrence of proliferation as discussed by Bell (1960), Braithwaite (1964, 1969), Bierhorst (1975) and Walker (1985). Generally, agamospory in ferns is scarce in epiphytic members, and as the habitat of *C. minutum* is either epiphytic or epipetric, it is interesting to observe the agamosporous habit in this species. We are still not sure if such a transformation in mode of reproduction depends on a particular evolutionary pathway. In groups other than Hymenophyllaceae, agamospory appears to be a fixed reproductive mode derived through evolution (Murakami & Iwatsuki 1990). The *Crepidomanes minutum* species complex may represent a good example for the study of the evolution of this mode of reproduction.

Phytochemistry

In parallel with the development of cytotaxonomy, especially in the mid 20th century, chemotaxonomy was one of the analytic methods in the field of biosystematics. Secondary chemical products in the cells were identified and used as indicators to trace the course of evolution of the species concerned. Basic data on the chemical compounds in pteridophytes was compiled in the latter half of the 20th century (Wallace & Markham 1978, Markham & Wallace 1980, Murakami & Tanaka 1988).

Molecular phylogeny

For the molecular phylogeny of pteridophytes, the first comprehensive accumulation of basic data was published by Hasebe et al. (1995). Since then, a great number of contributions has been made on the molecular systematics of the pteridophytes. The application of molecular data toward resolving the systematics of the pteridophytes was synthesized in PPG I (2016).

Preliminary attempts to use molecular methods for understanding the systematics of Hymenophyllaceae were made by Dubuisson and his colleagues (Dubuisson 1997, Dubuisson et al. 1998). Since then, three schools, with collaboration between them, have contributed to the molecular systematics of the Hymenophyllaceae: Pryer and her group (Pryer et al. 2001, Schuettpelz & Pryer 2006) in the United States, Dubuisson, Hennequin and their collaborators (Dubuisson et al. 2003a, b, Hennequin et al. 2003, 2006, 2008, 2010) in Paris, and Ebihara and his colleagues (Ebihara et al. 2002, 2004, 2006) in Tokyo-Tsukuba.

Based on an analysis of a variety of data, the generic system of the family was revised by Ebihara et al. (2006). The following list of Malesian species is arranged according their system.

Molecular techniques were also applied to analyze micro-evolution.

Studies of speciation in the Hymenophyllaceae have been fewer, although there are a number of species complexes that have been studied, including a variety using phenetic features. *Crepidomanes minutum* is a typical example. After a series of comprehensive studies of the family, Copeland (1958) lumped a number of names given to various forms of phenetic expression into the synonymy of his *Gonocormus minutus* (Blume) Bosch.

Braithwaite (1964) distinguished two forms, proliferous and sexually diploid *Trichomanes proliferum*e (a synonym of *Crepidomanes minutum*) and non-proliferous and apogamous *T. saxifragoides* C.Presl in his study of the cytology and reproductive mode in filmy ferns. Yoroi & Iwatsuki (1977) extended this type of research, including additional analytical methods, to propose that these two types could not be distinguished if we accepted wider variation and observed the two indicative features carefully for more individuals. Nitta et al. (2011) applied molecular data to show that distinct clades, which include a variety of hybrid races, form a reticulate evolutionary pattern within this species complex. The complex species structure is thus followed in recognizing *Crepidomanes minutum* in the broad sense.

Ebihara et al. (2005) showed another example of reticulate evolution of terribly variable phenetic features within the single species complex of *Vandenboschia radicans*. This species is also broadly defined to include a number of synonyms. A variety of hybrid combinations could be traced and the extensive variation in phenetic characters were elucidated within the reticulate evolution of this species complex.

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SYSTEMATICS

The Hymenophyllaceae have been treated as either bigeneric or multigeneric for many years. Since *Hymenophyllum* was recognized and separated from *Trichomanes* by Smith in 1793, both genera have been maintained for the family. In the mid 19th century, however, Presl (1843, 1848, 1849) and Van den Bosch (1859, 1861a, 1861b, 1861c, 1863) described a number of genera and proposed a multigeneric system for the family. Most botanists in 19th century, except for Presl and Van den Bosch, adopted the two genera

system in arranging the species of Hymenophyllaceae. This concept was followed by Christensen (1905–1906) in his Index Filicum and Christensen (1938).

During the latter half of the 19th century and the beginning of the 20th century, valuable contributions were made on comparative morphological observations of the Hymenophyllaceae. In addition to the detailed descriptions by Presl and van den Bosch, Mettenius (1864), Prantl (1875), Boodle (1900), Bower (1908) and others contributed greatly. Comprehensive data were added and compiled in the classical publications of Bower (1923), Goebel (1913, 1923) and Ogura (1938).

In the 1930s, Copeland made detailed observations on various characters, particularly on the Hymenophyllaceae mostly in the Old World and comprehensively revised the species. He published three monumental papers (Copeland 1933, 1937, 1938), and proposed a multigeneric system as his conclusion. In his Genera Filicum, Copeland (1947) recognized 34 genera in the family, mostly based on his detailed observations as well as in accord with his concept of a natural classification (Copeland 1929). His observations were followed by some Asian botanists and Itô (1949), Tagawa (1959), Ching (1959), Ohwi (1965), DeVol (1975) and Tagawa & Iwatsuki (1979) followed Copeland's multigeneric system in treatments in regional floras. Holttum published an excellent fern flora of Malaya (Holttum 1955) in which he adopted the bigeneric system for the Hymenophyllaceae, although he recognized all the trichomanoid genera of Copeland as infrageneric taxa. Croxall (1975) followed the concept of Holttum and the subgenera of *Trichomanes* in Holttum (1955) were treated as independent genera. Most European and American botanists insisted on following the traditional bigeneric system, except for Pichi Sermolli (1970, 1973, 1977a, 1977b, 1981) and Kunkel (1965), who recognized Copeland's system in part or in whole. Kunkel divided the family into two, treating Trichomanaceae as a distinct family.

Morton made detailed observations mostly on American species of the Hymenophyllaceae, and revised *Hymenophyllum* sect. *Sphaerocionium* comprehensively (Morton 1947). He also observed species of other groups, and proposed a subdivision of the two genera recognized in the family (Morton 1968). In naming subgenera and sections, he used Copeland's generic names and the definitions given by Copeland in creating subdivisions for the two broadly recognized genera.

Iwatsuki (1975, 1977a, 1977b, 1978, 1981, 1982, 1984, 1985, 1991) made a series of observations on various taxonomic characters of filmy ferns. Since the Hymenophyllaceae form a specially differentiated group, especially in laminar construction, it is invaluable to evaluate the characters based on careful observations of various morphological features, including their developmental stages, to derive at a systematic classification. Such observations were made in parallel with a revision of the species. The work was accompanied by careful comparisons of the species to yield evidence for revising some species groups.

Based on such observations, Iwatsuki (1984, 1990) proposed a generic and infrageneric system and enumerated the Asian species, excluding those from Malesia (Iwatsuki 1985). This was an oligogeneric system of eight genera. Among the eight genera recognized, three, *Cardiomanes* C.Presl in New Zealand, *Serpyllopsis* Bosch and *Hymenoglossum* C.Presl in Antarctic America, were monotypic and restricted to particular localities. The other five genera were subdivided into a number of subgenera and sections,

many of which were in accordance with Copeland's genera or Morton's subgenera and sections. Since Copeland did not recognize taxa at a rank between genera and species, the subgenera and sections in Morton's and Iwatsuki's systems in some parts coincide with Copeland's genera.

Until the end of the 20th century, taxonomic studies depended mostly on comparative morphology, in addition to information from cytotaxonomy and chemotaxonomy. Information from molecular systematics has been added since then and a number of clarifications have been made to former understandings of systematic treatises by using this new phylogenetic information (Dubuisson 1997, Pryer et al. 2001, Dubuisson et al. 2003a, 2003b, Ebihara et al. 2002, 2004, Hennequin et al. 2003, 2006). Based on the newly acquired information from molecular phylogeny, the new oligogeneric system proposed by Ebihara et al. (2006) is followed in the present treatise. Nine genera are recognized and a number of subgenera and sections are enumerated. Neotropical *Trichomanes* is not represented in Malesia, but the eight other genera are in the Malesian region and are distinguished by the following key (see below).

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KEY TO THE GENERA

1a. Rhizome creeping widely, more than several centimetres long 2
b. Rhizome short or erect 9
2a. Rhizomes nearly glabrous or with sparse pale hairs; involucres usually bivalvate . . . . . **6. Hymenophyllum**
b. Rhizomes with reddish or darker hairs; involucres not bivalvate, campanulate to tuberous 3

3a. Roots absent or replaced by root-like shoot 4
b. Roots present 5
4a. Pseudoveins parallel to true veins absent; venation anadromous . . . . . **4. Crepidomanes** (subg. **Crepidomanes**)
b. Pseudoveins parallel to true veins present; venation catadromous . . . . . **5. Didymoglossum**
5a. Roots few, fine, usually less than 0.15 mm diam. . . . . **7. Polyphlebium**
b. Roots numerous, more than a few in every millimeter, generally more than 0.2 mm diam. 6
6a. Fronds pinnate to bipinnatifid . . . . . **8. Vandenboschia**
b. Fronds bipinnate to more compound 7
7a. Abortive fronds present . . . . . **4. Crepidomanes** (subg. **Nesopteris**)
b. Abortive fronds absent 8
8a. Minute clavate hairs on stipe and rachis absent . . . . . **1. Abrodictyum**
b. Minute clavate hairs present on stipe and rachis . . . . . **8. Vandenboschia**
9a. Fronds pinnate to bipinnatifid . . . . . **3. Cephalomanes**
b. Fronds bipinnate or more compound 10
10a. Hairs on stipe and rachis elongate, bristle-like, light reddish 11
b. Elongate bristle-like hairs absent 12
11a. Laminar cells reduced; less than 3 rows of cells between midrib and blade margins . . . . . **1. Abrodictyum**
b. Laminar cells not reduced; more than 3 rows of cells between midrib and blade margins . . . . . **2. Callistopteris**
12a. Laminar cell walls slightly or quite thick, wavy or pitted . . . . . **1. Abrodictyum**
b. Laminar cell walls thin, straight . . . . . **4. Crepidomanes** (subg. **Nesopteris**)

1. ABRODICTYUM

Abrodictyum C.Presl, Abh. Königl. Böhm. Ges. Wiss., ser. 5, 3 (1843) 20, pl. 7; Copel., Philipp. J. Sci. 67 (1938) 85; Gen. Fil. (1947) 44; Ebihara et al., Blumea 51 (2006) 242. — *Trichomanes* L. sect. *Abrodictyum* (C.Presl) T.Moore, Index Fil. (1857) cx; C.V.Morton, Contr. U.S. Natl. Herb. 38 (1968) 185. — *Trichomanes* L. sect. *Eutrichomanes* C.Presl subsect. *Abrodictyum* (C.Presl) Alderw., Malayan Ferns (1908) 83. — *Cephalomanes* C.Presl subg. *Abrodictyum* (C.Presl) K.Iwats., Acta Phytotax. Geobot. 35 (1984) 176. — Type: *Abrodictyum cumingii* C.Presl.

Trichomanes L. subg. *Pachychaetum* C.Presl, Abh. Königl. Böhm. Ges. Wiss., ser. 5, 3 (1843) 16; C.V.Morton, Contr. U.S. Natl. Herb. 38 (1968) 187. — *Cephalomanes* C.Presl subg. *Pachychaetum* (C.Presl) K.Iwats., Acta Phytotax. Geobot. 35 (1984) 177. — Type: *Trichomanes rigidum* Sw. (= *Abrodictyum rigidum* (Sw.) Ebihara & Dubuisson).

Trichomanes L. subg. *Macroglena* C.Presl, Abh. Königl. Böhm. Ges. Wiss., ser. 5, 5 (1848) 333; Copel., Philipp. J. Sci. 51 (1933) 258; Holttum, Rev. Fl. Malaya 2 (1955) 103. — *Macroglena* (C.Presl) Copel., Philipp. J. Sci. 67 (1938) 82; Gen. Fil. (1947) 44; K.Iwats., Hikobia, Suppl. 1 (1981) 59. — *Cephalomanes* C.Presl subg. *Macroglena* (C.Presl) K.Iwats., Acta Phytotax. Geobot. 35 (1984) 176. — Lectotype (designated by Christensen, Index Filic. (1906) xv): *Trichomanes meifolium* Willd. (= *Abrodictyum meifolium* (Willd.) Ebihara & K.Iwats.).

Habrodictyon C.Presl ex Bosch, Verslagen Meded. Afd. Natuurk. Kon. Akad. Wetensch. 11 (1861) 321. — Type: *Habrodictyon cumingii* (C.Presl) Bosch (= *Abrodictyum cumingii* C.Presl).

Trichomanes L. sect. *Leptomanes* Prantl, Unters. Morph. Gefässkrypt. 1 (1875) 52. — Type: *Trichomanes smithii* Hook. (= *Abrodictyum cumingii* C.Presl).

Trichomanes L. sect. *Selenodesmium* Prantl, Unters. Morph. Gefässkrypt. 1 (1875) 53. — *Selenodesmium* (Prantl) Copel., Philipp. J. Sci. 67 (1938) 80; Gen. Fil. (1947) 42. — Type: *Trichomanes rigidum* Sw. (= *Abrodictyum rigidum* (Sw.) Ebihara & Dubuisson).

Rhizome ascending or short creeping, short and rather thick, c. 1.5 mm diam., or long-creeping and bearing dense bright brown hairs; *fronds* oblong-lanceolate to oblong, mediocre or larger in size, normally more than 5 cm long, bipinnate or more compound, in some species cubic in construction, or segments not arranged in a single plane; ultimate segments round to moderately acute at apex, entire and flat, or very narrow, without any laminar expansion, or up to 4 rows of tetragonal laminar cells at each side of veins; in some species internal cells distinctly elongate, elongate cells arranged in good order in the same direction, forming shorter continuous and distinct cell walls; *internal cell walls* thin and straight, or thick and pitted; *sori* campanulate, the lips more or less distinctly dilated; receptacles long-extruded.

Distribution — About 25 species widely distributed in the Old World tropics; 8 species throughout *Malesia*.

Habitat & Ecology — Terrestrial on moist clay ground in mossy forests at various elevations, from lower elevations to summit zone. Some terrestrial species spontaneously climb on the base of tree trunks; some others are typically epiphytic on mossy tree trunks or epipetric on moist rocks near streams in dense forests, and some are restricted to tree fern trunks.

Taxonomy — Both Copeland (1938, 1947) and Morton (1968) treated *Abrodictyum* as monotypic, and Copeland compared it with *Macroglena*, especially with *M. caudata*, while Morton placed it in *Trichomanes* subg. *Trichomanes* as an ally of *Trichomanes* sects. *Crepidium* and *Pleuromanes*. According to the key to subgenera given by Morton (1968), however, the first cited character leads *Abrodictyum* to subg. *Pachychaetum*.

More than ten species have been referred to *Macroglena* s.str. Copeland (1938, 1947) circumscribed his *Macroglena* rather broadly, enumerating 12 species from the Old World. Iwatsuki (1981) traced the relationships of each species included in *Macroglena* at that time, reconstructing *Macroglena* as to include the following four species rather strictly: two are closely related Malesian species, *A. pluma* and *A. idoneum*; Polynesian *A. asae-grayi* (Bosch) Ebihara & K.Iwats. is also close to the above two; another species to be added was *A. clathratum*, which was originally recorded from Taiwan, and now known also from Luzon. On the other hand, the African form of *Trichomanes meifolium*, the type species of *Macroglena*, was elucidated by molecular data to be related to subg. *Pachychaetum*. Molecular data now indicate that *Macroglena* s.str., excluding the type species, should be united with *Abrodictyum* s.str. at the rank of subgenus.

KEY TO THE SUBGENERA

1a. Rhizome short, ascending or creeping; laminar cells large, often more than 0.1 mm long, tetragonal to elongate, arranged variously . . . . . **1.** Subg. **Abrodictyum**

b. Rhizome short, erect, or short-creeping; laminar cells smaller, less than 70 micrometre diam., tetragonal, close to each other . . . . . **2.** Subg. **Pachycaetum**

1. Subgenus **Abrodictyum**

Abrodictyum C.Presl, Abh. Königl. Böhm. Ges. Wiss., ser. 5, 3 (1843) 20, pl. 7. — *Trichomanes* L. sect. *Abrodictyum* (C.Presl) T.Moore, Index Fil. (1857) cx. — *Trichomanes* L. subsect. *Abrodictyum* (C.Presl) Alderw., Malayan Ferns (1908) 83. — *Cephalomanes* C.Presl subg. *Abrodictyum* (C.Presl) K.Iwats., Acta Phytotax. Geobot. 35 (1984) 176. — Type: *Abrodictyum cumingii* C.Presl.

Habrodictyon C.Presl ex Bosch, Verslagen Meded. Afd. Natuurk. Kon. Akad. Wetensch. 11 (1861) 321. — Type species: *Habrodictyon cumingii* (C.Presl) Bosch (= *Abrodictyum cumingii* C.Presl).

Trichomanes L. sect. *Leptomanes* Prantl, Unters. Morph. Gefässkrypt. 1 (1875) 52. — Type: *Trichomanes smithii* Hook. (= *Abrodictyum cumingii* C.Presl).

Rhizome ascending or short creeping on tree fern trunks, or creeping, short and rather thick, c. 1.5 mm diam., or long-creeping and bearing dense bright brown hairs; *fronds* oblong-lanceolate to oblong, more than 5 cm long, bipinnate or more compound, in some species cubic in construction, or segments not arranged in a single plane; ultimate segments moderately acute at apex, entire and flat, or very narrow, without any laminar expansion, or up to 4 rows of tetragonal laminar cells at each side of veins; in some species internal cells distinctly elongate, elongate cells arranged orderly in the same direction, forming shorter continuous and distinct cell walls; *internal cell walls* thin and straight, or thick and pitted; sori campanulate, the lips a little to distinctly dilated; receptacles extruded. Chromosome numbers: $n = 36$.

Distribution — About 15 species in the Old World (Asia to the Pacific); Thailand (Peninsular), Taiwan, S Japan (Bonin), Polynesia, Australia, New Zealand; 5 species throughout *Malesia*.

Habitat & Ecology — Two species, *A. boninense* Tagawa & K.Iwats. and *A. cumingii*, occupy a special habitat on the intermingling adventitious roots on the surface of tree fern trunks, usually at middle elevations, in mist zones. Two additional species from Malesia are terrestrial on moist clay ground in mossy forests at higher elevations; they are neither epipetric nor epiphytic except in some particular cases where they climb up the base of tree trunks. Other species are epiphytic in dense forests at middle elevations.

Taxonomy — *Abrodictyum* was originally considered to be monotypic and was defined easily by the special form and arrangement of the laminar cells of the one species. A species from Bonin was later distinguished from the type species based on distinct differences from *A. cumingii* in the construction of the laminae (Iwatsuki, Acta Phytotax. Geobot. 17 (1958) 165). This second species, *A. boninense*, bridges the morphology of particular laminar cells between *A. cumingii* and *A. caudatum* (Brack.) Ebinara & K.Iwats. of Polynesia, and also the relationship to the New Zealand *A. strictum* (Menzies ex Hook. & Grev.) Ebihara & K.Iwats. The delimitation of *Abrodictyum*, thus became difficult. Iwatsuki (Hikobia, Suppl. 1 (1981) 59–66) moved a few additional species from *Macroglena* to *Abrodictyum*, but reports on chromosome numbers (Braithwaite, Bot. J. Linn. Soc. 71 (1975) 185) suggest further studies are needed. Molecular data show that *Abrodictyum* s.str. is in the same clade as *Macroglena* p.p. including *A. caudatum*.

There are interesting evolutionary trends in the cellular characteristics in *Abrodictyum*. The cells are extraordinarily elongate and perpendicularly arranged to the veins in *A. cumingii*. Formally, *A. cumingii* was considered to warrant generic distinction by

itself, but the recognition of *A. boninense* suggests further reference to the cellular construction of other species, including *A. caudatum* and *A. flavofuscum* (Bosch) Ebinara & K.Iwats., both of which should be placed under *Abrodictyum*, as is done here. The other distinct tendency is a reduction in laminar expansion, typically represented in *A. idoneum* and *A. pluma*. The artificial definition of *Macroglena* based on this feature was criticized by Iwatsuki (1981), and many of the species formerly included in *Macroglena* are here placed in *Abrodictyum*.

KEY TO THE SPECIES

1a. Rhizome ascending or short creeping; fronds usually arranged in a single plane; ultimate segments consisting of more than several rows of laminar cells, most of the internal cells distinctly elongate; elongate cells arranged orderly in the same direction, forming shorter, continuous and distinct cell walls; internal cell walls thin and straight; growing on intermingled adventitious roots on the surface of tree fern trunks usually at middle elevations in mist zones . . . . . **2. A. cumingii**

b. Rhizome creeping, short and rather thick, c. 1.5 mm diam., or long-creeping, bearing dense bright brown hairs; fronds often cubic in construction, or segments not arranged in a single plane; ultimate segments very narrow, up to 4 rows of tetragonal laminar cells at each side of veins; internal cell walls thick and pitted; terrestrial on moist clay ground in mossy forests at higher elevations 2

2a. Ultimate segments very narrow, setaceous, not in one plane but in cubic arrangement, laminar cells obsolete or only in one row at each side of costa **4. A. pluma**

b. Ultimate segments narrow but not really setaceous, arranged in one plane, laminar cells 2–4 rows at each side of costa 3

3a. Pagina not distinctly clathrate, internal cell walls thin and straight 4

b. Pagina distinctly clathrate, internal cell walls thick, coarsely pitted . . . . . **1. A. clathratum**

4a. Terrestrial ferns with erect or short ascending rhizome; fronds medium sized, to 10 cm long; stipes rather sparsely hairy; ultimate segments narrow, with 2–4 cells at each side of costa . . . . . **3. A. idoneum**

b. Epiphytic or epipetric ferns with creeping rhizome; fronds larger, usually 20–50 cm long; stipes with dense bristles throughout, bristles 8 mm long or more; ultimate segments direct variously, not arranging in one plane but forming more or less cubic construction of fronds, broader, usually with 3–6 larger and elongate cells rather obliquely arranged at each side of costa . . . . . **5. A. schlechteri**

1. Abrodictyum clathratum (Tagawa) Ebihara & K.Iwats.

Abrodictyum clathratum (Tagawa) Ebihara & K.Iwats. in Ebihara et al., Blumea 51 (2006) 243; J.X.Liu et al. in C.Y.Wu et al., Fl. China 2–3 (2013) 194. — *Trichomanes clathratum* Tagawa, Acta Phytotax. Geobot. 8 (1939) 164. — *Macroglena* sp.: K.Iwats. & M.G.Price, S.E. Asian Stud. 14 (1977) 552. — *Cephalomanes clathratum* (Tagawa) K.Iwats., J. Fac. Sci. Univ. Tokyo, Sect. 3, Bot. 13 (1985) 547. — Type: *Tagawa 2293* (holo KYO), Taiwan.

Rhizome widely creeping, c. 1.5 mm diam., densely covered with hairs, bearing fronds with some spaces, bearing roots; roots dark, usually less than 0.2 mm diam., densely covered with dark brownish hairs, irregularly branching; hairs multicellular, more or less articulated, bright brown or darker in older portion, 2–3 mm long. *Stipes* terete or very narrowly winged in upper portion, hairy throughout but caducous except for the basal portion, 1.5–5 cm long; *fronds* oblong, round to moderately acute at apex, cuneate to subcordate at base; 5–11 cm long, (1.5–)2–4 cm wide, tripinnate to quadripinnatifid; *rachis* winged throughout, caducously hairy; *pinnae* up to 15 pairs, lower ones reduced in size, middle ones larger, subdeltoid to ovate oblong, round at apex, cuneate at very shortly stalked base, to 2 cm long, 1.5 cm wide; larger *pinnules* often arranged in cubic form, with up to 12 segments, short-stalked; ultimate segments round to moderately acute at apex, entire, pale yellow green, brownish in dried specimens; *laminar cells* larger, pagina looked clathrate; *internal cell walls* thick, coarsely pitted. *Sori* solitary at apex of basal acroscopic segments of pinnules of upper pinnae, thus in one row at each side of pinna rachis; *involucres* shallowly cup-shaped, c. 1 mm long, c. 1 mm diam. at truncate mouth; receptacles long-extruded. — **Fig. 1d–f.**

Distribution — Taiwan; in *Malesia*: Philippines (Luzon, only two collections, from Mt Burnay and Mt Pulog).

Habitat & Ecology — Terrestrial on clayey ground in moist mossy forests on or below ridges. Altitude: 1800–2500 m.

Note — In discussing the relationship of this species, Iwatsuki (Hikobia, Suppl. 1 (1981) 61), briefly commented on the cell wall morphology: the thick, coarsely pitted internal cell walls were not identical with those of *A. pluma*, but were in common with many other species of *Macroglena* s.str. It was suggested that the 'other' species should be excluded from the *A. pluma* group, and this is followed here. *Abrodictyum clathratum* appears close to *A. pluma* based on the similarity in morphology of the rhizome, frond construction, structure of the sori, ecology and molecular data.

2. **Abrodictyum cumingii** C.Presl

Abrodictyum cumingii C.Presl, Abh. Königl. Böhm. Ges. Wiss., ser. 5, 3 (1843) 21, t. 7; K.Iwats., Acta Phytotax. Geobot. 17 (1958) 165; J.L.Tsai & W.C.Shieh in H.L.Li et al., Fl. Taiwan 1 (1994) 100, pl. 35; J.X.Liu et al. in C.Y.Wu et al., Fl. China 2–3 (2013) 94. — *Habrodictyon cumingii* (C.Presl) Bosch, Hymenophyll. Javan. (1861) 17, t. 12. — *Trichomanes cumingii* (C.Presl) C.Chr., Index Filic. (1905) 3; Copel., Philipp. J. Sci. 51 (1933) 257, pl. 56: 1–2. — *Cephalomanes cumingii* (C.Presl) K.Iwats., Acta Phytotax. Geobot. 35 (1984) 176; J. Fac. Sci. Univ. Tokyo, Sect. 3, Bot. 13 (1985) 545. — Lectotype (designated here): *Cuming 208* (lecto PRC; isolecto B, BM, E, K, L, MICH, P, US), Philippines, Luzon. Other syntype: *Cuming 358* (B, BM, E, GH, K, L, P, PRC), Philippines, Mindoro.

Trichomanes smithii Hook., Hooker's Icon. Pl. 8 (1844) t. 704; Sp. Fil. 1 (1848) 138. — *Habrodictyon smithii* (Hook.) Bosch, Verslagen Meded. Afd. Natuurk. Kon. Akad. Wetensch. 11 (1861) 321 — Lectotype (designated here): *Cuming 208* (lecto K 000557926, upper plant; isolecto B, BM, E, L, MICH, P, PRC, US), Philippines, Luzon. Other syntype: *Cuming 358* (B, BM, E, GH, K, L, P, PRC), Philippines, Mindoro.

Trichomanes warburgii Christ in Warb., Monsunia 1 (1900) 55. — Type: *Warburg 14106* (holo P), Philippines.

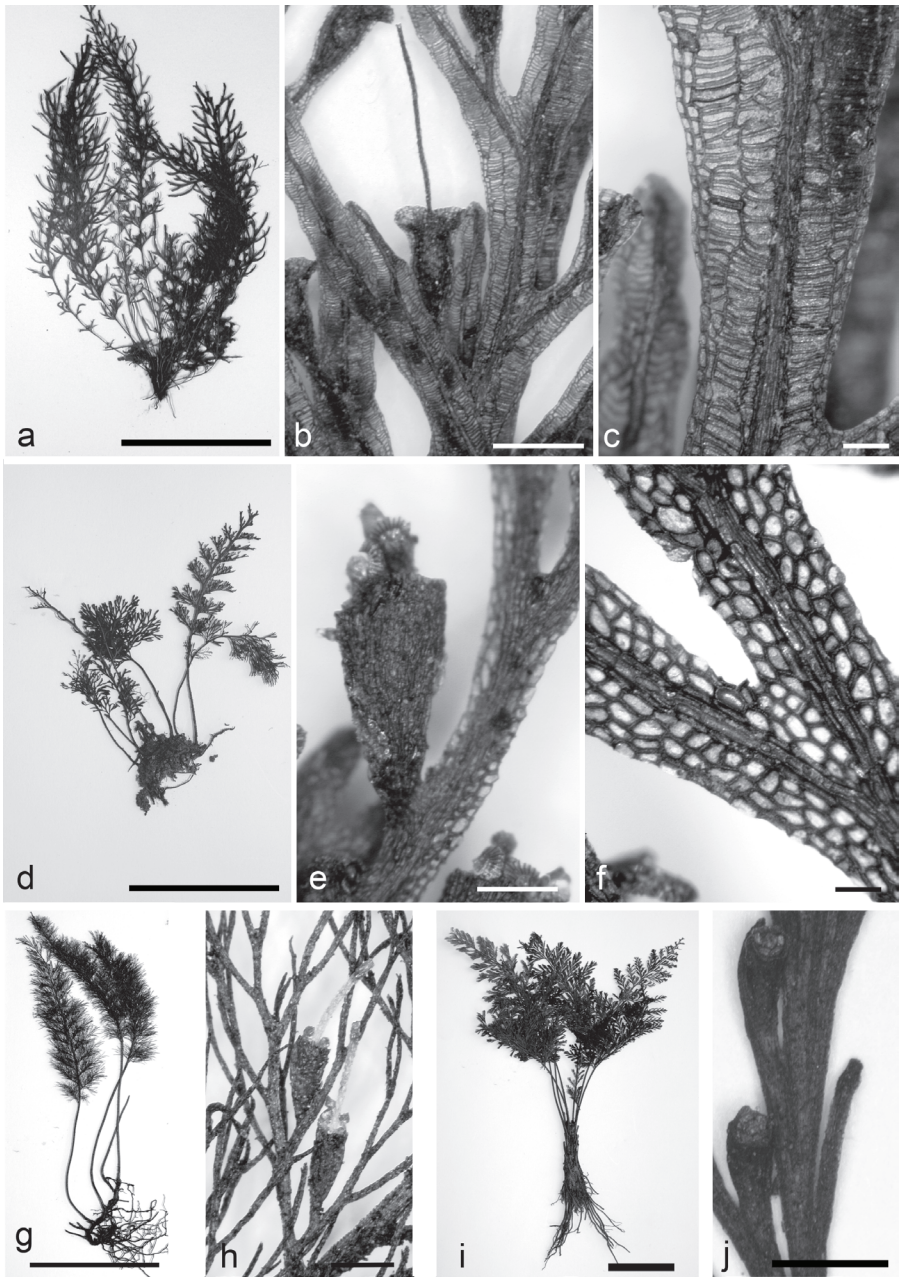

Fig. 1. a–c. *Abrodictyum cumingii* C.Presl. a. Fronds; b. sorus; c. laminar cells. — d–f. *A. clathratum* (Tagawa) Ebihara & K.Iwats. d. Fronds; e. sorus; f. laminar cells. — g, h. *A. pluma* (Hook.) Ebihara & K.Iwats. g. Fronds; h. sori. — i, j. *A. obscurum* (Blume) Ebihara & K.Iwats. i. Fronds; j. sorus (a–c: *Iwatsuki et al. P-1212*, Luzon, Philippines, KYO 00010999; d–f: *Iwatsuki et al. P-825*, Luzon, Philippines, KYO 00010998; g, h: Jaman s.n., Pahang, Malaysia, TNS; i, j: *Iwatsuki et al. S-358*, Sumatra, Indonesia, TI 00047643). — Scale bars: a, d, g, i = 5 cm; b, h, j = 1 mm; c, f = 0.1 mm; e = 0.5 mm.

Rhizome short, ascending or creeping among intricate adventitious roots on tree fern trunks, to 0.8 mm diam., bearing roots and fronds radially, densely covered with castaneous hairs; roots dark, scabrous, to 0.3 mm diam.; hairs dense at apex of rhizome, brown to bright brown, multicellular, articulated, to 3 mm long. *Stipes* densely crowded at the top of rhizome, terete, wiry, scabrous, brown to dark stramineous, glabrous or sparsely hairy near the base, 1–6 cm long; *fronds* oblong lanceolate, round to moderately acute at apex, gradually narrowing towards round to cuneate base, (2–)6–9(–13) cm long, to 3 cm wide, bipinnate to tripinnatifid with a few pinnules or segments; *rachis* similar to stipes, more slender and winged upwards, to middle, or sometimes upper middle, glabrous; *pinnae* larger, sessile, with several segments; ultimate segments usually elongate, moderately acute at apex, entire and flat at margin, 0.6–0.7 mm broad, to 2 cm long, green to pale green; *cells in laminae* transversely elongate and arranged along long cell walls, forming lines along shorter walls, sometimes referred to as false veinlets (Presl 1843), thus 1–3 rows of cells at each side of costae, in addition to single row of marginal cells; *internal cell walls* thin, nearly straight. *Sori* at terminal of short acroscopic branch, thus seemingly in one row at each side of costae, or sometimes 2 to 3 on each pinna; *involucres* campanulate or funnel-shaped with long tubes and dilated mouth, the tubes more than 1 mm long, c. 0.3 mm diam., winged on both sides, the mouth more than 0.3 mm in width, to 1 mm diam., the cells of involucre subquadrangular, arranged regularly, but never elongate; receptacles long-extruded. — **Fig. 1a–c.**

Distribution — Taiwan; in *Malesia*: Philippines (Luzon, Negros, Leyte, Polillo, Mindoro, Mindanao), Sulawesi, Moluccas and New Guinea.

Habitat & Ecology — Restricted to the trunks of tree ferns (and on oak trees in New Guinea); rooted in the intermingled adventitious roots on the trunk surface, usually in mist zones. Altitude: 500–2000 m.

3. **Abrodictyum idoneum** (C.V.Morton) Ebihara & K.Iwats.

Abrodictyum idoneum (C.V.Morton) Ebihara & K.Iwats. in Ebihara et al., Blumea 51 (2006) 243; K.Hori et al., J. Jap. Bot. 94 (2018) 35; K.Iwats. et al., PhytoKeys 119 (2019) 113. — *Trichomanes bifidum* C.Presl, Abh. Königl. Böhm. Ges. Wiss., ser. 5, 3 (1843) 43, non Vent. (1810) — *Trichomanes idoneum* C.V.Morton, Contr. U.S. Natl. Herb. 38 (1968) 272. — *Macroglena idonea* (C.V.Morton) Parris, Malayan Nat. J. 50 (1997) 257. — Lectotype (designated here): *Cuming 400* (lecto PRC; isolect B, BM, GH, MICH, K, PRC, US), Peninsular Malaysia, Malacca.

Trichomanes gemmatum J.Sm. [J. Bot. (Hooker) 3 (1841) 417, nom. nud.] in Hook. & Baker, Syn. Fil. (1867) 87, p.p. (except plants from Brasil); Copel., Philipp. J. Sci. 51 (1933) 269, pl. 61: f. 2; Tardieu & C.Chr. in Lecomte, Fl. Indo-Chine 7, 2 (1939) 69; Holttum, Rev. Fl. Malaya 2 (1955) 104, f. 40. — *Macroglena gemmata* (J.Sm. ex Baker) Copel., Philipp. J. Sci. 67 (1938) 84; Tagawa & K.Iwats. in Smitinand et al., Fl. Thailand 3 (1979) 98; K.Iwats., Hikobia, Suppl. 1 (1981) 62. — *Cephalomanes gemmatum* (J.Sm.) K.Iwats., J. Fac. Sci. Univ. Tokyo, Sect. 3, Bot. 13 (1985) 547. — Type: probably from Brasil as noted in C.V.Morton (Contr. U.S. Natl. Herb. 38 (1973) 272–273), although *Cuming 400* (K, MICH), Malacca, was one of the specimens cited.

Macroglena meifolia auct. non (Bory ex Willd.) Copel.: sensu Copel., Fern Fl. Philipp. 1 (1958) 80, p.p.

Rhizome creeping, not very long, irregularly branching, variable in size, usually in parallel with the size of plants, 0.6–1.7 mm diam., densely covered with hairs or glabrescent in age; hairs brown, multicellular, sometimes semi-articulated, commonly 1–2 mm long. *Stipes* close together, very narrowly to distinctly winged throughout,

with wings of 2–5 cells wide on each side, sparsely hairy, commonly the same length as, or a little longer than laminae, 2.5–7 cm long in fully mature plants, or more or less variable, stout and to 1 mm diam., or slender; *fronds* four or five times pinnately divided, oblong, round to moderately acute at apex, round or broadly cuneate at base, 3–10(–15) cm long, 1.5–4(–7) cm wide, and still variable in size and form; *rachis* like the upper part of stipes, narrowly winged with 1–4 rows of cells at each side; *pinnae* oblong subdeltoid to nearly circular, round to acute at apex, cuneate at base; ultimate segments setaceous, arranged in one plane or forming a more or less cubic construction of fronds, very narrow, consisting of veins and commonly 2–3(–4) rows of laminar cells at each side of veins, moderately acute at apex, entire at margin, commonly to 1 cm long, 0.2 mm broad, but variable in size and form. *Laminar cells* larger; *internal cell walls* thin, straight. *Sori* on short acroscopic segments of acroscopic pinnules, more or less curved downwards, or tending to direct the lower surface of fronds; involucres cup-shaped, truncate at apex, c. 1.2 mm long, c. 0.7 mm diam.; receptacles long-extruded.

Distribution — Thailand (Peninsular), Vietnam, Myanmar; in *Malesia*: Peninsular Malaysia, Borneo, Philippines, Moluccas (Seram) and New Guinea; Admiralty Islands.

Habitat & Ecology — On moist clayey ground and on humus rich ridges in dense forests, usually in the mossy zone near the summit.

Note — Some plants are difficult to refer to either this species or to *A. pluma*, for the development of the laminar surface is represented by various intermediate forms. Development in *A. pluma*, as noted in Lin et al. (J. Jap. Bot.78 (2003) 38–41), suggests that it may be a variant of *A. idoneum*.

4. Abrodictyum pluma (Hook.) Ebihara & K.Iwats.

Abrodictyum pluma (Hook.) Ebihara & K.Iwats. in Ebihara et al., Blumea 51 (2006) 243; C.W.Chen et al., Sol Amazing (2017) 106; K.Iwats. et al., PhytoKeys 119 (2019) 113. — *Trichomanes pluma* Hook., Hooker's Icon. Pl. 10 (1854) t. 997; Hook. & Baker, Syn. Fil. (1868) 466. — Type: *Lobb s.n.* (holo K), Malay Islands.

Trichomanes schultzei Brause, Bot. Jahrb. Syst. 49 (1912) 8. — Type: *Schultze 304h* (holo B), New Guinea.

Trichomanes meifolium Willd. var. *linearis* Brause, Bot. Jahrb. Syst. 56 (1920) 39. — Lectotype (designated here): *Ledermann 7713* (lecto B 20 0105179), Papua New Guinea. Other syntype: *Ledermann 9171* (B, BM), Papua New Guinea.

Trichomanes meifolium Willd. var. *contracta* Brause, Bot. Jahrb. Syst. 56 (1920) 39. — Type: *Ledermann 12143* (holo B), Papua New Guinea.

Trichomanes meifolium auct. non Willd.: Willd., Sp. Pl. 5 (1810) 509, excluding type; Copel., Philipp. J. Sci. 51 (1933) 265, pl. 59; Holttum, Rev. Fl. Malaya 2 (1955) 103. — *Macroglena meifolia* (Willd.) Copel., Philipp. J. Sci. 67 (1938) 83; Fern Fl. Philipp. 1 (1958) 80; Tagawa & K.Iwats. in Smitinand et al., Fl. Thailand 3 (1979) 98, f. 5–8; K.Iwats., Hikobia, Suppl. 1 (1981) 62, excluding type. — *Cephalomanes meifolium* (Willd.) K.Iwats., Acta Phytotax. Geobot. 35 (1984) 177; J. Fac. Sci. Univ. Tokyo, Sect. 3, Bot. 13 (1985) 546, excluding type.

Rhizome creeping, rather thick, to 1.5 mm diam., irregularly branched, bearing stipes close to each other, densely covered by the hairs or glabrescent with age; hairs multicellular, more or less articulated, 1.5 mm or more in length, often appressed, brown to bright brown. *Stipes* seemingly terete, but actually very narrowly winged with a single row of cells at each side, hairy, rather densely at base, gradually sparser upwards, usually

thick, to 1.2 mm diam., usually shorter than laminae, (2–)5–8(–12) cm long; *laminae* four or five times pinnately divided, oblong lanceolate to narrowly lanceolate, or oblong in smaller fronds, gradually narrowing towards acute apex, or the apex moderately acute in smaller fronds, the base round to roundly cuneate, 10–22 cm long, 2–4(–5) cm wide, but more variable in size; *rachis* like the upper part of stipes, narrowly winged and sparsely hairy throughout; *pinnae* commonly c. 20 pairs, shortly stalked, larger ones oblong to oblong subdeltoid, round to moderately acute at apex round to broadly cuneate at base, tri- to quadripinnate; pinna rachis narrowly winged, nearly straight or forming a little zigzag-form; ultimate segments linear, setaceous, consisting of only the veins or with a row of laminar cells at each side, sometimes more than 5 mm long, directing not in one plane, or recurving towards not only distal direction but also lower than adaxial surface as well as upper than abaxial surface, thus forming cubic construction of laminae. *Laminar cells* few, larger, c. 150 µm long; *internal cell walls* thin, straight. *Sori* solitary, terminal on short acroscopic branch of acroscopic pinnules, thus usually arranged in one row at each side of pinna rachis, dispersed on whole of the fronds but tending to be in upper portion, commonly recurved downwards; *involucres* cup-shaped, truncate at mouth, commonly c. 0.8 mm long, c. 0.5 mm diam., but variable in size and form; receptacles long-extruded. Chromosome numbers: $n = 33$ (Braithwaite, Bot. J. Linn. Soc. 71 (1975) 170). — **Fig. 1g, h.**

Distribution — Thailand (Peninsular), Vietnam; in *Malesia*: throughout; Solomon Islands.

Habitat & Ecology — Terrestrial on humus rich, peaty, and/or moist clayey ground or slightly climbing up the moss-covered base of tree trunks; usually in dense mossy forests, often along ridges, especially in summit areas. Altitude: commonly at middle to higher elevations, 750–2200 m.

Notes — In New Guinea and the Moluccas there are seemingly two forms of *Abrodictyum pluma*. The smaller form bears oblong to broadly oblong laminae; plants more delicate with rhizomes less than 1 mm diam., fronds smaller, often less than 10 cm including stipe, laminae broadly oblong, round to moderately acute, the ultimate segments with a row of larger laminar cells at each side of veins, thus seemingly less setaceous, and the laminar construction is less cubic. This is the form named var. *alatum*; another name, var. *lineare* Brause, was applied to a similar form as cited above; it is unclear whether the distinction is established or not.

The size of the largest available specimen is *BS (Merrill) 6072* (BO), from Mt Halcon, Mindoro, with the following measurements: rhizome 2.5 mm diam., stipes 1.7 mm diam., 12 cm long, laminae oblong subdeltoid, acute to acuminate at apex, 14 cm long, 8.5 cm wide. The longest fronds are on the specimen *Dransfield 4044* (BO), Air Sirab, Padang, Sumatra, with the lamina 24 cm long, and 5.5 cm wide.

5. **Abrodictyum schlechteri** (Brause) Ebihara & K.Iwats.

Abrodictyum schlechteri (Brause) Ebihara & K.Iwats. in Ebihara et al., Blumea 51 (2006) 243; C.W.Chen et al., Sol Amazing (2017) 107; K.Iwats. et al., PhytoKeys 119 (2019) 113. — *Trichomanes schlechteri* Brause, Bot. Jahrb. Syst. 49 (1912) 10; Copel., Philipp. J. Sci. 51 (1933) 268, pl. 60. — *Macroglena schlechteri* (Brause) Copel., Philipp. J. Sci. 67 (1938) 84; K.Iwats., Hikobia,

Suppl. 1 (1981) 63. — Lectotype (designated here): *Schlechter 19612* (lecto B 20 0106769; isolecto B 20 0106770, E, K, KYO, L, P, UC, US), Papua New Guinea.

Trichomanes compactum Alderw., Nova Guinea 14 (1924) 57; Copel., Philipp. J. Sci. 51 (1933) 265, pl. 59. — *Macroglena compacta* (Alderw.) Copel., Philipp. J. Sci. 67 (1938) 84. — Lectotype (designated here): *Lam 1559* (lecto BO; isolecto BM, L, MICH, SING, US), New Guinea. Other syntype: *Lam 1721* (BM, BO, L, MICH, SING, US), New Guinea.

Trichomanes compactum Alderw. f. *pauperculum* Alderw., Nova Guinea 14 (1924) 58. — Lectotype (designated here): *Lam 1721*, p.p. (lecto BO; isolecto L, SING), New Guinea.

Callistopteris muluensis K.Iwats., Acta Phytotax. Geobot. 21 (1965) 97, f. 2. — Type: *Hotta 14799* (holo KYO), Borneo, Sarawak.

Rhizome short creeping to ascending, bearing leaves closely spaced or nearly in fascicles at apex, thick roots in lower part, the apex densely covered with the bristles; bristles or hairs multicellular, consisting of more than a dozen cells, straight in lower half and more or less articulated and warty in distal half, pointed at apex, to 8 mm or often more in length, red brown, shining, the base more or less enlarged. *Stipes* terete in appearance, and very narrowly winged, wings of only one row of cells throughout and down to the base, densely covered with the bristles, rather short comparatively with the fronds, 1–5 cm long, and exceptionally to 15 cm long, to 3 mm diam., stramineous to brownish throughout, or more or less dark at the base; *fronds* quadripinnate to quasi-pinnatifid, narrowly oblong or lanceolate to linear-lanceolate, gradually narrowing to both ends, acuminate to caudate at apex, irregularly cuneate at base, 12–50 cm long, (2–)3–4.5(–6) cm wide, or smaller leaves often soriferous; *rachis* like the upper portion of stipes, gradually becoming thinner upwards, with shorter and less patent bristles; *pinnae* more than 30 pairs in larger leaves, shortly stalked in larger ones, usually close to each other and less than 1 cm from the next one, caudate-oblong or narrower, round to moderately acute at apex, cuneate at base, to 6 cm long, 1 cm wide; pinna rachis winged like the ultimate segments, bearing short hairs; *pinnules* often irregularly arranged, bearing the segments in various directions, thus laminae showing cubic construction; ultimate segment often elongate, commonly 2–4 cm long, sometimes elongate to more than 1.2 cm long, 0.3–0.6 mm broad, entire, slender, gradually narrowing in distal portion into acute to caudate-acute apex. *Laminar cells* often elongate in surface view, in 3–6 rows at each side of costae, very oblique or more or less longitudinally arranged; *internal cell walls* more or less thick, straight, rarely pitted. *Sori* solitary, on short acroscopic segments or often axillary in appearance, arranged in one row at each side of pinnule rachis, but often only few, or in one row at each side of pinna rachis, dispersed on the whole laminae; *involucres* cup-shaped with wings and truncate mouth, 1–1.5 mm long, to 1 mm diam. at mouth; receptacles long-extruded.

Distribution — *Malesia*: Borneo (Sabah, Sarawak), Moluccas (Seram) and New Guinea; Solomon Islands (Guadalcanal).

Habitat & Ecology — Epiphytic on mossy tree trunks and epipetric on moist rocks near streams in dense forests. Altitude: from low to mid elevations, 850–3000 m (850–1500 m in Borneo and 1200–3000 m in New Guinea).

Notes — Locally fairy common but the areas are restricted.

Abrodictyum schlechteri was originally described under *Trichomanes* and then placed in *Macroglena*, although it differs from other members of this 'genus' in having semi-articulated long hairs on the stipes and lacking short articulated hairs on the

upper surface of the rachis. The principal construction of the hairs on the stipes is the same as in *Callistopteris apiifolia*, and the difference seems to be only in appearance. Laminar cells narrow, very obliquely or longitudinally arranged, and thus the laminae are narrower, by which character it was included in *Macroglena* by Copeland (1938).

The fresh leaves are green to dark green but turn to reddish brown in dried specimens.

2. Subgenus **Pachychaetum** (C.Presl) K.Iwats.

Abrodictyum C.Presl subg. *Pachychaetum* (C.Presl) K.Iwats., Acta Phytotax. Geobot. 35 (1984) 177. — *Trichomanes* L. subg. *Pachychaetum* C.Presl, Abh. Königl. Böhm. Ges. Wiss., ser. 5, 3 (1843) 16; C.V.Morton, Contr. U.S. Natl. Herb. 38 (1968) 187. — Type: *Abrodictyum rigidum* (Sw.) Ebihara & Dubuisson.

Trichomanes L. subg. *Macroglena* C.Presl, Abh. Königl. Böhm. Ges. Wiss., ser. 5, 5 (1848) 333; Copel., Philipp. J. Sci. 51 (1933) 258; Holttum, Rev. Fl. Malaya 2 (1955) 103. — *Macroglena* (C.Presl) Copel., Philipp. J. Sci. 67 (1938) 82; Gen. Fil. (1947) 44; K.Iwats., Hikobia, Suppl. 1 (1981) 59. — *Cephalomanes* C.Presl subg. *Macroglena* (C.Presl) K.Iwats., Acta Phytotax. Geobot. 35 (1984) 176. — Lectotype (designated by Christensen, Index Filic. (1906) xv): *Trichomanes meifolium* Willd. (= *Abrodictyum meifolium* (Willd.) Ebihara & K.Iwats.

Trichomanes L. sect. *Selenodesmium* Prantl, Unters. Morph. Gefässkrypt. 1 (1875) 53. — *Selenodesmium* (Prantl) Copel., Philipp. J. Sci. 67 (1938) 80; Gen. Fil. (1947) 42. — *Trichomanes* L. subg. *Selenodesmium* (Prantl) Holttum, Rev. Fl. Malaya 2 (1955) 108. — Type: *Trichomanes rigidum* Sw. (= *Abrodictyum rigidum* (Sw.) Ebihara & Dubuisson).

Rhizome short creeping, bearing fronds not clustered but close together, with dense dark hairs; *fronds* bi- to tri-pinnate, usually arranged in one plane; *ultimate segments* with at least three rows of laminar cells at each side of veins except for the distal portion; *laminar cells* usually tetragonal, with *internal cell walls* thick and coarsely pitted; mouth of involucre truncate or slightly dilated.

Distribution — Pantropical, 15 species (see below), of which 3 in *Malesia*.

Taxonomy — Subgenus *Pachychaetum* is distinct in having segments with an acute apex and usually with setaceous segments split from pinnules, truncate mouth of involucre, and semiarticulate hairs on the stipes.

About 10 species are currently enumerated in the group of *A. rigidum*, or under *Selenodesmium*, although revision is badly needed, especially for the widespread species, such as the tropical American *Abrodictyum rigidum*, IndoMalesian *Abrodictyum obscurum*, Polynesian *Abrodictyum dentatum* (Bosch) Ebihara & K.Iwats. and New Zealand *Abrodictyum elongatum* (A.Cunn.) Ebihara & K.Iwats. Iwatsuki (1981) suggested separating five species of the group of *Abrodictyum setaceum* from *Macroglena* s.str. and including them in the group of *Abrodictyum rigidum*. This is followed here under the generic name *Abrodictyum*. Subgenus *Pachychaetum* thus includes 15 rather ill-defined species from all tropical areas on earth.

Morphology — The rhizome in subg. *Pachychaetum* as here defined is short and erect, although it is actually very short creeping and bearing fronds close to each other. The construction is radial, with the leaves arranged radially, giving the appearance of bearing fronds only dorsally. The stipes are close to each other and the appearance of the rhizome often leads to it being described as erect. The pattern of dissection of the main axes is pinnate, and open dichotomous distally. Larger laminae usually have

branching veins, and finely dissected forms have uninervate ultimate lobes and vein endings forming denticulations.

KEY TO THE SPECIES

1a. Ultimate segments with distinct laminar expansion throughout with 3–6 rows of laminar cells on each side of costa . . . . . **7. A. obscurum**
b. At least the distal part of ultimate segments setaceous with at most one row of laminar cells on each side of costa 2
2a. Laminae developed only at sinus-bottom, most ultimate segments setaceous . . . . . **8. A. setaceum**
b. Laminae with 2–6 rows of laminar cells on each side of lower half of ultimate segments . . . . . **6. A. kalimantanense**

6. Abrodictyum kalimantanense (K.Iwats. & M.Kato) Ebihara & K.Iwats.

Abrodictyum kalimantanense (K.Iwats. & M.Kato) Ebihara & K.Iwats. in Ebihara et al., Blumea 51 (2006) 244. — *Macroglena kalimantanensis* K.Iwats. & M.Kato, Acta Phytotax. Geobot. 31 (1980) 31; K.Iwats., Hikobia, Suppl. 1 (1981) 64. — Type: *Iwatsuki et al. B-1888* (holo KYO; iso BO, K, L, MO, TI), Borneo, Kalimantan.

Rhizome short, erect or ascending, bearing 3–8 fronds and numerous stout roots, the thickness of which is nearly the same as, or even thicker than, the stipe. *Stipes* stout, dark brown throughout, to 10 cm long, a half to five-sixth of the length of the lamina, bearing very narrow wings with 1–3 rows of narrow cells, somewhat densely hairy throughout; *lamina* narrowly oblong to lanceolate, broadest at a quarter from the base, round to subtruncate at base, gradually narrowing toward long acuminate apex, commonly 7–12 cm long, 1.5–2.7 cm wide, the largest one to 20 by 6 cm, tripinnate to quadripinnatifid; rachis like stipe, very narrowly winged or seemingly terete, hairy; lateral *pinnae* commonly 10–20 pairs, the upper ones indistinct, merging into indistinct apical portion, lower and middle pinnae oblong, oblique to patent, or the basal one often little deflexed, round at apex, round to subtruncate at acroscopic base, cuneate at basiscopic base, shortly stalked, commonly to 1.3 by 0.5 cm, the larger ones to 3.5 by 1.2 cm; *pinnules* 4 or 5 pairs, the distal ones adnate at base and becoming indistinct, various in size, form and dissection; ultimate segments several for each pinnule, more than half of the basal portion fused to the neighboring to develop typical laminar expansion, distal portion setaceous, bearing commonly 1, or rarely 2–3 row(s) of laminar cells at each side of veinlets, the setaceous portion 0.3–1 (rarely to 3) mm long; pagina hardly clathrate, dark brown, texture membranous, harsh; *laminar cells* larger, narrower, 0.05–0.07 mm long; *internal cell walls* thick, coarsely pitted; hairs on stipe, rachis and basal part of pinna rachis multicellular, polished brown to dark brown, to 3 mm long, not very stiff and semiarticulated but those at basal portion of stipe bristle-like; hairs on higher axes shorter, of 2 or 3 cells, brown, to 0.1 mm long. *Sori* solitary at acroscopic base of pinnules, cup-shaped, very narrowly winged, c. 1 mm long, 0.5 mm diam., the mouth of involucre truncate or little dilated in young stage; receptacles long-extruded.

Distribution — *Malesia*: Borneo (E Kalimantan: 3 collections).

Habitat & Ecology — On the wet, muddy foot of perpendicular cliffs under continuous spray in dense gloomy forests. Altitude: c. 350 m.

Note — In general features, *A. kalimantanense* is similar to *A. setaceum*, but has the laminar expansion at the sinus more developed. The setaceous portion of the segments, or veinlet with a row of cells on both sides, is usually less than half the length, i.e., between the junction to the opposite veinlets and the apex. In this feature, *A. kalimantanense* is intermediate between *A. setaceum* and *A. obscurum,* the latter has no setaceous part of the ultimate segments.

7. Abrodictyum obscurum (Blume) Ebihara & K.Iwats.

Abrodictyum obscurum (Blume) Ebihara & K.Iwats. in Ebihara et al., Blumea 51 (2006) 244; J.X.Liu et al. in C.Y.Wu et al., Fl. China 2–3 (2013) 94; C.W.Chen et al., Sol Amazing (2017) 104; K.Iwats. et al., PhytoKeys 119 (2019) 113. — *Trichomanes obscurum* Blume, Enum. Pl. Javae 2 (1828) 227; Bosch, Hymenophyll. Javan. (1861) 23, pl. 17; Copel., Philipp. J. Sci. 51 (1933) 233, pl. 43–44; Tardieu & C.Chr. in Lecomte, Fl. Indo-Chine 7, 2 (1939) 69; Holttum, Rev. Fl. Malaya 2 (1955) 108, f. 44; Sledge, J. Linn. Soc. Bot. 60 (1968) 307. — *Didymoglossum obscurum* (Blume) Hassk., Obs. Bot. Fil. 2 (1857) 22. — *Selenodesmium obscurum* (Blume) Copel., Philipp. J. Sci. 67 (1938) 81; Fern Fl. Philipp. 1 (1958) 79; Ching, Fl. Reipubl. Popularis Sin. 2 (1959) 191; Croxall, Austral. J. Bot. 23 (1975) 541; Tagawa & K.Iwats. in Smitinand et al., Fl. Thailand 3 (1979) 99; J.L.Tsai & W.C.Shieh in H.L. Li et al., Fl. Taiwan 1 (1994) 127, pl. 48. — *Cephalomanes obscurum* (Blume) K.Iwats., J. Fac. Sci. Univ. Tokyo, Sect. 3, Bot. 13 (1985) 547. — Lectotype (designated by Morton, Contr. U.S. Natl. Herb. 38 (1974) 381): *Zippel s.n.* (lecto L), Java.

Trichomanes obscurum Blume var. *adnatum* Blume, Enum. Pl. Javae 2 (1828) 227. — Type: *Blume s.n.* (holo L), Java.

Trichomanes obscurum Blume var. *obtusiusculum* Blume, Enum. Pl. Javae 2 (1828) 227. — Type: *Blume s.n.* (holo L), Java.

Didymoglossum longisetum C.Presl, Abh. Königl. Böhm. Ges. Wiss., ser. 5, 3 (1843) 49. — Syntypes: *Cuming 134* (E, GH, GOET, L, MICH, P, PRC n.v., UC), Philippines; *Cuming 189* (E, GH, GOET, MICH, L, P, PRC n.v., US), Philippines.

Trichomanes caruifolium Roxb., Calcutta J. Nat. Hist. 4 (1844) 519; C.V.Morton, Contr. U.S. Natl. Herb. 38 (1968) 381. — Lectotype (designated by Morton, Contr. U.S. Natl. Herb. 38 (1974) 382 who indicated it as 'holotype'): *Reinwardt 2430*, right-hand plant (lecto BR 00000510306; isolecto BM, G, K), Peninsular Malaysia.

Trichomanes papillatum Müll.Berol., Bot. Zeitung (Berlin) 12 (1854) 751. — Syntypes: *Cuming 134* (B, GH, L, MICH, P), Philippines; *Cuming 189* (B, GH, L, MICH, P, US), Philippines.

Trichomanes saxatile T.Moore, Gard. Chron. 1862 (1862) 45. — *Selenodesmium saxatile* (T.Moore) Parris, Malayan Nat. J. 50 (1997) 259. — *Abrodictyum saxatile* (T.Moore) Parris, Fern Gaz. 20 (2018) 305. — Type: collection not specified (K? n.v.), Borneo.

Trichomanes latipinnum Copel., Philipp. J. Sci., C. 6 (1911) 71. — Type: *Copland King 108* (holo MICH), Papua New Guinea, Waria River.

Trichomanes englerianum Brause, Bot. Jahrb. Syst. 56 (1920) 37. — Lectotype (designated here): *Ledermann 11026a* (B 20 0104494; isolecto B, BM), Papua New Guinea, Hunsteinspitze.

Trichomanes extravagans Copel., Philipp. J. Sci. 51 (1933) 240, pl. 48. — *Selenodesmium extravagans* (Copel.) Copel., Philipp. J. Sci. 67 (1938) 81; Fern Fl. Philipp. 1 (1958) 80. — Lectotype (designated here): *BS (Ramos & Edaño) 28465* (lecto MICH 1191067; isolecto BO, P, UC, US), Philippines, Luzon.

KEY TO THE VARIETIES

1a. Lower portion of rachis and stipes terete; mouth of involucres hardly dilated. . . . . **a.** var. **obscurum**

b. Rachis and at least upper portion of stipes persistently winged; mouth of involucres more or less dilated . . . . . **b.** var. **siamense**

a. var. **obscurum**

Type as species.

Rhizome stout, short creeping, ascending, or suberect, c. 2 mm diam., bearing stout roots below, several leaves near the apex, hairy at apex; hairs brown to dark brown, shining, slender, straight with thick cell walls, to 5 mm long, very dense at the apex, caducous with age. *Stipes* stramineous to darker, terete in appearance but very narrowly winged nearly to the base when young, wings mostly broken off when older, hairy throughout or caducous in the upper portion, commonly 7–15 cm long, but size variable, proportionately a little shorter than the blades; *blade* bipinnate to tripinnatifid, oblong subtriangular, gradually narrowing towards caudate-acuminate apex, round to broadly cuneate at base, 12–20 cm long, 5–18 cm wide, but the size and form very variable, even the small fronds of less than 2 cm long well soriferous, and larger ones nearly 30 cm long; *rachi*s very narrowly winged throughout, more or less forming zigzag in upper portion; *pinnae* nearly 20 pairs, lower ones subpatent, ascending and falcate in the upper ones, narrowly oblong, round to moderately acute at apex, cuneate and shortly stalked at base; pinna rachis similar to rachis, distal part broadly winged to form terminal pinnule-like collections of segments; *pinnules* oblong or subrhomboid, round at apex, cuneate at subsessile base, oblique, cut in various degrees at margin, often having nearly free secondary pinnules, commonly c. 1 cm long, 2.5 cm wide; lobes of pinnules or secondary pinnules with 2–5 segments, serrate at margin, each dentation at apex of veinlets; several veins in basiscopic side of basiscopic pinnules often becoming lamina-less; lamina-less veinlets and some lobes of pinnules often rolled in, forming the blades in a cubic construction. *Laminar cells* tetragonal in appearance, more than several rows at each side of midribs; *internal cell walls* thick and coarsely pitted. *Sori* solitary, on short basal acroscopic branch of a few basal acroscopic lobes, or secondary pinnules, and dispersed over nearly whole surface of fronds; *involucres* cup-shaped, truncate or bilabiate at apex, often narrowly winged but constricted at base, to 1.5 mm long, 0.6–0.7 mm diam.; receptacles long-extruded. Chromosome numbers: $n = 33, 36$ (Manton & Sledge, Philos. Trans., Ser. B 238 (1954) 136; Manton in Holttum, Rev. Fl. Malaya 2 (1955) 623); Ghatak, Nucleus (Calcutta) 20 (1977) 106). — **Fig. 1i, j.**

Distribution — Sri Lanka, India, Nepal, Bhutan, China (Yunnan, Hainan), Taiwan, Myanmar, Thailand, Vietnam, S Japan (Ryukyu, Bonin); in *Malesia*: throughout; Solomon Islands and Australia (N Queensland).

Habitat & Ecology — On clayey slopes, usually along streamlets in dark places in moist gloomy forests. Altitude: from low to mid or rarely higher elevations, to 2700 m.

b. var. **siamense** (Christ) K.Iwats.

Abrodictyum obscurum (Blume) Ebihara & K.Iwats. var. *siamense* (Christ) K.Iwats. in Ebihara et al., Blumea 51 (2006) 244; J.X.Liu et al. in C.Y.Wu et al., Fl. China 2–3 (2013) 95. — *Trichomanes siamense* Christ, Bot. Tidsskr. 24 (1901) 103. — *Selenodesmium siamense* (Christ) Ching & Chu H.Wang, Acta Phytotax. Sin. 8 (1959) 138; Ching, Fl. Reipubl. Popularis Sin. 2 (1959) 138. — *Cephalomanes obscurum* (Blume) K.Iwats. var. *siamense* (Christ) K.Iwats., J. Fac. Sci. Univ. Tokyo, Sect. 3, Bot. 13 (1985) 548. — Lectotype (designated here): *J.Schmidt 401* (lecto C; isolecto BM, PE), Thailand, Koh Chang.

Plants smaller; *stipes* to 4 cm long, narrowly winged; *blade* narrowly oblong to oblong lanceolate, gradually narrowing towards acute apex, to 4 cm long, 2 cm wide, bipinnate, or in larger pinnae pinnules are dissected; *pinnae* sessile, or the lower ones stalked with wings decurrent on rachis. *Sori* as in the type variety.

Distribution — China (Guangxi, Guangdong, Hainan), Thailand, Cambodia and Japan (S Ryukyu); in *Malesia*: Peninsular Malaysia, Borneo and Sulawesi.

Habitat & Ecology — On moist clayey slopes and on moist muddy rocks along streamlets in dark moist forests, from low to mid elevations, from sea level to 2000 m.

Note — A recent, still unpublished molecular study suggests that this form is sufficiently distinct from the typical variety to warrant specific status pending further taxonomic analysis.

8. Abrodictyum setaceum (Bosch) Ebihara & K.Iwats.

Abrodictyum setaceum (Bosch) Ebihara & K.Iwats. in Ebihara et al., Blumea 51 (2006) 244. — *Trichomanes setaceum* Bosch, Ned. Kruidk. Arch. 5(2) (1861) 176; Copel., Philipp. J. Sci. 51 (1933) 260, pl. 57: f. 1. — *Macroglena setacea* (Bosch) Copel., Philipp. J. Sci. 67 (1938) 84; Fern Fl. Philipp. 1 (1958) 81; K.Iwats., Hikobia, Suppl. 1 (1981) 64. — Syntypes: *Aman s.n.* (n.v.), Sumatra, Ins. Banca; *Gaudichaud s.n.* (n.v.), Singapore.

Trichomanes setigerum Backh., Cat. (1861) 14; T.Moore, Gard. Chron. 1862 (1862) 45; Holttum, Rev. Fl. Malaya 2 (1955) 104. — *Cephalomanes setigerum* (Backh.) I.M.Turner, Asian J. Trop. Biol. 1 (1995) 26. — *Macroglena setigera* (Backh.) Parris, Malayan Nat. J. 50 (1997) 257. — *Abrodictyum setigerum* (Backh.) Parris, Fern Gaz. 20 (2018) 305, nom. inval. — Type: collection not specified (K n.v.), Borneo.

Trichomanes merrillii Copel., Philipp. J. Sci. 1., Suppl. 2 (1906) 144, t. 1. — Lectotype (designated here): *Merrill 716* (lecto MICH 1191081; isolecto B, GH, P, SING, US), Philippines, Paragua.

Rhizome stout and short, erect, at most a few centimeters tall, bearing stout roots downwards, and commonly 3–5 leaves near the top, covered by the hairs at apex; hairs dark brown to nearly black, straight, patent, with thick walls, c. 2 mm long, somewhat enlarged at base. *Stipes* terete in appearance, very narrowly winged by a wing of one row of cells nearly towards the base, stramineous or dirty brown, densely hairy throughout, shorter than laminae, commonly to 7 cm and rarely to 12 cm long, to 2 mm diam.; fronds tripinnate to quadripinnatifid, oblong, gradually narrowing towards round to acute apex, round to broadly cuneate at base, 10–15(–20) cm long, 3–5(–7) cm wide, or smaller leaves soriferous; *rachis* like the stipes, gradually becoming thinner upwards, bearing sparse hairs, very narrowly winged nearly to the apex; *pinnae* 15–20 pairs, 5–8 mm remote, or sometimes more than 1 cm remote, patent or slightly ascending, oblong to oblong lanceolate, round to moderately acute at apex, cuneate and shortly stalked at

base, to 3.5 cm long, 1.5 cm wide; pinna rachis like rachis, very narrowly winged, glabrescent, thinner towards distal end; *pinnules* sessile or nearly so, with bipinnatifid or pinnate construction bearing many segments mostly in one level; the ultimate division deeply cut, and ultimate segments usually longer, distal part of 3–5 mm long bearing only one row of cells for laminar expansion, and distinct membrane at sinus between segments. *Laminar cells* in one row of cells in most of the ultimate segments and pinna rachis and other axes; *internal cell walls* thick, coarsely pitted. *Sori* solitary, on short basal acroscopic segments of secondary pinnules, or often fertile segments very short and seemingly axillary, arranged commonly in one row at each side of pinna rachis, dispersed evenly on whole of the laminae, or often gathering to the center of laminae; *receptacles* cup shaped, with truncate mouth, c.1.2 mm long, 0.5 mm diam.; receptacles very long-extruded.

Distribution — *Malesia*: Peninsular Malaysia (Perak), Borneo and Philippines (Palawan).

Habitat & Ecology — Terrestrial on muddy sandstone rocks along streams and in crevices of rocks and the base of cliffs in dense montane forests. Altitude: from low to mid elevations, 1000–2000 m.

2. CALLISTOPTERIS

Callistopteris Copel., Philipp. J. Sci. 67 (1938) 64; Gen. Fil. (1947) 40; Ebihara et al., Blumea 51 (2006) 248; J.X.Liu et al. in C.Y.Wu et al., Fl. China 2–3 (2013) 95. — *Trichomanes* L. sect. *Callistopteris* (Copel.) C.V.Morton, Contr. U.S. Natl. Herb. 38 (1968) 190. — *Cephalomanes* C.Presl subg. *Callistopteris* (Copel.) K.Iwats., Acta Phytotax. Geobot. 35 (1984) 176. — Type: *Callistopteris apiifolia* (C.Presl) Copel.

Rhizome terrestrial or epipetric, suberect or slightly ascending, bearing fronds fascicled; stipes stout, brownish to stramineous, densely covered with long, multicellular, bright brown hairs or glabrescent; *fronds* finely dissected, quadripinnate or more compound; ultimate segments narrow or to 0.8 mm in breadth, entire and flat at margin; *sori* campanulate, truncate; receptacles long-extruded.

Distribution — Six species; India (Nicobar Islands), Thailand (Peninsular), Vietnam, S China (Hainan), Taiwan, Japan (Yakushima, S Ryukyu); *Malesia*: 2 species, very common throughout; Micronesia, Polynesia including Hawaii, Australia, Norfolk Isl. and Lord Howe Isl.

Habitat & Ecology — Generally epipetric, usually in moist places in lowlands near streams in deep shade or very rarely terrestrial or even epiphytic on the base of tree trunks.

Morphology — A description of the morphological characters of *Callistopteris* was given in Iwatsuki (Hikobia, Suppl. 1 (1981) 59–66), including a summary of descriptions of various species in the genus from various floras and revisions.

Rhizomes are usually short and stout; erect to ascending with fasciculate leaves and usually stout, irregularly branching roots. The surface of the rhizome is covered with hairs, although older portions are often glabrescent.

The stipes are comparatively stout, comprehensively hairy or with dense bristles, and they have a central stele. The hairs are long, multicellular, patent, bright brown, stiff

and bristle-like, and very dense. The stele is more or less triangular in cross section. The laminae are pinnately dissected. The pattern of dissection is pinnate on the main axes, and open dichotomous on distal portions. Finely dissected forms have uninervate ultimate lobes.

The most distinctive trichomes are the hairs on the stipes of *Callistopteris*. The laminae are mostly unistratose except on the veins. False veinlets have not been observed in any of the species of *Callistopteris*.

The sori are campanulate with a truncate or dilated mouth; the receptacles are long-extruded, persistent, and straight.

Taxonomy — In addition to the five species included in *Callistopteris* by Copeland (1938), *C. superba* (Backh.) Ebihara & K.Iwats. is also included here, although it was placed in *Vandenboschia* by Copeland (1938). Among the six species recognized here for the genus, four species have a rather restricted distribution area outside Malesia: *C. baldwinii* (D.C.Eaton) Copel. in Hawaii, *C. baueriana* (Endl.) Copel. on Norfolk and Lord Howe Islands, *C. calyculata* Copel. in Rapa and SE Polynesia and *C. polyantha* (Hook.) Copel. in the Society Islands. The type species, *C. apiifolia*, is widely distributed throughout the area of the genus.

Callistopteris is often considered to be related to *Crepidomanes* subg. *Nesopteris* (cf. Copeland 1938). However, they seem to have evolved independently and in parallel from a mother stock, as is shown by the molecular data.

