

A Review of Philippine
Hookeriaceous Taxa
(Musci)

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ABSTRACT

Tan, Benito, and Harold Robinson. A Review of Philippine Hookeriaceous Taxa (Musci). *Smithsonian Contributions to Botany*, number 75, 41 pages, 63 figures, 1990.—The limits of the Hookeriaceae are discussed with the exclusion of some recently added elements, *Cyathophorum*, *Cyathophorella*, and *Dendrocyathophorum*. Of the genera traditionally placed in the family, *Chaetomitrium* is also excluded, but briefly reviewed. Segregate families based on peristome structure, such as the Daltoniaceae, are rejected. Papillose peristomes show at least three basically distinct types in the Hookeriaceae and they probably evolved at least three separate times. Keys are furnished to the 11 genera and 36 species of Hookeriaceae recognized in the Philippines and to the 17 species of *Chaetomitrium* in the country. Eleven species are newly reported from the country including four in *Chaetomitrium*, four in *Distichophyllum*, two in *Leskeodon*, and one in *Calyptrochaeta*. *Bryobrothera* is reported from the country. Ten new synonyms are cited. Five new combinations, *Calyptrochaeta microblasta*, *C. ramosa*, *Distichophyllum nigricaulis* var. *elmeri*, *Daltonia robbinsii*, and *Leskeodon brevicuspidatus*, and one new name, *Chaetomitrium schofieldii*, are proposed. Lectotypes are selected for *Calyptrochaeta ramosa* (Fleischer) Tan & Robinson, *Distichophyllum brevicuspes* Fleischer, *D. nigricaulis* Mitten ex Bosch & Lacoste, *D. gracilicaulis* Fleischer, *Lepidopilum sumatranum* Bosch & Lacoste, and *Hookeriopsis wichurae* Fleischer. New records reported from other countries include *Daltonia armata* for Sumatra and *Achrophyllum dentatum* and *Distichophyllum subnigricaulis* for New Guinea.

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A Review of Philippine Hookeriaceous Taxa (Musci)

Benito Tan and Harold Robinson

Introduction

The present study has a primary aim of reviewing the members of the family Hookeriaceae in the Philippines. For this purpose, keys and descriptions are provided for species known from that country with accompanying illustrations of leaf structure (Figures 1-34) for some critical groups. In addition, observations are made on the limits of the family and possible subdivisions within the family. The interpretations of peristome characters are based on SEM studies of their detailed structure (Figures 35-63). The family limits and potential subdivisions of the family are considered first, and these are followed by the systematic review of the family in the Philippines.

The family Hookeriaceae has been repeatedly revised in recent years by Miller (1971), Crosby (1974), and Buck (1987). Its relationship with other pleurocarpous families was discussed by Robinson (1971, 1986) who suggested a previously unrecognized closeness to the Sematophyllaceae and Hypnaceae.

Buck (1987), believing in the heterogeneous nature of the family delineation and following the leads given by his predecessors (Miller, 1971; Crum, 1984; Allen, 1987a), proposed a formal split into five groups: Hookeriaceae (sensu stricto), Daltoniaceae, Callicostaceae, Leucomiaceae, and Adellotheciaceae. Although Buck (1987) based his new familial treatment on a combined consideration of both the sporophytic and gametophytic characters, the placement of some genera, in our opinion, is still unsatisfactory. For example, the circumscription of the redefined Hookeriaceae fide Buck (1987) is not convincing. His placement of *Cyathophorum*, *Cyathophorella*, and *Dendrocyathophorum*, traditionally of the

Hypopterygiaceae, in the vicinity of *Hookeria* is, at least, controversial.

Buck (1987) justified his transfer of three cyathophoroid genera from the Hypopterygiaceae to the Hookeriaceae on the following shared character combination: little or un-branched stems, unbordered leaves, double costae, and hexagonal and porose leaf cells. The ranked foliation of the cyathophoroid genera is thought to have evolved separately from that of *Hypopterygium*. However, a close re-examination of these similarities between the cyathophoroids and the hookerioids suggests to us that they are more likely the result of convergent evolution. The double costae of the *Cyathophorum* group are short, and the ranking of the leaves is unlike anything in the Hookeriaceae. Furthermore, leaves with hexagonal cells with or without borders are a rather widespread specialization. None of these characters seems particularly indicative of a close relation between the *Cyathophorum* group and the Hookeriaceae including *Hookeria*.

One distinctive gametophytic difference between the cyathophoroid and hookerioid taxa is their stem anatomy. In the former group, the stem anatomy shows a layer of thick-walled epidermis surrounding the cortex and a large central strand consisting of numerous small, hexagonal, and thin-walled hydroid cells. There is cellular differentiation within the strand. This is true in most members of Hypopterygiaceae (cf. Frey and Richter, 1982). In contrast, most hookerioid genera do not have a differentiated central strand in the stem. In a few genera like *Hookeria*, *Calypstrochaeta*, and *Achrophyllum* where central differentiation occurs in the stem, the central strand is a weakly defined group of parenchyma cells.

Also, the leaf cell anatomy varies between the two groups. In *Cyathophorella*, *Cyathophorum*, *Dendrocyathophorum*, and *Hypopterygium*, the leaf cells have well developed pits on lateral walls, a feature seen comparatively rarely in members of Hookeriaceae. Furthermore, *Cyathophorella hookeriana* (Griffith) Fleischer and *Dendrocyathophorum paradoxum* (Brothrus) Dixon have distinct foliose pseudoparaphyllia which are

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not matched in the Hookeriaceae. The structures that look like small pseudoparaphyllia in a few Hookeriaceae such as *Callicostella* and *Achrophyllum* have a different aspect and should be examined more carefully.

As to sporophytic characters, Noguchi (1952) has emphasized and illustrated their similarity in Hypopterygiaceae. For example, *Cyathophorum* and *Dendrocyathophorum* have a cucullate calyptra and a cross-striated, unfurrowed exostome with cilia present on the endostome, characters allegedly incongruent in Hookeriaceae. The exception is *Cyathophorella* which appears to have a papillose exostome with a median zigzag line, reminiscent of the daltoniaceous exostome. In spite of the fact that the cyathophorelloid exostome is generally papillose, careful microscopic examination shows the dense papillae are sometimes borne on low ridges or folds formed on the outer surface of the exostome. We tend to interpret this as a modified hypopterygioid peristome.

Furthermore, the outer and inner layers of the exostome in *Cyathophorum* and *Cyathophorella* are more or less equal in thickness, unlike the daltoniaceous or hookeriaceous type of exostome described by Allen and Crosby (1986) and Buck and Vitt (1986). This is reflected in the fact that the exostomial teeth neither bend outward nor curve inward when wet.

Considering all the evidence at hand, we prefer to keep the three cyathophoroid genera in or near the Hypopterygiaceae.

We also examined under the SEM the papillose exostomes of *Actinodontium*, *Daltonia*, *Distichophyllidium*, and *Leskeodon* in an effort to understand their inter-relationship. Much to our surprise, the details of their peristomial designs are different and can be described in three types based on the size and thickening of each of the dorsal and ventral exostomial plates, the presence or absence of high trabeculae on both sides of the plate, and the alignment and composite nature of surface papillae (Figures 35–63). These three types are: the daltonioid, actinodontoid (lepidopiloid?), and distichophyllidioid. The exostome of Asiatic *Leskeodon* can be included under the daltonioid type. Clearly, this reinforces the view of Buck (1987) that it is phylogenetically incorrect to place all hookeriaceous taxa with papillose peristomes in a single separate family. We consider this as evidence that the character of exostomial papillosity has arisen independently at least three times in the family Hookeriaceae, perhaps more. Future work will probably show that papillose peristomes have also arisen at least twice in the related family Sematophyllaceae.

On the other hand, hookeriaceous taxa like *Calyptrochaeta*, *Callicostella*, and *Distichophyllum*, with cross-striolate exostomial teeth and with a distinct median gap, are relatively uniform in the details of their peristomial designs. The reported "striae" are actually distinctive plate-like extensions from the outer or dorsal exostomial layer forming a pile or stack between the well developed dorsal trabeculae (Figures 35, 38). They are termed "lamellulae" here for want of a technical term. They may or may not be studded with papillae.

Because the scope of our study is restricted to the Philippine

species and related taxa, the results do not provide us with an adequate basis for a new interpretation of the family organization. We are accepting, therefore, a broadly defined family in this treatment. We suspect that the tendency to subdivide the family results more from the richness of striking characteristics than from excessive phyletic diversity in the family.

For those who seek a homogenous or natural familial classification with a narrower family concept, we suggest that a narrower Hookeriaceae may contain only *Hookeria*. The segregated Callicostaceae of Crum (1984) and Buck (1987), at its best, would represent those elements with two costae distinct from the base, including *Bryodusenina* H. Robinson. The Daltoniaceae, at its best, represents the forms with a single costa or a costa branched above the base, including *Achrophyllum*, *Adelothecium*, and *Bryobrothera*. The present authors, do not accept the implication of other studies that the forms with single costae are primitive in the group. As suggested by Robinson (1975, 1986), all the strongly costate forms, both the single and double, are derived from basically short and doubly costate forms of the type seen in the related families Ptychomniaceae, Leucomiaceae, and Sematophyllaceae. Some of the genera with single costae such as *Calyptrochaeta* and *Achrophyllum* betray traces of their double-costate ancestry by the branching of their costae.

Most of the genera with the specialized isodiametric median leaf cells seem to fall within the daltoniaceous group of the family. Nevertheless, the characteristic, in combination with a contrasting border of narrow cells, is found in such callicostaceous genera as *Cyclodictyon* and in scattered genera elsewhere among the mosses, including some of the acrocarps like *Mnium* and *Tortula mniifolia* (Sullivant) Mitten. The character alone cannot be considered as evidence for or against close relationship. The highly specialized nature of the leaf cells in the daltoniaceous series, however, supports the specialized nature of the group within the Hookeriales.

Our revisionary study of Philippine taxa falls within the old familial limit circumscribed by Fleischer (1908) and Bartram (1939), excluding *Chaetomitrium* Dozy & Molkenboer and *Chaetomitriopsis* Fleischer. *Chaetomitrium*, *Chaetomitriopsis*, and *Dimorphocladon* Dixon (Dixon, 1922) are three related genera in the Hookeriaceae, sensu lato, which occupy a relatively isolated position. Their discordant features are the narrowly oblong to vermiform, often prorate leaf cells, much enlarged perichaetial leaves, and a hypnaceous peristome. We agree with Buck (1987) in transferring these three genera to Hypnaceae sensu Nishimura et al. (1984), or at least into some family closer to the Hypnaceae. However, in order to account for all the taxa treated in the Hookeriaceae by Bartram (1939), we include a tentative key to the revised Philippine species of *Chaetomitrium*.

In 1939, Bartram described some 30 species and 10 genera of Philippine Hookeriaceae. In the over 50 years since, additional collections made by local and foreign botanists have increased the number of known taxa significantly. The present revision

treats a total of 53 species distributed in 12 genera, including *Chaetomitrium*. Eleven new records of Philippine mosses, ten new synonyms, five new combinations, and one new name, *Chaetomitrium schofieldii*, are reported. Two taxa, *Chaetomitrium seriatum* Brotherus ex Bartram and *Eriopus microblastus* Brotherus, are resurrected from synonymy, and *Distichophyllum elmeri* Brotherus is resurrected as a variety of *D. nigricaula*. Lectotypes are selected for *Calyptrochaeta ramosa*, *Distichophyllum brevicuspis*, *D. nigricaula*, and *Hookeriopsis wichurae*, and for two of the names in synonymy, *Distichophyllum gracilicaule* and *Lepidopilum sumatranum*. In addition, *Daltonia armata* is reported new to Sumatra, and, *Achrophyllum dentatum* and *Distichophyllum subnigricaula* as new records for New Guinea.

Excluding *Chaetomitrium*, only three species, or about 5%, of the Philippine species of Hookeriaceae are locally endemic. They are *Calyptrochaeta microblasta* (Brotherus) Tan & Robinson, *Distichophyllum santosii* Bartram, and *Leskeodon philippinensis* Brotherus.

The specimens cited in the text are limited to (1) types studied, (2) any changes in the published identification of specimens, and (3) recent collections not listed in Bartram (1939) and which represent new locality records for the country. In the case of foreign collection citations, they represent significant range extensions in the region. Type specimens of several species from adjacent areas were studied for possible new synonyms.

ABBREVIATIONS.—Abbreviations used to indicate the location of specimens examined in this study are as follows:

B	Botanisches Museum, Berlin-Dahlem, Germany
BISH	Bernice P. Bishop Museum, Honolulu, Hawaii
BM	British Museum (Natural History)
BO	Herbarium Bogoriense, Bogor, Indonesia
BR	Jardin Botanique de l'Etat, Bruxelles, Belgium
CAHP	University of the Philippines at Los Baños
FH	Farlow Herbarium at Harvard University, Cambridge,

	Massachusetts (includes the Bartram and Fleisher Herbariums)
G	Conservatoire de Jardin botaniques, Geneva, Switzerland
H	Botanical Museum, University of Helsinki, Finland
H-BR	Helsinki: Brotherus Herbarium (part of the Botanical Museum, University of Helsinki, Finland)
HIRO	Botanical Institute, Hiroshima University, Hiroshima, Japan
L	Rijksherbarium, Leiden, Netherlands
MICH	University of Michigan, Ann Arbor, Michigan
NICH	Hattori Botanical Laboratory, Nichinan, Japan
NY	New York Botanical Garden, N.Y., New York
PC	Laboratoire de Cryptogamie, Muséum National d'Histoire Naturelle, Paris, France
PNOC	Herbarium of the Philippine National Oil Corporation
U	Botanical Museum and Herbarium, Utrecht, Netherlands
US	United States National Herbarium, Smithsonian Institution, Washington, D.C.