KEY TO THE SPECIES

1a. Rhizome erect, with tufted fronds; fronds narrowly deltoid to oblong subdeltoid; hairs on stipes patent, not articulated or bristle-like, those on rachis articulated; segments 0.2–0.5 mm broad . . . . . **1. C. apiifolia**

b. Rhizome ascending to short creeping, with close fronds; fronds narrowly oblong to oblong-lanceolate; hairs on stipes semiarticulated or not bristle-like, those on rachis not articulated, nor bristle-like; segments c. 0.8 mm broad . . **2. C. superba**

1. Callistopteris apiifolia (C.Presl) Copel.

Callistopteris apiifolia (C.Presl) Copel., Philipp. J. Sci. 67 (1938) 65; Fern Fl. Philipp. 1 (1958) 75; Tagawa & K.Iwats. in Smitinand et al., Fl. Thailand 3 (1979) 85; J.X.Liu et al. in C.Y.Wu et al., Fl. China 2–3 (2013) 95; C.W.Chen et al., Sol Amazing (2017) 108; K.Iwats. et al., PhytoKeys 119 (2019) 113. — *Trichomanes apiifolium* C.Presl, Abh. Königl. Böhm. Ges. Wiss., ser. 5, 3 (1843) 16, 44; Bosch, Hymenophyll. Javan. (1861) 26, t. 19; Hook. & Baker, Syn. Fil. (1867) 86; Christ, Bull. Herb. Boissier 6 (1898) 141; Copel., Philipp. J. Sci. 51 (1933) 227, pl. 42: f. 1. — *Cephalomanes apiifolium* (C.Presl) K.Iwats., Acta Phytotax. Geobot. 35 (1984) 176; J. Fac. Sci. Univ. Tokyo, Sect. 3, Bot. 13 (1985) 545. — Lectotype (designated here): *Cuming 137* (lecto PRC; isolecto B, GH, K, MICH, P, US), Philippines. Other syntype: *Cuming 190* (B, BM, GH, K, L, MICH, P, PRC), Philippines.

Trichomanes eminens C.Presl, Abh. Königl. Böhm. Ges. Wiss., ser. 5, 3 (1843) 16, 44. — Lectotype (designated here): *Cuming 207* (lecto PRC; isolecto BM, K, L, MICH, P, US), Philippines, Luzon.

Trichomanes myrioplasium Kunze, Bot. Zeitung (Berlin) 4 (1846) 477. — Type: *Zollinger 1762* (holo B n.v.), Java.

Trichomanes exaltatum Brack., U.S. Expl. Exped., Filic. 16 (1854) 259. — Type: *Wilkes C 19* (holo US), Fiji.

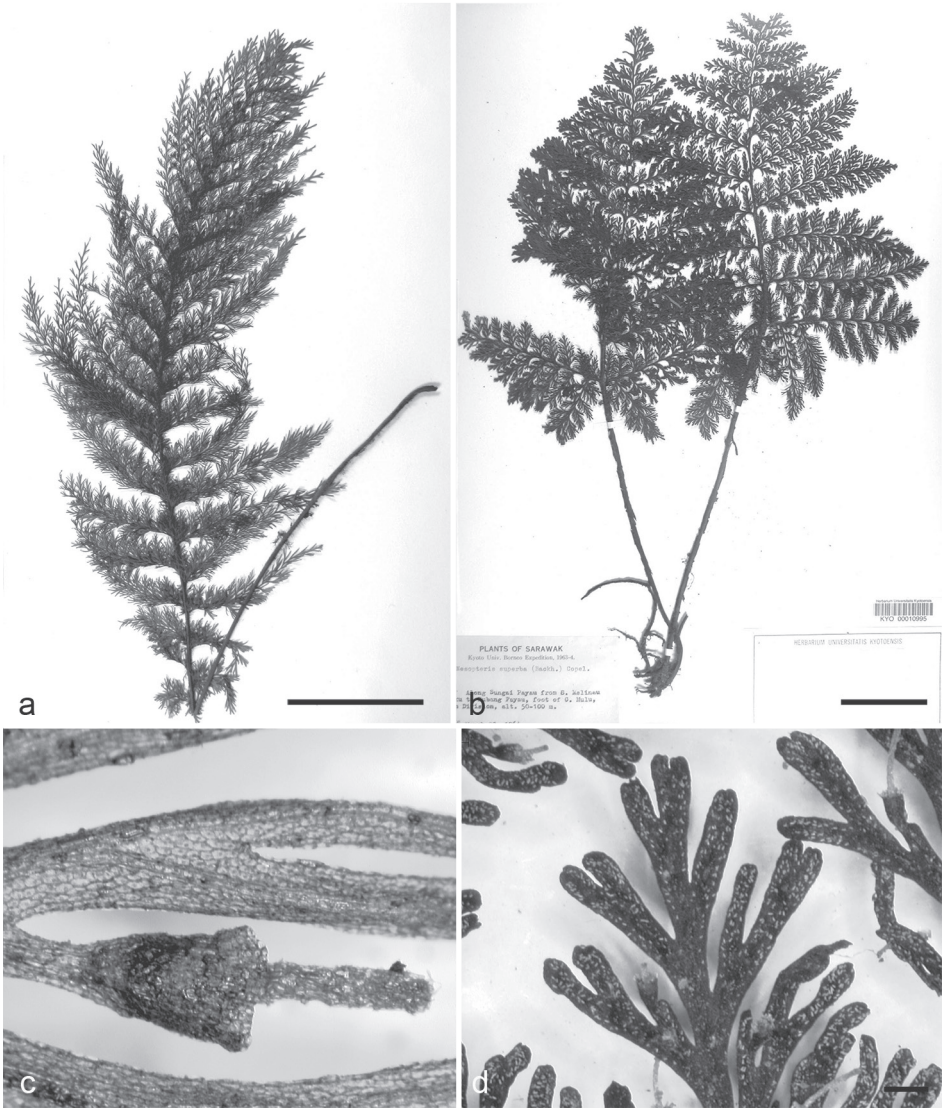

Fig. 2. a, c. *Callistopteris apiifolia* (C.Presl) Copel. a. Frond; c. sorus. — b, d. *C. superba* (Backh.) Ebihara & K.Iwats. b. Fronds; d. segments with sori (a, c: *Iwatsuki et al. P-1023*, Luzon, Philippines, KYO 00010993; b, d: *Hotta 15319*, Sarawak, Malaysia, KYO 00010995). — Scale bars: a, b = 5 cm; c, d = 1 mm.

Rhizome short, erect or rarely ascending, sometimes forming mass of stocks more than 5 cm in height, bearing tuft of fronds at apex and many roots, hairy at apex; roots to 1.8 mm diam., bearing very dense minute root hairs, often carrying muddy soil even in the dried specimens. *Stipes* terete, to 2.5 mm diam., stramineous to brownish, densely covered with bristles, (5–)8–15(–25) cm long, usually c. half-length of fronds; bristles or hairs reddish brown to brilliantly dark brown, shining, multicellular, patent or little

downy, 4–7(–12) mm long, the base more or less enlarged; *fronds* oblong lanceolate to broadly oblong, 15–40(–55) cm long, 7–10(–16) cm wide, or smaller leaves often soriferous, acuminate at apex, gradually narrowing towards narrowly cuneate, cuneate or round base, tripinnate to quadripinnate or more compound; *rachis* like the upper part of stipes, terete or narrowly winged in the upper part, densely hairy throughout; pinnae 15–20 pairs, lower pinnae smaller than the middle ones, ascending or patent, middle pinnae larger, subsessile or very shortly stalked, 1–2(–3) cm apart, ascending, narrowly oblong subdeltoid, broadly cuneate at base, gradually narrowing towards long-acuminate apex, to 10 cm long, 3 cm wide, the upper pinnae becoming smaller upwards; pinna rachis nearly straight or slightly bending upwards, in distal portion terete, or narrowly winged, hairy throughout, but the hairs less dense and shorter than those on stipes; larger *pinnules* oblong to rhomboid, moderately acute to round at apex, cuneate at sessile base, to 2 cm long, 1 cm wide; secondary pinnules with (1–)5–6(–8) pinnately arranged segments and winged costae; ultimate segments round to acute at apex, entire, 2–3.5(–5) mm long, 0.2–0.5 mm broad, pale green, brownish in old specimens, delicate and easily broken, often imbricate to each other; *laminar cells* tetragonal in surface view, in several rows at each side of costae, with thin and straight *internal cell walls*. *Sori* solitary at apex of short segments, or on 1–3 basal acroscopic secondary pinnules usually in one row at each side of pinnule rachis, dispersed on whole of the surface of fronds but more or less tending to be in the upper portion; *involucres* cup-shaped, 1–1.5 mm long, c. 0.7–1 mm diam., the mouth truncate, usually broadly open, the base gradually narrowing with slight constriction; receptacles long-extruded, sometimes more than 4 mm long. Chromosome numbers: $n = 36$ (Braithwaite, Fern Gaz. 10 (1969) 82, Bot. J. Linn. Soc. 71 (1975) 170; Mitui, J. Jap. Bot. 51 (1976) 49). — **Fig. 2a, c.**

Distribution — India (Nicobar Islands), Thailand (Peninsular), Vietnam, S China (Hainan), S Japan, Taiwan; in *Malesia*: Peninsular Malaysia, Sumatra, Java, Borneo, Philippines, Lesser Sunda Islands, Sulawesi, Moluccas and New Guinea; Polynesia, east to Samoa.

Habitat & Ecology — Epipetric on moist muddy rocks along streams in dense gloomy forests and partly in light places. Altitude: from low to mid elevations, rarely to 3000 m.

Notes — A lovely impression is given by the fascicled, larger, pale to yellow green leaves. *Callistopteris apiifolia* is one of the most handsome filmy ferns, although it is not easy to cultivate outside humid greenhouses.

As in the most filmy ferns, *C. apiifolia* may have sori even when the fronds are still young; in such cases the involucres are more or less dilated with broader lips. Smaller plants, less than 10 cm long, often bear sori and are thus fully mature. In such plants, the rachis of the pinna is often broadly winged, like the ultimate segments, and thus the dissection is less distinct, often tripinnate or at most quadripinnatifid. The ultimate segments are more than 5 mm long in such forms and in general appearance is even similar to the species of *Vandenboschia*.

A specimen from Timor (*Posthumus 3331*, SING) has broader segments, c. 0.8 mm in breadth, and larger laminar cells.

2. Callistopteris superba (Backh.) Ebihara & K.Iwats.

Callistopteris superba (Backh.) Ebihara & K.Iwats. in Ebihara et al., Blumea 51 (2006) 249. — *Trichomanes superbum* Backh., Cat. (1861) 15; T.Moore, Gard. Chron. 1862 (1862) 44, non Bosch (Ned. Kruidk. Arch. 5 (1863) 203); Copel., Philipp. J. Sci. 51 (1933) 221, pl. 39; Holttum, Rev. Fl. Malaya 2 (1955) 108. — *Nesopteris superba* (Backh.) Copel., Philipp. J. Sci. 67 (1938) 66; K.Iwats. & M.Kato, Acta Phytotax. Geobot. 31 (1980) 30. — *Cephalomanes superbum* (Backh.) I.M.Turner, Asian J. Trop. Biol. 1 (1995) 26. — Type: *Day ex H.Low s.n.* (n.v.), Borneo.

Trichomanes hispidulum Mett. in Kuhn, Linnaea 35 (1868) 389. — Syntype: *Motley ex Lobb s.n.* (K), Borneo.

Trichomanes ignobile Ces., Felci (1876) 9. — Syntypes: *Beccari s.n.* (FI, K, MICH), Borneo, Sarawak.

Rhizome ascending or suberect, bearing fronds closely, densely hairy at apex; hairs multicellular, brown, rather setose, to 2 mm long; roots many, thick, to 1.7 mm diam., blackish, bearing short dark hairs or glabrescent. *Stipes* to 30 cm long, dark in dried condition, hairy at base, bearing rather dense, long, multicellular, semiarticulate, brown hairs to 4 mm in length, distinctly winged nearly to the base, the wings to 2 mm broad, blackish in dried condition, entire, flat, often broken in the old specimens; *fronds* quadripinnate to quasipinnatifid, subdeltoid or ovate subtriangular, acute to acuminate at apex, broadly cuneate to subtruncate at base, to 25 cm long, 25 cm wide at base; *basal pinnae* the largest, unequally subtriangular, the basal basiscopic pinnule more than twice as large as the third and fourth, middle pinnae oblong-lanceolate, moderately acute at apex, widest at middle portion or at base, broadly cuneate at base, shortly but distinctly stalked, 7–10 cm long, 2–3.5 cm wide, *upper pinnae* gradually becoming smaller upwards; *rachis* and pinna rachis more or less stout, bearing rather dense brown, multicellular, semi-articulated or straight hairs, 2–4 mm in length, distinctly winged throughout with entire, flat wings as wide or wider than breadth of the segments; larger pinnules unequally oblong subdeltoid, shortly stalked or subsessile, round to very moderately acute at apex, broadly cuneate at base, 2–3.5 cm long, 1–1.5 cm wide; pinnule rachis seemingly the same as ultimate segments; *secondary pinnules* pinnate or bipinnatifid, usually with 10 or less segments, to 1 cm long, 0.5 mm wide; ultimate segments c. 0.8 mm broad, entire, usually enrolled inside in dried condition, nearly black when dried, minutely hairy on the veinlets underneath or glabrescent; sometimes the involute lower surface covered with short glandular cilia of whitish yellow colour, similar to those on the mouth of involucres, often caducous. *Laminar cells* not particular, larger in size than those of *C. apiifolia*; *internal cell walls* thin, not coarsely pitted, often wavy. *Sori* solitary at apex of short segments, immersed or broadly winged; *involucres* cup-shaped, c. 0.8 mm long, 0.5 mm diam., truncate and never dilated at mouth; cilia pale brown to whitish yellow, dense at the edge of mouth; receptacles long-extruded. — **Fig. 2b, d.**

Distribution — *Malesia*: Peninsular Malaysia (Perak, Johore), Singapore, Sumatra and Borneo (Brunei, Sarawak, Kalimantan).

Habitat & Ecology — Terrestrial on loamy soils and in wet marshy places, usually in dense gloomy forests at lower elevations.

Notes — *Callistopteris superba* is often described as having an erect rhizome or caudex, although it is short creeping, and even when it appears to be erect the stipes are closely spaced, never having the habit of an erect rhizome with fascicled fronds.

All the segments are dark when dried and recurved, and thus the fronds of dried specimens appear corrugated. The distinct impression is given to this species by the combination of such features as the blackish colour of the plants, stout stipe and rachis with distinct flat wings, numerous, robust roots and ovate subdeltoid fronds. Copeland placed *C. superba* in his subg. *Vandenboschia* (Philipp. J. Sci. 51 (1933) 21) and later in *Nesopteris* (Philipp. J. Sci. 67 (1938) 66), but the molecular data do not support either of these treatments.

Trichomanes ignobile is based on a juvenile plant whose affinity is undoubtedly here.

3. CEPHALOMANES

Cephalomanes C.Presl, Abh. Königl. Böhm. Ges. Wiss., ser. 5, 3 (1843) 17, pl. v; Bosch, Hymenophyll. Javan. (1861) 30; Copel., Philipp. J. Sci. 67 (1938) 66; Gen. Fil. (1947) 40; K.Iwats., Acta Phytotax. Geobot. 35 (1984) 176, emend.; Ebihara et al., Blumea 51 (2006) 248. — *Lacostea* Bosch sect. *Cephalomanes* (C.Presl) Prantl, Unters. Morph. Gefässkrypt. 1 (1875) 50. — *Trichomanes* L. subg. *Cephalomanes* (C.Presl) C.Chr., Index Filic. (1906) xiv; Holttum, Rev. Fl. Malaya 2 (1955) 102. — *Trichomanes* L. sect. *Cephalomanes* (C.Presl) C.V.Morton, Contr. U.S. Natl. Herb. 38 (1968) 189. — Type: *Cephalomanes atrovirens* C.Presl.

[*Trichomanes* L. 'subg.' *Schizophlebium* Bosch in Miq., Pl. Jungh. 5 (1857) 551, nom. nud.]

Rhizome erect or ascending, bearing accumulated fronds and usually hairy roots; *stipes* fascicled or close together, stout, hairy, green to darker; *fronds* unipinnate, or pinnatifid in one species (*C. crassum*), bearing characters of rheophytes; *pinnae* narrowly oblong, acroscopic side serrate, deeply cut in basiscopic side; *internal cell walls* thick and coarsely pitted; *sori* solitary at margin of pinnae, *involucres* campanulate, the mouth truncate; receptacles long-extruded. Chromosomes: $n = 32$ (Manton in Holttum, Rev. Fl. Malaya 2 (1955) 623; Mitui, J. Jap. Bot. 51 (1967) 34; Braithwaite, Fern Gaz. 10 (1969) 82).

Distribution — Five species are known in the Old World tropics; India, Myanmar, Thailand, Indo-China, S China (Hainan), Taiwan, S Japan (Ryukyu), Micronesia, Melanesia, Polynesia, south to Australia (Queensland); all the five species are throughout *Malesia*.

Habitat & Ecology — Epipetric or terrestrial usually in streambeds and on rocks along streams, on sandy ground near ravines and terrestrial on gentle slope usually near streamlets and thus in very wet places in deep shade or in gaps in the crown at lower elevations. *Cephalomanes* is distinct in its rheophytic habitat: *C. javanicum* and *C. atrovirens* are typically rheophytic, having slender fronds, pinnae and pinnules with narrower angles to the rachis and costae.

Morphology — A comprehensive description of the morphological characteristics of *Cephalomanes* is given in Iwatsuki (J. Jap. Bot. 66 (1991) 134–146).

The rhizomes are usually short and stout, erect to ascending with fasciculate leaves. They bear usually stout, irregularly branching roots. The surface of the rhizome is covered with hairs, but the older portions are often glabrescent. The inner structure is observed as typically protostelic. The roots are internally diarch.

The stipes are close to each other, and are comparatively stout, hairy or glabrescent, and have the stele in the center. The stele is more or less triangular in cross section. The laminae are pinnately dissected. The least dissected laminae are in *C. crassum*, which

has deeply pinnatifid laminae. *Cephalomanes* typically has once pinnate laminae and the vein ends form denticulations, with most branching veins in the larger laminae.

The laminae are mostly unistratose, except on the veins. False veinlets have not been observed in any species of *Cephalomanes*. The construction of the internal cell walls is used to distinguish subgenera, although more careful observations are necessary.

Gametophytes — The gametophytic characters have not been studied in detail in *Cephalomanes*.

Taxonomy — The concept of *Cephalomanes* has been fixed since the time of Presl (1843) and Van den Bosch (1861), although the rank at which it is recognized differs according to the authors. The pinnate fronds with more or less rheophytic morphological characteristics lead to the easy definition of the genus.

Cephalomanes is well defined by simply pinnate fronds, but the aberrant *C. crassum* has pinnatifid fronds. The genus as a whole usually grows in rheophytic habitats.

All chromosome numbers have been reported as $n = 32$ or $n = 64$. The basic number $x = 32$ is unique among the Hymenophyllaceae. Species classification, in contrast, is difficult and various.

KEY TO THE SPECIES

1a. Fronds monomorphic, pinnate, with more than ten pairs of free pinnae 2
b. Fronds subdimorphic, pinnae only at base, or only a few basal pinnae free and more than twenty pinnae adnate to rachis at base . . . . . **2. C. crassum**
2a. Mouth of involucre dilated 3
b. Mouth of involucre truncate or hardly dilated 4
3a. Stipe usually to 5 cm long, less than one-third length of frond; pinnae more or less cut to lacerate . . . . . **1. C . atrovirens**
b. Stipe more than 10 cm long, more than half as long as frond; pinnae only shallowly cut . . . . . **3. C. densinervium**
4a. Sori salient, not immersed in notches; mouth of involucre usually longer than apex of lobes . . . . . **4. C. javanicum**
b. Sori in notches on margin; mouth of involucre usually shorter than apex of lobes . . . . . **5. C. singaporianum**

1. Cephalomanes atrovirens C.Presl

Cephalomanes atrovirens C.Presl, Abh. Königl. Böhm. Ges. Wiss., ser. 5, 3 (1843) 18, t. 5; Copel., Philipp. J. Sci. 67 (1938) 67; Fern Fl. Philipp. 1 (1958) 77; Tindale, Contr. New South Wales Natl. Herb., Fl. Ser. 201 (1963) 45; Croxall, Austral. J. Bot. 23 (1975) 540; K.Iwats., J. Fac. Sci. Univ. Tokyo, Sect. 3, Bot. 13 (1985) 549; J. Jap. Bot. 66 (1991) 140; C.W.Chen et al., Sol Amazing (2017) 110; K.Iwats. et al., PhytoKeys 119 (2019) 113. — *Trichomanes atrovirens* (C.Presl) Kunze, Bot. Zeitung (Berlin) 5 (1847) 371; Copel., Philipp. J. Sci. 51 (1933) 251, pl. 52: f. 3, pl. 55: f. 2. — *Trichomanes javanicum* Blume var. *atrovirens* (C.Presl) C.Chr., Index Filic. (1906) 635. — Lectotype (designated by Croxall (1975) 540, see Field, Austral. Syst. Bot. 33 (2020) 22): *Cuming 169* (lecto K; isolecto B, GH, L, MICH, PRC), Philippines, Luzon.

Trichomanes alatum Bory, Voy. Monde, Crypt. 1 (1828) 282, t. 38, f. 2, non Sw., nec Schkuhr, nec Hook. — *Trichomanes boryanum* Kunze, Farrnkräuter 1 (1847) 237, pl. 97; Copel., Philipp. J. Sci. 51 (1933) 254, pl. 52: f. 4. — *Cephalomanes alatum* (Bory) C.Presl, Abh. Königl. Böhm.

Ges. Wiss., ser. 5, 5 (1848) 334. — *Cephalomanes boryanum* (Kunze) Bosch, Ned. Kruidk. Arch. 4 (1859) 351, nom. superfl. — *Lacostea boryana* (Kunze) Prantl, Unters. Morph. Gefässkrypt. 1 (1875) 50, nom. illeg. — *Trichomanes javanicum* Blume var. *alatum* C.Chr., Index Filic. (1905) 168; Index Filic. (1906) 635. — Type: *Durville s.n.* (n.v.), New Guinea, Waigeo.

[*Trichomanes rhomboideum* J.Sm., J. Bot. (Hooker) 3 (1841) 417, nom. nud.]

Cephalomanes curvatum Bosch, Ned. Kruidk. Arch. 4 (1859) 351. — *Trichomanes javanicum* Blume var. *curvatum* (Bosch) C.Chr., Index Filic. (1906) 638. — Lectotype (designated by Iwatsuki, J. Jap. Bot. 66 (1991) 140 as 'type'): *Cuming 184* (lecto K; isolecto B, PRC), Philippines.

Cephalomanes australicum Bosch, Ned. Kruidk. Arch. 5(2) (1861) 139; J. Bot. Néerl. 1 (1861) 341. — *Trichomanes javanicum* Blume var. *australicum* (Bosch) C.Chr., Index Filic. (1905) 168. — Lectotype (designated here): *Cuming 8* (K), New Caledonia.

Cephalomanes wilkesii Bosch, Ned. Kruidk. Arch. 5(2) (1861) 140; J. Bot. Néerl. 1 (1861) 345. — *Trichomanes javanicum* Blume var. *wilkesii* (Bosch) C.Chr., Index Filic. (1905) 169. — Syntypes: *Wilkes Expedition 24* (GH, US), Samoa; on the labels of both syntypes the locality is noted as Samoa?, but the prologue records Fiji as locality.

Trichomanes kingii Copel., Philipp. J. Sci., C. 6 (1911) 72; Philipp. J. Sci. 51 (1933) 253, pl. 53: f. 2. — *Cephalomanes kingii* (Copel.) Copel., Philipp. J. Sci. 67 (1938) 68. — Type: *Copland King S13* (holo MICH), New Guinea.

Trichomanes acrosorum Copel., Philipp. J. Sci., C. 6 (1911) 72; Philipp. J. Sci. 51 (1933) 254, pl. 53: f. 3. — *Cephalomanes acrosorum* (Copel.) Copel., Philipp. J. Sci. 67 (1968) 68; C.W. Chen et al., Sol Amazing (2017) 109. — Type: *Copland King 352* (holo MICH), New Guinea, Lakekamu.

Trichomanes acrosorum Copel. var. *alatum* Alderw., Bull. Jard. Bot. Buitenzorg, sér. 2, 11 (1913) 23. — Type: *Janowski 52* (holo BO), New Guinea, near Leparei River.

Trichomanes ledermannii Brause, Bot. Jahrb. Syst. 56 (1920) 35. — *Cephalomanes ledermannii* (Brause) Copel., J. Arnold Arbor. 24 (1943) 440. — Lectotype (designated here): *Ledermann 8638* (lecto B 20 0105007), Papua New Guinea. Other syntype: *Ledermann 9622* (B, NY).

Trichomanes maluense Brause, Bot. Jahrb. Syst. 56 (1920) 36. — Lectotype (designated by Iwatsuki, J. Jap. Bot. 66 (1991) 140 as 'type'): *Ledermann 6843* (lecto B; isolecto L, US), Papua New Guinea.

Trichomanes acranthum H.Ito in Nakai, Iconogr. Pl. Asiae Orient. 2 (1937) 109, t. 45. — *Cephalomanes acranthum* (H.Ito) Tagawa, Acta Phytotax. Geobot. 14 (1950) 45; Seriz., Sci. Rep. Takao Mus. Nat. Hist. 7 (1975) 14. — Type: *S. Sonohara & H. Ito s.n.* (holo TI), Japan, Ryukyu.

Cephalomanes densinervium auct. non (Copel.) Copel.: H.Ito, Bot. Mag. (Tokyo) 67 (1954) 215.

Two subspecies are distinguished of which only the typical one occurs in Malesia.

KEY TO THE SUBSPECIES

1a. Mouth of involucres slightly dilated, dilated lips to 0.3 mm broad. — S Ryukyu, Philippines, New Guinea to Solomon Islands and Australia (Queensland) . . . . . **a.** subsp. **atrovirens**

b. Mouth of involucre conspicuously dilated, dilated lips usually 0.5 mm broad. — Micronesia, Melanesia and Polynesia . . . . **b.** subsp. **boryanum** (not in Malesia)

a. subsp. **atrovirens**

Type as the species

Rhizome erect, bearing a close tuft of fronds; roots many, stout, irregularly branching, the main roots 0.5–1 mm diam. *Stipes* of larger fronds 2–7(–10) cm long, to 1.5 mm diam., terete, with very narrow wings of one, or at most two, row(s) of cells at least on

the upper portion and apparently decaying with age, hairy; hairs on stipes multicellular, consisting of 5–9 cells, stiff and bristle-like, dark brown, to 2 mm long, caducous. *Fronds* simply pinnate, lanceolate to linear lanceolate, attenuate at apex, broadest at middle portion and gradually narrowing towards base, 10–17 cm long in well-grown plants, (2.5–)3–4(–5) cm wide at widest portion; *rachis* like the upper part of stipes, narrowly winged, or the wings of lower part decaying in age and of upper part persistent, hairy like the stipes; *pinnae* 20 or more pairs, very shortly stalked or sessile, with stalks to 0.5 mm long, imbricate or overlapping to the neighboring ones, largest ones narrowly oblong, round to obtuse at distal end, subentire or toothed at the end of each vein, narrowly cuneate at acroscopic and dimidiate at basiscopic bases, 1.7–2.2(–2.5) cm long, 4–7(–8) mm broad, the upper ones smaller upwards, more obliquely placed, sessile or adnate at base, lower ones smaller downwards, shortly stalked, more patently placed; costae forming angles of 45–60° to rachis; veins distinct, close, 1 or 2 (or 3) times forked, the ends forming teeth at margin of pinnae. *Sori* on the upper pinnae, usually on acroscopic margin of pinnae, tending to the posterior part of it, paratactic, or on the tip of proximal veinlets, usually placed at sinus-bottom, or when several sori borne close together to the acroscopic margin cut, rarely with uni- or bi-nervate linear segments, shortly stalked or subsessile; *involucres* tubular or campanulate, narrowly winged, to 2 mm long, 0.7 mm diam., the mouth dilated, usually above the line of pinna-margin; receptacles long-extruded, often to 5 mm long.

Distribution — S Japan (Ryukyu: Iriomote Isl.); in *Malesia*: Philippines, Sulawesi, Moluccas (Seram, Halmahera, Tanimbar, Aror) and New Guinea; Micronesia, Vanuatu, Australia (NE Queensland) and Solomon Islands.

Habitat & Ecology — On wet muddy rocks and sandy ground, usually along streams in deep shade and in gaps in canopy. Altitude: usually at lower elevations to 600 m, but sometimes to 2200 m.

Note — Subspecies *boryanum* (Kunze) Ebihara & K.Iwats. in Polynesia is distinguished by the more conspicuously dilated mouth of the involucres and is allopatric with the Malesian subspecies. Subspecie *boryanum* is variable in arrangement and dissection of the pinnae, texture, arrangement, size, form of the sori and other features. Two particular forms in New Guinea are maintained at the rank of forma.

KEY TO THE FORMS

1a. Sori on normal pinnae, not confined to apical part of fronds 2
b. Sori born in a terminal spike or restricted to apex of fronds. — Endemic to New Guinea . . . . . **2.** forma **acrosorum**
2a. Rachis terete, wingless at least in the lower portion; sori not or short-stalked. . . . . **1.** forma **atrovirens**
b. Rachis narrowly winged throughout; sori distinctly stalked. — Endemic to New Guinea . . . . . **3.** forma **kingii**

1. forma **atrovirens**

Type as the species.

Rachis terete, wingless at least in the lower portion. Sori on normal pinnae, not confined to apical part of fronds, not or shortly stalked

Distribution, Habitat & Ecology — See under subspecies.

2. forma **acrosorum** (Copel.) K.Iwats.

Cephalomanes atrovirens C.Presl forma *acrosorum* (Copel.) K.Iwats., J. Jap. Bot. 66 (1991) 141. — *Trichomanes acrosorum* Copel., Philipp. J. Sci., C. 6 (1911) 72; Philipp. J. Sci. 51 (1933) 254, pl. 53, f. 3. — *Cephalomanes acrosorum* (Copel.) Copel., Philipp. J. Sci. 67 (1938) 68. — Type: *Copland King 352* (holo MICH), Papua New Guinea, Lakekamu.

Sori born in a terminal spike or restricted to apex of fronds.

Distribution — *Malesia*: Papua New Guinea.

Habitat & Ecology — Terrestrial and epipteric in creeks in hill forests at elevations below 600 m.

3. forma **kingii** (Copel.) K.Iwats.

Cephalomanes atrovirens C.Presl forma *kingii* (Copel.) K.Iwats., J. Jap. Bot. 66 (1991) 141. — *Trichomanes kingii* Copel., Philipp. J. Sci., C. 6 (1911) 72; Philipp. J. Sci. 51 (1933) 253, pl. 53: f.2. — *Cephalomanes kingii* (Copel.) Copel., Philipp. J. Sci. 67 (1938) 68. — Type: *Copland King S13* (holo MICH), Papua New Guinea.

Rachis narrowly winged throughout. Sori on normal pinnae, not confined to apical part of fronds, distinctly stalked.

Distribution — *Malesia*: Papua New Guinea.

Habitat & Ecology — Epipetric in waterfalls.

2. Cephalomanes crassum (Copel.) M.G.Price

Cephalomanes crassum (Copel.) M.G.Price, Contr. Univ. Michigan Herb. 17 (1990) 268; K.Iwats., J. Jap. Bot. 66 (1991) 144. — *Trichomanes crassum* Copel., Philipp. J. Sci. 51 (1933) 256, pl. 54, 55: f. 3; Fern Fl. Philipp. 1 (1958) 78. — Lectotype (designated by Ebihara & Iwatsuki, Mem. Natl. Mus. Nat. Sci. (Tokyo) 46 (2010) 95): *BS (G. Lopez) 40804* (lecto MICH; isolecto P, US), Philippines, Leyte.

Rhizome short, erect to ascending, bearing a rosette of fronds; bristles dense on the apical part of rhizome, more or less caducous, brown to dark brown, shining, multicellular, at least the lower half articulated, to 2 mm long. *Fronds* fascicled, dimorphic, the fertile ones narrow and erect, the sterile ones wider and rosette-like. *Sterile fronds*: stipes short, 1–2 cm long, terete, bearing bristles or nearly glabrous in the older fronds; laminae narrowly to linear lanceolate, round to moderately acute at apex, gradually narrowing towards base, to 40 cm long, 5.5 cm wide (Samar plants are smaller, to 25 by 5 cm), pinnatifid throughout, or a few lower (small) pinnae free (but sessile), bluish green in the fields (Price 1990) and dark green in dried specimens; rachis brownish to darker on the underside, densely covered by the bristles, upper surface glabrous; *pinnae*

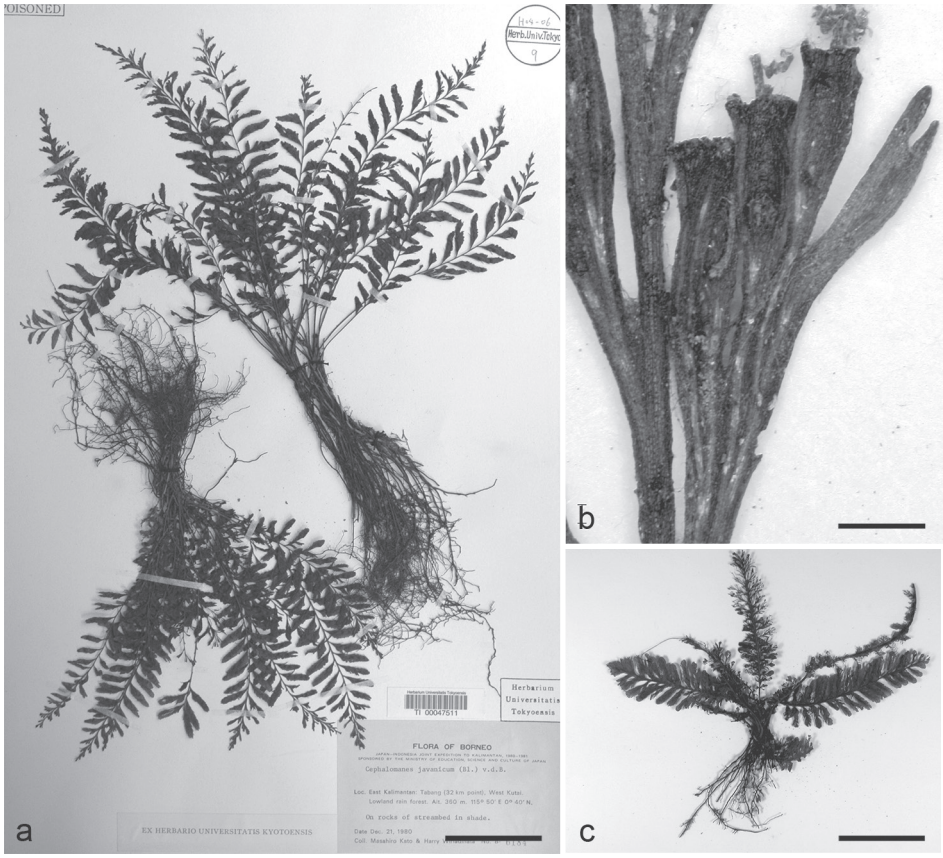

Fig. 3. a, b. *Cephalomanes javanicum* (Blume) C.Presl. a. Specimen; b. sori. — c. A specimen of *C. crassum* (Copel.) M.G.Price (a, b: *Kato & Wiriadnata B-6184*, East Kalimantan, Indonesia, TI 00047511; c: *Price & Hernaez 806*, Samar, Philippines, KYO 00010997).

up to 50 pairs, narrowly oblong, the larger ones more or less falcate, oblique, round to obtuse at apex, subentire or slightly dentate, adnate at base, to 4 cm long, 0.7 cm broad; the apex of veinlets forming small dentations; *cells* large, the larger ones to 0.2 mm diam., *internal cell walls* thick, pitted. *Fertile fronds* rather rare, the one found on *Price & Hernaez 806* (KYO, MICH): c. 8 cm long, 1 cm wide (sterile fronds of this plant are 10–17 by 4 cm); pinnae round to subquadrangular, more or less dissected, each bearing 1–6 sori; *sori* cup-shaped, not immersed, nor stalked, c. 3 mm long, 1 mm diam. at mouth, subtruncate or more or less blunt at mouth, distinctly winged; the receptacles long-extruded. — **Fig. 3c.**

Distribution — *Malesia*: Philippines (Leyte, Samar, 2 collections), Sulawesi (*Hicks 205* [K] – new record).

Habitat & Ecology — In primary forests, on limestone and limestone-derived soils.

Note — *Cephalomanes crassum* is unique in this genus in having incompletely pinnate fronds and being semidimorphic.

3. **Cephalomanes densinervium** (Copel.) Copel.

Cephalomanes densinervium (Copel.) Copel., Philipp. J. Sci. 67 (1938) 67. — *Trichomanes densinervium* Copel., Philipp. J. Sci, C. 6 (1911) 71; Philipp. J. Sci. 51 (1933) 253, pl. 53: f.1; K.Iwats., J. Jap. Bot. 66 (1991) 142. — Type: *Copland King 150* (holo MICH), Papua New Guinea.

Trichomanes infundibulare Alderw., Nova Guinea 14 (1924) 55. — Lectotype (designated by Iwatsuki, J. Jap. Bot. 66 (1991) 142, as 'type'): *Lam 439* (lecto BO; isolecto L), New Guinea, Mamberamo River.

Rhizome erect, bearing a close tuft of fronds; roots stout, many, tufted, the main roots 1–1.5 mm diam., bearing slender side roots. *Stipes* 6–14 cm long, to 1.8 mm diam., terete, with very narrow wings of usually one row of cells at upper portion and decaying with age, hairy though caducous; hairs multicellular, consisting of 5–8 cells, bristle-like, dark brown, stiff but not very thick, to 2.5 mm long. *Fronds* simply pinnate, lanceolate or narrowly so, acute to moderately attenuate at apex, broadest at middle or lower one-third portion, and round to subtruncate at base, 13–17 cm long in well-grown plants, 3–4.5 cm wide at broadest portion; rachis like the upper part of stipes, very narrowly winged, the wings of lower part decaying with age and of upper part more or less persistent, hairy like the stipes; *pinnae* 18–30 pairs, the lower ones shortly stalked with stalks to 0.7 mm long, the upper ones sessile, in most cases overlapping with the neighboring ones, patent or more or less oblique, largest ones oblong, round to obtuse at distal end, subentire or toothed at the end of each vein, subauriculate to broadly cuneate, or rarely cuneate, at acroscopic side, and narrowly cuneate to dimidiate at basiscopic bases, to 2.3 cm long, 1 cm broad, the upper ones smaller upwards, more obliquely placed and less stalked to adnate at base, a few lower ones smaller downwards, patent to deflecting; veins distinct on both surfaces, close to each other, 1 or 2 (or 3) times forked, the ends forming teeth at margin of pinnae. *Sori* throughout the plants or sometimes only at the upper parts of fronds, restricted to the acroscopic side of pinnae, or commonly on the posterior half of the acroscopic margin, paratactic, at sinus-bottom, more or less distinctly stalked; *involucres* tubular or campanulate, distinctly winged, to 2.5 mm long, 0.7 mm diam., the mouth dilated, with lips c. 0.3 mm broad, usually above the line of pinna-margin; receptacles long-extruded, often more than 5 mm long.

Distribution — *Malesia*: New Guinea; Solomon Isl. (Santa Ysabel).

Habitat & Ecology — Terrestrial, beside creeks in forests and on slopes of ultrabasic rocks behind mangroves. Altitude: from sea level to c. 1000 m.

4. **Cephalomanes javanicum** (Blume) C.Presl

Cephalomanes javanicum (Blume) C.Presl, Abh. Königl. Böhm. Ges. Wiss., ser. 5, 5 (1848) 334; Bosch, Ned. Kruidk. Arch. 4 (1859) 350; Hymenophyll. Javan. (1861) 30, pl. 22; Copel., Philipp. J. Sci. 67 (1938) 67; Ching, Fl. Reipubl. Popularis Sin. 2 (1959) 189, pl. 14: f. 1-4; Tagawa & K.Iwats. in Smitinand et al., Fl. Thailand 3 (1979) 96; K.Iwats., J. Fac. Sci. Univ. Tokyo, Sect. 3, Bot. 13 (1985) 548; J. Jap. Bot. 66 (1991) 142; J.X.Liu et al. in C.Y.Wu et al., Fl. China 2–3 (2013) 95; C.W.Chen et al., Sol Amazing (2017) 112; K.Iwats. et al., PhytoKeys 119 (2019) 113. — *Trichomanes javanicum* Blume, Enum. Pl. Javae 2 (1828) 224; Copel., Philipp. J. Sci. 51 (1933) 246, pl. 52: f.1; Tardieu & C.Chr. in Lecomte, Fl. Indo-Chine 7, 2 (1939) 68; Holttum, Rev. Fl. Malaya 2 (1955) 102, f. 38. — *Lacostea javanica* (Blume) Prantl, Unters. Morph. Gefässkrypt. 1 (1875) 50. — Type: *Blume s.n.* (holo L 0544656), Java.

Cephalomanes zollingeri Bosch in Miq., Pl. Jungh. 5 (1857) 552; Hymenophyll. Javan. (1861) 31, pl. 23; Ned. Kruidk. Arch. 4 (1859) 351. — *Lacostea zollingeri* (Bosch) Prantl, Unters. Morph. Gefässkrypt. 1 (1875) 50; Pic.Serm., Webbia 31 (1977) 50. — Lectotype (designated by Iwatsuki, J. Jap. Bot. 66 (1991) 143): *Zollinger 1464* (lecto L; isolecto P), Java.

Cephalomanes rhomboideum Bosch, Ned. Kruidk. Arch. 4 (1859) 350; Hymenophyll. Javan. (1861) 33, pl. 24. — *Lacostea rhomboidea* (Bosch) Prantl, Unters. Morph. Gafässkrypt. 1 (1875) 50. — Lectotype (designated by Iwatsuki, J. Jap. Bot. 66 (1991) 143): *Cuming 169 pt*. (lecto K; isolecto L), Philippines.

Trichomanes javanicum Blume var. *intercalatum* Christ, Philipp. J. Sci., C. 2 (1907) 156. — Syntypes: *Elmer 6214* (MICH), Philippines, Luzon, Benguet; *Loher s.n*. (n.v.), Philippines, Luzon, Mount Maquiling; *Loher s.n*. (n.v.), Philippines, Oriud.

Trichomanes foersteri Rosenst., Repert. Spec. Nov. Regni Veg. 13 (1914) 213; Copel., Philipp. J. Sci. 51 (1933) 255. — Type: *W. Grashoff 43* (possible syntype S), Sumatra.

Rhizome short, erect, bearing numerous roots, 6–15 fronds in tuft, densely hairy at apex. *Roots* thick, to or often more than 1 mm diam., bearing thin branching which again branch under angle of nearly 90° to those of higher order, dark brown to blackish, bearing short, dense root hairs, dark brown to blackish, mostly 0.3–0.5 mm long. *Stipes* commonly 2–5 mm long, thicker than the roots, or to or more than 1 mm diam. near the base, densely hairy throughout or caducous, dark brown or dusty brown; *laminae* pinnate without any apical pinna, narrowly lanceolate, (3–)7–13(–25) cm long, to 3(–5) cm wide at broadest middle portion; *rachis* like the upper portion of stipes, nearly straight to the top, very narrowly winged throughout in upper portion, hairy on the under surface, brown to dark in dried condition; hairs slender, to 1.5 mm long, multicellular, straight or a little woolly, brown to dark brown; *lateral pinnae* usually more than 25 pairs, alternate, lower ones with short, winged stalks, the narrow wings of stalks often decurrent down to the rachis but never continuous with the next ones in lower portion, larger ones more or less ascending, oblong, round to very moderately acute at apex, the base cuneate, or obsolete at basiscopic base and subtruncate at acroscopic base, sometimes obscurely auricled at acroscopic base, margin dentate, either with veinlets ending in each tooth-apex, or often irregularly cut down nearly to costae; upper pinnae becoming smaller and narrower upwards, more ascending, sessile or decurrent and forming very narrow wings on rachis; costae of pinnae straight, glabrous, or sparsely hairy near base; veins pinnate in basal ones, forked in the others, ending in the apex of dentations, distinct on both surfaces. *Pinnae* dark green to deep blue green, usually dark green to blackish in dried specimens. *Sori* at anterior branches of forked veins or more often at simple veinlets, arranged on upper margin of upper pinnae except for distal portion, usually 1–5 on a pinna, cup-shaped with truncate mouth, 1.2–1.7 mm long, to 0.8 mm diam., usually extruding, but the mouth nearly in the same line as pinna-margin, very narrowly winged with very narrowly winged short stalk; receptacles long-extruded, often more than 5 times the length of involucre but often destroyed in herbarium specimens. Chromosome number: $n = 32$ (Manton in Holttum, Rev. Fl. Malaya 2 (1955) 623; Braithwaite, Fern Gaz. 10 (1969) 82; Mitui, J. Jap. Bot. 51 (1976) 34). — **Fig. 3a, b.**

Taxonomy — Three varieties are distinguished.

KEY TO THE VARIETIES

1a. Sori commonly 2–3 mm long, on normal pinnae and not confined to apical part of fronds 2
b. Sori larger, commonly 4 mm long, borne in a terminal spike or panicle . . . . . **c.** var. **sumatranum**
2a. Sori on acroscopic margin of pinnae, not on basiscopic margin **a.** var. **javanicum**
b. Sori gathered on distal portion of pinnae and gathered toward acroscopic margin, or sometimes on basiscopic margin . . . . . **b.** var. **asplenioides**

a. var. **javanicum**

Type as the species

Fronds commonly several on one stock, variable in size and form; stipes sometimes exceeding 10 cm long, rather densely hairy, brown to darker; *laminae* linear lanceolate, acuminate to long-attenuate at apex, widest at lower one-third portion, narrowing towards round to subtruncate base, often to 25 cm long, 4.5 cm wide; lateral *pinnae* commonly more than 25 pairs, or to 40 pairs, not very deeply imbricate to the next ones, round and serrate to denticulate at apex, serrate at acroscopic and subentire at basiscopic sides, shortly stalked at cuneate base, *costae* placed rather widely, c. 60–85° to rachis, texture thin papyraceous, green to dark green in living condition, dark brown when dried. *Sori* on the acroscopic side of lateral pinnae, not particularly in the apical portion of fronds, distributed from inner one-third portion toward distal and basal ends, never on basiscopic side; *involucres* 2–2.5 mm long, 0.7–1 mm diam., cup-shaped with truncate mouth, 2–2.5 mm long, c. 0.8 mm diam., hardly winged; often the fertile segments deeply cut at the side, but the pinnae not lacerate.

Distribution — N India, Nepal, Bhutan, Myanmar, Thailand, Vietnam; in *Malesia*: Peninsular Malaysia, Sumatra, Borneo, Java and the Moluccas (Ambon and Seram).

Habitat & Ecology — On muddy rocks, often in streambeds or at least along streams in deep shade, usually in rheophytic habitats and at the edge of forests. Altitude: from low to mid elevations, or to 2200 m.

b. var. **asplenioides** (C.Presl) K.Iwats.

Cephalomanes javanicum (Blume) C.Presl var. *asplenioides* (C.Presl) K.Iwats., J. Fac. Sci. Univ. Tokyo, Sect. 3, Bot. 13 (1985) 549; J. Jap. Bot. 66 (1991) 143; K.Iwats. et al., PhytoKeys 119 (2019) 113. — *Trichomanes asplenioides* C.Presl, Abh. Königl. Böhm. Ges. Wiss., ser. 5, 3 (1843) 37, 129, nom illeg., non Sw. 1788. — *Cephalomanes asplenioides* (C.Presl) C.Presl, Abh. Königl. Böhm. Ges. Wiss., ser. 5, 5 (1848) 334. — *Trichomanes javanicum* Blume var. *asplenioides* (C.Presl) C.Chr., Index Filic. (1906) 635; Kunze, Farrnkräuter (1847) 218, pl. 89; Copel., Philipp. J. Sci. 51 (1933) 249, pl. 52: f. 2, pl. 55: f. 1. — *Trichomanes preslii* C.V.Morton, Contr. U.S. Natl. Herb. 38 (1968) 190. — Lectotype (designated by Morton, Contr. U.S. Natl. Herb. 38 (1974) 382 as 'holotype'): *Cuming 184* (lecto PRC; isolecto GH, K, L, P, US), Philippines, Luzon.

Trichomanes oblongifolium C.Presl, Abh. Königl. Böhm. Ges. Wiss., ser. 5, 3 (1843) 129; Copel., Philipp. J. Sci. 51 (1933) 249, pl. 52: f. 2, pl. 55: f. 1. — *Cephalomanes oblongifolium* C.Presl, Abh. Königl. Böhm. Ges. Wiss., ser. 5, 5 (1848) 334; Epimel. Bot. (1851) 19, pl. 10; Copel., Philipp. J. Sci. 67 (1938) 67; Philipp. J. Sci. 73 (1941) 467; Fern Fl. Philipp. 1 (1958) 78. — Lectotype

(designated by Iwatsuki, J. Jap. Bot. 66 (1991) 142 as 'type'): *Cuming 169 pt*. (lecto PRC; isolecto B, K, L, MICH, P, US), Philippines.

Trichomanes laciniatum Roxb., Calcutta J. Nat. Hist. 4 (1844) 518; C.V.Morton, Contr. U.S. Natl. Herb. 38 (1968) 382. — *Cephalomanes laciniatum* (Roxb.) DeVol in H.L.Li et al., Fl. Taiwan 1 (1975) 98, pl. 30; J.L.Tsai & W.C.Shieh in H.L.Li et al., Fl. Taiwan 1 (1994) 103, pl. 37. — Lectotype (designated by Morton, Contr. U.S. Natl. Herb. 38 (1974) 382): *Reinwardt 2430*, left-hand plant (lecto BR 00000698776), Molucca Is. (locality doubted by Morton).

Trichomanes suffrutex Alderw., Nova Guinea 14 (1924) 56. — Syntypes: *Lam 1197* (BO, K, L, SING, US), New Guinea; *Lam 1334* (BO? n.v.), New Guinea.

Fronds in most cases less than 10 on one stock, larger in size, mostly more than 20 cm long, though fully soriferous even in smaller fronds less than 8 cm long; *stipes* commonly 2–7 cm long, brown, hairy and not smooth on the surface, very narrowly winged; *laminae* linear-lanceolate, acuminate to caudate at apex; *lateral pinnae* usually more than 25 pairs, the larger ones shortly but distinctly stalked, ascending, the costae forming an angle of 60–80°, narrowly oblong, round at minutely serrate apex, nearly parallel at denticulate or subentire lateral margin, cuneate at base, to 2.5 cm long, 7 mm broad, not or rarely lacerate. *Sori* having a tendency to gather at the distal end or acroscopic side of distal portion of pinnae, or often extending to basiscopic side, commonly in upper ones but not restricted to the apical ones, usually at the end of veinlets, not on specialized notches; *involucres* in many cases immersed in laminar expansion, commonly c. 2 mm long, 0.8 mm diam.; receptacles long-extruded. Chromosome number: $n = 32$ (Mitui, J. Jap. Bot. 51 (1976) 34).

Distribution — S Japan (Ryukyu), Taiwan; in *Malesia*: Pulau Tioman near Peninsular Malaysia, Borneo, Philippines, Moluccas (Seram) and New Guinea.

Habitat & Ecology — On moist rocks, usually along streams in gaps of the canopy.

Note — At the edge of the distribution area, the identification of *C. javanicum* becomes easier, although it is rather difficult to distinguish the three varieties, especially when they grow sympatrically.

c. var. **sumatranum** (Alderw.) K.Iwats.

Cephalomanes javanicum (Blume) C.Presl var. *sumatranum* (Alderw.) K.Iwats., J. Fac. Sci. Univ. Tokyo, Sect. 3, Bot. 13 (1985) 549; J. Jap. Bot. 66 (1991) 143. — *Trichomanes sumatranum* Alderw., Bull. Dépt. Agric. Indes Néerl. 18 (1908) 4; Copel., Philipp. J. Sci. 51 (1933) 248, pl. 53: f.4; Tardieu & C.Chr. in Lecomte, Fl. Indo-Chine 7, 2 (1939) 68. — *Cephalomanes sumatranum* (Alderw.) Copel., Philipp. J. Sci. 67 (1938) 67; Ching, Fl. Reipubl. Popularis Sin. 2 (1959) 188. — Type: *Burck 87* (holo BO), Sumatra.

Fronds usually more than 10 on one stock, comparatively smaller in size; *stipes* to 5 cm long, or exceptionally a little longer, *laminae* in largest ones 20 cm long, 4.5 cm wide; texture membranous, dark green in living condition, and black in dried specimens; *pinnae* at most 20 pairs, narrowly oblong to lanceolate, narrowly cuneate and distinctly stalked at base, round to moderately acute at apex, often lacerate and forming linear segments with veinlets and very narrow laminae, *costae* commonly placed on rachis with angle of 35–45°. *Sori* usually gathering at apical portion of fronds, forming terminal spikes or panicles, the soriferous uppermost pinnae often without any development

of laminar surfaces; *involucres* larger than those of the other varieties, often to 4 mm long, 1.2 mm diam., with long-extruded receptacles.

Distribution — China (Hainan), Vietnam; in *Malesia*: Sumatra, Borneo and Java.

Habitat & Ecology — On moist muddy rocks, usually in streambeds in shade or in partly open places. Altitude: from low to mid elevations.

Note — This is a typical form of a so-called rheophytic plant, although the genus as a whole has a tendency to grow restricted to rheophytic habitats. Var. *sumatranum* is typically rheophytic in morphological features, too, including the smaller size of plants, narrower and often lacerate pinnae oriented on the rachis at an acute angle, more tightly attached stipes which retain the fronds longer, and sori borne on panicles that lack the development of laminar expansion.

5. **Cephalomanes singaporianum** Bosch

Cephalomanes singaporianum Bosch, Ned. Kruidk. Arch. 4 (1859) 351; Copel., Philipp. J. Sci. 67 (1938) 67; K.Iwats., J. Jap. Bot. 66 (1991) 144. — *Trichomanes javanicum* Hook. & Grev., Icon. Filic. (1830) ad pl. 240, nom. illeg., non Blume (1828), see former species. — *Lacostea singaporiana* (Bosch) Prantl, Unters. Morph. Gefässkrypt. 1 (1875) 50, non *L. javanica* (Blume) Prantl. — *Trichomanes singaporianum* (Bosch) Alderw., Bull. Jard. Bot. Buitenzorg, sér. 2, 20 (1915) 25; Copel., Philipp. J. Sci. 51 (1933) 247, pl. 52: f. 5; Holttum, Rev. Fl. Malaya 2 (1955) 103, f. 39. — Type: *Wallich s.n.* (holo K), Singapore.

Trichomanes christii Rosenst., Bull. Jard. Bot. Buitenzorg, sér. 2, 2 (1911) 27, nom. illeg., non Copel. (1906). — *Trichomanes rosenstockii* Alderw., Bull. Jard. Bot. Buitenzorg, sér. 2, 7 (1912) 27. — Lectotype (designated here): *Jaheri 641* (lecto BO), Borneo. Other syntypes: *Jaheri 290* (BO), Borneo; *Jaheri 824* (BO), Borneo; *Jaheri 825* (BO), Borneo.

Trichomanes borneense Alderw., Bull. Jard. Bot. Buitenzorg, sér. 2, 20 (1915) 25. — Type: *Teuscher s.n.* (holo BO), W Borneo.

Rhizome erect, bearing a close tuft of fronds; roots many, stout, main roots branching bearing slender side roots, to 1.5 mm diam. *Stipes* of largest plants more than 20 cm long, commonly in well-grown plants 7–14 cm long, 1.2–1.5 mm diam., terete, with very narrow caducous wings usually with one row of cells, hairy; hairs on stipes multicellular, consisting of 5–9 cells, bristle-like or the septae more or less apparent, brown to dark brown, to 2.5 mm long, caducous. *Fronds* simply pinnate, narrowly lanceolate to narrowly oblong, acute to attenuate at apex, broadest at middle, lower one-third, or even at basal portion, round to subtruncate at base, 12–25 cm long in well-grown plants, 3–6(–8) cm wide at broadest portion; rachis like the upper part of stipes, very narrowly winged, the wings of lower part decaying with age and of upper part more or less persistent, hairy like the stipes; *pinnae* 15–25 pairs, the lower ones stalked with stalks to 1 mm long, the upper ones sessile to adnate at base, not imbricate or more or less overlapping the neighboring ones, patent or more or less oblique, largest ones narrowly subquadrangular, acute to round at apex, incised to lobed at acroscopic margin, subentire to dentate at basiscopic margin, subauriculate and then cuneate at acroscopic and dimidiate at basiscopic bases, to 4.5 cm long, 1.2 cm broad, commonly 3–3.8 cm long and 0.8–1 cm broad, the upper ones more obliquely placed and less stalked to adnate at base, a few basal pinnae smaller downwards but often the basal pinnae the longest, patent or a little deflexed; veins distinct on both surfaces, 1–3 times forked, the

ends forming more or less distinct teeth at margin of pinnae; texture coriaceous, dark green or paler. *Sori* usually throughout the plants, at bottom of notches at acroscopic margin of pinnae, commonly on posterior half of acroscopic side of pinnae; *involucres* tubular or campanulate, broadly winged, to 1.5 mm long, 0.5 mm diam., the mouth truncate, usually immersed in notches and below the level of pinna-margin; receptacles long-extruded, often to 5 mm long.

Distribution — *Malesia*: Peninsular Malaysia, Singapore, Sumatra and Borneo.

Habitat & Ecology — Terrestrial on clay soils and in rain forests. Altitude: usually from lowlands to 600 m.

Note — Species of *Cephalomanes* are mostly in streambeds and accordingly are more or less rheophytic with slender and obliquely placed pinnae, but *C. singaporianum* is exceptional in having lateral pinnae nearly patent and by being terrestrial in habitat. The colour also differs from other species of *Cephalomanes* in being green and not becoming dark when dried.

4. CREPIDOMANES

Crepidomanes (C.Presl) C.Presl, Epimel. Bot. (1851) 258; Copel., Philipp. J. Sci. 67 (1938) 58; Gen. Fil. (1947) 39; K.Iwats., Acta Phytotax. Geobot. 35 (1984) 173, emend.; in Kubitzki, Fam. Gen. Vasc. Pl. 1 (1990) 161, f. 83 F-H, p.p.; Ebihara et al., Blumea 51 (2006) 237. — *Trichomanes* L. subg. *Crepidomanes* C.Presl, Epimel. Bot. (1851) 17; Holttum, Rev. Fl. Malaya 2 (1955) 99. — Type: *Crepidomanes intramarginale* (Hook. & Grev.) C.Presl.

Gonocormus Bosch, Hymenophyll. Javan. (1861) 7; Copel., Philipp. J. Sci. 67 (1938) 56; Gen. Fil. (1947) 38. — *Trichomanes* L. sect. *Gonocormus* (Bosch) Christ, Farnkr. Erde (1897) 27. — *Trichomanes* L. subg. *Gonocormus* (Bosch) C.Chr., Index Filic. (1906) xiv, 634. — *Crepidomanes* (C.Presl) C.Presl sect. *Gonocormus* (Bosch) K.Iwats., Acta Phytotax. Geobot. 35 (1984) 174. — Type: *Gonocormus minutus* (Blume) Bosch (= *Crepidomanes minutum* (Blume) K.Iwats.).

Crepidopteris Copel., Philipp. J. Sci. 67 (1938) 57, nom. illeg., non C.Presl in Sternb. (1838). — *Didymoglossum* Desv. subg. *Crepidium* C.Presl, Abh. Königl. Böhm. Ges. Wiss., ser. 5, 3 (1843) 23. — *Crepidophyllum* C.F.Reed, Amer. Fern J. 38 (1948) 88, nom. illeg., non Herzog (1926). — *Reediella* Pic.Serm., Webbia 24 (1970) 719. — Type: *Crepidopteris humilis* (G.Forst.) Copel. (= *Crepidomanes humile* (G.Forst.) Bosch).

Nesopteris Copel., Philipp. J. Sci. 67 (1938) 65; Gen. Fil. (1947) 40. — *Trichomanes* L. subg. *Nesopteris* (Copel.) Holttum, Rev. Fl. Malaya 2 (1955) 108. — *Trichomanes* L. sect. *Nesopteris* (Copel.) C.V.Morton, Contr. U.S. Natl. Herb. 38 (1968) 190. — *Cephalomanes* (C.Presl) C.Presl subg. *Nesopteris* (Copel.) K.Iwats., Acta Phytotax. Geobot. 35 (1984) 176. — Type: *Nesopteris grandis* (Copel.) Copel. (= *Crepidomanes grande* (Copel.) Ebihara & K.Iwats.).

[*Taschneria* C.Presl, Epimel. Bot. (1851) 258, nom. nud.; Copel., Philipp. J. Sci. 51 (1933) 174, as a group. —] *Trichomanes* L. sect. *Taschneria* C.Chr., Index Filic. (1906) xv. — *Crepidomanes* (C.Presl) C.Presl sect. *Taschneria* (C.Chr.) K.Iwats., Acta Phytotax. Geobot. 35 (1984) 175. — Type: *Trichomanes filicula* Bory (= *Crepidomanes bipunctatum* (Poir.) Copel.).

Rhizome short, suberect to long-creeping, filiform to rather stout, wiry or densely hairy; root absent or numerous and robust in subg. *Nesopteris*; *fronds* principally pinnately decompound, rarely simple or biforked (*C. parvifolium* and *C. vitiense*), pinnation anadromous; ultimate segments entire, flat; false veinlets absent or present in sect. *Crepidomanes* (but *C. vitiense* without false veinlets), without any direct connection with true veins; marginal *laminar cells* differentiated in sect. *Crepidium*; all axes of fronds proliferous in sect. *Gonocormus*; *sori* paratactic, solitary at apex of segments, usually

immersed; *involucres* cup-shaped or campanulate, the mouth truncate, more or less dilated, or bilabiate, receptacles long-extruded. Chromosome numbers $n = 36$, or its multiples.

Distribution — About 25 species throughout the tropics of the Old World, northward to N Japan, southward to Australia (Queensland). Fifteen species throughout *Malesia*.

Habitat & Ecology — Terrestrial on wet sandy or humus-rich ground, saxifragous on mossy rocks, or epiphytic usually near streams in dense evergreen forests. Terrestrial species are typical in subg. *Nesopteris*.

Morphology — For most species of *Crepidomanes*, the rhizomes are long-creeping, densely hairy or glabrescent. In subg. *Nesopteris* most species have short, stout rhizomes.

Gametophytes — Yoroi (Sci. Rep. Tokyo Kyoiku Daigaku B 15 (1972) 81–110; J. Jap. Bot. 51 (1976) 257–267) made observations of the general morphology.

KEY TO THE SUBGENERA AND SECTIONS

1a. Rhizome long-creeping; fronds distant, commonly at most 15 cm long; plants mostly epiphytic or epipetric . . . . . 2 (**a.** subg. **Crepidomanes)**
b. Rhizome short, erect, or very narrowly creeping; fronds close together, mature ones usually more than 20 cm long; plants terrestrial . . . . . **b.** subg. **Nesopteris**
2a. Segments without false veinlets; axis gemmiferous or not 3
b. False veinlets present; or if absent, without gemmae . . . **aa.** sect. **Crepidomanes**
3a. Marginal cells not differentiated; axis gemmiferous or not 4
b. One or two marginal rows of cells differentiated from others, elongate; axis not gemmiferous . . . . . **ab.** sect. **Crepidium**
4a. Axis never gemmiferous; fronds simple and entire, or lobed with a few lobes like the simple form . . . . . **aa.** sect. **Crepidomanes** (*C. vitiense*)
b. Axis gemmiferous; fronds simple with dentate margin or pinnate . . . . . **ac.** sect. **Gonocormus**

a. Subgenus **Crepidomanes**

Type: as the genus.

aa. Section **Crepidomanes**

Type: as the genus.
Including *Taschneria*.

Rhizome long-creeping, filiform, bearing blackish or dark brownish hairs rather densely; *stipes* terete, hairy at base, usually shorter than fronds; *fronds* pinnately decompound, digitate, or in an extremely dwarfed form forming one (simple) or two (forked) segments; ultimate *segments* entire, flat or slightly undulate; false veinlets submarginal or oblique, never connected with true veinlets, or absent in *C. vitiense*; *laminar cells* not specialized, unistratose except for veinlets, with straight, thin, *internal cell walls*, or thicker in *C. intramarginale*; *sori* solitary at apex of segments, often immersed;

involucres campanulate or lower half in tubes, the lips bilabiate or dilated; receptacles long-extruded.

Distribution — Old World tropics, from Africa to Polynesia; very common throughout *Malesia* (9 species).

Habitat & Ecology — On moist mossy rocks and cliffs, on basal tree trunks, or on branches of trees in dense forests, often along streams, usually in lowlands.

Taxonomy — The presence of false veinlets often places this section close to *Didymoglossum*, although the distribution of the false veinlets is distinct between them: false veinlets are principally connected to true veins in *Didymoglossum*, but are completely separate from true veins in sect. *Crepidomanes*. This difference appears trivial, but the two groups also differ in chromosomes, pinnation pattern, and morphology of the involucres. They are likely not as closely related as indicated by the presence of false veinlets.

The pinnation pattern of this subgenus accords well with the other sections and subgenus combined here with sect. *Crepidomanes*. The most valuable key characters do not raise any questions in placing sect. *Crepidomanes* here.

The type species of subg. *Crepidomanes*, which has unique bistratose laminae, is not present in Malesia. All other species of the subgenus have unistratose laminae.

KEY TO THE SPECIES

1a. False veinlets present 2
b. False veinlets absent . . . . . **9. C. vitiense**
2a. Mouth of involucres bilabiate; pinnae oriented to rachis at angles of less than 70°; epiphytic and epipteric 3
b. Mouth of involucres broadly dilated; pinnae oriented to rachis at nearly a right angle; epiphytic often on smaller branches of trees . . . . . **3. C. christii**
3a. Fronds moderate in size, mature fronds usually more than 4 cm long, more or less firm in texture 4
b. Fronds smaller, usually to 4 cm long, texture soft and delicate 5
4a. Submarginal veinlets continuous or occasionally interrupted, additional oblique striae none or few . . . . . **1. C. bipunctatum**
b. Submarginal veinlets obsolete, with abundant oblique striae . . . **5. C. latealatum**
5a. Submarginal veinlets present, continuous or interrupted; fronds bi- or tri-pinnately compound or digitate in appearance 6
b. Submarginal veinlets obsolete; fronds simple to pinnately compound . . . . . **7. C. pervenulosum**
6a. Fronds bipinnate to tripinnatifid, segments arranged pinnately 7
b. Fronds digitate in appearance 8
7a. Two rows of normal cells present outside submarginal strands . . . **2. C. brevipes**
b. Only one row of normal cells present outside submarginal strands . . **4. C. kurzii**
8a. Submarginal veinlets continuous, seldom interrupted; segments to 15 in number . . . . . **6. C. latemarginale**
b. Submarginal veinlets continuous, though often interrupted and duplicated; segments to 6 in number . . . . . **8. C. rupicola**

1. **Crepidomanes bipunctatum** (Poir.) Copel.

Crepidomanes bipunctatum (Poir.) Copel., Philipp. J. Sci. 67 (1938) 59; Fern Fl. Philipp. 1 (1958) 72; Ching, Fl. Reipubl. Popularis Sin. 2 (1959) 162, pl. 12: f. 8; Croxall, Austral. J. Bot. 23 (1975) 533; Tagawa & K.Iwats. in Smitinand et al., Fl. Thailand 3 (1979) 90; K.Iwats., J. Fac. Sci. Univ. Tokyo, Sect. 3, Bot. 13 (1985) 536; J.X.Liu et al. in C.Y.Wu et al., Fl. China 2–3 (2013) 96; C.W.Chen et al., Sol Amazing (2017) 113; K.Iwats. et al., PhytoKeys 119 (2019) 112. — *Trichomanes bipunctatum* Poir. in Lam., Encycl. 8 (1808) 69; Bedd., Ferns Brit. India (1968) ad pl. 283; Copel., Philipp. J. Sci. 51 (1933) 177, pl. 18: f. 1–4; Tardieu & C.Chr. in Lecomte, Fl. Indo-Chine 7, 2 (1939) 63; Holttum, Rev. Fl. Malaya 2 (1955) 99, f. 35. — Type: *Petit-Thouars s.n.* (holo P), Madagascar.

Trichomanes bilabiatum Nees & Blume, Nova Acta Phys.-Med. Acad. Caes. Leop.-Carol. Nat. Cur. 11 (1823) 123, t. 13: f. 2; Copel., Philipp. J. Sci. 51 (1933) 179, pl. 18: f. 5–6; Holttum, Rev. Fl. Malaya 2 (1955) 99, f. 36. — *Crepidomanes bilabiatum* (Nees & Blume) Copel., Philipp. J. Sci. 67 (1938) 59; K.Iwats., Acta Phytotax. Geobot. 17 (1958) 161; Sledge, J. Linn. Soc. Bot. 60 (1968) 306; Tagawa & K.Iwats. in Smitinand et al., Fl. Thailand 3 (1979) 90; J.L.Tsai & W.C.Shieh in H.L.Li et al., Fl. Taiwan 1 (1994) 105. — Lectotype (designated here): *Blume s.n.* (lecto L sheet no. 908328-818), Java.

[*Hymenophyllum campanulatum* Wall., Numer. List. (1829) no. 2199, nom. nud.] — *Trichomanes campanulatum* Roxb., Calcutta J. Nat. Hist. 4 (1844) 518, B. — Lectotype (designated by Morton, Contr. U.S. Natl. Herb. 38 (1974) 381): *Buchanan s.n.* (lecto BR; isolecto BM), [Myanmar,] Chittagong.

Didymoglossum griffithii Bosch, Ned. Kruidk. Arch. 5(3) (1863) 141; Copel., Philipp. J. Sci. 51 (1933) 193. — *Trichomanes griffithii* (Bosch) Panigrahi, Phytologia 31 (1975) 256. — *Crepidomanes griffithii* (Bosch) R.D.Dixit & B.Ghosh in R.D.Dixit, Census Indian Pteridophytes (1984) 91. — Type: *Griffith s.n.* (holo K), Nepal.

Trichomanes bilobatum Alderw., Bull. Jard. Bot. Buitenzorg sér. 2, 20 (1915) 24. — Type: *Backer 9890* (holo BO? n.v.), Java, Mt Hyang.

Trichomanes bipunctatum Poir. var. *venulosa* Rosenst., Hedwigia 56 (1915) 350. — *Trichomanes venulosum* (Rosenst.) Copel., Philipp. J. Sci. 51 (1933) 186, pl. 22: f. 1–2. — *Crepidomanes venulosum* (Rosenst.) Copel., Philipp. J. Sci. 67 (1938) 60. — *Crepidomanes bipunctatum* (Poir.) Copel. var. *venulosum* (Rosenst.) Croxall, Austral. J. Bot. 23 (1975) 534. — Syntypes: *Bamler 117* (B, NY), New Guinea.

Trichomanes pseudocapillatum Alderw., Nova Guinea 14 (1924) 54. — Type: *Lam 693* (holo BO), New Guinea.

Crepidomanes sarawakense K.Iwats., Acta Phytotax. Geobot. 21 (1965) 96, f. 1. — *Trichomanes sarawakensis* (K.Iwats.) Croxall, Bot. J. Linn. Soc. 85 (1982) 73. — Type: *Hirano & Hotta 781* (holo KYO), Sarawak.