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Family HOOKERIAACEAE

HOOKERIAACEAE Schimper, Corollarium Bryologiae Europaeae, 101, 1855.

Key to the Genera of Philippine Hookeriaceae

1. Leaf margins strongly erose or irregularly dentate *Achrophyllum*
 Leaf margins not strongly erose or dentate 2
2. Costa single, reaching at least half the leaf length 3
 Costae double, branched above the base, short, or lacking 6
3. Leaves scarcely complanate, isomorphous, oblong-lanceolate, lanceolate to lanceolate-linear *Daltonia*
 Leaves complanate, usually dimorphous, ovate-oblong, lingulate, obovate, or spatulate 4
4. Exostome teeth without median furrow, papillose *Leskeodon*
 Exostome teeth with median furrow, cross-striolate 5
5. Leaves without differentiated marginal cells, cells of lamina with strongly incrassate walls, sometimes mamilllose *Bryobrothera*
 Leaves usually with elongate marginal cells, cells of lamina with thin or scarcely thickened walls, not mamilllose *Distichophyllum*

6. Costae strong, reaching at least half the leaf length 7
Costae weak, short, or none 10
7. Leaf borders distinctly differentiated; leaf cells round to hexagonal, large, more than 30 μm in diameter *Cyclodictyon*
Leaf borders not or weakly differentiated; leaf cells oval, rhomboidal to elongate, longer than wide, less than 30 μm wide 8
8. Exostome teeth papillose *Actinodontium*
Exostome teeth cross-striolate 9
9. Costae reaching near the apex, strongly protruding abaxially *Callicostella*
Costae reaching only half the leaf length or less, not or weakly protruding abaxially *Hookeriopsis*
10. Leaf cells broadly oval-rhomboidal, large, more than 18 μm wide, very thin-walled *Hookeria*
Leaf cells narrowly rhomboidal, oblong, fusiform, elongate, or vermiform, less than 18 μm wide, firm-walled 11
11. Leaf borders distinctly differentiated; setae strongly spinose or hirsute *Calyptrochaeta*
Leaf borders not or weakly differentiated; setae smooth or papillose, at most scabrous 12
12. Leaves strongly divergent or deflexed (*Chaetomitriopsis*)
Leaves imbricate, complanate, at most erect-spreading (*Chaetomitrium*)

Genus *Achrophyllum*

Achrophyllum Vitt & Crosby, Bryologist, 75:174, 1972. [Type: *Hookeria quadrifaria* J.E. Smith (= *Achrophyllum quadrifarium* (J.E. Smith) Vitt & Crosby).]

The name, *Pterygophyllum* Bridel, is invalid having originally included the type species of the genus *Hookeria*. The name has been replaced by *Achrophyllum* (Crosby, 1972; Vitt and Crosby, 1972).

The main distribution centers of the genus are in the Southern Hemisphere with two species reaching Malesia: *A. javense* is widespread, while *A. dentatum* (Hooker f. & Wilson) Vitt & Crosby is reported here for New Guinea.

NOTE ON *Pterygophyllum novae-guineae*

Bartram (1961) described *Pterygophyllum novae-guineae* as a much more robust plant than *P. dentatum*, having longer leaves that are coarsely toothed above with multicellular teeth. However, the plant size and the leaf dentation of *Achrophyllum dentatum* are variable features noted by Sainsbury (1955) in New Zealand populations. In addition, our own examination of herbarium specimens of *Achrophyllum dentatum* from New Zealand, Australia, and Chile further shows that the length of the leaf costa and the shape of the leaves are equally variable. We think that the two species are best treated as synonyms. Thus, *A. dentatum* is reported here as new to New Guinea (= *Pterygophyllum novae-guineae*, syn. nov.).

Achrophyllum javense is also known from New Guinea. It differs from *A. dentatum* in having an acute to acuminate leaf apex and a much more strongly erose leaf margin. In *A.*

dentatum, the laminal cells are 45–60 μm in diameter, the leaf apices are mostly obtuse or rounded and the cells of the marginal teeth are 30–36(–60) μm in diameter.

SPECIMENS STUDIED.—PAPUA NEW GUINEA. Morobe District: Mt. Kaindi, vicinity of Wau, *Weber & McVean B-34871* (US, as *Pterygophyllum novae-guineae*). Western Highland: Wabag area, Sugarloaf Mt., *Robbins 2828* (holotype of *Pterygophyllum novae-guineae*, FH); *ibid*, *Hoogland & Schodde 7225* (FH).

Achrophyllum javense

Achrophyllum javense (Dixon ex Froehlich) Iwatsuki, Tan, & Touw, J. Hattori Bot. Lab, 44:149, 1978.

Pterygophyllum javense Dixon ex Froehlich, Ann. Naturh. Mus. Wien, 59:99, 1953. [Type: Java, im Urwalde Oben Tjibodas, leg. *Schiffner* (Cryptogam. Exsicc. Museo Hist. Natur. Vindobonensi 4372, isotype, US!)]

Plants tufted, sparingly branched. Stems to 6 cm tall and ~3 mm wide including the leaves. Stem cross-section with a layer of hyalodermis surrounding the thickened outer cortical cells, and a small central strand. Leaves moderately complanate, strongly contorted to crisped when dry, variable in size and shape. Lateral leaves mostly oblanceolate, occasionally ovate and lanceolate. Dorsal and ventral leaves ovate to oblong. Leaf apices acute to acuminate; unbordered leaf margins strongly and irregularly toothed, with several cells forming each of the tooth segments measuring to 75 μm long. Costa single, short, often branched above the base. Leaf cells round-hexagonal, 36–40 μm in diameter, smooth, thin-walled, slightly thickened at corners, becoming rectangular and elongate at base. Rhizoidal propagules formed from the leaf cells. Sporophytes not seen.

SPECIMENS STUDIED.—PHILIPPINES. Luzon: Mt. Pulo, *Jacob B 196* (B, L, NY); Mt. Data, *Nishimura 6725* (HIRO, US). Mindoro: Mt. Halcon, *Tan 87-095, 87-185* (CAHP). Mindanao: Mt. Apo, *Tan 82-232, 82-330* (CAHP); Mt. Hilong-Hilong, Cabadbaran, *Tan 84-403, 84-436* (CAHP).

REMARKS.—This is a species of humid and humic habitats in mossy forests. It was first reported for the country by Iwatsuki and Sharp (1968) from Mt. Data in northern Luzon. It is easily identified by its filmy leaves that have large leaf cells and an erose marginal dentation.

Genus *Actinodontium*

Actinodontium Schwaegrichen, Spec. Musc. Suppl., 2:75, 1826. [Type: *A. ascendens* Schwaegrichen.]

Key to the Philippine Species of *Actinodontium*:

- Leaves ovate to lanceolate, the apices acute to short acuminate; capsules ovoid-oblong, less than 2 mm long *A. ascendens*
 Leaves narrowly lanceolate, the apices long acuminate; capsules oblong-cylindric, more than 2 mm long *A. raphidostegum*

Actinodontium ascendens

FIGURES 47-50

Actinodontium ascendens Schwaegrichen, Spec. Musc. Suppl., 2(2):75, 1826. [Type: Java, sine loco, *Reinwardt s.n.* (G?), not seen.]

REMARKS.—Tixier (1978) reported this taxon as new to the Philippines based on a collection he made from the Benguet Highlands in northern Luzon. In the same article, he disputed Bartram's (1939) Philippine report of *A. raphidostegum* by remarking that the latter is a very small species found in shady forest habitats. All of the herbarium specimens of *Actinodontium* from the Benguet Highlands seen by us are *A. raphidostegum*, which grows as an epiphyte on the trunks of various vascular plant species in semi-open to openly disturbed environments such as roadsides and lawns. Efforts to relocate Tixier's collection have so far failed. An earlier record of *A. ascendens* in the Philippines (Williams, 1914) was corrected to *A. raphidostegum* by Bartram (1939).

Based on our field records and examination of herbarium specimens, the two species are actually of the same size range and both grow epiphytically on tree trunks in both primary and disturbed forests.

Actinodontium ascendens can be distinguished by its broadly acute leaf apices in wet condition, and also by the ovoid capsules. A good illustration of it can be found in Fleischer (1908, fig. 176). It is not uncommon in the Malesian region and is also known from Sri Lanka, Thailand, and Java. It is probably present in the Philippines, but because we have not seen a Philippine specimen, we remain uncertain about its presence.

This is a genus of small, epiphytic plants, very much like *Daltonia* in general habit. The leaves are silky yellow-green or dark-green, and densely cover the stem. They are doubly costate, but the costae do not protrude abaxially. The stem cross-section consists of a weakly differentiated epidermis enclosing a group of parenchyma cells. Often, a cluster of brown, thin-walled stem epidermal cells grows outward from the leaf insertion forming a pseudo-alar structure. The calyptra is mitrate and the base is laciniate instead of fringed with cilia. The erect capsule is without collenchymatous exothecial cells.

Two species have been reported from the Philippines; but one, *A. ascendens*, lacks a definitive herbarium record.

Actinodontium raphidostegum

Actinodontium raphidostegum (C. Müller) Bosch & Lacoste, Bryol. Jav., 2:37, 1862.

Hookeria raphidostega C. Müller, Syn., 2:677, 1851. [Type: Java, *Blume s.n.* (B, destroyed).]

Plants small, less than 2 cm tall, forming scanty tufts on trunks of trees, *Pandanus*, and bamboo culms. Stems simple or branched, densely covered by somewhat flexuose leaves, often with a purplish tinge. Leaves 2–2.5 mm long, shiny green, slightly shrunken when dry, erect-spreading when wet, oblong-lanceolate, gradually acuminate into a narrow point, the margins recurved, weakly serrulate near apex, otherwise entire. Costae double, long, more than half the length of the lamina. Leaf cells elongate-rhomboidal, (45–)51–135 μm long and 12–21 μm wide, thin-walled, becoming short-oval to hexagonal toward apex, narrower near margin, more rectangular and laxer at base. Perichaetial leaves small, lanceolate, acute to obtuse, ecostate. Perigonal leaves similar. Calyptra mitrate, laciniate at base. Setae short, about 5 mm long. Operculum rostrate. Capsules oblong-cylindric, to 3 mm long. Exothecial cells not collenchymatous, but thickened along the vertical walls. Exostome teeth papillose, with a distinct median zigzag line, opening outward when wet. Spores green, papillose.

SPECIMENS STUDIED.—PHILIPPINES. Luzon: Mt. Santo Tomas, *Tan s.n.*, 29–30 Nov, 1986 (CAHP); Baguio, MSAT campus, *Onraedt 84.P.10783* (CAHP); Imugan, Nueva Visaya, *Tan 84-13* (CAHP); Mt. Banahao, *Iwatsuki & Sharp 16453*, (NICH, CAHP). Mindoro: Mt. Halcon, *Tan 87-119* (CAHP). Mindanao: Mt. Apo, *Tan 82-261* (CAHP).

REMARKS.—This species is variable in the length of its leaf cells, leaf apices and capsules. Indeed, in some herbarium specimens the leaf apices are intermediate between acute and acuminate. The illustration of *A. ascendens* in Dozy and Molkenboer's *Bryologia Javanica* (1855–70) clearly shows a variation of leaf apices, ranging from broadly acute to short acuminate, like that of *A. rhabdostegum*. The two taxa may eventually prove to be synonymous.

Actinodontium rhabdostegum is widespread in the Malaysian region.

Genus *Bryobrothera*

Bryobrothera Thériot, Rev. Bryol., 47:26, 1920. [Type: *B. crenulata* (Brotherus & Paris) Thériot.]

The position of this monotypic genus has been shown to be with the Hookeriaceae by Norris and Robinson (1979). The latter authors have shown the geographical range to include Queensland, Australia, Fiji, the Solomon Islands, and the type locality, New Caledonia. The Philippine record is reported by Tan and Koponen (1989).

Bryobrothera crenulata

Bryobrothera crenulata (Brotherus & Paris) Thériot, Rev. Bryol., 47:26, 1920. *Mesochaete crenulata* Brotherus & Paris, Oefv. Finsk. Vet.-Soc. Foerh., 51:19, 1908. [Type: New Caledonia, Mt. Dzumac, *Le Rat s.n.* (H), not seen.] *Calomnion dixonii* Bartram, Bishop Mus. Occ. Pap., 11:9, 1936. [Types: Fiji, Viti Levu, near summit of Mt. Victoria, *Gillespie 4114* (holotype, BISH; isotype, FH), not seen.]

Plants small, mat-forming. Stems prostrate, complanate-foliate. Lateral leaves elliptical to oblong, 0.5–1.5 mm long, somewhat asymmetrical. Median and ventral leaves smaller, broadly oblong to obovate, symmetrical. Leaf apices broadly acute to obtuse; margins crenulate to weakly toothed above, entire below, without elongate cells. Costa single, percurrent or ending below the apex. Leaf cells mostly isodiametric, 10–12 μm , with thick walls, smooth to slightly mamilllose. Plants dioicous. Calyptra mitrate, plicate toward base, sparingly pilose. Setae 3–4 mm long, smooth. Operculum rostrate. Capsule horizontal to pendent, 0.8–1.2 mm long. Exothecial cells collenchymatous. Exostome teeth cross-striate with a distinct longitudinal median furrow.