Rhizome long-creeping, irregularly branching, bearing dense dark hairs, 0.3–0.5 mm diam., appearing thicker with hairs. *Stipes* (0.8–)1.5–4(–7) cm long, very narrowly winged throughout or terete near the base, bearing sparse brown hairs c. 1 mm in length; wings at most two rows of cells at each side, green or dark green in older fronds. *Fronds* tripinnate to quadripinnatifid or tripinnatifid in smaller ones, ovate-subdeltoid or narrowly oblong to oblong, variable in shape and size, usually longer than stipes, (1.2–)2.5–8(–14) cm long, 1.2–5(–8) cm wide, acute at apex, widest at base or gradually narrowing downwards; rachis narrowly winged, straight, green to stramineous, bearing sparse brown hairs mixed with pale brownish, clavate hairs; *pinnae* largest at base or rarely at middle or higher portion, larger ones oblong-subtriangular, acute to acuminate at apex, cuneate to broadly cuneate at base, sessile, to 6 cm long, 2 cm wide; pinna rachis winged and similar to the segments in appearance; *pinnules* narrowly oblong to ovate, acute to moderately acute at apex, larger ones pinnate to bipinnatifid,

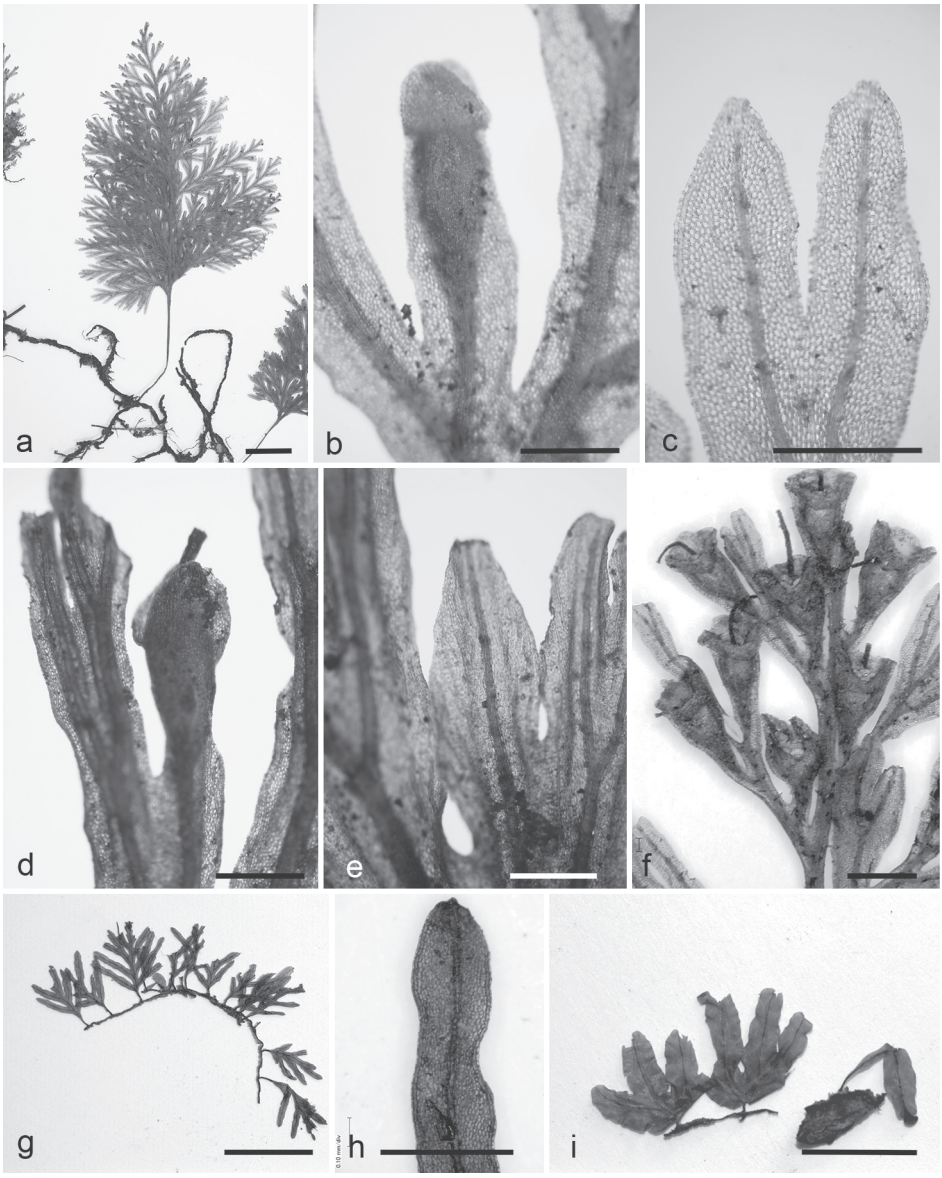

Fig. 4. a–c. *Crepidomanes bipunctatum* (Poir.) Copel. a. Fronds; b. sorus; c. laminar cells with submarginal false veinlets. — d, e. *C. latealatum* (Bosch) Copel. d. Sorus; e. laminar cells with oblique false veinlets. — f. Sori of *C. christii* (Copel.) Copel. — g, h. *C. kurzii* (Bedd.) Tagawa & K.Iwats. g. Specimen; h. frond segment with submarginal false veinlets. — i. Fronds of *C. vitiense* (Baker) Bostock (a–c: *Sugawara et al. SB2007-55*, Sabah, Malaysia, TNS 764882; d, e: *Amoroso 5396*, Mindanao, Philippines, TNS 1113517; f: *Ebihara et al. 000226-038*, Mt Kinabalu, Malaysia, TNS; g, h: *Kato et al. 8335*, Kalimantan Timur, Indonesia, KYO 00010994; i: *Kokawa & Hotta 582*, Sabah, Malaysia, KYO 00010985).

sessile, to 1.5 cm long, 0.8 cm wide; ultimate segments, usually 2–4(–6) mm long, 0.3–0.6 mm broad, narrowly lanceolate, round to moderately acute at apex, entire and flat at margin, sometimes more or less involute, bearing pale brownish clavate hairs on the veins underneath, green to deep green, brownish in dried specimens. *False veinlets* submarginal and continuous along the margin of segments, 2 rows of cells outside the false veinlets, occasionally interrupted or with more than two rows of normal cells outside; additional oblique false veinlets none or occasionally observed. *Sori* at apex of segments, from basal acroscopic pinnules outwardly, solitary; *involucre* tuberous, winged, bilabiate at apical one-fifth to one-fourth, 2–3.5 mm long, c. 0.7 mm diam.; lips narrowly subdeltoid, acute to acuminate but not pointed at apex, c. 0.8 mm long, 0.5 mm at base; receptacles long-extruded. Chromosome numbers: $n = 36$ (Manton & Sledge, Philos. Trans., Ser. B, 238 (1954) 136; Manton in Holttum, Rev. Fl. Malaya 2 (1955) 62; Braithwaite, Fern Gaz. 10 (1969) 82, Bot. J. Linn. Soc. 71 (1975) 170; Mitui, J. Jap. Bot. 51 (1976) 34). — **Fig. 4a–c.**

Distribution — Widely distributed in the tropics of the Old World, from Madagascar, Mascarene Islands, Sri Lanka, S & SE Continental Asia; in *Malesia*: common throughout; Melanesia and Polynesia east to Tahiti, south to Australia (NE Queensland).

Habitat & Ecology — Epiphytic and epipetric, on basal tree trunks and on mossy rocks, often near rivers in dark jungle at lower elevations, sometimes on high branches of trees, often forming mats or mixed with mosses. Altitude: lowlands to 2000 m.

Notes — The typical form is identified by its continuous submarginal false veinlets with two regular rows of normal cells outside them. In such typical forms the submarginal false veinlets are rarely interrupted and there is no additional oblique veinlet. However, the morphology and distribution of false veinlets is variable; submarginal false veinlets are often interrupted and additional oblique veinlets are observed. The form with interrupted submarginal false veinlets has long been separated and listed in floras under the name *C. bilabiatum*. As there is variation in the distribution of the false veinlets, *C. bilabiatum* is here united with *C. bipunctatum* pending further analysis. The form and size of the fronds is also extremely variable throughout the wide distribution area.

In New Guinea collections with the fronds less than 4 cm long are found, even in a fully mature state; in western Malesia, such forms are identified as *C. brevipes*. The New Guinean plants are always coarse in the texture of the fronds and differ from the dwarf western Malesian form, which has a more tender texture and delicate appearance.

2. **Crepidomanes brevipes** (C.Presl) Copel.

Crepidomanes brevipes (C.Presl) Copel., Philipp. J. Sci. 67 (1938) 60; Fern Fl. Philipp. 1 (1958) 71; Tagawa & K.Iwats. in Smitinand et al., Fl. Thailand 3 (1979) 91; K.Iwats., J. Fac. Sci. Univ. Tokyo, Sect. 3, Bot. 13 (1985) 537; K.Iwats. et al., PhytoKeys 119 (2019) 112. — *Didymoglossum brevipes* C.Presl, Abh. Königl. Böhm. Ges. Wiss., ser. 5, 3 (1843) 23, 47. — *Trichomanes brevipes* (C.Presl) Baker in Hook. & Baker, Syn. Fil. (1867) 84; Copel., Philipp. J. Sci. 51 (1933) 182, pl. 20. — Lectotype (designated here): *Cuming 316* (lecto PRC; isolecto BM, GH, K), Philippines.

Didymoglossum undulatum C.Presl, Abh. Königl. Böhm. Ges. Wiss., ser. 5, 3 (1843) 23, 48. — Type: *Cuming s.n.* (n.v.), Philippines.

Trichomanes melanorhizon Hook., Sp. Fil. 1 (1845) 140; Hooker's Icon. Pl. (1848) t. 705. — Lectotype (designated here): *Cuming 316* (lecto K 000375498; isolecto BM, GH, LE, PRC), Philippines.
Didymoglossum anomalum Bosch, Ned. Kruidk. Arch. 5(3) (1863) 140. — Type: *Wilke's expedition* (holo US), Philippines.

Rhizome long-creeping, irregularly branching, slender, c. 0.2 mm diam., densely covered with dark brownish hairs, including these more than 0.7 mm diam. *Stipes* 2–5(–10) mm long, winged nearly to the base, green to stramineous, blackish near base, hairy throughout but caducous in upper portion; *fronds* oblong-ovate or broadly oblong in larger ones, round to moderately acute at apex, round to broadly cuneate at base, widest at middle or lower one-third portion, 1–2(–5) cm long, 0.8–1.4(–3) cm wide, tripinnatifid to tripinnate; *rachis* more or less zigzag, distinctly winged throughout, wings continuous to those of pinna rachis, entire, flat, with continuous marginal false veinlets; *pinnae* shortly stalked, larger ones bipinnatifid to bipinnate, round to moderately acute at apex; pinna rachis distinctly winged and having same appearance as segments, decurrent and continuous to wings of rachis; *pinnules* simple or bi- or tri-forked, or pinnately divided in larger ones; ultimate segments acute to moderately acute at apex, entire and often crenulate at margin, c. 0.5 (or at most 0.8) mm broad; texture thin and delicate, green; *false veinlets* or submarginal strands continuous at margin of segments and of wings of axes, usually two rows of normal cells outside the strands, oblique striae none or few. *Sori* solitary at apex of short axillary segments, with tuberous base and bilabiate mouth, c. 1.5 mm long, 0.7 mm diam.; tuberous basal portion of *involucres* immersed in segments or broadly winged, bilobed portion c. a quarter of whole of involucres, subdeltoid, round to acute at apex, to 0.4 mm long; receptacles long-extruded.

Distribution — Thailand (Peninsular); in *Malesia*: Sumatra, Java, Borneo, Philippines, Sulawesi, Moluccas (Seram) and New Guinea; Micronesia.

Habitat & Ecology — Epiphytic and epipetric, mixed with mosses on high branches of large trees and on wet rocks along streamlets in dense forests. Altitude: at lower elevations, usually to 500 m or sometimes to 1000 m.

Note — *Crepidomanes brevipes* is similar to *C. bipunctatum* in general characters. It is sometimes difficult to distinguish from dwarf forms of the latter. *Crepidomanes brevipes* is more delicate in general habit, and the segments are narrower. In general habit, it is somewhat similar to *C. christii*, although *C. christii* has bilabiate involucres, pinnae more or less ascending and a habitat on the bark of the main trunks of larger trees and on mossy rocks.

3. Crepidomanes christii (Copel.) Copel.

Crepidomanes christii (Copel.) Copel., Philipp. J. Sci. 67 (1938) 60; Fern Fl. Philipp. 1 (1958) 73; Tagawa & K.Iwats. in Smitinand et al., Fl. Thailand 3 (1979) 88; K.Iwats., J. Fac. Sci. Univ. Tokyo, Sect. 3, Bot. 13 (1985) 540. — *Trichomanes christii* Copel., Philipp. J. Sci. 1, Suppl. 4 (1906) 251; Philipp. J. Sci. 51 (1933) 185, pl. 21; Holttum, Rev. Fl. Malaya 2 (1955) 100, f. 37. — *Crepidomanes barnardianum* (F.M.Bailey) Tindale subsp. *christii* (Copel.) Croxall, Austral. J. Bot. 23 (1975) 532. — Lectotype (designated by Ebihara & Iwatsuki, Mem. Natl. Mus. Nat. Sci. (Tokyo) 46 (2010) 96): *Merrill 1819* (lecto MICH; isolecto GH, P, SING, UC, US), Philippines, Mindoro.
Trichomanes recedens Rosenst., Meded. Rijks-Herb. 11 (1912) 2. — Type: *Winkler s.n.* (n.v.), Borneo.

Trichomanes paniculatum Alderw., Bull. Jard. Bot. Buitenzorg, sér. 2, 16 (1914) 38. — Type: *Backer 5837* (holo BO), Java.

Trichomanes microlirion Copel., Philipp. J. Sci., C. 10 (1915) 146. — Type: *Brooks 172* (n.v.), Borneo, Tringos.

Rhizome long-creeping, irregularly branching, slender, to 0.35 mm diam., densely covered with black hairs. *Stipes* short, (0.5–)1.2–2 cm long, terete, stramineous or greenish, blackish at basal portion, bearing sparse brown hairs; *fronds* oblong, broadest at middle, narrowing downwards, gradually narrowing towards round to moderately acute apex, tripinnatifid to tripinnate, 2–6 cm long, 1.2–3.5 cm wide; rachis straight, mostly terete or narrowly winged upwards, sparsely hairy; *pinnae* largest at middle or below it, larger pinnae narrowly oblong, round at apex, broadly cuneate and shortly stalked at base, usually placed patent to rachis, to 2 cm long, 7 mm wide; upper *pinnae* gradually smaller upwards, sessile or decurrent at base, less divided; pinna rachis placed on rachis with angles of 85–90°, nearly straight, winged and taking similar appearance to segments; *pinnules* pinnatifid to pinnate, round at apex, usually cuneate, to 8 mm long, 3.5 mm wide; *ultimate segments* narrowly oblong to lanceolate, acute to round at apex, entire and flat at margin, commonly 0.7–1.8 mm long, 0.4–0.6 mm broad; texture thin, green, brown in dried condition, brown hairs sparsely on veins underneath. *False veinlets* continuous along margin of segments and wings of axes, two regular rows of normal laminar cells outside them, oblique striae none or few. *Sori* solitary at apex of short segments, often gathering near apex, tuberous, broadly winged, dilated at mouth, 1.5–2 mm long, c. 1 mm diam., the dilated lips c. 0.4 mm broad; receptacles long-extruded. — **Fig. 4f.**

Distribution — Thailand (Peninsular); in *Malesia*: Peninsular Malaysia, Sumatra, Borneo and the Philippines.

Habitat & Ecology — Usually on twigs and on small trees, very rarely on rocks and on basal tree trunks; in dark places or in lighter part of jungles, often near streams, locally abundant. Altitude: usually in lowlands.

Notes — The distribution of false veinlets is similar to the situation in *C. bipunctatum*, although they are different in the structure of the sorus, construction of the fronds, and habitats. Still, they are sometimes confused.

Crepidomanes christii often grows on the higher portions of trees, on twigs. The fronds are oriented perpendicular to the substrate. The pinna rachis is usually oriented on the rachis at a broad angle or the frond is mostly rectangular. It is not known if there is any relationship between habitat and leaf construction.

4. Crepidomanes kurzii (Bedd.) Tagawa & K.Iwats.

Crepidomanes kurzii (Bedd.) Tagawa & K.Iwats., Acta Phytotax. Geobot. 26 (1975) 169; in Smitinand et al., Fl. Thailand 3 (1979) 92, f. 5:10; Croxall, Austral. J. Bot. 23 (1975) 534; K.Iwats., J. Fac. Sci. Univ. Tokyo, Sect. 3, Bot. 13 (1985) 535; J.X.Liu et al. in C.Y.Wu et al., Fl. China 2–3 (2013) 98; C.W.Chen et al., Sol Amazing (2017) 116; K.Iwats. et al., PhytoKeys 119 (2019) 112. — *Trichomanes kurzii* Bedd., Ferns Brit. India 2 (1868) ad t. 286; Handb. Ferns Brit. India (1883) 40, f. 20; Tardieu & C.Chr. in Lecomte, Fl. Indo-Chine 7, 2 (1939) 62; Sledge, J. Linn. Soc. Bot. 60 (1968) 304; Tagawa & K.Iwats., Acta Phytotax. Geobot. 24 (1970) 177. — Lectotype (designated by Croxal (1975); see Field, Austral. Syst. Bot. 33 (2020) 19): *Kurz s.n.* (lecto BM; isolecto K), S Andaman Islands.

[*Trichomanes nanum* Bosch, Ned. Kruidk. Arch. 5(3) (1863) 206, nom. illeg., non Hook. (1844). — Type: *Griffith s.n.* (holo K; iso L), India, Assam.]

Trichomanes nymanii Christ in K.Schum. & Lauterb., Fl. Schutzgeb. Südsee, Nachtr. (1905) 36; Copel., Philipp. J. Sci. 51 (1933) 187, pl. 19: f. 4. — *Crepidomanes nymanii* (Christ) Copel., Philipp. J. Sci. 67 (1938) 60. — Lectotype (designated here): *Nyman 506* (lecto B 200096759; isolecto P), New Guinea, Sattelberg.

Trichomanes perpusillum Alderw., Bull. Jard. Bot. Buitenzorg, sér. 2, 16 (1914) 37. — Type: *Schlechter s.n.* (holo BO), New Guinea.

Crepidomanes nanophyllum Tagawa, Acta Phytotax. Geobot. 9 (1940) 142; Tagawa & K.Iwats., S.E. Asian Stud. 5 (1967) 42. — *Trichomanes nanophyllum* (Tagawa) C.V.Morton, Contr. U.S. Natl. Herb. 38 (1968) 183. — Type: *Tagawa 2413* (holo KYO), Taiwan.

Rhizome long-creeping, irregularly branching, filiform, c. 0.1 mm diam., with dense blackish hairs. *Stipes* to 3 mm long, winged nearly to the base, greenish, dark at base; *fronds* oblong to oblong lanceolate, round at apex, cuneate at base, at most 1.5 cm long, 6 mm wide, pinnate-bipinnatifid; *rachis* winged throughout, wings of the lower portion at most 0.2 mm broad, entire, flat, broader in the upper portion; lateral *pinnae* simple or biforked, or in extremely larger ones with 3 or 4 lobes; simple pinnae or *ultimate segments* elongate sometimes to 5 mm long, c. 0.7 mm broad, acute at apex, entire and flat at margin; pagina clathrate, pale bluish green, thin in texture; submarginal *false veinlets* continuous, with one row of normal cells outside them. *Sori* at apex of ultimate segments, often gathering at apical portion of fronds; *involucres* tuberous with dilated mouth, c. 1.2 mm long, to 1 mm broad in pressed specimens; mouth dilated forming very narrow lips; receptacles extruded. — **Fig. 4g, h.**

Distribution — Sri Lanka, India (including Andaman Is.), Myanmar, Thailand, Vietnam, China (Hong Kong), Taiwan, Japan (S Ryukyu); in *Malesia*: Peninsular Malaysia, Philippines, Moluccas (Seram), New Guinea; Solomon Islands, Samoa and Australia (NE Queensland).

Habitat & Ecology — Epipetric on wet rocks, often along streams in dense gloomy forests. Altitude: at lower elevations to 350 m.

Note — Holttum (Rev. Fl. Malaya 2 (1955) 101) treated *C. kurzii* as a synonym of *T. latemarginale* and introduced confusion between these species. Both occur in Peninsular Malaysia.

5. **Crepidomanes latealatum** (Bosch) Copel.

Crepidomanes latealatum (Bosch) Copel., Philipp. J. Sci. 67 (1938) 60; H.Ito, Fil. Jap. Ill. (1944) pl. 475; J. Jap. Bot. 24 (1949) 125; Ching, Fl. Reipubl. Popularis Sin. 2 (1959) 165; Tagawa & K.Iwats. in Smitinand et al., Fl. Thailand 3 (1979) 89; K.Iwats., J. Fac. Sci. Univ. Tokyo, Sect. 3, Bot. 13 (1985) 537; J.L.Tsai & W.C.Shieh in H.L.Li et al., Fl. Taiwan 1 (1994) 105, pl. 38; J.X.Liu et al. in C.Y.Wu et al., Fl. China 2–3 (2013) 97; K.Iwats. et al., PhytoKeys 119 (2019) 112. — *Didymoglossum latealatum* Bosch, Ned. Kruidk. Arch. 5(3) (1863) 138; Copel., Philipp. J. Sci. 51 (1933) 192, pl. 25, 26. — *Trichomanes latealatum* (Bosch) Christ, Verh. Naturf. Ges. Basel 11 (1896) 424; Tardieu & C.Chr. in Lecomte, Fl. Indo-Chine 7, 2 (1939) 64; Holttum, Rev. Fl. Malaya 2 (1955) 101. — Type: *Griffith s.n.* (holo K), Assam.

Didymoglossum plicatum Bosch, Ned. Kruidk. Arch. 5(3) (1863) 139; Copel., Philipp. J. Sci. 51 (1933) 193. — *Trichomanes plicatum* (Bosch) Bedd., Ferns Brit. India 2 (1868) t. 285; Tardieu & C.Chr. in Lecomte, Fl. Indo-Chine 7, 2 (1939) 65; Sledge, J. Linn. Soc. Bot. 60 (1968) 305. — *Crepidomanes plicatum* (Bosch) Ching, Fl. Reipubl. Popularis Sin. 2 (1959) 171. — Lectotype (designated by

Morton, Contr. U.S. Natl. Herb. 38 (1968) 381): *Griffith s.n.* (lecto K), Malacca. Other syntypes: *Teijsman* (n.v.), Sumatra; *Thwaites 2985* (L), Sri Lanka; *Walker s.n.* (K), Sri Lanka.

Didymoglossum euphlebium Bosch, Ned. Kruidk. Arch. 5(3) (1863) 142; Copel., Philipp. J. Sci. 51 (1933) 193. — *Trichomanes euphlebium* (Bosch) Panigrahi, Phytologia 31 (1975) 256. — *Crepidomanes euphlebium* (Bosch) R.D.Dixit & B.Ghosh in R.D.Dixit, Census Indian Pteridophytes (1984) 91. — Type: *Griffith s.n.* (holo K), India, Assam.

Didymoglossum insigne Bosch, Ned. Kruidk. Arch. 5(3) (1863) 143; Copel., Philipp. J. Sci. 51 (1933) 193. — *Trichomanes insigne* (Bosch) Bedd., Ferns Brit. India 2 (1868) t. 284 C; Tardieu & C.Chr. in Lecomte, Fl. Indo-Chine 7, 2 (1939) 64. — *Crepidomanes insigne* (Bosch) S.H.Fu, Ill. Handb. Chin. Pl. Pterid. (1957) 39; Ching, Fl. Reipubl. Popularis Sin. 2 (1959) 168, pl. 11: f. 9–12. — Type: *Griffith s.n.* (holo K), India.

Trichomanes rothertii Alderw., Bull. Jard. Bot. Buitenzorg, sér. 2, 1 (1911) 13. — Type: *Bünnemeijer 9040a* (holo BO), Sumatra.

Trichomanes filicula auct. non Bory: Bedd., Ferns S. India (1863) pl. 7; Ferns Brit. India 2 (1868) pl. 283; Makino, Phan. Pter. Jap. Icon. 1 (1899) pl. 15.

Trichomanes bipunctatum auct. non Poir.: Ogata, Icon. Filic. Jap. 1 (1928) pl. 45.

Rhizome long-creeping, irregularly branching, thin but seemingly thicker because of the dense hairs. *Stipes* (0.8–)1.5–5(–8) cm long, very narrowly winged throughout or terete near the base, dark and with blackish hairs in lowest portion, green to stramineous and sparsely hairy in middle and upper portions; wings broader and 4–8 rows of cells in upper portion, very narrow downwards. *Fronds* tripinnate to quadripinnatifid or smaller tripinnatifid ones often fully soriferous, narrowly oblong to oblong subdeltoid, variable to some extent in size and outline, usually longer than stipes, (1–)2.5–8(–12) cm long, 1.5–6 cm wide, acute to moderately acute at apex, widest at lower portion and usually narrowing downwards; *rachis* straight, greenish, narrowly winged, bearing sparse both brown, setose hairs and pale brownish, clavate hairs; *pinnae* largest in lower middle ones, larger ones narrowly oblong, acute to moderately acute at apex, cuneate or broadly so at base, sessile or decurrent, to 7 cm long, 2.5 cm wide; pinna rachis distinctly winged and seemingly like segments, placed on rachis at 50–80°; *pinnules* narrowly oblong or variable in form, moderately acute to round at apex, larger ones pinnate to bipinnatifid, decurrent, to 1.2 cm long, 0.6 cm wide; *ultimate segments* 2–4 mm long, 0.3–0.6 mm broad, but variable in size, linear lanceolate, moderately acute to acuminate at apex, entire and flat, or more or less wavy to crisped, bearing dark club-shaped hairs rather densely on the veins underneath, green to deep green, brownish in dried specimens. No continuous submarginal *false veinlets*; oblique false veinlets many, variable in length. *Sori* at apex of segments, solitary, distributed from basal acroscopic pinnules outwards, usually many; *involucres* tuberous, winged, bilabiate at apical one-fifth to one-third, 2.2–2.7 mm long, to 1.5 mm diam.; lips subdeltoid or narrower, round to acuminate at apex, irregularly wavy or subentire; receptacles long-extruded, fragile. Chromosome number: $n = 36$ (Vijayakanth et al., Caryologia 71 (2018) 382), $2n = 72$ (Ghatak, Nucleus (Calcutta) 7 (1964) 95). — **Fig. 4d, e.**

Distribution — Sri Lanka, India, Nepal, Bhutan, continental Southeast Asia generally, north to C China and Japan; throughout *Malesia*.

Habitat & Ecology — Epipetric on muddy or mossy rocks, or epiphytic on the base of tree trunks, or sometimes on the upper trunk, often along or near streamlets from low to mid elevations.

Note — Forms comparable with *C. bipunctatum*, but having only oblique striae without any trace of submarginal false veinlets are lumped with *C. latealatum*. The biological delimitation of this species complex is pending. A detailed discussion of the variation in *C. latealatum* in the Sino-Japanese floristic region and a long list of synonyms was given by Iwatsuki (1985: 537–540).

6. Crepidomanes latemarginale (D.C.Eaton) Copel.

Crepidomanes latemarginale (D.C.Eaton) Copel., Philipp. J. Sci. 67 (1938) 60; Ching, Fl. Reipubl. Popularis Sin. 2 (1959) 154; Tagawa & K.Iwats. in Smitinand et al., Fl. Thailand 3 (1979) 91; K.Iwats., J. Fac. Sci. Univ. Tokyo, Sect. 3, Bot. 13 (1985) 535; J.L.Tsai & W.C.Shieh in H.L.Li et al., Fl. Taiwan 1 (1994) 107; J.X.Liu et al. in C.Y.Wu et al., Fl. China 2–3 (2013) 97. — *Trichomanes latemarginale* D.C.Eaton, Proc. Amer. Acad. Arts 4 (1858) 111; Hook. & Baker, Syn. Fil. (1867) 79; Copel., Philipp. J. Sci. 51 (1933) 189, pl. 24; Tardieu & C.Chr. in Lecomte, Fl. Indo-Chine 7, 2 (1939) 63; Holttum, Rev. Fl. Malaya 2 (1955) 101. — Lectotype (designated here): *C. Wright s.n.* (lecto GH 00022246; isolecto B, K, L, PE), China, Hong Kong.

Crepidomanes yunnanense Ching & P.C.Chiu in Ching, Fl. Reipubl. Popularis Sin. 2 (1959) 169. — Type: *Chu 2741* (holo PE), China, Yunnan.

Crepidomanes intramarginale auct. non (Hook. & Grev.) C.Presl: Ching, Fl. Reipubl. Popularis Sin. 2 (1959) 163.

Rhizome long-creeping, irregularly branching, bearing fronds commonly several millimeters apart, slender, c. 0.15 mm diam., densely hairy with brown, soft hairs. *Stipes* to 1 cm long, winged and greenish in upper portion, terete, dark, and hairy in lower portion; *fronds* pinnately compound in one plane and bipinnate, but often digitate in appearance, usually with 5–15 segments, oblong to ovate in outline, round both at apex and base, 1–1.5(–2.2) cm long, 0.8–1.5 cm wide; *rachis* often very short, winged to appear like segments; *ultimate segments* narrowly lanceolate, usually round at apex, entire and flat, to 5 mm long, commonly 2 mm broad, green to deep green. Submarginal *false veinlets* continuous, bearing two rows of laminar cells outside it; oblique false veinlets few or sparsely dispersed, usually short; *internal cell walls* thin, straight. *Sori* solitary at apex of segments, immersed; *involucres* cup-shaped, very broadly winged or forming apical portion of segments, 1–1.5 mm long, c. 1 mm diam. near mouth; lips bilabiate, more than 0.5 mm long, to 2 mm broad, round and entire; receptacles long-extruded. Chromosome numbers: $2n$ = c. 108 (Yoroi, J. Jap. Bot. 51 (1976) 264).

Distribution — India (Assam), Thailand, Vietnam, China (Yunnan, Hunan, Zhejiang, Guangdong, Hainan, Hong Kong, Fujian), Taiwan, Japan (S Ryukyu); in *Malesia*: Peninsular Malaysia and Java.

Habitat & Ecology — On moist, muddy rocks in dense gloomy forests, usually near streamlets at lower elevations.

Note — As a dwarf species, the collections are not sufficient to determine the extent of the wide distribution area.

7. Crepidomanes pervenulosum (Alderw.) Copel.

Crepidomanes pervenulosum (Alderw.) Copel., Philipp. J. Sci. 67 (1938) 60; K.Iwats. et al., PhytoKeys 119 (2019) 112. — *Trichomanes pervenulosum* Alderw., Philipp. J. Sci., C. 11 (1916) 103, pl. 5, f. 2; Copel., Philipp. J. Sci. 51 (1933) 188, pl. 19: f. 3, pl. 22: f. 2–3. — Lectotype (designated here): *C.B. Robinson 1947* (lecto BO; isolecto A, GH, K, L, MICH, NY, P, US), Moluccas, Ambon.

Rhizome long-creeping, irregularly branching, bearing fronds usually more than several millimeters apart, slender, less than 1 mm diam., densely hairy with brown, soft hairs. *Stipes* to 0.5 mm long, terete or winged in upper portion, hairy with short, brown, more or less stiff hairs, or caducous; *fronds* simple to pinnately decompound, simple fronds like the segments of pinnately decompound ones, linear, round at apex, entire and flat, and nearly parallel at edges, narrowly cuneate at base, to 8 mm long, 1.5 mm broad, biforked fronds often equally forked at apical quarter or less portion, rarely unequally forked even near the basal portion, forked segments like the simple fronded form but shorter in length, larger fronds with up to 7 segments, principally arranged in one pinnate plane but often irregularly pinnate to bipinnatifid, each segment like the simple fronded form and often shorter; *rachis* and pinna rachis, if any, winged throughout taking similar appearance to segments; *false veinlets* all oblique, numerous in number, to 0.5 mm long, 2–3(–5) rows of cells at each side of true veins, rarely straight or wavy; texture membranous. *Laminar cells* not modified except for false veinlets; *internal cell walls* straight, thin. *Sori* solitary at apex of segments, immersed; *involucres* cup-shaped, very broadly winged, c. 1 mm long, 1 mm diam. near mouth; lips dilated or separated into two parts and distinctly dilated, to 0.4 mm broad; receptacles long-extruded.

Distribution — *Malesia*: Borneo (East Kalimantan: Gunung Buntung, *Kato & Wiriadinata B-5343bis,* KYO), Moluccas (Ambon, Seram).

Habitat & Ecology — On moss-covered bark of basal tree trunks.

8. Crepidomanes rupicola (Racib.) Copel.

Crepidomanes rupicola (Racib.) Copel., Philipp. J. Sci. 67 (1938) 59; Fern Fl. Philipp. 1 (1958) 73; J.X.Liu et al. in C.Y.Wu et al., Fl. China 2–3 (2013) 98. — *Trichomanes rupicola* Racib., Pteridoph. Buitenzorg (1898) 24; Copel., Philipp. J. Sci. 51 (1933) 181, pl. 19: f. 3. — Lectotype (designated here): *Raciborski s.n.* (lecto BO; isolecto L, MICH, P), Java, G. Pantja.

Trichomanes formosanum Y.Yabe, Bot. Mag. (Tokyo) 19 (1905) 31, f. 1–4. — Type: *K. Miyake s.n.* (holo TI), Taiwan.

Rhizome long-creeping, filiform, less than 0.1 mm diam., densely covered with dark brownish hairs, thus appearing c. 0.3 mm diam. *Stipes* filiform, terete, very short, 1–3 mm long, greenish, hairy or glabrescent; *fronds* with up to 6 lobes, seemingly digitately arranged, or simple, simple fronds like lobes of multi-lobed fronds that are orbicular in outline, round to cuneate at base, round to obtuse at apex, to a little more than 1 cm long, 1 mm wide; *pinnae* simple or at most forked, all the lobes univeined; ultimate segments or simple fronds narrowly oblong to linear, round or slightly notched at apex, entire and flat at margin, to nearly 1 cm long, 2 mm broad; pagina thin, pale green (green even on specimens after many years), nearly transparent; submarginal *false veinlets* usually obsolete, or sometimes present but interrupted and duplicated to the next row, many oblique striae present. *Sori* at apices of ultimate lobes, solitary, campanulate; *involucres* with tuberous basal portion and dilated mouth, tuberous portion completely immersed in lobe-apex, c. 1.8 mm long, 0.7 mm diam., broadly winged by lobes or same width as lobes, dilated mouth to 1.7 mm diam., 0.5 mm in breadth; receptacles elongate, extruded from dilated mouth.

Distribution — Taiwan; in *Malesia*: Java, the Philippines (Luzon, Palawan, Mindanao) and the Lesser Sunda Island (Flores).

Habitat & Ecology — Epipetric on shaded surface of large boulders, often overhanging streams, but above the reach of floods. Altitude: 100–1000 m.

Note — The division of the frond axis is typically pinnate, but as the rachis is indistinct, the division appears digitate; on fronds with six lobes there is one forked pinna and four alternate simple pinnae.

9. **Crepidomanes vitiense** (Baker) Bostock

Crepidomanes vitiense (Baker) Bostock in Orchard, Fl. Australia 48 (1998) 706; Ebihara et al., Taxon 53 (2004) 945; J.X.Liu et al. in C.Y.Wu et al., Fl. China 2–3 (2013) 99; C.W.Chen et al., Sol Amazing (2017) 119; K.Iwats. et al., PhytoKeys 119 (2019) 112. — *Trichomanes vitiense* Baker, J. Linn. Soc., Bot. 9 (1866) 338, t. 8: f. D; Copel., Philipp. J. Sci. 51 (1933) 157, pl. 9: f. 1, 2; K.Iwats., Fern Gaz. 11 (1975) 192. — *Microtrichomanes vitiense* (Baker) Copel., Philipp. J. Sci. 67 (1938) 37; Croxall, Austral. J. Bot. 23 (1975) 525. — Type: *Milne s.n.* (holo K), Fiji.

Trichomanes powellii Baker in Hook. & Baker, Syn. Fil. (1867) 76. — *Trichomanes digitatum* Sw. var. *powellii* (Baker) Christ, Bot. Jahrb. Syst. 23 (1897) 336. — *Microtrichomanes powellii* (Baker) Pic.Serm., Webbia 45 (1991) 346. — Lectotype (designated here): *Powell 128* (lecto K; isolecto BM), Samoa.

Trichomanes asnykii Racib., Natuurk. Tijdschr. Ned.-Indië 59 (1900) 238, pl. 2: f. 6; Copel., Philipp. J. Sci. 51 (1933) 158 (‘*T. aswijkii*’); K.Iwats., Fern Gaz. 11 (1975) 122. — Lectotype (designated here): *Raciborski s.n.* (lecto BO; isolecto KYO, L, US), Java.

Rhizome long-creeping, very densely covered with blackish hairs, c. 0.8 mm diam. including hairs. *Stipes* very short, usually to 5 mm long, filiform, terete, glabrous except hairy base; *fronds* simple, forked, or at most with four digitately arranged lobes, when forked with nearly the same lobes similar to simple fronds, or in more divided cases with three or four lobes similar to each other; simple fronds or lobes of divided forms narrowly oblong or more or less quadrangular in outline, round or more commonly notched at apex, entire and flat or undulate at margin, round at base, largest ones to 2 cm long, 7 mm broad, reddish brown in dried condition; *costae* (or veins) simple in simple fronds, or uninervate in each lobe; forked fronds with two lobes similar to simple fronds, or just consisting of two simple fronds. *Sori* solitary at apices of lobes, campanulate; *involucres* with tuberous lower half and dilated mouth, tuberous portion immersed to frond apex nearly halfway, c. 1.5 mm long, 0.8 mm diam., distal dilated portion c. 2.2 mm diam., distinctly dilated, entire; receptacles elongate, long-extruded from lips. — **Fig. 4i.**

Distribution — Taiwan; in *Malesia*: Java, Borneo, Moluccas (Seram) and New Guinea; Solomon Islands, Vanuatu, New Caledonia, Fiji, Samoa, and Australia (Queensland, New South Wales).

Habitat & Ecology — Epipetric on moist rocks in dense gloomy forests, rarely epiphytic on tree trunks in montane forests. Altitude: from low to mid elevations.

Note — *Crepidomanes vitiense* was placed under *Microtrichomanes* by Copeland (1933, 1938), but the molecular analysis showed that it merges into *Crepidomanes* (cf. Ebihara et al. 2004).

ab. Section **Crepidium** (C.Presl) Ebihara & K.Iwats.

Crepidomanes (C.Presl) C.Presl subg. *Crepidomanes* sect. *Crepidium* (C.Presl) Ebihara & K.Iwats. in Ebihara et al., Blumea 51 (2006) 239. — *Didymoglossum* Desv. subg. *Crepidium* C.Presl, Abh. Königl. Böhm. Ges. Wiss., ser. 5, 3 (1843) 23. — *Trichomanes* L. sect. *Crepidium* (C.Presl) C.Chr., Index Filic. (1906) xv; C.V.Morton, Contr. U.S. Natl. Herb. 38 (1968) 184. — *Crepidopteris* Copel., Philipp. J. Sci. 67 (1938) 57, nom. superfl. non C.Presl in Sternb. (1838); Gen. Fil. (1947) 39. — *Trichomanes* L. subg. *Crepidopteris* (Copel.) Holttum, Rev. Fl. Malaya 2 (1955) 98. — *Crepidophyllum* C.F.Reed, Amer. Fern J. 38 (1948) 88, nom. superfl., non Herzog (1926). — *Reediella* Pic.Serm., Webbia 24 (1970) 719. — *Crepidomanes* (C.Presl) C.Presl subg. *Crepidium* (C.Presl) K.Iwats., Acta Phytotax. Geobot 35 (1984) 174. — Type: *Crepidomanes humile* (G.Forst.) Bosch.

See species for description.

Distribution — Thailand, S China, Taiwan, Japan (Ryukyu); in *Malesia*: throughout; Pacific Islands and Australia (Queensland).

Habitat & Ecology — On moss-covered and muddy rocks and on the base of tree trunks, commonly along streams in dense forests.

Taxonomy — The general characteristics of sect. *Crepidium* are similar to those of sect. *Crepidomanes*, and distinct in particular in the modified marginal cells. The two rows of marginal laminar cells are elongate parallel to the lamina-margin and are 2–4 times as long as wide. The cross walls run obliquely downward and inward from the margin; the outer ones are hyaline and slightly thickened, while the walls of the inner rows are thicker and darker. This feature is distinct, but is a special modification. The reason for such a particular modification has not been elucidated.

10. Crepidomanes humile (G.Forst.) Bosch

Crepidomanes humile (G.Forst.) Bosch, Hymenophyll. Javan. (1861) 16, pl. 11; K.Iwats., Acta Phytotax. Geobot. 35 (1984) 174; J. Fac. Sci. Univ. Tokyo, Sect. 3, Bot. 13 (1985) 532; J.X. Liu et al. in C.Y. Wu et al., Fl. China 2–3 (2013) 98; C.W.Chen et al., Sol Amazing (2017) 114; K.Iwats. et al., PhytoKeys 119 (2019) 112. — *Trichomanes humile* G.Forst., Prodr. (1786) 84; Hook. & Baker, Syn. Fil. (1867) 80; Copel., Philipp. J. Sci. 51 (1933) 164, pl. 12; Ogata, Icon. Fil. Jap. 6 (1935) pl. 296; Holttum, Rev. Fl. Malaya 2 (1955) 98, f. 34. — *Didymoglossum humile* (G.Forst.) C.Presl, Abh. Königl. Böhm. Ges. Wiss., ser. 5, 3 (1843) 23. — *Crepidopteris humilis* (G.Forst.) Copel., Philipp. J. Sci. 67 (1938) 58; H.Ito, Fil. Jap. Ill. (1944) pl. 474; Copel., Fern Fl. Philipp. 1 (1958) 70; Ching, Fl. Reipubl. Popularis Sin. 2 (1959) 174. — *Crepidophyllum humile* (G.Forst.) C.F.Reed, Amer. Fern J. 38 (1948) 89; DeVol in H.L.Li et al., Fl. Taiwan 1 (1975) 106, pl. 34. — *Reediella humilis* (G.Forst.) Pic.Serm., Webbia 24 (1970) 719; Croxall, Austral. J. Bot. 23 (1975) 531; Tagawa & K. Iwats. in Smitinand et al., Fl. Thailand 3 (1979) 87; J.L.Tsai & W.C.Shieh in H.L.Li et al., Fl. Taiwan 1 (1994) 125, pl. 47. — Lectotype (designated by Nicolson & Fosberg, Regnum Veg. 139 (2003) 108): *G. Forster 302-464* (lecto K; possible isolecto BM as *G. Forster 302*), Society Islands.

Trichomanes luzonicum C.Presl, Abh. Königl. Böhm. Ges. Wiss., ser. 5, 3 (1843) 16, 42. — Lectotype (designated here): *Cuming 98* (lecto PRC; isolecto GH, L, MICH, P), Philippines.

Trichomanes lauterbachii Christ in K.Schum. & Lauterb., Fl. Schutzgeb. Südsee 1 (1900) 108. — Lectotype (designated here): *Lauterbach 2825a* (lecto B; isolecto BM, S), New Guinea, Bismarck-Ebene.

Trichomanes filiculoides Christ in K.Schum. & Lauterb., Fl. Schutzgeb. Südsee 1 (1900) 108. — Lectotype (designated here): *Lauterbach 535c* (lecto B), New Guinea. Other syntypes: *Lauterbach 541* (B, L, UC), New Guinea; *Lauterbach 988* (B), New Guinea.

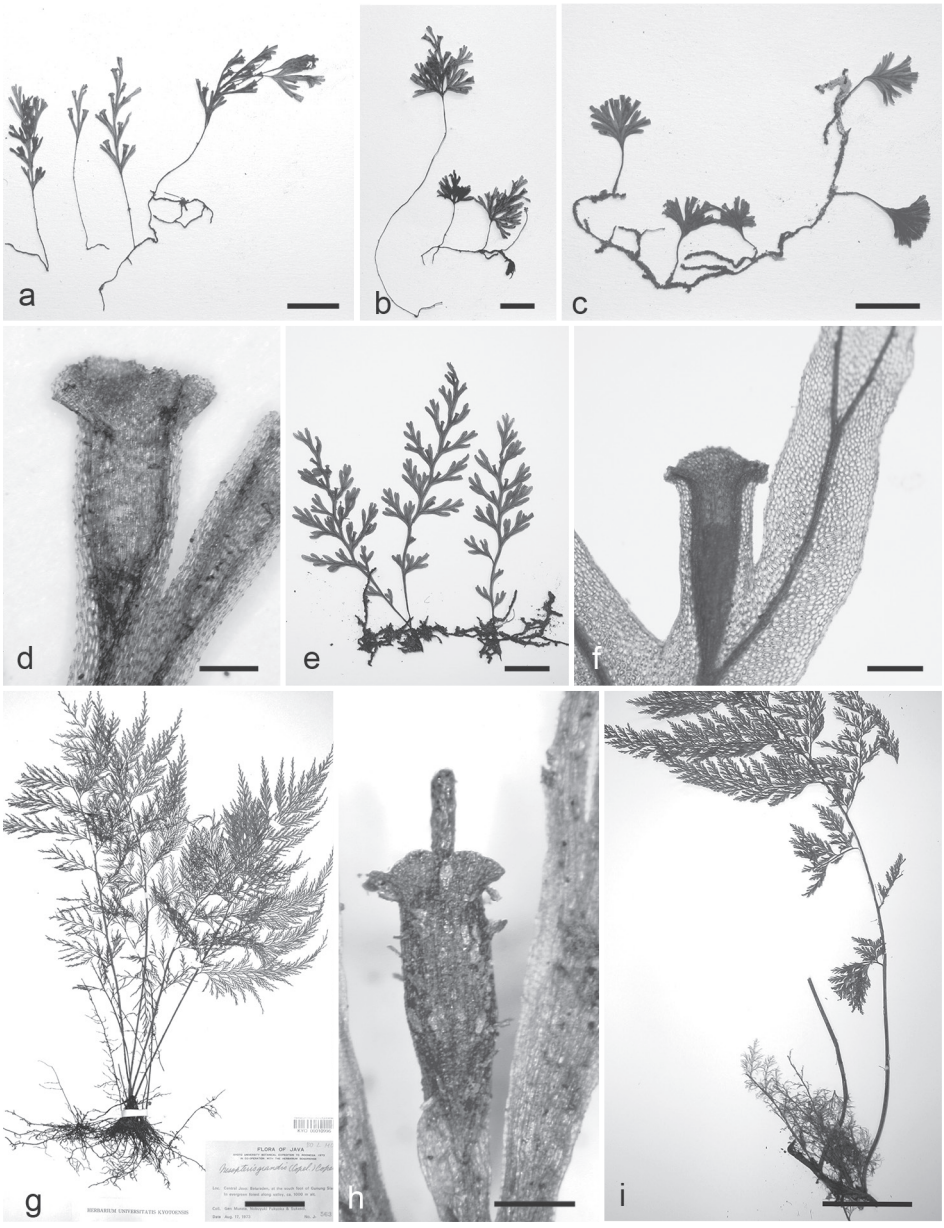

Fig. 5. a–d. *Crepidomanes minutum* (Poir.) Copel. a. Specimen with pinnately divided fronds; b. specimen with proliferous flabellate fronds; c. specimen with flabellate fronds; d. sorus. — e, f. *C. humile* (G.Forst.) Bosch. e. Specimen; f. sorus. — g, h. *C. grande* (Copel.) Ebihara & K.Iwats. g. Specimen; h. sori. — i. Aphlebiae on a rhizome of *C. aphlebioides* (Christ) I.M.Turner (a: *Ebihara et al. 000224-014*, Mt Kinabalu, Malaysia, TNS 766160; b: *Ebihara et al. 000223-012*, Mt Kinabalu, Malaysia, TNS 766158; c: *Ebihara 040922-06*, Luzon, Philippines, TNS 1107010; d: *Ebihara et al. 000224-014*, Mt Kinabalu, Malaysia, TNS 766160; e, f: *Iwatsuki et al. A-504*, Ambon, TNS 1195441; g, h: *Murata et al. J-563*, Java, Indonesia, KYO 00010996; i: *Kato et al. C-13883*, Seram, Indonesia, TI 00047803).

Trichomanes gracillimum Copel., Philipp. J. Sci. 51 (1933) 168, pl. 13. — *Crepidopteris gracillima* (Copel.) Copel., Philipp. J. Sci. 67 (1938) 58; Fern Fl. Philipp. 1 (1958) 70. — *Crepidophyllum gracillimum* (Copel.) C.F.Reed, Amer. Fern J. 38 (1948) 89. — Lectotype (designated by Ebihara & Iwatsuki, Mem. Natl. Mus. Nat. Sci. (Tokyo) 46 (2010) 95): *BS (Ramos) 33383* (lecto MICH; isolecto P, SING), Philippines, Luzon.

Rhizome long-creeping on rocks or rarely on basal tree trunks, very slender, c. 0.3 mm diam., densely covered by blackish hairs, thus making appearance of rhizome 1–1.5 mm diam. and velvety, irregularly branching, fragile. *Stipes* usually short, (2–)7–12 mm long, the lower half dark and with blackish hairs, the upper half green, narrowly winged; *fronds* bipinnatifid to tripinnatifid, ovate in small and lanceolate to oblong-lanceolate in larger ones, round at apex, subtruncate, round, or cuneate at base, 1–3(–8) cm long, 2(–3) cm wide; rachis winged, wings c. 0.4 mm on both sides, entire, flat, bearing short, caducous hairs; *pinnae* patent to ascending, sessile, usually with 2–7 pinnately arranged segments, to 1 cm long, 7 mm wide; ultimate segments round at apex, flat or a little wavy, entire, commonly c. 1.2 mm broad, green to pale green. *Laminar cells* unistratose, with thin and straight cell walls; double rows of marginal cells of segments and wings elongate parallel to margin, with cross walls running obliquely. *Sori* solitary on basal acroscopic segments of pinnae, tuberous with narrow wings, c. 1.7 mm long, 0.4 mm diam., the mouth dilated, more than 1 mm diam.; receptacles extruded. Chromosome numbers: $2n = 72$ (Braithwaite, Fern. Gaz. 10 (1969) 82, Bot. J. Linn. Soc. 71 (1975) 170). — **Fig. 5e, f.**

Distribution — India (Andaman and Nicobar Islands), Thailand (Peninsular), Taiwan, Japan (S Ryukyu); throughout *Malesia*; Micronesia and Polynesia, east to French Polynesia and south to New Zealand (Kermadec Islands).

Habitat & Ecology — On muddy rocks and on the base of tree trunks, usually in accumulated soil; commonly along streamlets in dense lowland forests. Altitude: to middle elevations.

Notes — As usual in such widely distributed species, *C. humile* forms a variable species complex. It is somewhat doubtful to lump all the materials from a wide area into a single species, but we have no evidence at present to draw any taxonomic lines of demarcation among them.

From the Philippines, a form with narrower wings on the rachis and involucres consisting of a few rows of cells, or less than 0.3 mm broad, was specifically separated by Copeland (1933). Similar forms occur even outside the Philippines. This form, called *C. gracillimum*, is here included in this widely distributed species. Among the variation in some phenetic characters, there is variation in the width of the wings in this species.

ac. Section **Gonocormus** (Bosch) K.Iwats.

Crepidomanes (C.Presl) C.Presl subg. *Crepidomanes* sect. *Gonocormus* (Bosch) K.Iwats., Acta Phytotax. Geobot. 35 (1984) 174. — *Gonocormus* Bosch, Hymenophyll. Javan. (1861) 7; Copel., Philipp. J. Sci. 67 (1938) 56; Gen. Fil. (1947) 38. — Type: *Gonocormus minutus* (Blume) Bosch (= *Crepidomanes minutum* (Blume) K.Iwats.).

Rhizome creeping, usually very long, often forming a mat of fronds, hairy; *fronds* pinnate in one plane, variously proliferous often with side leaves, or seemingly flabel-

late with very short rachis; *segments* entire, flat or distinctly recurved; *laminar cells* not modified, sometimes very large; *internal cell walls* not coarsely pitted; *involucres* cup-shaped or campanulate, the mouth dilated; receptacles long-extruded. Chromosome numbers: $n = 36$ and its multiples.

Distribution — Widely distributed throughout the Old World tropics, Africa to Polynesia, north to N Japan (Hokkaido) and south to Australia (Victoria). One species common throughout *Malesia*.

Habitat & Ecology — Terrestrial, saxifragous, or epiphytic; most species live near streams.

Taxonomy — The species taxonomy is terribly difficult in sect. *Gonocormus*; all forms of the section from Malesia are lumped into a single species.

11. **Crepidomanes minutum** (Blume) K.Iwats.

Crepidomanes minutum (Blume) K.Iwats., J. Fac. Sci. Univ. Tokyo, Sect. 3, Bot. 13 (1985) 524; J.X.Liu et al. in C.Y.Wu et al., Fl. China 2–3 (2013) 98; C.W.Chen et al., Sol Amazing (2017) 117; K.Iwats. et al., PhytoKeys 119 (2019) 112. — *Trichomanes minutum* Blume, Enum. Pl. Javae 2 (1828) 223; Copel., Philipp. J. Sci. 51 (1933) 148; Holttum, Rev. Fl. Malaya 2 (1955) 96; Yoroi & K.Iwats., Acta Phytotax. Geobot. 28 (1977) 152. — *Gonocormus minutus* (Blume) Bosch, Hymenophyll. Javan. (1861) 7, pl. 3; Copel., Philipp. J. Sci. 67 (1938) 57; Fern Fl. Philipp. 1 (1958) 68; Ching, Fl. Reipubl. Popularis Sin. 2 (1959) 175, pl. 12: f. 1–6; J.L.Tsai & W.C.Shieh in H.L.Li et al., Fl. Taiwan 1 (1994) 108, pl. 39, photo 44. — *Trichomanes proliferum* Blume var. *minutum* (Blume) C.A.Hameed, K.P.Rajesh & Madhus., Filmy Ferns S. India (2003) 258. — Lectotype (designated by Croxall, Austral. J. Bot. 23 (1975) 529 as 'holotype'): *Blume s.n.* (lecto L; isolecto P), Java.

Trichomanes bifolium Blume, Enum. Pl. Javae 2 (1828) 224. — Type: *Blume s.n.* (holo L n.v.), Java.

Trichomanes proliferum Blume, Enum. Pl. Javae 2 (1828) 224; Hook., Sp. Fil. 1 (1844) 118, pl. 29B; Copel., Philipp. J. Sci. 51 (1933) 150; Tardieu & C.Chr. in Lecomte, Fl. Indo-Chine 7, 2 (1939) 66; Holttum, Rev. Fl. Malaya 2 (1955) 97, f. 33; Sledge, J. Linn. Soc. Bot. 60 (1968) 299, pl. 1. — *Gonocormus prolifer* (Blume) Prantl, Unters. Morph. Gefässkrypt. 1 (1875) 51; Ching, Fl. Reipubl. Popularis Sin. 2 (1959) 178, pl. 12: f. 7; Croxall, Austral. J. Bot. 23 (1975) 528; Tagawa & K.Iwats. in Smitinand et al., Fl. Thailand 3 (1979) 81. — *Crepidomanes proliferum* (Blume) Bostock in Orchard, Fl. Australia 48 (1998) 706. — Lectotype (designated by Sledge, J. Linn. Soc. Bot. 60 (1968) 299; see Field (Austral. Syst. Bot. 33 (2020) 29): *Blume s.n.* (lecto L 0052391), Java.

Trichomanes diffusum Blume, Enum. Pl. Javae 2 (1828) 225; Copel., Philipp. J. Sci. 51 (1933) 149. — *Gonocormus diffusus* (Blume) Bosch, Hymenophyll. Javan. (1861) 9, pl. 4; Copel., Philipp. J. Sci. 67 (1938) 57; K.Iwats., Acta Phytotax. Geobot. 17 (1958) 162. — Type: *Blume s.n.* (holo L 0052381), Java.

Trichomanes palmatum C.Presl, Abh. Königl. Böhm. Ges. Wiss., ser. 5, 3 (1843) 16, 39. — Lectotype (designated here): *Cuming 209* (lecto PRC; isolecto GH, K, L, P), Philippines.

Trichomanes saxifragoides C.Presl, Abh. Königl. Böhm. Ges. Wiss., ser. 5, 3 (1843) 39; Sledge, J. Linn. Soc. Bot. 60 (1968) 298. — *Gonocormus saxifragoides* (C.Presl) Bosch, Hymenophyll. Javan. (1861) 9; Croxall, Austral. J. Bot. 23 (1975) 529; Tagawa & K.Iwats. in Smitinand et al., Fl. Thailand 3 (1979) 80. — *Crepidomanes saxifragoides* (C.Presl) P.S.Green, Kew Bull. 48 (1993) 618; C.W.Chen et al., Sol Amazing (2017) 118. — Lectotype (designated by Croxall, Austral. J. Bot. 23 (1975) 529 as 'holotype'): *Cuming 256* (lecto K; isolecto B, GH, L, MICH, P, PRC, US), Philippines, Luzon.

Trichomanes subpinnatifidum Bosch, Ned. Kruidk. Arch. 5(2) (1861) 141; in Goddijn, Meded. Rijks-Herb. 38 (1919) 25, f. 14. — Type: *Gardner s.n.* (holo L 0052386), Sri Lanka.

Trichomanes teysmannii Bosch, Ned. Kruidk. Arch. 5(2) (1861) 142; Copel., Philipp. J. Sci. 51 (1933) 150, pl. 6, f. 1–3. — *Gonocormus teysmannii* Bosch, Hymenophyll. Javan. (1861) 10 pl. 5; Tagawa

& K.Iwats., S.E. Asian Stud. 5 (1967) 40. — *Crepidomanes teysmannii* (Bosch) Parris, Fern Gaz. 20 (2018) 305. — Type: *Teijsmann s.n.* (holo L), Sumatra.

Trichomanes gracile Bosch, Ned. Kruidk. Arch. 5(2) (1861) 157. — Type: *Kuhl & van Hasselt 71* (holo L), Java.

Trichomanes assimile Mett. in Kuhn, Linnaea 35 (1868) 386. — *Gonocormus assimilis* (Mett.) Parris, Fern Gaz. 14 (1994) 256. — Lectotype (designated here): *McGillivray 53* (lecto B; isolecto P 4 sheets, S), Vanuatu.

Trichomanes hosei Baker, J. Linn. Soc., Bot. 22 (1887) 223, pl. 12; Copel., Philipp. J. Sci. 51 (1933) 137, pl. 2, f. 2–4. — Type: *Hose 16* (holo K), Sarawak, Matang.

Trichomanes alagense Christ, Philipp. J. Sci., C. 3 (1908) 270; Copel., Philipp. J. Sci. 51 (1933) 152, pl. 6, f. 4–7. — *Gonocormus alagensis* (Christ) Copel., Philipp. J. Sci. 67 (1938) 57; Fern Fl. Philipp. 1 (1958) 69. — Lectotype (designated here): *Merrill 6062* (lecto MICH 1191060; isolecto P 2 sheets), Philippines, Mindoro.

Trichomanes matthewii Christ, Notul. Syst. (Paris) 1 (1909) 56. — *Gonocormus matthewii* (Christ) Ching, Fl. Reipubl. Popularis Sin. 2 (1959) 177. — Lectotype (designated here): *Matthew 26* (lecto P 00623412; isolecto BM, K 2 sheets, PE), China.

Trichomanes novoguineense Brause, Bot. Jahrb. Syst. 49 (1912) 7. — *Gonocormus novoguineensis* (Brause) Copel., Philipp. J. Sci. 73 (1941) 467. — *Crepidomanes novoguineense* (Brause) Parris, Fern Gaz. 20 (2018) 305. — Type: *Schultze 33 (35)* (holo B), Papua New Guinea.

Trichomanes brooksii Copel., Philipp. J. Sci., C. 12 (1917) 45. — Type: *Brooks & Hewitt s.n.* (holo MICH), Sarawak.

Trichomanes subtilissimum Brause, Bot. Jahrb. Syst. 56 (1920) 33. — Type: *Ledermann 8493* (holo B), Papua New Guinea.

Gonocormus australis Ching, Acta Phytotax. Sin. 8 (1959) 137, 163; Fl. Reipubl. Popularis Sin. 2 (1959) 176. — Lectotype (designated here): *E. Smith 1397* (lecto PE 00042630; isolecto BM, K), China.

Gonocormus siamensis Tagawa & K.Iwats., Acta Phytotax. Geobot. 22 (1967) 99, f. 3; in Smitinand et al., Fl. Thailand 3 (1979) 81. — Type: *Tagawa et al. T-4813* (holo KYO; iso K), Thailand.

Trichomanes parvulum auct. non Poir.: Blume, Enum. Pl. Javae 2 (1828) 223; Hook., Sp. Fil. 1 (1844) 118, pl. 39A; Hook. & Baker, Syn. Fil. (1867) 75; Copel., Philipp. J. Sci. 51 (1933) 145, pl. 5; Tardieu & C.Chr. in Lecomte, Fl. Indo-Chine 7, 2 (1939) 65.

Rhizome long-creeping, irregularly branching, slender, c. 0.15 mm diam., bearing brown hairs, or older portions glabrescent and wiry. *Stipes* variable in morphology, slender, similar to rhizome but hairy dense at base and very sparsely upwards, green to stramineous, terete, often proliferous or bearing dormant buds, very short or to 3 cm long in larger fronds; *fronds* variable in form and size, smaller ones often flabellate or rachis becoming extremely short, simple and deeply incised between the veins, with short, narrow, deep green, glabrous segments, larger ones principally pinnately decompound in one plane, oblong-lanceolate, moderately acute at apex, bipinnate to quadripinnatifid, but if all axes of fronds bear proliferations then the construction of fronds can be complex, to 12 cm long, 3 cm wide, but commonly to 8 cm long; *rachis* like the upper part of stipes, very short to form a flabellate construction of fronds or elongate in pinnately decompound fronds, bearing proliferation in various ways, sparsely hairy; *pinnae* of the pinnately decompound fronds nearly flabellate to oblong subdeltoid, subsessile to shortly stalked; *ultimate segments* narrow, entire, deep green, commonly to 0.3 mm broad, but variable to some extent, often flat or involute to some extent. *Laminar cells* without modification near the margin of laminae; *internal cell walls* thin and straight. *Sori* immersed in the apices of segments or stalked, tuberous to

campanulate, c. 3 mm long, 1 mm diam., often broadly winged; the mouth more or less dilated, the lips 0.3 mm in width; receptacles long-extruded. Chromosome numbers: $2n = 72$, 108, 144 and $n = 36$ or 'n' = '$2n$' = 72 for the plants outside Malesia (Bell, New Phytol. 59 (1960) 53; Braithwaite, Fern Gaz. 10 (1969) 82, Bot. J. Linn. Soc. 71 (1975) 169; Yoroi & Iwatsuki, Acta Phytotax. Geobot. 28 (1977) 156); normally sexual or agamosporous. — **Fig. 5a–d.**

Distribution — Thus defined broadly, *Crepidomanes minutum* is very widely distributed in the Palaeotropics, Africa to Polynesia, north to Siberia and N Japan (Hokkaido) and south to Australia (Victoria); throughout *Malesia*.

Habitat — Usually forming mats on wet mossy rocks and on the base of tree trunks in dense gloomy forests, but it also grows on rather dry cliffs and higher up on tree trunks and on the thinner branches of trees. The wide range of habitats may explain the wide range of morphological variation. Altitude: from lowlands to 3000 m.

Notes — The definition and circumscription of *Crepidomanes minutum* does not accord well with the usual species concept, but is comparable with a so-called species complex. At the moment, there is no conclusive evidence for establishing taxonomic differences among the specimens treated here, except to recognize only a wide range of variation in various characters.

Blume (1828) distinguished four forms in Java, all with vegetative proliferations: *Trichomanes diffusum* is the least proliferous form, although the fronds are not typically flabellate. Both species described by Presl (1843), on the contrary, have flabellate fronds. As I have noted already, even the so-called flabellate form, *T. saxifragoides*, bears distinct proliferations. *Trichomanes teysmanni* is the largest form in this complex. Until the time of Van den Bosch (1861), all typical forms of variation in the *Crepidomanes minutum* complex were distinguished and named. All efforts made until now to recognize species within this particular group were not successful.

The lectotype of *Trichomanes minutum* in L is a form with several fan-shaped fronds repeated on an elongate rachis; an isolectotype in P is a form with only one fan-shaped frond. In this species, such a variation is often observed even within a single population and it is possible to include these forms in one collection, though there is no evidence if the different sheets of specimens under the same number were collected in one population or not.

Trichomanes alagense has the sori gathered near the apex of the fronds and their larger involucres are supported by longer stalks. Other species described from neighboring areas are also referred here and reduced to this species complex.

Some specimens from middle elevations of New Guinea, 2000–2500 m alt., are noted as being erect herbs and larger in size, to 7 cm tall. The features are those of *T. minutum*, but the habit appears to be different. *Trichomanes novoguineense* appears to be based on one such form.

Yoroi & Iwatsuki (1977) reported both normal sexual and agamosporous reproductive patterns in this species complex, and this is a particular case. We were unable to detect any geographical or morphological distinction between the two reproductive types. More analysis is needed to determine more precisely the relationships among the various forms in this species complex.

The taxonomy of the species was further illuminated by modern technology (Nitta et al., Amer. J. Bot. 98 (2011) 1782–1800), which showed a reticulate pattern of evolution of infraspecific variation in various hybrid populations between slightly differentiated local populations. The *C. minutum* species complex is still producing variation where differentiation is being promoted by divergence and convergence of various populations. Under such circumstances, it is recommended that one complex species be recognized at the moment, pending further analysis of the relationships among various populations.

b. Subgenus **Nesopteris** (Copel.) Ebihara & K.Iwats.

Crepidomanes (C.Presl) C.Presl subg. *Nesopteris* (Copel.) Ebihara & K.Iwats., Blumea 51 (2006) 239. — *Nesopteris* Copel., Philipp. J. Sci. 67 (1938) 65; Gen. Fil. (1947) 40. — Type: *Crepidomanes grande* (Copel.) Ebihara & K.Iwats.

Rhizome suberect or ascending, with fronds clustered on the top, hairy; hairs on stipes and rachis, if any, dark brown, coarse, appressed, and rather sparse; *laminae* finely dissected, quasi- to quadripinnate; pinnae, pinnules and segments placed in one plane; ultimate segments usually round to moderately acute at apex; *laminar cells* with straight and thin cell walls; *sori* campanulate, the mouth truncate or little dilated; receptacles long-extruded, but feasible, rarely on the dried specimens.

Distribution — Four species in Taiwan, Japan (S Ryukyu); throughout *Malesia*; east to Polynesia.

Habitat & Ecology — Wet rocks, muddy crevices of cliffs usually near streams, terrestrial on the humus rich floor of dense forests and epiphytic on the base of tree trunks, usually at lower elevations.

Taxonomy — The definition and circumscription of subg. *Nesopteris* were given by Copeland (1938) and followed by the botanists since then. Molecular data show that *Nesopteris* should be included in *Crepidomanes* along with *T. aphlebioides*, a species having long-creeping rhizome. *Trichomanes superbum* was formerly placed in *Nesopteris*, based on sorus construction, although it is tentatively placed here in *Callistopteris* indicated by its vegetative features.

Among the Malesian species of subg. *Nesopteris*, *C. grande* is often misidentified as *Vandenboschia maxima*, especially when the rhizome is missing. Thus, it is rather doubtful to circumscribe the species in this way as defined by a specific sorus construction. The information currently available is too little to revise the systematics of this subgenus.

KEY TO THE SPECIES

1a. Abortive fronds present at base of normal fronds . . . . . **12. C. aphlebioides**
b. Abortive fronds absent 2
2a. Mouth of involucres truncate, ciliate . . . . . **15. C. thysanostomum**
b. Mouth of involucres more or less dilated, not ciliate 3

3a. Lips not so distinct, or diam. of mouth including lips between half and two-thirds the length of involucres . . . . . **13. C. grande**
b. Mouth of involucres distinctly dilated, diam. including lips similar to the length of involucres . . . . . **14. C. intermedium**

12. **Crepidomanes aphlebioides** (Christ) I.M.Turner

Crepidomanes aphlebioides (Christ) I.M.Turner, Asian J. Trop. Biol. 1 (1995) 26; C.W.Chen et al., Sol Amazing (2017) 112; K.Iwats. et al., PhytoKeys 119 (2019) 112. — *Trichomanes tenuissimum* Christ in K.Schum. & Lauterb., Fl. Schutzgeb. Südsee (1901) 106, nom. illeg., non Bosch (1861). — *Trichomanes aphlebioides* Christ in C.Chr., Index Filic. (1906) 635; Holttum, J. Malayan Branch Roy. Asiat. Soc. 6 (1928) 18, pl. 4; Rev. Fl. Malaya 2 (1955) 105, f. 42; Copel., Philipp. J. Sci. 51 (1933) 219, pl. 38, f. 5–8; Croxall, Austral. J. Bot. 23 (1975) 526. — *Vandenboschia aphlebioides* (Christ) Copel., Philipp. J. Sci. 67 (1938) 54; Tindale, Vict. Naturalist 71 (1955) 191. — Type: *Lauterbach 494* (holo P; iso L), Papua New Guinea.

Trichomanes pulcherrimum Copel., Philipp. J. Sci., C. 9 (1914) 227. — Lectotype (designated here): *Brooks 26S* (lecto MICH 1191090; isolecto P), Sumatra.

Rhizome long-creeping, often climbing on rocks and trees, 2.8–3.5 mm diam., irregularly branching, rather densely covered by hairs, glabrescent with age, bearing roots, aphlebia, and leaves; hairs dark brown, to 5 mm long, slender, hard in texture, remaining dust-like on rhizome after falling. *Aphlebiae* c. two between the adjacent leaves, shortly stalked or subsessile, pinnately divided as minute leaves, tri- to quadripinnate, oblong, with acute apex and cuneate base, c.10 cm long, 3 cm wide, but variable in size and form; rachis and pinna rachis distinctly winged, to 1.2 mm broad; pinnae shortly stalked, ascending; ultimate segments often bending, spreading in various directions resulting in somewhat cubic construction of aphlebiae, often elongate to 3–5 mm, setaceous, usually with only one row of laminar cells at each side of costae, 0.15–0.2 mm broad, entire, acute at apex. *Stipes* commonly 2–7 cm apart, stout, to 2.5 mm diam., very narrowly winged nearly to the base, stramineous and dark at the base, hairy at basal portion, glabrescent upwards or bearing minute hairs in very young leaves, usually much shorter than blades, often only 2 cm long or more commonly 15–25 cm long; blade quadripinnate to quasipinnatifid, oblong to oblong ovate, gradually narrowing toward acute to acuminate apex, round to broadly cuneate at base, often very large and c. 70 cm long, 25 cm wide; *rachis* like the upper part of stipes, winged; *lateral pinnae* 12–20 pairs, lower pinnae of larger leaves 4–5 cm apart, ascending, lanceolate to linear subtriangular, gradually narrowing towards acuminate or caudate apex, distinctly stalked and broadly cuneate at base, the largest one c. 20 cm long, 3.5 cm wide; *pinnules* narrowly oblong, more or less falcate, round to moderately acute at apex, cuneate at base, stalked in larger ones but sessile in distal smaller ones; secondary pinnules with several pinnate pinnae, rhomboid in outline in larger ones, round to moderately acute at apex; secondary pinnule rachis very broadly winged with less divided segments; larger tertiary pinnules less dissected, with ultimate segments distinct only in the apical portion; ultimate segments entire, round at apex, c. 0.4 mm broad, straight, or often bending. *Sori* solitary, on short basal acroscopic segments of tertiary pinnules, dispersing evenly over the surface of blades; *involucres* deeply cup-shaped, strongly dilated at mouth, 1.5–1.8 mm long, to 0.5 mm diam.; lips of mouth to 0.5 mm broad; receptacles long-extruded. — **Fig. 5i.**

Distribution — *Malesia*: Peninsular Malaysia, Sumatra, Borneo, Java, Moluccas and New Guinea; Admiralty Islands, Solomon Islands, Vanuatu, Fiji, Australia (NE Queensland).

Habitat & Ecology — Terrestrial in rocky valleys and creeping epiphyticly in dense forests in lowlands. Altitude: from sea level to 500 m.

Note — Peculiar small fronds having segments without laminar expansion are the first leaves on axillary branches of the rhizome and develop less to form the so-called aphlebia: the plants are thus heterophyllous.

13. Crepidomanes grande (Copel.) Ebihara & K.Iwats.

Crepidomanes grande (Copel.) Ebihara & K.Iwats. in Ebihara et al., Blumea 51 (2006) 239. — *Trichomanes grande* Copel., Philipp. J. Sci., C. 6 (1911) 70; Philipp J. Sci. 51 (1933) 224, pl. 40: f. 1–4. — *Nesopteris grandis* (Copel.) Copel., Philipp. J. Sci. 67 (1938) 66; Fern Fl. Philipp. 1 (1958) 76. — *Cephalomanes grande* (Copel.) K.Iwats., Acta Phytotax. Geobot. 35 (1984) 176. — Lectotype (designated here): *Copeland 1739* (lecto MICH 1191072; isolecto P), Philippines, Mindanao.

Trichomanes millefolium C.Presl, Abh. Königl. Böhm. Ges. Wiss., ser. 5, 3 (1843) 16, 43, nom. illeg., non Desv. (1828); Bosch, Hymenophyll. Javan. (1861) 27, pl. 20. — *Trichomanes preslianum* Nakai, Bot. Mag. (Tokyo) 40 (1926) 261. — Syntypes: *Cuming 162* (GH, L), Philippines.

Trichomanes elatum Bosch, Ned. Kruidk. Arch. 5(2) (1861) 177, nom. illeg., non G.Forst. (1786), nec Desv. (1827). — Lectotype (designated here): *Korthals s.n., '176'* (lecto L, 2 sheets, L3648227, L.3648228), Sumatra. Other syntypes: *Cuming 162* (GH, L), Philippines; *LaBik in H Webb* (L), Ambon; *Milne s.n.* (L), Fiji.

[*Trichomanes anceps* Wall. var. β: Hook., Sp. Fil. 1 (1846) 135, pl. 40C, f.3.]

Trichomanes roemerianum Rosenst., Nova Guinea 8 (1912) 717. — Syntypes: *von Roemer 773* (BO, L), New Guinea; *von Roemer 1138* (BO, L), New Guinea.

Trichomanes pseudoarbuscula Alderw., Nova Guinea 14 (1924) 57. — Lectotype (designated here): *Lam 1492* (lecto BO; isolecto L), New Guinea, Doormantop.