SPECIMENS STUDIED.—PHILIPPINES. Mindanao: Mt. Hilong-Hilong, Cabadbaran, Agusan Norte Province, *Tan & Navarez*

84-520 (CAHP, H).

REMARKS.—The complanate and matted habit is rather distinctive for this species. In addition, the strong single costa and the unbordered leaves distinguish the species from most other members of the family. Because of the latter combination of characters, the species was placed in other families such as the Calomniaceae and Rhizogoniaceae before sporophytes were discovered (Norris and Robinson, 1979). Sporophytes are still known only from the Norris Queensland collection.

Recently, Akiyama (1988) reported *Calomnion complanatum* (Hooker f. & Wilson) Lindberg, a New Zealand endemic, from the island of Seram (Ceram) in Indonesia. Both the illustrations by Akiyama and the geography favor identification of the material as *Bryobrothera*. *Bryobrothera* has been mistaken for *Calomnion* before, and the two are similar in the strong costae and unbordered leaves. Nevertheless, the leaves of *C. complanatum* are markedly 3-ranked, its lateral leaves are oblong-lanceolate with sharply acute to shortly acuminate apices, and sporophytes, when present, are terminal. The leaves of *B. crenulata*, on the other hand, are not 3-ranked, the lateral leaves are oblong-elliptical, never lanceolate, its leaf apices are mostly obtuse, and sporophytes, when present, are lateral.

Genus *Callicostella*

Callicostella (C. Müller) Mitten, nom. cons., J. Linn. Soc. Bot. Suppl., 1:136, 1859. [Type: *C. papillata* (Montagne) Mitten.]

The generic name *Callicostella* has been shown to be a later synonym by Crosby (1975) who replaced it with an earlier name, *Schizomitrium* Bruch, Schimper, & Gumbel. However, the name *Callicostella*, which has long been in use, was proposed for conservation by Koponen and Isoviita (1984). The proposal was approved at the 1987 Berlin Congress.

The genus is characterized by the presence of two strong and abaxially protruding leaf costae. The calyptra is notable in being large, covering the entire capsule, strongly plicate and lacinate at base, but without a hairy basal fringe. The calyptra proper is only sparsely hairy, being scabrous near the tip. The exostome teeth are typically hookeriaceous with a cross-striate pattern and a distinct median furrow.

There are two known Philippine species of *Callicostella* in this largely neotropical genus. Buck (1987) placed *Callicostella* with *Callicosta* and other Hookeriaceae having a double costa in the family *Callicostaceae* of Crum (1984).

Key to the Philippine Species of *Callicostella*

- Leaf cells papillose *C. papillata*
 Leaf cells smooth *C. prabaktiana*

Callicostella papillata

Callicostella papillata (Montagne) Mitten, J. Linn. Soc. Bot., Suppl. 1:136, 1859.

Hookeria papillata Montagne, London J. Bot., 3:632, 1844. [Type: Java, Prov. Buitenzorg, *Miquel s.n.* (U), not seen.]

Plants mat-forming, light yellow to dark green in color. Main stems long, creeping, pinnately to subpinnately branched, the secondary branches 2–5 cm long and less than 1 mm wide including leaves. Stem cross-section without a central strand. Leaves complanate, somewhat flexuose, two strong costae forming two plicae on the leaf blade when dry, ovate to oblong-lanceolate, 1.0–1.5 mm long, broadly acute to abruptly acuminate. Leaf costae reaching near the apex, protruding abaxially, the costal surfaces smooth to strongly toothed near the distal end, at times lamellate. Leaf margins plain, without a clearly differentiated border, irregularly toothed to lower half, at times serrulate. Leaf cells hexagonal-oval, shortly oblong to rhomboidal, 5–15 μm long and 6–9 μm wide, angular, thin to thick-walled, but not pitted, mostly with a single papilla over the lumen, cells elongate and smooth near the base; the marginal leaf cells shorter, projecting apically. Perichaetial leaves mostly lanceolate, slightly smaller than the vegetative leaves; the margins serrate. Synoicous or autoicous. Setae smooth below, weakly papillose above, 1–2 cm long. Capsules ovoid-cylindric, horizontal to inclined. Exothecial cells colenchymatous. Exostomes cross-striate with a large median furrow.

SPECIMENS STUDIED.—PHILIPPINES. Luzon: Lamao River, Bataan Prov., *Williams 852* (US); National Botanic Garden, Real, Quezon Prov., *Tan 81-455* (CAHP); Tignaong, Tayabas Prov., *Leiberg 1230* (US). Panay: Jamindan, Capiz Prov., *Ramos & Edaño* (Bur. Sci.) *31226, 31090* (US). Mindanao: District of Zamboanga, *Merrill 8359* (US); TIMEX logging area west of Ipil, Mt. Silligain, Zamboanga Prov., *Hale & Banaag 25306* (US).

REMARKS.—Although this species is noted for its polymorphism, few have described the observed variations in detail. In general, the ventral leaves, which are in direct contact with the moist substrate, tend to be more lanceolate and long-acuminate than the dorsal and lateral leaves. Also, the cells of the ventral leaves become more rhomboidal-oblong in outline with only thin walls. Often the single papilla over the cell lumen is weakly developed and may be absent from the cells of many ventral leaves. Plants having only a few papillose leaf cells are often incorrectly named *C. prabaktiana*. The marginal teeth of the leaves are equally variable. Each tooth segment may be formed by one to many cells, often becoming bigeminate to trigeminate apically. The abaxial surface of the leaf costa can vary from smooth to spinose or even lamellate. These variable characters appear to be unreliable bases for specific as well as infra-specific classification.

As presently interpreted, *C. papillata* is widespread in the paleotropics. It is very common in Philippine lowland rainforests.

Callicostella prabaktiana

Callicostella prabaktiana (C. Müller) Bosch & Lacoste, Bryol. Jav., 2:40, 1862.

Hookeria prabaktiana C. Müller, Syn., 2:678, 1851. [Type: Java, Mt. Prabakti, *Zollinger 3503* (B), destroyed.]

Plants like *C. papillata* in general habit. The leaf cells more oval-oblong, smooth or slightly mamillate, with thick walls.

SPECIMENS STUDIED.—PHILIPPINES. Luzon: Bicol National Park, Camarines Sur Prov., *Tan 74-413* (US, CAHP). Polillo: *Leiberg 1224* (US).

REMARKS.—Contrary to the claim of Bartram (1939), this is actually a rare or uncommon species in the Philippines. We have seen only three undoubted collections from the region. Except for the smooth leaf cells, it resembles the preceding species in most details. As in *C. papillata*, the leaf shapes, marginal dentation of the leaf, and the abaxial surface ornamentation of leaf costae of *C. prabaktiana* are variable characters.

One Philippine specimen of *C. prabaktiana* with lamellate leaf costae (*Leiberg 1224*, US) was named *C. beccariana* (Hampe) Jaeger by Brotherus. However, this plant has some leaves with smooth to spinose costae.

Most specimens of *C. prabaktiana* have been collected from very wet environments, a condition that appears to cause the partial disappearance of leaf papillae in *C. papillata*. When more collections of these two species are studied and analyzed in the light of a better understanding of the environmental effects on the morphogenesis of moss plant organs, specially the leaf papilla formation, the two may prove to be conspecific.

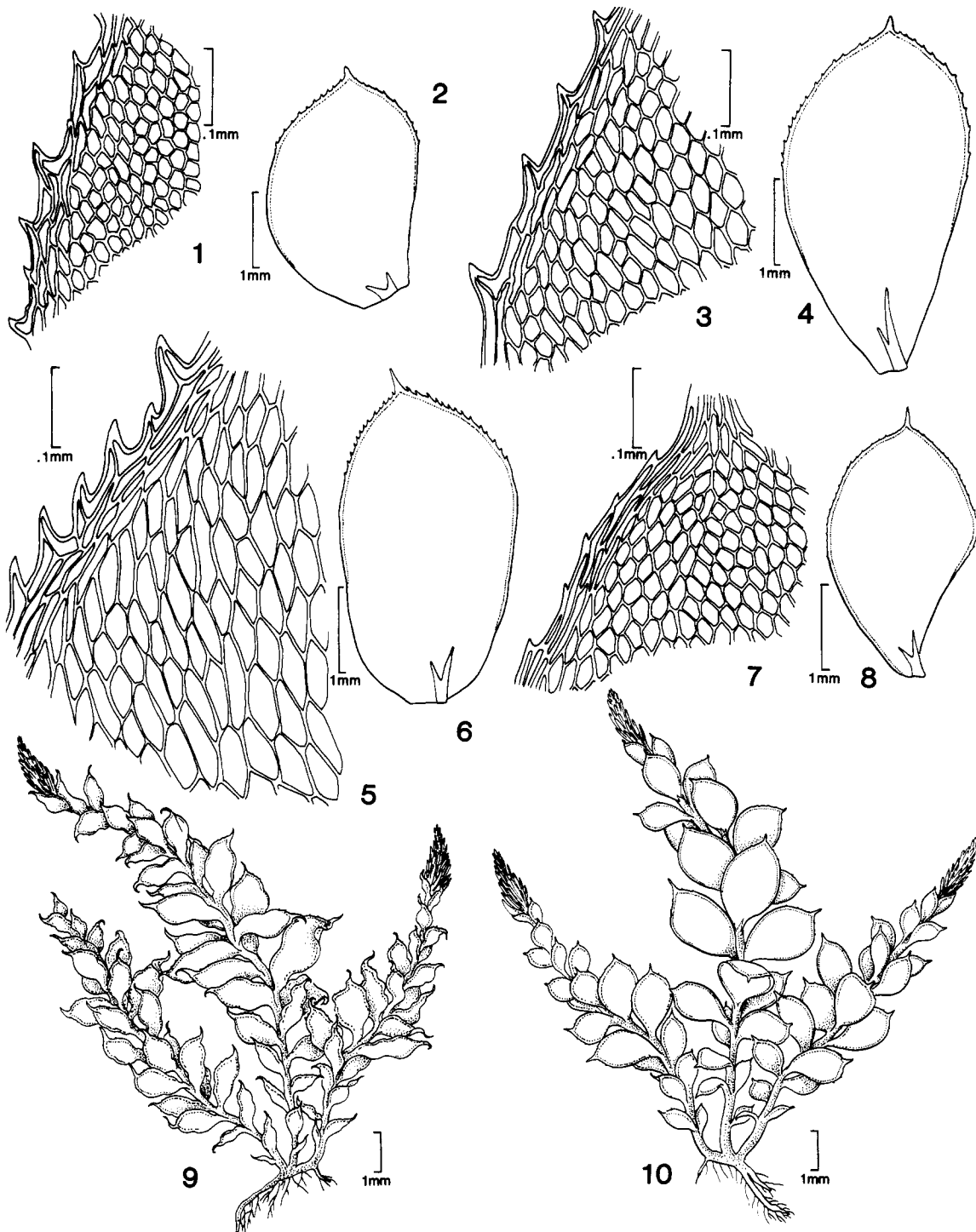
Callicostella prabaktiana is known also from Java, Borneo, peninsular Malaya, and Indochina.

Genus *Calyptrochaeta*

Calyptrochaeta Desvaux, Mém. Soc. Linn. Paris, 3:226, 1825. [Type: *Leskea cristata* Hedwig (= *Calyptrochaeta cristata* (Hedwig) Desvaux).]

The generic name *Eriopus* Bridel has been found to be illegitimate (Margadant 1959; Crosby 1974), and has been replaced by *Calyptrochaeta*. The genus is characterized by a complanate and heterophyllous foliation, often with attenuated branches bearing numerous filiform propagules in the leaf axils, and a spinose or hirsute seta.

In the Philippines, species concepts have traditionally been based on variation in a few gametophytic characters such as the leaf border, leaf cell morphology, and the leaf outline. As the plants infrequently produce sporophytes, reproduction usually occurs by means of the asexual propagules on the stems. It is possible that the various species treated here may represent clonally perpetuated microspecies with a fixed suite of characters. Until breeding studies and transplanting experiments are conducted for the genus, we are accepting the narrowly defined species concepts proposed by various authors.



FIGURES 1-10.—*Calypstrochaeta*. 1, 2, *C. parviretis* (Java: Gedeh, *Fleischer*, type, FH): 1, upper leaf cells; 2, whole leaf. 3, 4, *C. ramosa* (Philippines: Luzon, Mt. Banahao, *Merrill 7523*, type of *Eriopus flaccidus*, FH): 3, upper leaf cells; 4, whole leaf. 5, 6, *C. remotifolia* (Java: Tjiburnum, *Fleischer*, FH): 5, upper leaf cells; 6, whole leaf. 7-10, *C. microblasta* (Philippines: Sibuyan Is., Mt. Giting-Giting, *Tan & Hernaez 87-447*, US): 7, upper leaf cells; 8, whole leaf; 9, plant, dry; 10, plant, wet.