Rhizome short, erect, never becoming very tall, bearing several fronds in a tuft and many stout roots, the apex covered with hairs; roots more or less wiry, to 1 mm diam., irregularly branching, with dense dark brownish root hairs, often with muddy soil even on dried specimens; hairs dark brown, to 5 mm long, but commonly shorter, straight but not so thick-walled. *Stipes* terete in appearance and very narrowly winged throughout, dirty brownish, to 25 cm long, usually shorter than fronds, sparsely hairy with brownish hairs c. 2 mm long, rather densely pubescent with short brownish hairs of less than 0.5 mm long, caducous, glabrescent; *fronds* ovate-oblong to oblong, round to broadly cuneate at base, acute to acuminate at apex, 15–25 cm long, 10–15 cm wide, quadripinnate in larger ones; *rachis* like the upper part of stipes, becoming more slender upwards, distinctly winged, the wings to 0.7 mm broad on each side, caducously pubescent; *pinnae* more than 10 distinct pairs, lower ones more or less reduced or larger ones distinctly stalked, oblong to oblong subdeltoid, acute to acuminate at apex, to 12 cm long, 5 cm wide; pinna rachis usually bending upwards, winged throughout, caducously pubescent; larger *pinnules* narrowly oblong, round to moderately acute at apex, cuneate at stalked base 1.5–2.5(–4.5) cm long, 0.5–1 cm wide; pinnule rachis winged throughout with an appearance like the segments; *secondary pinnules* with 1–7 pinnately arranged segments; *ultimate segments* round to subtruncate at apex, entire, rarely bifurcate in larger secondary pinnules, commonly c. 0.5 mm broad, green to pale

green, more or less shaggy and easily broken when dried, often very densely pubescent underneath, hairs glandular, caducous. *Sori* at apex of basal acroscopic segments of secondary pinnules on upper pinnae, thus often in one row near pinna rachis; *involucres* campanulate, distinctly dilated at mouth usually with lips of more than 0.2 mm in width, 1.5–2 mm long, 0.6–0.8 mm diam. or c. 1 mm diam. at mouth; receptacles long-extruded. — **Fig. 5g, h.**

Distribution — *Malesia*: Sumatra, Java, Borneo, Philippines, Sulawesi, Moluccas (Ambon, Seram), New Guinea; Solomon Islands and Micronesia.

Habitat & Ecology — Epipetric on damp muddy cliffs and terrestrial, often near streams in evergreen hill forests. Altitude: low elevations to c. 1000 m.

Note — Plants from New Guinea have involucres more or less dilated at the mouth.

14. **Crepidomanes intermedium** (Bosch) Ebihara & K.Iwats.

Crepidomanes intermedium (Bosch) Ebihara & K.Iwats. in Ebihara et al., Blumea 51 (2006) 240; C.W.Chen et al., Sol Amazing (2017) 115; K.Iwats. et al., PhytoKeys 119 (2019) 112. — *Trichomanes intermedium* Bosch, Ned. Kruidk. Arch. 5(2) (1861) 179; J. Bot. Néerl. 1 (1861) 361; Copel., Philipp. J. Sci. 51 (1933) 226, pl. 40: f. 5. — *Nesopteris intermedia* (Bosch) Copel., Philipp. J. Sci. 67 (1938) 66. — Lectotype (designated here): *Wilkes Expedition (Brackenstock) 18* (lecto L 3583734; isolecto GH, P, US), Fiji.

Trichomanes millefolium C.Presl var. *anceps* Alderw., Malayan Ferns, Suppl. 1 (1921) 106. — Lectotype (designated here): *Lam 815* (lecto BO; isolecto L, SING), New Guinea. Other syntype: *Lam 1198* (BO, L, SING), New Guinea.

Trichomanes maximum Blume var. *grandiflorum* Rosenst., Repert. Spec. Nov. Regni Veg. 5 (1908) 371. — Syntypes: *Werner 51, Ros. Fil. Novog. no 7* (L, P), New Guinea.

Rhizome short, erect, not becoming very tall, bearing more or less stout roots below and several leaves near the apex, densely hairy at apex; hairs dull brown to darker, more or less appressed, to 5 mm long or more, straight but not thick-walled. *Stipes* terete, narrowly winged nearly towards the base, stramineous or deeply so, dark at base, sparsely hairy but glabrescent at base and upwards, shorter than blades but proportionately usually more than four-fifths of the blades, 15–20 cm long in leaves of standard size; *blades* quadripinnate to in larger leaves quasipinnatifid, oblong orbicular, round to moderately acute at apex, broadest at middle portion, round to subcordate at base, 20–35 cm long, 12–20 cm wide in the leaves of standard size; *rachis* like the upper part of stipes, winged throughout, densely covered with minute hairs when young, glabrous with age; hairs 0.2–0.4 mm long, pale brown, warty, caducous; pinnae oblong to lanceolate, broader in lower ones, gradually narrowing to acute apex, cuneate at base, shortly stalked; *pinna rachis* similar to rachis and thinner, winged throughout, minute hairy when young, glabrous with age, more or less in zigzag form especially at distal portion; *pinnules* oblong or narrowly so, ascending, round to moderately acute at apex, cuneate at very shortly stalked base; pinnule rachis stalked, placed with acute angle to pinna rachis, distinctly winged like the segments; secondary segments with one to several segments; *ultimate segments* often involute or recurved, mostly arranged in one plane, sometimes elongate to 5 mm or more long, 0.5 mm broad in standard size, entire, round or obtuse at apex, bearing dense small hairs in young leaves, glabrous with age. *Laminar cells* several rows at each side of midribs, more or less elongate in surface

view; *internal cell walls* thin. *Sori* solitary on very short basal acroscopic segments, nearly axial in appearance, thus usually near the axis of various leaves and dispersing over the whole surface of blades but not dense at marginal portion of blades, pinnae, and pinnules; *involucres* cup-shaped with distinctly dilated margin, 1.5–2 mm long, to 0.8 mm diam. excluding lips, the dilated lips 0.3–0.5 mm wide; receptacles long-extruded. Chromosome numbers: n = c. 36 (Braithwaite, Fern Gaz. 10 (1969) 82, Bot. J. Linn. Soc. 71 (1975) 170).

Distribution — *Malesia*: Moluccas (Seram, Ambon), New Guinea, Admiralty Islands; Solomon Islands, Fiji, and Samoa.

Habitat & Ecology — Terrestrial and epipetric, on clay banks and muddy rocks, usually along streams in dense forests. Altitude: lower elevations to 1600 m.

Notes — When the dilated mouth opens fully, its diam. including the width of the lips is nearly similar to the length of the involucres. In *C. grande*, however, the diam. of the mouth, including the dilated lips, measures between half to two-thirds the length of the involucres. In vegetative features, *C. intermedium* is not very distinct from *C. grande*.

Trichomanes millefolium var. *anceps* is a form with broader wings on the main axes, thicker texture of the laminae and more decidedly curved or bent ultimate segments. Studies are pending for this form, which is known only from the type collection.

15. Crepidomanes thysanostomum (Makino) Ebihara & K.Iwats.

Crepidomanes thysanostomum (Makino) Ebihara & K.Iwats. in Ebihara et al., Blumea 51 (2006) 240; J.X.Liu et al. in C.Y.Wu et al., Fl. China 2–3 (2013) 99. — *Trichomanes thysanostomum* Makino, Bot. Mag. (Tokyo) 12 (1898) 193 (in Japanese); Bot. Mag. (Tokyo) 13 (1899) 46; Ogata, Icon. Fil. Jap. 7 (1936) pl. 348. — *Nesopteris thysanostoma* (Makino) Copel., Philipp. J. Sci. 67 (1938) 66; Fern Fl. Philipp. 1 (1958) 77; J.L.Tsai & W.C.Shieh in H.L.Li et al., Fl. Taiwan 1 (1994) 122, pl. 45. — *Cephalomanes thysanostomum* (Makino) K.Iwats., J. Fac. Sci. Univ. Tokyo, Sect. 3, Bot. 13 (1985) 546. — Lectotype (designated by Iwatsuki (1985) 546): *Y. Tashiro s.n.* (lecto TI), Japan, Ryukyu.

Trichomanes blepharistomum Copel., Philipp. J. Sci. 51 (1933) 225, pl. 41. — *Nesopteris blepharistoma* (Copel.) Tagawa, J. Jap. Bot. 26 (1951) 186; K.Iwats., Acta Phytotax. Geobot. 17 (1958) 163. — *Nesopteris thysanostoma* (Makino) Copel. var. *blepharistoma* (Copel.) Seriz., J. Jap. Bot. 50 (1975) 15. — Type: *BS (Edaño) 79659* (holo MICH), Philippines, Luzon.

Rhizome short, suberect or slightly ascending, densely hairy at apex, bearing several fronds in tuft at apex, and many roots; roots dark, to 1 mm diam., irregularly branching, densely covered with dark root hairs, often with mud even in the dried specimens. *Stipes* dark brownish, winged nearly to the base, sparsely hairy, to 25 cm long; hairs dark brown, shining, multicellular, to 3 mm long, not articulated; *fronds* oblong to narrowly oblong, rarely ovate oblong, acute to acuminate at apex, gradually narrowing towards base, 30–50 cm long, 10–15 cm wide, quadripinnatifid to quadripinnate; *pinnae* in more than 12 alternate pairs, lower ones more or less reduced in size, larger ones narrowly oblong, gradually narrowing towards long acuminate apex, cuneate and distinctly stalked at base, to 12 cm long, 3 cm wide; pinna rachis nearly straight or more or less bending upwards, winged throughout, narrow near base and broader at distal portion taking an appearance of segments, upper pinnae becoming smaller upwards; larger *pinnules* distinctly stalked, narrowly oblong subdeltoid to rhomboid, acute to moder-

ately acute at apex, cuneate at base, 2–2.5(–3.5) cm long, 0.6–1 cm wide; *secondary pinnules* with 1–8 pinnately arranged segments; *ultimate segments* round to subtruncate at apex, entire, rarely bifurcate in larger secondary pinnules, green to pale green, rather rigid and easily broken when dried, pubescent underneath. *Sori* solitary at apex of short basal acroscopic segments of secondary pinnules, thus often in one row at each side near pinnule rachis; *involucres* campanulate, c. 2 mm long, 0.7 mm diam., distinctly stalked, the mouth truncate, often with distinct horns; receptacles long-extruded. Chromosome numbers: *2n* = 108 (Yoroi, J. Jap. Bot. 52 (1977) 211).

Distribution — Taiwan, Japan (S Ryukyu); in *Malesia*: Philippines (Luzon, Batan and Mindoro).

Habitat & Ecology — Terrestrial on wet clay slopes and epipetric on wet muddy rocks, often near streams in dense evergreen forests. Altitude: from low elevations to 800 m.

5. DIDYMOGLOSSUM

Didymoglossum Desv., Mém. Soc. Linn. Paris 6 (1827) 330; C.Presl, Abh. Königl. Böhm. Ges. Wiss., ser. 5, 3 (1843) 22, t. 8: f. A; Copel., Philipp. J. Sci. 67 (1938) 76; Gen. Fil. (1947) 42; Croxall, Austral. J. Bot. 23 (1975) 540; Ebihara et al., Blumea 51 (2006) 235. — *Trichomanes* L. sect. *Didymoglossum* (Desv.) T.Moore, Index Fil. (1857) cx; Wess.Boer, Acta Bot. Neerl. 11 (1962) 277. — *Trichomanes* L. subg. *Didymoglossum* (Desv.) C.Chr., Index Filic. (1906) xiv; C.V.Morton, Contr. U.S. Natl. Herb. 38 (1968) 190; Holttum, Rev. Fl. Malaya 2 (1955) 94; K.Iwats., Acta Phytotax. Geobot. 35 (1984) 175. — Type: *Didymoglossum muscoides* (Sw.) Desv.

Lecanium C.Presl, Abh. Königl. Böhm. Ges. Wiss., ser. 5, 3 (1843) 11, t. 1, nom. illeg., non Reinw. (1825); Copel., Philipp. J. Sci. 67 (1938) 79; Gen. Fil. (1947) 42. — *Hemiphlebium* C.Presl sect. *Lecanium* (C.Presl) Prantl, Unters. Morph. Gefässkrypt. 1 (1875) 46. — *Trichomanes* L. sect. *Lecanium* (C.Presl) Christ, Farnkr. Erde (1897) 25; C.V.Morton, Contr. U.S. Natl. Herb. 38 (1968) 192; K.Iwats., Acta Phytotax. Geobot. 35 (1984) 175. — *Lecanolepis* Pic.Serm., Webbia 28 (1973) 449. — Type: *Lecanium membranaceum* (L.) C.Presl (= *Didymoglossum membranaceum* (L.) Vareschi).

Microgonium C.Presl, Abh. Königl. Böhm. Ges. Wiss., ser. 5, 3 (1843) 19, t. 6: f. A, B; Bosch, Hymenophyll. Javan. (1861) 5; Copel., Philipp. J. Sci. 67 (1938) 61; Gen. Fil. (1947) 39; M.Nishida, J. Jap. Bot. 32 (1957) 154; Croxall, Austral. J. Bot. 23 (1975) 537. — *Hemiphlebium* C.Presl sect. *Microgonium* (C.Presl) Prantl, Unters. Morph. Gefässkrypt. 1 (1875) 46. — *Trichomanes* L. sect. *Microgonium* (C.Presl) Christ, Farnkr. Erde (1897) 24; Wess.Boer, Acta Bot. Neerl. 11 (1962) 277; C.V.Morton, Contr. U.S. Natl. Herb. 38 (1968) 191; K.Iwats., Acta Phytotax. Geobot. 35 (1984) 175. — *Trichomanes* L. subg. *Microgonium* (C.Presl) Holttum, Rev. Fl. Malaya 2 (1955) 91. — Type: *Microgonium cuspidatum* (Willd.) C.Presl (= *Didymoglossum cuspidatum* (Willd.) Ebihara & Dubuisson).

Hemiphlebium C.Presl, Abh. Königl. Böhm. Ges. Wiss., ser. 5, 3 (1843) 25, t. 9; C.V.Morton, Contr. U.S. Natl. Herb. 38 (1968) 200. — *Trichomanes* L. sect. *Hemiphlebium* (C.Presl) T.Moore, Index Fil. (1857) cx. — *Trichomanes* L. subg. *Hemiphlebium* (C.Presl) Christ, Farnkr. Erde (1897) 23. — *Trichomanes* L. subsect. *Hemiphlebium* (C.Presl) Alderw., Malayan Ferns (1908) 83. — Type species: *Hemiphlebium pusillum* (Sw.) C.Presl (= *Didymoglossum pusillum* (Sw.) Desv.).

Trichomanes auct. non L.: K.Iwats., Acta Phytotax. Geobot. 35 (1984) 175, emend.; in Kubitzki, Fam. Gen. Vasc. Pl. 1 (1990) 161.

Rhizome creeping, filiform, or in some American species ascending or erect, bearing roots or sometimes the roots regenerating; *fronds* simple, or in some American species

pinnatifid, pinnate or rarely bipinnate; *false veinlets* present or absent in some American species; hairs at margin of lobes (subg. *Didymoglossum*), thick-walled, brownish, persistent; *venation* catadromous, in one plane with epitactic sori; *involucres* tubular, the apex truncate or dilated; *receptacles* filiform, extruded beyond the mouth of involucres.

Distribution — More than 30 species are credited to *Didymoglossum*. About 15 of them are in the Old World, mostly in the tropics, 6 in *Malesia*. Detailed information on the distribution of the American species of *Didymoglossum* is given in Wessels Boer (1962).

Habitat & Ecology — Most of the Malesian species grow in moist places, usually near streamlets in dense forests at lower elevations and rarely in the mossy zone. There are epiphytic as well as epipetric species; most of the Malesian representatives are either on the surface of moist rocks or on tree trunks, often covering wide areas in the manner of bryophytes. *Didymoglossum tahitense* is very tightly appressed to the substrate and resembles a hepatic.

Morphology — *Didymoglossum* has nearly the same number of species in the Old World as in the New. The morphology of the American species was comprehensively treated by Wessels Boer (1962). Iwatsuki (Mem. Fac. Sci. Kyoto Univ., Ser. Biol. 7 (1978) 31–43) also made detailed observations on the morphology of *Didymoglossum* and compared it with *Crepidomanes*.

The roots are in many cases obsolete, substituted by rhizoids on the rhizomes. Critical embryological observations have not been made of the roots, although it is speculated that secondary adventitious roots do not develop. The rhizome of subg. *Didymoglossum* is wide-creeping, slender, thread-like, bearing hairs, rhizoids and, less commonly, roots. The inner structure of the rhizomes is typical of smaller species in the family, having a hymenophyllaceous protostele (Schneider, Bot. J. Linn. Soc. 132 (2000) 29–46).

The frond construction of subg. *Didymoglossum* is simple to, at most, deeply pinnatifid. The margin of the frond is entire, crenate, wavy, or lobed. Venation is rather difficult to trace, as it is often deformed in the simple fronds and mostly observed as catadromous.

False veinlets have been observed in all species of subg. *Didymoglossum*. The pattern of their distribution and histology was reported by Wessels Boer (1962) and Iwatsuki (1978). In most cases, the false veinlets are continuous with the true veins, and in this pattern of distribution the false veinlets are distinct from those of *Crepidomanes* sect. *Crepidomanes*. The histological construction is only veins without vascular bundles, or cells similar to those in true veins except for the tracheids and sieve elements.

The sori are solitary and terminal on the veins. Involucres are campanulate with a more or less dilated mouth. The receptacle more or less extrudes from the lips of the involucres.

Gametophytes — Yoroi (J. Jap. Bot. 67 (1992) 169–176) observed gametophytes and embryos of *D. tahitense*, although sexual regeneration in *Didymoglossum* was mostly studied in the New World species. *Didymoglossum petersii* is an example where gametophytes are separate from the sporophytes (Pinson et al., Amer. Fern J. 107 (2017) 257–264).

Taxonomy — According to the system of Copeland (1938), four genera have false veinlets. Among them, *Crepidomanes* is separated from the other three and placed by

itself. As the distribution pattern of the false veinlets is distinct in *Crepidomanes*, it may safely be separated from the other three even solely by this particular feature. Morton (1968) considered that *Microgonium*, *Didymoglossum* and *Lecanium* formed a closely related group and treated them as a distinct subgenus of *Trichomanes* s.lat. next to *Trichomanes* subg. *Trichomanes*. Based on cytological observations, Braithwaite (Bot. J. Linn. Soc. 71 (1975) 167–189) supported the union of these three taxa into a distinct genus, and molecular evidence supports this (Ebihara et al., Blumea 51 (2006) 221–280). Two subgenera are referred to *Didymoglossum*; both occur in Malesia.

KEY TO THE SUBGENERA

1a. Submarginal false veinlets absent; marginal hairs present or absent . . . . . **a.** subg. **Didymoglossum**
b. Submarginal false veinlets present; marginal hairs absent . . . . . **b.** subg. **Microgonium**

a. Subgenus **Didymoglossum**

Nomenclature and type: as the genus.

Rhizome slender, long-creeping, lacking roots, bearing rhizoids and hairs; *fronds* simple to pinnatifid, usually small in size; *false veinlets* usually connecting with true veins; *hairs* at margin of fronds, thick-walled, brownish, simple or fascicled, or lacking, *involucres* tubular with dilated mouth; receptacles filiform, extruded but not very long.

Distribution — About 20 species are recorded from the tropics of the New World; 4 species are recorded from *Malesia*.

KEY TO THE SPECIES

1a. Margin of fronds with hairs . . . . . **1. D. exiguum**
b. Margin of fronds glabrous 2
2a. Fronds sessile, peltate, undersurface bearing hairs along veins . . . **4. D. tahitense**
b. Fronds stipitate, attached at base (not peltate), undersurface glabrescent 3
3a. Fronds much less than 1 cm long, sterile ones circular to rounded-oblong, main veins sometimes obsolete near apex . . . . . **2. D. motleyi**
b. Fronds 1–2.5 cm long or longer, oblong to oblong-lanceolate, main veins usually distinct . . . . . **3. D. sublimbatum**

1. Didymoglossum exiguum (Bedd.) Copel.

Didymoglossum exiguum (Bedd.) Copel., Philipp. J. Sci. 67 (1938) 78; Croxall, Austral. J. Bot. 23 (1975) 540; Tagawa & K.Iwats. in Smitinand et al., Fl. Thailand 3 (1979) 96, f. 5–12. — *Hymenophyllum exiguum* Bedd., Ferns Brit. India 2 (1868) pl. 275. — *Trichomanes exiguum* (Bedd.) Baker in Hook. & Baker, Syn. Fil., ed. 2 (1874) 464; Copel., Philipp. J. Sci. 51 (1933) 205, pl. 32: f. 1, 2; Holttum, Rev. Fl. Malaya 2 (1955) 94: f. 31; Sledge, J. Linn. Soc. Bot. 60 (1968) 297; K.Iwats., J. Fac. Sci. Univ. Tokyo, Sect. 3, Bot. 13 (1985) 543. — Lectotype (designated by Croxall, Austral.

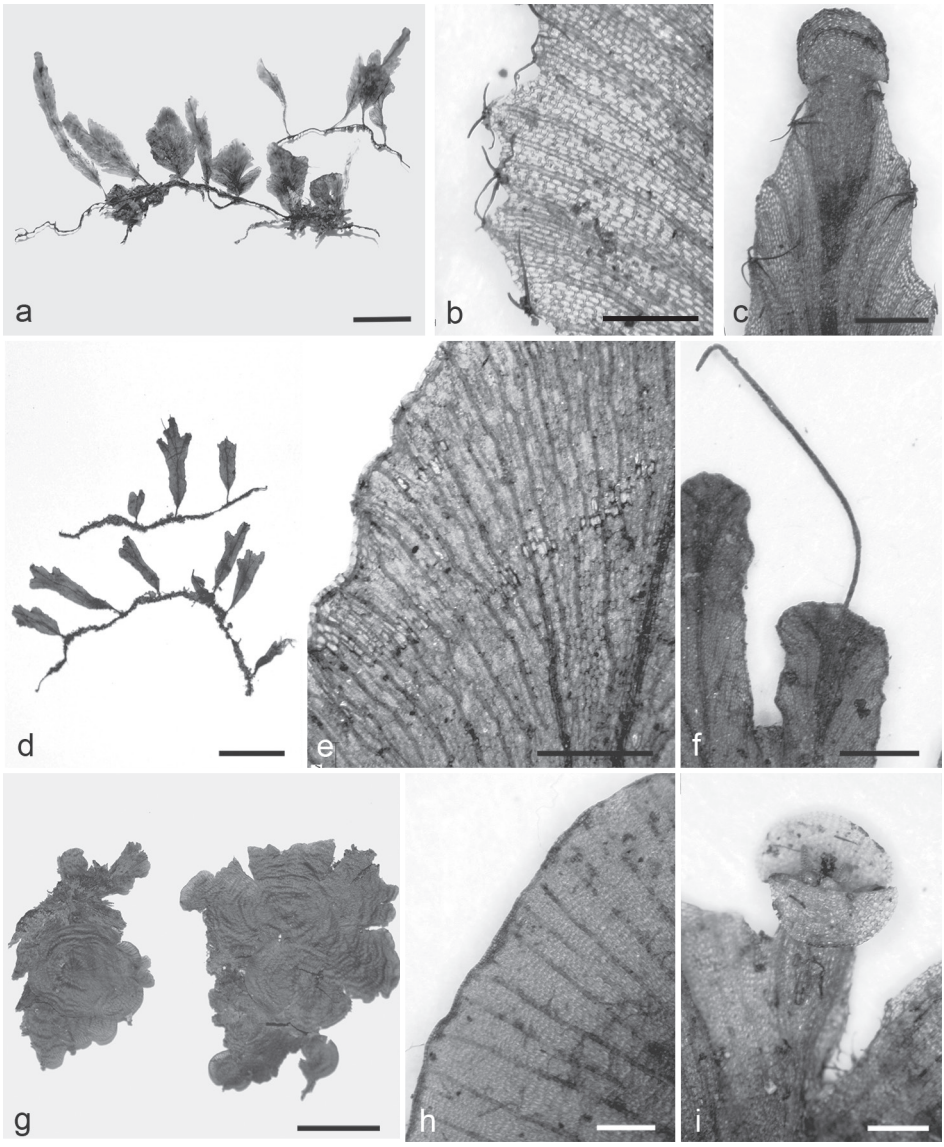

Fig. 6. a–c. *Didymoglossum exiguum* (Bedd.) Copel. a. Specimen; b. false veinlets and dark brown hairs at frond margin; c. sorus. — d–f. *D. bimarginatum* (Bosch) Ebihara & K.Iwats. d. Specimen; e. false veinlets; f. sorus. — g–i. *D. tahitense* (Nadeaud) Ebihara & K.Iwats. g. Specimen; h. false veinlets; i. sorus (a–c: *Tagawa et al. T5579*, Thailand, KYO; d–f: *Kato et al. C-2167*, Seram, Indonesia, TI; g–i: *Kato et al. C-4788*, Seram, Indonesia, TI).

J. Bot. 23 (1975) 540 as 'holotype'): *Beddome s.n.* (lecto K; isolecto BM), South India, Wynaad & Coorg.

Trichomanes paradoxum Domin, Biblioth. Bot. 20(85) (1913) 10, pl. 2: f. 4. — Type: *Domin 4* p.p. (PR n.v.), Australia, Bellenden Ker.

Rhizome long-creeping, on moist rocks, very slender, usually less than 0.1 mm diam., covered by dark brownish hairs, roots absent. *Stipes* c. 2 mm long, or less in sterile fronds, delicate, brownish to dark, often hairy at base; *fronds* simple; sterile ones ovate to ovate-lanceolate, with rounded base, entire, 3–5 mm long, 1–3 mm broad; fertile fronds lanceolate, oblanceolate, or narrowly elliptic, round at apex, round reniform, cuneate or attenuate at base, slightly crenulate at margin, to 7 mm long, 3 mm broad; *veins* simple, typically arriving at apex; *false veinlets* many, mostly joined to true veins like branches, simple or forked; hairs at apex of small crenulae at margin of frond, simple, geniculate, or fascicled, to 0.5 mm long, dark brown, thick-walled. *Sori* solitary at apex of fronds, more or less immersed, campanulate, c. 1.7 mm long including mouth, 0.5 mm diam., mouth bilabiate, lips c. 0.5 mm long, 0.8 mm broad, dark brown at edge, receptacles extruded. — **Fig. 6a–c.**

Distribution — Seychelles, Sri Lanka, South India, Thailand; in *Malesia*: Peninsular Malaysia (two collections); Australia (N Queensland).

Habitat — Epipetric on moist rocks, usually near streamlets in dense montane forests at lower elevation.

Note — *Didymoglossum exiguum* was collected in Malesia only at Ginting Simpah (*Holttum 28315*, K, SING) and near Lake Chenderon (*M. Allen 3095*, SING). As this tiny fern has been collected in various places infrequently, it is highly likely that more Malesian localities will be added in the future. A unique record from Australia is in a locality far from the next closest cite in Peninsular Malaysia, but is questionable (Field & Renner, Austral. Syst. Bot. 32 (2019) 111–122).

2. Didymoglossum motleyi (Bosch) Ebihara & K.Iwats.

Didymoglossum motleyi (Bosch) Ebihara & K.Iwats. in Ebihara et al., Blumea 51 (2006) 236; J.X.Liu et al. in C.Y.Wu et al., Fl. China 2–3 (2013) 107; Senterre et al., Phytotaxa 292 (2017) 201; K.Iwats. et al., PhytoKeys 119 (2019) 111. — *Trichomanes motleyi* Bosch, Ned. Kruidk. Arch. 5(2) (1861) 145; Hook. & Baker, Syn. Fil. (1867) 73; Copel., Philipp. J. Sci. 51 (1933) 201, pl. 30: f. 1–4; Tardieu & C.Chr. in Lecomte, Fl. Indo-Chine 7, 2 (1939) 61; Holttum, Rev. Fl. Malaya 2 (1955) 92, f. 30; Sledge, J. Linn. Soc. Bot. 60 (1968) 296; K.Iwats., J. Fac. Sci. Univ. Tokyo, Sect. 3, Bot. 13 (1985) 542. — *Microgonium motleyi* (Bosch) Bosch, Hymenophyll. Javan. (1861) 5, pl. 1; Copel., Fern Fl. Philipp. 1 (1958) 75; Croxall, Austral. J. Bot. 23 (1975) 538; Tagawa & K.Iwats. in Smitinand et al., Fl. Thailand 3 (1979) 94; J.L.Tsai & W.C.Shieh in H.L.Li et al., Fl. Taiwan 1 (1994) 118. — *Hemiphlebium motleyi* (Bosch) Prantl, Unters. Morph. Gefässkrypt. 1 (1875) 46. — Lectotype (designated by Field, Austral. Syst. Bot. 33 (2020) 21): *Motley 203* (lecto L 0051894; isolecto GH, K, L 0051895, MICH), Borneo.

Trichomanes beccarianum Ces., Felci (1876) 8, t. 1: f. 2.; Copel., Philipp. J. Sci. 51 (1933) 200, pl. 29. — *Microgonium beccarianum* (Ces.) Copel., Philipp. J. Sci. 67 (1938) 63; Fern Fl. Philipp. 1 (1958) 74; M.Nishida, J. Jap. Bot. 32 (1957) 155, f. 1; Ching, Fl. Reipubl. Popularis Sin. 2 (1959) 159, pl. 13: f. 8. — *Didymoglossum beccarianum* (Ces.) Senterre & Rouhan in Senterre et al., Phytotaxa 292 (2017) 210; C.W.Chen et al., Sol Amazing (2017) 121. — Lectotype (designated by Croxall, Austral. J. Bot. 23 (1975) 539 as 'holotype'): *Beccari s.n.* (lecto RO n.v.; isolecto BM, FI, K, MICH), Sarawak.

Trichomanes pannosum Ces., Rendiconto Accad. Napoli 16 (1877) 24, 28. — Syntypes: *Beccari s.n.* (FI, RO), Indonesia, New Guinea, Monte Arfak (Beccari collection so identified in K is *D. tahitense*.).

Trichomanes cognatum Ces., Rendiconto Accad. Napoli 16 (1877) 24, nom. illeg., non C.Presl (1843). — *Trichomanes motleyi* Bosch var. *cognatum* (Ces.) C.Chr., Index Fil. (1905) 637. — Type: *Beccari s.n.* (holo FI), Indonesia, New Guinea, Andai.

Trichomanes cultratum Baker, J. Bot. 17 (1879) 293; Copel., Philipp. J. Sci. 51 (1933) 202, pl. 30, f. 5–7. — *Microgonium cultratum* (Baker) Copel., Philipp. J. Sci. 67 (1938) 67. — Lectotype (designated by Croxall, Austral. J. Bot. 23 (1975) 539 as 'holotype'): *Horne 1078* (lecto K; isolecto GH, MICH), Fiji.

Trichomanes sayeri F.Muell. & Baker, Ann. Bot. (London) 5 (1891) 195. — Lectotype (designated by Tindale, Contr. New South Wales Natl. Herb., Fl. Ser. 201 (1963) 33 as 'holotype'): *Sayer s.n.* (lecto BRI; isolecto BM, K, MEL), Australia, Queensland.

Trichomanes minutissimum Alderw., Philipp. J. Sci., C. 11 (1916) 102, pl. 5: f. 1; K.I.Goebel, Flora 124 (1930) 397, f. 11–19. — Type: *C.B. Robinson 1944* p.p. (holo BO), Moluccas, Ambon.

Rhizome creeping on rocks and on the base of tree trunks, very slender, 0.1–0.2 mm diam., covered with blackish hairs, thus taking an appearance of c. 1 mm diam., or subglabrous, irregularly branching. *Stipes* invisible, to 1 mm in length, similar in appearance to rhizomes, covered with blackish hairs, very narrowly winged; *fronds* simple, variable in size and form, commonly round, or narrower or elongate, subcordate, rounded, cuneate, or attenuate at base, usually round at apex, subentire and flat except for soriferous portion, to 3 mm both in length and width; *veins* simple, reaching the apical margin only in fertile fronds; *false veinlets* many, submarginal veinlets absent, 2–6 rows of cells between false veinlets. *Sori* at terminal of simple veins, usually at deep cleft between apical lobes, thus extruded and without wings, campanulate, usually on 0.5–0.6 mm long stalks, commonly c. 1.5 mm long, 0.5 mm wide, with more or less dilated mouth c. 1 cm diam., receptacles extruded. Chromosome numbers: $n = 34$ (Manton & Sledge, Philos. Trans., Ser. B, 238 (1954) 136; Braithwaite, Fern Gaz. 10 (1969) 82).

Distribution — Seychelles, Sri Lanka, S India (Andaman Islands), Taiwan, Japan (S Ryukyu), continental SE Asia (Myanmar, Thailand and Vietnam); throughout *Malesia*; Micronesia, Melanesia, east to Fiji, and south to Australia (N Queensland).

Habitat & Ecology — On moist rocks and on the base of tree trunks, often near streamlets in moist dense forests at low elevations.

Note — *Trichomanes motleyi* and *T. beccarianum* were united by Holttum (1955) and Sledge (1968); *T. sayeri* was considered to be the same by Tindale (Contr. New South Wales Natl. Herb., Fl. Ser. 201 (1963) 33); and Croxall (1975) reduced *T. cultratum* to the *D. motleyi* species complex. A detailed description of the structure of these forms awaits further elucidation. The variation in the dwarf forms has often been postponed in comparative morphological studies. Senterre et al. (2017) revised the *D. motleyi* complex in their floristic study of the Seychelles. Their study covered the Malesian species and provided data suggesting subdivision of the complex to include several species as formerly proposed by Copeland (1933) and others. The actual classification of the Malesian species is, however, still difficult as we have insufficient data on the dwarf plants of this complex in the Old World tropics.

3. **Didymoglossum sublimbatum** (Müll.Berol.) Ebihara & K.Iwats.

Didymoglossum sublimbatum (Müll.Berol.) Ebihara & K.Iwats. in Ebihara et al., Blumea 51 (2006) 236; J.X.Liu et al. in C.Y.Wu et al., Fl. China 2–3 (2013) 107. — *Trichomanes sublimbatum* Müll. Berol., Bot. Zeitung (Berlin) 12 (1854) 737; Copel., Philipp. J. Sci. 51 (1933) 198, pl. 28: f. 1–2; Tardieu & C.Chr. in Lecomte, Fl. Indo-Chine 7, 2 (1939) 62; Holttum, Rev. Fl. Malaya 2 (1955) 92, f. 29; K.Iwats., J. Fac. Sci. Univ. Tokyo, Sect. 3, Bot. 13 (1985) 542. — *Microgonium sublimbatum* (Müll.Berol.) Bosch, Hymenophyll. Javan. (1861) 6, pl. 2; Tagawa & K.Iwats. in Smitinand et al., Fl. Thailand 3 (1979) 94. — *Hemiphlebium sublimbatum* (Müll.Berol.) Prantl, Unters. Morph. Gefässkrypt. 1 (1875) 46. — Lectotype (designated here): *Zollinger 865* (lecto B; isolecto K, MEL, P), Java.

Trichomanes papuanum Brause, Bot. Jahrb. Syst. 56 (1920) 32. — Lectotype (designated by Croxall, Kew Bull. 41 (1986) 523 as 'holotype'): *Ledermann 7835* (lecto B; isolecto BM 2 sheets), Papua New Guinea.

Trichomanes muscoides auct. non Sw.; Hook. & Baker, Syn. Fil. (1867) 75, p.p.

Rhizome long-creeping on rocks and on the base of tree trunks, very slender, 0.1–0.2 mm diam., densely covered with blackish hairs of 0.4–0.7 mm in length, thus having an appearance c. 1 mm diam. *Stipes* commonly to 4 mm long, but sometimes to 8 mm long, usually covered by the blackish hairs similar to those on rhizome, sometimes caducous; *fronds* simple, variable in form and size, lanceolate, oblong, subquadrangular, roundly obtriangular, oblong with dilated apical portion, or roundish, the base narrowly cuneate to round or subcordate, the apical portion and both sides flat or slightly undulate, subentire or more or less wavy, or lobed especially in fertile ones, 1–1.7 cm long, commonly to 0.7 cm, but rarely more than 1 cm in width; *veins* simple or branched, *false veinlets* numerous, usually continuous to true veins, 3–7 rows of cells between false veinlets, submarginal false veinlets absent. *Sori* solitary at apex of veinlets; *involucres* campanulate, c. 2 mm long, gradually expanding to the mouth of 1.5–2 mm diam., usually with broad wings forming lobes; receptacles extruded, not very long.

Distribution — India (Assam), China (Yunnan, Guizhou, Guangxi), Myanmar, Thailand, Vietnam; throughout *Malesia*.

Habitat & Ecology — Epipetric on wet rocks and epiphytic on the base of tree trunks; usually in dense gloomy forests. Altitude: lower elevations to 1500 m.

4. **Didymoglossum tahitense** (Nadeaud) Ebihara & K.Iwats.

Didymoglossum tahitense (Nadeaud) Ebihara & K.Iwats. in Ebihara et al., Blumea 51 (2006) 236; J.X.Liu et al. in C.Y.Wu et al., Fl. China 2–3 (2013) 107; C.W.Chen et al., Sol Amazing (2017) 123; K.Iwats. et al., PhytoKeys 119 (2019) 111. — *Trichomanes tahitense* Nadeaud, Énum. Pl. Tahiti (1873) 18; K.Iwats., J. Fac. Sci. Univ. Tokyo, Sect. 3, Bot. 13 (1985) 541. — *Microgonium tahitense* (Nadeaud) Tindale, Contr. New South Wales Natl. Herb., Fl. Ser. 201 (1963) 4, pl. 5: f. 3; Croxall, Austral. J. Bot. 23 (1975) 539. — Type: *Nadeaud s.n.* (holo P n.v.), Tahiti.

Trichomanes peltatum Baker, J. Linn. Soc. 9 (1866) 336, pl. 8, f. C, nom. illeg., non Poir. (1808); Hook. & Baker, Syn. Fil. (1867) 73. — *Hemiphlebium peltatum* (Baker) Luerss., Bot. Centralbl. 3(11) (1882) 28. — Lectotype (designated by Croxall, Austral. J. Bot. 23 (1975) 539): *Powell 125* (lecto K; isolecto GH, MICH), Samoa.

Microgonium omphalodes Vieill. ex E.Fourn., Ann. Sci. Nat., Bot. sér. 5, 18 (1873) 255, nom. illeg.; Ching, Fl. Reipubl. Popularis Sin. 2 (1959) 158, pl. 13: f. 3–6; J.L.Tsai & W.C.Shieh in H.L.Li et al., Fl. Taiwan 1 (1994) 119, pl. 43. — *Trichomanes omphalodes* (Vieill. ex E.Fourn.) C.Chr., Index Filic. (1906) 646; Copel., Philipp. J. Sci. 51 (1933) 203, pl. 31: f. 1–6; Ogata, Icon. Fil. Jap.

5 (1933) pl. 248. — Syntypes: *Deplanche 175* (P), New Caledonia; *Powell 128* (K n.v.), Samoa; *Vieillard 2166* (GH, P? n.v.), New Caledonia.

Rhizome long-creeping, filiform, 0.2–0.3 mm diam., densely covered with long dark brownish hairs, thus appearing to be more than 1 mm diam., irregularly branching, attached tightly on rock surfaces or on tree trunks. *Fronds* sessile, peltately attached to the rhizome nearly at the center, circular or orbicular in outline, commonly 1–3 cm diam., continuously growing marginally, often becoming larger in size, thin, attached tightly to substratum especially with the hairs on the undersurface of veins, margin entire, wavy or notched, the surface flat or more or less wavy; *veins* seemingly dichotomous, in fact a first few times divided pinnately with lateral branches very close, then distal portion dichotomous, arriving at the very margin of fronds; *false veinlets* branched off from the true veins or less often independent from them, in most cases arriving at the frond margin, rather densely placed, with 3–6 rows of cells between adjacent false veinlets, densely hairy on the lower surface. *Sori* at end of veinlets, often at the bottom of small notches, many at margin of fronds; *involucres* campanulate, more or less immersed or free, to 4 mm long, 1–1.5 mm diam., the mouth distinctly dilated. — **Fig. 6g–i.**

Distribution — Vietnam, Taiwan, S Japan (Ryukyu and Bonin); in *Malesia*: Java, Borneo, Moluccas (Seram), New Guinea; Polynesia, Micronesia, Melanesia, south to Australia (NE Queensland).

Habitat & Ecology — On moist rocks and on moist tree trunks in dense montane forests; commonly along or near rivers; tightly attaching to the substrate. Altitude: from lowlands to 600 m.

Notes — *Didymoglossum tahitense* is morphologically distinct from other species in subg. *Didymoglossum* in the growth habit with unlimited meristem, circular sessile fronds with peltate construction, fronds tightly attached to the substrate and with numerous hairs on the (true and false) veins on the abaxial surface. These features are all distinct from a morphological point of view and indicate the distinctness of *D. tahitense* from other members of the subgenus.

This widespread species has never been recorded from Sumatra and the Philippines.

b. Subgenus **Microgonium**

Didymoglossum Desv. subg. *Microgonium* (C.Presl) Ebihara & K.Iwats. in Ebihara et al., Blumea 51 (2006) 236. — *Microgonium* C.Presl, Abh. Königl. Böhm. Ges. Wiss., ser. 5, 3 (1843) 19, pl. 6: f. A–B; Copel., Philipp. J. Sci. 67 (1938) 61; Gen. Fil. (1947) 39. — Type: *Didymoglossum cuspidatum* (Willd.) Ebihara & K.Iwats.

Rhizome long-creeping, filiform, to 0.5 mm diam., deeply covered with dark hairs, root absent; *stipes* often quite reduced to 1 cm; *fronds* usually simple, or sometimes lobed to pinnatifid, to 3 by 2 cm, venation catadromous, continuous submarginal false veinlets present, longitudinal false veinlets parallel to the true veins present; *sori* epitactic or pantotactic, often immersed in the laminae, tubular, lips often dilate, receptacles extruded.

Distribution — About 10 species in the tropics of the Old World, Africa to Polynesia, two species in *Malesia*; 4 species by definition are known in the tropics of the New World.

Taxonomy — *Microgonium* was formerly defined as a group of species with dwarf, simple fronds bearing false veinlets and without stiff hairs at the margin of the fronds. The absence of marginal hairs separated *Microgonium* from *Didymoglossum*, which has marginal hairs. Four American species were referred to *Microgonium* by definition. They are very similar to species of *Didymoglossum* in most features except for the presence of marginal hairs. The presence of marginal hairs was thought to be an important character when *Didymoglossum* was defined, although *Didymoglossum* is here re-defined to include species without marginal hairs. The discrimination of the two subgenera under *Didymoglossum* is rather obvious, although the species included in subg. *Microgonium* have submarginal false veinlets. Thus defined, there are about 10 species included here.

Copeland (Philipp. J. Sci. 67 (1938) 61; Gen. Fil. (1947) 40) related his *Microgonium* to *Crepidomanes* s.str., and considered that the former had evolved from the latter by dwarfing of the fronds.

Tagawa & Iwatsuki (S.E. Asian Stud. 5 (1967) 39; Acta Phytotax. Geobot. 26 (1975) 169) referred *M. minutifolium* and *M. parvifolium* to *Microgonium* based on the simple construction of their fronds. As noted in Iwatsuki (Mem. Fac. Sci. Kyoto Univ., Ser. Biol. 7 (1978) 37, 42), the distribution pattern of false veinlets in these species is distinctly the *Crepidomanes* type, and the simple-fronded *T. parvifolium* is undoubtedly derived by reduction in frond size from a species of *Crepidomanes*. By differences in the distribution pattern of the false veinlets, *Trichomanes* subg. *Didymoglossum* can be distinguished from *Crepidomanes* subg. *Crepidomanes* only by phenetic features.

As usual with extremely small forms, species of subg. *Microgonium* are often variable, especially in the form and size of the fronds. Various names have been given to various local forms, and a variety of forms may better be noted here to show the variability within species.

KEY TO THE SPECIES

1a. Veins and false veinlets numerous, usually more than 5 per 1 mm; lobes not distinct at apical portion of frond . . . . . **5. D. bimarginatum**

b. Veins and false veinlets rather sparse, usually 2 or 3 per 1 mm; distinct lobes present at apical portion of frond . . . . . **6. D. mindorense**

5. Didymoglossum bimarginatum (Bosch) Ebihara & K.Iwats.

Didymoglossum bimarginatum (Bosch) Ebihara & K.Iwats. in Ebihara et al., Blumea 51 (2006) 236; J.X.Liu et al. in C.Y.Wu et al., Fl. China 2–3 (2013) 106; K.Iwats. et al., PhytoKeys 119 (2019) 111. — *Trichomanes bimarginatum* Bosch, Ned. Kruidk. Arch. 5(2) (1861) 143; Copel., Philipp. J. Sci. 51 (1933) 208, pl. 33: f. 1–4; Holttum, Rev. Fl. Malaya 2 (1955) 92; Sledge, J. Linn. Soc. Bot. 60 (1968) 296; K.Iwats., J. Fac. Sci. Univ. Tokyo, Sect. 3, Bot. 13 (1985) 543. — *Microgonium bimarginatum* Bosch, Hymenophyll. Javan. (1861) 7; Ann. Sci. Nat., Bot. sér. 4, 15 (1861) 91; Copel., Philipp. J. Sci. 67 (1938) 61; Croxall, Austral. J. Bot. 23 (1975) 537; Tagawa & K.Iwats. in Smitinand et al., Fl. Thailand 3 (1979) 95; J.L.Tsai & W.C.Shieh in H.L.Li et al., Fl. Taiwan 1 (1994) 118. — *Hemiphlebium bimarginatum* (Bosch) Luerss., Bot. Centralbl. 3(9) (1882) 439. — Lectotype (designated by Croxall (1975) 537, see Field, Austral. Syst. Bot. 33 (2020) 20): *Thwaites CP 2986* (lecto L; isolecto BM, GH, K, P 3 sheets, PDA, S), Sri Lanka.

Trichomanes neilgherrense Bedd., Ferns S. India (1863) pl. 6; Hook. & Baker, Syn. Fil. (1867) 74; Bedd., Handb. Ferns Brit. India (1883) 37. — Type: *Herb. Beddome s.n.* (holo BM; iso K), India, Nilgiris.

Rhizome long-creeping on rocks or rarely on basal tree trunks, filiform, usually less than 0.3 mm diam., densely covered with blackish rhizoids, giving appearance of thickness sometimes to 1.2 mm. *Stipes* commonly to 3 mm diam., densely covered by hairs, becoming blackish with age, often with decurrent base of laminae resembling wings; *fronds* simple, variable in size and form, round, oblong, or with broader apical portion, the base cuneate, round, or subtruncate, rarely cordate, apical portion to both sides more or less undulate, subentire to variously lobed especially in fertile ones, to 1.5 cm long, 0.2–1 cm broad for the fronds more than 1 cm in length; *veins* simple or with several branches, with many false veinlets usually joining the true veins, usually more than 5 per 1 mm, 2–5 rows of cells between the false veinlets, submarginal false veinlets continuous. *Sori* solitary at apex of veinlets, usually forming lobes with broad wings, campanulate, c. 2 mm long, 0.5 mm diam., with dilated mouth to 1.5 mm diam., receptacles extruded. Chromosome number: $n = 68$ (Vessey & Barlow, Proc. Linn. Soc. New South Wales 88 (1963) 303; Braithwaite, Bot. J. Linn. Soc. 71 (1975) 170). — **Fig. 6d–f.**

Distribution — Sri Lanka, India, Myanmar, Thailand, Taiwan, Japan (S Ryukyu); throughout *Malesia*; Micronesia, Melanesia, Polynesia, east to Samoa, and south to Australia (Queensland).

Habitat & Ecology — Epipetric or epiphytic, on the surface of rocks and on the basal part of tree trunks, usually in dense forests at various elevations.

6. Didymoglossum mindorense (Christ) K.Iwats.

Didymoglossum mindorense (Christ) K.Iwats. in Ebihara et al., Blumea 51 (2006) 236; C.W.Chen et al., Sol Amazing (2017) 122. — *Trichomanes mindorense* Christ, Philipp. J. Sci., C. 3 (1908) 270; Copel., Philipp. J. Sci. 51 (1933) 209, pl. 34: f. 1–2. — *Microgonium mindorense* (Christ) Copel., Philipp. J. Sci. 67 (1938) 61; Fern Fl. Philipp. 1 (1958) 74; Croxall, Austral. J. Bot. 23 (1975) 537. — Lectotype (designated by Croxall 1975, see Field (Austral. Syst. Bot. 33 (2020) 21): *Merrill 6066* (lecto P; isolecto GH, K, MICH, US), Philippines, Mindoro.

Trichomanes craspedoneurum Copel., Philipp. J. Sci., C. 7 (1912) 53; Philipp. J. Sci. 51 (1933) 208, pl. 33: f. 5–7. — *Microgonium craspedoneurum* (Copel.) Copel., Philipp. J. Sci. 67 (1938) 61; Fern Fl. Philipp. 1 (1958) 74; M.Nishida, J. Jap. Bot. 32 (1957) 156, f. 3, pl. 1c. — Type: *J.B. Leiburg s.n.* (holo US 593183), Philippines, Luzon.

Rhizome long-creeping, slender but more or less wiry, 0.1–0.2 mm diam., densely covered by dark brown to blackish hairs, thus having the appearance of a thicker diam. *Stipes* short, to 5 mm long, slender but stout, more or less densely hairy, very narrowly winged nearly to the base; *fronds* simple, deeply lobed at margin in the upper part, and the lobed upper portion becoming wider, narrowly cuneate to long-attenuate to shortly stiped, commonly c. 2 cm both in length and width; lobes to 5 mm long, 2–3 mm broad, round at apex, entire, commonly slightly wider near the base; *veins* rather lax, true veins pinnately branched, *false veinlets* branched from true veins, variable in number, few and inconspicuous, usually 2 or 3 per 1 mm, or many and evident, all connected with an intramarginal strand that is continuous along the margin of fronds leaving two rows

of cells outside of it. *Sori* at margin of upper portion of fronds, 1–5(–8) on each frond; *involucres* tubular, immersed in the frond margin, commonly c. 2 mm long, mouth dilated, round; receptacles slender, extruded.

Distribution — *Malesia*: Borneo, Philippines and New Guinea; Admiralty Islands, Solomon Islands and Australia (NE Queensland).

Habitat & Ecology — Epipetric and epiphytic on moist rocks and near the base of tree trunks, usually in gloomy dense forests. Altitude: at low elevations, to 600 m.

Note — *Didymoglossum mindorense* is distinguished from *D. bimarginatum* as noted in the key to the species, although the distinction requires further study as *D. bimarginatum* is variable and often some plants can hardly be identified to either of them. *Didymoglossum mindorense* and *Trichomanes craspedoneurum* were distinguished by differences in size. The former is more slender and longer, although it was impossible to find any particular feature to discriminate these two forms.

6. HYMENOPHYLLUM

Hymenophyllum Sm., Mém. Acad. Roy. Sci. Turin 5 (1793) 418; Copel., Philipp. J. Sci. 64 (1937) 77; Philipp. J. Sci. 68 (1938) 37; Gen. Fil. (1947) 34; C.V.Morton, Contr. U.S. Natl. Herb. 38 (1968) 153; K.Iwats., Acta Phytotax. Geobot. 35 (1984) 170; in Kubitzki, Fam. Gen. Vasc. Pl. 1 (1990) 159, f. 83 C–E; Ebihara et al., Blumea 51 (2006) 226. — Lectotype (designated by Presl, Abh. Königl. Böhm. Ges. Wiss., ser. 5, 3 (1843) 31): *Hymenophyllum tunbrigense* (L.) Sm.

Cardiomanes C.Presl, Abh. Königl. Böhm. Ges. Wiss., ser. 5, 3 (1843) 12; Copel., Gen. Fil. (1947) 37. — Type: *Cardiomanes reniforme* (G.Forst.) C.Presl (= *Hymenophyllum nephrophyllum* Ebihara & K.Iwats.).

Meringium C.Presl, Abh. Königl. Böhm. Ges. Wiss., ser. 5, 3 (1843) 24, t. 8 B; Copel., Philipp. J. Sci. 67 (1938) 39; Gen. Fil. (1947) 35. — Type: *Meringium meyenianum* C.Presl (= *Hymenophyllum serrulatum* (C.Presl) C.Chr.).

Leptocionium C.Presl, Abh. Königl. Böhm. Ges. Wiss., ser. 5, 3 (1843) 26, t. 9: f. D; Copel., Gen. Fil. (1947) 36. — Type: *Leptocionium dicranotrichum* C.Presl (= *Hymenophyllum dicranotrichum* (C.Presl) Sadeb.).

Myrmecostylum C.Presl, Abh. Königl. Böhm. Ges. Wiss., ser. 5, 3 (1843) 27, t. 10: f. A. — Type: *Myrmecostylum tortuosum* (Hook. & Grev.) C.Presl (= *Hymenophyllum tortuosum* Hook. & Grev.).

Ptychophyllum C.Presl, Abh. Königl. Böhm. Ges. Wiss., ser. 5, 3 (1843) 28, t. 11: f. E. — Type: *Ptychophyllum plicatum* (Kaulf.) C.Presl (= *Hymenophyllum plicatum* Kaulf.).

Hymenophyllum Sm. subg. *Craspedophyllum* C.Presl, Abh. Königl. Böhm. Ges. Wiss., ser. 5, 3 (1843) 33. — *Craspedophyllum* (C.Presl) Copel., Philipp. J. Sci. 67 (1938) 27; Gen. Fil. (1947) 33. — Type species: *Craspedophyllum marginatum* (Hook. & Grev.) Copel. (= *Hymenophyllum marginatum* Hook. & Grev.).

Sphaerocionium C.Presl, Abh. Königl. Böhm. Ges. Wiss., ser. 5, 3 (1843) 33, t. 4: f. B, 10: f. B–C; Copel., Philipp. J. Sci. 67 (1938) 28; Gen. Fil. (1947) 33; K.Iwats., J. Fac. Sci. Univ. Tokyo, Sect. 3, Bot. 13 (1982) 207; Acta Phytotax. Geobot. 35 (1984) 173; in Kubitzki, Fam. Gen. Vasc. Pl. 1 (1990) 160. — *Hymenophyllum* Sm. sect. *Sphaerocionium* (C.Presl) C.Chr., Index Filic. (1906) xv; C.V.Morton, Contr. U.S. Natl. Herb. 29 (1947) 139. — *Hymenophyllum* Sm. subg. *Sphaerocionium* (C.Presl) C.Chr., Index Filic., Suppl. 3 (1934) 5; Copel., Philipp. J. Sci. 64 (1937) 164; C.V.Morton, Contr. U.S. Natl. Herb. 38 (1968) 168. – Lectotype (designated by Copeland (1938) 28): *Sphaerocionium hirsutum* (L.) C.Presl (= *Hymenophyllum hirsutum* (L.) Sw.).

Hymenoglossum C.Presl, Abh. Königl. Böhm. Ges. Wiss., ser. 5, 3 (1843) 35; Copel., Gen. Fil. (1947) 37. — Type: *Hymenoglossum cruentum* (Cav.) C.Presl (= *Hymenophyllum cruentum* Cav.).

Trichomanes L. sect. *Pleuromanes* C.Presl, Epimel. Bot. (1851) 17. — *Pleuromanes* (C.Presl) C.Presl, Epimel. Bot. (1851) 258; Copel., Philipp. J. Sci. 67 (1938) 55; Gen. Fil. (1947) 38. — Type: *Pleuromanes acutum* (C.Presl) C.Presl (= *Hymenophyllum pallidum* (Blume) Ebihara & K.Iwats.).

[*Amphipterum* C.Presl, Epimel. Bot. (1851) 258, nom. nud.] — *Hymenophyllum* Sm. subg. *Amphipterum* Copel., Philipp. J. Sci. 64 (1937) 68. — *Amphipterum* (Copel.) Copel., Philipp. J. Sci. 67 (1938) 46; Gen. Fil. (1947) 35. — Type: *Amphipterum fuscum* (Blume) C.Presl (= *Hymenophyllum fuscum* (Blume) Bosch).

[*Dermatophlebium* C.Presl, Epimel. Bot. (1851) 258, nom. nud. — *Hymenophyllum* Sm. sect. *Dermatophlebium* C.Chr., Index Filic. (1906) xv, nom. nud.]

[*Leucomanes* C.Presl, Epimel. Bot. (1851) 258, nom. nud.]

[*Mecodium* C.Presl, Epimel. Bot. (1851) 258, nom. nud.] — *Hymenophyllum* Sm. subg. *Mecodium* Copel., Philipp. J. Sci. 64 (1937) 93. — *Mecodium* (Copel.) Copel., Philipp. J. Sci. 67 (1938) 17; Gen. Fil. (1947) 33. — Type: *Mecodium polyanthos* (Sw.) Copel. (= *Hymenophyllum polyanthos* (Sw.) Sw.).

Pachyloma Bosch, Verslagen Meded. Afd. Natuurk. Kon. Akad. Wetensch. 11 (1861) 318, nom. illeg., non DC. (1828). — Type: *Pachyloma marginatum* (Hook. & Grev.) Bosch (= *Hymenophyllum marginatum* Hook. & Grev.).

Serpyllopsis Bosch, Verslagen Meded. Afd. Natuurk. Kon. Akad. Wetensch. 11 (1861) 318; Copel., Gen. Fil. (1947) 37. — Type: *Serpyllopsis caespitosa* (Gaudich.) C.Chr. (= *Hymenophyllum caespitosum* Gaudich.).

Craspedoneuron Bosch, Verslagen Meded. Afd. Natuurk. Kon. Akad. Wetensch. 11 (1861) 322; Copel., Philipp. J. Sci. 67 (1938) 14. — *Trichomanes* L. sect. *Craspedoneuron* (Bosch) Prantl, Unters. Morph. Gefässkrypt. 1 (1875) 52. — Lectotype (designated by Copeland (1938) 14): *Craspedoneuron album* (Blume) Bosch (= *Hymenophyllum pallidum* (Blume) Ebihara & K.Iwats.).

Diploöphyllum Bosch, Verslagen Meded. Afd. Natuurk. Kon. Akad. Wetensch. 11 (1861) 322. — Lectotype (designated by Christensen, Index Filic. (1906) xv): *Diplophyllum dilatatum* (G.Forst.) Bosch (= *Hymenophyllum dilatatum* (G.Forst.) Sw.).

Gonocormus Bosch sect. *Microtrichomanes* Mett. ex Prantl, Unters. Morph. Gefässkrypt. 1 (1875) 51. — *Microtrichomanes* (Mett. ex Prantl) Copel., Philipp. J. Sci. 67 (1938) 35; Gen. Fil. (1947) 34. — Type: *Microtrichomanes digitatum* (Sw.) Copel. (= *Hymenophyllum digitatum* (Sw.) Fosberg).

Hymenophyllum Sm. subg. *Hemicyatheon* Domin, Biblioth. Bot. 20(85) (1913) 20. — *Hemicyatheon* (Domin) Copel., Philipp. J. Sci. 67 (1938) 27; Gen. Fil. (1947) 33. — Type: *Hemicyatheon baileyanum* (Domin) Copel. (= *Hymenophyllum baileyanum* Domin).

Hymenophyllum Sm. subg. *Buesia* C.V.Morton, Bot. Gaz. 93 (1932) 336. — *Buesia* (C.V.Morton) Copel., Philipp. J. Sci. 67 (1938) 47; Gen. Fil. (1947) 36. — Type: *Buesia mirifica* (C.V.Morton) Copel. (= *Hymenophylllum mirificum* C.V.Morton).

Hymenophyllum Sm. subg. *Myriodon* Copel., Philipp. J. Sci. 64 (1937) 73. — *Myriodon* (Copel.) Copel., Philipp. J. Sci. 67 (1938) 47; Gen. Fil. (1947) 35. — Type: *Myriodon odontophyllus* (Copel.) Copel. (= *Hymenophyllum brassii* C.Chr.).

Hymenophyllum Sm. subg. *Apteropteris* Copel., Philipp. J. Sci. 64 (1937) 176. — *Apteropteris* (Copel.) Copel., Philipp. J. Sci. 67 (1938) 34; Gen. Fil. (1947) 34. — Type: *Apteropteris malingii* (Hook.) Copel. (= *Hymenophyllum malingii* (Hook.) Mett.).

Rosenstockia Copel., Gen. Fil. (1947) 36. — Type: *Rosenstockia rolandi-principis* (Rosenst.) Copel. (= *Hymenophyllum rolandi-principis* Rosenst.).

Rhizome long-creeping, filiform or wiry, glabrous or sparsely covered with brown hairs; *fronds* pinnately compound, seemingly digitate or simple; *veins* all free, anadromous, uninervate in ultimate segments (or with a few veinlets in *H. rolandi-principis*); *lamina*e unistratose or 2–4 cells thick in some particular species; *sori* solitary at terminal at ultimate segments, paratactic; *involucres* valvate or tuberous with bilabiate mouth with more or less cleft lips; receptacles capitate, clavate, to filiform, included in the valves, or exserted. Chromosome numbers: various, $x = 11–36$.

Distribution — Ten subgenera are recognized and more than 350 species are known throughout the area of this family (Ebihara et al. 2006). Five of the 10 subgenera, including 63 species, are present in *Malesia*.

Habitat & Ecology — Most of the species of *Hymenophyllum* are epiphytic or epipetric with long-creeping rhizomes. Their habitat is usually in the mossy zone and in places where atmospheric humidity is comparatively high. When the environment around them becomes dry, the plants dry and often shrink, but they extend their fronds when humidity returns. In such dry conditions, they can survive for very long times, even for several weeks, and in this way they are resistant to drought, somewhat like the habit of mosses. In general, Hymenophyllaceae typically have unistratose laminae, and no intercellular spaces have been observed, even in laminae of more than one cell thick. It is therefore fairly difficult for *Hymenophyllum* to maintain humidity within the plant body.

Morphology — *Hymenophyllum* is rather broadly defined and exhibits diverse morphological features.

The rhizomes are mostly long-creeping, wiry, less hairy except very young portions. They are slender, usually to 2 mm diam., dorsiventral, with subcollateral protostele, the roots being few and fine. The long rhizomes often intermingle, thus forming a mat of fronds on tree trunks and on rocks, giving the appearance of mosses.

Fronds are medium to small; the longest ones, as in *H. longifolium*, attain a length of 50 cm. The smaller ones, as observed in fully mature plants of *H. lobbii*, have fronds at most 1.5 cm in length. Fully mature fronds in other genera of Hymenophyllaceae (e.g., *Didymoglossum*) are less than 1 cm long, and some fronds are simple. In *Hymenophyllum*, however, even simple fronds, as in *H. nephrophyllum*, are more than 10 cm diam. Most species have a pinnate dissection, although the fronds of some species have a digitate appearance, as in *H. digitatum*.

The stipe and rachis are winged or not, and wings can be flat or crisped, entire or dentate. The laminae are mostly unistratose, but in some cases more than one layer of cells have been observed. Even in multistratose laminae, however, intercellular spaces are never observed. Cell walls are thin and straight or more or less thickened and coarsely pitted.

Sori are solitary at the apex of the ultimate segments. Involucres are bivalvate or campanulate with bilobed lips; or the lips of the involucre are divided nearly to the middle or even nearly to the base. The receptacle is capitate or clavate and included or long-extruded beyond the edge of the lips.

Gametophytes — The general morphology of the gametophytes of *Hymenophyllum* are ribbon-like. Observations of the gametophytes of *Hymenophyllum*, totalling c. 30 species, were made by, e.g., Stokey (Bot. Gaz. 101 (1940) 759–790, Bot. Gaz. 109 (1948) 363–380); Atkinson (Phytomorphology 10 (1960) 26–36); Yoroi (Sci. Rep. Tokyo Kyoiku Daigaku, Sect. B. 15 (1972) 81–110).

Taxonomy — *Hymenophyllum* was broadly treated in Christensen (1906) and the Old World species in Copeland's classical paper in 1937. Copeland (1938, 1947) later subdivided the genus into more than ten genera, recognizing 34 genera in all for the family. Since then, two alternative systems have been applied to the family; Copeland's system of splitting, which recognizes more than 30 genera, and a principally bigeneric

system. According to Copeland's system, the Malesian species of *Hymenophyllum* s.lat. should be separated into several genera, such as *Amphipterum*, *Hymenophyllum*, *Mecodium*, *Meringium*, *Myriodon*, *Sphaerocionium*.

Molecular data indicate that the species of *Hymenophyllum* s.lat. form a unique clade, even including some species formerly treated as *Trichomanes* s.lat. (e.g., *Pleuromanes*). It has been elucidated that *Hymenophyllum* should be delimited more broadly (Ebihara et al. 2006).

In *Hymenophyllum* in the broader sense, there are 10 subgenera, 5 of which are in the Malesian region.

KEY TO THE SUBGENERA

1a. Stellate hairs present on fronds, and/or fronds dichotomously divided . . . . . **e.** subg. **Sphaerocionium**
b. Stellate hairs absent on fronds, and/or fronds not dichotomously divided 2
2a. Lower surface of fronds glaucous or covered with whitish multicellular hairs . . . . . **d.** subg. **Pleuromanes**
b. Lower surface of fronds neither glaucous nor with whitish multicellular hairs . . 3
3a. Rhizome thick, more than 0.4 mm diam., nearly glabrous or with scattered pale hairs . . . . . **b**. subg. **Globosa**
b. Rhizome filiform, less than 0.4 mm diam., with scattered short brown hairs . . . 4
4a. Margin of segments toothed . . . . . **a**. subg. **Hymenophyllum**
b. Margin of segments entire 5
5a. Laminar cell walls more or less thick and not necessarily straight; sori each with a thickened base, on short acroscopic segments near rachis . . . . . **a**. subg. **Hymenophyllum**
b. Laminar cell walls thin and straight; sori lacking a thickened base . . . . . **c.** subg. **Mecodium**

a. Subgenus **Hymenophyllum**

Hymenophyllum Sm. subg. *Hymenophyllum*. — *Hymenophyllum* Sm. subg. *Euhymenophyllum* C.Presl, Abh. Königl. Böhm. Ges. Wiss., ser. 5, 3 (1843) 31, nom. illeg. — Literature and type: as the genus.

Other synonymous genus names (see under genus): *Amphipterum* (Copel.) Copel., *Buesia* (C.V.Morton) Copel., *Craspedophyllum* (C.Presl) Copel., *Leptocionium* C.Presl, *Meringium* C.Presl, *Myriodon* (Copel.) Copel., *Pachyloma* Bosch.

Didymoglossum Desv. subg. *Chilodium* C.Presl, Abh. Königl. Böhm. Ges. Wiss., ser. 5, 3 (1843) 23. — *Hymenophyllum* Sm. subg. *Chilodium* (C.Presl) Croxall, Austral. J. Bot. 23 (1975) 515. — *Hymenophyllum* Sm. sect. *Chilodium* (C.Presl) K.Iwats., Acta Phytotax. Geobot. 35 (1984) 171. — Type: *Hymenophyllum neesii* (Blume) Hook. (= *Hymenophyllum denticulatum* Sw.).

Hymenophyllum Sm. subg. *Sphaerodium* C.Presl, Abh. Königl. Böhm. Ges. Wiss., ser. 5, 3 (1843) 31. — *Hymenophyllum* Sm. sect. *Sphaerodium* (C.Presl) C.Chr., Index Filic. (1905) xvi. — Type: *Hymenophyllum wilsonii* Hook.

Hymenophyllum Sm. sect. *Acanthotheca* Nakai, Bot. Mag. (Tokyo) 40 (1926) 242. — Type: *Hymenophyllum acanthoides* (Bosch) Rosenst.

Hymenophyllum Sm. sect. *Eupectinum* Diem & J.S.Licht., Darwiniana 11 (1959) 655. — Type: *Hymenophyllum pectinatum* Cav. (= *Hymenophyllum polyanthos* (Sw.) Sw.).

Hymenophyllum Sm. sect. *Pseudomecodium* K.Iwats., Acta Phytotax. Geobot. 35 (1984) 172. — *Pseudomecodium* (K.Iwats.) Satou, Hikobia 12 (1997) 269. — Type: *Hymenophyllum exsertum* Wall.

Rhizome long-creeping, filiform, wiry, nearly glabrous or covered with thick-walled, brownish hairs, dense at apical portion; *stipes* terete or narrowly winged in upper portion, in some species with accessory wings; *fronds* remote, simple to quadripinnatifid, pinnate in one plane, or seemingly pectinate in dwarfed ones; *ultimate segments* entire or toothed, usually flat or more or less crisped, each with a single veinlet. *Sori* solitary at apex of ultimate segments, *involucres* bivalvate, deeply cleft or forming more or less campanulate basal portion with cleft lips nearly to half-way, lips entire or serrate, receptacles included or slightly extruded beyond valves.

Distribution — Cosmopolitan, c. 250 species; 39 species in *Malesia*.

Habitat & Ecology — Epiphytic on trunks and branches of trees in dense forests and epipetric on moss-covered, moist rocks, especially in cooler regions and at higher elevations; sometimes withstanding long periods of drought.

Taxonomy — In Copeland' system (1938; Gen. Fil. (1947) 33), most of the species included here were treated as species of *Amphipterum*, *Craspedophyllum*, *Meringium*, *Myriodon*, *Buesia* and others. The comparative morphology and taxonomy of subg. *Hymenophyllum* was treated in detail by Iwatsuki (Gard. Bull. Singapore 30 (1977) 63) as *Meringium* and related genera.

KEY TO SPECIES

1a. Accessory wings present on various axes of fronds, either on upper (abaxial) or lower (adaxial) surface or on both surfaces 2
b. Accessory wings absent on axes of fronds 6
2a. Margin of ultimate segments entire; axes of fronds lamellate on lower surface only or on both surfaces (*H. ledermannii*) 3
b. Margins of ultimate segments serrulate; axes of fronds lamellate on both upper and lower surfaces 5
3a. Axes of fronds lamellate only on lower surface 4
b. Axes of fronds lamellate on both upper and lower surfaces. **24. H. ledermannii**
4a. Fronds bipinnatifid or more decompound, hairy only on axes . . . **15. H. fuscum**
b. Fronds pinnatifid to pinnate, hairy throughout . . . . . **39. H. trichophorum**
5a. Fronds larger, 20–30 cm long, with stipes 10–20 cm in length; stipes and rachis stout, densely hirsute . . . . . **16. H. geluense**
b. Fronds smaller, c 15 cm long, with stipes 4–5 cm in length; stipes and rachis slender, less densely hairy or glabrescent . . . . . **23. H. laminatum**
6a. Typical lamina present, and axes winged only in the plane of the fronds 7
b. Typical lamina wanting and replaced by veinless teeth . . . . . **6. H. brassii**
7a. Margin of segments and wings more or less toothed 8
b. Margin of segments and wings entire 37
8a. Margin of segments distinctly serrate throughout 9
b. Margin of segments subentire or rarely toothed 35

9a. Margin of segments serrate by irregular arrangement of laminar cells; fronds pinnate, usually more than 4 cm long 10
b. Margin of segments toothed with setose dark brown hairs; fronds flabellate or pinnatifid, less than 3 cm long . . . . . **21. H. johorense**
10a. Involucre bivalvate, deeply cleft nearly to the base . . . . . **32. H. peltatum**
b. Involucre campanulate in basal portion, with bilabiate lips 11
11a. Rachis terete in basal portion, wings of upper part of rachis narrow and flat . 12
b. Rachis winged throughout, with more or less crisped wings 26
12a. Mature fronds normally 3 cm long or longer 13
b. Fronds less than 3 cm long 25
13a. Lips of involucres entire or nearly so 14
b. Lips of involucres with evident short teeth 22
14a. Internal cell walls of laminae thick and coarsely pitted 15
b. Internal cell walls of laminae uniformly thin . . . . . **5. H. bontocense**
15a. Fronds normally more than 6 cm long, more or less lax 16
b. Fronds to 6 cm long, more or less compact 20
16a. Hairs on stipe more or less dense or caducous, brownish, never articulate, to 1.5 mm long 17
b. Hairs on stipes very dense, pale brown, semiarticulate, to 4 mm long . . . . . **36. H. rubellum**
17a. Hairs on frond axes to 0.5 mm long; sori covering entire frond, c. 2 mm long 18
b. Hairs on frond axes to 1 mm long; sori usually in one row on each side of rachis, c. 3 mm long . . . . . **13. H. firmum**
18a. Rachis densely hairy 19
b. Rachis with sparse brown hairs . . . . . **11. H. edentulum**
19a. Ultimate segments c. 7 mm broad, sori larger; dried specimens reddish brown to dark . . . . . **22. H. klabatense**
b. Ultimate segments 7–10 mm broad, sori mediocre in size; dried specimens deep green or brownish . . . . . **38. H. serrulatum**
20a. Sori less than 4 mm long, dark green to brownish 21
b. Sori larger, c. 4 mm long, blackish . . . . . **27. H. melanosorum**
21a. Ultimate segments 1.5–2.5 mm broad . . . . . **2. H. archboldii**
b. Ultimate segments c. 0.8 mm broad . . . . . **8. H. campanulatum**
22a. Fronds coriaceous, compact 23
b. Fronds papyraceous, normal or not particularly compact 24
23a. Texture papyraceous; lips of involucres nearly entire . . . . . **18. H. hieronymi**
b. Texture soft papyraceous; lips of involucres distinctly dentate, very minutely wavy . . . . . **30. H. ovatum**
24a. Soral tubes with prominent projections . . . . . **17. H. gorgoneum**
b. Soral tubes without prominent projections . . . . . **28. H. merrillii**
25a. Fronds pinnate, rachis terete throughout . . . . . **4. H. blandum**
b. Fronds bipinnatifid, rachis terete in lower portion, winged distally **25. H. lobbii**
26a. Wings of stipes not toothed 27
b. Wings of stipes toothed 31

27a. Axes of fronds hairy but not densely so 28
b. All axes of fronds and margin of segments conspicuously hairy 30
28a. Fronds elongate; receptacles extruded from involucres 29
b. Fronds deltoid; receptacles included under edge of lips of involucres . . . . . **34. H. ramosii**
29a. Fronds not black when dried; ultimate segments c. 1 mm broad, dentition regular, with few cells . . . . . **19. H. holochilum**
b. Fronds blackish in dried specimens; ultimate segments 0.3–0.7 mm broad, dentition sharp and distinct, with several rows of cells . . . . . **35. H. rosenstockii**
30a. Hairs on fronds caducous and sparse on older portions, not articulated, c. 0.8 mm long; involucres c. 2.5 mm long, often darkly tinted . . . . . **7. H. bryophilum**
b. Hairs on fronds dense, persistent, subarticulate, sometimes more than 2 mm long; involucres c. 1.8 mm long, rarely darkly tinted . . . . . **14. H. foersteri**
31a. Wings of stipes flat or at most somewhat crisped 32
b. Wings of stipes distinctly contorted 33
32a. Wings of stipes flat 34
b. Wings of stipes more or less crisped . . . . . **10. H. denticulatum**
33a. Sori normal in size, c. 2.5 mm long, diameter slightly larger than breadth of segments . . . . . **20. H. hosei**
b. Sori distinctly larger, c. 3.5 mm long, diameter c. 3 times as large as breadth of segments . . . . . **26. H. macrosorum**
34a. Hairs of frond axes brownish, dense . . . . . **1. H. acanthoides**
b. Hairs of frond axes reddish, very dense . . . . . **9. H. cardunculus**
35a. Rachis winged throughout, wings decurrent on upper portion of stipe; margin of segments entire 36
b. Rachis terete at base; margin of segments spontaneously toothed. — Plants of elevations below 1000 m . . . . . **33. H. penangianum**
36a. Stipes very narrowly winged nearly to base; larger fronds quadripinnatifid; rachis and pinna rachis glabrous. — Plants of elevations above 1200 m . . . . . **29. H. microchilum**
b. Stipes terete or upper portion very narrowly winged; fronds tripinnatifid; undersurface of rachis and pinna rachis sparsely hairy. — Plants of mid elevations, around 1000 m . . . . . **37. H. seramense**
37a. Receptacles extruded from lips of involucres 38
b. Receptacles included under edge of lips of involucres . . . . . **12. H. exsertum**
38a. Fronds thin, membranous; hairs on frond axis adpressed, persistent; lips of involucres elongate, triangular. — Endemic to Batu Isl., Sumatra . . . **3. H. batuense**
b. Fronds coarse in texture; hairs on frond axis patent, deciduous; lips of involucres broadly rounded . . . . . **31. H. pachydermicum**

1. Hymenophyllum acanthoides (Bosch) Rosenst.

Hymenophyllum acanthoides (Bosch) Rosenst., Bull. Jard. Bot. Buitenzorg, ser. 2, 2 (1911) 25; C.Chr., Mitt. Inst. Allg. Bot. Hamburg 7 (1928) 144; Copel., Philipp. J. Sci. 64 (1937) 45, pl. 17; Holttum, Rev. Fl. Malaya 2 (1955) 80, f. 20; K.Iwats., J. Fac. Sci. Univ. Tokyo, Sect. 3, Bot. 13 (1985) 512; K.Iwats. et al., PhytoKeys 119 (2019) 111. — *Didymoglossum acanthoides* Bosch in Miq., Pl.

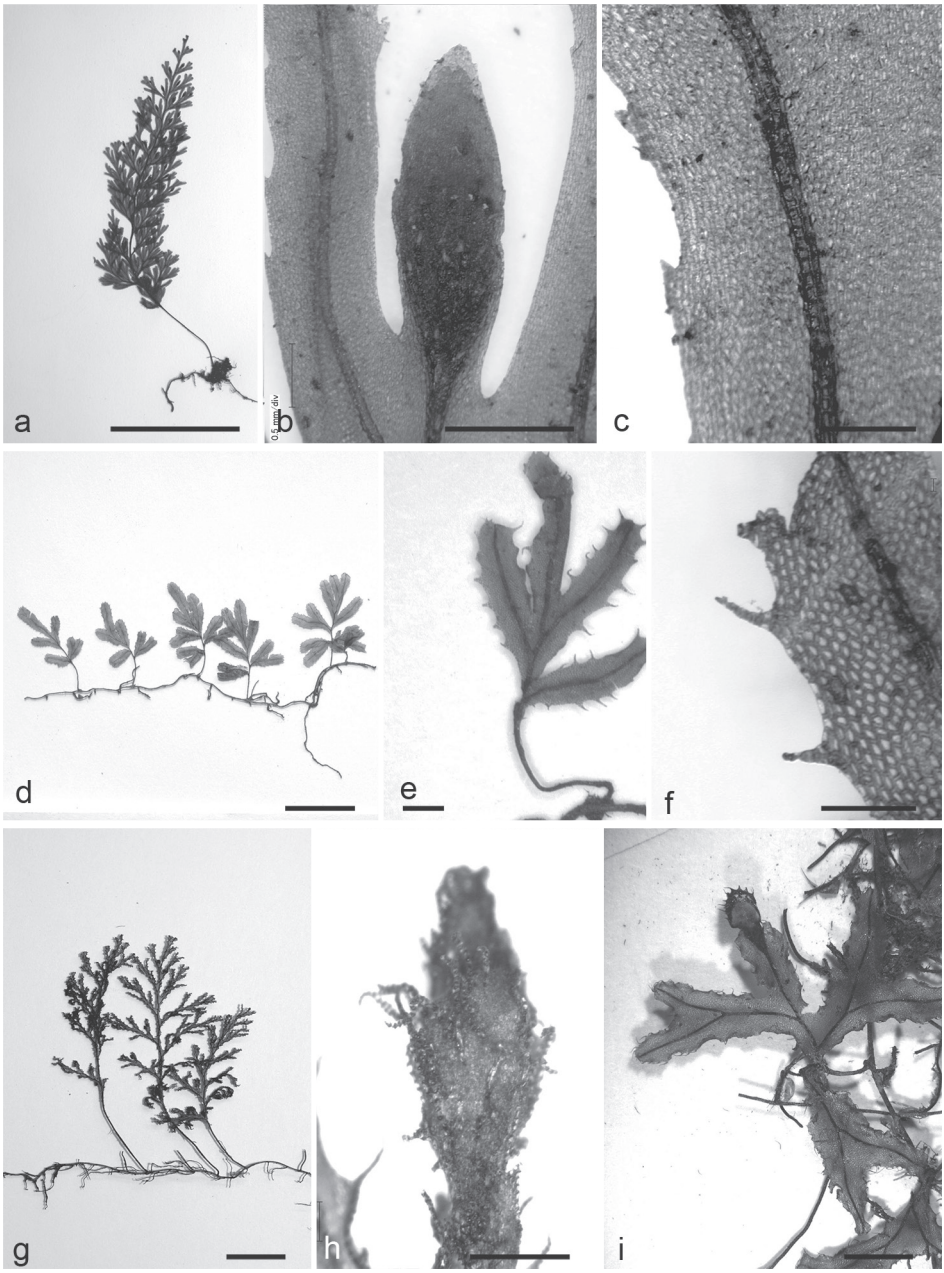

Fig. 7. a–c. *Hymenophyllum serrulatum* (C.Presl) C.Chr. a. Frond; b. sorus; c. toothed margin of lamina. — d. Fronds of *H. blandum* Racib. — e, f. *H. lobbii* T.Moore ex Bosch. e. Frond; f. sharply toothed margin of lamina. — g, h. *H. acanthoides* (Bosch) Rosenst. g. Fronds; h. sorus. — i. Frond of *H. joho-rense* Holttum (a–c: *Togashi 6222218*, Cameron Highland, Malaysia, TI 00047149; d: *Shimizu et al. M-13515*, Pahang, Malaysia, TI 00001093; e, f: *Arikawa 277C*, Mt Kinabalu, Malaysia, TNS 766187; g, h: *Kato et al. C-1754*, Seram, Indonesia, TI; i: *Price 1158*, Luzon, Philippines, KYO 00010955).

Jungh. 5 (1857) 560 — *Leptocionium acanthoides* (Bosch) Bosch, Ned. Kruidk. Arch. 4 (1859) 383; Hymenophyll. Javan. (1861) 42, pl. 32. — *Meringium acanthoides* (Bosch) Copel., Philipp. J. Sci. 67 (1938) 42; Fern Fl. Philipp. 1 (1958) 63; Ching, Fl. Reipubl. Popularis Sin. 2 (1959) 151; Tagawa & K.Iwats. in Smitinand et al., Fl. Thailand 3 (1979) 78, f. 5-5. — Lectotype (designated here): *van Gesker s.n.* (lecto L 1258467 upper plants; isolecto P), Java, Gede.

Hymenophyllum sabinifolium Baker in Hook. & Baker, Syn. Fil. (1867) 71. — Lectotype (designated here): *Zollinger 3623* (lecto K 001090293; isolecto L), Java, Salak.

Hymenophyllum australe Willd. var. *fimbriatum* auct. non (J.Sm.) C.Chr.: C.Chr. & Holttum, Gard, Bull. Singapore 7 (1934) 213.

Rhizome long-creeping, slender, c. 0.2 mm diam., covered with brownish hairs when young, glabrescent or glabrous in older portion, brown; bearing slender, blackish, less densely hairy roots rather sparsely. *Stipes* 1–3 cm apart, winged at least on upper portion, 0.7–4 cm long, densely hairy with brownish hairs; *fronds* variable in size and form, bipinnate to tripinnatifid, oblong-subdeltoid to ovate, moderately acute at apex, broadly cuneate to subcordate at base, 1–3.5 cm long and wide (at most 5 cm long in the largest ones); rachis and all divisions of fronds about equally winged, giving appearances like ultimate segments, toothed, moderately to exceedingly crisped; larger *lateral pinna*e with several segments, ovate to oblong, round at apex, unequally cuneate at base; *ultimate segments* round or obtuse at apex, c. 1 mm wide, sharply and irregularly toothed and conspicuously crisped at margin, the fronds never extending in one plane. *Internal cell walls* nodulose-thickened in optical section, more thickened and wavy or short-toothed near the surface. *Sori* at apex of short acroscopic segments, usually in apical part of fronds and arranged along rachis, large, sessile, winged at the base; *involucres* tubular with bilabiate mouth, cleft more or less halfway down, winged, also with a few accessory projections on the tube; lips round to moderately acute at apex, sharply, irregularly, and densely toothed; receptacles elongate, apparently extruded. — **Fig. 7g, h.**

Distribution — S India, Thailand (Peninsular); throughout *Malesia*.

Habitat & Ecology — Epiphytic and epipetric, on moss-covered bark of tree trunks, on twigs and on rocks in dense montane forests and in dry forests near streams. Altitude: from sea level to 1200 m.

Note — *Hymenophyllum acanthoides* is a common species variable in size, form and degree of crisping, as in the case of such widely distributed species in various habitats belonging to the group of *H. denticulatum*. This distinct species may be recognized by the more sharply and densely crisped margin of the segments and wings. Less crisped forms of this species somewhat resemble *H. denticulatum*, although the discrepancy between these two species is clear: in *H. acanthoides* the margin of the segments is distinctly crisped throughout, though in *H. denticulatum* not throughout.

2. Hymenophyllum archboldii (Copel.) C.V.Morton

Hymenophyllum archboldii (Copel.) C.V.Morton, Contr. U.S. Natl. Herb. 38 (1968) 167. — *Meringium archboldii* Copel., Philipp. J. Sci. 73 (1941) 462, t. 3. — Lectotype (designated here): *Brass 12328* (lecto MICH 1190740; isolecto BM, BO, BRI, GH, L), New Guinea, Idenburg River.

Rhizome long-creeping, slender, wiry, c. 0.2 mm diam. *Stipes* filamentous, terete, sparsely hairy or glabrous, 1.5–2 cm long, c. 0.1 mm diam.; *fronds* narrowly oblong, round at apex, gradually narrowing downwards, (2–)4–6 cm long, to 1.7 cm wide,

bipinnatifid; rachis terete in lower portion, winged with decurrent base of pinnae in upper portion, sparsely hairy beneath or glabrescent; *pinnae* simple or bi- to tri-forked, sessile or decurrent at base; *ultimate segments* obtuse at apex, sparsely minute-dentate and flat at margin, 1.5–2.5 mm broad. *Sori* apical on short acroscopic segments, arranged in one row at each side of rachis; *involucre* deeply immersed in lower half, cleft to halfway; lips moderately acute at apex, entire; receptacles clavate, extruded beyond the lips of involucres.

Distribution — *Malesia*: New Guinea (known only from the type collection).

Habitat & Ecology — Massed on a mossy tree at c. 1800 m altitude.

Note — *Hymenophyllum archboldii* is in the group of *H. holochilum*, but is distinct in having very broad ultimate segments, terete stipes and lower portion of the rachis and bipinnatifid fronds.

3. Hymenophyllum batuense Rosenst.

Hymenophyllum batuense Rosenst., Bull. Jard. Bot. Buitenzorg, ser. 2, 2 (1911) 22; Copel., Philipp. J. Sci. 64 (1937) 23. — Syntypes: *Raap 579* (BM, BO), Sumatra, Batu Is.

Rhizome long-creeping, slender, 0.15–0.2 mm diam., bearing brownish hairs. *Stipes* terete, filiform, 1–1.5 cm long, hairy; hairs thin, persistent, reddish brown, multicellular, to more than 1 mm long; *fronds* bipinnate, oblong to oblong-lanceolate, round to moderately acute at apex, round to broadly cuneate at base, 3.5–5 cm long, to 2.3 cm wide, reddish brown in dried specimens; rachis winged throughout with flat and entire wings, hairy, more or less zigzag in upper portion; *pinnae* pinnate, narrowly oblong sessile at cuneate base, moderately acute at apex; pinna rachis winged, appearing like ultimate segments, hairy beneath; *ultimate segments* round or obtuse at apex, entire and flat at margin, c. 1 mm broad, their costae densely hairy beneath. *Sori* terminal at apices of short basal acroscopic pinnules, thus arranged in one row at each side of rachis; *involucres* obconic, with tuberous lower half and bilabiate upper portion, to 2.5 mm long, 1.7 mm diam.; lips triangular, acuminate at apex, entire; receptacles long-extruded.

Distribution — *Malesia*: Sumatra (Batu Island; known only from the type collection).

Habitat & Ecology — Not recorded.

Note — The hairs on all axes of the fronds are reddish brown, multicellular, to more than 1 mm in length, and dense throughout, although they are more slender than those of *H. pachydermicum*. The fronds are generally more delicate and loosely constructed. As noted in the original description, *H. batuense* is somewhat similar to *H. holochilum* in its general appearance, although morphological features indicate its systematic position within this section. The only record is the type collection, so no further information is available.

4. Hymenophyllum blandum Racib.

Hymenophyllum blandum Racib., Pteridoph. Buitenzorg (1898) 20; Copel., Philipp. J. Sci. 64 (1937) 50, pl. 18; Holttum, Rev. Fl. Malaya 2 (1955) 77, f. 18; K.Iwats., J. Fac. Sci. Univ. Tokyo, Sect. 3, Bot. 13 (1985) 512; J.X.Liu et al. in C.Y.Wu et al., Fl. China 2–3 (2013) 104; K.Iwats. et al., PhytoKeys 119 (2019) 111. — *Meringium blandum* (Racib.) Copel., Philipp. J. Sci. 67 (1938) 43; Fern

Fl. Philipp. 1 (1958) 63; Tagawa & K.Iwats. in Smitinand et al., Fl. Thailand 3 (1979) 78; J.L.Tsai & W.C.Shieh in H.L.Li et al., Fl. Taiwan 1 (1994) 115. — Lectotype (designated here): *Raciborski s.n.* (lecto BO; isolecto K, L, P), Java, Salak.

Hymenophyllum herterianum Brause, Bot. Jahrb. Syst. 56 (1920) 43; Copel., Philipp. J. Sci. 64 (1937) 54, pl. 21: f. 3. — Lectotype (designated here): *Ledermann 8869* (lecto B 20 0101494; isolecto BM, MICH), Papua New Guinea, Kaiserin Augusta Fluss.

Rhizome filiform, c. 0.1 mm diam., long-creeping, wiry, with sparse long brown hairs. *Stipes* slender, usually c. 2 mm long, not winged, sparsely hairy throughout, glabrescent except at the base; *fronds* pinnate-bipinnatifid in plan or digitate in appearance, with c. 10 segments, suborbicular to oblong-ovate in outline, typically c. 1 cm in both length and width, or exceptionally to 5 cm long; *rachis* slender, winged only near the apex, sparsely hairy; *pinnae* simple or forked or sometimes with 3 lobes of which the basal acroscopic one may be forked again; *ultimate segments* (or simple pinnae) round at apex, c. 0.8 mm long, to almost 2 times as broad, thin or firm, the margin denticulate with rather long teeth, flat; pale green in colour, axis dark; *internal cell walls* thin, straight. *Sori* solitary on segments, near the apex of the frond only, rather short; *involucres* with tuberous base and rather short bilabiate lips, cleft to halfway down, c. 1.6 mm long, less than 1 mm broad; lips subdeltoid, moderately acute at apex, often reflexed; receptacles protruding much in old sori. — **Fig. 7d.**

Distribution — Thailand (Peninsular) and Taiwan; in *Malesia*: Peninsular Malaysia, Sumatra, Borneo, Java, Philippines, Sulawesi, Lesser Sunda Islands (Flores), Moluccas (Seram) and New Guinea.

Habitat & Ecology — Epiphytic and epipetric on tree trunks and on moist, muddy rocks in dense montane forests. Altitude: from middle to higher elevations, 700–2700 m; in New Guinea 1000–2700 m.

Note — The New Guinean form has been distinguished as *H. herterianum* because of the variable fronds, although no such forms can be separated taxonomically from *H. blandum*. Actually, some forms from New Guinea, such as *H. holochilum*, are referred to *H. blandum*. Fronds to 2.5 cm long have a terete rachis, which is characteristic of *H. blandum*.

5. Hymenophyllum bontocense Copel.

Hymenophyllum bontocense Copel., Philipp. J. Sci. 64 (1937) 33, pl. 12; K.Iwats., J. Fac. Sci. Univ. Tokyo, Sect. 3, Bot. 13 (1985) 511. — *Meringium bontocense* (Copel.) Copel., Philipp. J. Sci. 67 (1938) 41; Fern Fl. Phillip. 1 (1958) 60; Tagawa & K.Iwats. in Smitinand et al., Fl. Thailand 3 (1979) 76, f. 5–15. — Lectotype (designated by Ebihara & Iwatsuki, Mem. Natl. Mus. Nat. Sci. (Tokyo) 46 (2010) 95): *BS (Ramos & Edaño) 37735* (lecto MICH; isolecto P). Other syntype: *BS (Ramos & Edaño) 37932* (MICH, US), Philippines, Luzon.

Rhizome slender, long-creeping, hairy on younger portion, glabrescent, c. 0.2 mm diam.; hairs thin, brown, to 1.2 mm long. *Stipes* slender, wingless or very narrowly winged in the upper portion, hairy with hairs similar to those on rhizome, 1–2 mm long; *rachis* distinctly winged in upper portion, hairy, wings of rachis flat, entire or very slightly dentate; *fronds* oblong to oblong lanceolate, round or very moderately acute at apex, bipinnate or tripinnate in larger ones, 4–6 cm long, 1.3–2.2 cm wide; *pinnae*

6–8 pairs, all sessile, upper ones gradually reducing in size, larger ones oblong ovate in outline, round to obtuse at apex, unequally cuneate at base; *ultimate segments* of pinnae 5–8, round at apex, sharply serrate at margin, c. 1.5 mm broad, bearing brown hairs on costae underneath; green in colour; *internal cell walls* thin, not coarsely pitted. *Sori* at apices of short acroscopic segments, usually on the basal ones only, thus arranged in one row at each side of rachis; *involucres* obconic, with bilabiate mouth cleft nearly halfway down, c. 1.5 mm long, to 0.8 mm diam.; the lips acute, entire; receptacles long-extruded.

Distribution — Thailand (Peninsular); in *Malesia*: Philippines.

Habitat & Ecology — Epiphytic or epipetric on the base of tree trunks and on moist mossy rocks in dense evergreen forests on hills and in montane limestone forests. Altitude: at mid elevations, 1200–1500 m.

Note — *Hymenophyllum bontocense* is distinct in its discriminating characters (narrow and flat wings only on the upper part of rachis, involucres campanulate in basal portion with bilabiate and entire margin, and in the morphology of the cell walls), although such features are observable on only a restricted number of specimens.

6. Hymenophyllum brassii C.Chr.

Hymenophyllum brassii C.Chr., Brittonia 2 (1937) 273. — *Meringium brassii* (C.Chr.) Copel., Philipp. J. Sci. 73 (1941) 463; C.W.Chen et al., Sol Amazing (2017) 126. — *Myriodon brassii* (C.Chr.) Copel., Gen. Fil. (1947) 36. — Lectotype (designated here): *Brass 4114* (lecto BM 001044219; isolecto BO, BRI, GH, MICH, NY), New Guinea, Mt Tafa.

Hymenophyllum sabinifolium Baker var. *imbricata* Brause, Bot. Jahrb. Syst. 56 (1920) 45. — Lectotype (designated here): *Ledermann 13057* (lecto B 20 0102751; isolecto BM, MICH), New Guinea, Felsspitze.

Hymenophyllum sabinifolium Baker var. *irregularis* Brause, Bot. Jahrb. Syst. 56 (1920) 45. — Syntypes: *Ledermann 10116* (B, BM), Papua New Guinea, Lordberg; *Ledermann 12796* (B, BM), Papua New Guinea, Lordberg. On the label of *Ledermann 10116* in B is a note that it is the lectotype.

Hymenophyllum odontophyllum Copel., Philipp. J. Sci. 64 (1937) 73, pl. 35. — *Myriodon odontophyllus* (Copel.) Copel., Philipp. J. Sci. 67 (1938) 47. — Type: *Ledermann 13057* (holo MICH; iso B, BM), New Guinea.

Rhizome long-creeping, wiry, with very sparse pale hairs or glabrescent, c. 0.3 mm diam. *Stipes* slender, 1.5–5 cm long, glabrous, terete, or with sparse scaly accessories on upper portion; *fronds* tripinnatifid-tripinnate, oblong-lanceolate or much elongate, 6–10(–18) cm long, commonly c. 2 or to 4 cm wide; *rachis* like upper part of stipes, bearing rather dense scaly accessories apparently in various directions; *pinnae* 15–20 pairs or even more, ascending, oblong-ovate, narrowly oblong or lanceolate and falcate, round to moderately acute at apex, cuneate and shortly petiolate at base in larger ones, commonly 1–1.7 cm long, c. 0.7 mm wide, and sometimes becoming extraordinarily larger, even forming so-called side-leaves; pinna rachis similar to rachis, or winged in distal portion; *ultimate segments* linear, round at apex, deeply incised to form scaly accessories of the same pagina as normal laminae, or often occupied only by scaly accessories without any normal laminae remained; *internal cell walls* rather thick, slightly wavy. *Sori* at apex of short acroscopic branch of segments, c. 2 mm long, 1.5 mm broad; *involucres* tuberous with bilabiate mouth, the tubers with dense accessories; lips short,

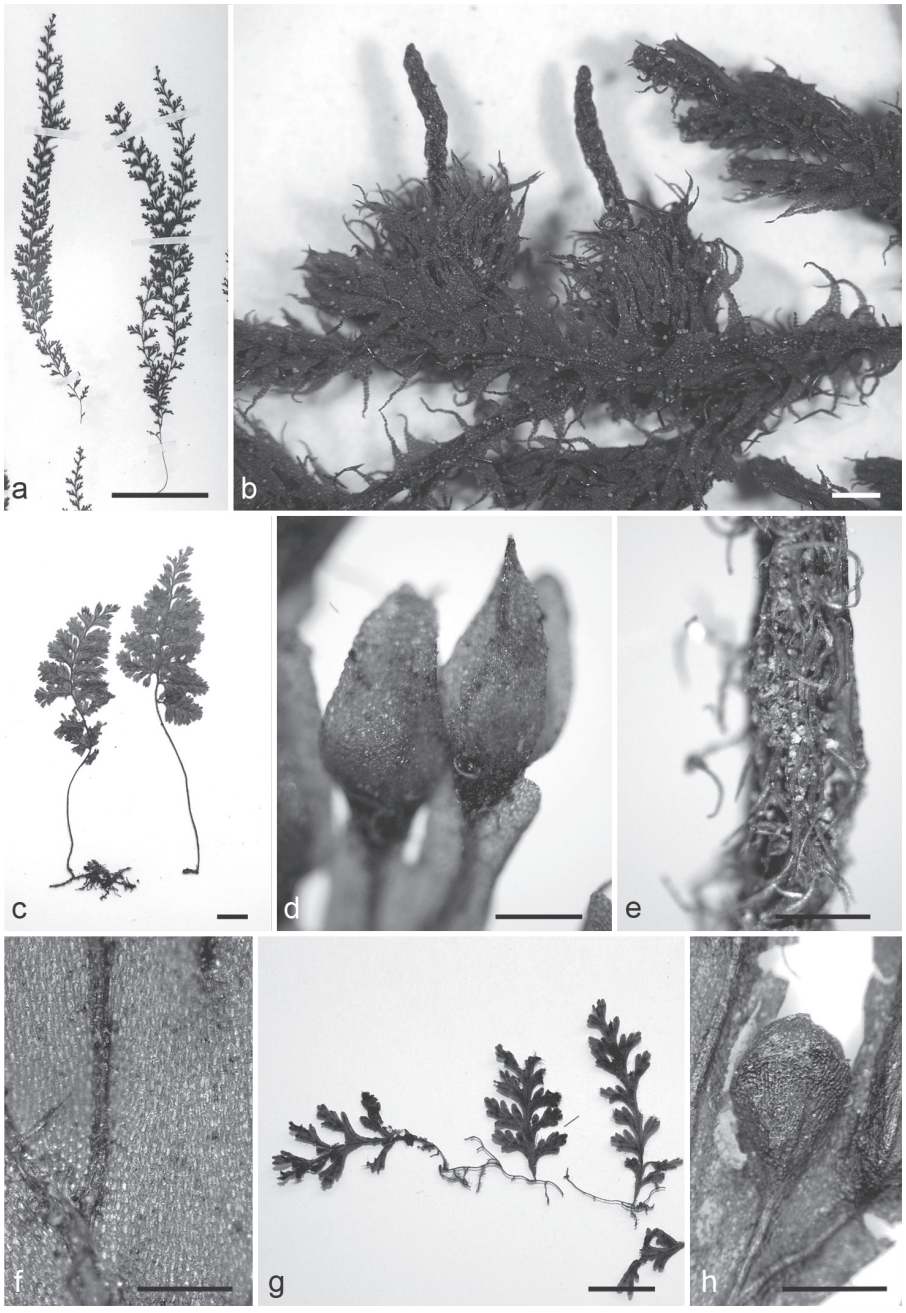

Fig. 8. a, b. *Hymenophyllum brassii* C.Chr. a. Fronds; b. sori. — c–f. *H. exsertum* Wall. c. Fronds; d. sori; e. stipe covered by multicellular hairs on the abaxial side; f. laminar cells. — g, h. *H. pachydermicum* Ces. g. Fronds; h. sorus (a, b: *Kalkman 5016*, Papua New Guinea, KYO; c–f: *Shimizu et al. 13238bis*, Pahang, Malaysia, KYO; g, h: *Kokawa & Hotta 4075*, Sabah, Malaysia, KYO 00010991).

round, finely splitting into sharp teeth of the same pagina as scaly accessories; receptacles long-extruded. — **Fig. 8a, b.**

Distribution — *Malesia*: New Guinea; Solomon Islands.

Habitat & Ecology — Epiphytic on upper and middle part of trunk of larger trees in mid-montane, mossy, subalpine forests and in shrubbery. Altitude: at mid to high elevations, 1400–3300 m.

7. Hymenophyllum bryophilum C.Chr.

Hymenophyllum bryophilum C.Chr., Brittonia 2 (1937) 274. — *Meringium bryophilum* (C.Chr.) Copel., Philipp. J. Sci. 75 (1941) 359. — Lectotype (designated here): *Brass 4262* (lecto BM 001044322; isolecto BO, GH, MICH, US), New Guinea, Mt Albert Edward.

Rhizome long-creeping, wiry, slender, c. 0.2 mm diam., with very sparse pale brown hairs, or glabrescent. *Stipes* usually short, 1–2(–3) cm long, sparsely hairy, terete; *fronds* linear, moderately acute at apex, round to narrowly cuneate at base, 15–25 cm long, nearly the same in width throughout or broader in upper portion, 1.8–2.5 cm wide, sometimes bearing extraordinarily elongate pinnae (showing a form of so-called side-leaves); rachis narrowly winged, hairy throughout; *pinnae* usually more than 25 pairs, subquadrangular, with 5–8 subdigitately arranged segments or in larger ones bipinnatifid, 0.5–2 cm long, 0.5–0.8 mm wide, or sometimes enlarged as to form side-leaves; *ultimate segments* linear, acute to moderately acute at apex, sparsely dentate at margin, hairy throughout, but caducous and nearly glabrous in older specimens; hairs brownish, multicellular, c. 0.8 mm long; *internal cell walls* rather thick, wavy. *Sori* terminal on short axillary segments at basal acroscopic side of pinnae, thus arranged in one line at each side of rachis; *involucres* campanulate, or with tuberous lower half and bilabiate upper portion, c. 2.5 mm long, 1.2 mm broad, with distinct accessories on tuberous portion; lips c. 1.5 mm in width, round, sharply dentate, densely hairy; receptacles long-extruded.

Distribution — *Malesia*: New Guinea.

Habitat & Ecology — Epiphytic, pendulous from tree trunks in upper montane forests and in subalpine shrubby places at higher elevations. Altitude: 3100–3800 m.

Notes — The fronds are usually narrowly lanceolate in outline and some pinnae may elongate extraordinarily, resulting in an irregular wider portion of the fronds. This feature is characteristic of other species of *Hymenophyllum*, especially in New Guinea.

M.S.Clemens s.n. (BO) is a particularly densely hairy form, although the morphology is quite similar to the type collection, except in the dense hairiness. *Brass 4313* in BO, determined by Christensen as *H. geluense* var. *apiciflora*, is a stouter form of this species.

Christensen (1937) noted that *H. bryophilum* is near *H. foersteri*, which is much more densely hairy and with longer and thinner hairs and pilose-ciliate segments. The specimens cited by Christensen (*Brass 4261*, *4435*) appear somewhat different from *Brass 4262*, but agree in all the important characters.

8. Hymenophyllum campanulatum Christ

Hymenophyllum campanulatum Christ, Philipp. J. Sci., C. 2 (1907) 155; Copel., Philipp. J. Sci. 64 (1937) 32, pl. 11. — *Meringium campanulatum* (Christ) Copel., Philipp. J. Sci. 67 (1938) 40; Fern Fl. Philipp. 1 (1958) 60. — Lectotype (designated here): *Whitford 1549* (lecto P 00622014; isolecto MICH, PNH, US), Philippines, Negros, Mt Silay.

Rhizome long-creeping, wiry, very slender, c. 0.3 mm diam., branched and intricate, hairy; hairs multicellular, downy, pale brown, to 1.5 mm long, rather dense in younger portion but glabrescent. *Stipes* to 1.5 cm long, terete, slender, glabrescent; *fronds* oblong to oblong-lanceolate, round to moderately acute at apex, to 4 cm long, 1 cm wide, bipinnatifid, compact; *rachis* sparsely hairy with brown, multicellular hairs to 1.5 mm long, winged only towards the top; *pinnae* sessile and minutely decurrent at base towards rachis, with at most 8 segments; *ultimate segments* c. 0.8 mm broad, round to obtuse at apex, rather sparsely but sharply toothed. *Sori* at apex on short axillary branch of ultimate segments, campanulate; *involucres* c. 1.5 mm long, cleft to the middle; tube smooth and glabrous except for few hairs at base on dorsal side; lips ovate, rounded at apex, entire; receptacles extruded.

Distribution — *Malesia*: Philippines (Negros).

Habitat & Ecology — Not recorded. Seemingly epiphytic on tree trunks.

Note — *Hymenophyllum campanulatum* is very close to *H. edentulum* and should possibly be reduced to it. More collections from Negros may elucidate it further. In addition to the type materials, *FB (Curran & Foxworthy) 13605* and *13643* (MICH) were also examined.

9. Hymenophyllum cardunculus C.Chr.

Hymenophyllum cardunculus C.Chr., Mitt. Inst. Allg. Bot. Hamburg 7 (1928) 144; Copel., Philipp. J. Sci. 64 (1937) 47. — *Meringium cardunculus* (C.Chr.) Copel., Philipp. J. Sci. 67 (1938) 42. — Lectotype (designated here): *Hans Winkler 745* (lecto HBG; isolecto MICH, UC), Borneo, Bukit Mehipit.

Rhizome long-creeping, wiry, c. 0.3 mm diam., densely reddish pilose or glabrescent. *Stipes* c. 3.5 cm long, narrowly winged in upper portion with wings flat but dentate, densely hairy throughout; hairs multicellular, often more than 1.5 mm long, reddish brown; *fronds* subdeltoid, ovate, oblong or oblanceolate, round to moderately acute at apex, 3–5 cm long, 2–3 cm wide, tripinnatisect; *rachis* densely hairy beneath and reddish pilose as stipes, winged with toothed and distinctly crisped wings; *pinnae* largest at base, subdeltoid, upper ones subquadrangular to narrowly oblong; *ultimate segments* elongate, moderately acute to round at apex, to 0.7 mm broad, sharply toothed and distinctly crisped at margin. *Sori* at apices of short acroscopic axillary segments or usually arranged in one row at each side along rachis, campanuliform, 1.8–2.5 mm long, 1–1.5 mm diam.; *involucres* cleft to c. halfway down, with various accessary projections, hairs or teeth on surfaces; lips acute at apex, sharply denticulate; receptacles elongate, distinctly extruded.

Distribution — *Malesia*: Sumatra, Borneo, Philippines, Moluccas (Ambon and Halmahera).

Habitat & Ecology — Epiphytic and epipetric, on mossy tree trunks, on tree roots, and on moist mossy rocks in dense forests. Altitude: 1000–1800 m.

Note — *Hymenophyllum cardunculus* is similar to *H. acanthoides*, but differs from it only in the dense reddish hairs on the stipe and rachis, a character not difficult to observe.

10. Hymenophyllum denticulatum Sw.

Hymenophyllum denticulatum Sw., J. Bot. (Schrader) 1800(2) (1801) 100; Syn. Fil. (1806) 148, 375; Bedd., Handb. Ferns Brit. India (1883) 34; Copel., Philipp. J. Sci. 64 (1937) 41, pl. 15; Tardieu & C.Chr. in Lecomte, Fl. Indo-Chine 7, 2 (1939) 57; Holttum, Rev. Fl. Malaya 2 (1955) 79; Sledge, J. Linn. Soc. Bot. 60 (1968) 291; K.Iwats., J. Fac. Sci. Univ. Tokyo, Sect. 3, Bot. 13 (1985) 511; J.X.Liu et al. in C.Y.Wu et al., Fl. China 2–3 (2013) 104; K.Iwats. et al., PhytoKeys 119 (2019) 111. — *Trichomanes denticulatum* (Sw.) Poir. in Lam., Encycl. 8 (1808) 75; Blume, Enum. Pl. Javae 2 (1828) 226. — *Didymoglossum denticulatum* (Sw.) Hassk., Obs. Bot. Fil. 2 (1858) 16. — *Leptocionium denticulatum* (Sw.) Bosch, Ned. Kruidk. Arch. 4 (1859) 382; Hymenophyll. Javan. (1861) 39, pl. 29. — *Meringium denticulatum* (Sw.) Copel., Philipp. J. Sci. 67 (1938) 42; Fern Fl. Philipp. 1 (1958) 62; Ching, Fl. Reipubl. Popularis Sin. 2 (1959) 150; Tagawa & K.Iwats. in Smitinand et al., Fl. Thailand 3 (1979) 77; J.L.Tsai & W.C.Shieh in H.L.Li et al., Fl. Taiwan 1 (1994) 116, pl. 42. — Type: *Thunberg s.n.* (UPS n.v.), Java.

Hymenophyllum dichotomum Cav., Descr. Pl. (1802) 276; Nees & Blume, Nova Acta Phys.-Med. Acad. Caes. Leop.-Carol. Nat. Cur. 11 (1823) 127, pl. 13, f. 4; Blume, Enum. Pl. Javae 2 (1828) 222. — *Myrmecostylum dichotomum* (Cav.) C.Presl, Abh. Königl. Böhm. Ges. Wiss., ser. 5, 3 (1843) 28. — *Leptocionium dichotomum* (Cav.) Bosch, Ned. Kruidk. Arch. 4 (1859) 384. — Type: *Neés s.n.* (holo MA), Philippines, not Chile as stated (see Christensen, Index Filic., Suppl. 3 (1934) 114 and Copeland, Philipp. J. Sci. 67 (1937) 44).

Hymenophyllum humile Nees & Blume, Nova Acta Phys.-Med. Acad. Caes. Leop.-Carol. Nat. Cur. 11 (1823) 125, pl. 13: f. 3. — *Trichomanes neesii* Blume, Enum. Pl. Javae 2 (1828) 226 (non *T. humile* G.Forst. 1786). — *Didymoglossum neesii* (Blume) C.Presl, Abh. Königl. Böhm. Ges. Wiss., ser. 5, 3 (1843) 115 (non *D. humile* C.Presl). — *Hymenophyllum neesii* (Blume) Hook., Sp. Fil. 1 (1844) 99, nom. superfl.; Brack., U.S. Expl. Exped., Filic. 16 (1854) 266; Harr., J. Linn. Soc., Bot. 16 (1877) 26; Christ, Bull. Herb. Boissier 6 (1898) 141. — *Leptocionium neesii* (Blume) Bosch, Ned. Kruidk. Arch. 4 (1859) 383, nom. superfl.; Hymenophyll. Javan. (1861) 40, pl. 30. — *Meringium neesii* (Blume) B.Nair, Bull. Bot. Surv. India 11 (1969) 186, nom. superfl. — Type: *Blume s.n.* (holo L 0051712; isolecto L 0061094), Java.

[*Trichomanes aculeatum* J.Sm. in Hook., J. Bot. 3 (1841) 417, nom. nud., non Sw. (1788).] — *Didymoglossum aculeatum* Bosch in Miq., Pl. Jungh. 5 (1857) 559. — *Leptocionium aculeatum* (Bosch) Bosch, Ned. Kruidk. Arch. 4 (1859) 383; Hymenophyll. Javan. (1861) 41, pl. 31. — *Hymenophyllum aculeatum* (Bosch) Racib., Pteridoph. Buitenzorg (1898) 21; Christ, Philipp. J. Sci., C. 2 (1907) 155. — Lectotype (designated here): *van Gesker 33* (L), Java. The name by J.Smith is a nomen nudum, thus the specimen on which it is based, *Cuming 146* (L), is not a type.

Hymenophyllum brachyglossum A.Braun ex Kunze, Bot. Zeitung (Berlin) 5 (1847) 227; Copel., Philipp. J. Sci. 64 (1937) 40. — *Meringium brachyglossum* (A.Braun ex Kunze) Copel., Philipp. J. Sci. 67 (1938) 42. — Type: *Beccari s.n.* (holo K), Borneo, Sarawak.

Didymoglossum braunii Bosch in Miq., Pl. Jungh. 5 (1857) 560; Ned. Kruidk. Arch. 4 (1859) 383. — *Leptocionium braunii* (Bosch) Bosch, Ned. Kruidk. Arch. 4 (1859) 383; Hymenophyll. Javan. (1861) 43, pl. 33. — Syntypes: *Reinwardt s.n.* ('herb. Sonder' n.v.), Java; *Teijsman s.n.* (L, P), Java.

Didymoglossum ferox Hassk., Obs. Bot. Fil. 2 (1857) 17. — Syntypes: *Luerssen 11264* (BO [4660] P [44]), Java.

Hymenophyllum subrotundum Alderw., Bull. Jard. Bot. Buitenzorg, sér. 2, 20 (1915) 19. — Lectotype (designated here): *Matthew s.n.* (lecto BO; isolecto BM, K), Sumatra, Padang Panjung.

Rhizome slender, long-creeping, wiry, with rather sparse brown hairs. *Stipes* to 3 cm long, hairy, winged upwards to rachis; wings more or less toothed at margin; *fronds*

bipinnate to tripinnatifid, oblong-ovate to oblong-lanceolate, to c. 8(–12) cm long, 3.5(–5.5) cm wide; *rachis* distinctly winged throughout; wings of rachis more or less crisped and conspicuously toothed at margin; *pinnae* oblong-ovate to lanceolate, round at apex, unequally cuneate at base, usually with less than 10 segments; *ultimate segments* linear-oblong, round to obtuse at apex, sharply toothed at margin, decurrent at base to form wings of axes, to 5 mm long, 1.3 mm broad; the wings of rachis and costae (sometimes the ultimate segments also) toothed and crisped to varying degree; *internal cell walls* rather thick, coarsely pitted. *Sori* apical on short acroscopic segments, usually near rachis in the upper part of fronds; *involucres* obconic, tubular with bilabiate mouth, with accessory wings; lips ± as long as obconic base, bluntly triangular to semi-elliptic, round to moderately acute, distinctly serrate at margin; receptacles extruded when old.

Distribution — Sri Lanka, NE India, Myanmar (Moulmein), Thailand (Peninsular), Vietnam, S China (Guangdong, Guangxi, Hainan), Taiwan, Japan (S Ryukyu); throughout *Malesia*; east to Fiji.

Habitat & Ecology — Epiphytic and epipetric on mossy tree trunks, on bark and on twigs, on rocks in montane forests; in both dense rain forests and in dry deciduous forests. Altitude: from low to mid elevations, or to 2700 m.

Notes — *Hymenophyllum denticulatum* is one of the widespread and variable species, better called a composite species, probably including more than several species not recognized based on current information.

Hymenophyllum brachyglossum was recognized by Copeland as a distinct species after examining the confusion around the names, including those proposed by himself. The first author tried to follow Copeland's identifications of 1933, both in L and GH, but it was difficult to follow his notes on the specimens; *H. brachyglossum* cannot be discriminated from *H. denticulatum*.

Didymoglossum braunii was published independently from *Hymenohyllum brachyglossum*, though there was no distinct difference between the two. The ultimate segments of the type specimen of *D. braunii* are very sharply and distinctly serrate at the margin and the lips are finely serrate to nearly fimbriate.

11. Hymenophyllum edentulum (Bosch) C.Chr.

Hymenophyllum edentulum (Bosch) C.Chr., Index Filic. (1905) 360; Copel., Philipp. J. Sci. 64 (1937) 24, pl. 7. — *Leptocionium edentulum* Bosch, Ned. Kruidk. Arch. 5(3) (1863) 148. — *Meringium edentulum* (Bosch) Copel., Philipp. J. Sci. 67 (1938) 41. — Lectotype (designated here): *Lobb s.n.* (lecto K; isolecto L), Borneo, Sarawak. Other syntype: *Griffith s.n.* (BO, K, L), India, Assam.

Hymenophyllum bakeri Copel., Sarawak Mus. J. 2 (1917) 309; Philipp. J. Sci. 64 (1937) 29; C.Chr., Mitt. Inst. Allg. Bot. Hamburg 7 (1928) 143. — *Trichomanes denticulatum* Baker in Hook. & Baker, Syn. Fil. (1867) 82, nom. superfl., non Houtt. (1783), nec Poir. (1808). — *Meringium bakeri* (Copel.) Copel., Philipp. J. Sci. 67 (1938) 40; Fern Fl. Philipp. 1 (1958) 59. — Type: *Motley s.n.* (holo K), Borneo.

Rhizome long-creeping, wiry, slender, irregularly branching, bearing sparse brownish hairs or glabrescent, c. 0.3 mm diam. *Stipes* slender, glabrous or hairy at base, terete, 0.7–1.5(–3) cm long; *fronds* bipinnate-tripinnatifid, ovate to oblong, moderately acute to acute at apex, round to cuneate at base, 3–6(–12) cm long, 0.7–2.5(–4) cm wide; *rachis* straight or more or less zigzag and winged in upper portion, terete in lower

portion, bearing sparse brown hairs, wings of rachis flat and entire at margin; *pinnae* shortly stalked in larger ones, narrowly oblong, ascending and falcate, round to moderately acute at apex, narrowly cuneate at base, larger ones to 2 cm long, 0.5 cm wide; *pinnules* pinnatifid down to a narrowly winged pinna rachis, larger ones with several segments; *ultimate segments* linear, round at apex, flat and serrate at margin, c. 0.7 mm broad, bearing brown hairs on costae underneath; *internal cell walls* slightly thickened, wavy. *Sori* at apex of short acroscopic axillary segments, usually tending to gather along rachis; *involucres* campanulate, immersed in segments, more or less cleft halfway down, sparsely, deciduously hairy on one side, otherwise smooth, 1.5–2 mm long, to 1 mm diam.; lips bilabiate, triangular to rounded, entire; receptacles eventually extruded.

Distribution — India (Assam); in *Malesia*: Peninsular Malaysia, Sumatra, Borneo (Sabah, Sarawak) and Philippines (Palawan & Mindanao).

Habitat & Ecology — Epiphytic on tree trunks and rotten logs and epipetric, often on moist sandstone, in dense forests. Altitude: often from lowlands to 1500 m.

Notes — *Hymenophyllum edentulum* is similar to *H. serrulatum* in some features. Holttum (Rev. Fl. Malaya 2 (1955) 79) suggested uniting them, but *H. edentulum* is less hairy and has a very slender rachis, the internal cell walls are only slightly thickened and broadly wavy near the surface and the sori are usually smaller.

Hymenophyllum edentulum is reported from Borneo, based on *Lobb s.n.*, in the original description, although Copeland (1937) doubted the identification; he was concerned with another syntype, *Griffith s.n.*, collected in Assam. The identification of the Assam and Borneo specimens are still doubtful, although the species is here broadly construed to include plants from both areas.

12. Hymenophyllum exsertum Wall.

Hymenophyllum exsertum Wall. in Hook., Sp. Fil. 1 (1844) 109, t. 38 A; Bedd., Handb. Ferns Brit. India (1883) 30, f. 16; C.Chr., Contr. U.S. Natl. Herb. 26 (1931) 330, pl. 24; Copel., Philipp. J. Sci. 64 (1937) 153, pl. 83; Tardieu & C.Chr. in Lecomte, Fl. Indo-Chine 7, 2 (1939) 53; Holttum, Rev. Fl. Malaya 2 (1955) 86, f. 28; K.Iwats., J. Fac. Sci. Univ. Tokyo, Sect. 3, Bot. 13 (1985) 513; J.X.Liu et al. in C.Y.Wu et al., Fl. China 2–3 (2013) 102. — *Mecodium exsertum* (Wall.) Copel., Philipp. J. Sci. 67 (1938) 23; Ching, Fl. Reipubl. Popularis Sin. 2 (1959) 73; Tagawa & K.Iwats. in Smitinand et al., Fl. Thailand 3 (1979) 73, f. 5-13. — Lectotype (designated by Morton, Contr. U.S. Natl. Herb. 38 (1973) 245): *Buchanan-Hamilton s.n.* (BM, Morton photograph 6592), Nepal.

Rhizome long-creeping, wiry, hairy throughout, laxly branched, c. 0.3 mm diam. *Stipes* remote, slender, hairy on the abaxial side, (1.5–)3–5 cm long, terete or sometimes winged on the upper part; *fronds* very variable in shape and size, oblong ovate, oblong or oblong-lanceolate, round to acute at apex, tripinnatisect, (2–)7–10 cm long, (1–)2.5–4 cm wide; *rachis* like the upper part of stipes, hairy throughout, more densely on abaxial side, winged throughout by flat wings, wings of the upper part broader, to 0.8 mm on both sides; *pinnae* many, more than 12 pairs, longer ones on lower part of fronds oblong to oblong-lanceolate, slightly falcate, round to moderately acute at apex, at most 2.5 cm long, 1 cm wide; *pinnules* with a few to several segments, in larger ones pinnately decompound; *ultimate segments* to 1.5 mm long, 1 mm broad, entire and flat, brownish in dried condition; hairs on all axes, rather sparse on upper axis, brown, to 2 mm long; *internal cell walls* rather thick, coarsely reticulate-pitted, more or less wavy.

Sori usually on upper portion of pinnae, dispersing from near rachis outwardly, the base constricted; *involucres* bivalvate to the very base; lips subtriangular, moderately acute, entire and flat, to 2 mm long, 1 mm broad; receptacles clavate, included in the lips. Chromosome numbers: $n = 21$, $2n = 42$ (Manton & Sledge, Philos. Trans., Ser. B, 238 (1954) 136, Mehra & Singh, J. Genet. 55 (1957) 380; Ghatak, Nucleus (Calcutta) 7 (1964) 30). — **Fig. 8c–f.**

Distribution — India, Sri Lanka, Nepal, Bhutan, China (Yunnan, Sichuan, Guangdong, Hainan, Xizang, Fujian, Hong Kong), Myanmar, Thailand, Vietnam, Laos and Cambodia; in *Malesia*: Peninsular Malaysia.

Habitat & Ecology — Epiphytic, usually in masses on mossy tree trunks in dense montane forests. Altitude: 1200–1800 m.

Note — *Hymenophyllum exsertum* is a species of southern and continental Southeast Asia and extending to Peninsular Malaysia in Malesia. It is another variable species throughout its wide area of distribution, although the Malesian specimens are only slightly variable in the size and form of the fronds as described above.

13. **Hymenophyllum firmum** Alderw.

Hymenophyllum firmum Alderw., Nova Guinea 14 (1924) 28; Copel., Philipp. J. Sci. 64 (1937) 57. — *Meringium firmum* (Alderw.) Copel., Philipp. J. Sci. 67 (1938) 44. — Lectotype (designated here): *Lam 1944* (lecto BO; isolecto L, U), New Guinea, Doorman Summit.

Hymenophyllum subfirmum Alderw., Nova Guinea 14 (1924) 28. — Lectotype (designated here): *Lam 1501* (lecto BO; isolecto BM, L), New Guinea, Doorman Summit.

Rhizome long-creeping, wiry, c. 0.7 mm diam., densely covered by brownish hairs, irregularly branching and bearing many roots with dense root hairs. *Stipes* terete throughout, or very narrowly winged in uppermost portion with wings of 1–3 rows of cells, sparsely hairy, hairs more dense at basal portion, 8–15 cm long; *fronds* rather irregularly oblong-subdeltoid in outline, acute to acuminate at apex, subtruncate to moderately broad cuneate at base, 10–22 cm long, to 15 cm wide, quadripinnate to pentapinnatifid; *rachis* like the upper part of stipes, very narrowly winged with entire wings; *larger pinnae* stalked, subtriangular, acuminate at apex, broadly cuneate at base, smaller pinnae oblong subdeltoid to narrowly oblong, sessile; pinna rachis distinctly winged, hairy; *larger pinnules* like smaller pinnae, secondary pinnules of larger pinnae with several segments; *ultimate segments* linear, round to moderately acute at apex, sparsely denticulate at margin, to 4 mm long, 0.2 mm broad; axes of every order, including costae of segments, hairy beneath, hairs pale brownish, multicellular, to 1 mm long; *internal cell walls* thick, wavy. *Sori* terminal on very short axillary segments, appearing as on pinna rachis; *involucres* with shallow tuberous portion and deeply cleft bilabiate part, c. 3 mm long, 1.2 mm diam.; lips round, slightly crenate; receptacles long-extruded.

Distribution — *Malesia*: New Guinea.

Habitat & Ecology — Epiphytic on mossy tree trunks and on fallen tree trunks. Altitude: 700–3200 m.

Notes — There is no distinct difference between *H. firmum* and *H. subfirmum*, even between the type specimens in BO.

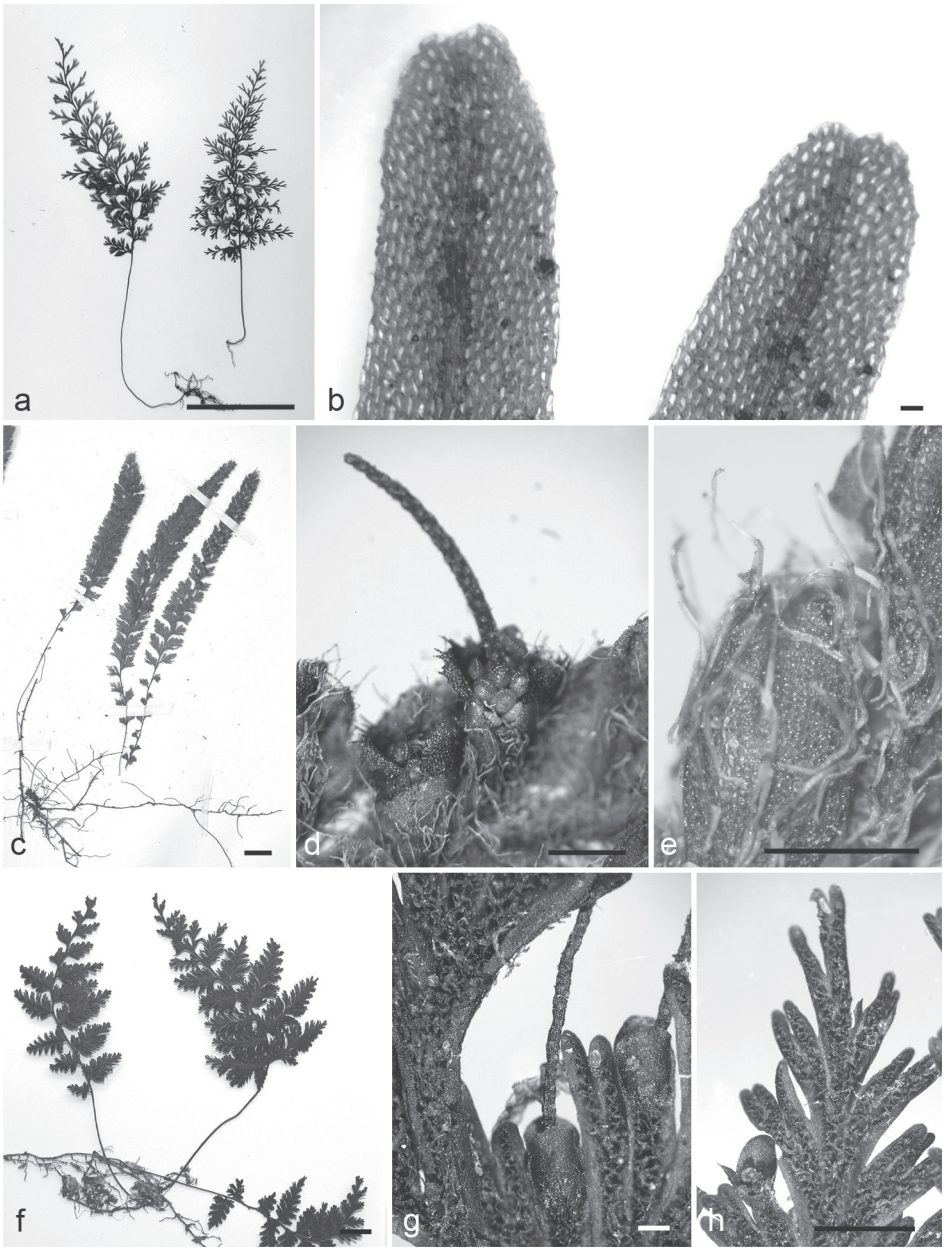

Fig. 9. a, b. *Hymenophyllum penangianum* C.G.Matthew & Christ. a. Fronds; b. laminar cells. — c–e. *H. foersteri* Rosenst. c. Fronds; d. sorus; e. multicellular, subarticulate hairs. — f–h. *H. fuscum* (Blume) Bosch. f. Fronds; g. sorus; h. accessory wings on lower surface (a, b: *Hotta 15190*, Sarawak, Malaysia, KYO; c–e: *van Balgooy 99*, Papua New Guinea, KYO 00010962; f–h: *Hotta & Tamin 144*, Sumatra, Indonesia, KYO).

Copeland indicated that the fronds become black when dried, although it may be variable. *Hymenophyllum firmum* is another variable species, based on the ample collections preserved in various herbaria, especially in such features as width of the segments, dentition at the margin of the segments, density of hairs on the axes of the fronds, size of the fronds, thickness of the rachis and stipes, and lips of the involucre, which range nearly entire to minutely toothed at the apex.

14. Hymenophyllum foersteri Rosenst.

Hymenophyllum foersteri Rosenst., Repert. Spec. Nov. Regni Veg. 12 (1913) 165; Copel., Philipp. J. Sci. 64 (1937) 58, pl. 23. — *Meringium foersteri* (Rosenst.) Copel., Philipp. J. Sci. 73 (1941) 463. — Syntypes: *Keysser B 31* (BM, S, UC), New Guinea, Bolan.

Rhizome long-creeping, rather densely hairy or glabrescent, c. 0.3 mm diam.; hairs multicellular, pale brown, to 1.8 mm long. *Stipes* filiform, terete, bearing hairs or glabrescent, c. 0.2 cm or less diam., (0.5–)1.5–3 cm long; *fronds* linear, moderately acute at apex, gradually narrowing downward or with several reduced pinnae on upper portion of stipes, sometimes elongate to 30 cm long, but usually 5–15 cm long, to 1.5 cm wide in the widest portion, bipinnate-tripinnatifid; *rachis* terete in lower portion, or pinnae decurrent on rachis to form very narrow wings, or winged in upper portion with wings flat but serrate at margin, densely hairy; *pinnae* many, close to each other, usually with intervals of less than 5 mm, forming a parallelogram or narrowly oblong, oblique, round to obtuse at apex, cuneate at shortly stalked or sessile base, to 1.3 cm long, 5 mm wide; pinna rachis winged like segments, densely hairy; *pinnules* simple to triforked; *ultimate segments* round at apex, c. 1 mm broad, densely hairy on costae and at margin, margin dentate at hair-base; hairs on rachis, pinna rachis, costae and margin of segments pale brown to whitish, multicellular, subarticulate, sometimes more than 2 mm long, persistent on fronds like thick matt. *Sori* at apex of short axillary branch of segments at basal acroscopic position of pinnae, or arranged in one row close to each side of rachis, campanulate with bilobed apex, sometimes tinted darkish; *involucres* c. 1.8 mm long, 0.8 mm diam.; bilobed portion in upper one-fourth, round or moderately acute; densely hairy on whole surface, margin of lips hairy, with short projections at base of hairs; involucres extruded. — **Fig. 9c–e.**

Distribution — *Malesia*: New Guinea.

Habitat & Ecology — Epiphytic; abundant on tree trunks in subalpine forests and on rock surfaces in mixed coniferous montane forests. Altitude: 2400–3950 m.

Note — The hairiness of the fronds is somewhat similar to species of subg. *Sphaerocionium*, although all the hairs are simple.

15. Hymenophyllum fuscum (Blume) Bosch

Hymenophyllum fuscum (Blume) Bosch, Hymenophyll. Javan. (1861) 62, pl. 51, 52B; Copel., Philipp. J. Sci. 64 (1937) 69, pl. 31. — *Trichomanes fuscum* Blume, Enum. Pl. Javae 2 (1828) 225. — *Amphipterum fuscum* (Blume) C.Presl, Epimel. Bot. (1851) 258; Copel., Philipp. J. Sci. 67 (1938) 46. — *Didymoglossum fuscum* (Blume) Hassk., Obs. Bot. Fil. 2 (1857) 19. — Type: *Blume s.n.* (holo L), Java.

Hymenophyllum dipteroneuron A.Braun ex Kunze, Bot. Zeitung (Berlin) 5 (1847) 225. — Type: Unknown (n.v.), Java.

Hymenophyllum zollingerianum Kunze, Bot. Zeitung (Berlin) 6 (1848) 305; Bosch, Hymenophyll. Javan. (1861) 61, pl. 50, 52A. — *Didymoglossum zollingerianum* (Kunze) Hassk., Obs. Bot. Fil. 2 (1857) 20 ('*zollingeri*'). — Lectotype (designated here): *Zollinger 1725* (lecto B; isolecto L), Java. Other syntype: *Zollinger 2308* (L, LE, P), Java.

Rhizome long-creeping on trunks or on branches of trees, usually forming a mat of leaves, wiry, c. 0.4 mm diam., bearing pale brownish hairs rather sparsely or glabrescent. *Stipes* not very thin, 3–8 cm long, with rather dense brown multicellular hairs, very narrowly winged throughout; *fronds* oblong-subdeltoid in smaller ones to broadly lanceolate in larger ones, variable in size and form, 4–20(–35) cm long, 3.5–5.5 cm wide in widest middle or lower portion, usually gradually narrowing to acute apex, narrowing towards base in larger fronds and broadly cuneate in smaller ones; *rachis* winged throughout with entire and flat wings, hairy on both the upper and lower sides; *pinnae* several to more than 25 pairs, alternate, oblong subdeltoid to narrowly oblong, to 2.5 cm long, 1 cm wide; *pinnules* with a few to several segments, never free from each other, or pinnae not fully pinnate; pinna rachis and veins hairy on lower surface but less densely on upper surface, bearing two accessory wings on lower surface; accessory wings c. 2 mm broad, entire, flat or more or less crisped, the same in pagina with rachis wings and laminae throughout the leaves; *ultimate segments* linear, moderately acute at apex, entire, flat, c. 0.7 mm broad, usually dark green in the field and reddish brown when dried; *internal cell walls* thin, wavy. *Sori* terminal on short branch of acroscopic side of segments; *involucres* campanulate with tuberous lower half and bilabiate upper portion; lips triangular, moderately acute at apex, entire, glabrous; several accessories continuous from accessory wings on surface of tuberous portion; receptacles long-extruded. — **Fig. 9f–h.**

Distribution — *Malesia*: Sumatra, Java and Lesser Sunda Islands (Flores and Bali).

Habitat & Ecology — Confined to moss-covered tree trunks and branches in misty zone, usually along ridges near the top of mountains. Altitudes: 1000–2000 or to 2500 m.

Note — *Hymenophyllum fuscum*, common in the mossy zone in West Malesia, is variable in the size and form of the fronds. Two synonyms are names that were given to different forms, but they are indistinguishable from *H. fuscum*. Plants of the Lesser Sunda Islands have narrower accessory wings, but they are not distinct from Javanese plants.

16. Hymenophyllum geluense Rosenst.

Hymenophyllum geluense Rosenst., Repert. Spec. Nov. Regni Veg. 5 (1908) 372; Copel., Philipp. J. Sci. 64 (1937) 72, pl. 33. — *Amphipterum geluense* (Rosenst.) Copel., Philipp. J. Sci. 67 (1938) 47. — Syntypes: *Werner 48* (B, BM, L, S), New Guinea, Mt Gelu.

Hymenophyllum geluense Rosenst. var. *apiciflora* Rosenst., Repert. Spec. Nov. Regni Veg. 12 (1913) 526. — Type: *Keysser 257* (holo n.v.; iso B, S), Papua New Guinea, Sattelberg.

Hymenophyllum geluense Rosenst. var. *minor* Rosenst., Repert. Spec. Nov. Regni Veg. 12 (1913) 526. — Type: *Keysser 239 p* (n.v.), Papua New Guinea.

Rhizome long-creeping on tree trunks, forming a mat of fronds, wiry, c. 1 mm diam., with rather dense pale brownish hairs. *Stipes* rigid, terete, 10–20 cm long, densely covered with hairs of 2–3 mm in length; *fronds* pinnately decompound, oblong lanceolate

to narrowly so, 20–30 cm long, 2–3(–8) cm wide at widest portion; *rachis* like upper part of stipes, narrowly winged, rather densely hairy; *lateral pinnae* many, lower ones bipinnate, to 10 cm long, 3–4 cm wide; *ultimate segments* slender, moderate, round, or obtuse at apex, toothed and flat at margin, c. 0.4 mm broad; veins thicker, reddish brown, with accessory wings on both upper and lower surfaces, the wings rather irregularly denticulate at margin, flat; *cells* slightly elongate, *internal cell walls* broadly and shallowly reticulate-pitted, finely wavy. *Sori* on acroscopic branch of pinnules, terminal to short segments; *involucres* tuberous in lower half and bilabiate at upper portion, c. 2.5 mm long, 1.2 mm broad, with accessories on tuberous portion; lips round, nearly entire; receptacles long-extruded.

Distribution — *Malesia*: New Guinea.

Habitat & Ecology — Epiphytic on mossy tree trunks in dense forests in summit zone and terrestrial among mosses in coniferous or lower subalpine forests at higher elevations. Altitude: 800–3700 m.

17. **Hymenophyllum gorgoneum** Copel.

Hymenophyllum gorgoneum Copel., Philipp. J. Sci. 64 (1937) 60, pl. 26; C.W.Chen et al., Sol Amazing (2017) 129. — *Meringium gorgoneum* (Copel.) Copel., Philipp. J. Sci. 67 (1938) 44. — Lectotype (designated by Ebihara & Iwatsuki, Mem. Natl. Mus. Nat. Sci. (Tokyo) 46 (2010) 96): *Brass 3304* (lecto MICH; isolecto BRI, GH, UC), Solomon Islands, Ysabel.

Rhizome long-creeping, densely covered with hairs, 0.5–0.8 mm diam.; hairs persistent, thin and straight, pale, to 1.5 mm long. *Stipes* dark, terete, sparsely hairy, 3–5 cm long; *fronds* subdeltoid or oblong-ovate, subacute to moderately acute at apex, widest at base or slightly narrowed towards base, (3–)5–10(–20) cm long, to 10 cm at widest basal portion, tripinnate to quadripinnatifid; *rachis* very narrowly winged throughout, with entire and flat wings of less than 0.2 mm broad on each side, rather densely hairy beneath; hairs pale brown, multicellular, semiarticulated; *pinnae* linear to linear subdeltoid, very shortly stalked in lower ones; pinna rachis winged to with similar feature as segments, hairy beneath; *pinnules* sessile, decurrent at base to wings of pinna rachis; *ultimate segments* c. 0.5 mm broad, apex round, margin dentate and flat. *Sori* at apex of short axillary branch at acroscopic base of basal acroscopic secondary pinnules, thus arranged in one row along each side of rachis, or more widely distributed in some cases, with campanulate basal portion and bilobed apical portion; *involucres* c. 3 mm long, 1.5 mm diam., basal campanulate portion not immersed in segments, often tinted blackish, bearing various projections on surface, upper bilobed portion cleft to halfway, moderately acute at apex, entire; receptacles long-extruded.

Distribution — *Malesia*: New Guinea, Bismarck & Admiralty Islands; Solomon Islands.

Habitat & Ecology — Epiphytic on tree trunks, on branches of trees, on tree roots, on fallen tree trunks and terrestrial on mossy ground in dense montane forests, often on ridges from mid to high elevations. Altitude: 600–3400 m.

Notes — The general appearance of the vegetative features are more or less similar to *H. firmulum*, although the large blackish sori are distinct. The cristate lip of the involucre is another distinct feature to discriminate this species from allied ones.

The smaller fronds are similar to *H. melanosorum*, but the two species are different in: *H. gorgoneum*: fronds larger, usually more than 15 cm long, usually flat; segments flat, toothed with thin, sharp teeth. *Hymenophyllum melanosorum*: fronds smaller, normally less than 6 cm long, rarely to 12 cm long, often curled in cubic form; segments more or less involute sharply toothed with scale-like appearance of the teeth.

18. Hymenophyllum hieronymi (Brause) C.Chr.

Hymenophyllum hieronymi (Brause) C.Chr., Index Filic., Suppl. 3 (1934) 114. — *Trichomanes hieronymi* Brause, Bot. Jahrb. Syst. 49 (1912) 6, f. 1A. — Lectotype (designated here): *Schlechter 19701* (lecto B 20 0104652; isolecto BM, E, K, L, P, US), Papua New Guinea, Kaiser-Wilhelmsland.

Rhizome long-creeping, wiry, c. 0.2 mm diam., hairy or glabrescent; hairs multicellular, more or less articulated, pale brown, to 2 mm long. *Stipes* to 1.2 cm long, terete, rather densely hairy with brownish, setose hairs; *fronds* remotely placed, oblong subdeltoid to broadly oblong, moderately acute at apex, round at base, 3.5–5 cm long, to 3 cm wide, bipinnate to tripinnatifid; rachis like the upper portion of stipes, densely hairy, winged; *lateral pinnae* to 10 in pairs, lower ones reduced in size, middle ones the largest; largest pinnae oblong to narrowly oblong, round at apex, cuneate at base, pinnate or bipinnatifid, to 1.5 cm long, 0.7 cm wide; pinna rachis rather densely hairy with soft brownish hairs; *ultimate segments* simple or rarely biforked, narrow, round to obtuse at apex, wavy and flat at margin, to 1 mm broad; veins underneath rather densely hairy, upper surface of fronds glabrous. *Sori* solitary at apex of basal acroscopic segments, thus arranged in one row at each side of pinna rachis; *involucres* campanulate with bilabiate mouth, 1.5–2 mm long, c. 1 mm diam., lips cleft nearly halfway down, entire or very minutely wavy at margin; receptacles long-extruded.

Distribution — *Malesia*: Papua New Guinea (known only from the type collection).

Habitat & Ecology — Not recorded.

Note — *Hymenophyllum hieronymi* was placed in synonymy under *H. ovatum*, from which it is distinct in its soft papyraceous texture and nearly entire margin of the lips of the involucre.

19. Hymenophyllum holochilum (Bosch) C.Chr.

Hymenophyllum holochilum (Bosch) C.Chr., Index Filic. (1905) 226, 362; Copel., Philipp. J. Sci. 64 (1937) 34, pl. 14; Holttum, Rev. Fl. Malaya 2 (1955) 77, f. 17; K.Iwats., J. Fac. Sci. Univ. Tokyo, Sect. 3, Bot. 13 (1985) 511; J.X.Liu et al. in C.Y.Wu et al., Fl. China 2–3 (2013) 104; C.W.Chen et al., Sol Amazing (2017) 130; K.Iwats. et al., PhytoKeys 119 (2019) 111. — *Didymoglossum holochilum* Bosch in Miq., Pl. Jungh. 5 (1856) 561. — *Leptocionium holochilum* (Bosch) Bosch, Ned. Kruidk. Arch. 4 (1859) 383; Hymenophyll. Javan. (1861) 44, pl. 34. — *Meringium holochilum* (Bosch) Copel., Philipp. J. Sci. 67 (1938) 41; Fern Fl. Philipp. 1 (1958) 62; Ching, Fl. Reipubl. Popularis Sin. 2 (1959) 149; Tagawa & K.Iwats. in Smitinand et al., Fl. Thailand 3 (1979) 77, f. 5–4. — Type: *Hasskarl s.n.* (holo L), Java.

Didymoglossum affine Bosch in Miq., Pl. Jungh. 5 (1856) 562. — *Leptocionium affine* (Bosch) Bosch, Ned. Kruidk. Arch. 4 (1859) 383; Hymenophyll. Javan. (1861) 45, pl. 35. — *Hymenophyllum affine* (Bosch) Racib., Pteridoph. Buitenzorg (1898) 20, nom. illeg., non Brack. (1854). — *Hymenophyllum boschii* Rosenst., Bull. Jard. Bot. Buitenzorg, sér. 2, 2 (1911) 24. — Type: *Molkenboer s.n.* (n.v.), Java.

Hymenophyllum kurzii Prantl, Unters. Morph. Gefässkrypt. 1 (1875) 54. — Syntypes: *Kurz 293* (M), Java; *Kurz 720* (M n.v.), Java; *Kurz 722* (M), Java.

Hymenophyllum tunbrigense (L.) Sm. var. *exsertum* F.M.Bailey, Rep. Bellenden-Ker Range (1889) 74. — Lectotype (designated by Croxall, Austral. J. Bot. 23 (1975) 516): *Bailey s.n.* (lecto BRI; isolecto BM, K, NSW), Australia, Queensland.