Key to the Philippine Species of *Calyptrochaeta*

1. Plants large, more than 4 cm long; lateral leaves oblong-lanceolate, flaccid and strongly wrinkled when dry 2
 Plants small to medium size, less than 4 cm long; lateral leaves ovate-elliptic, firm or slightly wrinkled when dry 4
2. Upper leaf cells mostly oblong, elliptic to fusiform, ratio of length to width (3-5:1), frequently thin-walled; leaf borders, especially near the apex, consisting of (2)3-4 rows of elongate-linear cells; perichaetial leaves with blunt to short acute apices *C. remotifolia*
 Upper leaf cells mostly oval, rhomboidal, or hexagonal, ratio of length to width (1-3:1), thin to moderately thick-walled with thickened corners; leaf borders, especially near apex, consisting of 2(-3) rows of elongate-linear cells; perichaetial leaves with acuminate or abruptly mucronate apices 3
3. Upper leaf cells mostly hexagonal to oval, often collenchymatous; marginal teeth of leaf weak to moderately strong *C. parviretis*
 Upper leaf cells mostly rhomboidal, not collenchymatous; marginal teeth of leaf strong to very strong *C. ramosa*
4. Lateral leaves ovate to broadly elliptic; upper leaf cells collenchymatous; the upper leaf borders at most with 2 rows of elongated cells; filiform propagules borne in leaf axils *C. parviretis*
 Lateral leaves mostly obovate-elliptic to broadly oblanceolate; upper leaf cells not collenchymatous; upper leaf border with (3-)4 rows of linear cells; filiform propagules borne terminally on attenuate branches with small, modified leaves *C. microblasta*

***Calyptrochaeta microblasta* (Brotherus) Tan & Robinson, new combination**

FIGURES 7-10

Eriopus microblastus Brotherus, Philipp. J. Sci., 8C (Bot.):82, 1913, basionym. [Types: Philippines, Luzon, Mt. Banahao, *Robinson Bur. Sci. 9813* (holotype, H-BR!; isotypes, FH!, NY!).]

Plants small to medium size, tuft forming. Stems mostly branched at base, less than 4 cm tall, laxly foliate. Attenuate propaguliferous branches often naked or with very small leaves. Leaves complanate, slightly wrinkled when dry. Lateral leaves obovate to elliptic, slightly asymmetrical at base, strongly cuspidate, 2-3 mm long and 1-1.5 mm wide, the margins serrate to serrulate, with 3-4 rows of linear cells all around. Costae double, short. Laminal cells broadly rhomboidal to hexagonal, becoming laxer and rectangular near base. Dorsal and ventral leaves variable in shape, ovate to lanceolate, smaller in size; areolation and marginal serration similar to lateral leaves. Perichaetial leaves much reduced in size, with long-acuminate apices. Setae mostly appearing terminal on branches, 4-6 mm long, very spinose. Operculum conic. Capsules ovoid, 1 mm long.

SPECIMENS STUDIED.—PHILIPPINES. Luzon: Mt. Babatuging, Cagayan Prov., *Edaño* (Bur. Sci.) 3335, det. by Dixon as *Eriopus propagulifer*, in sched. (US, FH). Sibuyan Island: Mt. Giting-Giting, *Tan & Hernaez 87-447* (CAHP, US). Panay Island: Antique Prov., Mt. Madyaas, *M. Price s.n.*, Jan 15-16,

1987 (CAHP). Negros: Cuernos Mt., *Palmore 2843* (FH); *ibid*, *Magdamo 23* (FH). Mindanao: Mt. Hilong-Hilong, Cabadbaran, Agusan Prov., *Tan & Navarez 84-471, proparte* (CAHP).

REMARKS.—*Calyptrochaeta microblasta* was considered a synonym of *C. parviretis* by Bartram (1939). The species, however, can be distinguished from all other Philippine species by the following characters: (1) plant size small, with a lax foliation and a firm leaf texture that gives the plant the aspect of a species of *Epipterygium*; (2) strong leaf borders, especially near the apex, consisting of 3-4 rows of linear cells; (3) short upper leaf cells as in *C. parviretis*; (4) leaf apices to 450 µm long, consistently longer than all other species of Philippine *Calyptrochaeta*.

In addition, the presence of a nearly naked mass of filiform propagules borne terminally on attenuated branches is unusual and is known only from a few other taxa in the family (Allen, 1987b).

Calyptrochaeta microblasta is a Philippine endemic (Brotherus, 1913). It has been collected from several islands in the country, mostly from limestone areas.

Calyptrochaeta parviretis

FIGURES 1, 2

Calyptrochaeta parviretis (Fleischer) Iwatsuki, Tan & Touw, J. Hattori Bot. Lab., 44:150, 1978.
Eriopus parviretis Fleischer, Musci Fl. Buitenzorg, 3:1008, 1908. [Type: West

Java, Pangerango, Kandang Badak, *Fleischer s.n.* (FH).]

Plants large, tuft-forming. Main stem long, often creeping, secondary stems complanately foliate, 4–5 cm tall, erect or inclined, branched, often attenuate at tip with bundles of brown, filiform propagules borne in the leaf axils. Stem cross-section with weakly differentiated central strand. Lateral leaves wrinkled when dry, at times flat, broadly ovate to elliptic, asymmetrical, 3 mm long and 2 mm wide, cuspidate or shortly acuminate. Costae double, very short. Leaf border distinct, toothed near apex, consisting of mostly 2 rows of elongate cells. Upper leaf cells mostly oval to short rhomboidal, 30–45(75) μm long and 12–18 μm wide, thickened at corners, becoming laxer and rectangular near base. Dorsal and ventral leaves smaller, mostly broadly ovate, the leaf border less serrulate. Dioicous. Perichaetial leaves small, lanceolate, about 1 mm long, acuminate, ecostate. Calyptra hairy, lacinate at base. Seta 5–6 mm long, spinose. Capsule erect or inclined, ovoid. Exostome teeth cross-striate, with median furrow.

SPECIMENS STUDIED.—PHILIPPINES. Mindoro: Mt. Halcon, *Tan 87-447* (CAHP). INDONESIA. Celebes: Soputan Mt., *Alston 15921* (FH).

REMARKS.—This species is often confused with *C. remotifolia*. The latter is a bigger plant with leafy stems more than 4 mm wide. The upper leaf cells of *C. parviretis* are shorter, often collenchymatous, and the leaf border consists of 2(3) rows of elongated cells. *Calyptrochaeta parviretis* can also be difficult to separate from *C. ramosa*. The latter, however, is a large plant similar in size to *C. remotifolia*.

Calyptrochaeta parviretis is a widespread species in the Malesian region.

Calyptrochaeta ramosa (Fleischer) Tan & Robinson, new combination

FIGURES 3, 4, 35–38

Eriopus ramosus Fleischer, Musci Fl. Buitenzorg, 3:1007, 1908, basionym. [Types: West Java, Tjibeureum, am Gedeh, Fleischer s.n. (lectotype, with sporophyte, FH!; isolectotype H-BR!); am Kandang-Badak, *Fleischer s.n.* (syntype, without sporophyte, FH!).]

Cyathophorum limbatulum Renauld & Cardot, Rev. Bryol., 23:108, 1896, syn. nov. [Type: Java, Tjiboda, *Massart s.n.*, 1856 (isotype, FH!).]

Eriopus flaccidus Brother, Philipp. J. Sci., 13C (Bot.):213, 1918, syn. nov. [Types: Philippines, Luzon, Mt. Banahao, *Merrill 7523* (holotype, H-BR!; isotypes, NY1, FH!).]

Plants as large or larger than *C. remotifolia*, some secondary stems to 10 cm tall and 4–5 mm wide. Leaf shape and areolation like *C. remotifolia*, except the border with only 2(–3) rows of elongate cells and the perichaetial leaves with acuminate apices. Perigonal leaves like the perichaetial leaves, but with the marginal borders less defined. Sporophyte as in *C. parviretis*.

SPECIMENS STUDIED.—PHILIPPINES. Luzon: Mt. Pulog, *Tan 82-149* (CAHP); Mt. Banahao, *Merrill 7523* (FH).

REMARKS.—This species apparently differs from *C. remotifolia* in having narrower leaf borders and acuminate perichae-

tial leaves. The upper leaf cells, measuring 36–90 μm long and 15–24 μm wide, are intermediate between those of *C. parviretis* and *C. remotifolia*. In the protologue, Fleischer (1908) compared *C. ramosa* to *C. remotifolia*. However, it is more similar to *C. parviretis*, both in terms of leaf areolation and the acuminate perichaetial leaf morphology.

The illustration and type description of *Eriopus spinosus* (Noguchi, 1937) from Taiwan is probably a juvenile form of *C. ramosa*.

Eriopus flaccidus was described by Brotherus (1918) as a more slender plant with flaccid leaves and shortly spinose setae in comparison with *C. ramosa*. However, Bartram (1939) compared it to *C. remotifolia* and stated that the differences between the two taxa are hardly characters of taxonomic importance for the genus. We concur with his observation that the name is a synonym, but we consider it to be a synonym of *C. ramosa*. *Eriopus flaccidus* and *Calyptrochaeta ramosa* both have similar narrow leaf borders consisting of 2(–3) rows of elongate cells, and both have acuminate perichaetial leaves.

The type specimen of *Cyathophorum limbatulum* was studied. It is a juvenile plant of *Calyptrochaeta ramosa*. The characters used by Fleischer (1908) in maintaining the species are untenable.

This formerly Javan species is here reported as new to the Philippines.

Calyptrochaeta remotifolia

FIGURES 5, 6

Calyptrochaeta remotifolia (C. Müller) Iwatsuki, Tan, & Touw, J. Hattori Bot. Lab., 44:150, 1978.

Eriopus remotifolius C. Müller, Bot. Zeit., 5:828, 1847. [Type: Java, Mt. Gédé, *Reinwardt s.n.* (B, destroyed; L?).]

Plants large, as in *C. ramosa*, secondary stems to 5–6 mm tall. Lateral leaves oblong to oblanceolate, asymmetrical, wrinkled when dry. Leaf margins strongly toothed, with (3)4 rows of linear cells near the apex. Costae double, short. Upper leaf cells rhomboidal to fusiform, (90)105–126(150) μm long and 21–30 μm wide. Dorsal and ventral leaves variable, mostly lanceolate or elliptic, the marginal teeth less strong. Perichaetial leaves with blunt or round apices, occasionally shortly acute. Calyptra and capsule as in *C. parviretis*.

SPECIMENS STUDIED.—PHILIPPINES. Luzon: Mt. Pulog, *Tan 75-154* (CAHP); Mt. Banahao, *Tan 84-99* (CAHP). Negros: Mt. Canlaon, *Iwatsuki & Sharp* (NICH 263395). INDONESIA. Sumatra: Brastagi, *Holtum 15488* (US). JAVA. Tjiburnum, *Fleischer* (FH).

REMARKS.—Among its local congeners, this species and *C. parviretis* are commonly seen in mossy forests from mid- to high altitudes (~500–2500 m). Past circumscriptions of the two species have emphasized the size and shape of the upper leaf cells, which vary greatly in lateral, dorsal, and ventral leaves from the same plant. The use of the leaf cell size should be confined only to mature lateral leaves. We found the width of the leaf border also a reliable diagnostic character. The

perichaetial leaf apices of both taxa which were nicely illustrated by Fleischer (1908), are another useful character to distinguish the two taxa.

Calypstrochaeta remotifolia may prove difficult to separate from *C. ramosa*. The latter has, in general, shorter leaf cells in the upper half of the leaf and narrower leaf borders. Also, the perichaetial leaves of *C. ramosa* have acuminate apices, which are unlike the blunt perichaetial leaves of *C. remotifolia*.

Genus *Cyclodictyon*

Cyclodictyon Mitten, J. Linn. Soc. Bot., 7:163, 1864. [Type: *C. laetevirens* (Hooker & Taylor) Mitten.]

This genus is distinctive in having strong, double costae, a clearly differentiated leaf border, and lax leaf cells that are large, round to hexagonal, and smooth. It is largely a neotropical taxon with only one species represented in the Philippines.

Cyclodictyon blumeanum

Cyclodictyon blumeanum (C. Müller) O. Kuntze, Rev. Gen. Pl., 2:835, 1891. *Hookeria blumeana* C. Müller, Syn., 2:676, 1851. [Type: Java, *Blume s.n.* (B, destroyed).]

Plants mat-forming, stems creeping, irregularly branched, branches to 1.5 cm long and 1.5–2 mm wide including the leaves, light green in color. Leaves complanately arranged, slightly flexuose when dry, ovate to oblong-lanceolate, 1–1.5 mm long and about 1 mm wide, broadly acute to acuminate. The leaf margins plain, entire below, slightly toothed above near the apex. The leaf borders narrow, with 2 rows of linear cells. Leaf cells large, (36–)45–60 µm wide, smooth, round-hexagonal above, becoming rectangular below near base. Autoicous. Calyptra naked, mitrate, lacinate at base. Setae to 2 cm long. Capsules ovoid-oblong, horizontal. Exostome teeth transversely striolate, with a wide median gap.

SPECIMENS STUDIED.—PHILIPPINES. Luzon: Mt. Data, *Nishimura 6721* (HIRO, US); Mt. Makiling, *Nishimura 6967* (HIRO, US).

REMARKS.—*Cyclodictyon blumeanum* is a widespread species in the Philippines preferring humid and shaded places such as creek banks and wet cliff faces. Under an ordinary 10× field lens, the flexuose leaves (in dry state) exhibit the soft texture

and also conspicuous net-like leaf cell areolation also found in *Hookeria* and *Leskeodon*. The distinctive double costae forming two deep plicae on the leaf blade will distinguish this taxon from *Hookeria* or *Leskeodon*. A beautiful illustration of this species can be found in Mohamed and Damanhuri-Mohamed (1986).

This species is widespread in Southeast Asia and the Pacific Islands.

Genus *Daltonia*

Daltonia Hooker & Taylor, Musci Brit., 80, 1818, nom. cons. [Type: *D. splachnoides* (J.E. Smith) Hooker & Taylor.]