Hymenophyllum boschii Rosenst. var. *euryglossa* Rosenst., Bull. Jard. Bot. Buitenzorg, sér. 2, 2 (1911) 24. — Syntypes: *Beccari PS 440* (n.v.), Sumatra; *Hallier 407* (BO n.v.), Borneo.

Hymenophyllum subdimidiatum Rosenst., Meded. Rijks-Herb. 11 (1912) 1. — Lectotype (designated by Croxall, Austral. J. Bot. 23 (1975) 517): *Schlechter 14799* (lecto L; isolecto BM, K, M, MICH, NSW, P), New Caledonia.

Hymenophyllum elberti Rosenst., Meded. Rijks-Herb. 14 (1912) 31; Copel., Philipp. J. Sci. 64 (1937) 38. — Syntypes: *Elbert (C.Gruendler) 2312* (BM, L), Lombok.

Hymenophyllum pseudotunbrigense Watts, Proc. Linn. Soc. New South Wales 39 (1915) 766. — Lectotype (designated by Croxall, Austral. J. Bot. 23 (1975) 517): *Waller P1813* (NSW), Australia, Queensland.

Hymenophyllum babindae Watts, Proc. Linn. Soc. New South Wales 39 (1915) 766, pl. 87, f. 5. — Lectotype (designated by Croxall, Austral. J. Bot. 23 (1975) 517): *Watts s.n.* (lecto NSW; isolecto BRI), Australia, Queensland.

Hymenophyllum holochilum (Bosch) C.Chr. var. *subgenuinum* Alderw., Bull. Jard. Bot. Buitenzorg, sér. 2, 20 (1915) 19. — Type: *Backer 10214* (holo BO), Java.

Hymenophyllum rufifolium Alderw., Bull. Jard. Bot. Buitenzorg, sér. 2, 28 (1918) 28; Copel., Philipp. J. Sci. 64 (1937) 38. — Lectotype (designated here): *Bünnemeijer 925* (lecto BO; isolecto BM), Sumatra.

Hymenophyllum rufifrons Alderw., Bull. Jard. Bot. Buitenzorg, sér. 2, 28 (1918) 28; Copel., Philipp. J. Sci. 64 (1937) 38. — Lectotype (designated here): *Brooks 295/S* (lecto BO; isolecto BM, P), Sumatra.

Hymenophyllum hamuliferum Alderw., Bull. Jard. Bot. Buitenzorg, sér. 2, 28 (1918) 29. — Lectotype (designated here): *Bünnemeijer 2057* (lecto BO; isolecto BM, L, MICH), Sumatra, Bangka.

Hymenophyllum lingganum Alderw., Bull. Jard. Bot. Buitenzorg, sér. 3, 5 (1922) 208. — Lectotype (designated here): *Bünnemeijer 6621* (lecto BO; isolecto L, MICH), Sumatra, Lingga Island.

Hymenophyllum ellipticosorum Alderw., Nova Guinea 14 (1924) 27; Copel., Philipp. J. Sci. 64 (1937) 39. — Type: *Lam 1469* (holo BO), New Guinea, Indenburg River.

Hymenophyllum nutantifolium Alderw., Nova Guinea 14 (1924) 27; Copel., Philipp. J. Sci. 64 (1937) 39. — Type: *Lam 1470* (holo BO n.v.), New Guinea, near Doorman Summit.

Hymenophyllum viride Rosenst. ex Copel., Philipp. J. Sci. 64 (1937) 59. — Lectotype (designated by Croxall, Austral. J. Bot. 23 (1975) 517): *Schlechter 14799* (lecto L; isolecto BM, K, MICH, NSW, P, US), New Caledonia.

Meringium latifolium Copel., Philipp. J. Sci. 73 (1941) 461. — *Hymenophyllum latifolium* (Copel.) C.V.Morton, Contr. U.S. Natl. Herb. 38 (1968) 167. — Lectotype (designated here): *Brass 11091* (lecto MICH 1190743; isolecto BM, BO, GH, K, L), New Guinea, Bele River.

Meringium bartlettii Copel., Philipp. J. Sci. 73 (1941) 464. — *Hymenophyllum bartlettii* (Copel.) C.V.Morton, Contr. U.S. Natl. Herb. 38 (1968) 167. — Lectotype (designated here): *Bartlett 15973* (lecto MICH 15973; isolecto PNH, UC), Philippines, Mindanao, Davao.

Meringium laxum Copel., Univ. Calif. Publ. Bot. 18 (1942) 217. — *Hymenophyllum laxum* (Copel.) C.V.Morton, Contr. U.S. Natl. Herb. 38 (1968) 167. — Type: *Clemens 12343A* (holo MICH; iso UC), New Guinea, Rowlinson Range.

Rhizome slender, wiry, with rather sparse pale brown hairs, c. 0.3 mm diam. *Stipes* 1–4 cm long, terete or very narrowly winged on upper portions with a row of cells on each side, more or less bearing dense brown hairs of up to 1.5 mm in length; *fronds* oblong to oblong-lanceolate, round to moderately acute at apex, round to cuneate at

base, 3–10 cm long, 1.7–4 cm wide, bipinnatifid to tripinnatifid; rachis slender, hairy on lower surface, wingless or very narrowly winged in lower portion with usually flat and not toothed wings; *pinnae* close, 5–9(–12) alternate pairs, oblong to ovate, spreading or somewhat oblique, with 2–7(–12) segments; *pinnules* usually simple, rarely forked or sometimes trilobed; ultimate segments linear or broader, round at apex, distinctly and sharply toothed at margin but not crisped, c. 1 mm or to 1.5 mm broad. *Sori* solitary, on basal acroscopic lobes of pinnae, often in one row at each side of rachis, but may be more widely distributed, base hollow, inversely conical, more or less winged, with 1–3 rows of longitudinal ridges at the base on the lower surface; *involucres* with tuberous base and bilabiate upper portion, cleft to halfway, c. 2 mm long, 1 mm broad; lips shorter than hollow base, subdeltoid, moderately acute at apex, subentire or irregularly toothed; receptacles of mature sori extruded. Chromosome numbers: $2n = 21$ (Braithwaite, Bot. J. Linn. Soc. 71 (1975) 169).

Distribution — Taiwan, Thailand (Peninsular); throughout *Malesia*; Solomon Islands, Vanuatu, Fiji, New Caledonia, Australia.

Habitat & Ecology — Epiphytic on tree trunks and on branches of large trees in tropical evergreen forests. Altitude: at low to middle elevations, to 2300 m, or even to 3700 m on Mt Kinabalu (Sabah, N Borneo).

Notes — This is another variable species complex, and many names have been proposed for the plants probably belonging to this species.

Hymenophyllum brevipes has narrower segments, which are reminiscent of the morphology of *H. ramosii*; *H. elbertii* is only slightly different from *H. holochilum* except in the rather loose arrangement of the segments; the Sumatran *H. rufifolium* again has very narrow ultimate segments, to 0.6 mm broad, and occurs between 1200 and 1900 m altitude; *H. rufifrons* is another Sumatran plant with larger fronds, divided more amply, to 10 cm long, 5 cm wide, tripinnate-quadripinnatifid and with distinct wings on the rachis; *H. latifolium* has broadly oblong fronds and is more or less distinct in having larger, thick sori; *Meringium laxum* has longer fronds with laxly placed pinnae and ultimate segments, although narrow wings at the very base of the rachis; *M. bartlettii* has sharper teeth on the margin of the segments and sori gathered on the apical portion of the fronds and the lips of the involucres minutely but sharply dentate. The type of *H. rosenstockii* appears somewhat similar to *H. blandum*. Several specimens from New Guinea and the Admiralty Islands in the Kew Herbarium that were annotated by Croxall as *H. rosenstockii* should be included in the *H. holochilum* complex, although the fronds are oblong to oblong-subdeltoid and not narrowly oblong as in the common form of *H. holochilum*; the rhizome is stouter, c. 0.4 mm diam. and with rather dense brownish hairs. *Hymenophyllum ellipticosorum* is reduced to *H. holochilum*. It is larger, with narrowly winged stipes 2–3 cm long, subtripinnatifid linear-lanceolate fronds 3–6 cm to 20 cm long, 1.5–2.5(–3) cm wide, subglabrous; ultimate segments 7.5–10 mm long and 1–1.6(–2) mm broad, distinctly dentate margins; sori solitary on ultimate segments, 1.5–2 mm long, c. 0.8 mm diam., and usually with a constriction at the base where they connect with the apex of the segments; and receptacles long extruded.

20. Hymenophyllum hosei Copel.

Hymenophyllum hosei Copel., Philipp. J. Sci., C. 12 (1917) 46; C.Chr., Mitt. Inst. Allg. Bot. Hamburg 7 (1928) 143; Copel., Philipp. J. Sci. 64 (1937) 45, pl. 16. — *Meringium hosei* (Copel.) Copel., Philipp. J. Sci. 67 (1938) 42. — Lectotype (designated here): *Hose 730* (lecto MICH 1190651; isolecto B, K, P, PNH), Borneo, Sarawak.

Rhizome long-creeping, wiry, c. 0.3 mm diam., hairy, with brown multicellular hairs c. 1.5 mm long, caducous. *Stipes* 2–5 cm long, slender, winged in upper portions or nearly to the base, hairy or glabrescent; *fronds* tripinnatifid, oblong to oblong-lanceolate, moderately acute at apex, (2–)4–7(–12) cm long, in average c. 2.5 cm wide or variable in size; *rachis* straight or slightly zigzag in upper portion, hairy beneath, distinctly winged throughout; wings flat or rarely crisped, narrowly black margined, distinctly toothed or often entire in the lower part; *lateral pinnae* very shortly stalked or sessile, acute to moderately so at apex; pinna rachis winged to have appearance similar to segments, with dentate wings, hairy beneath; *pinnules* simple to pinnatifid with 2–6 segments; *ultimate segments* 0.7–1 mm broad, round at apex, hairy on costae underneath or glabrescent, the margin flat, dentate, often black margined; *internal cell walls* more or less thickened, coarsely pitted. *Sori* at apex of short auxiliary branch of ultimate segments, c. 2.5 mm long, 1 mm diam., campanulate; *involucres* tuberous in lower portion with accessories on the surface, the mouth bilabiate, cleft to one-third to two-fifth way down, subtriangular, acute at apex, distinctly dentate; receptacles long-extruded beyond lips.

Distribution — *Malesia*: Borneo and Moluccas (Seram).

Habitat & Ecology — Epiphytic on tree trunks and epipetric on moist mossy rocks in both dense tropical forests and dry forests. Altitude: from lowlands to 2300 m.

Note — *Hymenophyllum hosei* may be a form derived from *H. denticulatum*, but has fewer denticulations on the wings and ultimate segments of the flat margin. The margin of the segments is denticulate, evenly flat and arranged in one plane and never crisped. In this feature, *H. hosei* is in a position between *H. denticulatum* and *H. serrulatum*; from the latter, *H. hosei* is distinct in the winged rachis and stipes.

21. Hymenophyllum johorense Holttum

Hymenophyllum johorense Holttum, Gard. Bull. Straits Settlem. 4 (1929) 408, f.; Copel., Philipp. J. Sci. 64 (1937) 51, pl. 19; Holttum, Rev. Fl. Malaya 2 (1955) 80, f. 21. — *Microtrichomanes johorense* (Holttum) Copel., Philipp. J. Sci. 67 (1938) 96. — *Meringium johorense* (Holttum) Copel., Fern Fl. Philipp. 1 (1958) 64. — Lectotype (designated here): *Holttum 10755* (lecto SING; isolecto BM, BO, K), Peninsular Malaysia, Gunong Belumut.

Hymenophyllum reductum Copel., Philipp. J. Sci. 64 (1937) 53, pl. 20. — *Meringium reductum* (Copel.) Copel., Philipp. J. Sci. 67 (1938) 43; Fern Fl. Philipp. 1 (1958) 64. — Type: *Elmer 9747* (holo MICH; iso GH), Philippines, Negros.

Rhizome long-creeping, very slender, c. 0.15 mm diam., wiry, bearing pale brownish hairs rather sparsely. *Stipes* 0.6–1 cm long, filiform, terete nearly throughout, glabrous except for hairy base; *fronds* broadly oblong but often irregular in dwarfed form, narrowly cuneate and decurrent on stipes at base, to 2 cm long, 1 cm wide, seemingly dichotomously branching twice or three times; *ultimate segments* 3–5, 5–12 mm long,

c. 2 mm broad, unequal, ascending; edge of segments bearing numerous stiff, reddish brown hairs of c. 0.5 mm long. *Sori* at apices of ultimate segments, with more or less immersed tubes; *involucres* with short, narrow, hollow, conical in basal one-third portion, with accessary projections rather sparsely on basal portion, c. 2 mm long, 1.5 mm diam.; lips cleft to c. two-thirds way to the base, almost circular in outline, round, strongly toothed, the teeth bearing hairs like those at edge of segments; receptacles extruded from edge of lips. — **Fig. 7i.**

Distribution — *Malesia*: Peninsular Malaysia (Johore: G Belumut), Borneo (Sabah: Mt Kinabalu) and Philippines (Luzon: Mt Makiling, Mt Isarog; Tayabas: Mt Binusag; Negros).

Habitat & Ecology — In close mats on mossy tree trunks. Altitude: at the summit zone and at higher elevations, 1000–3000 m.

Notes — The hairs at the margin of the ultimate segments are distinct, multicellular, brown and thick, but are not the same as those of *H. digitatum*. The hairs of *H. johorense* were described and discussed in detail by Iwatsuki (Gard. Bull. Singapore 30 (1977) 68–69).

Philippines plants are larger and with broader segments and give a different impression than the Malay-Bornean plants. The diagnostic features of branching pattern and hairiness are the same throughout the above areas.

Copeland (1937) reviewed the concept of Christensen that *H. perparvulum* might be an earlier homonym of *H. johorense*, but that is a form of *H. lobbii* and is not referable here; *H. perparvulum* has pinnately divided fronds with ultimate segments sharply toothed but not setose at the margin.

22. **Hymenophyllum klabatense** Christ

Hymenophyllum klabatense Christ, Verh. Naturf. Ges. Basel 11 (1894) 4; Copel., Philipp. J. Sci. 64 (1937) 30; K.Iwats. et al., PhytoKeys 119 (2019) 111. — *Meringium klabatense* (Christ) Copel., Philipp. J. Sci. 67 (1938) 40; Fern Fl. Philipp. 1 (1958) 59. — Type: *Sarasin s.n.* (holo P), Sulawesi, Mt Klabat.

Rhizome long-creeping, wiry, slender, 0.5–0.7 mm diam., irregularly branching, bearing dense brownish hairs; hairs brown to pale brownish, persistent, to 1.5 mm long. *Stipes* terete, densely hairy throughout, not very thick but stout, (3–)6–9(–12) cm long; *fronds* oblong-subdeltoid to oblong-lanceolate, widest at basal or lower middle portion, gradually narrowing towards acute apex, tripinnate to quadripinnatifid, (4–)8–14 cm long, to 6 cm wide; *rachis* like the stipes, slender upwards, hairy, winged with narrow, entire wings in upper portion; *larger pinnae* shortly stalked, ascending, oblong, moderately acute at apex; secondary pinnae sessile, with winged pinna rachis; *ultimate segments* narrow, 0.2–0.4(–0.7) mm broad, rather sparsely minutely denticulate, round to moderately acute at apex, flat, reddish brown or dark in dried condition; *internal cell walls* thin and straight. *Sori* campanulate, more than 2 mm long, c. 1 mm diam., dark at maturity; lips bilabiate to halfway, round to moderately acute at apex, entire; receptacles extruded.

Distribution — *Malesia*: Philippines (Mindanao), Sulawesi and Moluccas (Seram).

Habitat & Ecology — Epiphytic on moss-covered trees, on basal trunks and on branches in deep shade in mossy forests at middle to high elevations.

Note — *Hymenophyllum klabatense* has been referred to as a local form credited to Sulawesi, but is discriminated from *H. serrulatum* in having narrower segments, c. 0.7 mm broad, larger sori and dried specimens brownish. This was noted by Copeland (1937) as: "…hardly more than a local form of *H. meyeniaum* with less hairy axes, thinner walls, and narrower segments than are usual in that variable species.". Sori are large, sometimes to 3 mm long and 1.5 mm diam. This is a form from Sulawesi, although there are comparable specimens from the Philippines and Seram. It was actually difficult to conclude that *H. klabatense* is a distinct species, as *H. serrulatum* is usually very broadly defined, but ample collections from Seram showed it to be distinct. *Hymenophyllum klabatense* is close to *H. serrulatum*, and is also comparable with *H. rosenstockii*, which may be referred to as a dwarf derivative of the latter species.

23. Hymenophyllum laminatum Copel.

Hymenophyllum laminatum Copel., Philipp. J. Sci., C. 6 (1911) 70; Philipp. J. Sci. 64 (1937) 73, pl. 34. — *Amphipterum laminatum* (Copel.) Copel., Philipp. J. Sci. 67 (1938) 47. — Lectotype (designated here): *Copland King 341* (lecto MICH 1190653; isolecto BM, NSW), Papua New Guinea, Lakekamu.

Rhizome long-creeping on tree trunks, wiry, 0.3–0.5 mm diam., hairy with pale brownish hairs. *Stipes* slender, densely hairy at base with longer hairs, rather sparsely hairy or glabrescent upwards, 4–5 cm long; *fronds* lanceolate, bipinnate, gradually narrowing towards acute apex, cuneate at base, c. 15 cm long, 2.5–3.5 cm wide; *rachis* slender, like upper portion of stipes, narrowly winged, with articulated hairs or glabrescent; *pinnae* lanceolate, acute at apex, deeply pinnatisect nearly to pinna rachis; *ultimate segments* oblanceolate to obovate, denticulate at margin; veins with accessory wings on both upper and lower surfaces, the wings continuous, nearly entire or rarely wavy at margin, flat; the cells of normal lamina somewhat elongate; *internal cell walls* broadly and shallowly reticulate-pitted, nearly straight or finely wavy. *Sori* at apex of very short acroscopic branch of segments, tuberous in lower half, bilabiate in upper portion, c. 2.5 mm long, 1 mm broad, with accessories on tuberous portion; lips round, irregularly dentate at margin; receptacles long-extruded.

Distribution — *Malesia*: Papua New Guinea.

Habitat & Ecology — Epiphytic on high branches of trees in lower montane, usually dense, forests. Altitude: 1650–3300 m.

Note — Similar to *H. geluense*, but differing from it in the less dense hairs on the stipe and rachis. *Hymenophyllum laminatum* is generally more delicate, but the features of the accessary wings are similar in the two species.

24. Hymenophyllum ledermannii Brause

Hymenophyllum ledermannii Brause, Bot. Jahrb. Syst. 56 (1920) 41; Copel., Philipp. J. Sci. 64 (1937) 70, pl. 32. — *Amphipterum ledermannii* (Brause) Copel., Philipp. J. Sci. 67 (1938) 47. — Lectotype (designated here): *Ledermann 9408* (lecto B 20 0101917; isolecto BM, MICH, S), Papua New Guinea. Other syntype: *Ledermann 8993* (B), Papua New Guinea, Etappenberg.

Hymenophyllum ledermannii Brause var. *nutans* Brause, Bot. Jahrb. Syst. 56 (1920) 42. — Lectotype (designated here): *Ledermann 10117* (lecto B 20 0101920; isolecto B 20 0101917), Papua New Guinea. Other syntype: *Ledermann 9171a* (B), Papua New Guinea.

Rhizome long-creeping on tree trunks, wiry, c. 0.8 mm diam., with sparse pale brownish multicellular hairs, glabrescent. *Stipes* slender, terete, or very narrowly winged except for very base, sparsely hairy, 7–12 cm long; *fronds* oblong-ovate to lanceolate, obtuse at apex, pinnate-bipinnatifid to bipinnate-tripinnatifid, 10–15 cm long, 2.5–7 cm wide, reddish brown in dried condition, glabrous; *rachis* like upper portion of stipes, narrowly winged throughout, distinctly hairy with long hairs; *pinnae* petiolate, 10–15 pairs, more or less truncate at apex, broadly cuneate at base, c. 3 cm long, 1.7 cm wide; *ultimate segments* linear, entire at margin, moderately acute at apex; both sides of pinnule rachis and veins with narrow, entire, flat or slightly undulate accessory wings; *internal cell walls* thin, wavy. *Sori* on acroscopic branch of pinnae, usually along rachis; *involucre*s tuberous at basal half and bilabiate at upper portion, c. 2.5 mm long, 1 mm broad; tuberous portion with accessories continuous from accessory wings; lips round at apex, entire; receptacles long-extruded.

Distribution — *Malesia*: New Guinea.

Habitat & Ecology — Epiphytic on mossy tree trunks in dense forests. Altitude: 850–2800 m.

Note — Most closely resembling the West Malesian *H. fuscum* in various characters. Variation in the form and size of the fronds is seen in parallel in the two species.

25. Hymenophyllum lobbii T.Moore ex Bosch

Hymenophyllum lobbii T.Moore ex Bosch, Ned. Kruidk. Arch. 5(3) (1863) 176; C.Chr., Gard. Bull. Straits Settlem. 7 (1934) 215; Copel., Philipp. J. Sci. 64 (1937) 49; Croxall, Austral. J. Bot. 23 (1975) 516. — *Meringium lobbii* (T.Moore ex Bosch) Copel., Philipp. J. Sci. 67 (1938) 43. — Lectotype (designated by Croxall 1975: 516): *Lobb s.n.* (lecto K), Ins. Malasicae (see Field, Austral. Syst. Bot. 33 (2020) 24). Other syntype: *Griffith s.n.* (K n.v.), India orientalis (Assam).

Trichomanes serratulum Baker in Hook. & Baker, Syn. Fil. (1867) 80; Domin, Biblioth. Bot. 20(85) (1913) 15, pl. 3, f. 4. — Type: *Lobb s.n.* (holo K), Borneo.

Hymenophyllum subflabellatum Ces., Felci (1876) 8. — Type: *Beccari s.n.* (holo FI), Borneo, Sarawak.

Hymenophyllum perparvulum Alderw., Bull. Jard. Bot. Buitenzorg, sér. 2, 16 (1914) 18; Copel., Philipp. J. Sci. 64 (1937) 52. — Lectotype (designated here): *Matthew 664* (lecto BO; isolecto BM, K), Sumatra, Mt Singgalong.

Rhizome long-creeping on tree trunks, very slender, 0.1–0.2 mm diam., wiry, with sparse short brown hairs, glabrescent. *Stipes* filiform, terete, 2–3.5 mm long, glabrous except for hairy base; *fronds* broadly oblong to oblong-lanceolate, round at apex, round to broadly cuneate at base, to 1.5 cm long, 5 mm wide, pinnately dissected to bipinnatifid, or at most with several segments on a pinna; *rachis* hairy, terete in lower portion, narrowly winged in distal half, wings entire, flat; *lower pinnae* sessile, forked or with to four lobes, upper pinnae simple; *ultimate segments* linear, round to moderately acute at apex, c. 3 mm long, 0.5 mm broad, sparsely but sharply toothed at margin. *Sori* at apices of ultimate segments, usually immersed, with tuberous and immersed base and bilabiate upper portion; *involucres* cleft three-fourths way down; lips orbicular, sharply dentate; receptacles extruded. — **Fig. 7e, f.**

Distribution — *Malesia*: Sumatra and Borneo; Australia (Queensland).

Habitat & Ecology — Epiphytic, confined to tree trunks, usually forming large mats in thick moss on trunks of large trees, in dense moist forests. Altitude: from low elevations to 2400 m.

Note — *Hymenophyllum perparvulum* has pinnate-bipinnatifid fronds with more than ten ultimate segments. Fronds are at most 1.5 cm long, 0.8 cm wide; rachis wingless in basal half or distinctly winged in distal portion, hairy with long, brown, multicellular hairs; segments less than 1 mm broad, round to obtuse at apex, densely dentate at flat margin, never setiferous; involucres deeply cleft more than halfway, lips round, distinctly dentate.

26. Hymenophyllum macrosorum Alderw.

Hymenophyllum macrosorum Alderw., Bull. Jard. Bot. Buitenzorg, sér. 2, 16 (1914) 18; Copel., Philipp. J. Sci. 64 (1937) 48. — *Meringium macrosorum* (Alderw.) Copel., Philipp. J. Sci. 67 (1938) 43. — Lectotype (designated here): *Matthew 705* (lecto BO; isolecto BM, K, L), Sumatra, Mt Singgalang.

Rhizome long-creeping, c. 0.4 mm diam., with sparse pale brown hairs more than 1 mm long. *Stipes* with narrow wings on upper portion or nearly to the base, hairy in lower portion with hairs similar to those on rhizome; *fronds* oblong to oblong-lanceolate, moderately acute at apex, round to cuneate at base, 5–8 cm long, 1.5–3 cm wide, quadripinnatifid; rachis narrowly winged throughout, wings to 0.5 mm broad on each side of rachis, distinctly dentate, flat; *lateral pinnae* narrowly oblong, ascending, round at apex, sessile or very shortly stalked at base; pinna rachis winged with wings like those of rachis, hairy on lower surface; *pinnules* simple or with to three segments; *ultimate segments* linear, round to obtuse at apex, c. 0.6 mm broad, sparsely but sharply dentate at margin, often involute in dried condition, minutely hairy on costa underneath. *Sori* solitary, at apices of short acroscopic segments of pinnae or arranged in one row on each side of rachis, large in size, usually dark and distinct; *involucres* campanulate with bilabiate mouth, c. 3.5 mm long, 2 mm or more diam.; lower tuberous portion with irregular accessories on surface, bilabiate portion c. one-third on distal side, lips round to moderately acute at apex, entire; receptacles long-extruded.

Distribution — *Malesia*: Sumatra, Borneo.

Habitat & Ecology — Epiphytic on the undersurface of moss-covered tree trunks in upper montane forests. Altitude: 2700–3400 m.

Note — The ultimate segments are narrow, c. 0.6 mm in width, and the sori have campanulate involucres more than 2 mm in width. *Hymenophyllum macrosorum* is distinct in the large sori, especially when compared with the narrow ultimate segments and long extruded receptacles.

27. Hymenophyllum melanosorum (Copel.) C.V.Morton

Hymenophyllum melanosorum (Copel.) C.V.Morton, Contr. U.S. Natl. Herb. 38 (1968) 167; K.Iwats. et al., PhytoKeys 119 (2019) 111. — *Meringium melanosorum* Copel., Philipp. J. Sci. 73 (1941) 462. — Lectotype (designated here): *Brass & Meijer Drees 10327* (lecto MICH 1190745; isolecto BM, BO, BRI, L), New Guinea, Mt Wilhelmina.

Rhizome long-creeping, hairy but glabrescent, dark, 0.3–0.5 mm diam.; hairs brownish, multicellular, semiarticulated. *Stipes* terete, sparsely hairy with long brown hairs, 2–5 cm long; fronds oblong to oblong-subdeltoid, round to moderately acute at apex, round at usually widest base, 3–5 cm long, to 2 cm wide, tripinnate to quadripinnatifid; *rachis* winged throughout or terete in basal portion, sparsely hairy beneath; *pinnae* short-stalked in basal ones, semiquadrangular or oblong ovate; pinna rachis winged throughout, very sparsely hairy beneath; *ultimate segments* round at apex, flat and distinctly toothed at margin, or more or less involute, 0.7–1 mm broad, with teeth to 1 mm in length. *Sori* seemingly directly on basal acroscopic position of secondary pinnules, thus arranged in one row at each side of rachis, large and distinctly blackish, with deep tuberous portion and bilabiate mouth; *involucres* c. 4 mm long, 2 mm diam., with various projections on surface; lips on apical one quarter portion, bilabiate, round and entire, or very minutely wavy; receptacles thick, very long-extruded, blackish.

Distribution — *Malesia*: Moluccas (Ambon and Seram) and New Guinea.

Habitat & Ecology — Epiphytic on mossy tree trunks and on tree fern trunks in subalpine and mossy montane forests, usually in calcareous areas. Altitude: (1000–) 2000–3800 m.

Note — In the finely dissected frond construction and large blackish sori, *H. melanosorum* resembles *H. gorgoneum*. The long, distinct teeth at the margin of the segments with several rows of cells at their base are reminiscent of *H. ooides*.

28. Hymenophyllum merrillii Christ

Hymenophyllum merrillii Christ, Philipp. J. Sci., C. 2 (1907) 154; Copel., Philipp. J. Sci. 64 (1937) 33, pl. 13. — *Meringium merrillii* (Christ) Copel., Philipp. J. Sci. 67 (1938) 41; Fern Fl. Philipp. 1 (1958) 61. — Lectotype (designated here): *Merrill 3927* (lecto P 00623490; isolecto MICH, PNH), Philippines, Luzon, Province of Pampanga. Other syntype: *Loher s.n.* (P), Philippines, Luzon, Mariveles.

Rhizome long-creeping, wiry, slender, 0.15–0.2 mm diam., sparsely but persistently hairy with pale brown hairs. *Stipes* short, to 2 cm long, terete, sparsely hairy throughout with brown hairs to 1.2 mm in length; *fronds* oblong-lanceolate, acute at apex, gradually narrowing towards round base, 3–6 cm long, to 2 cm wide, bipinnatifid; *rachis* winged only at apical portion, hairy throughout; lateral *pinnae* sessile or very shortly stalked in larger ones, ovate with several segments; *ultimate segments* to 1.5 mm broad, round to acute at apex, flat and sharply dentate at margin, sometimes with uncut central areas of the pinnae, c. 2 mm or more broad, hairy on costae underneath; *internal cell walls* irregular and slightly irregularly thickened near surface. *Sori* at apices on short acroscopic branch of segments, thus arranged in one row at each side of rachis, campanulate, 2.2–3 mm long, to 1.2 mm diam.; *involucre*s cleft nearly to halfway down, with accessary projections like hairs and teeth; lips broadly rounded to subtriangular with acute apex, subentire or minutely denticulate; receptacles extruded.

Distribution — *Malesia*: Philippines (Luzon: Mts Arayat, Mariveles, Maquiling).

Habitat — Epiphytic on moss-covered branches of trees in dense forests. Altitude: at mid elevations, 900–1100 m.

Note — *Hymenophyllum merrillii* is similar to *H. holochilum*, but distinguished from it by terete lower portion of the rachis, smaller size and narrower fronds, reddish colour and thicker texture. Those features are very variable in the *H. holochilum* complex and it is not clear that this endemic species can be distinguished in particular areas.

29. Hymenophyllum microchilum (Baker) C.Chr.

Hymenophyllum microchilum (Baker) C.Chr., Mitt. Inst. Allg. Bot. Hamburg 7 (1928) 7; Gard. Bull. Straits Settlem. 7 (1934) 212. — *Trichomanes microchilum* Baker, Trans. Linn. Soc. London, Bot. 4 (1894) 250. — *Meringium microchilum* (Baker) Parris in Beaman et al., Pl. Mt. Kinabalu 1 (1992) 84. — Type: *Haviland 1478* (holo K), Borneo, Sabah, Mt Kinabalu.

Hymenophyllum hallierii Rosenst., Bull. Jard. Bot. Buitenzorg, sér. 2, 2 (1911) 23; Copel., Philipp. J. Sci. 64 (1937) 23. — Type: *Hallier 1791* (holo n.v.; iso BO), Borneo.

Hymenophyllum polyanthos auct. non (Sw.) Sw.: Copel., Philipp. J. Sci. 64 (1937) 97, p.p.

Rhizome long-creeping, dark, sparsely hairy or glabrescent, 0.2–0.4 mm diam. *Stipes* very narrowly winged nearly to the base with flat and entire wings, glabrous, commonly 5–7 cm long; *fronds* oblong-lanceolate, acute to moderately acute at apex, gradually narrowing to round base, commonly 6–10 cm long, to 5 cm wide, quadripinnatifid; *rachis* very narrowly winged throughout, wings at most 0.1 mm broad at each side of rachis, flat, entire; *pinnae* rather widely placed from each other, not imbricate, stalked in lower ones, oblong-subdeltoid to oblong-lanceolate; pinna rachis winged and look like a part of the segments, glabrous; *ultimate segments* round to moderately acute at apex, entire and flat at margin, c. 0.5 mm broad. *Sori* at apex of very short axillary segments at acroscopic base of basal acroscopic secondary pinnules, or arranged in one row nearly to rachis, or distributed more widely; *involucres* with basal tuberous portion and upper one-third of bilobed mouth, c. 2 mm long, 1 mm diam.; lips moderately acute at apex, entire; receptacles long-extruded.

Distribution — *Malesia*: Borneo (Sarawak and Sabah).

Habitat & Ecology — Epiphytic on tree trunks and on the lower surface of the main branches of larger trees in dense montane forests and epipetric on mossy rocks along streams in dense forests. Altitude: 1200–2400 m.

Notes — *Hymenophyllum microchilum* was reduced to *H. polyanthos* by Copeland (1937), but it is distinctly different from that species in the long extruded receptacles with tuberous basal portion of the involucres. It resembles *H. penangianum* and *H. seramense* in various key characters, and may form a single species with them in W Malesia.

Hymenophyllum hallierii was placed near *H. lobbii* by Copeland (1937: 24), but is identical with *H. microchilum* in all the key characters.

30. Hymenophyllum ovatum Copel.

Hymenophyllum ovatum Copel., Philipp. J. Sci., C. 6 (1911) 70; Philipp. J. Sci. 64 (1937) 56, pl. 22. — *Meringium ovatum* (Copel.) Copel., Philipp. J. Sci. 67 (1938) 43. — Lectotype (designated here): *Copland King B32* (lecto MICH 1190661; isolecto BRI, NSW), Papua New Guinea, Gira.

Rhizome long-creeping, filiform, c. 0.2 mm diam., with sparse long pale brown hairs or glabrescent. *Stipes* 1–7 cm long, dark, terete, hairy; *fronds* oblong-subdeltoid to ovate in outline, acute to moderately so at apex, round to subtruncate at base, 3.5–6(–12) cm

long, 1.5–2.5(–7) cm wide; rachis dark, terete in lower portion, hairy on lower surface, hairs multicellular, more or less semiarticulate, downy, often to 1.5 mm long, brownish to pale brownish; *lateral pinnae* less than 10 pairs, more or less imbricate, sessile, rotundate to round at apex, pinnatifid to costae, nearly parallel or slightly narrowing distally; *pinnules* simple or larger ones biforked or trilobed (or the largest ones quadrilobed); pinna rachis broadly winged with similar appearance to segments, hairy; *ultimate segments* narrow, 0.6–0.8(–1) mm broad, obtuse at apex, hairy on costae underneath, more or less reddish, flat, distinctly toothed at margin, with dense oblique (or falcate) teeth; *internal cell walls* irregularly thickened, more or less toothed near the surface of laminae. *Sori* at apices of segments, or arranged in distal position of upper part of fronds, or more in number nearly throughout the upper portion of fronds, large, c. 2 mm long; *involucres* campanulate, bilobed down to halfway, rather densely hairy, c. 2.5 mm long, 1.2 mm diam.; lips broadly ovate, distinctly dentate very minutely wavy at apex; receptacles long-extruded.

Distribution — *Malesia*: New Guinea.

Habitat — Epiphytic on exposed tree roots in montane forests at various elevations. Altitude: from lowlands to 2000 m.

31. **Hymenophyllum pachydermicum** Ces.

Hymenophyllum pachydermicum Ces., Felci (1876) 8; Copel., Philipp. J. Sci. 64 (1937) 20, pl. 5; K.Iwats. et al., PhytoKeys 119 (2019) 111. — *Meringium pachydermicum* (Ces.) Copel., Philipp. J. Sci. 67 (1938) 41. — Syntypes: *Beccari s.n.* (FI, K, MICH), Borneo, Sarawak, Gunong Poe.

Hymenophyllum pedicularifolium Ces., Rendiconto Accad. Napoli 16 (1877) 24, 28; Baker, Ann. Bot. (Oxford) 5 (1891) 193; Copel., Philipp. J. Sci. 64 (1937) 40. — Syntypes: *Beccari s.n.* (BM, FI, K), Papua New Guinea, Monte Arfak.

Trichomanes vestitum Baker, Bull. Misc. Inform. Kew (1894) 7. — *Hymenophyllum vestitum* C.Chr., Gard. Bull. Straits Settlem. 7 (1934) 213, nom. illeg., non Bosch (1863). — Type: *Hose 266* (holo K; iso P), Sarawak.

Hymenophyllum ringens Christ, Ann. Jard. Bot. Buitenzorg 19 (1904) 34. — Lectotype (designated here): *Sarasin 2014* (lecto P 00623430), Sulawesi. Other syntype: *Sarasin 2039* (P), Sulawesi.

Hymenophyllum halconense Copel., Philipp. J. Sci., C. 2 (1907) 144. — Lectotype (designated here): *Merrill 6084* (lecto MICH 1190648; isolecto BM, P), Philippines, Mindoro.

Hymenophyllum taliabense Alderw., Bull. Jard. Bot. Buitenzorg, sér. 2, 16 (1914) 18. — Lectotype (designated here): *Atje 261 p.p.* (lecto BO; isolecto K, L), Sumatra, Taliabo.

Hymenophyllum pilosum Alderw., Bull. Jard. Bot. Buitenzorg, sér. 2, 16 (1914) 57. — Lectotype (designated here): *Matthew 631* (lecto BO; isolecto BM, K, L, MICH), Sumatra.

Hymenophyllum pilosum Alderw. var. *nirmalanum* Alderw., Bull. Jard. Bot. Buitenzorg, sér. 2, 16 (1914) 57. — Type: *Backer 10968* (holo BO? n.v.), Java, Nirmala.

Hymenophyllum clemensiae Copel., Philipp. J. Sci., C. 12 (1917) 46. — Lectotype (designated by Ebihara & Iwatsuki, Mem. Natl. Sci. Mus. (Tokyo) 46 (2010) 96): *Clemens 10780* (lecto MICH; isolecto UC), Borneo, Mt Kinabalu.

Hymenophyllum pulchrum Copel., Philipp. J. Sci. 64 (1937) 22, pl. 6. — *Meringium pulchrum* (Copel.) Copel., Philipp J. Sci. 67 (1938) 42. — Lectotype (designated here): *BS (Reillo) 16214* (lecto MICH 1190666; isolecto CM, GH, L, NSW, UC, US), Philippines.

Rhizome long-creeping, delicate, c. 0.2 mm diam., intricate, with dense reddish brown hairs or older portions glabrescent; bearing roots irregularly with irregularly and densely beset root hairs. *Stipes* terete, winged only on the top or nearly throughout,

slender, ± hairy, 1–3 cm long; hairs rather dense on all axes of fronds, multicellular, subarticulate, reddish brown to brown, to more than 1 mm long; *fronds* variable in size and form, 1.5–6(–8) cm long, c. 2 cm wide, bipinnate, fuscous brown; rachis winged throughout, usually not very narrowly, the wings entire and flat at margin, on the lower surface covered with dense rusty to fuscous, somewhat deciduous hairs; *pinnae* proximate, oblong, c. 1 cm long, 0.6 cm broad, obliquely incised-pinnatifid, with mostly simple, entire segments less than 1 mm wide, the lowest pinnae usually reduced and with cuneate bases; *ultimate segments* round at apex, entire and flat at margin, dark brown in dried condition, 1–3 cm long, c. 1 mm broad; *internal cells* more or less elongate or rectangular, the walls very much thickened and coarsely pitted, appearing coarsely and rather regularly toothed in optical section. *Sori* on shortened basal acroscopic segments of pinnae above the middle of the frond, thus in one row along each side of rachis; *involucres* campanulate, tuberous and immersed or nearly free at base, c. 1.5 mm long, cleft c. halfway down, tube hairy on the back; lips variable, usually broadly rounded and entire but sometimes narrowed or emarginate, or very obscurely toothed; receptacles extruded. — **Fig. 8g, h.**

Distribution — *Malesia*: Sumatra, Java, Borneo, Philippines, Sulawesi, Moluccas (Seram) and New Guinea.

Habitat & Ecology — Epiphytic on tree trunks in lowlands and often in the summit zone; populations forming large mats. Altitude: 100–1800 (or to 2200) m.

Notes — Two Javan collections, *Backer 10968* and *Donk s.n.* (both in BO), have a rather loose construction of the pinnation pattern; the label of the former specimen has the name *Hymenophyllum pilosum* Alderw. var. *mirmalanum* n. var. This is very common in Seram, where the plants bear long, dense hairs,

Hymenophyllum pulchrum was described as a local form of *H. pachydermicum* with more delicate, linear-elliptic fronds, less hairy throughout. The variation of *H. pachydermicum* in the Philippines indicates that it should not be divided into separate species.

32. Hymenophyllum peltatum (Poir.) Desv.

Hymenophyllum peltatum (Poir.) Desv., Mém. Soc. Linn. Paris 6 (1827) 333. — *Trichomanes peltatum* Poir. in Lam., Encycl. 8 (1808) 76. — Type: *Bory de St.-Vincent s.n.* (holo P), Ile de France (Mauritius).

Hymenophyllum unilaterale Willd., Sp. Pl. 5 (1810) 521. — Type: *Willdenow 117* (holo n.v.; iso P), Mascarene Islands.

Hymenophyllum perfissum Copel., Philipp. J. Sci., C. 12 (1917) 47; Philipp. J. Sci. 64 (1937) 80, pl. 39. — Lectotype (designated by Ebihara & Iwatsuki, Mem. Natl. Mus. Nat. Sci. (Tokyo) 46 (2010) 96): *Clemens 10588* (lecto MICH; isolecto BM, L, PNH, US), Borneo, Mt Kinabalu.

Rhizome long-creeping, wiry, 0.15–0.2 mm diam., sparsely covered with brown, caducous hairs. *Stipes* c. 1 cm apart from the next ones, terete, sparsely hairy, 0.7–1.5 cm long. *Fronds* bipinnate to tripinnatifid, oblong-lanceolate to lanceolate, gradually narrowing towards acute apex, subtruncate at base, 3–6 cm long, to 1.5 cm wide at widest middle lower to basal portion; *rachis* very sparsely hairy or glabrescent, very narrowly winged throughout with flat and entire wings; larger *pinnae* with to 6 pinnately arranged segments, very shortly stalked; *ultimate segments* oblong, round at apex, flat, to 0.8 mm broad, rather sparsely but sharply dentate at margin; hairs sparse

if any, brown, multicellular, c. 1 mm long. *Sori* solitary at apex of ultimate segment on posterior side of pinna rachis, usually gathering to upper portion of fronds, bivalvate, deeply cleft towards base; *involucres* oblong ovate, round or very moderately acute at apex, entire; receptacles clavate, included. Chromosome number: $n = 11$ (Brownlie, Trans. & Proc. Roy. Soc. New Zealand 85 (1958) 213).

Distribution — Cosmopolitan, mostly temperate to warm temperate regions, S Africa, Mascarene Isls.; in *Malesia*: Borneo (Mt Kinabalu) and New Guinea (Mt Victoria); New Zealand, Australia, Tristan da Cunha

Habitat & Ecology — Epiphytic on base of mossy tree trunks and epipetric on moist rocks in upper montane forests. Altitude: 2950–3270 m in Borneo and 3270–3550 m in New Guinea.

33. Hymenophyllum penangianum Matthew & Christ

Hymenophyllum penangianum Matthew & Christ, J. Linn. Soc., Bot. 39 (1909) 214; Copel., Philipp. J. Sci. 64 (1937) 19, pl. 4; Holttum, Rev. Fl. Malaya (1955) 81, f. 22. — *Meringium penangianum* (Matthew & Christ) Copel., Philipp. J. Sci. 67 (1938) 41. — Lectotype (designated here): *Matthew 90* (lecto SING; isolecto BM, K), Peninsular Malaysia, Penang.

Hymenophyllum semifissum Copel., Philipp. J. Sci., C. 10 (1915) 145; C.Chr., Gard. Bull. Straits Settlem. 4 (1929) 376. — Lectotype (designated by Ebihara & Iwatsuki, Mem. Natl. Mus. Nat. Sci. (Tokyo) 46 (2010) 96): *BS (Native Collector) 2607* (lecto MICH; isolecto NY), Borneo, Mt Merinjak.

Hymenophyllum leptocarpum Copel., Brittonia 1 (1931) 71. — Type: *Clemens 22018* (holo MICH; iso NY, UC), Borneo, Upper Kejong River.

Rhizome very slender, c. 0.4 mm diam., long-creeping, bearing sparse pale brownish hairs. *Stipes* 1–3 cm long, bearing scattered hairs, not winged or narrowly winged near the apex; *fronds* 4–7.5 cm long, to 2.5 cm wide; main *rachis* winged throughout or in upper half only, bearing scattered hairs on the lower surface; *pinnae* oblique, well-spaced, 1–2 cm long, the largest ones usually with 3 segments on each side, one or more of those on the acroscopic side sometimes forked; *ultimate segments* 3–6 mm long and under 1 mm broad, edges entire but often slightly sinuous. *Sori* 1–3 on each pinna, terminal on the lower acroscopic lobes; free lips bluntly triangular, nearly equal in length to the conical hollow basal portion; receptacles of mature sori extruded far beyond the lips. — **Fig. 9a, b.**

Distribution — *Malesia*: Peninsular Malaysia and Borneo.

Habitat & Ecology — Epiphytic on rather small trees and on fallen and rotten logs in alluvial forests. Altitude: from low to mid elevations, 150–2900 m.

34. Hymenophyllum ramosii Copel.

Hymenophyllum ramosii Copel., Philipp. J. Sci. 64 (1937) 34, pl. 9: f. 4–6. — *Meringium ramosii* (Copel.) Copel., Philipp. J. Sci. 67 (1938) 41; Fern Fl. Philipp. 1 (1958) 61. — Lectotype (designated by Ebihara & Iwatsuki, Mem. Natl. Mus. Nat. Sci. (Tokyo) 46 (2010) 96): *BS (Ramos & Edaño) 38550* (lecto MICH; isolecto US), Philippines, Mindanao, Mt Lipa.

Rhizome long-creeping, wiry, c. 0.6 mm thick, rather densely hairy in younger portion, more or less caducous; hairs very thin, light brown, to 1.5 mm long. *Stipes* 2–7 cm

long, sparsely hairy or glabrescent, distinctly winged nearly to the base; wings flat, entire, to 0.4 mm broad at each side; *fronds* subdeltoid to pentagonal, acute to acuminate at apex, subtruncate to cordate at base, 4–7 cm long, to 7 cm wide, tripinnatifid to quadripinnatifid; *rachis* winged throughout with wings like those on stipes, distinct nearly to the apex, sparsely hairy; lateral *pinnae* several pairs, the lowest ones distinctly the largest, stalked, more or less asymmetrically subtriangular, acute at apex, broadly cuneate at base, to 5 cm long, 2.5 cm wide, upper pinnae gradually smaller upwards, oblong-subdeltoid, moderately acute at apex, shortly stalked or sessile; pinna rachis winged with wings like those on stipes but narrower; larger *pinnules* with more than 15 segments, secondary pinnules at most with three segments; *ultimate segments* round to moderately acute at apex, flat and sharply dentate at margin, sparsely hairy on costae underneath, 0.6–0.8 mm broad, often involute when dry. *Sori* at apices of segments, often gathering at apical portion of fronds, campanulate with bilabiate mouth, to 2 mm long, 1.2 mm diam.; *involucres* cleft nearly to two-thirds way down; lips subdeltoid, moderately acute at apex, distinctly denticulate; receptacles thick, extruded beyond lips.

Distribution — *Malesia*: Philippines (Mindanao: Davao) and Papua New Guinea.

Habitat & Ecology — Epiphytic on lower tree trunks in mossy forests. Altitude: 2000–2300 m.

Note — There are still some doubts about combining the Philippines and Papua New Guinean plants in one species, although they are similar to each other in having such discriminating features as distinct stipes with flat, entire wings, subtriangular fronds usually shorter than the stipe and finely divided, very narrow ultimate segments.

35. **Hymenophyllum rosenstockii** Brause

Hymenophyllum rosenstockii Brause, Bot. Jahrb. Syst. 56 (1920) 43; Copel., Philipp. J. Sci. 64 (1937) 53, pl 21, f. 1–2; K.Iwats. et al., PhytoKeys 119 (2019) 111. — *Meringium rosenstockii* (Brause) Copel., Philipp. J. Sci. 67 (1938) 43. — Lectotype (designated here): *Ledermann 8842* (lecto B 20 0102724; isolecto MICH) , Papua New Guinea, Hunsteinspitze. Other syntype: *Ledermann 9087a* (B, BM), Papua New Guinea, Hunsteinspitze.

Hymenophyllum brevidens Alderw., Bull. Jard. Bot. Buitenzorg, sér. 2, 7 (1912) 20; Copel., Philipp. J. Sci. 64 (1937) 39. — Lectotype (designated here): *d'Armandville 238* (lecto BO; isolecto BM), New Guinea, Johannes-Keyts Mts.

Rhizome long-creeping, slender, wiry, with rather sparse brownish hairs. *Stipes* slender, 1–2(–3) cm long, terete or rarely winged at upper portion with the wings decurrent from fronds, very sparsely hairy, thinner than rhizome; *fronds* bipinnate to tripinnatifid, lanceolate to oblong in outline, narrowing downwards and truncate at base, gradually narrower upwards, (0.8–)1.5–2.5(–3.5) cm long, 0.8–1.5(–2.2) cm wide; *rachis* like the upper part of stipes, very sparsely hairy, winged in the upper portion, with narrow, flat, entire wings; *pinnae* alternately placed, usually several in pairs, larger ones pinnatifid in plan; *ultimate segments* narrower, 0.3–0.7 mm broad, sharply dentate at margin, not crisped, blackish when dried. *Sori* axillary, gathering to upper central portion; *involucres* tubular, deeply cleft in upper half, c. 2 mm or more long, 0.7–1.2 mm diam., lips acute at apex, entire; receptacles long-extruded.

Distribution — *Malesia*: Moluccas (Seram) and New Guinea (Hunsteinspitze and Etappenberg).

Habitat & Ecology — Epiphytic on mossy tree trunks in dense mossy forests. Altitude: (800–)1000–1800 m.

Note — The black fronds when dried, larger involucres, narrower segments, sharp and distinct dentation with several rows of cells and generally smaller size are the main characters to recognize *H. rosenstockii*, but also suggest affinity with *H. melanosorum*, which occurs in the same distribution area.

36. Hymenophyllum rubellum Rosenst.

Hymenophyllum rubellum Rosenst., Nova Guinea 8 (1912) 716; Copel., Philipp. J. Sci. 64 (1937) 56. — *Meringium rubellum* (Rosenst.) Copel., Philipp. J. Sci. 67 (1938) 43. — Lectotype (designated here): *von Roemer 767* (lecto B; isolecto K, L), New Guinea, Hellwig-Gebirge. Other syntype: *von Roemer 1305* (n.v.), New Guinea, Hellwig-Gebirge.

Hymenophyllum cernuum A.Gepp in Gibbs, Fl. Arfak Mts (1917) 68; Copel., Philipp. J. Sci. 64 (1937) 72. — Lectotype (designated here): *Gibbs 5964* (lecto BM 001044227; isolecto P), Papua New Guinea, Arfak Mts.

Hymenophyllum cincinnatum A.Gepp in Gibbs, Fl. Arfak Mts. (1917) 68; Copel., Philipp. J. Sci. 64 (1937) 40. — Lectotype (designated here): *Gibbs 5989* (lecto BM 001045156; isolecto K, P), Papua New Guinea, Arfak Mts.

Trichomanes lasiophyllum Alderw., Nova Guinea 14 (1924) 54. — Lectotype (designated here): *Lam 1739* (lecto BO; isolecto BM, L), New Guinea.

Rhizome long-creeping, rather thick, 0.7–1 mm diam., irregularly branching, densely covered with hairs in younger portion; hairs persisting but glabrescent in very old portion, pale brown, multicellular, semiarticulate, thin, more or less stiff or tender, to 4 mm long. *Stipes* stout, narrowly winged except basal portion, dark brown, densely hairy or glabrescent in older ones; hairs on stipes multicellular, semiarticulate, light brown, thin and tender, to 3 mm long; *fronds* oblong to oblong-lanceolate, acuminate to caudate at apex, broadly cuneate at base, quadripinnatifid, (10–)15–25 cm long, 7–15 cm wide at widest portion; *rachis* winged throughout with wings flat and entire, rather densely hairy; lateral *pinna*e usually more than 12 pairs, larger ones with distinct stalks, oblong-subtriangular, acuminate at apex, asymmetrically cuneate at base; pinna rachis narrowly winged, hairy; *pinnules* sessile or shortly stalked in larger ones, larger secondary pinnules with several segments; *ultimate segments* round at apex, denticulate, c. 0.3 mm broad. *Sori* solitary, at apices of very short, acroscopic, axillary segments; *involucres* campanulate, with cleft lips of upper one-third portion, 2–2.5(–3.5) mm long, 1.2–1.7(–2.3) mm diam., with accessary wings and stiff hairs on surface of lower portion; lips bilabiate at upper one-third portion of involucres, round, entire, glabrous, sometimes tinted dark at margin; receptacles stiff and long-extruded.

Distribution — *Malesia*: New Guinea.

Habitat & Ecology — Epiphytic on mossy tree trunks and tree roots, also terrestrial on mossy ground, in forests on ridge crests and in semi-open areas. Altitude: common at mid elevations, from lowlands to 3600 m.

Note — *Hymenophyllum cernuum* was inferred to be a slender form of *H. ledermannii* by Copeland (1937), although it is a synonym of *H. rubellum*.

37. Hymenophyllum seramense K.Iwats., M.Kato & Ebihara

Hymenophyllum seramense K.Iwats., M.Kato & Ebihara, J. Jap. Bot. 96 (2021) 229, f. 1. — Type: *Kato, Ueda & Fanani 12623* (holo TI 00003339; iso BO). Moluccas, Seram, Kecamatan Kaitaru, along a trail from Tihulale to Gunong Toniwel

Hymenophyllum sp. 1: K.Iwats. et al., PhytoKeys 119 (2019) 111.

Rhizome slender, c. 0.2 mm diam., long-creeping, bearing brown hairs in younger portion, caducous. *Stipes* to 6 cm long, terete or very narrowly winged in upper portion, glabrous except for the base; *fronds* tripinnatifid, oblanceolate in outline, widest at upper 1/3–1/4 portion, gradually narrowing downwards, to 13 cm long, 3 cm wide; *rachis* narrowly winged with flat, entire wings, very sparsely hairy in lower surface; *pinnae* largest at upper 1/3–1/4 portion of fronds, larger ones with short stalks, oblong subdeltoid, cuneate at base, round at apex, to 2.5 cm long, 1 cm wide, gradually reducing in size downwards, lower ones extremely reduced to just a few segments; pinna rachis winged throughout; secondary pinnae with 1–5 segments; *ultimate segments* narrow, round to obtuse at apex, to 3 mm long, 0.7 mm broad, flat and entire. *Sori* without constriction at base, campanulate, bilabiate at upper half, c. 1.2 mm long, to 1 mm diam.; lips as long as conical basal portion, moderately acute at apex, entire; receptacles distinctly extruded.

Distribution — *Malesia*: Moluccas (Seram).

Habitat & Ecology — Epiphytic on mossy tree trunks in mossy forest. Altitude: 980–1190 m.

Note — Only one collection of *H. seramense* is available, but the soral structure is distinct. As indicated by the various morphological characters, it should be allied with *H. penangianum* and *H. microchilum*.

38. Hymenophyllum serrulatum (C.Presl) C.Chr.

Hymenophyllum serrulatum (C.Presl) C.Chr., Index Filic. (1905) 367; Holttum, Rev. Fl. Malaya 2 (1955) 78, f. 19; K.Iwats., J. Fac. Sci. Univ. Tokyo, Sect. 3, Bot. 13 (1985) 511; C.W.Chen et al., Sol Amazing (2017) 134; K.Iwats. et al., PhytoKeys 119 (2019) 111. — *Didymoglossum serrulatum* C.Presl, Abh. Königl. Böhm. Ges. Wiss., ser. 5, 3 (1843) 23, 48, 140. — *Leptocionium serrulatum* (C.Presl) Bosch, Ned. Kruidk. Arch. 4 (1859) 383. — Lectotype (designated here): *Cuming 221* (lecto PRC; isolecto B, BM, GH, K, L, P), Philippines, Luzon.

Hymenophyllum bivalve J.Sm., J. Bot. (Hooker) 3 (1841) 418, nom. illeg., non (G.Forst.) J. Bot. (Schrader) 1800(2): 99 (1801). — *Hymenophyllum smithii* Hook., Sp. Fil. 1 (1844) 97, pl. 35B; Bedd., Handb. Ferns Brit. India (1883) 34; Christ, Bull. Herb. Boissier 6 (1898) 140. — Lectotype (designated here): *Cuming 221* (lecto K 000420453; isolecto B, BM, GH, L, P, PRC), Philippines. Other syntype: *Cuming 264* (B, BM, GH, K, L, P, PRC), Philippines.

[*Meringium meyenianum* C.Presl, Abh. Königl. Böhm. Ges. Wiss., ser. 5, 3 (1843) 24, pl. 8B, nom. nud.]. — *Trichomanes meyenianum* Bosch, Ned. Kruidk. Arch. 4 (1859) 379 — *Leptocionium preslii* Bosch, Ned. Kruidk. Arch. 4 (1859) 384, nom. superfl. — *Leptocionium violaceum* Bosch, Ned. Kruidk. Arch. 5(3) (1863) 147, nom. superfl. — *Hymenophyllum preslii* (Bosch) Rosenst., Bull. Jard. Bot. Buitenzorg, sér. 2, 2 (1911) 25, nom. superfl. — *Hymenophyllum meyenianum* (Bosch) Copel., Philipp. J. Sci. 64 (1937) 25, pl. 8. — *Meringium meyenianum* (Bosch) Copel., Fern Fl. Philipp. 1 (1958) 58; Tagawa & K.Iwats. in Smitinand et al., Fl. Thailand 3 (1979) 76. — Type: *Meyen s.n.* (holo B).

Hymenophyllum multifidum (G.Forst.) Sw. var. *novoguineense* Rosenst., Repert. Spec. Nov. Regni Veg. 12 (1913) 166. — Type: *Keysser B30* (holo n.v.; iso BM), New Guinea.

Hymenophyllum torricellianum Alderw., Bull. Jard. Bot. Buitenzorg, sér. 2, 11 (1913) 14; Copel., Philipp. J. Sci. 64 (1937) 39. — Syntypes: *Schlechter 14543* (B, BM, K, P), New Guinea, Torricelli Gebirge.

Hymenophyllum vittatum Copel., Philipp. J. Sci. 64 (1937) 31, pl. 9, f. 1–3. — *Meringium vittatum* (Copel.) Copel., Philipp. J. Sci. 67 (1938) 40; Fern Fl. Philipp. 1 (1958) 59. — Lectotype (designated by Ebihara & Iwatsuki, Mem. Natl. Mus. Nat. Sci. (Tokyo) 46 (2010) 95): *FB (Curran) 13099* (lecto MICH), Philippines, Tayabas.

Hymenophyllum bicolanum Copel., Philipp. J. Sci. 64 (1937) 31, pl. 10. — *Meringium bicolanum* (Copel.) Copel., Philipp. J. Sci. 67 (1938) 40; Fern Fl. Philipp. 1 (1958) 60. — Lectotype (designated by Ebihara & Iwatsuki, Mem. Natl. Mus. Nat. Sci. (Tokyo) 46 (2010) 95): *BS (Edaño) 76555* (lecto MICH), Philippines, Luzon.

Rhizome slender, long-creeping, irregularly branching, wiry, c. 0.3 mm diam., covered with stiff, light brownish hairs, glabrescent. *Stipes* terete and lacking wings, 1–3 cm or to 7 cm long, hairy throughout or nearly glabrous in very old portions. *Fronds* tripinnatifid, oblong-lanceolate to oblong-ovate, acute to acuminate at apex, narrowing towards the base, variable in size, commonly 6–8 cm long, but sometimes to 30 cm long or more, commonly 2–3 cm or to 4.5 cm wide; *rachis* terete in lower portion, narrowly winged upwards with narrow flat wings, slightly hairy beneath; larger *pinnae* oblong-subtriangular, acute or moderately so at apex, unequally cuneate at sessile base, commonly 1–3 cm or sometimes to 3 cm or rather more in length, basal pinnae sometimes widely spaced and reduced in size; *ultimate segments* linear, round to moderately acute at apex, 7–10 mm broad, the margin flat, irregularly minutely toothed or nearly entire, pale green and brown when dried up, dark on axes; hairs rather dense on all axes, brown, multicellular, c. 1 mm long. *Sori* solitary at the apices of short basal acroscopic segments in the upper part of fronds; *involucre* campanulate with bilabiate mouth cleft to the middle portion; lips about as long as the hollow base, bluntly triangular, moderately acute to acute, nearly entire; receptacles extruded when old. Chromosome numbers: $n = 21$ (Manton & Sledge, Philos. Trans., Ser. B, 238 (1954) 136, Manton in Holttum, Rev. Fl. Malaya 2 (1955) 623; Braithwaite, Fern Gaz. 10 (1969) 82). — **Fig. 7a–c.**

Distribution — Thailand (Peninsular) and Vietnam; in *Malesia*: throughout.

Habitat & Ecology — Epiphytic and epipetric, on mossy tree trunks and on moist rocks in deep shade in evergreen forests at low to mid elevations, or from lowlands to 2200 m.

Notes — Examples from 2400–2700 m elevation in New Guinea may be referred to *H. serrulatum*, although the fronds are larger, 15–20 cm long and more than 10 cm wide at their widest.

Both *H. vittatum* and *H. bicolanum* were described by Copeland (1937) from different provinces of Luzon. Particular diagnostic characters were enumerated, but they are not useful for discriminating special forms as distinct taxa in such a variable coenospecies as *H. serrulatum*.

Specimens identified as *H. polyodon* from Papua New Guinea and the Bismarck Archipelago appear to be stouter and larger forms of *H. serrulatum*.

39. Hymenophyllum trichophorum (Alderw.) Ebihara & K.Iwats.

Hymenophyllum trichophorum (Alderw.) Ebihara & K.Iwats. in Ebihara et al., Blumea 51 (2006) 229. — *Trichomanes trichophorum* Alderw., Nova Guinea 14 (1924) 53. — Lectotype (designated here): *Lam 1551* (lecto BO; isolecto L), New Guinea, near Doorman Summit.

Amphipterum humatoides Copel., Philipp. J. Sci. 73 (1941) 465. — Lectotype (designated here): *Brass 12638* (lecto MICH 1190021; isolecto A, BO, BRI, FI, GH, L), New Guinea. Other syntype: *Brass 11867* (MICH), New Guinea.

Rhizome long-creeping on branches of trees or tree trunks, wiry, c. 0.4 mm diam., persistently hairy with brownish hairs. *Stipes* like rhizome diam., narrowly winged except very base, rather sparsely hairy, 3–7 cm long; *fronds* pinnatifid to pinnate, oblong to narrowly so, round at apex, broadly cuneate at base, 2–4 cm long, 1.5–2 cm wide at widest basal portion; *rachis* winged throughout with decurrent base of pinnae, hairy on lower surface; *pinnae* several to 10 pairs, oblong-subdeltoid, round to moderately acute at apex, entire or undulate by vein-apex, decurrent at base to rachis or nearly free in larger ones, to 1.5 cm long, 0.5 cm broad, with pinnately branched veins; lower surface of pinna rachis and veins with accessory wings; laminae apparently very thick, dark brown to nearly blackish in dried specimens, hairy throughout; hairs on upper surface restricted on veins, simple, branched or stellate, deep brown, thick and straight, those on lower surface rather dense, simple and multicellular, often articulate. *Sori* at apex of upper pinnae, large; *involucres* with shallow tuberous base and narrow bilabiate portion, c. 3 mm long, 2.5 mm broad; lips at most 0.5 mm broad, round, entire, often tinted black at least in marginal portion; receptacles stout, very long-extruded.

Distribution — *Malesia*: New Guinea.

Habitat & Ecology — Epiphytic on tree tops and on branches 3 cm diam., usually in ridge-crest forests and on rocks of landslides. Altitude: lower subalpine forests at higher elevations, 1800–3400 m.

Notes — Typical *H. trichophorum* has accessary wings only on the lower surface of the fronds. Short accessary wings, however, sometimes occur at the branching of the veins on the upper surface of the fronds. In this feature, *H. trichophorum* appears to be close to *H. ledermanni*. Unipinnate fronds with dense simple hairs on the lower surface and branched or stellate hairs on the upper surface and distinctly large sori are distinct features of this species.

A collection from Sumatra, *Surbeck 242* in L, should be identified as *H. trichophorum*, although it is doubtful to attribute this species to Sumatra based only on this collection. There may be confusion on the label of this particular specimen.

b. Subgenus **Globosa** (Prantl) Ebihara & K.Iwats.

Hymenophyllum Sm. subg. *Globosa* (Prantl) Ebihara & K.Iwats. in Ebihara et al., Blumea 51 (2006) 231. — *Hymenophyllum* Sm. sect. *Globosa* Prantl, Unters. Morph. Gefässkrypt. 1 (1875) 55. — Type: *Hymenophyllum junghuhnii* Bosch.

Sphaerocionium C.Presl sect. *Glabra* C.Presl, Abh. Königl. Böhm. Ges. Wiss., ser. 5, 3 (1843) 34, non *Hymenophyllum* Sm. sect. *Glabra* Prantl (1875). — Lectotype (designated by Morton, Contr. U.S. Natl. Herb. 38 (1968) 172): *Hymenophyllum caudiculatum* Mart.

Rhizome long-creeping, filiform to wiry, usually glabrous; *stipes* to 15 cm long; *fronds* mediocre to larger among the filmy ferns, elliptic to subdeltoid, tri- to quadri-

pinnate; margin of segments usually entire, minutely serrate in some species. *Sori* at apex of ultimate segments; *involucres* bivalvate, entire or serrate; receptacles included, capitate to clavate.

Distribution — About 25 species are included in this subgenus in tropics and temperate regions of Asia and Pacific areas; one species is recorded from southern part of S America. Fourteen species in *Malesia*.

Habitat & Ecology — Epiphytic and epipetric, on mossy tree trunks and on moist rocks in forests and in semi shaded places from low to mid elevations.

Taxonomy — The species included in subg. *Globosa* are usually placed in *Hymenophyllum* in the strict sense, or in *Mecodium* by Copeland and his followers. They form a distinct clade based on molecular phylogeny, and are distinguished in phenetic features by thicker, glabrous rhizomes and a dorsiventral protostele.

KEY TO THE SPECIES

1a. Receptacles filiform to columnar, involucres triangular to subdeltoid, longer than wide or rarely reniform with the length nearly the same as the width 2
b. Receptacles capitate, involucres distinctly broader than long 9
2a. Receptacles included in involucres 3
b. Receptacles extruded beyond edge of lips of involucres . . . . . **42. H. edanoi**
3a. Fronds normally over 7 cm long; segments many; wings of axes flat or undulate 4
b. Fronds dwarf, usually less than 6 cm long at maturity, or segments few; wings of axes and ultimate segments distinctly crisped at margin 6
4a. Lips of involucre entire or at most crenate. 5
b. Lips of involucre toothed; segments often laxly placed with some irregularly elongated ones . . . . . **49. H. productum**
5a. Fronds brownish green, usually to 15(–25) cm long, oblong to narrowly oblong, or subdeltoid, rarely widest at base, rachis winged throughout . **40. H. angulosum**
b. Fronds clearly green, larger, more than (10–)15 cm long, oblong-subdeltoid and widest at base, rachis terete near base . . . . . **43. H. emarginatum**
6a. Lips of involucres entire to crenate 7
b. Lips of involucres toothed to fimbriate 8
7a. Fronds larger, commonly 8–12 cm long; wings of axes distinctly crisped . . . . . **50. H. reinwardtii**
b. Fronds smaller, to 10 cm long; wings exceedingly crisped, margin appearing as if toothed . . . . . **52. H. thuidium**
8a. Margin of segments distinctly crisped, lips of involucres fimbriate. . . . . **44. H. fimbriatum**
b. Margin of segments flat or undulate, lips of involucres toothed **46. H. javanicum**
9a. Margin of wings and ultimate segments flat 10
b. Margins of wings and ultimate segments more or less crisped . . **41. H. badium**
10a. Fronds generally ovate to oblong ovate 11
b. Fronds narrowly lanceolate . . . . . **48. H. longifolium**

11a. Fronds larger, usually over 10 cm long 12
b. Fronds smaller, usually to 10 cm long 14
12a. Head of receptacles widened, clavate to capitate 13
b. Head of receptacles globose. . . . . **45. H. imbricatum**
13a. Involucres crenate; wings o f rachis usually narrower than or same as segments . . . . . **41. H. badium**
b. Involucres entire; wings of rachis broad, often more than 1 mm on each side, flat and entire . . . . . **47. H. junghuhnii**
14a. Receptacles capitate; fronds regularly pinnate; segments normally placed . . . . . **51. H. salakense**
b. Receptacles clavate; fronds irregularly branched; segments laxly placed . . . . . **53. H. treubii**

40. Hymenophyllum angulosum Christ

Hymenophyllum angulosum Christ, Philipp. J. Sci., C. 3 (1908) 269; Copel., Philipp. J. Sci. 64 (1937) 109, pl. 50; C.W.Chen et al., Sol Amazing (2017) 125; K.Iwats. et al., PhytoKeys 119 (2019) 110. — *Mecodium angulosum* (Christ) Copel., Philipp. J. Sci. 67 (1938) 20; Fern Fl. Philipp. 1 (1958) 49. — Lectotype (designated here): *Merrill 6080* (lecto P 00622001; isolecto MICH, NY, US), Philippines, Mindoro, Mt Halcon.

Hymenophyllum todjambuense Kjellb., Bot. Jahrb. Syst. 66 (1933) 41; Copel., Philipp. J. Sci. 64 (1937) 114. — *Mecodium todjambuense* (Kjellb.) Copel., Philipp. J. Sci. 67 (1938) 20. — Type: *Kjellberg 3505* (holo S (S-P-5272) 'Herb. Celebicum Kjellberg'; iso BM, S 3 sheets), [Indonesia], Sulawesi, Todjamboe.

Rhizome long-creeping, wiry, slender, c. 0.3 mm diam., covered with pale brown hairs at apex, glabrous except for the very apex; roots irregularly from rhizome, rather densely beset with brownish root hairs, sometimes more than 3 mm long. *Stipes* 2–9 cm long, finely filiform, terete or very narrowly winged on the uppermost portion, glabrous or beset with several brownish hairs at very base; *fronds* tripinnatifid, ovate or broadly lanceolate, round to moderately acute at apex, round to subtruncate at base, but outline of fronds often becoming irregular, 3–5(–11) cm long, 1.5–3(–4.5) cm wide; *rachis* straight, filiform, very narrowly winged, wings flat, entire, at most 0.15 mm broad at each side; *lateral pinnae* largest at middle or lower one-third portion, to 2.5 cm long, 1.5 cm wide, sessile or very shortly stalked in a few lower ones, pinnate with a few basal pinnules forked or with 3 or 4 segments, pinna rachis winged forming nearly the same appearance with ultimate segments; *ultimate segments* often elongate to 8 mm long, round to obtuse at apex, entire and flat at margin, (0.8–)1(–1.3) mm in width, emarginate; pinnae and segments rather loosely beset, giving generally a rather irregular appearance of fronds. *Sori* at apices of short ultimate segments, usually distributed in upper portion of fronds; *involucres* round-ovate, rounded at base, 1.8–2.7 mm long, c. 1.5 mm broad; valves deeply cleft nearly to the base, broadly rounded, flat, subentire to crenate-lobed; receptacles clavate, included in valves.

Distribution — *Malesia*: Borneo (one collection from Kalimantan), Philippines (Luzon, Batan, Mindoro), Sulawesi (one collection), Moluccas (Seram), New Guinea; Solomon Islands and Vanuatu.

Habitat & Ecology — Epiphytic at base of tree trunks from lower to mid-montane forests at elevations of 750–1800 m.

Notes — The rather irregular and loose branching pattern with flat segments in frond construction in *H. angulosum* is a characteristic feature. This species appears to be in the group of *H. emarginatum* in soral and vegetative characters, but not in the particular branching pattern.

The margin of the lips is entire in the type of *H. todjambuense*, the only collection from Sulawesi.

Endert 4232 from Kalimantan in BM (duplicate in MICH) is annotated as *Hymenophyllum endertii* C.Chr. and is filed under *H. treubii*; the receptacles are not capitate with entire lips. This is the only collection of *H. angulosum* from Borneo (Kalimantan).