Daltonia is a conserved generic name with a complicated nomenclatural history (Crosby, 1968). Having bordered leaves with a single costa, it bears a resemblance to *Distichophyllum*. However, the two genera are different in the degree of homogeneity of leaf cells as seen from the apex to the base. In *Daltonia*, only the proximal basal leaf cells are different in shape and larger in size than the rest of the laminal cells, while in *Distichophyllum*, the lower half of the leaf consists of enlarged rectangular-elongate cells that are morphologically different from the round-hexagonal upper leaf cells. Overall, the leaves of *Daltonia* also are narrower and more erect-spreading than the leaves of *Distichophyllum*.

In addition, the exostome teeth on the outer surface of *Daltonia* are papillose while those of *Distichophyllum* are strongly cross-striated.

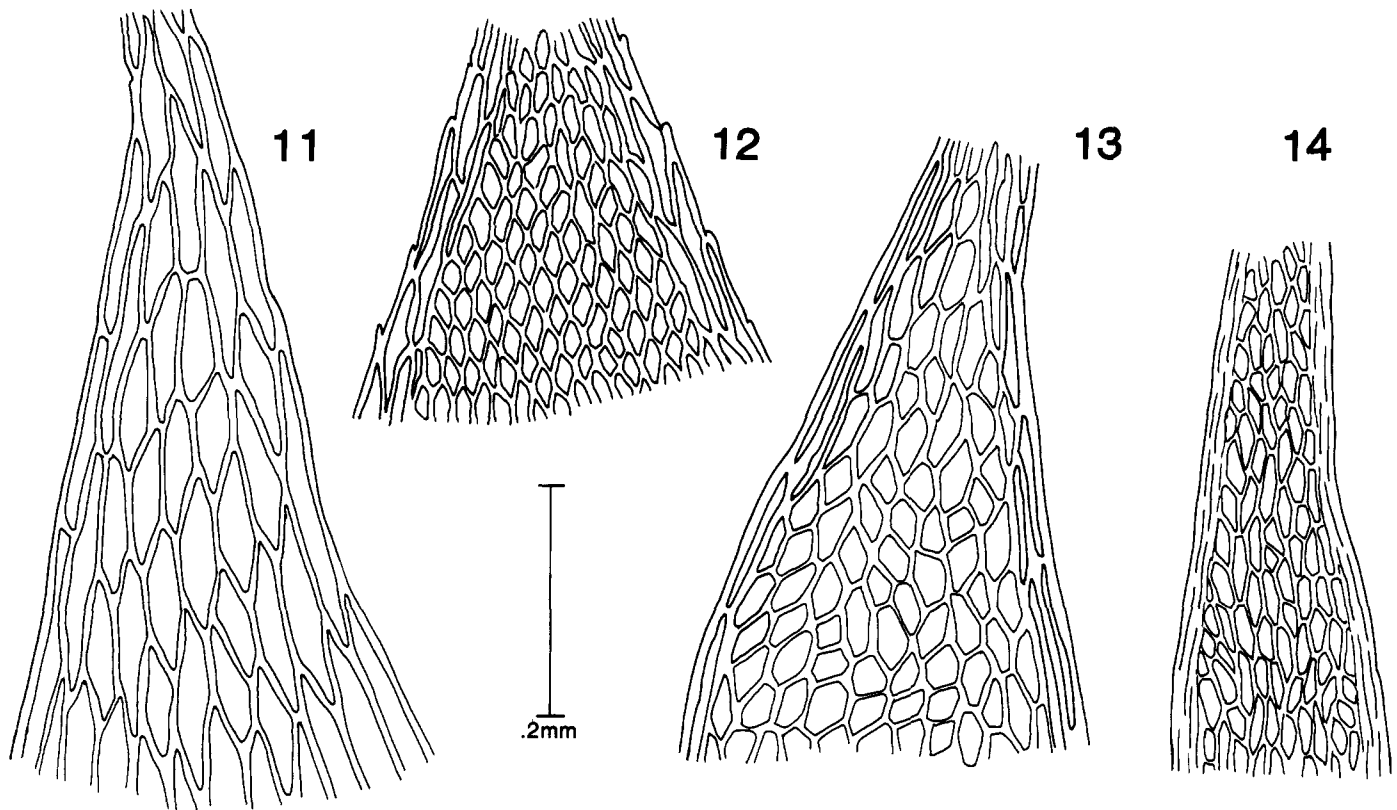
Daltonia, like *Actinodontium*, develops a bulging group of colored, thin-walled, pseudo-alar cells at the leaf insertion that are of stem origin. This feature is not well developed in *Distichophyllum*.

The New World members of the genus have been revised by Bartram (1931) who considered the perigonal/perichaetial leaves, the peristome, the operculum, and the calyptra to be fairly stable characters, not useful for species delineation. In the Philippines, this also is true and the species are separated mainly on vegetative leaf characters.

There are four epiphytic species of *Daltonia* known from the Philippines. Their small size and tendency to grow in sparse patches probably contributes to the small number of collections deposited in various herbaria.

Key to the Philippine Species of *Daltonia*

1. Leaf apices aristate or abruptly mucronate 2
 Leaf apices acute to acuminate 3
2. Upper leaf cells large, more than 30 µm long; setae strongly tuberculate-spinose above *D. armata*
 Upper leaf cells small, less than 30 µm long; seta scabrous above *D. aristifolia*
3. Leaves strongly twisted or contorted when dry, oblong-lanceolate, the margins plain, the apices acute *D. contorta*
 Leaves slightly flexuose when dry, narrowly lanceolate to linear, the margins recurved, the apices acuminate *D. angustifolia*



FIGURES 11-14.—*Daltonia* upper leaf cells: 11, *D. armata* (Philippines: Zamboanga, Dansalan, Zwickey 638, FH); 12, *D. contorta* (Philippines: Baguio, Williams 1666, US); 13, *D. aristifolia* (New Guinea: Robbins 2797a, B); 14, *D. angustifolia* (Philippines: Mt. Canlaon, Merrill 6813, US).

Daltonia angustifolia

FIGURE 14

Daltonia angustifolia Dozy & Molkenboer, Ann. Sci. Nat. Bot., sér. 3, 2:302, 1844. [Type: Borneo, sine loco, *Korthals s.n.* (L), not seen.]

Daltonia revoluta Brotherus, Philipp. J. Sci., 5C (Bot.):156, 1910. [Type: Philippines, Luzon, Mt. Pulog, Curran, Merritt & Zschokke Bur. Sci. 16405 (isotype, NY).]

Plants small, yellowish green, tuft forming. Stems simple or branched, without central strand, 5-10 mm tall. Leaves crowded, flexuose when dry, erecto-patent when moist, 2-3 mm long, narrowly lanceolate to linear, with a well-differentiated border of 2-3(4) rows of linear cells, the margins entire, strongly recurved on both sides. Costa single, strong, ending some distance below the apex. Leaf cells oval to narrowly rhomboidal and short fusiform, 21-30 μm long and 4-6 μm wide, slightly thick-walled, becoming rectangular and lax only at base. Synoicous. Perichaetial leaves shorter and narrower. Calyptra strongly fringed with long hairs at base, covering only the operculum. Setae 5-10 mm long, scabrous in

the upper half. Capsules ovoid, erect to inclined, 1 mm long; the exothecial cells collenchymatous. Exostome teeth reflexed when wet, papillose throughout; endostomial segments narrowly elongate, papillose throughout.

SPECIMENS STUDIED.—PHILIPPINES. Luzon: Mt. Pulog, Tan 82-200 (CAHP); Mt. Data, Nishimura 6788, 6796 (HIRO, US); Baguio, Williams 1665 (US). Mindoro Is.: Mt. Halcon, Tan 87-181 (CAHP). Negros: Mt. Canlaon, Merrill 6813 (US). Mindanao: Mt. Apo, Tan 82-270 (CAHP).

REMARKS.—Widespread in Southeast Asia and Australasia, this species is best distinguished by its long-acuminate leaf apices and recurved leaf margins. The margins of *D. contorta* are plain. The broad basal leaf border of *D. angustifolia* is not as abruptly differentiated as in *D. contorta*. In the former, the basal leaf border merges imperceptibly into the adjacent leaf cells. Several varieties have been treated by Fleischer (1908), Bartram (1939) and Sainsbury (1955). Considering the great variation of vegetative characters seen in the few collections available for study, we have refrained from making comments on the infraspecific taxa.

Daltonia aristifolia

FIGURE 13

Daltonia aristifolia Renaud & Cardot, Rev. Bryol., 23:105, 1896. [Type: Java, Tjibodas, Massart inter 1395 (BR?), not seen.]

Plants nearly of the same size as in *D. angustifolia*. Leaves also narrowly lanceolate, but with long, aristate apices. Costae reaching $2/5-1/2$ of the leaf length. Leaf borders clearly differentiated, reaching the apex, entire, the margins plane or recurved. Leaf cells of somewhat irregular shapes, mostly oval-hexagonal, mixed with short oblong, rhomboidal to fusiform ones, (9-)15-30(-60) μm long and 6-9 μm wide, thin-walled, becoming more or less rectangular at leaf base. Autoicous. Sporophytes as in *D. angustifolia*, but exothelial cells thin-walled, slightly collenchymatous.

SPECIMENS STUDIED.—PHILIPPINES. Mindanao: Mt. Apo, Tan & Aguila 82-230 (CAHP). NEW GUINEA: Robbins 2797a (B). SRI LANKA: Hübschmann s.n. (B).

REMARKS.—This species is distinctive in having leaves with long hairpoints and comparatively small cells. Some forms of *D. angustifolia* develop unusually long-acuminate leaf apices and may key to *D. aristifolia*. The arista of *D. aristifolia*, however, is made up of several thick-walled, pitted, linear cells, similar to the leaf border cells. In *D. angustifolia*, the long leaf apex consists of cells that are not different from other upper leaf cells.

Daltonia baldwinii Brothrus from Hawaii has similar long aristate leaf tips, but the leaf cells are longer than those of *D. aristifolia*. The leaf costa of the former also reaches $2/3$ of the leaf length.

Daltonia aristifolia is a widespread species in tropical Asia. Its presence in the Philippines was first reported by Tan and Iwatsuki (1983).

Daltonia armata

FIGURE 11

Daltonia armata Bartram, Farlowia, 1:508, 1944. [Type: Philippines, Mindanao, Sacred Mountain, Lanao, Zwickey 638 (holotype, FH!).]

Plants small, as in *D. angustifolia*. Stems to 10 mm tall. Leaves flexuous when dry, narrowly lanceolate, gradually becoming aristate, or oblong-lingulate, 4 mm long, blades slightly folded at the lower half. Leaf costa reaching $2/3$ the leaf length. Leaf borders weakly differentiated, with 1-2 rows of linear cells, the margins plane above, entire, and narrowly recurved below. Leaf cells oblong-fusiform above, 54-75 μm long and 12-16 μm wide, thin-walled, becoming laxly elongate below. Setae 5-7 mm long, strongly scabrous above. Capsules ovoid, 1 mm long.

SPECIMENS STUDIED.—PHILIPPINES. Zamboanga, Dansalan, Zwickey 638 (FH). INDONESIA. Sumatra: Batang-Karo, Westkriods, no collector, ex Herb. Borg., sub *Daltonia spiniseta* Fleischer, nom. nud. (FH).

REMARKS.—According to Bartram (1944), this Philippine species resembles *D. aristifolia* in its aristate leaf apices, but differs from the latter in having longer leaf cells (Figure 11) and a strongly tuberculate seta.

Daltonia armata is hereby reported as new to Sumatra based on a specimen at FH named *D. spiniseta* in sched. by Fleischer. Apparently, Fleischer too was impressed by the strongly scabrous to nearly spinose setae of the present species.

Daltonia contorta

FIGURES 12, 43-46

Daltonia contorta C. Müller, Syn., 2:660, 1851. [Type: Java, sine loco, Blume s.n. (B, destroyed).]

Plants small to medium size. Stems to 1-3 cm long. Leaves strongly contorted or twisted when dry, lanceolate, long-acuminate. Leaf borders strongly differentiated, consisting of 4-5 rows of linear cells at base; leaf margins not recurved. Leaf cells oval to short-rhomboidal, 15-36 μm long and 6-9 μm wide, thick-walled, becoming rectangular at base. Calyptra strongly fringed at base. Setae 5-6 mm long, nearly smooth or weakly papillose throughout. Operculum conic. Capsules variable in shape, ovoid to cylindric, 1-1.5 mm long.

SPECIMENS STUDIED.—PHILIPPINES. Luzon: Mt. Data, Tan & Aguilar 81-92 (CAHP); ibid, Nishimura 6528, 6758 (HIRO, US); Baguio, Williams 1666 (US).

REMARKS.—The leaves of *D. contorta* are strongly twisted when dry, befitting the species epithet. The acute to acuminate leaf apices with plane leaf margins are also diagnostic; although the last mentioned character is inconspicuous in the dry state.

Daltonia contorta is also known from Sri Lanka, Java, Fiji, and Hawaii. All Philippine collections, thus far, come from the Island of Luzon (Bartram, 1939).

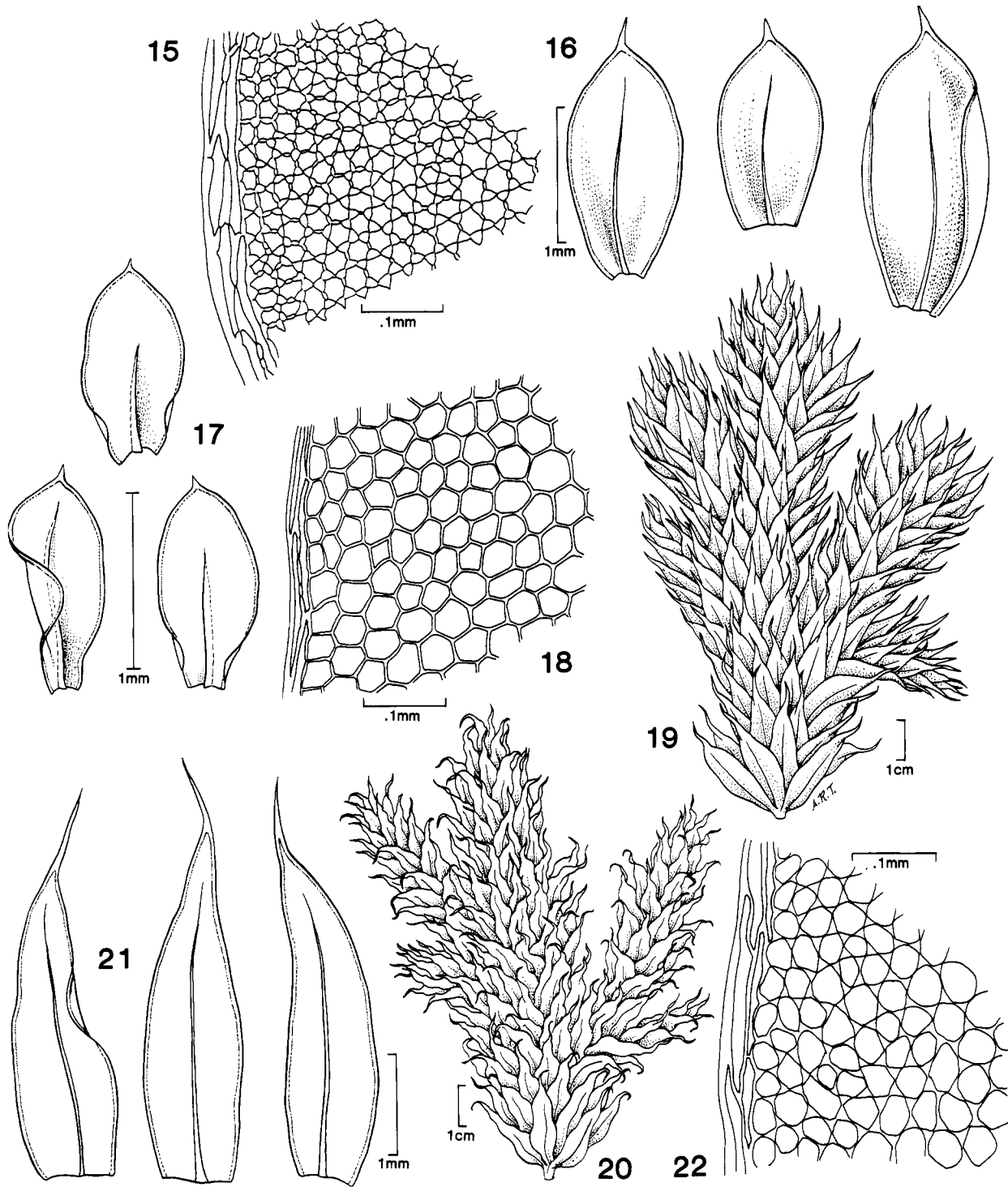
Genus *Distichophyllum*

Distichophyllum Dozy & Molkenboer, Musci Frond. Ined. Archip. Indici, 4:99, 1846.

This is one of the large genera in the Hookeriaceae with about 65 species in tropical Asia and Oceania. It is also the largest genus in the family in the Philippines.

The genus is characterized by somewhat complanate foliation, bordered leaves with rounded to hexagonal upper leaf cells, a single costa, short setae, and capsules with a typical hookericeous exostome.

Like *Actinodontium* and *Daltonia*, the stem cross-section shows little or no internal differentiation. A central strand is absent in all of the Philippine species studied. However, many stem parenchyma cells develop a "sieve plate" structure with elliptic pits on their transverse walls, a peculiar feature illustrated by Fleischer (1908, fig. 168) and Noguchi (1956). *Hookeria* is another genus in the family with a similar sieve



FIGURES 15-22.—*Distichophyllum*: 15, 16, *D. subcuspidatum* (Philippines: Sibuyan Is., Mt. Giting-Giting, Tan & Hernaez 87-468, CAHP): 15, upper leaf cells; 16, whole leaves. 17, 18, *D. brevicuspes* (Philippines: Semper s.n., L): 17, whole leaves; 18, upper leaf cells. 19-22, *D. kinabaluense* (Philippines: Sibuyan Is., Mt. Giting-Giting, Tan & Hernaez 87-446, CAHP): 19, plant, wet; 20, plant, dry; 21, whole leaves; 22, upper leaf cells.

plate development in the stem cell walls, but the stem cross-section of *Hookeria* shows a weakly differentiated central strand.

The degree of heterophylly and leaf density along the stem axis is variable in *Distichophyllum*. Compared to the lateral rows of leaves, the two alternate rows of median leaves are variable both in their leaf morphology and leaf cell areolation. Thus, the foliar taxonomic characters described below in the species treatment refer only to the mature, lateral leaves. Furthermore, the leaf habit in dry state, the degree of homogeneity of cell size in the upper half of the leaf, the length of leaf costa, and the width of the leaf border are all variable to some extent. Still, within a limited range of variation, they can be used effectively for separation of related species.

The perichaetial and perigonial leaves, surprisingly, are rather uniform in many species. They are often small ($\sim 1/3-1/5$ the size of lateral leaves), ovate-lanceolate, acute-acuminate, weakly bordered, and ecostate. Consequently, they do not have taxonomic significance. In contrast, the length and the papilosity of the setae are important diagnostic characters which correlate well with the sectional division of the genus. In general, section *Mniadelphus* Mitten includes large species with leaves more than 3 mm long and scabrous to papillose setae. The small species belonging to section *Distichophyllum* have leaves less than 3 mm long and have smooth, short setae. Also, the calyptra, which covers half of the capsule, is rather uniformly mitrate and fringed with a row of long hairs at its base. Many species differ in having a scabrous or papillose,

hairy or smooth calyptral surface; but, these would have limited practical systematic value since collections often lack calyptrae even when parts of the sporophyte are present. Capsules, when present, are generally ovoid-cylindric with collenchymatous exothecial cells. In the following treatment, these sporophytic characters are not mentioned unless the Philippine specimens bear them.

The majority of the Philippine species of *Distichophyllum* are dioicous, or at least reportedly so. Perichaetia are commonly seen in collections, but perigonia and sporophytes are infrequently encountered. Compared to *Calyptrochaeta* and *Leskeodon*, species of *Distichophyllum* usually do not produce filiform brood bodies in the leaf axils or on the adaxial leaf surfaces.

Philippine *Distichophylla* are commonly found in wet, humid, and shaded sites such as creek banks and dripping wet cliffs inside rainforests. A few species have become epiphytic on tree trunks and branches in humid, montane forests. Perhaps as an adaptation to this environment, the leaves of epiphytic taxa tend to be less complanate and the plants more tufted.

In 1939, Bartram treated seven species of *Distichophyllum* in the Philippine archipelago. The number increased to nine in the checklist of Iwatsuki and Tan (1979). Our present study, which includes three as new synonyms, shows a total of 14 species, five of which are new additions to the local moss flora. *Distichophyllum jungermannioides* and *D. nigricaula* var. *nigricaula* have not been found in the Philippines, however, they are included in the key inside parentheses since they are likely to occur in the country.

Key to the Philippine Species and Varieties of *Distichophyllum*

1. Leaf apices coarsely toothed, denticulate or serrulate 2
 Leaf apices entire 3
2. Leaf apices coarsely toothed *D. santosii*
 Leaf apices finely denticulate *D. obtusifolium*
3. Plants small, stems less than 25 mm long and not more than 3 mm wide including
 the lateral leaves 4
 Plants large, stems more than 25 mm long and 3 mm wide including the lateral
 leaves 16
4. Leaf apices long-acuminate to aristate or cuspidate, the acumen more than 100 μ m
 long 5
 Leaf apices round or obtuse, mucicous or shortly mucronate, the acumen if present,
 less than 100 μ m long 7
5. Leaf cells small, less than 15 μ m wide, weakly or not collenchymatous
 *D. cuspidatum*
 Leaf cells large, more than 15 μ m wide, strongly collenchymatous 6
6. Leaves oblong-elliptic, the apices broadly cuspidate; upper leaf cells mostly 15–21
 μ m wide, pitted *D. subcuspidatum*
 Leaves narrowly lanceolate, the apices gradually acuminate to aristate; upper leaf
 cells mostly 21–33 μ m wide, not clearly pitted *D. kinabaluense*

7. Leaf apices round to obtuse, mucous 8
 Leaf apices apiculate or short-mucronate 9
8. Leaves less than 2 mm long, broadly obovate from a short narrow base to nearly orbicular, the apices cucullate *D. catinifolium*
 Leaves more than 2 mm long, spatulate to oblanceolate from a long narrow base, the apices not cucullate *D. mittenii*
9. Leaf borders wide, of 3-4(-5) rows of linear cells, especially in the lower half of the leaf 10
 Leaf borders narrow, of 1-2(-3) rows of linear cells in the lower half of the leaf 11
10. Upper submarginal leaf cells small, 9-15 μm wide, clearly smaller than the paracostal ones; leaf borders more than 30 μm wide; leaf apices shortly mucronate, mucros less than 30 μm long *D. nigricaula* var. *elmeri*
 Upper submarginal leaf cells large, 21-30 μm wide, not or slightly smaller than the paracostal ones; leaf borders less than 30 μm wide; leaf apices stoutly apiculate, acumina 30-60 μm long (*D. nigricaula* var. *nigricaula*)
11. Leaf apices with stout acumen, more than 70 μm long 12
 Leaf apices with short apiculus, less than 70 μm long 13
12. Leaves more than 2 mm long, not carinate at base along the costa; the submarginal leaf cells much smaller than the inner ones, slightly collenchymatous, not pitted *D. collenchymatosum*
 Leaves less than 2 mm long, often carinate at base along the costa; the submarginal leaf cells not distinctly smaller than the inner ones, clearly collenchymatous and pitted *D. brevicuspis*
13. Leaves more than 2 mm long, narrowly oblanceolate to spatulate *D. mittenii*
 Leaves less than 2 mm long, oblong-ovate to obovate and broadly lingulate 14
14. Upper leaf cells mostly less than 15 μm wide, thick-walled; costae well developed, reaching $\frac{2}{3}$ of the leaf length *D. maibarae*
 Upper leaf cells mostly more than 15 μm wide, thin-walled; costae weak, reaching only midleaf 15
15. Leaf apices apiculate, acumina less than 20 μm long; upper leaf cells more or less homogenous from margin to costa *D. subnigricaula*
 Leaf apices short-mucronate, acumina more than 20 μm long; upper submarginal leaf cells smaller than the inner ones (*D. jungermannioides*)
16. Leaves more than 2.5 mm long, oblanceolate, lingulate to spatulate 17
 Leaves less than 2.5 mm long, ovate-oblong to short-obovate 21
17. Upper leaf cells more than 20 μm wide, more or less homogenous in size from margin to costa 18
 Upper submarginal leaf cells less than 20 μm wide, distinctly smaller than the paracostal ones 19
18. Leaf apices round or with short mucro, cucullate *D. cucullatum*
 Leaf apices broadly obtuse, apiculate, not cucullate *D. tortile*
19. Leaves indistinctly or not bordered in the upper half *D. osterwaldii*
 Leaves distinctly bordered all around 20
20. Leaf borders with 1-2 rows of linear cells; leaf apices round, with a tiny mucro *D. mittenii*
 Leaf borders with 2-3 rows of linear cells; leaf apices pointed, with distinct apiculus *D. collenchymatosum*
21. Leaf borders with 2-3 rows of linear cells, not clearly differentiated at leaf base *D. collenchymatosum*
 Leaf borders with 3-4(-5) rows of linear cells, strongly differentiated in the lower half of leaf 22

22. Upper submarginal leaf cells more than 18 μm wide, not distinctly smaller than the paracostal cells; leaf borders narrow, less than 30 μm wide
 (*D. nigricaula* var. *nigricaula*)
 Upper submarginal leaf cells less than 18 μm wide, distinctly smaller than the paracostal cells; leaf borders strong, more than 30 μm wide 23
23. Leaf apices with well developed apiculus; the costae reaching more than $\frac{2}{3}$ the leaf length, at times percurrent *D. nigricaula* var. *cirratum*
 Leaf apices round, with a tiny mucro; the costae at most reaching $\frac{2}{3}$ of the leaf length *D. nigricaula* var. *elmeri*

Distichophyllum brevicuspis

FIGURES 17, 18

Distichophyllum brevicuspis Fleischer, Musci Fl. Buitenzorg, 3:979, 1908.
 [Types: West Java, am Poentjak Pass, *Fleischer s.n.* (lectotype, FH!); West Java, bei Tjibodas, *Fleischer s.n.* (syntype, FH!).]

Plants small, mat-forming. Stems to 1.5 cm long, 1.5 mm wide with leaves. Leaves oblong-elliptic to lingulate with a narrow, short, somewhat carinate leaf base, 1–2 mm long, cuspidate, the acumina (60–)75–90 μm long, the borders narrow, with 1–2 rows of linear cells. Leaf cells hexagonal-polygonal, (18–)21–27 μm , thin-walled, collenchymatous, homogenous throughout the upper half. Gametangia and sporophytes not seen.