41. Hymenophyllum badium Hook. & Grev.

Hymenophyllum badium Hook. & Grev., Icon. Filic. 1 (1828) t. 76; Copel., Philipp. J. Sci. 64 (1937) 144, pl. 76; Tardieu & C.Chr. in Lecomte, Fl. Indo-Chine 7, 2 (1939) 53; Holttum, Rev. Fl. Malaya 2 (1955) 83, f. 25; K.Iwats., J. Fac. Sci. Univ. Tokyo, Sect. 3, Bot. 13 (1985) 520; J.X.Liu et al. in C.Y.Wu et al., Fl. China 2–3 (2013) 101; K.Iwats. et al., PhytoKeys 119 (2019) 110. — *Sphaerocionium badium* (Hook. & Grev.) C.Presl, Abh. Königl. Böhm. Ges. Wiss., ser. 5, 3 (1843) 35. — *Mecodium badium* (Hook. & Grev.) Copel., Philipp. J. Sci. 67 (1938) 23; Fern Fl. Philipp. 1 (1958) 53; Ching, Fl. Reipubl. Popularis Sin. 2 (1959) 137, pl. 10: f. 1-6; Tagawa & K.Iwats. in Smitinand et al., Fl. Thailand 3 (1979) 72; J.L.Tsai & W.C.Shieh in H.L.Li et al., Fl. Taiwan 1 (1994) 112. — *Hymenophyllum javanicum* Spreng. var. *badium* (Hook. & Grev.) Bedd., Handb. Ferns Brit. India (1883) 33. — Syntypes: *Wallich s.n.* (K), Nepal; *von Schlagintweit s.n.* (K), India, Sikkim, West Bengal, Singhalia ridge.

Hymenophyllum crispatum Wall. in Hook. & Grev., Icon. Fil. 1 (1828) pl. 77; Bedd., Ferns S. India (1873) pl. 207; Copel., Phillip. J. Sci. 64 (1937) 148, pl. 77. — *Mecodium crispatum* (Wall.) Copel., Phillip. J. Sci. 67 (1938) 23. — Syntypes: *Hooker f. s.n.* (K), India, Assam; *Wallich 169* (K), Nepal; *Wallich 173* (K), Tundooa.

Sphaerocionium macrocarpum C.Presl, Abh. Königl. Böhm. Ges. Wiss., ser. 5, 3 (1843) 35, 61, 127, 153. — *Hymenophyllum macrocarpum* (C.Presl) Bosch, Ned. Kruidk. Arch. 4 (1859) 55. — Lectotype (designated by Iwatsuki, J. Fac. Sci. Univ. Tokyo, Sect. 3, Bot. 13 (1985) 520): *Cuming 130* (lecto L; isolecto BM, MICH, P, PRC), Philippines.

Hymenophyllum crispatum Wall. var. *majus* Hook., Sp. Fil. 1 (1846) 105. — Type: *Cuming 220* (holo n.v.; iso BM), Philippines.

Hymenophyllum latilobum Bonap., Notes Ptéridol. 13 (1921) 103; Tardieu & C.Chr., Bull. Mus. Natl. Hist. Nat., sér. 2, 6 (1934) 287. — Type: *Bourret 129 bis* (P n.v.), Vietnam, Tonkin.

Hymenophyllum pleiocarpum Alderw., Bull. Jard. Bot. Buitenzorg, sér. 3, 5 (1922) 208; Copel., Philipp. J. Sci. 64 (1937) 149, pl. 78 — Lectotype (designated here): *Bünnemeijer 9142* (lecto BO; isolecto L), Sumatra. Other syntypes: *Bünnemeijer 9243* (BO), Sumatra; *Bünnemeijer 9245* (BO, K, L), Sumatra; *Bünnemeijer 9313* (BO, L, P), Sumatra.

Rhizome long-creeping, irregularly branching, wiry, covered with brownish hairs at younger portions or glabrescent, 0.5–0.8 mm diam., the rootlets irregularly from rhizome, with dense long root hairs. *Stipes* hard, glabrous, to 1.2 mm diam., to 10 cm long, winged except the basal portion, the wings entire, almost flat or distinctly crispate, gradually narrowing downwards, the broader ones c. 1 mm on each side. *Fronds* variable to some extent in size and form, usually oblong, occasionally broader or narrower, acute at apex, rarely narrowing towards base or the basal pinnae largest, tripinnate to

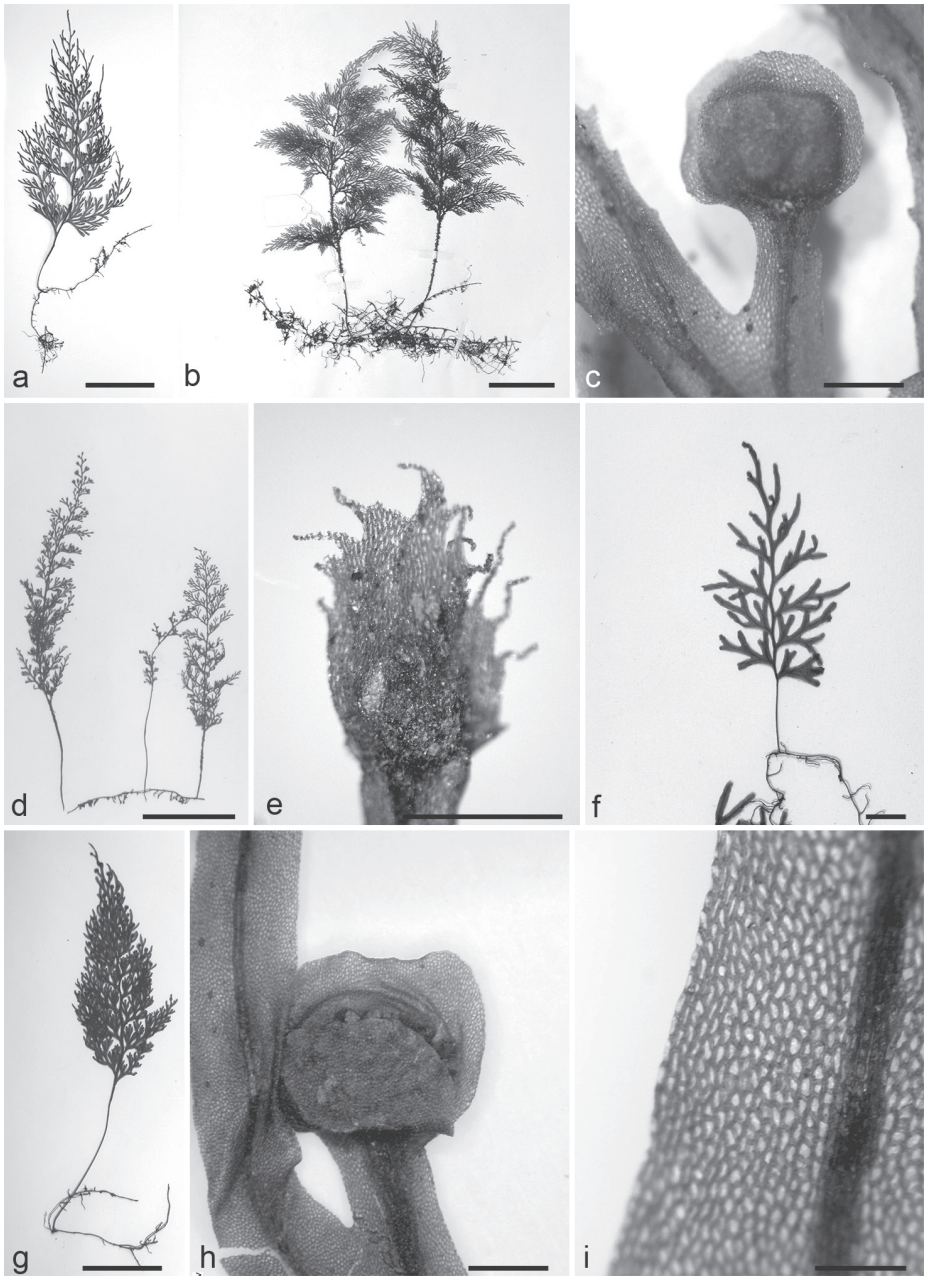

Fig. 10. a. Frond of *Hymenophyllum productum* Kunze. — b, c. *H. reinwardtii* Bosch. b. Fronds; c. sorus. — d, e. *H. fimbriatum* J.Sm. d. Fronds; e. a sorus. — f. Frond of *H. treubii* Racib. — g–i. *H. badium* Hook. & Grev. g. Frond; h. sorus; i. laminar cells (a: *Iwatsuki et al. M-13650*, Pahang, Malaysia, TI 00047106; b, c: *van Balgooy 216*, Mt Wilhelm, Papua New Guinea, KYO 00010964; d, e: *Tagawa 3347*, Taiwan, KYO 00011000; f: *Molesworth-Allen 2704*, Perak, Malaysia, KYO 00010990; g–i: *Copeland s.n.*, Luzon, Philippines, TI 00000818).

quadripinnatifid, (5–)10–13(–25) cm long, to 7 cm wide; *rachis* like the upper part of stipes, winged throughout, wings to 1.2 mm broad, entire, nearly flat, wavy or crisped; *pinnae* to 10 pairs, the larger ones oblong to oblong-lanceolate, acute or moderately acute at apex, shortly stalked, to 4 cm long, 1.5 cm wide, upper ones gradually smaller; *ultimate segments* narrowly oblong or the terminal ones often somewhat and irregularly elongate, round to obtuse at apex, entire and flat at margin, c. 1 mm or broader, the wings of costae and the higher axes not distinctly crisped. *Internal cell walls* thin and uniform, rarely a little thicker. *Sori* many on a frond; *involucres* orbicular-reniform, deeply cleft to the very base in forming two distinct valves, 1.5–2.5 mm long, somewhat broader; lips round, entire but occasionally crenate or undulate; receptacles capitate, included. — **Fig. 10g–i.**

Distribution — India, Nepal, Bhutan, Myanmar, Thailand, Vietnam, S & SW China, Taiwan, C & S Japan; common throughout *Malesia*.

Habitat & Ecology — Epiphytic and epipetric; on mossy tree trunks and on damp rocks, usually in dense evergreen forests; rather common at various altitudes, from lowlands to 2700 m.

Notes — *Hymenophyllum badium* is one of the most variable filmy ferns, making it rather difficult to delimit the species.

Hymenophyllum crispatum is a form of *H. badium*. It differs in having more distinctly crispate wings on the axes, narrower involucres often longer than broad, and generally smaller fronds, subdeltoid in outline. All of these discriminating features vary to some extent.

42. Hymenophyllum edanoi (Copel.) C.V.Morton

Hymenophyllum edanoi (Copel.) C.V.Morton, Contr. U.S. Natl. Herb. 38 (1968) 173. — *Mecodium edanoi* Copel., Philipp. J. Sci. 81 (1952) 2; Fern Fl. Philipp. 1 (1958) 50. — Type: *PNH (Edaño 378) 3897* (holo PNH; iso L, MICH), Philippines, Mindoro, Mt Ilong.

Rhizome long-creeping, wiry, sparsely hairy, c. 0.8 mm diam.; hairs on rhizome pale brown, downy, multicellular, semiarticulate, to 1.5 mm long, caducous. *Stipes* 3–5 cm long, slender, terete, castaneous, practically glabrous in mature condition except for the very base; *fronds* oblong to oblong-lanceolate, moderately acute at apex, gradually narrowing downwards, to 16 cm long, 5.5 cm wide, tripinnate or quadripinnatifid in most dissected part; *rachis* terete in the lower part, narrowly winged in the upper part with entire wings; lateral *pinnules* placed with loose intervals, sometimes more than 3 cm apart from the next one, oblong-ovate, the largest ones c. 3.5 cm long, 1.5 cm wide, shortly stalked; pinna rachis more or less zigzag, winged showing similar appearance as ultimate segments; pinnules simple to pinnatifid with at most five segments; *ultimate segment*s 1–1.6 mm broad, entire, flat, distal ones at the top of pinnae often elongate to more than 1 cm long. *Sori* at apices of short acroscopic branch of pinnules or secondary pinnules; *involucres* bivalvate, cleft nearly to the base, c. 2 mm long, 1.5–2 mm broad; valves longer than broad, round to moderately acute at apex, entire; receptacles clavate, elongate to some extent and shortly extruded from lips of valves.

Distribution — *Malesia*: Philippines (Mindoro: Mt Halcon & Mt Ilong; Luzon: Mt Isarog).

Habitat & Ecology — Not stated.

Note — *Merrill 6080* (A) is typical *H. angulosum* while *Merrill 6082* from Mt Halcon (A, P) is identified as this species with the general mode of the fronds similar to *H. angulosum* in having rather loosely arranged pinnules and segments. It appears that the plants comprising these two specimens grew side by side on Mt Halcon.

43. Hymenophyllum emarginatum Sw.

Hymenophyllum emarginatum Sw., J. Bot. (Schrader) 1800(2) (1801) 101; Syn. Fil. (1806) 148, 377; Copel., Philipp. J. Sci. 64 (1937) 118, pl. 58; Holttum, Rev. Fl. Malaya 2 (1955) 84. — *Trichomanes emarginatum* (Sw.) Poir. in Lam., Encycl. 8 (1808) 76. — *Mecodium emarginatum* (Sw.) Copel., Philipp. J. Sci. 67 (1938) 20; Fern Fl. Philipp. 1 (1958) 52. — Type: *Thunberg s.n.* (holo S, Herb. Sw.), Java.

Hymenophyllum eximium Kunze, Bot. Zeitung (Berlin) 4 (1846) 478; Bosch, Hymenophyll. Javan. (1861) 57, pl. 46. — Lectotype (designated here): *Zollinger 1264* (lecto B; isolecto P), Java.

Hymenophyllum leptodictyon Müll.Berol., Bot. Zeitung (Berlin) 12 (1854) 734. — Syntypes: *Blume s.n.* (n.v.), Java; *Cuming s.n.* (n.v.), Philippines; *Zollinger s.n.* (n.v.), Java.

Hymenophyllum inclinatum Bosch in Miq., Pl. Jungh. (1856) 570. — Lectotype (designated here): *van Gesker s.n.* (lecto L 0544630; isolecto P), Java. Other syntype: *Al. Brown H.Bogor 269* (L), Java.

Hymenophyllum cumingii Bosch, Ned. Kruidk. Arch. 4 (1859) 395, nom. illeg., non C.Presl (1843). — Syntypes: *Cuming 212* (BM, GH, K, L, MICH, P, PNH, PRC, US), Philippines, Luzon.

Hymenophyllum modestum Bosch, Ned. Kruidk. Arch. 5(3) (1863) 163. — Lectotype (designated here): *Cuming 212* (lecto K 000420346; isolecto BM, GH, L, MICH, P, PNH, PRC, US), Philippines, Luzon.

Hymenophyllum pantotactum Alderw., Bull. Jard. Bot. Buitenzorg, sér. 2, 7 (1912) 20. — Type: *Backer 304* (holo BO), Java.

Rhizome long-creeping, irregularly branching, wiry, 0.7–1 mm diam., densely covered with brownish hairs in younger portions, glabrescent, or glabrous in older portion; roots irregularly from rhizome, bearing long root hairs. *Stipes* terete or very narrowly winged in upper portion with wings of at most 1 or 2 cells in row, 7–10(–15) cm long, glabrous or very sparsely hairy, covered with rather dense brownish hairs at base; *fronds* to 25 cm long, 15 cm wide, quadripinnate or even more compound, oblong subdeltoid or variable like ovate, oblong, or lanceolate, acute to acuminate at apex, subtruncate to broadly cuneate at base; *rachis* straight, practically terete in lower portion, but actually very narrowly winged with at most 1 or 2 cells in row, distinctly but narrowly winged in upper portion, glabrous; lateral *pinnae* subdeltoid to oblong, distinctly petiolate in larger ones, to 12 cm long, 6 cm wide; pinna rachis narrowly winged in lower portion, broadly winged to appear like segments in distal portion; secondary *pinnules* with axes winged and appearing like segments; *ultimate segments* round to moderately acute at apex, often extremely elongate in outermost ones, falcate and more than 1.5 cm long in elongate ones, entire and flat at margin, c. 1 mm broad, all axes glabrous on both surfaces. *Sori* at apex of short acroscopic axillary segments, usually nearly to rachis, pinna rachis, and rachis of secondary pinna, more or less constricted at base; *involucres* bivalvate, deeply cleft nearly to the base, orbicular, longer than broad, c. 1.5 mm long, lips round to moderately acute at apex, entire or slightly undulate; receptacles clavate, included.

Distribution — *Malesia*: Peninsular Malaysia, Sumatra to Java and Flores, and to the Philippines.

Habitat & Ecology — Epiphytic on mossy tree trunks and epipetric, usually in dense forests. Altitude: at middle to higher elevations, 1000–2500 m, or to 3300 m on Mt Kinabalu.

Notes — *Hymenophyllum emarginatum* is one of the largest species of this subgenus. It has clavate receptacles and narrower involucres. It is a characteristic species on tree trunks at middle elevations in western Malesia.

Hymenophyllum dilatatum and *H. demissum* Sw., both New Zealand species, were often confused in the past with *H. emarginatum*.

44. Hymenophyllum fimbriatum J.Sm.

Hymenophyllum fimbriatum J.Sm., J. Bot. (Hooker) 3 (1841) 418; Hook., Sp. Fil. 1 (1844) 102, pl. 36C; Bosch, Hymenophyll. Javan. (1861) 55; Copel., Philipp. J. Sci. 64 (1937) 122, pl. 60; Tardieu & C.Chr. in Lecomte, Fl. Indo-Chine 7, 2 (1939) 54; K.Iwats., J. Fac. Sci. Univ. Tokyo, Sect. 3, Bot. 13 (1985) 520; J.X.Liu et al. in C.Y.Wu et al., Fl. China 2–3 (2013) 104; K.Iwats. et al., PhytoKeys 119 (2019) 110. — *Mecodium fimbriatum* (J.Sm.) Copel., Philipp. J. Sci. 67 (1938) 21; Fern Fl. Philipp. 1 (1958) 52. — Lectotype (designated here): *Cuming 218* (lecto K 000420361; isolecto A, B, BM, G, H, L, P), Philippines, Luzon.

Hymenophyllum fraternum Harr., J. Linn. Soc., Bot. 16 (1877) 26, nom. illeg., non C.Presl (1843). — *Hymenophyllum steerei* C.Chr., Index Filic. (1905) 361, 368. — Type: *Steere s.n.* (holo MICH), Philippines, Panay.

Rhizome long-creeping, wiry, irregularly branching, c. 0.5 mm diam. or thicker, hairy with dark brownish hairs when young, glabrescent; roots irregularly from rhizome, densely beset with long, dark brownish root hairs. *Stipes* 2–7 cm long, winged nearly throughout, with wings to 1 mm broad on each side, entire but decidedly crisped; *fronds* oblong to oblong-ovate, acute or moderately so at apex, broadly cuneate to subtruncate at base, 5–10 cm long, 2.5–5 cm wide at widest middle portion, tripinnate to quadripinnatifid; *rachis* nearly straight or slightly zigzag in upper part, winged throughout, wings similar to those on stipes or less crisped; lateral *pinnae* ascending, shortly stalked in larger ones, oblong-subdeltoid to oblong, moderately acute to round at apex, broadly cuneate at base, 2–4.5 cm long in larger ones, to 1.8 cm wide; pinna rachis winged giving appearance just like the ultimate segments; larger *pinnules* pinnate to bipinnatifid or secondary pinnules forked or tri-forked; *ultimate segments* to 1 mm broad, round to obtuse at apex, the margin entire, moderately undulate to more or less crisped. *Sori* at apices of nearly all the ultimate segments of apical portion of fronds, more or less constricted at base; *involucres* deeply cleft nearly to the base, oblong, 1.2–1.6 mm long, 0.8–1.3 mm broad; lips fimbriate-toothed at apex but the teeth somewhat deciduous; receptacles cylindrical, included in valves. — **Fig. 10d, e.**

Distribution — Vietnam, Taiwan; in *Malesia*: Borneo (Sarawak), Philippines, Moluccas (Seram) and New Guinea.

Habitat & Ecology — Epiphytic on tree trunks in primary forests. Altitude: from middle to higher elevations, (600–)1300–2500 m.

Note — In every specimen of this species from the Philippines the lips of involucres are distinctly fimbriate. In the Seram specimens, identified as this species, on the

contrary, the fimbriate lips are not very distinct; Vietnamese plants are similar to plants from Seram in this feature. They are distinct from *H. javanicum*, however, in the smaller, oblong lanceolate fronds. Two Sarawak collections are from 600–900 m elevation.

45. Hymenophyllum imbricatum Blume

Hymenophyllum imbricatum Blume, Enum. Pl. Javae 2 (1828) 220; Copel., Philipp. J. Sci. 64 (1937) 137, pl. 70, 71; Holttum, Rev. Fl. Malaya 2 (1955) 85; C.W.Chen et al., Sol Amazing (2017) 131; K.Iwats. et al., PhytoKeys 119 (2019) 110. — *Mecodium imbricatum* (Blume) Copel., Philipp. J. Sci. 67 (1938) 22; Fern Fl. Philipp. 1 (1958) 53. — Type: *Blume s.n.* (holo L), Java.

Hymenophyllum formosum Brack., U.S. Expl. Exped., Filic. 16 (1854) 268, pl. 32, f. 3; Bosch, Hymenophyll. Javan. (1861) 59, pl. 47, 48. — Lectotype (designated here): *Brackenridge* in *Wilkes Exped. s.n.* (lecto US 00134560; isolecto GH, K, NY, YU), Tahiti.

Rhizome long-creeping, brown, bearing brown, multicellular hairs rather densely in younger portion, glabrescent in older portion, 0.4–0.8 mm diam.; roots in irregular intervals from rhizomes, dark brown, bearing dark brown root hairs rather densely. *Stipes* to 10 cm or even more in length, terete throughout or very slightly winged towards upper portion, glabrescent except for hairy base; *fronds* quadripinnatifid or more compound, subdeltoid to oblong in outline, acute to acuminate at apex, round to broadly cuneate at base, to 25 cm long and 10 cm wide, variable in size and smaller ones less than 7 cm long, easily soriferous; *rachis* distinctly winged throughout, narrow at base, more widely upwards, nearly as broad as ultimate segments, entire, flat; larger *pinnae* oblong-subdeltoid to oblong, more or less falcate, acuminate at apex, shortly petiolate at cuneate base, to 7 cm long, 3 cm wide, smaller ones narrowly oblong, sessile at base; pinna rachis similar to ultimate segments; *pinnules* of larger pinnae similar to uppermost pinnae; *ultimate segments* straight or curved, round at apex, entire and flat at margin, 1–1.2(–1.5) mm broad, terminal ones sometimes elongate, more than 1 cm long; *internal cell walls* thin, straight. *Sori* at apices of short acroscopic branch of ultimate segments, dispersing over the complete surface of fronds with a tendency to gather in upper portion; *involucres* bivalvate, cleft almost to the shallow obconic base; lips almost circular, entire, usually broader than long, 1.5–2 mm diam.; receptacles capitate, much swollen at apex, included.

Distribution — *Malesia*: Peninsular Malaysia, Sumatra, Java, Philippines, Sulawesi, Lesser Sunda Islands (Flores), Moluccas, New Guinea; Solomon Islands, Vanuatu, New Caledonia, Fiji, Samoa and Tahiti.

Habitat & Ecology — Epiphytic on mossy tree trunks in dense forests. Altitude: 1000–2600 m; to 3400 m in New Guinea.

Note — In general, *H. imbricatum* is similar to *H. emarginatum* in size and form of the fronds, although the soral characters are quite different.

46. Hymenophyllum javanicum Spreng.

Hymenophyllum javanicum Spreng., Syst. Veg. 4 (1827) 132; Bosch, Hymenophyll. Javan. (1861) 50, pl. 40; Bedd., Handb. Ferns Brit. India (1883) 32; Copel., Philipp. J. Sci. 64 (1937) 120, pl. 59; Tardieu & C.Chr. in Lecomte, Fl. Indo-Chine 7, 2 (1939) 54; Holttum, Rev. Fl. Malaya 2 (1955) 83, f. 24; Sledge, J. Linn. Soc. Bot. 60 (1968) 294; Croxall, Austral. J. Bot. 23 (1975) 521; K.Iwats., J. Fac. Sci. Univ. Tokyo, Sect. 3, Bot. 13 (1985) 519; J.X.Liu et al. in C.Y.Wu et al., Fl. China

2–3 (2013) 103; C.W.Chen et al., Sol Amazing (2017) 132; K.Iwats. et al., PhytoKeys 119 (2019) 110. — *Mecodium javanicum* (Spreng.) Copel., Philipp. J. Sci. 67 (1938) 20; Tagawa & K.Iwats. in Smitinand et al., Fl. Thailand 3 (1979) 71; J.L.Tsai & W.C.Shieh in H.L.Li et al., Fl. Taiwan 1 (1994) 113. — Lectotype (designated by Field, Austral. Syst. Bot. 33 (2020) 204): Nees & Blume, Nova Acta Phys.-Med. Acad. Caes. Leop.-Carol. Nat. Cur. 11 (1823) 128, t. 14: f. 1.

Hymenophyllum erosum Blume, Enum. Pl. Javae 2 (1828) 221; Bosch, Hymenophyll. Javan. (1861) 54, pl. 43. — Lectotype (designated here): *Blume s.n.* (lecto L), Java. Other syntype: *Reinwardt s.n.* (L), Moluccas.

Hymenophyllum daedaleum Blume, Enum. Pl. Javae 2 (1828) 222. — Lectotype (designated here): *Blume s.n.* (lecto L 0051725; isolecto K), Java, Bantam.

Hymenophyllum micranthum Bosch in Miq., Pl. Jungh. 5 (1857) 566; Hymenophyll. Javan. (1861) 52, pl. 41. — Type: *van Gesker s.n.* (holo L 0544628), Java.

Rhizome long-creeping, wiry, slender, c. 0.5 mm diam., laxly branched, bearing brownish hairs rather sparsely. *Stipes* remote, glabrous but the very base hairy, 2–5 cm long, winged except near the base; wings becoming broader upwards, entire, more or less crisped at edge. *Fronds* oblong-subdeltoid, acute to moderately acute at apex, tripinnate to quadripinnatifid, glabrous, 4–7(–15) cm long, 3–4(–7) cm wide at the widest basal portion; *rachis* straight or zigzag in very upper portion, winged like upper portion of stipes; *pinnae* 5 or more pairs, the basal ones to 3 cm long, 2 cm wide, oblong-subdeltoid, moderately acute to round at apex, broadly cuneate to round at base, shortly stalked, upper ones gradually becoming smaller upwards, oblong in outline; pinna rachis like rachis, more or less zigzag throughout; *ultimate segments* narrow, round to obtuse at apex, entire but undulate or crisped at margin, to 4 mm long, 0.6–1 mm broad, decurrent onto all axes forming distinct, wavy or crisped wings of c. 0.8 mm wide; *internal cell walls* thin, straight. *Sori* scattered usually on the apical parts of pinnae; *involucres* bivalvate, deeply cleft to the very base; valves subdeltoid to oblong, 1.2–1.6 mm long, to 1 mm broad, the lips finely toothed; receptacles clavate to filiform, wholly included in the involucres. Chromosome numbers: $n = 36$ (Braithwaite, Bot. J. Linn. Soc. 71 (1975) 169), $2n = 72$ (Manton & Sledge, Philos. Trans., Ser. B, 238 (1954) 136), $2n = 108$ (Mehra & Singh, J. Genet. 55 (1957) 380).

Distribution — Sri Lanka, India, Myanmar, Thailand, Vietnam, Taiwan; throughout *Malesia*; Oceania east to Marquesas, south to Australia (Queensland).

Habitat & Ecology — Epiphytic on mossy tree trunks in dense tropical evergreen forests. Altitude: rather common at medium to higher elevations, 600–2800 m.

Note — *Hymenophyllum javanicum*, one of the most common and widely distributed species in the family, is variable in the size and form of the fronds; the characteristics of the segment margin and involucres are distinct.

47. Hymenophyllum junghuhnii Bosch

Hymenophyllum junghuhnii Bosch in Miq., Pl. Jungh. 5 (1857) 570; Hymenophyll. Javan. (1861) 60, pl. 49; Copel., Philipp. J. Sci. 64 (1937) 141, pl. 73. — *Mecodium junghuhnii* (Bosch) Copel., Philipp. J. Sci. 67 (1938) 22; K.Iwats. et al., PhytoKeys 119 (2019) 110. — Lectotype (designated by Copeland 1937): *Junghuhn s.n.* (lecto L 0051727 / 908.282.194), Java. Other syntypes: *Blume s.n.* (n.v.), Java; *Reinwardt s.n.* (n.v.), Java.

Hymenophyllum bamlerianum Rosenst., Repert. Spec. Nov. Regni Veg. 10 (1912) 323. — *Mecodium bamlerianum* (Rosenst.) A.F.Braithw., Brit. Fern Gaz. 10 (1969) 82. — Syntypes: *Bamler S 50* (CAL, GH, M, S), New Guinea.

Hymenophyllum raapii Gand., Bull. Soc. Bot. France 60 (1913) 29. — Type: *Raap s.n.* (n.v.), Java, Tjibodas.

Hymenophyllum opacum Copel., Philipp. J. Sci. 64 (1937) 151, pl. 81. — *Mecodium opacum* (Copel.) Copel., Philipp. J. Sci. 67 (1938) 23. — Type: *Docters van Leeuwen 10946* (holo L; iso MICH), New Guinea, Mt Nassau.

Rhizome long-creeping, stout, commonly c. 0.7 mm and often to nearly 1 mm diam., hairy; hairs multicellular, semiarticulate, soft, brown, to 1 mm long. *Stipes* terete, or very narrowly winged in upper portion, to 15 cm long, nearly glabrescent except for hairy base; wings of stipes very narrow, at most 0.5 mm broad, entire, flat, glabrous; *fronds* oblong-subdeltoid to broadly oblong, acute to acuminate at apex, round to cuneate at base, commonly 12–25 cm long, 4–12 cm wide, quadripinnatifid to quadripinnate; *rachis* distinctly winged, wings of rachis broader in distal portion, more than 1 mm at each side of rachis, entire and very flat; *pinnae* shortly stalked in lower larger ones with winged stalks, asymmetrically oblong-subtriangular or narrower, larger ones c. 8 cm long, 2.5 cm wide; pinna rachis similar to rachis, broadly winged, winged pinna rachis broader than ultimate segments; larger *pinnules* like smaller pinnae, sessile, bipinnatifid to bipinnate with several to more than a dozen segments; *ultimate segments* usually 2–3 mm long, c. 1.2 mm broad or broader, shallowly cut with neighboring ones, sometimes distal ones extraordinarily elongated to 1.5 cm long, entire and flat at margin, glabrous, soft papyraceous in texture; *internal cell walls* thin, straight. *Sori* large, solitary at apices of ultimate segments, practically on all segments and dispersing from apex downwardly, or from along axes outwardly; *involucres* bivalvate, deeply cleft nearly to the very base; valves broadly orbicular, to 3 mm broad, 2 mm long, entire and flat at margin; receptacles capitate, large, included in valves.

Distribution — *Malesia*: Sumatra, Java, Borneo, Lesser Sunda Islands, Moluccas (Seram) and New Guinea.

Habitat & Ecology — Epiphytic on tree trunks and on branches of tall trees in dense evergreen forests. Altitude: medium to high elevations, (600–)1200–3000 m.

Notes — *Hymenophyllum junghuhnii* is one of the largest filmy ferns and is handsomely pendulous on tree trunks in evergreen jungles. It is distinct among other species by a combination of such features as larger fronds, entire, flat margins of the segments and wings, broadly winged rachis and pinna rachis and large sori with the margins of the valves round and entire.

Hymenophyllum opacum from New Guinea has many sori with valves longer than wide; the frond is oblong-subdeltoid, c. 15 cm long; the wings of the stipes and rachis are more or less crisped; and the internal cell walls are thicker. No other specimens from New Guinea are identical with *H. badium* or *H. salakense*, and *H. opacum* is hardly referable to those species. The type of *H. opacum* appears to be an incomplete form of *H. junghuhnii*.

48. Hymenophyllum longifolium Alderw.

Hymenophyllum longifolium Alderw., Bull. Jard. Bot. Buitenzorg, sér. 2, 16 (1914) 17; Copel., J. Arnold Arbor. 10 (1929) 175; Philipp. J. Sci. 64 (1937) 142, pl. 74; K.Iwats. et al., PhytoKeys 119 (2019) 110. — *Mecodium longifolium* (Alderw.) Copel., Philipp. J. Sci. 67 (1938) 23. — Lectotype (designated here): *Rachmat 615* (lecto BO; isolecto L), Sulawesi, Goenoeng Boesoe.

Rhizome long-creeping, wiry, c. 0.5 mm diam., bearing sparse long, brown, multicellular hairs or glabrescent. *Stipes* not very long, broadly winged in uppermost portion and narrowly in lower portion, hairy at base; *fronds* lanceolate, mostly in parallel and gradually narrowing towards acute apex, basal *pinnae* usually becoming smaller downwards, (15–)20–35(–60) cm long, (4–)6–8(–12) cm wide nearly throughout, tripinnate to quadripinnatifid; *rachis* straight, glabrous, distinctly winged; wings of rachis broad, more than 1 mm on each side of rachis, entire, flat, distinct throughout; *pinnae* more than 30 pairs, shortly stalked with broadly winged stalks, asymmetrically oblong-subdeltoid, ± falcate, c. 5.5 cm or to 8 cm long, c. 2.2 cm or to 3 cm wide, nearly in the same size except for upper ones or slightly becoming smaller upwards; pinna rachis like rachis, distinctly and broadly winged throughout, wings broader than ultimate segments; *ultimate segments* oblong to linear oblong, round or retuse at apex, 1.2–1.5 mm broad, shallowly incised to the neighboring ones; *internal cell walls* thin, straight. *Sori* solitary at apex of ultimate segments, bivalvate; *involucres* deeply cleft nearly to the very base, usually broader than long, 1–1.2 mm long, 1.4–1.8(–2.2) mm broad, entire or roughly undulate at margin; receptacles capitate, bearing a number of sporangia, included.

Distribution — *Malesia*: Sulawesi, Moluccas (Seram) and New Guinea.

Habitat & Ecology — Epiphytic on mossy tree trunks in dense evergreen forests from lowlands to medium elevations to 2600 m.

Note — The above description of vegetative characters is based mostly on the lectotype; the particular form of the fronds is peculiar to this species. In characters other than the form of the fronds, *H. longifolium* is similar to *H. junghuhnii* and is hardly separable in some cases. Some collections have wider fronds, to 12 cm, or fronds oblong-lanceolate in outline and gradually narrowing toward both the apex and base. Such variation in the form of the fronds may result from the habitat of the plants concerned. Some Javan collections referred to *H. longifolium* have much narrower fronds, although they appear to be narrower forms of *H. junghuhnii*.

49. Hymenophyllum productum Kunze

Hymenophyllum productum Kunze, Bot. Zeitung (Berlin) 6 (1848) 305; Bosch, Hymenophyll. Javan. (1861) 56, pl. 45; Copel., Philipp. J. Sci. 64 (1937) 113, pl. 54; Holttum, Rev. Fl. Malaya 2 (1955) 83, f. 26; K.Iwats., J. Fac. Sci. Univ. Tokyo, Sect. 3, Bot. 13 (1985) 519; J.X.Liu et al. in C.Y.Wu et al., Fl. China 2–3 (2013) 103; K.Iwats. et al., PhytoKeys 119 (2019) 110. — *Mecodium productum* (Kunze) Copel., Philipp. J. Sci. 67 (1938) 20; Fern Fl. Philipp. 1 (1958) 51; Tagawa & K.Iwats. in Smitinand et al., Fl. Thailand 3 (1979) 71, f. 5-1. — Syntypes: *Zollinger 74* (P), *Zollinger 363z* (B, L), Java; *Zollinger 365a.x* (n.v.), Java; *Zollinger 1851* (L), Java.

Rhizome slender, c. 0.5 mm diam., wiry, nearly glabrous or brown hairy in younger portion, irregularly branching. *Stipes* remote, glabrous but hairy at the very base, commonly c. 5 cm long, winged in the upper half; wings flat or slightly undulate; *fronds* oblong to oblong-lanceolate, acute at apex, tripinnate to quadripinnatifid, herbaceous, green to deep green, glabrous throughout, (5–)10–15(–25) cm long, to 5 cm wide; rachis like the upper part of stipes, slightly zigzag in upper part, winged throughout; wings flat, continuous, 0.4–0.8 mm wide; *pinnae* up to 10 pairs, the basal ones triangular-rhomboid, acute at apex, at the base subtruncate anteriorly and cuneate posteriorly,

short-stalked, to 5 cm long, 2 cm wide; *pinnules* c. 5 pairs, with 5–10 segments; upper pinnae gradually becoming smaller; *ultimate segments* narrow, entire and flat at margin, obtuse to retuse at apex, 0.8–1.2 mm broad, the uppermost usually elongate, to twice as long as normal ones; *internal cell walls* thin, straight. *Sori* at apices of ultimate segments, constricted below the base of involucre; *involucres* bivalvate, divided down almost to the base, just triangular, long-acuminate at apex, round at base, 1.2–1.8 mm long, less than 1 mm wide; the lips toothed; receptacles clavate to somewhat columnar, included. — **Fig. 10a.**

Distribution — Thailand (Peninsular), China (Hainan), Taiwan; in *Malesia*: Peninsular Malaysia, Sumatra, Borneo, Java, Philippines, Sulawesi, Moluccas (Buru and Seram) and New Guinea to Bismarck Archipelago.

Habitat & Ecology — Epiphytic on mossy tree trunks in dense evergreen forests at middle to higher elevations, rarely in lowland forests. Altitude: (800–)1000–1800 m, to 3000 m in New Guinea.

Note — New Guinean plants are much more variable in size and form, often elongating to more than 40 cm in length, but less than 5 cm wide; they also occupy a much wider habitat, ranging from lower montane rain forests to subalpine forests (750–3000 m elevation).

50. Hymenophyllum reinwardtii Bosch

Hymenophyllum reinwardtii Bosch, Ned. Kruidk. Arch. 4 (1859) 399; Hymenophyll. Javan. (1861) 52, pl. 42; Copel., Philipp. J. Sci. 64 (1937) 115, pl. 55; K.Iwats. et al., PhytoKeys 119 (2019) 110. — *Hymenophyllum dichotomum* auct. non Cav.: Blume, Enum. Pl. Javae 2 (1828) 222. — *Mecodium reinwardtii* (Bosch) Copel., Philipp. J. Sci. 67 (1938) 20; Fern Fl. Philipp. 1 (1958) 51. — Type: *Reinwardt 1689* (holo L), Moluccas, Tidore.

Hymenophyllum bismarckianum Christ in K.Schum. & Lauterb., Fl. Schutzgeb. Südsee, Nachtr. (1905) 34; Copel., Philipp. J. Sci. 64 (1937) 117. — Lectotype (designated here): *Schlechter 14030* (lecto P 00622009; isolecto B, BM, BO, BR, K, P), Papua New Guinea, Bismark Gebirge.

Hymenophyllum copelandianum Alderw., Bull. Jard. Bot. Buitenzorg, sér. 2, 7 (1912) 19. — Lectotype (designated here): *Elmer 11799* (lecto BO; isolecto BM, L, NY, US), Philippines, Mindoro, Mt Apo.

Hymenophyllum australe auct. non Willd.: Christ, Philipp. J. Sci., C. 2 (1907) 156; Copel., Leafl. Philipp. Bot. 3 (1910) 800.

Rhizome long-creeping, wiry, c. 0.5–0.8 mm diam., bearing sparse pale brownish hairs or glabrescent. *Stipes* to 10 cm long, distinctly winged except near base; wings of stipes 0.8–1.5 mm broad, distinctly crisped throughout; *fronds* oblong-subdeltoid to oblong in outline, usually widest at base, gradually narrowing towards moderately acute apex, quadripinnate to pentapinnatifid in basal portion, (5–)8–12(–30) cm long, (2–)3–6(–12) cm wide; *rachis* straight but slightly zigzag in upper portion, distinctly winged throughout with the wings like those on stipes; lateral *pinnae* up to 10 pairs below indefinite apical portion, lowest one the largest, shortly stalked, asymmetrically oblong-subdeltoid to oblong, round to moderately acute at apex, 1.5–3(–5) cm long, 1–2(–2.5) cm wide, upper lateral pinnae gradually becoming smaller upwards; pinna rachis winged with crisped wings and seemingly like ultimate segments; *pinnules* and secondary pinnules like smaller lateral pinnae in upper portion; *ultimate segments* round to moderately acute at apex, c. 0.6–1 mm broad, entire, more or less crisped. *Sori* solitary, at apices of ultimate segments, 1.5–2 mm diam.; *involucres* orbicular in outline,

bivalvate or deeply cleft nearly to the base, round, entire or very minutely crenate at margin; receptacles clavate, included. — **Fig. 10b, c.**

Distribution — *Malesia*: Sumatra, Borneo, Java, Philippines, Sulawesi, Moluccas (Seram and Tidore), New Guinea; Micronesia.

Habitat & Ecology — Epiphytic on tree trunks, larger fronds usually erect or pendulous. Altitude: lower montane to mossy forests, and in subalpine forests in New Guinea, 1000–3300 m.

Note — New Guinean plants are variable in various characters, especially in the size and form of the fronds, sometimes becoming more than 30 cm long and 12 cm wide.

51. Hymenophyllum salakense Racib.

Hymenophyllum salakense Racib., Pteridoph. Buitenzorg (1898) 18; Copel., Philipp. J. Sci. 64 (1937) 143, pl. 75. — *Mecodium salakense* (Racib.) Copel., Philipp. J. Sci. 67 (1938) 23. — Lectotype (designated here): *Raciborski s.n.* (lecto BO; isolecto BM, K, L, P), Java, Salak.

Rhizome long-creeping, wiry, 0.5–0.8 mm diam., glabrous or hairy with brown, multicellular, subarticulate hairs. *Stipes* distinctly winged nearly to the base, with entire and flat wings, sparsely hairy, usually less than 10 cm long; *fronds* oblong-subdeltoid to orbicular, the apex round, moderately acute or acute, round to cuneate at base, c. 10 cm long; rachis distinctly winged throughout with entire and flat wings, thus usually broader than ultimate segments or more than 3 mm broad, very sparsely hairy; lower *pinnae* stalked with distinct, winged petioles, asymmetrically oblong-subdeltoid; pinna rachis like rachis but less broad; *ultimate segments* round to moderately acute at apex, entire and flat at margin, 1.5–2 mm broad, terminal ones often extraordinarily elongate to be more than 2 cm long, usually very dark brown to blackish in dried condition; *internal cell walls* thin, straight. *Sori* at apices of ultimate segments, practically on all the segments, dispersing from distal portion inwardly; *involucres* bivalvate, deeply cleft nearly to the very base, very large in size and to more than 3 mm long, 4 mm broad; valves orbicular to broadly so, lips entire or more or less undulate, glabrous; receptacles capitate, large, completely included below lips of valves.

Distribution — *Malesia*: Sumatra, Java, Borneo and Philippines.

Habitat & Ecology — Epiphytic, usually on mossy tree trunks, and epipetric, often on moist mossy rocks, in dense evergreen forests. Altitude: 1200–1700 m.

Notes — In many specimens, *H. salakense*, at a glance, looks like a less mature form of either *H. junghuhnii* or *H. badium*, though the type specimen is fully fertile. Specimens referred to *H. salakense* were collected from various localities and bear mature sori. As is natural in such forms, the stipes are winged nearly to the base.

All the materials from New Guinea referred to this species appear to be *H. junghuhnii*.

52. Hymenophyllum thuidium Harr.

Hymenophyllum thuidium Harr., J. Linn. Soc., Bot. 16 (1877) 25; Christ, Philipp. J. Sci., C. 2 (1907) 154; Copel., Philipp. J. Sci. 64 (1937) 116, pl. 56; K.Iwats. et al., PhytoKeys 119 (2019) 110. — *Mecodium thuidium* (Harr.) Copel., Philipp. J. Sci. 67 (1938) 20; Fern Fl. Philipp. 1 (1958) 52. — Type: *Steere s. n.* (holo K n.v.; iso GH, MICH, MO, P, PH, UC, US), Philippines, Mts of Panav.

Hymenophyllum physocarpum Christ in K.Schum. & Lauterb., Fl. Schutzgeb. Südsee, Nachtr. (1905) 35, pl. 1A. — Lectotype (designated here): *Schlechter 14529* (lecto B 20 0102359; isolecto BM, BO, K, P), Papua New Guinea, Torricelli Gebirge.

Rhizome long-creeping, wiry, rather thick, or 0.5–0.8 mm diam., bearing rather sparse pale brownish hairs or glabrescent. *Stipes* winged almost or quite to base, wings to 0.7 mm wide, actually entire at margin but distinctly crisped to appear dentate; *fronds* oblong-subdeltoid to oblong-lanceolate, acute to moderately so at apex, widest at base or more or less narrowing towards one or two basal pairs, quadripinnate, to 10 cm long, 8 cm wide; *rachis* nearly straight or more or less zigzag in uppermost portion, distinctly winged throughout with very much crisped margin; lowest lateral *pinnae* asymmetrically subtriangular or deltoid, acute to moderately so at apex, shortly stalked, middle lateral pinnae oblong-subdeltoid, broadly cuneate and shortly stalked at base, upper lateral pinnae narrowly oblong, sessile; pinna rachis winged with distinctly crisped wings; *pinnules* and secondary pinnules like upper smaller pinnae, larger ones shortly stalked; *ultimate segments* round to moderately acute at apex, 0.3–0.5 mm broad, actually entire but appearing sharply dentate by very distinct crispation at margin. *Sori* solitary at apices of ultimate segments, usually tending to be in upper portion of fronds; *involucres* suborbicular, deeply cleft nearly to the base, round at minutely crenate (or variable from nearly entire to distinctly toothed) flat margin, 1–1.5 mm both in width and in length, or more than twice as broad as ultimate segments; receptacles with sterile columnar base and slightly enlarged head, included in valves.

Distribution — *Malesia*: Borneo, Philippines, Moluccas (Seram) and New Guinea.

Habitat & Ecology — Epiphytic on mossy tree trunks in dense rain forests. Altitude: middle elevations, 350–1500 m.

Note — The involucre of the type specimen of *H. physocarpum* has distinctly toothed lips and is distinct in this feature from *H. thuidium*. Other collections from New Guinea (*Brass 23572*, *Cheeseman s.n.* in BM) with the same characteristic need further study.

53. Hymenophyllum treubii Racib.

Hymenophyllum treubii Racib., Pteridoph. Buitenzorg (1898) 15; Copel., Philipp. J. Sci. 64 (1937) 140, pl. 72; Holttum, Rev. Fl. Malaya 2 (1955) 84, f. 27 — *Mecodium treubii* (Racib.) Copel., Philipp. J. Sci. 67 (1938) 22. — Lectotype (designated here): *Raciborski 215* (lecto BO; isolecto B, BM, K, L, MICH, US), Java, Salak.

Hymenophyllum treubii Racib. var. *novoguineense* Rosenst., Repert. Spec. Nov. Regni Veg. 12 (1913) 526. — Syntypes: *Keysser 239p* (B, BM, CAL, NY, S, UC), New Guinea, Sattelberg.

Rhizome long-creeping, wiry, 0.2–0.3 mm diam., glabrous or hairy in younger portion with dark brownish hairs. *Stipes* terete in lower portion, narrowly winged towards apex, glabrous, 1–4 cm long; *fronds* bipinnate to tripinnatifid, oblong to oblong-lanceolate, rather irregularly branching, round to obtuse at apex, 6–10 cm long, 2.5–5 cm wide; *rachis* winged throughout, wings entire, flat, widening towards distal portion, rachis including its wing to 2 mm broad; *pinnae* close but not overlapping, oblique, with few rather distant segments, pinnate-bipinnatifid but segments arrange rather irregularly, or each division often asymmetrical, acroscopic pinnules sometimes less developed or particular ultimate segments in various position extraordinarily elongate; *ultimate*

segments simple or forked, c. 2 mm broad, the simple segments commonly 5–10 mm long or even more, flat throughout, sterile segments not toothed, round or notched at apex; *internal cell walls* thin, straight. *Sori* usually a few, at apices of ultimate segments in distal part, bivalvate; *involucres* obconic in the base, cleft almost or quite to the base; valves semicircular or oblong, c. 2 mm long, 2.5 mm broad, lips almost round and slightly and irregularly toothed; receptacles short, clavate, with its apex thickened, wholly included in valves. Chromosome numbers: $n = 36$ (Braithwaite, Fern Gaz. 10 (1969) 82). — **Fig. 10f.**

Distribution — *Malesia*: Peninsular Malaysia to Moluccas.

Habitat & Ecology — Epiphytic and epipetric; on mossy tree trunks and on moist rocks in dense montane forests. Altitude: at middle elevations, 800–1700 m.

Note — All the New Guinean specimens referred to *H. treubii*, that we have seen, have a columnar receptacle and are correctly placed under *H. angulosum*. It is doubtful that *H. treubii* occurs in New Guinea.

c. Subgenus **Mecodium**

Hymenophyllum Sm. subg. *Mecodium* Copel. See under the genus for related synonyms, literature and type.

Hymenophyllum Sm. sect. *Glabra* Prantl, Unters. Morph. Gefässkrypt. 1 (1875) 54. — Type: *Hymenophyllum polyanthos* (Sw.) Sw.

Hymenophyllum Sm. sect. *Corrugatae* K.Iwats., Acta Phytotax. Geobot. 35 (1984) 173. — Type: *Hymenophyllum ooides* F.Muell. & Baker.

Rhizome long-creeping, filiform, nearly glabrous; *stipes* to 10 cm long: *fronds* pinnate to quadripinnatifid, elliptic to subdeltoid, or forming an irregular outline in one species (*H. ooides*); *ultimate segments* entire at margin, corrugated in one species (*H. ooides*); *sori* at apex of ultimate segments, *involucre* bivalvate, entire at margin; receptacles included in involucres. Basic chromosome number: $x = 28$.

Distribution — More than 35 species, cosmopolitan; 5 species in *Malesia*.

Habitat — Commonly epiphytic on tree trunks and epipetric on mossy rocks in the northern edge of its distribution in the temperate zone.

Taxonomy — *Mecodium* was recognized as a distinct genus by Copeland (Philipp. J. Sci. 68 (1938) 47) and delimited rather broadly to include all the species of subg. *Globosa*. The basic chromosome number indicates the distinctness of this group and molecular data support it. This is a group of species closely related to a broadly recognized *H. polyanthos*.

KEY TO THE SPECIES

1a. Ultimate segments entire and flat or irregularly crisped; extraordinarily larger lateral pinnae, if any, not so large as forming side leaves 2

b. Ultimate segments entire and distinctly crisped to form corrugated fronds; some lateral pinnae becoming larger to give the appearance of side leaves . . . . . **56. H. ooides**

2a. Fronds pinnate, extraordinarily larger pinnae few, if any 3
b. Fronds pinnate, often bearing extraordinarily larger pinnae resulting in rather irregular outline of fronds 4
3a. Sori crowded apically . . . . . **57. H. paniculiflorum**
b. Sori not crowded apically, dispersed throughout the frond . . . **58. H. polyanthos**
4a. Rachis more or less straight, bearing blackish galls at middle of fronds . . . . . **54. H. copelandii**
b. Rachis more or less zigzag, not bearing any galls . . . . . **55. H. novoguineense**

54. Hymenophyllum copelandii C.V.Morton

Hymenophyllum copelandii C.V.Morton, Contrib. U.S. Natl. Herb. 38 (1968) 173; C.W.Chen et al., Sol Amazing (2017) 127. — *Mecodium archboldii* Copel., Philipp. J. Sci. 73 (1941) 458, t. 1, nom. illeg., nom. superfl. — Lectotype (designated here): *Brass 14067* (lecto MICH 1190737; isolecto A, BM, BO, BRI, FI, K, L 2 sheets, TI), New Guinea, Idenburg River.

Rhizome long-creeping, wiry, slender, 0.3–0.4 mm diam., bearing brown hairs rather sparsely at apex or nearly glabrous in mature portion. *Stipes* to 5 cm long, very narrowly winged in upper portion, glabrous; *fronds* linear-lanceolate, gradually narrowing towards acute apex and gradually narrowing towards base, generally 25 cm long, 4 cm wide, and sometimes more than 50 cm long, tripinnatifid-tripinnate; *rachis* like the upper portion of stipes, very sparsely hairy with brown hairs, winged throughout with narrow, flat, entire wings, bearing blackish galls in the midst of the frond; lateral *pinnae* more than 25 pairs, lower ones often very much reduced to auricles, middle pinnae the largest, falcately narrowly oblong, sessile at base, narrowing towards acute apex, often irregularly elongate, larger ones c. 3 cm long, 1 cm wide; *pinnules* with several ultimate segments, pinnate in arrangement; *ultimate segments* round to obtuse at apex, entire and flat at margin, to 1 mm broad. *Sori* solitary at apex of every ultimate segment; *involucres* bivalvate, ovate-oblong, moderately acute at apex, c. 2 mm long, a little more than 1 mm broad.

Distribution — *Malesia*: New Guinea; Solomon Islands.

Habitat & Ecology — Creeping in moss on trunks and branches of canopy trees, from sea level to 2300 m.

Note — Somewhat similar to *H. novoguineense*, but the pinnae may elongate extraordinarily to form an irregular outline of the fronds; sometimes bearing strange blackish galls in middle of fronds.

55. Hymenophyllum novoguineense (Rosenst.) K.Iwats.

Hymenophyllum novoguineense (Rosenst.) K.Iwats. in Ebihara et al., Blumea 51 (2006) 231. — *Hymenophyllum blumeanum* Spreng. var. *novoguineense* Rosenst., Repert. Spec. Nov. Regni Veg. 5 (1908) 371. — *Mecodium novoguineense* (Rosenst.) Copel., Philipp. J. Sci. 73 (1941) 458. — Type: *Werner 49a* (holo n.v.; iso S, UC, US), New Guinea, Mt Gelu.

Rhizome long-creeping, wiry, 0.3–0.4 mm diam., glabrous, dark. *Stipes* terete or very narrowly winged in upper portion, slender but stiff, dark throughout, glabrous, 10–15 cm long but very reduced scar of pinnae usually coming down nearly 3–5 cm

up the rhizome; *fronds* to 40 cm long, 4–7 cm wide, and often rachis branching to bear a few side-fronds having a total width c. twice as wide as a single frond, tripinnate to quadripinnatifid; *rachis* slightly zigzag in upper portion, winged throughout or terete in basal portion; wings to 0.3 mm broad on each side, entire, flat; *pinnae* oblong to oblong-lanceolate, round at apex, sometimes a few to several middle or upper ones becoming abnormally larger or rachis branching to form side fronds, pinnae of normal size, at most 4 cm long, 1.5 cm wide, larger ones shortly stalked; *pinnules* pinnate with a few forked or at most quadrate secondary pinnules; *ultimate segments* round at apex, entire and flat at margin, at most 1 mm in width. *Sori* on terminal of ultimate segments, on practically every segment, usually tending to gather in upper portion; *involucres* bivalvate, deeply cleft to more than halfway, the basal portion immersed in segments; valves nearly circular, round to moderately acute at apex, entire and flat at margin, 1–1.3 mm long, to 1 mm broad; receptacles clavate, included below lips of involucres.

Distribution — *Malesia*: New Guinea.

Habitat & Ecology — Locally common; pendulous epiphytes on lower surface of old leaning trees in more or less mossy forests on ridge crests at 1600–3300 m elevation.

56. Hymenophyllum ooides F.Muell. & Baker

Hymenophyllum ooides F.Muell. & Baker, J. Bot. 23 (1890) 105; Copel., Philipp. J. Sci. 64 (1937) 107. — *Mecodium ooides* (F.Muell. & Baker) Copel., Philipp. J. Sci. 67 (1938) 19. — Type: *MacGregor s.n.* (holo K), New Guinea.

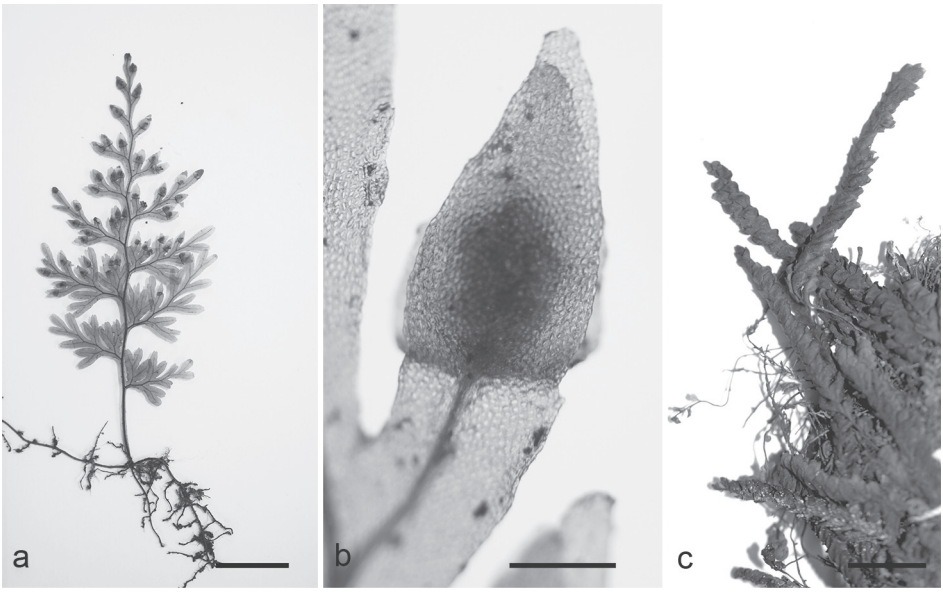

Fig. 11. a, b. *Hymenophyllum polyanthos* (Sw.) Sw. a. Fronds; b. sorus. — c. fronds of *H. ooides* F.Muell. & Baker (a, b: *Sugawara et al. SB2007-8,* Sabah, Malaysia, TNS 766195; c: *van Balgooy 453*, Papua New Guinea, KYO 00010978).

Rhizome long-creeping, wiry, c. 0.2 mm diam., dark brown to blackish, bearing very sparse pale brownish hairs or glabrescent. *Stipes* short, or to 3 cm long, finely filiform, glabrous, very narrowly winged in upper portion; *fronds* 2–3-pinnate, pendulous, variable in size and form, lanceolate or irregularly broader with many bipinnate pinnae (side-leaves), 5–30 cm long, c. 3 cm wide in the middle portion, gradually narrowing to both ends; *rachis* thread-like, narrowly winged throughout, glabrous; *pinnae* numerous in number, close to each other, ovate to lanceolate, usually pinnate, 1–2 cm long, 3–5 mm wide, or on some larger pinnae bipinnate or once or twice dichotomously cleft, elongate to more than 10 cm long side-leaves; *ultimate segments* obovate, obtuse, emarginate, c. 1.5 cm long, often cuneate at base, more or less crisped and complicated; *internal cell walls* thin, the marginal ones slightly, irregularly thickened; laminar tissue dark and nearly opaque. *Sori* terminal on ultimate segments, distal and acropetal, or on all segments of the upper pinnae; *involucres* immersed at base in the lamina of the segments, to 1.5 cm long, 1 cm broad, cuneate at base, lips rounded, entire; receptacles clavate, slender, included, often elongate nearly at the margin of lips. — **Fig. 11c.**

Distribution — *Malesia*: Sulawesi and New Guinea.

Habitat & Ecology — Epiphytic and saxifragous, pendulous, in mossy forests. Altitude: 1700–3800 (or to 4400) m.

Note — Fronds are typically elongate and linear-lanceolate in outline. Some lateral pinnae may sometimes elongate to more than 10 cm long, or to the same length as the fronds themselves, and form broad, fully tripinnate fronds, or they may bear a few elongate, bipinnate pinnae in addition to the typical shorter bipinnate pinnae. The pinnules are very narrow and distinctly crisped throughout, sometimes with larger terminal portions, or are more or less flat and deeply imbricate even forming unipinnate fronds. Sometimes, both of the above forms are intermixed on one frond to give the appearances of several fronds in bundles.

57. Hymenophyllum paniculiflorum C.Presl

Hymenophyllum paniculiflorum C.Presl, Abh. Königl. Böhm. Ges. Wiss., ser. 5, 3 (1843) 32, 55; Bosch, Hymenophyll. Javan. (1861) 49, pl. 39; Christ, Philipp. J. Sci., C. 2 (1907) 155; Copel., Philipp. J. Sci. 64 (1937) 110, pl. 51. — *Mecodium paniculiflorum* (C.Presl) Copel., Philipp. J. Sci. 67 (1938) 19; Fern Fl. Philipp. 1 (1958) 50. — Lectotype (designated here): *Cuming 214* (lecto PRC; isolecto BM, GH, L, P), Philippines, Luzon.

Hymenophyllum coloratum A.Braun ex Bosch in Miq., Pl. Jungh. 5 (1857) 565; Ned. Kruid. Arch. 5(3) (1863) 198. — Type: *Herb. A. Braun* (n.v.), Java.

Hymenophyllum discosum Christ, Bull. Herb. Boissier 6 (1898) 140. — Type: *Loher s.n.* (holo n.v.; iso K), Philippines, Luzon.

Rhizome long-creeping, wiry, to 0.2 mm diam., bearing brownish hairs or glabrescent. *Stipes* filiform, (1.4–)2–4.5(–6.5) cm long, very narrowly winged nearly to the base, glabrous or hairy at the very base; wings very narrow, to c. 0.2 mm broad at each side, entire and flat; *fronds* ovate to oblong, moderately acute at apex, cuneate at base, usually broadest at middle portion, nearly as long as stipes or usually c. 4 cm long, 1.5 cm wide, tripinnatifid, brownish green; *rachis* uniformly, narrowly but distinctly winged, wings very narrow, entire and flat at margin; *pinnae* sessile, bipinnatifid to bipinnate, or with several pairs of simple or two- to three-forked segments; *segments*

numerous, round to moderately acute at apex, entire, flat or more or less involute in dried condition, 0.5–0.7 mm broad. *Sori* large, at apices of practically all the short segments of upper part of fully fruiting fronds, usually forming particular fertile zone or panicles in narrower apical portion of mature fronds; *involucres* bivalvate, deeply divided nearly to the base; valves ovate to orbicular, proportionally larger in size, 2–2.5 mm long, 1.5–2 mm broad, at least twice as broad as the segments, entire or at most dully crenate at margin; receptacles cylindrical, without conspicuous sporangiophores and included in the valves.

Distribution — *Malesia*: Borneo, Java, Philippines and Lesser Sunda Islands.

Habitat & Ecology — Epiphytic and saxifragous, on tree trunks and on moist rocks. Altitude: at higher elevations and in the summit zone, 2000–3700 m.

Note — *Hymenophyllum paniculiflorum* is recognized by its larger sori usually accumulated near the apical portion of the fronds. The sori appear to be borne below the soral zone of the fronds. In addition to the soral character, *H. paniculiflorum* has sparse, downy hairs on the lower surface of the rachis.

58. Hymenophyllum polyanthos (Sw.) Sw.

Hymenophyllum polyanthos (Sw.) Sw., J. Bot. (Schrader) 1800(2) (1801) 102; Syn. Fil. (1806) 149; Hook., Sp. Fil. 1 (1844) 107; Bedd., Handb. Ferns Brit. India (1883) 30; Copel., Philipp. J. Sci. 64 (1937) 97, pl. 46, 47; Tardieu & C.Chr. in Lecomte, Fl. Indo-Chine 7, 2 (1939) 54; Holttum, Rev. Fl. Malaya 2 (1955) 81, f. 23; Sledge, J. Linn. Soc. Bot. 60 (1968) 293; K.Iwats., J. Fac. Sci. Univ. Tokyo, Sect. 3, Bot. 13 (1985) 516; J.X.Liu et al. in C.Y.Wu et al., Fl. China 2–3 (2013) 103; K.Iwats. et al., PhytoKeys 119 (2019) 111. — *Trichomanes polyanthos* Sw., Prodr. (1788) 137. — *Mecodium polyanthos* (Sw.) Copel., Philipp. J. Sci. 67 (1938) 19; Fern Fl. Philipp. 1 (1958) 49; Tagawa & K. Iwats. in Smitinand et al., Fl. Thailand 3 (1979) 70; J.L.Tsai & W.C.Shieh in H.L.Li et al., Fl. Taiwan 1 (1994) 113, pl. 41. — Type: *Swartz s.n.* (holo S n.v.; iso BM n.v.), Jamaica.

Hymenophyllum pectinatum Nees & Blume, Nova Acta Phys.-Med. Acad. Caes. Leop.-Carol. Nat. Cur. 11 (1823) 124, t. 12: f. 5, nom. illeg., non Cav. (1802). — *Hymenophyllum blumeanum* Spreng., Syst. Veg. 4 (1827) 131. — Lectotype (designated by Iwatsuki, J. Fac. Sci. Univ. Tokyo, Sect. 3, Bot. 13 (1985) 516): *Blume s.n.* (lecto K; isolecto L), Java.

Hymenophyllum tenellum D.Don, Prodr. Fl. Nepal. (1825) 12. — Syntypes: *Hamilton s.n.* (K), Nepal; *Wallich s.n.* (n.v.), Nepal.

Hymenophyllum pycnocarpum Bosch, Pl. Jungh. 1 (1856) 564; Hymenophyll. Javan. (1861) 48, pl. 37; Christ, Philipp. J. Sci. 2 (1907) 155. — Type: *van Gesker s.n.* (holo L), Java, Mt Gedé.

Hymenophyllum microsorum Bosch, Ned. Kruidk. Arch. 5(3) (1863) 155. — *Mecodium microsorum* (Bosch) Ching, Fl. Reipubl. Popularis Sin. 2 (1959) 143. — Type: *Hooker f. & T. Thomson s.n.* (holo K), India, Sikkim.

Hymenophyllum osmundoides Bosch, Ned. Kruidk. Arch. 5(3) (1863) 164; Tardieu & C.Chr. in Lecomte, Fl. Indo-Chine 7, 2 (1939) 55. — *Mecodium osmundoides* (Bosch) Ching, Fl. Reipubl. Popularis Sin. 2 (1959) 147, pl. 10: f. 7–11. — Type: *Hooker f. & T. Thomson s.n.* (holo K; iso GH), India, Khasia.

Hymenophyllum sphaerocarpum Bosch, Ned. Kruidk. Arch. 5(3) (1863) 167. — Type: *Hooker f. & T. Thomson 329* (holo K n.v.; iso B, GH), India, Sikkim.

Hymenophyllum subdemissum Christ, Bull. Herb. Boissier 6 (1898) 140. — *Mecodium subdemissum* (Christ) Parris in Beaman et al., Pl. Mt Kinabalu (1992) 82. — Type: *Loher 928* (holo K), Philippines, Luzon, Volcan Maquiling.

Hymenophyllum polyanthos (Sw.) Sw. var. *microglossum* Ridl., J. Malayan Branch Roy. Asiat. Soc. 4 (1926) 12. — Type: *Ridley 14200* (holo SING), Peninsular Malaysia, Perak.

Hymenophyllum nitiduloides Copel., Philipp. J. Sci. 64 (1937) 112, pl. 52. — *Mecodium nitiduloides* (Copel.) Copel., Philipp. J. Sci. 67 (1938) 19; Fern Fl. Philipp. 1 (1958) 50. — Lectotype (designated by Ebihara & Iwatsuki, Mem. Natl. Sci. Mus. (Tokyo) 46 (2010) 96): *BS (Ramos) 23577* (lecto MICH; isolecto US), Philippines, Sorsogon.

Mecodium hainanense Ching, Acta Phytotax. Sin. 8 (1959) 161; Fl. Reipubl. Popularis Sin. 2 (1959) 143. — Lectotype (designated here): *C. Wang 35803* (lecto PE 00042634; isolecto GH), China, Hainan.

Rhizome long-creeping, irregularly branching, wiry, slender, usually less than 0.2 mm diam., with light brown hairs in young portion, older portion dark and glabrous; the rootlets densely hairy, the hairs brown, to 1 mm long. *Stipes* (1–)2–7(–9) cm long, very narrowly winged nearly to the base, wings less than 0.3 mm broad, entire, flat, easily broken and lacking in old leaves. *Fronds* very variable both in size and form, commonly lanceolate to oblong or subdeltoid, acute to acuminate at apex, more or less narrowing towards base, 3–12 cm long, 1.5–5(–8) cm wide, tripinnatifid or even bipinnate forms of less than 2 cm in length bearing sori, light green, brownish or darker when dried; *rachis* bearing minute transparent hairs or glabrescent, winged throughout, wings very narrow, entire, flat; *pinnae* less than 10 pairs, the largest ones in the middle portion, reducing in size both upward and downward, the larger ones oblong-subdeltoid or oblong-lanceolate, often falcate; *ultimate segments* linear or narrowly lanceolate, round to obtuse or moderately acute at apex, the margin entire and flat, commonly c. 0.8 mm broad or 0.6–1 mm broad; *internal cell walls* thin, straight, rarely rather thick. *Sori* scattered usually on the upper part of fronds, solitary at apex of segments or on short acroscopic branches of them; *involucres* bivalvate, cleft almost to the base, subdeltoid or reniform, c. 1 mm in length, usually longer than the breadth; lips round to acute, entire or more or less crenate; receptacles clavate, included. Chromosome numbers: $n = 27$ (Mehra & Singh, J. Genet. 55 (1957) 380), $n = 28$ (Manton & Sledge, Philos. Trans. Ser. B 238 (1954) 144), $2n = 56$ (Tatuno & Takei, Bot. Mag. (Tokyo) 82 (1969) 126). — **Fig. 11a, b.**

Distribution — Tropics and subtropics throughout the world, north to central Japan; throughout *Malesia*.

Habitat & Ecology — Epiphytic and epipetric, on tree trunks and on branches of trees, on mossy rocks and on moist, perpendicular cliffs, in dense montane forests and in semi-shaded places. Altitude: from low to high elevations, to 3000 m.

Notes — The phenotype of *H. polyanthos* is quite variable, especially in form, size and construction of the fronds. The habitat is also variable, no positive relationship has been traced between morphological variation and ecology. While Fraser-Jenkins et al. (Ferns Fern-Allies Nepal (2015) 147) applied the name '*H. tenellum* D.Don' to Asian plants instead of *H. polyanthos*, Hsu et al. (Syst. Bot. 44 (2019) 753–767) recently recognized five species belonging to the complex even within Taiwan. This cosmopolitan species may not be a species in our modern concept, but a species complex (Vasques et al., Pl. Syst. Evol. 305 (2019) 811–825), although it is still awaiting global taxonomic revision.

Hymenophyllum subdemissum is recognized as distinct by some botanists based on the oblong outline of the fronds and somewhat larger sori.

In some specimens, especially those under the name of *H. blumeanum* from Java and New Guinea, a few pinnae are extraordinarily elongated to give a more or less irregular outline to the fronds. Such morphology suggests that *H. polyanthos* is related to *H. ooides* through morphological similarity to *H. copelandii*. Plants of *H. polyanthos* with elongate fronds, some attaining a length of 40 cm and at most 4 cm wide and having the lower lateral pinnae reduced, are abundant in New Guinea.

Plants that were named *H. nitiduloides* are characterized by having stipes 1–2 cm long, terete, glabrous; fronds 1.5–2.5 cm long, subflabellate or pinnatifid with forked segments; rachis and costae broadly winged; segments to 8 mm long, 1–1.5 mm broad, brownish green; sori on all but the lower segments immersed at base; lips round or slightly elongate, entire; and receptacles cylindrical and included. The combination of these characters shows the extremely variable morphology of *H. polyanthos*.

d. Subgenus **Pleuromanes** (C.Presl) Ebihara & K.Iwats.

Hymenophyllum Sm. subg. *Pleuromanes* (C.Presl) Ebihara & K.Iwats. See under the genus for related synonyms, literature and type.

Other synonymous (infrageneric) genus names (see under genus for related synonyms, literature and types): *Leucomanes* C.Presl, *Craspedoneuron* Bosch.

Rhizome long-creeping, slender, hairy at apex, glabrescent in older portion; hairs multicellular, semiarticulate, shining brown; *fronds* pinnately decompound, often glaucous underneath, variously hairy with multicellular hairs; *laminar cells* 2 or 3 layers near the veinlets, thick-walled, marginal row of cells smaller, more or less elongate, thin-walled; *sori* solitary on segments, tuberous or campanulate, with distinctly dilated mouth; *involucres* long-extruded.

Distribution — Four species, present in Sri Lanka, Thailand, Indo-China, China (Hainan), Taiwan; throughout *Malesia*; east to the Society Islands and Marquesas.

Habitat & Ecology — Usually pendulous on moist rocks, mossy cliffs, and on tree trunks in dense gloomy forests, usually in the mossy zone. Colonies are rather loose and often mixed with mosses, and rarely in very wet places in the water spray.

Taxonomy — Subgenus *Pleuromanes* is distinguished by the multicellular hairs of pilose fronds, glaucous lower-surface of the fronds, and laminae consisting of more than one layer of cells near the veinlets. A local form in Luzon (Philippines) is sometimes specifically distinguished by usually having narrowly oblong to linear laminae with a hardly glaucous, sparsely hairy lower surface. Such a form occurs throughout the range of subg. *Pleuromanes* and is less distinct in the diagnostic features that define species.