SPECIMENS STUDIED.—PHILIPPINES: *Semper s.n.* (L!); Luzon: Mt. Tabayog, *Jacob B426* (L!).

REMARKS.—Known previously from Java, this species is a new addition to the Philippine flora. It is best recognized by its rather homogenous upper leaf cells, cuspidate leaf apices, and a somewhat carinate or folded leaf base. *Distichophyllum nigricaula* differs in having larger leaves (more than 2 mm long), larger paracostal leaf cells, more broadly cuspidate leaf apices, and stronger costae (Figures 23–28). The leaf borders of *D. nigricaula* are also stronger, consisting often of 3–4 rows of linear cells as compared to 1–2 rows for *D. brevicuspis*.

Distichophyllum subcuspidatum differs from the present species in having a concave, more expanded leaf blade in the upper half, and a leaf base that is not carinate.

Distichophyllum subcarinatum Noguchi & Iwatsuki from Borneo (Noguchi and Iwatsuki, 1972) was characterized as having a distinctly carinate leaf and a short leaf acumen. Although the cells of *D. subcarinatum* were described as non-collenchymatous, it was illustrated in the original publication with collenchymatous leaf cells. It appears likely that *D. subcarinatum* may be a synonym of *D. brevicuspis*.

In the Fleischer Herbarium (FH), both syntypes are present. The specimen from Poentjak Pass is selected as the lectotype because of its abundance of material.

Distichophyllum catinifolium

Distichophyllum catinifolium Froehlich, Ann. Naturh. Mus. Wien, 59:98, 1953.

[Type: Sumatra, Mt. Singgalang, *Meijer 6157* (isotype, L!).]

Distichophyllum hattorii Noguchi & Iwatsuki, J. Hattori Bot. Lab., 36:472, 1972, syn. nov. [Type: North Borneo: Mt. Kinabalu, *Z. Iwatsuki NICH 679a* (holotype, NICH!).]

Plants small, forming dense mats. Stems prostrate, to 2 cm long, 2 mm wide with leaves. Leaves contorted when dry, imbricate when wet, shortly obovate to orbicular, to about 1 mm long, the apices obtuse to round, at times with small apiculus, cucullate. Costae short but clearly developed, reaching $\frac{2}{3}$ of the leaf length. Leaf borders narrow, with 1–2 rows of linear cells, the margins entire, somewhat incurved. Leaf cells lax, hexagonal-rounded, 12–16 μm , thin-walled, more or less homogenous throughout upper half of leaf. Perichaetial leaves small, broadly ovate, round to obtuse. Setae 5–6 mm long, smooth. Capsules not seen.

REMARKS.—The type of *Distichophyllum catinifolium* was compared with *D. hattorii* and found to be identical. The round, cucullate leaf apices coupled with the lax and thin-walled leaf areolation are unmistakable. The other Philippine species having similarly cucullate leaf apices is *D. cucullatum*, but the latter is a large plant with spatulate leaves. Unfortunately the better known binomial, *D. hattorii*, postdates *D. catinifolium* by 19 years.

The present species was first reported for the Philippines from Mt. Data by Iwatsuki and Tan (1980). We add here a second locality: the Philippine National Botanic Garden, Quezon Province, Luzon (*Tan 81-456*, CAHP). It is also known from several localities in Borneo and Sumatra.

Distichophyllum collenchymatosum

Distichophyllum collenchymatosum Cardot, Bull. Soc. Bot. Genève, sér. 2, 3:278, 1911. [Type: Japan, Yakushima, *Faurie 1156 in part* (holotype, PC), not seen.]

Plants small to medium size. Stems slender, to 4 cm long and 3 mm wide with lateral leaves. Leaves contorted when dry, broadly oblong, elliptic to lingulate, 2–3 mm long and 1.5 mm

wide, with well developed acumina (60–)75–90(–100) μm long. Leaf borders with 2–3 rows of linear cells, entire, slightly undulate. Costae strong, reaching beyond $2/3$ of the leaf length. Leaf cells hexagonal to round, (18–)21–30(–33) μm wide, slightly collenchymatous, markedly decreasing in size toward the margins in the upper half of the leaf. Calyptra smooth above. Setae 15–20 mm long, smooth.

SPECIMEN STUDIED.—PHILIPPINES. Negros: Mt. Talinis (Cuernos Mt.), *A. de Jesus, s.n.* Oct.–Nov. 1982 (CAHP).

REMARKS.—*Distichophyllum collenchymatosum* is a subtropical species in East Asia with its southern limit in the central Philippines (Tan and Iwatsuki, 1983). It can be confused with *D. nigricaulis*, from which it differs in having a narrower leaf border. In spite of its species epithet, this species does not develop leaf cells that are as strongly collenchymatous as in some other local species.

Distichophyllum cucullatum

Distichophyllum cucullatum Bartram, Lloydia, 5:279, 1942. [Type: West Irian, Lake Habbema, *Brass 9500* (holotype, FH1).]

Plants large, stems to 5 cm long and 4 mm wide including the leaves. Leaves long-spathulate to obovate, 2–3 mm long and 1.25–2 mm wide, the apices round, with very small apiculus, mostly cucullate. Leaf borders narrow, of 1–2 rows of linear cells. Costae weak, reaching $1/2$ of the leaf length. Leaf cells large, hexagonal to polygonal, (18–)24–36(–45) μm , thin-walled, laxly arranged in the expanded orbicular upper part of the leaf, the submarginal cells slightly smaller than the medial ones. Setae strongly hirsute, 5–7 mm long. Capsules cylindrical, to 1 mm long, neck elongated.

SPECIMENS STUDIED.—PHILIPPINES. Mindanao: Muralong Mt., near Kabasalan, Zamboanga, *Ebalo 731* (MICH, CAHP).

REMARKS.—This species is easily recognized by its large size and spatulate leaves that are cucullate at the apex. The Philippine specimen compares well with the type of *D. cucullatum*, differing only in the smaller plant size. Because of its large size, *Distichophyllum cucullatum* is unlikely to be confused with the much smaller species, *D. catinifolium*, which also has similarly cucullate leaf apices. According to Bartram (1942), the setae of *D. cucullatum* are papillose, while those of *D. catinifolium* are smooth.

Distichophyllum cucullatum was known previously only from New Guinea. Its extension to the island of Mindanao in the southern Philippines is a disjunctive distribution pattern shared by a few other mosses such as *Plagiotheciopsis oblonga* (Brotherus) Brotherus ex Dixon (Tan, 1987).

Distichophyllum cuspidatum

FIGURES 29, 30

Distichophyllum cuspidatum (Dozy & Molkenboer) Dozy & Molkenboer, Musci Frond. Ined. Archip. Indici, 4:101, 1846.

Hookeria cuspidata Dozy & Molkenboer, Ann. Sc. Nat., ser. 3, 2:305,

1844. [Types: Java, prope Limbang, *Zippelius s.n.*, *Korthals s.n.* (L); Sumatra, Batang-Bessie, *Korthals s.n.* (L).]

Plants forming aggregate tufts. Stems to 2 cm long. Leaves twisted when dry, not complanate, 1–1.5 mm long and 1–1.25 mm wide, mostly elliptic-oblong to oblanceolate, rarely narrowly lingulate, at times concave, long-cuspidate, weakly carinate at leaf base, the leaf acumina variable in length, 150–300(–360) μm long, the leaf borders well developed, consisting of 2–3 rows of thick-walled, elongate cells. Leaf margins entire, slightly revolute at leaf base; the costae reaching more than half the leaf length. Leaf cells small, round to hexagonal, (6–)9–15(–18) μm , thin to moderately thick-walled, weakly collenchymatous toward the apex. Setae smooth below, slightly to strongly papillose above, 3–5 mm long. Capsules short-ovoid to ovoid-oblong, erect or inclined.

SPECIMENS STUDIED.—PHILIPPINES. Sibuyan Is.: Mt. Giting-Giting, *Tan & Hernaez 87-528* (CAHP, US). INDONESIA. East Ceram: G. Selagor, near Kp. Selagor, *Buwalda 5731* (FH).

REMARKS.—Although *D. cuspidatum* was well illustrated by Dozy and Molkenboer (1846, pl. 33) and Fleischer (1908, fig. 169), this reportedly widespread species in Malesia and Oceania has not been well understood.

Recent authors (Bartram, 1939; Noguchi, 1956) have expanded its concept to include a number of species with similarly long-cuspidate leaf apices. The only Philippine specimen (Mt. Apo, *Williams 2672*) cited by Bartram (1939) as *D. cuspidatum* and the Taiwan specimens illustrated by Noguchi (1956) show a totally different leaf shape: ligulate with a narrowly triangular leaf apex terminating in a long arista (Figures 20, 21). The leaf cells of these specimens are also collenchymatous, a feature not typically seen in *D. cuspidatum*. In fact, *Williams 2672* is *D. kinabaluense*, a species Noguchi and Iwatsuki (1972) segregated from *D. cuspidatum* on the basis of their Bornean collections.

Furthermore, in *D. cuspidatum*, the broadest part of the leaf is just below the apex and is about 1 mm wide, while in the leaf of *D. kinabaluense* the broadest part is near the middle and is less than 1 mm wide (Figures 21, 30). These two taxa may prove to be conspecific, but for the present, we believe that they are distinct species.

Distichophyllum kinabaluense

FIGURES 19–22

Distichophyllum kinabaluense Noguchi & Iwatsuki, J. Hattori Bot. Lab., 36:474, 1972. [Types: Sabah, Mt. Silam, alt. 900–1000 m, *Iwatsuki NICH 5512* (holotype, NICH!; isotype, Herb. Noguchi!).]

Plants slightly larger than *D. cuspidatum*. Leaves contorted when dry, narrowly lanceolate, oblong-lingulate to short-ligulate, about 2 mm long, the upper half gradually narrowed to long aristate tips, the acumina 200–480 μm long, and slightly subcarinate at leaf base. Leaf costae distinct, reaching $2/3$ of the leaf length or shorter. Leaf margins entire, plane above,

revolute at leaf base. Leaf cells round to polygonal, (15-)18-27(-33) μm , thick-walled, subporose, collenchymatous, becoming more lax and rectangular below, the marginal rows of cells slightly smaller than the medial ones. Rhizoidal filiform brood bodies present in some leaf axils. Setae to 5 mm long, smooth throughout. Capsules not seen.

SPECIMENS STUDIED.—PHILIPPINES. Sibuyan Is.: Mt. Giting-Giting, *Tan & Hernaez 87-446* (CAHP), *87-452* (US). Mindanao: Mt. Apo, *Williams 2672*, sub *D. cuspidatum* (US); Mt. Malindang, Misamis Occidental Prov., *Reyes 15*, sub *Distichophyllum philippinense* Bartram, nom. nud. (NY).

REMARKS.—The above species description is based on the Philippine materials determined by us on the basis of the original description and illustration in Noguchi and Iwatsuki (1972). The identification has since been confirmed by examination of type material.

In *Distichophyllum kinabaluense* the length of the leaf acumina and costae can vary greatly in leaves taken from the same plant. For the distinctions from *D. cuspidatum* see the discussion under that species.

Distichophyllum iwatsukii Noguchi from Mt. Kinabalu, Borneo, was described as having a similar leaf cell areolation but the plants are larger with leafy stems up to 2.5 cm long and 4 mm wide (Noguchi and Iwatsuki, 1972). The leaf acumina of *D. iwatsukii* have been illustrated as shorter than those of *D. kinabaluense*. The relationship between these two taxa deserves more attention.

Distichophyllum maibarae

Distichophyllum maibarae Bescherelle, J. Bot. (Morot), 13:40, 1899. [Type: Central Japan, Maibara, *Faurie 11130* (holotype, BM), not seen.]

Plants small to medium size, in dense mats. Stems creeping, branched, to 1.5 cm long, less than 3 mm wide including the leaves. Leaves crisp and undulate when dry, somewhat imbricate when wet, oblong-lanceolate to slightly oblanceolate, 1-1.25 mm long and 0.5-0.75 mm wide, apiculate to shortly mucronate, the acumina (21-)30-50(-60) μm long. Leaf borders narrow, of about 2 rows of linear cells, becoming weakly differentiated near the apex and toward the base. Costae flexuose above, reaching $\frac{2}{3}$ of the leaf length. Leaf cells small, round to hexagonal, 9-15(-18) μm , not collenchymatous and more or less homogenous in the upper half of the leaf in fresh state. Calyptra rather hairy. Setae short, less than 10 mm long, smooth. Capsules small, ovoid, 1 mm long, the exothelial cells slightly mamilliose, collenchymatous.

SPECIMENS STUDIED.—PHILIPPINES. Batanes Is.: Mt. Iraya, *Tan 84-163* (CAHP). Luzon: Mt. Tabayog, *Jacob B 485* (sub *D. nigricaulis*), *B 314* (L, CAHP); Mt. Data, *Nishimura 6731* (HIRO).

REMARKS.—This Sino-Japanese species was first reported for the Philippines by Shin (1965), from the Batan Islands located at the far northern tip of the country. Since then, several collections have been made from the high mountains of

northern Luzon where the local flora has strong Himalayan and temperate Asian affinities.

Among its local congeners, *D. maibarae* is rather characteristic in its oblong-lingulate leaf shape with a short mucro consisting of a few short, oblong to rhomboidal cells. These cells contrast strongly with the linear border cells, but are similar to the adjacent laminal cells. Occasionally, specimens of *D. nigricaulis* may be found with a similar leaf apiculus, but the leaf borders of *D. nigricaulis* are always broader or more strongly developed than those of *D. maibarae*.