59. Hymenophyllum pallidum (Blume) Ebihara & K.Iwats.

Hymenophyllum pallidum (Blume) Ebihara & K.Iwats. in Ebihara et al., Blumea 51 (2006) 232; J.X.Liu et al. in C.Y.Wu et al., Fl. China 2–3 (2013) 105; C.W.Chen et al., Sol Amazing (2017) 133; K.Iwats. et al., PhytoKeys 119 (2019) 110. — *Trichomanes pallidum* Blume, Enum. Pl. Javae 2 (1828) 225; Copel., Philipp. J. Sci. 51 (1933) 141; Tardieu & C.Chr. in Lecomte, Fl. Indo-Chine 7, 2 (1939) 67; Holttum, Rev. Fl. Malaya 2 (1955) 97; Sledge, J. Linn. Soc. Bot. 60 (1968) 303. — *Pleuromanes pallidum* (Blume) C.Presl, Epimel. Bot. (1851) 258; Copel., Philipp. J. Sci. 67 (1938) 56; Fern Fl. Philipp. 1 (1958) 67; Ching, Fl. Reipubl. Popularis Sin. 2 (1959) 172, pl. 14: f. 5–8; Croxall, Austral. J. Bot. 23 (1975) 528; J.L.Tsai & W.C.Shieh in H.L.Li et al., Fl. Taiwan 1 (1994) 122, pl. 46. —

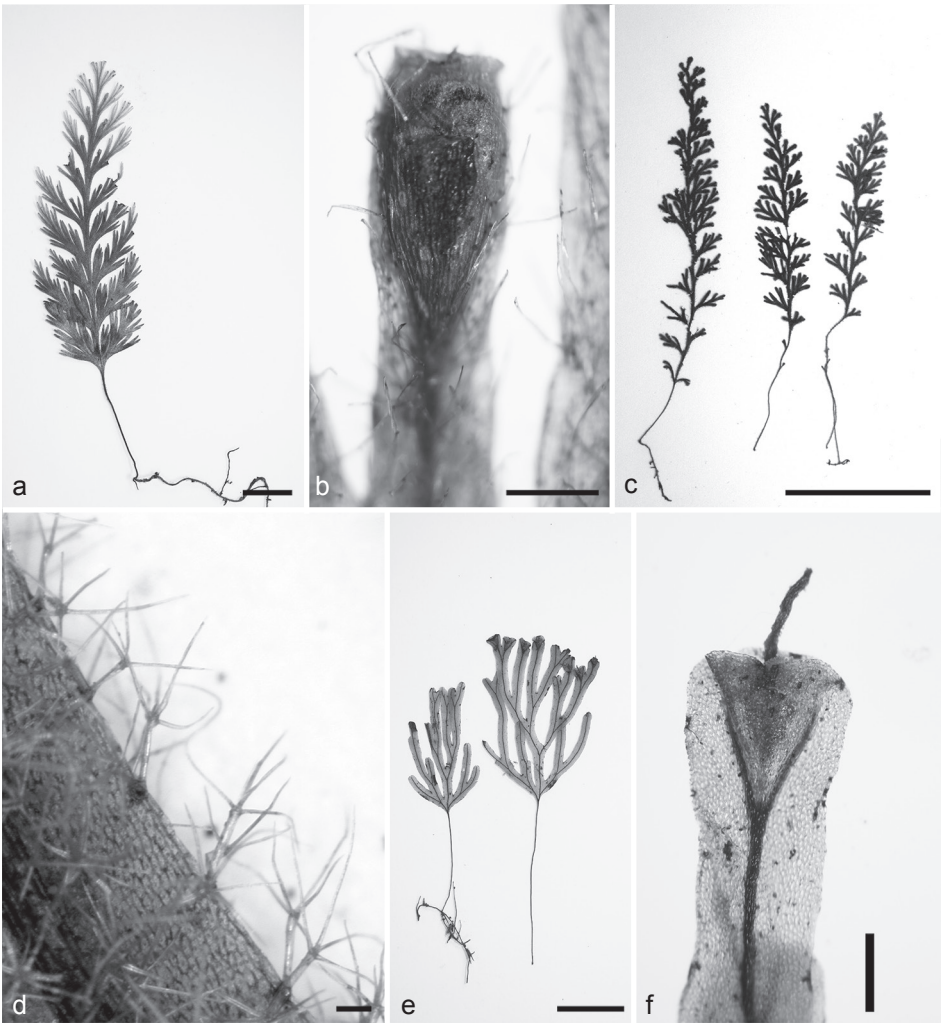

Fig. 12. a, b. *Hymenophyllum pallidum* (Blume) Ebihara & K.Iwats. a. Frond; b. sorus covered by long hairs. — c, d. *H. pilosissimum* C.Chr. c. Fronds; d. stellate hairs. — e, f. *H. digitatum* (Sw.) Fosberg. e. Fronds; f. sorus (a, b: (*Amoroso 5397*, Mindanao, Philippines, TNS 1113506; c, d: *Schram BW13422*, Wondiwoi Mts, New Guinea, Indonesia, KYO 00010943; e, f: *Ebihara et al. 000224-016*, Sabah, Malaysia, TNS 766162). — Scale bars: a, e = 1 cm; b = 0.5 mm; c = 5 cm; d = 0.1 mm; f = 1 mm.

Craspedoneuron pallidum (Blume) Bosch, Hymenophyll. Javan. (1861) 14, pl. 8. — *Crepidomanes pallidum* (Blume) K.Iwats., Acta Phytotax. Geobot. 35 (1984) 174; J. Fac. Sci. Univ. Tokyo, Sect. 3, Bot. 13 (1985) 523. — Type: *Blume s.n.* (holo L 0052385/sheet no. 908.325.30), Java.

Trichomanes album Blume, Enum. Pl. Javae 2 (1828) 226. — *Leucomanes album* (Blume) C.Presl, Epimel. Bot. (1851) 258. — *Craspedoneuron album* (Blume) Bosch, Hymenophyll. Javan. (1861) 12, pl. 7. — *Pleuromanes album* (Blume) Parris in Beaman et al., Pl. Mt. Kinabalu (1992) 87. — *Hymenophyllum album* (Blume) Parris, Fern Gaz. 20 (2018) 305. — Lectotype (designated here): *Blume s.n.* (lecto L 0544610/sheet no. 908.325.21; isolecto P), Java.

Trichomanes glaucofuscum Hook. in T.Nightingale, Oceanic Sketches (1835) 131; Sp. Fil. 1 (1844) 128. — Type: *T. Nightingale s.n.* (holo K), Samoa?

Trichomanes acutum C.Presl, Abh. Königl. Böhm. Ges. Wiss., ser. 5, 3 (1843) 42; Copel., Philipp. J. Sci. 51 (1933) 140. — *Pleuromanes acutum* (C.Presl) C.Presl, Epimel. Bot. (1851) 258; Copel., Philipp. J. Sci. 67 (1938) 56; Fern Fl. Philipp. 1 (1958) 67. — *Crepidomanes acutum* (C.Presl) K.Iwats., Acta Phytotax. Geobot. 35 (1984) 174. — *Hymenophyllum acutum* (C.Presl) Ebihara & K.Iwats. in Ebihara et al., Blumea 51 (2006) 232. — Lectotype (designated here): *Cuming 219* (lecto PRC; isolecto E, GH, K, L, P), Philippines.

Trichomanes braunii Bosch in Miq., Pl. Jungh. 5 (1857) 550. — *Craspedoneuron braunii* (Bosch) Bosch, Hymenophyll. Javan. (1861) 15, pl. 9. — Lectotype (designated here): *Blume s.n.* (lecto L sheet no. 908.325.43; isolecto P 3 sheets), Java.

Trichomanes glaucescens Bosch in Miq., Pl. Jungh. 5 (1857) 551. — Syntypes: *van Gesker s.n.* (L), Java; *Zollinger s.n.* (L? n.v.), Java, Mt Gede; *Zollinger s.n.* (L? n.v.), Java, Salak.

Pleuromanes retusum Copel., Philipp. J. Sci. 73 (1941) 466. — *Trichomanes retusum* (Copel.) C.V.Morton, Contr. U.S. Natl. Herb. 38 (1968) 186. — Lectotype (designated here): *Brass 12204* (lecto MICH 1190821; isolecto BO, BRI, FI, GH, K), New Guinea, Idenburg River.

Rhizome long-creeping on tree trunks and on rocks, usually on vertical surfaces, wiry, 0.3–0.5 mm diam., brown, sparsely covered by long hairs; roots blackish, wiry, hairy, slender; hairs multicellular, subarticulate, brown, shining, to 2 mm long. *Stipes* 3–10 cm long but variable in size, terete except for the uppermost winged portion, dark brown, bearing pale brown, long hairs, glabrescent; *fronds* bipinnate-tripinnatifid, oblong to oblong-subdeltoid, round to acute at apex, cuneate or round at base or subtruncate in some smaller forms, 5–8(–20) cm long, 1.5–2.5(–3.5) cm wide in common forms but variable to some extent; *rachis* winged throughout, showing similar appearance to the segments except for very base, hairy beneath; *pinnae* ascending, falcate, narrowly lanceolate to oblong, round at apex, cuneate at sessile or short-stalked base, to 3 cm long, 7 mm broad, in many cases still larger; *pinnules* simple or biforked, or rarely triforked; *ultimate segments* longer, more or less falcate, round to acute at apex, c. 0.7 mm broad, entire and flat at margin, glaucous beneath, hairy on the veins underneath; simple hairs on all axes of fronds, pale brown, more or less downy, to 2 mm long. *Laminar cells* bi- or tri-stratose in central portion near the veinlets, thick-walled in brownish appearance; one marginal row of cells smaller, more or less elongate, thin-walled, transparent. *Sori* solitary on segment, commonly on basal acroscopic position of pinnae, thus arranged in one row at each side of rachis, cup-shaped, immersed in segment or constricted at base; *involucres* forming cups, c. 1.7 mm long, 1 mm diam. at mouth, the mouth distinctly dilated; receptacles extruded. Chromosome numbers: $n = 36$ (Braithwaite, Fern Gaz. 10 (1969) 82). — **Fig. 12a, b.**

Distribution — Sri Lanka, India, Thailand (Peninsular), Laos, Vietnam, China (Hainan), Taiwan; throughout *Malesia*; Solomon Islands, Vanuatu, Australia (NE Queensland), New Caledonia, Fiji, Samoa, Society Islands.

Habitat & Ecology — Usually pendulous from moist rocks, mossy cliffs, and tree trunks in gloomy mossy forests at high or middle elevations, 1200–3000 m altitude. *Hymenophyllum pallidum* may be a good indicator of mossy forests where the substrate is not very wet.

Notes — The fronds on plants from Samoa attain a length to 40 cm, and appear to be a different species. It is difficult to distinguish them only by the difference in size.

The hairiness, abundance of glaucous waxy substance, and size and form of the fronds are also variable, and *H. pallidum* is defined here as a variable species, although one form with less glaucous and less hairy lower surface of the fronds has sometimes been separated specifically. Copeland believed *Plueromanes acutum* was restricted to northern Luzon, but such a form occurs over a very wide area, nearly throughout the range of the subgenus. Here, no specific differences are recognized between the two 'species' in the subgenus.

e. Subgenus **Sphaerocionium** (C.Presl) C.Chr.

Hymenophyllum subg. *Sphaerocionium* (C.Presl) C.Chr. See under the genus for related synonyms, literature and type.

Other synonymous (infrageneric) genus names (see under genus for related synonyms, literature and types): *Gonocormus* sect. *Microtrichomanes* Mett. ex Prantl, *Hymenophyllum* Sw. subg. *Apteropteris* Copel., *Dermatophlebium* C.Presl.

Rhizome filiform, wiry, bearing roots; *fronds* pinnately compound or small and palmate or subdigitate in appearance, hairy or subglabrous; hairs on fronds simple or stellate, pale in colour, usually longer, more than 0.5 mm long; *internal cell walls* thin and straight; *sori* solitary at apex of segments, usually immersed; *involucres* cleft, the lower immersed portion sometimes obconic with shallow, hollow base, usually as long as the diam.; receptacles filiform or clavate, included or extruded beyond the mouth of involucres.

Distribution — About 70 species are known in subg. *Spherocionium*, with the greatest number in the Neotropics. Morton (Contr. U.S. Natl. Herb. 29 (1947) 139–202) enumerated 52 species from the New World, covering all the sections and subsections of subg. *Sphaerocionium*. Iwatsuki (J. Fac. Sci. Univ. Tokyo, Sect. 3, Bot. 13 (1982) 203–215) listed 10 species from Asia and Oceania (both sections are represented in Oceania) with 5 species in *Malesia*. More than half a dozen species have been recorded from Africa.

Habitat & Ecology — The Malesian species are on mossy tree trunks in dense primitive forests at middle to higher elevations of higher mountains, often growing abundantly so as to cover the entire surface of tree trunks. The species are not restricted to the mossy zones. Colonies of the Malesian species are often very compact and scarcely mixed with bryophytes.

Three New Zealand species were carefully observed by Holloway (Trans. & Proc. New Zealand Inst. 54 (1923) 577–618). The ecology of the New World species was described by Morton (1947).

Morphology — Details of the anatomy are unknown for the species of subg. *Spherocionium*, although there are no distinct differences at least in external morphology between subg. *Sphaerocionium* and other subgenera of *Hymenophyllum*, except for those given in the diagnostic key to the subgenera.

Pubescence is one of the most characteristic features for distinguishing subg. *Spherocionium*. Morton (1947) distinguished the types of hairs, and Iwatsuki (1982) typified them to speculate on the interrelationships based on this feature. In transferring two Malesian species from *Trichomanes* and *Microtrichomanes* to *Hymenophyllum* subg.

Sphaerocionium, Iwatsuki (Fern Gaz. 11 (1975) 119) illustrated differences in the morphology of the hairs between *H. palmatifidum* and *H.* (*Microtrichomanes*) *digitatum*. The morphology of the hairs of *H. palmatifidum* falls completely within the range of variation of those of subg. *Sphaerocionium*, but not of *H. digitatum*. Nearly glabrous plants of *H. nitidulum* have the same kind of hairs as *H. palmatifidum*, although the hairs are extremely sparse.

The receptacles of the three Malesian species extruded beyond the lips of the involucre, which is campanulate in outline with bilabiate lips. The evolution of this feature appears to have occurred in parallel with the evolution of this feature in species of *Hymenophyllum* subg. *Hymenophyllum* in which *H. edanoi* has an extruded receptacle of the involucre. In the *H. serrulatum* group with included receptacles, *H. penangianum* and *H. seramense* are distinct in having extruded receptacles.

Gametophytes — The report on gametophytes was by Atkinson (Phytomorphology 10 (1960) 26–36), based on observations of *H. lyallii*.

Taxonomy — Morton (1947) revised the American species comprehensively, and distinguished two subgroups as subsections of sect. *Sphaerocionium* based on the distribution of the hairs, whether the hairs are on the leaf surfaces or not. In his system of Hymenophyllaceae proposed in 1968, Morton (Contr. U.S. Natl. Herb. 38 (1968) 168–170) divided subg. *Sphaerocionium* into 2 sections and sect. *Sphaerocionium* into 4 subsections (subsect. *Sphaerocionium* was listed under the name subsect. *Ciliata*). In addition to the two subsections distinguished by the distribution of hairs, subsect. *Plumosa* was recognized by having wings on the veins, as compared with those of the *Amphipterum* group of subg. *Hymenophyllum* in the Old World. Another subsection, South American *Leptocionium*, is reduced in the present system to subg. *Hymenophyllum*, too.

The species bearing hairs only on the veins and margin of the fronds and never on the laminar surfaces are more than 35 in number. There are no wings on the veins in any of these species. The diagnosis is rather artificial; the infrageneric classification, especially of the American species, needs further revision.

KEY TO THE SPECIES

1a. Fronds subdigitate, with very short rachis; hairs if any mostly simple, isolated, or forked 2
b. Fronds pinnate with elongate rachis; hairs dense, stellate, branches of hairs commonly 3–8, spreading . . . . . **63. H. pilosissimum**
2a. Fronds densely hairy 3
b. Fronds nearly glabrous or with occasional hairs . . . . . **61. H. nitidulum**
3a. Fronds setose, hairs simple, dark brownish at margin of segments . . . . . **60. H. digitatum**
b. Fronds with soft, simple and sometimes fascicled, nearly transparent hairs on costae and margin of segments . . . . . **62. H. palmatifidum**

60. Hymenophyllum digitatum (Sw.) Fosberg

Hymenophyllum digitatum (Sw.) Fosberg, Smithsonian Contr. Bot. 45 (1980) 1; J.X.Liu et al. in C.Y.Wu et al., Fl. China 2–3 (2013) 105; C.W.Chen et al., Sol Amazing (2017) 128; K.Iwats. et al., PhytoKeys 119 (2019) 110. — *Trichomanes digitatum* Sw., Syn. Fil. (1806) 370, 422; Hook. & Baker, Syn. Fil. (1867) 239, p.p.; Bedd., Ferns Brit. India 3 (1869) pl. 301; Handb. Ferns Brit. India (1883) 39, f. 19; Copel., Philipp. J. Sci. 51 (1933) 159, pl. 7: f. 3–4; Tardieu & C.Chr. in Lecomte, Fl. Indo-Chine 7, 2 (1939) 66; Holttum, Rev. Fl. Malaya 2 (1955) 94, f. 32. — *Gonocormus digitatus* (Sw.) Prantl, Unters. Morph. Gefässkrypt. 1 (1875) 51. — *Microtrichomanes digitatum* (Sw.) Copel., Philipp. J. Sci. 67 (1938) 36; Fern Fl. Philipp. 1 (1958) 55; Croxall, Austral. J. Bot. 23 (1975) 525; Tagawa & K.Iwats. in Smitinand et al., Fl. Thailand 3 (1979) 79, f. 5–6. — *Crepidomanes digitatum* (Sw.) K.Iwats., Acta Phytotax. Geobot. 35 (1984) 175; J. Fac. Sci. Univ. Tokyo, Sect. 3, Bot. 13 (1985) 540. — Type: *de Petit-Thouars s.n.* (n.v.), Mauritius and Réunion.

Trichomanes lanceum Willd., Sp. Pl. 5 (1810) 500; Hook. & Grev., Icon. Filic. 1 (1827) t. 33. — Type: (P? n.v.), 'Insula Borboniae' (= Réunion).

Trichomanes loreum Bory & Bel. in Bel., Voy. Indes Or. 2 (1833) 79. — Type: (P? n.v.), Ile de Mascareigne (= Mascarene Islands).

Trichomanes dichotomum Kunze, [Bot. Zeitung (Berlin) 5 (1847) 302, nom. nud.] Bot. Zeitung (Berlin) 6 (1848) 285; Bosch, Hymenophyll. Javan. (1861) 22, pl. 16; Copel., Philipp. J. Sci. 51 (1933) 160, pl. 7, f. 5; K.Iwats., Fern Gaz. 11 (1875) 121. — *Gonocormus dichotomus* (Kunze) Prantl, Unters. Morph. Gefässkrypt. 1 (1875) 51. — *Microtrichomanes dichotomum* (Kunze) Copel., Philipp. J. Sci. 67 (1938) 36. — *Hymenophyllum dichotomum* (Kunze) Fosberg, Amer. Fern J. 40 (1950) 135, nom. illeg., non Cav. (1802). — Type: *Zollinger 1707* (holo n.v.; iso BR, P 2 sheets), Java.

Trichomanes blumei Hassk., Obs. Bot. Fil. 2 (1857) 4. — Type: *Blume s.n.* (n.v.), Java.

Trichomanes flabelliforme Hassk., Obs. Bot. Fil. 2 (1857) 5. — Type: (? n.v.), Java.

Trichomanes flabellatum Bosch, Ned. Kruidk. Arch. 4 (1859) 353, nom. illeg., non Bory ex Desv. (1827); Hymenophyll. Javan. (1861) 19, pl. 13; K.Iwats., Fern Gaz. 11 (1975) 121. — *Gonocormus flabellatus* (Bosch) Prantl, Unters, Morph. Gefässkrypt. 1 (1875) 51. — Lectotype (designated here): *Blume s.n.* (lecto L 3568929; isolecto P), Java.

Trichomanes digitatum Sw. var. *major* Rosenst., Repert. Spec. Nov. Regni Veg. 12 (1913) 166. — Type: *Keysser B49* (holo n.v.; iso S), Papua New Guinea, Bolan.

Trichomanes piliferum Alderw., Bull. Jard. Bot. Buitenzorg, sér. 3, 5 (1922) 225. — Type: *Bakhuizen van den Brink 4116* (holo BO), Java.

Trichomanes taeniatum Copel., Bull. Bernice P. Bishop Mus. 93 (1932) 6, pl. 2. — *Microtrichomanes taeniatum* (Copel.) Copel., Philipp. J. Sci. 67 (1938) 37. — Lectotype (designated here): *Grant 3561* (lecto BISH; isolecto BO, K, MICH, NY, P, SING, UC, US), Tahiti.

Rhizome long-creeping, filiform, wiry, 0.1–0.2 mm diam., irregularly branching, bearing roots in irregular intervals, sparsely hairy; hairs on rhizome pale brown, downy, multicellular, to 1.2 mm long. *Stipes* slender, to 0.15 mm diam., dark brown, sparsely hairy or glabrescent, terete, wingless, 1–3(–5) cm long; *fronds* mainly pinnately divided, digitate to flabellate or monopodially branching in appearance, semicircular to oblong-lanceolate, smaller ones c. 1.5 cm in both length and width, larger ones 5–10 (–20) cm long, 3–7(–10) cm wide; *rachis* very short to elongate, winged throughout, in appearance the same as the segments; *pinnae* 1–3(–4) times dichotomously branching, or sometimes monopodial with a reduction of a few branches in smaller plants with 2 or 3 segments, larger ones more than 5 cm long; *ultimate segments* sometimes elongate, to 2.5 cm long, 1–2.2 mm broad, membranous, straight or a little curved, entire or a little crisped at margin, setose hairy, round, subacute or retuse at apex, dark green in living condition, dark brown to blackish in dried specimens; hairs setose, at

margin of segments and wings, with intervals of some 10 marginal cells, simple, dark brown to blackish, to 0.2 mm long. *Laminar cells* normal in size, *internal cell walls* thin, straight. *Sori* solitary at apex of segments, campanulate, usually immersed in segment-apex, campanulate portion c. 3 mm long, 1 mm diam.; mouth extruded outside the segment-apex, dilated at most for c. 0.5 mm; receptacles long-extruded. Chromosome numbers: $n = 36, 72$ (Braithwaite, Bot. J. Linn. Soc. 71 (1975) 169). — **Fig. 12e, f.**

Distribution — Tanzania, Madagascar, Mauritius, Réunion, Taiwan, Thailand (Peninsular), Vietnam; in *Malesia*: Peninsular Malaysia, Sumatra, Borneo, Java, Philippines, Lesser Sunda Islands (Flores), Moluccas (Seram, Tidore), New Guinea; Micronesia, Polynesia and Australia (NE Queensland; see Croxall, Austral. J. Bot. 23 (1975) 525).

Habitat & Ecology — Epiphytic on mossy tree trunks, usually in dense gloomy forests from low to mid elevations, often in the mossy zone to 3300 m.

Notes — It is rather difficult to delimit the specific boundary of such a dwarfed form; the following notes are necessary here.

1. The form named *Trichomanes dichotomum* is treated here as conspecific with *H. digitatum*, resulting in a vague description, especially in the size and form of the fronds and pinnae. The branching pattern, usually described as digitate for *Microtrichomanes*, is in fact pinnate with the rachis extremely reduced in length (Iwatsuki 1975). The branching of *T. dichotomum* was interpreted as monopodial by Copeland (1933), although the elongation of the rachis as the main axis is evident, even if the mature rachis is more or less zigzag in form. The pinnae of *Microtrichomanes* branch dichotomously, and larger pinnae of *T. dichotomum* appear to be monopodial in their branching pattern. This type of branching is the same as in sect. *Gonocormus*; principally dichotomous branching of the pinnae in reduced plants does not occur among the filmy ferns. Thus, the branching pattern in *T. dichotomum* is not particular, but the elongation of the rachis is comprehensive in this form, giving the size of fronds extraordinary variation in this species group. The variation in size and form is gradual, however, resulting in a diversity of intermediate forms. When two extreme forms are encountered, they appear to be quite different, but it is not realistic to distinguish them taxonomically until more evidence is available to support it.

2. The Malesian form of *H. digitatum* is variable in size and form as noted above. The type of *Trichomanes digitatum* is from Mauritius or Réunion. In E Africa the plants of this species bear 2–8 segments. In the smaller plants the coloration in the dry state is not really black or dark brown. A specimen from mainland Africa (*Schlieben 3028*, Tanganjika, in P, noted as 'var. *ulugurense* Reinw.') has long stipes and up to 10 segments with longer marginal setae. We still know the variation in the African plants insufficiently, but there is no evidence to distinguish the African from the Malesian forms. Thus, the distribution of *H. digitatum* extends to mainland Africa and Australia.

3. A Polynesian form having many ultimate segments compared with its size and green to darker fronds, even in dried condition, has been distinguished as *Trichomanes taeniatum*. This form is also included within the variation of *H. digitatum*, recognizing this species rather broadly.

4. It is rather difficult to specify the types of the species described earlier, so the designation of type specimens is postponed. The broader concept of *H. digitatum* adop-

ted here allows the application of this name to forms extending from continental Africa to Asia, as already noted by Copeland (1933).

61. **Hymenophyllum nitidulum** (Bosch) Ebihara & K.Iwats.

Hymenophyllum nitidulum (Bosch) Ebihara & K.Iwats. in Ebihara et al., Taxon 53 (2004) 941; J.X.Liu et al. in C.Y.Wu et al., Fl. China 2–3 (2013) 105; K.Iwats. et al., PhytoKeys 119 (2019) 109. — *Trichomanes nitidulum* Bosch in Miq., Pl. Jungh. 5 (1857) 547; Hymenophyll. Javan. (1861) 21, pl. 15; Copel., Philipp. J. Sci. 51 (1933) 155, pl. 7, f. l; Tardieu & C.Chr. in Lecomte, Fl. Indo-Chine 7, 2 (1939) 67; Sledge, J. Linn. Soc. Bot. 60 (1968) 302; K.Iwats., Fern Gaz. 11 (1975) 120. — *Gonocormus nitidulus* (Bosch) Prantl, Unters. Morph. Gefässkrypt. 1 (1875) 51. — *Microtrichomanes nitidulum* (Bosch) Copel., Philipp. J. Sci. 67 (1938) 37; J.L.Tsai & W.C.Shieh in H.L.Li et al., Fl. Taiwan 1 (1994) 119, pl. 44. — *Sphaerocionium nitidulum* (Bosch) K.Iwats., J. Fac. Sci. Univ. Tokyo, Sect. 3, Bot. 13 (1982) 211; 13 (1985) 522. — Lectotype (designated by Iwatsuki 1982: 211): *Junghuhn s.n.* (lecto L, sheet no. 908.325.785; isolecto L 3 sheets, P), Java.

Hymenophyllum sp.: Bosch, Hymenophyll. Javan. (1861) 21. — *Trichomanes inerme* Bosch, Meded. Rijks-Herb. 17 (1913) 23, f. 12. — Type: *Thwaites CP 3275* (holo L), Sri Lanka.

Trichomanes corticola Bedd., Ferns S. India (1863) 87, pl. 264. — *Hymenophyllum corticola* (Bedd.) Hook. in Thwaites, Enum. Pl. Zeyl. (1864) 397. — Lectotype (designated by Iwatsuki, J. Fac. Sci. Univ. Tokyo, Sect. 3, Bot. 13 (1982) 211 as 'type'): *Thwaites CP 3278* (lecto BM; isolecto B, GH, K, S), Sri Lanka.

Microtrichomanes zamboanganum Copel., Philipp. J. Sci. 81 (1952) 2. — Type: *Copeland Herbarium 11567* (holo MICH), Philippines.

Rhizome long-creeping, filiform, c. 0.1 mm diam., irregularly branching, bearing roots rather sparsely, sparsely hairy; hairs pale brownish, simple, to 1 mm long. *Stipes* filiform, similar to rhizome in size, hairy especially at basal portion, 0.5–2 cm long; hairs on stipes pale brownish, simple or forked, to 1 mm long; *fronds* digitate in appearance, semicircular in outline, commonly 1–2 cm in both length and width; mainly pinnate to bipinnatifid with very short rachis and closely placed alternate pinnae, and tending to be monopodial in less developed sterile fronds; *rachis* very short or often indistinct, winged; *pinnae* with 1–4(–8) segments apparently arranged dichotomously; *ultimate segments* round to obtuse at apex, entire at margin, 0.8–l.8 mm broad, green to deep green in living condition, dark green, brownish or dark brown when dried, glabrous or occasionally hairy; hairs on the fronds, if any, marginal, pale brown, simple or rarely forked, downy, usually c. 1 mm long. *Laminar cells* not very large; *internal cell walls* thin and straight. *Sori* solitary at apex of ultimate segments, usually on longer segments, several on one frond, immersed; *involucres* shallowly cup-shaped in the immersed portion, their diameter the same as or a little narrower than breadth of segments, the depth shallower than diameter, the mouth a little bilabiate with subtruncate and undulate lips; receptacles elongate, extruded.

Distribution — Sri Lanka, NE India, China (Guangxi, Yunnan), Taiwan, Vietnam; *Malesia*: Peninsular Malaysia, Sumatra, Borneo, Java and Moluccas (Seram).

Habitat & Ecology — Epiphytic usually in mats on mossy tree trunks in dense forests. Altitude: from mid elevations to 3100 m.

Notes — The distinct feature to distinguish this species from *H. palmatifidum* is usually given as its glabrous frond. Careful observation of *H. nitidulum,* however, reveals hairs everywhere on the fronds, although they are sparse. Young fronds especially and

the basal portion of the stipes usually bear hairs similar to those of *H. palmatifidum*. The occasional presence of hairs similar to those of *H. palmatifidum* may show that the seemingly glabrous nature of *H. nitidulum* is to reflect extremely sparse hairs. The close resemblance between *H. palmatifidum* and *H. nitidulum* is thus evident, although they differ also in the ratio between the length of laminae and the stipes and between lobe-breadth and lamina size.

Four sheets of specimens were used in preparing the original description. Among them in L only one specimen, L sheet no. 908.325.785, bears the specific name with the handwriting by Bosch.

62. Hymenophyllum palmatifidum (Müll.Berol.) Ebihara & K.Iwats.

Hymenophyllum palmatifidum (Müll.Berol.) Ebihara & K.Iwats. in Ebihara et al., Taxon 53 (2004) 941; K.Iwats. et al., PhytoKeys 119 (2019) 110. — *Trichomanes palmatifidum* Müll.Berol., Bot. Zeitung (Berlin) 12 (1854) 732; Bosch, Hymenophyll. Javan. (1861) 20, t. 14; Copel., Philipp. J. Sci. 51 (1933) 162, pl. 7: f. 6, pl. 11: f. 1; Holttum, Rev. Fl. Malaya 2 (1955) 95; K.Iwats., Fern Gaz. 11 (1975) 120. — *Gonocormus palmatifidus* (Müll.Berol.) Prantl, Unters. Morph. Gefässkrypt. 1 (1875) 51. — *Trichomanes digitatum* Sw. var. β *palmatifidum* (Müll.Berol.) Hook. & Baker, Syn. Fil. (1865) 76. — *Microtrichomanes palmatifidum* (Müll.Berol.) Copel., Philipp. J. Sci. 67 (1938) 36. — *Sphaerocionium palmatifidum* (Müll.Berol.) K.Iwats., J. Fac. Sci. Univ. Tokyo, Sect. 3, Bot. 13 (1982) 211. — Lectotype (designated by Iwatsuki (1982) 211): *Zollinger 1722* (lecto B; isolecto K, L, P 3 sheets), Java.

Hymenophyllum borneense Hook. in Hook. & Baker, Syn. Fil. (1866) 62. — Lectotype (designated here): *Lobb s.n.* (lecto K 001090205; isolecto BO), Borneo.

Trichomanes ridleyi Copel., Philipp. J. Sci. 51 (1933) 162, pl. 11: f. 2–3; Holttum, Rev. Fl. Malaya 2 (1955) 95; K.Iwats., Fern Gaz. 11 (1975) 120. — *Microtrichomanes ridleyi* (Copel.) Copel., Philipp. J. Sci. 67 (1938) 36. — Type: *Ridley 15909* (holo SING; iso K, MICH, PE, UC), Peninsular Malaysia, Pahang, Gunung Talian.

Rhizome long-creeping, filiform, less than 0.15 mm diam., irregularly branching, bearing roots rather sparsely, hairy; hairs on rhizome pale brownish, simple, c. 1 mm long, rather dense on younger portion, glabrescent in age. *Stipes* filiform, 1.5–2.5 (–5) cm long, variable in length and proportionately longer, terete, wingless, hairy; hairs on stipes rather dense on basal portion, pale brownish, simple or forked, c. 1 mm long; *fronds* digitate in appearance, but in fact pinnate to bipinnatifid with very short rachis and alternately placed pinnae, semicircular or ovate, round at apex, usually wider than long, 1–2(–3.5) cm both in length and width, but abnormally larger fronds not very rare; rachis very short or obsolete, winged or very rarely terete; *pinnae* a few pairs close to each other, with 1–4(–8) segments arranged dichotomously; *ultimate segments* round to obtuse at apex, sometimes elongate to 1.5 cm, entire at margin, 0.7–1.3 mm broad, green to dark green in living condition, brown to dark brown when dried, hairy at margin or sometimes on veins as well; hairs on fronds pale brown, downy, c. 0.3 mm long, fascicled with 1–5 hairs at margin of segments and on veins; laminar cells not very large; *internal cell walls* thin and straight. *Sori* solitary at apex of segments, more or less immersed; *involucres* obconic in immersed portion, usually the diameter equals the breadth of segments, nearly the same depth or shallower as the diameter, the mouth generally little bilabiate, round at lip margin; receptacles elongate, shortly extruded.

Distribution — Taiwan; in *Malesia*: Peninsular Malaysia, Sumatra, Borneo, Java, Lesser Sunda Islands (Flores), Moluccas (Seram) and New Guinea.

Habitat & Ecology — Epiphytic on mossy tree trunks usually in mossy zones at middle elevations.

Notes — *Trichomanes ridleyi* is known only from the type collection. It is similar to *H. palmatifidum* except for the rather irregular form of the fronds. In such dwarfed forms, the size and form of the fronds are variable, and even abnormal and irregular forms are not rare. Without additional collections of this peculiarly constructed form, it may be admissible to include *T. ridleyi* within the range of variation of *H. palmatifidum*. *Rensch 1199* from Flores (L) is a mixture of this species, *H. palmatifidum* and *H. digitatum*. The Flores specimen has less dense hairs and more elongate involucres forming the tuberous basal portion of the sori.

The hairs on the fronds are not stellate, as in *H. pilosissimum*, but are articulate at the margins and on the veins of the segments and they always detach in a group, which suggests that the hair group is a stellate hair without a stalk cell.

63. Hymenophyllum pilosissimum C.Chr.

Hymenophyllum pilosissimum C.Chr., Gard. Bull. Straits Settlem. 7 (1934) 213; Copel., Philipp. J. Sci. 64 (1937) 172; J.X.Liu et al. in C.Y.Wu et al., Fl. China 2–3 (2013) 105; S.Linds. et al., Thai Forest Bull., Bot. 42 (2014) 48. — *Sphaerocionium pilosissimum* (C.Chr.) Copel., Philipp. J. Sci. 67 (1938) 33; Fern Fl. Philipp. 1 (1958) 54; K.Iwats., J. Fac. Sci. Univ. Tokyo, Sect. 3, Bot. 13 (1982) 213. — Type: *Burbidge s.n.* (holo K; iso BM), Borneo, Kinabalu.

Hymenophyllum obtusum auct. non Hook. & Arn.: C.Chr., Index Filic. (1905) 365.

Rhizome long-creeping, slender, wiry, 0.2–0.3 mm diam., irregularly branching, covered with dense hairs or glabrescent in older portion; hairs slender, brown to pale brown, multicellular and simple or stellate, with a simple stalk cell and triforked, biforked, or simple multicellular arms, simple longest ones to 1.5 mm long; roots irregularly from rhizome, bearing brownish simple hairs. *Stipes* remote to each other, slender, 0.2–0.3 mm diam., commonly 2–4 cm long but variable according to the size of fronds, much shorter than laminae, terete in lower portion, narrowly winged in upper portion with at most three cells broad on each side, covered throughout with stellate hairs; *fronds* bipinnate to tripinnate, oblong-lanceolate to lanceolate, round to moderately acute at apex, widest at middle, or sometimes at upper or lower portion, (1.5–)4–7(–12) cm long, (1–)1.7–2.5(–3.5) cm wide, but variable in size and fully soriferous in smaller fronds of the size of 3 cm long; *rachis* distinctly winged throughout, winged rachis similar in appearance to segments, more or less zigzag in the upper portion, densely covered by stellate hairs; *pinnae* usually more than 10 pairs, the upper ones becoming smaller and indistinct, larger ones stalked, bipinnatifid, or with biforked or triforked pinnules, oblong-ovate in outline, sometimes to 4 cm long, more than 1 cm wide, winged throughout showing an appearance similar to segments, densely stellate-hairy; *ultimate segments* linear, round to moderately acute, or obtuse, or often retuse at apex, entire and hairy at margin, sometimes elongate to 1 cm long, commonly (0.7–)1.3–1.7 mm broad, uninervate with hairy veinlets, pale green in living condition, brown when dried. *Laminar cells* large, 0.1–0.12 mm long; *internal cell walls* thin, straight; *hairs* stellate, usually very dense on stipes, on both surfaces of all axes inclu-

ding veinlets, and at margin of segments as well as of wings of rachis and pinna rachis, usually solitary on veins but 2 or 3 hairs articulated at margin, each bearing one stalk cell and (1–)3–5(–6) unicellular arms, stalk cells tinted pale brown, thick, c. 0.3 mm long, arm cells needle-like, slender, stiff, semitransparent, to 0.7 mm long. *Sori* solitary at apex of ultimate segments, often at distal end of segment and apparently arranged marginal on upper part of fronds, deeply immersed, c. 0.8 mm long, 1–1.2 mm broad; *involucres* bivalvate in the upper two-thirds, shallowly cup-shaped in lower immersed portion, semicircular or a little wider, as broad as ultimate segments; receptacles short, clavate, included. — **Fig. 12c, d.**

Distribution — Thailand, Taiwan; in *Malesia*: Borneo, Philippines (Luzon, Catanduanes, Negros, Mindanao) and New Guinea.

Habitat — Epiphytic on mossy tree trunks, usually in a mat on lower part of trunks of medium sized trees, in dense and tall lower montane rain forests. Altitude: middle and higher elevations, 1000–2700 m.

Notes — The stellate hairs are densely arranged at the margin of the segments and wings, usually with two or three marginal laminar cells between the adjacent hairs. After the stellate hairs fall, the marginal cells are damaged, and often the entire arrangement of marginal cells is disordered. After many hairs have fallen, the margin of the segments and wings of older fronds appear to be denticulate.

The stipes and rhizome are seemingly similar, but the hairs on the stipes are stellate, while those on the rhizome are simple.

This is the only example in Malesia of the typical form of subg. *Sphaerocionium* with dense stellate hairs. They do not have any direct relationship to the American species. Although phenetically similar, the New Zealand *H. frankliniae* differs from our species in having hairs also on the surface of the lamina.

7. POLYPHLEBIUM

Polyphlebium Copel., Philipp. J. Sci. 67 (1938) 55; Ebihara et al., Blumea 51 (2006) 240. — *Phlebiophyllum* Bosch, Verslagen Meded. Afd. Natuurk. Kon. Akad. Wetensch. 11 (1861) 321, non Nees (1832). — *Trichomanes* L. sect. *Phlebiophyllum* (Bosch) Prantl, Unters. Morph. Gefässkrypt. 1 (1875) 52. — *Trichomanes* L. subg. *Polyphlebium* (Copel.) Allan, Fl. New Zealand 1 (1961) 34. — Type: *Polyphlebium venosum* (R.Br.) Copel.

Rhizome long-creeping, filiform, densely covered with blackish hairs, bearing a few and fine roots; *fronds* pinnate; ultimate segments round at apex, entire and flat; a single row (except for some species outside Malesia) of marginal cells modified, elongate parallel to lamina-margin, 2–3 times as long as wide; *involucre* of sori cup-shaped, with distinctly dilated mouth; receptacles long-extruded.

Distribution — About 15 species are known in the temperate regions, mostly in the southern hemisphere; one species in *Malesia*.

Habitat & Ecology — Epiphytic and epipetric in dense montane forests, from low to mid elevations.

Note — *Polyphlebium* resembles *Crepidomanes* and *Vandenboschia*, but is distinct from both in molecular features. It is defined by external morphology in having few, fine roots on the rhizome and modified marginal cells arranged in a single row.

1. Polyphlebium werneri (Rosenst.) Ebihara & K.Iwats.

Polyphlebium werneri (Rosenst.) Ebihara & K.Iwats. in Ebihara et al., Blumea 51 (2006) 241. — *Trichomanes werneri* Rosenst., Repert. Spec. Nov. Regni Veg. 5 (1908) 35; Copel., Philipp. J. Sci. 51 (1933) 170, pl. 16. — *Crepidopteris werneri* (Rosenst.) Copel., Philipp. J. Sci. 67 (1938) 58. — *Crepidophyllum werneri* (Rosenst.) C.F.Reed, Amer. Fern J. 38 (1948) 89. — *Reediella werneri* (Rosenst.) Pic.Serm., Webbia 24 (1970) 719. — Syntypes: *Werner 27* (B, L, NY, P, S, UC), New Guinea.
Reediella endlicheriana auct. non (C.Presl) Pic.Serm.: Croxall, Austral. J. Bot. 23 (1975) 530.

Rhizome long-creeping, filiform, irregularly branching, not wiry, to 0.15 mm diam.; hairs dense, dark brown to blackish, warty, minute. *Stipes* distinctly winged, nearly terete at basal portion, dark brown, hairy, upper portion green, glabrescent, to 1 cm long, proportionately much shorter than laminae; *fronds* tripinnate, oblong or broader, usually widest at upper portion, round at apex, gradually narrowing towards cuneate base, laminae to 5 cm long, 2 cm wide, rachis winged, giving appearance similar to the segments, bearing minute hairs, nearly straight; *pinnae* 4–8 pairs, but often several ones abbreviated, short-stalked, the larger ones bipinnate with pinnules of several segments; *ultimate segments* round to moderately acute at apex, entire and almost flat at margin, to 0.5 mm broad. *Laminar cells* unistratose, a single row of marginal cells modified, elongate parallel to lamina margin, 2–3 times as long as wide. *Sori* solitary, on short first acroscopic segments or acroscopic branches of pinnules, thus usually arranged in one row at each side of rachis or second rows often developed; *involucres* cup-shaped, with distinctly dilated mouth, 2–2.5 mm long, c. 0.7 mm diam., broadly winged throughout; lips c. 0.4 mm broad, the mouth becoming c, 1.7 mm diam.; receptacles long-extruded.

Distribution — *Malesia*: Borneo, New Guinea.

Habitat & Ecology — Epiphytic on mossy tree trunks in dense montane forests; collections were made between 700 and 1500 m altitude.

Note — *Polyphlebium werneri* is seemingly similar to *P. endlicherianum* and *P. vieillardii,* from the Pacific islands and Australia, respectively, but has narrower segments and is epiphytic. The modified cells at the margin are in a single row, the same as in the two Oceanic species. In general habit, *P. werneri* resembles *Crepidomanes humile* in some respects.

8. VANDENBOSCHIA

Vandenboschia Copel., Philipp. J. Sci. 67 (1938) 51; Gen. Fil. (1947) 37; Ebihara et al., Blumea 51 (2006) 241. — *Trichomanes* L. subg. *Vandenboschia* (Copel.) Holttum, Rev. Fl. Malaya 2 (1955) 105; Allan in Allan et al., Fl. New Zealand 1 (1961) 34. — Type: *Vandenboschia radicans* (Sw.) Copel.
Trichomanes L. sect. *Lacosteopsis* Prantl, Unters. Morph. Gefässkrypt. 1 (1875) 53. — *Lacosteopsis* (Prantl) Nakaike, Enum. Pterid. Jap.: Filic. (1975) 21. — Type: *Trichomanes radicans* Sw. (= *Vandenboschia radicans* (Sw.) Copel.).
Crepidomanes C.Presl subg. *Maiora* (Prantl) K.Iwats., Acta Phytotax. Geobot. 35 (1984) 174, p.p. — *Trichomanes* B *Maiora* Prantl, Unters. Morph. Gefässkrypt. 1 (1875) 52. — Type: *Trichomanes scandens* L. (= *Vandenboschia scandens* (L.) Copel.).

Rhizome long-creeping, or short in some species, bearing rather dense brownish hairs; *fronds* pinnate to pinnately decompound, small to mediocre in size; ultimate *segments* entire, uninervate, unistratose except for veins, *internal cell walls* in many

species rather thin and straight. *Sori* solitary at apex of ultimate segments; *involucres* campanulate, with truncate to dilated mouth; receptacles long-extruded. Chromosome base number: $x = 36$.

Distribution — More than 15 species throughout the tropics, extending to northern temperate regions; 4 species in *Malesia*.

Habitat — Epiphytic on tree trunks, epipetric on moist to mossy rocks and terrestrial on wet sandy ground; from low to mid elevations.

Morphology — Rhizome short, suberect to long-creeping, irregularly branching, and usually with dense, dark to bright brown unicellular hairs. On older portions, especially on tree trunks, the hairs are caducous and the rhizome is subglabrous. Anatomically, the protostele is reduced and the cortex is heterogenous. The roots are numerous, and more or less robust.

Fronds are pinnately divided, bipinnate in subg. *Lacosteopsis* to penta-pinnatifid in larger ones. There are no false veinlets and the venation is anadromous. Pagina is unistratose, and the cells are regularly arranged. Internal cell walls are in principal thin and straight, but in some species thick and coarsely pitted.

The sori are paratactic in arrangement, tubular to campanulate in form, with a nearly truncate to dilated mouth. Receptacles are long-extruded, the elongate portion sometimes more than several times as long as the involucres, and usually straight.

Taxonomy — *Vandenboschia* was once reduced to *Crepidomanes* s.lat. by Iwatsuki (1984), although it was recognized as subg. *Maiora* sect. *Maiora*. Molecular analysis elucidated that both Copeland's *Vandenboschia* and Iwatsuki's *Crepidomanes* are polyphyletic, and the systematics and nomenclature were thus revised by Ebihara et al. (Blumea 51 (2006) 237–242).

KEY TO THE SUBGENERA

1a. Terrestrial or saxicolous plants, or at most on the base of tree trunks; fronds decompound, at least tripinnate . . . . . **a.** subg. **Vandenboschia**

b. Scandent plants, usually on trunks or branches of trees; fronds lanceolate to narrowly so, simply pinnate . . . . . **b.** subg. **Lacosteopsis**

a. Subgenus **Vandenboschia**

Type: as the species.

Rhizome creeping but not very long; *fronds* bipinnate or more deeply compound, at least tripinnate; usually epipetric or terrestrial, rarely epiphytic.

Distribution — About 25 species, widely distributed in the tropics worldwide, also north to Britain and northern Japan, south to central South America (Brazil and Bolivia). Three species in *Malesia*.

Habitat & Ecology — On wet sandy ground and in muddy crevices of rocks, rarely climbing on tree trunks, usually in dense forests.

Taxonomy — Subgenus *Vandenboschia* is seemingly similar to *Crepidomanes* subg. *Nesopteris,* but the latter subgenus is distinct, even in phenetic features, in having an erect or ascending rhizome.

KEY TO THE SPECIES

1a. All axes narrowly winged, usually as wide as ultimate segments; rhizome glabrous on older portions 2
b. Axes broadly winged or pinnules less dissected; rhizome persistently covered with blackish hairs . . . . . **3. V. striata**
2a. Fronds broadly lanceolate to oblong; mouth of involucres distinctly dilated, lips to 0.5 mm broad . . . . . **1. V. johnstonensis**
b. Fronds ovate to oblong-subdeltoid; mouth of involucres truncate or a slightly dilated . . . . . **2. V. maxima**

1. Vandenboschia johnstonensis (F.M.Bailey) Copel.

Vandenboschia johnstonensis (F.M.Bailey) Copel., Philipp. J. Sci. 67 (1938) 54; Fern Fl. Philipp. 1 (1958) 65. — *Trichomanes johnstonense* F.M.Bailey, Proc. Roy. Soc. Queensland 1 (1884) 14, pl. 1; Lithogr. Ferns Queensland (1892) pl. 26; Domin, Biblioth. Bot. 20(85) (1913) 18; Copel., Philipp. J. Sci. 51 (1933) 217; Croxall, Austral. J. Bot. 23 (1975) 526. — *Crepidomanes johnstonense* (F.M. Bailey) K.Iwats., J. Fac. Sci. Univ. Tokyo, Sect. 3, Bot. 13 (1985) 532. — Lectotype (designated by Bostock & Spokes, Orchard, Fl. Australia 48 (1998) 140, see Field, Austral. Syst. Bot. 33 (2020) 20): *Kefford s.n.* (lecto BRI; isolecto MEL), Australia, Queensland.

Rhizome creeping rather long, bearing the leaves commonly less than 1 cm remote, 0.7–1 mm diam., nearly black, usually bearing hairs, glabrous with age; hairs red brown to bright dark brown, multicellular, to 5 mm long, more or less warty, rather dense roots irregularly from rhizome, with dense black hairs. *Stipes* narrowly winged nearly to the base, stramineous, dark at the base, hairy near the base, minutely beset with small hairs of pale brown colour and to 0.5 mm long when young or glabrous with age, usually less than 10 cm long, often one-fifth to one-fourth to the length of fronds; *fronds* tripinnate, narrowly oblong to oblong-lanceolate, round to acute at apex, round at base, broadest at middle portion, 10–15 cm long, 2–3.5 cm wide in the leaves of standard size but smaller ones often fully fertile; rachis like the upper part of stipes, slightly zigzag in the upper portion, distinctly winged and nearly the same width as the ultimate segments; *pinnae* 10–15(–18) pairs, stalked, subrhomboid to oblong, often falcate, bipinnate or rarely tripinnatifid in larger ones; pinna rachis placed at acute angle to rachis, bent upward, broadly winged, having nearly the same width as the ultimate segments, wings broader at sinus between axes; *pinnules* with one to several segments, less deeply cut with broader laminae at sinus between axes; ultimate segments hardly elongate, connected with the next ones by broader sinus, entire at margin, moderately acute, round, obtuse, or retuse at apex, c. 1 mm broad. *Sori* solitary on short basal acroscopic segments, dispersed evenly throughout the fronds; *involucres* deeply cup-shaped, distinctly dilated at mouth, 1.7–2.2 mm long, to 8 mm diam.; the lips to 0.5 mm broad, thus forming mouth c. 2 mm diam.; receptacles long extruded.

Distribution — *Malesia*: Philippines (Luzon, Negros, Leyte, Mindanao); Australia (Queensland).

Habitat & Ecology — Terrestrial in wet ground, often along rivers, or sometimes immersed in water when flooded, usually in dense forests. Altitude: lower elevations to 1000 m.

Note — In the size and form of the leaves, *V. johnstonensis* appears similar to *V. striata*, but the relationship is likely to *V. maxima* as indicated by the pale green leaves, wiry rhizome, sparser hairs, coarse texture and deeply cut leaves. In turn, *V. johnstonensis* differs from *V. maxima* in being smaller with lanceolate leaves and the mouth of involucres distinctly dilated. The most similar species of this group is *V. liukiuensis* (Y.Yabe) Copel. in Japan, which in all characters, except for the less dilated mouth of the involucres, is similar to *V. johnstonensis*.

2. Vandenboschia maxima (Blume) Copel.

Vandenboschia maxima (Blume) Copel., Philipp. J. Sci. 67 (1938) 54; Fern Fl. Philipp. 1 (1958) 65; H.Ito, Fil. Jap. Ill. (1944) pl. 470; Ching, Fl. Reipubl. Popularis Sin. 2 (1959) 182; J.X.Liu et al. in C.Y.Wu et al., Fl. China 2–3 (2013) 109; C.W.Chen et al., Sol Amazing (2017) 136; K.Iwats. et al., PhytoKeys 119 (2019) 112. — *Trichomanes maximum* Blume, Enum. Pl. Javae 2 (1828) 228; Bosch, Hymenophyll. Javan. (1861) 25, pl. 18; Copel., Philipp. J. Sci. 51 (1933) 217, pl. 38: f. 1–4; Ogata, Icon. Fil. Jap. 6 (1935) pl. 298; Tardieu & C.Chr. in Lecomte, Fl. Indo-Chine 7, 2 (1939) 72; Holttum, Rev. Fl. Malaya 2 (1955) 107, f. 43; Tagawa & K.Iwats. in Smitinand et al., Fl. Thailand 3 (1979) 83. — *Lacosteopsis maxima* (Blume) Nakaike, Enum. Pterid. Jap.: Filic. (1975) 22. — *Crepidomanes maximum* (Blume) K.Iwats., J. Fac. Sci. Univ. Tokyo, Sect. 3, Bot. 13 (1985) 531. — Lectotype (designated by Iwatsuki (1985) 532 as 'type'): *Blume s.n.* (lecto L; isolecto P), Java.

Hymenophyllum puellum Ces., Rendiconto Accad. Napoli 16 (1877) 24, 28. — Type: *Beccari s.n.* (holo FI), Papua New Guinea, Monte Arfak.

Macroglena obtusa Copel., Philipp. J. Sci. 84 (1955) 163. — *Trichomanes obtusum* (Copel.) C.V.Morton, Contr. U.S. Natl. Herb. 38 (1968) 188. — Type: *PNH (Edaño) 21369* (holo MICH), Philippines, Negros.

Rhizome creeping, commonly on rocks along streams, irregularly branching, not so long and bearing fronds rather closely, to 3 mm diam., densely covered with blackish bristles, or nearly glabrous and dark brown to black, or glaucous in older portion; *roots* wiry or tender, densely covered with dark brownish hairs; hairs multicellular, subarticulate, not straight, brown to dark, shining, to 3 mm long. *Stipes* shallowly grooved on upper surface, very narrowly winged throughout, green to stramineous with dark basal portion, to 25 cm long but variable in size, bearing blackish bristles near the base, nearly glabrous upwards; wings usually less than 0.4 mm broad, or a few laminar cells broad at each side, entire, flat; *fronds* quadripinnate or even more compoundly divided in some cases, ovate to oblong subdeltoid, acute to acuminate at apex, broadly cuneate to round at base, often more than 30 cm long, 20 cm wide, but smaller fronds of 15 cm in length and 6 cm width being fully fertile, variable in size and form; *rachis* like stipes, narrowly winged throughout, stramineous or pale green, bearing a few brownish multicellular hairs; *basal pinnae* the largest, or a few basal pinnae gradually becoming smaller downwards, more or less ascending, at angles of 47–70° to rachis, stalked, oblong-subtriangular, gradually narrowing towards acuminate apex, unequally broadly cuneate at base, basiscopic base often with wide space, to 12 cm long, 4.5 cm wide, *upper pinnae* gradually becoming smaller and narrower; pinna rachis winged throughout, similar to stipes and rachis but more slender; larger *pinnules* narrowly oblong, oblong-subdeltoid, or semi-parallelogrammoid, acute at apex, unequally or narrowly cuneate at base, basiscopic base often obsolete, to 3 cm long, 1.2 cm wide, somewhat

Fig. 13. a, b. *Vandenboschia maxima* (Blume) Copel. a. Specimen; b. sorus. — c, d. *V. striata* (D.Don) Ebihara. c. Specimen; d. frond segments. — e. fronds of *V. auriculata* (Blume) Copel. (a, b: *Ueda & Darnaedi B-8953*, Kalimantan Timur, Indonesia, TI 00000331; c, d: *De Wilde & De Wilde-Duyfjes 12329*, Sumatra, Indonesia, KYO 00010536; e: *Kato et al. C-14110*, Seram, Indonesia, TI 00047804).

falcate, ascending, shortly stalked, smaller ones oblong or nearly so, less divided and less stalked; *secondary pinnules* similar to smaller pinnules, shortly stalked, round at apex, cuneate at base; *tertiary pinnules* with 1–6 segments arranged bipinnatifidly, cuneate and sessile at base; *ultimate segments* round to moderately acute at apex, entire, flat or more or less recurved in dried condition, 0.4–0.6 mm broad, green, usually sinus covered by the laminae or segments less deeply incised; *laminar cells* tetragonal, *internal cell walls* thin and straight. *Sori* solitary, usually at apex of short basal acroscopic branch of secondary pinnules of upper pinnae, dispersed throughout the fronds; *involucres* cup-shaped, c. 1.5 mm long, 0.7 mm diam., the mouth hardly dilated and truncate in appearance, c. 1.2 mm diam.; receptacles long-extruded. Chromosome numbers: $n = 36$ (Braithwaite, Fern Gaz. 10 (1969) 82, Bot. J. Linn. Soc. 71 (1975) 169). — **Fig. 13a, b.**

Distribution — Thailand, Vietnam, Taiwan, Japan (Ryukyu); in *Malesia*: throughout; Melanesia, Micronesia, Polynesia.

Habitat & Ecology — Terrestrial on wet sandy ground and on muddy rocks, usually near streamlets in dark forests. Altitude: from lowlands to 2700 m.

3. **Vandenboschia striata** (D.Don) Ebihara

Vandenboschia striata (D.Don) Ebihara in J.X.Liu et al. in C.Y.Wu et al., Fl. China 2–3 (2013) 109. — *Trichomanes striatum* D.Don, Prodr. Fl. Nepal. (1825) 11; C.V.Morton, Contr. U.S. Natl. Herb. 38 (1968) 273. — Type: *Buchanan-Hamilton s.n.* (holo BM), Nepal.

[*Trichomanes anceps* Wall., Numer. List (1828) no. 166, nom. nud.]

Trichomanes birmanicum Bedd., Suppl. Ferns Brit. Ind. (1876) 3, pl. 349; Tardieu & C.Chr. in Lecomte, Fl. Indo-Chine 7, 2 (1939) 70; Tagawa & K.Iwats. in Smitinand et al., Fl. Thailand 3 (1979) 84, f. 5: 7; Ebihara, Bull. Natl. Mus. Nat. Sci. B, 35 (2009) 71. — *Trichomanes radicans* Sw. var. *birmanicum* (Bedd.) C.Chr., Index Filic. (1906) 636. — *Vandenboschia birmanica* (Bedd.) Ching, Acta Phytotax. Sin. 8 (1959) 135; Fl. Reipubl. Popularis Sin. 2 (1959) 185. — *Crepidomanes birmanicum* (Bedd.) K.Iwats., J. Fac. Sci. Univ. Tokyo, Sect. 3, Bot. 13 (1985) 530. — Type: *Parish 181* (holo K), Myanmar.

Trichomanes naseanum Christ, Bull. Soc. Bot. France 52 (Mém. 1) (1905) 11; Ogata, Icon. Fil. Jap. 1 (1928) pl. 46; Tardieu & C.Chr. in Lecomte, Fl. Indo-Chine 7, 2 (1939) 71. — *Vandenboschia radicans* (Sw.) Copel. var. *naseanum* (Christ) H.Ito, J. Jap. Bot. 24 (1949) 124; Tagawa, Col. Ill. Jap. Pterid. (1959) 45, 260, f. 69b — *Vandenboschia naseana* (Christ) Ching, Acta Phytotax. Sin. 8 (1959) 136; Fl. Reipubl. Popularis Sin. 2 (1959) 186; DeVol in H.L.Li et al., Fl. Taiwan 1 (1975) 115. — *Trichomanes radicans* Sw. var. *naseanum* (Christ) Lellinger, Amer. Fern J. 58 (1968) 157. — *Lacosteopsis orientalis* (C.Chr.) Nakaike var. *naseana* (Christ) Nakaike, Enum. Pterid. Jap.: Filic. (1975) 24. — *Crepidomanes radicans* (Sw.) K.Iwats. var. *naseanum* (Christ) K.Iwats., J. Fac. Sci. Univ. Tokyo, Sect. 3, Bot. 13 (1985) 530. — Lectotype (designated by Ebihara et al., Acta Phytotax. Geobot. 60 (2009) 32): *coll. unknown*, *Christ det. 1* (lecto P; isolecto TI), Japan, Ryukyu.

Trichomanes radicans auct. non Sw.: Sw., J. Bot. (Schrader) 1800(2) (1801) 97; Bedd., Ferns Brit. India 1 (1866) pl. 181; Copel., Philipp. J. Sci. 51 (1933) 213, pl. 53: f. 1–2; Holttum, Rev. Fl. Malaya 2 (1955) 107. — *Vandenboschia radicans* auct. non (Sw.) Copel.; Copel., Philipp. J. Sci. 67 (1938) 54; H.Ito, Fil. Jap. Ill. (1944) pl. 469; J.L.Tsai & W.C.Shieh in H.L.Li et al., Fl. Taiwan 1 (1994) 131, pl. 50. — *Crepidomanes radicans* auct. non (Sw.) K.Iwats: K.Iwats., J. Fac. Sci. Univ. Tokyo, Sect. 3, Bot. 13 (1985) 530; pertaining to the Asian specimens.

Rhizome long-creeping, (0.7–)1.5–2.2(–2.5) mm diam., densely covered with hairs and seemingly more than 5 mm diam., bearing wiry and hairy roots rather sparsely; hairs brown or blackish, multicellular, 0.7–2(–4) mm long, very dense throughout except on

the surface attached to substrata, slender, same as those on roots and stipe bases. *Stipes* usually broadly winged nearly towards base but often broken in older ones, terete only on the basal c. 5 mm portion, densely hairy at base with hairs similar to or longer than those on rhizome, stramineous to greenish, 2–6(–12) cm long. *Fronds* quadripinnatifid to quadripinnate, oblong or narrowly so, moderately acute to acuminate at apex, gradually narrowing towards round to broadly cuneate base, (17–)20–35(–70) cm long, (5–)6–10 cm wide at widest middle portion; *lateral pinnae* more than 12 pairs, middle or lower middle ones the largest, to 15 cm long, 3.5 cm wide, or commonly c. 12 cm long, 2.5 cm wide, unequally oblong subdeltoid, often more or less falcate, acute to acuminate at apex, subtruncate to broadly cuneate at acroscopic and narrowly cuneate at basiscopic bases, the *upper pinna*e gradually smaller upwards; *larger pinnules* bipinnatifid to bipinnate, oblong or narrowly so, often falcate, acute or moderately so at apex, broadly cuneate at acroscopic and very narrowly cuneate at basiscopic bases, shortly but distinctly stalked or subsessile, to 4 cm long, 1.2 cm wide, similar to the upper lateral pinnae; *secondary pinnules* with up to 12 ultimate segments, less divided, connected by wings; *ultimate segments* round, obtuse or moderately acute at apex, entire, sometimes involute when dry, 0.3–0.6 mm broad, glabrous, coarsely membranous, deep green when living, dark brown or blackish in dried specimens; all axes winged, with wings entire, flat, broader than ultimate segments, those on stipes to 1.5 mm broad at each side, on rachis to 1.2 mm broad, and on pinna rachis c. 0.6 mm broad, quite the same in pagina with ultimate segments, thus giving appearance of less deeply divided. *Internal cell walls* thin and straight. *Sori* solitary at apex of acroscopic branches of segments, usually below margin of pinnules, often bending slightly downward; *involucres* tuberous, narrower than ultimate segments or winged only on basiscopic side, to 2 mm long, 0.5 mm diam., the mouth dilated, to 1 mm diam., the lips to 0.2 mm broad; receptacles long-extruded. Chromosome numbers: $n = 36$ (Mitui, Sci. Rep. Tokyo Kyoiku Daigaku, B, 13 (1968) 286; J. Jap. Bot. 51 (1976) 34), $n = 72$ (Mehra & Singh, J. Genet. 55 (1957) 383). — **Fig. 13c, d.**

Distribution — N India, Nepal, Bhutan, Myanmar, Thailand, Laos, Vietnam, Central & S China, Taiwan, S Japan; in *Malesia*: throughout, but not very common.

Habitat — On moist, mossy rocks and cliffs, rarely on the base of tree trunks, and terrestrial on sandy streamsides, often forming colonies in dense gloomy forests, often along streamlets in lowlands in deep shade. Climbing only a few meters up tree trunks, and never climbing as high as *V. auriculata*.

Notes — *Vandenboschia striata* has been reduced to a form of *V. radicans* of the American tropics, but differs from it, beyond its geographical distribution, in being more blackish when dried and having broader ultimate segments and broader wings on the distal axes, which show the pagina less dissected. Smaller or stunted forms of *V. radicans* are often similar, but *V. striata* does not become as large as *V. radicans*, although more careful observations are badly needed to find evidence that show most exactly the features of these two species.

The discriminating characters to distinguish *V. striata* from *V. maxima* are: rhizome long-creeping, usually densely covered with dark brown hairs, more or less fleshy; fronds dissected less finely, or the wings of all axes broader than ultimate segments and occupying the sinus between segments; laminae dark green when alive and often

blackish in dried specimens, not very fragile. The characters of *V. maxima* in comparing with the noted ones of *V. striata* are: rhizome short creeping, bearing fronds closely, covered with blackish bristles, or caducous; fronds finely dissected, quadri-pinnate or even more compoundly divided; the wings of axes narrower than ultimate segments; laminae fresh green when alive and brownish in dried specimens, rather fragile.

The structure of the so-called *Trichomanes radicans* species complex was carefully examined in Japan and adjacent areas (Ebihara et al., Amer. J. Bot. 92 (2005) 1535–1547; Annals Tsukuba Bot. Gard. 24 (2005) 17–25; Acta Phytotax. Geobot. 60 (2009) 27–41; Ebihara, Bull. Natl. Mus. Nat. Sci. B, 35 (2009) 71–89).

b. Subgenus **Lacosteopsis** (Prantl) Ebihara & K.Iwats.

Vandenboschia Copel. subg. *Lacosteopsis* (Prantl) Ebihara & K.Iwats. in Ebihara et al., Blumea 51 (2006) 242. — *Trichomanes* L. sect. *Lacosteopsis* Prantl, Unters. Morph. Gefässkrypt. 1 (1875) 53; C.V.Morton, Contr. U.S. Natl. Herb. 38 (1968) 181. — *Lacosteopsis* (Prantl) Nakaike, Enum. Pterid. Jap.: Filic. (1975) 21, p.p. — Type: *Trichomanes luschnatianum* C.Presl (= *Vandenboschia rupestre* (Raddi) Ebihara & K.Iwats.).

Scandent plants, usually on trunks or branches of trees; *fronds* lanceolate to narrowly so, simply pinnate.

Distribution — Two species are recognized in subg. *Lacosteopsis*, they occur throughout the tropics except in Africa. One species is widely distributed in *Malesia*.

Habitat & Ecology — Both species are hemi-epiphytes climbing on tree trunks (Nitta & Epps, Brittonia 61 (2009) 392–397); from low to mid elevations.

4. Vandenboschia auriculata (Blume) Copel.

Vandenboschia auriculata (Blume) Copel., Philipp. J. Sci. 67 (1938) 55; H.Ito, Fil. Jap. Ill. (1944) pl. 471; Copel., Fern Fl. Philipp. 1 (1958) 66; Tagawa, Col. Ill. Jap. Pterid. (1959) 46, 260, f. 73; Ching, Fl. Reipubl. Popularis Sin. 2 (1959) 181, pl. 13: f. 1-2; DeVol in H.L.Li et al., Fl. Taiwan 1 (1975) 14; J.L.Tsai & W.C.Shieh in H.L.Li et al., Fl. Taiwan 1 (1994) 129, pl. 49; J.X.Liu et al. in C.Y.Wu et al., Fl. China 2–3 (2013) 108; K.Iwats. et al., PhytoKeys 119 (2019) 112. — *Trichomanes auriculatum* Blume, Enum. Pl. Javae 2 (1828) 225; Bosch, Hymenophyll. Javan. (1861) pl. 25; Bedd., Ferns Brit. India 1 (1866) pl. 182; Makino, Phan. Pter. Jap. Icon. 1 (1899) pl. 22; Ogata, Icon. Filic. Jap. 4 (1931) pl. 198; Copel., Philipp. J. Sci. 51 (1933) 223; Tardieu & C.Chr. in Lecomte, Fl. Indo-Chine 7, 2 (1939) 69; Holttum, Rev. Fl. Malaya 2 (1955) 105, f. 41; Tagawa & K.Iwats. in Smitinand et al., Fl. Thailand 3 (1979) 83. — *Cephalomanes auriculatum* (Blume) Bosch, Ned. Kruidk. Arch. 4 (1859) 352; Hymenophyll. Javan. (1861) 34, pl. 25. — *Lacostea auriculata* (Blume) Prantl, Unters. Morph. Gefässkrypt. 1 (1875) 50. — *Lacosteopsis auriculata* (Blume) Nakaike, Enum. Pterid. Jap.: Filic. (1975) 21. — *Crepidomanes auriculatum* (Blume) K.Iwats., J. Fac. Sci. Univ. Tokyo, Sect. 3, Bot. 13 (1985) 528. — Lectotype (designated here): *Blume s.n.* (lecto L 544643; isolecto L (8 sheets)]), Java.

Trichomanes dissectum J.Sm., J. Bot. (Hooker) 3 (1841) 417; Hook., Sp. Fil. 1 (1845) 140; Bedd., Ferns Brit. India 1 (1866) pl. 182. — Lectotype (designated here): *Cuming 129* p.p. (lecto K 000375471; isolecto GH, K, L, LE, P), Philippines, Luzon.

Trichomanes dimidiatum C.Presl, Abh. Königl. Böhm. Ges. Wiss., ser. 5, 3 (1843) 38. — Syntypes: *Cuming 129* (GH, K, L, LE, P, PRC), Philippines.

Rhizome long-creeping, scandent on tree trunks, rarely on rocks, 1.2–2.2 mm diam., green to darker, glabrous on upper surface, densely hairy beneath, roots lacking, bear-

ing leaves 1–5 cm from each other. *Stipes* short, less than 1 cm long, terete, green to darker, hairy at base with blackish hairs similar to those on rhizome, *fronds* pinnate, linear-lanceolate to lanceolate, acute to caudate-acuminate at apex, gradually narrowing downwards, to 35 cm long, 4.5 cm wide, the fully fertile ones a little narrower, rachis narrowly winged nearly to the base or terete, green or darker in lower portion, sparsely hairy, hairs pale brown, downy, multicellular, to 1.5 mm long, *pinnae* short-stalked, falcately oblong-subdeltoid, round at apex, cuneate at basiscopic and distinctly auriculate at acroscopic bases, lobed nearly to halfway, or auricles sometimes separated, to 2.5 cm long, 1.2 cm wide, auricles fan-shaped, round at apex, serrate at margin, lateral lobes commonly including 3–5 lobes, truncate, separated by sharp sinus 1–2 mm in depth, apical lobes round at apex, cuneate at base, *costae* distinct, branched off the veins in pinnate pattern, veins forked dichotomously two or three times. *Sori* terminal on veinlets, usually one on each lateral lobe, or in addition a few on basal acroscopic lobes (auricles), immersed or extruded with narrow wings; *involucre* cup-shaped with hardly dilated mouth, c. 1.7 mm long, 0.5 mm diam., mouth c. 0.6 mm diam.; receptacles long-extruded. Chromosome numbers: $n = 36$ (Mehra & Singh, J. Genet. 55 (1957) 384; Mitui, J. Jap. Bot. 41 (1966) 62; 42 (1976) 34; Wang & Sun, Acta Phytotax. Sin. 20 (1982) 60), $2n = 108$ (Mehra & Singh, J. Genet. 55 (1957) 384). — **Fig. 13e.**

Distribution — N India, Nepal, Bhutan, Myanmar, Thailand, Laos, Vietnam, Cambodia, China, Taiwan, S Japan; in *Malesia*: throughout, very common; Micronesia.

Habitat & Ecology — Climbing up trees, often to the slender branches, rarely creeping on mossy rocks in dense gloomy forests. Altitude: from lowlands to 1700 m.

INDEX TO SCIENTIFIC PLANT NAMES

Numbers refer to page numbers. Infrageneric epithets have been entered directly under the generic name to which they belong, preceded by the indication of their rank (subg., sect., etc.). Infraspecific epithets have been entered under the specific name to which they belong, preceded by the indication of their rank (subsp., var., etc.).

Synonyms (including nomina nuda) have been printed in *italics*. Page numbers in **bold** type denote main treatment.

List of revised families in Flora Malesiana Series I (Seed Plants)

List of revised families in Flora Malesiana Series II (Ferns and Fern allies)