The species is reported from mainland China, Taiwan, Japan, and the Philippines. In Indochina and the Himalayas the species may be present under the name, *D. sinuosulum* Dixon. The description and illustration of *D. sinuosulum* provided by Gangulee (1977) matches *D. maibarae*. Typical *D. sinuosulum* from the Malay Peninsula is not *D. maibarae* but is a synonym of *D. nigricaulis* var. *elmeri*.

The species may be in herbaria from other parts of Malesia under the name *D. montagneanum* (C. Müller) Bosch & Lacoste. If this turns out to be so, then *D. montagneanum*, which was recently redescribed by Townsend (1982) from the type deposited at Paris, is the oldest available name.

Distichophyllum mittenii

Distichophyllum mittenii Bosch & Lacoste, Bryol. Jav., 2:25, 1861. [Types: Java, sine loco, *Teysmann s.n.* (L); *Holle s.n.* (L); prope Toegoe, pr. Bogor, *Amann s.n.* (L), not seen.]

Plants medium to large size, mat-forming, laxly foliate, complanate. Stems simple or branched, prostrate or ascending, to 4 cm long and 4 mm wide including the leaves. Leaves slightly wrinkled to moderately crisped when dry, spatulate to obovate from a narrow leaf base, 2-3 mm long and 1.5 mm wide above midleaf, the apices broadly rounded above with one or two tiny apicula measuring less than 15 μm long. Costae strong, reaching near the apex. Leaf borders narrow, with 1(-2) rows of linear cells all around, the margins entire, undulate even when wet. Leaf cells hexagonal to polygonal, thick-walled, pitted, not collenchymatous, the submarginal cells in upper half of the leaf forming several rows of small (9-15 μm) cells; paracostal cells distinctly larger, 18-27 μm . Calyptra scabrous above. Setae scabrous, 7-8 mm long. Capsules ovoid to ovoid-oblong, the exothelial cells strongly mamilliose.

SPECIMENS STUDIED.—PHILIPPINES. Luzon: Mt. Makiling, *Pancho 4913* (CAHP); Mt. Banahao, *Pancho 1087* (CAHP); boundary of Albay and Sorsogon provinces, *A. de Jesus, s.n.* (PNOC). Negros: Dumaguete area, *Mack 1302* p.p. (NY). MALAYSIA. Malay Peninsula: Pahang, Fraser Hill, *Burkill & Holttum 8714* (FH); Selangor, Templer Park, *Manuel 2692*, sub *D. tortile* (NY).

REMARKS.—This is the most common species of *Distichophyllum* found in the Philippine rainforests. The most obvious characters are the very narrow leaf border in the upper half of the leaf with usually one row of linear cells, the minutely

mucronate leaf apices, and the several rows of submarginal cells distinctly smaller in size than the medial paracostal cells.

Distichophyllum nigricaula var. *cirratum* has similarly heterogeneous upper leaf cells, but its leaves are smaller and have broad, strongly developed borders consisting of 3–4 rows of linear cells. Furthermore, the leaf shapes of the two taxa are different, spatulate from a narrow base in *D. mittenii* versus oblong-elliptic to oblanceolate or lingulate in *D. nigricaula* var. *cirratum*. The Philippine specimen of *D. nigricaula* from Mt. Makiling (Hadden 137a) reported by Bartram (1939) consists of juvenile plants of *D. mittenii*.

Distichophyllum undulatum Dozy & Molkenboer ex Bosch & Lacoste has a similar leaf shape, leaf border, and leaf cell areolation, but differs from the present species in having an irregularly denticulate upper leaf border.

Distichophyllum mittenii is widely distributed in tropical Asia and Oceania, reaching as far south as New Caledonia and Vanuatu.

Distichophyllum nigricaula

FIGURES 23–28

Distichophyllum nigricaula Mitten ex Bosch & Lacoste, Bryol. Jav., 2:20, 1861. [Types: Java, Mt. Pangerango, *Motley s.n.* (lectotype, NY!); sine loco, *Teysmann s.n.* (syntypes, BO, L).]

REMARKS.—This is a variable species and several varieties have been described in the literature. Typically the infraspecific taxa are quite distinctive, but many intermediate forms can be found. One common feature present in all of the taxa closely related to *D. nigricaula* is a dark brown stem. Filiform brood bodies have been observed in Philippine specimens of *D. nigricaula*.

Distichophyllum nigricaula has been reported from Indochina to Malesia. Based on our examination of Philippine material, we recognize three varieties.

Distichophyllum nigricaula var. *nigricaula*

FIGURES 27, 28

Distichophyllum gracilicaule Fleischer, Musci Fl. Buitenzorg, 3:983, 1908, syn. nov. [Types: West Java, um Tjibodas am Gedeh, *Fleischer s.n.* (lectotype, FH!); am Poentjak, *Fleischer s.n.* (syntype, FH!).]

Plant small to medium size, dull yellow-green, mat-forming. Stems dark brown, prostrate to procumbent, slender, 2–6 cm long and ~2.5–3 mm wide including the leaves, laxly foliate. Leaves strongly crisped when dry, 2–2.5 mm long and 1–1.25 mm wide, short-ovate to obovate, at times broadly oblong, the apices rounded to broadly obtuse, shortly apiculate, the acumina 30–60 μm long. Leaf borders broad, well differentiated at leaf bases, with 2–3(–4) rows of linear cells and measuring 15–21(–30) μm wide. Costae moderately strong, to $\frac{2}{3}$ of the leaf length or shorter. Leaf cells round to hexagonal,

(18–)21–30(–39) μm , thin-walled, weakly collenchymatous near the apex, slightly decreasing in size toward the margins and becoming short-rectangular at base. Perichaetial leaves very small.

REMARKS.—There are two syntypes of *D. nigricaula* mentioned in the original publication. Since the species was attributed to Mitten by the authors of Bryologia Javanica (Dozy and Molkenboer, 1855–1870), the specimen at the New York Botanical Garden was selected as the lectotype.

In *Distichophyllum nigricaula*, the leaves tend to be more oblong and narrowly obovate, although broadly oblong ones are not rare. On the other hand, the leaves of *D. gracilicaule* are mostly broadly elliptic to broadly oblong, as illustrated by Fleischer (1908, fig. 168). These differences appear to be insignificant for the group, and the two taxa should be united.

When Fleischer (1908) described *D. gracilicaule*, he appears to have been misguided by his examination of atypical specimens of *D. nigricaula*. In his treatment of the two taxa, Fleischer stated that the costa of *D. nigricaula* is often percurrent and also that the submarginal cells are distinctly smaller than the inner ones. These distinctions are not found in the type specimen of *D. nigricaula*. As a result, many specimens of *D. nigricaula*, including those cited by Fleischer (1908) and by Bartram (1939), are misidentified. They are instead *D. nigricaula* var. *cirratum*, which has leaves with strong and undulate borders, a nearly percurrent costa, and several rows of distinctly smaller submarginal leaf cells. The leaf borders of var. *cirratum* are broader (about 30–42 μm wide) and have 3–4(–5) rows of linear cells, especially near the leaf bases. In var. *nigricaula*, the leaf border measures only 15–21(–30) μm wide and often consists of 2–3(–4) rows of linear cells near the base.

Although we have not seen any Philippine material of var. *nigricaula*, we include a species description based on our examination of the lectotype at NY for purposes of comparison. All previous reports of *D. nigricaula* from the Philippines, have proven to be either var. *cirratum* or var. *elmeri*.

Distichophyllum nigricaula var. *cirratum*

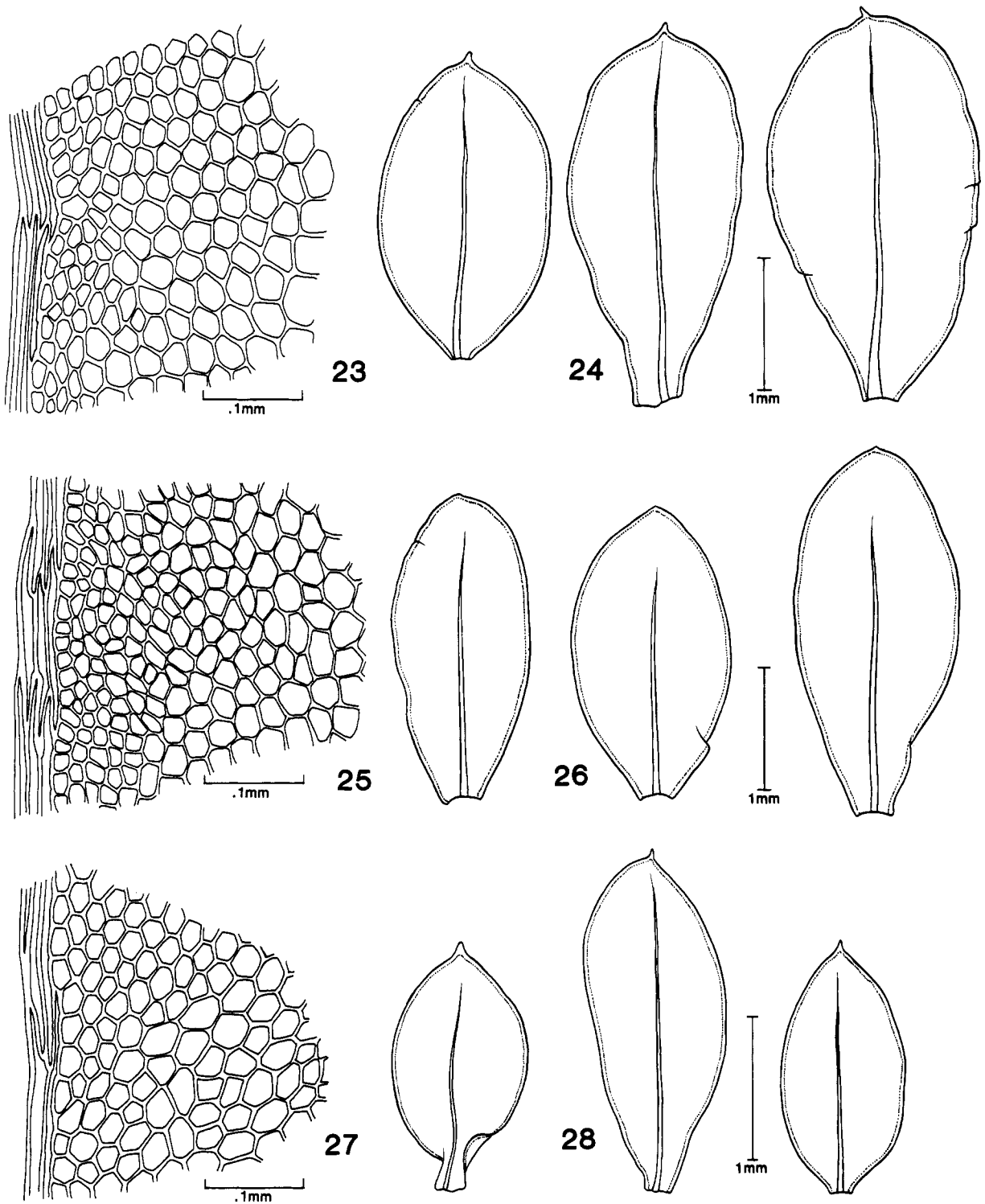
FIGURES 23, 24

Distichophyllum nigricaula var. *cirratum* (Renauld & Cardot) Fleischer, Musci Fl. Buitenzorg, 3:982, 1908.

Distichophyllum cirratum Renauld & Cardot, Rev. Bryol., 23:104, 1896. [Type: Java, Tjibodas, *Massart 1397* (isotype, FH!).]

Distichophyllum perundulatum Dixon, J. Linn. Soc. Bot., 50:106, 1935, syn. nov. [Type: North Borneo: Sarawak, Ulu Koyan, Oxford Exped. no. 1863 (holotype, BM!).]

Plants small to medium size, mat-forming. Stems dark brown, slender, 1.5–3 cm long and 2–2.5 mm wide including the leaves. Leaves strongly contorted when dry, 1–2.5 mm long and about 1 mm wide, oblong-elliptic, oblanceolate to short-lingulate, the margins entire, undulate, with strong



FIGURES 23-28.—*Distichophyllum nigricaulle* varieties: 23, 24, *D. n. var. cirratum* (Java: Tjibodas, Massart s.n., type of *D. cirratum*, FH); 23, upper leaf cells; 24, whole leaves. 25, 26, *D. n. var. elmeri* (Philippines: Baguio, Elmer 8716, FH); 25, upper leaf cells; 26, whole leaves. 27, 28, *D. n. var. nigricaulle* (Java: Pangerango, Molley, type of *D. nigricaulle*, NY); 27, upper leaf cells; 28, whole leaves.

apiculus, the leaf acumina (54–)60–105 μm long. Leaf borders strong, 30–42 μm wide, with 3–4(–5) rows of thick-walled linear cells well differentiated at leaf bases. Costae strong, reaching near apex, at times percurrent. Leaf cells hexagonal-polygonal, moderately thick-walled, forming 6–8 rows of small submarginal cells, 9–18 μm , and large paracostal cells, 21–33 μm . Sporophytes not seen.

SPECIMENS STUDIED.—PHILIPPINES. Luzon: Mt. Makiling, *Tan 84-66* (CAHP). INDONESIA. Java: Tjibodas, *Massart s.n.* (FH).

REMARKS.—When *D. cirratum* was first described by Renault and Cardot (1896), it was compared to *D. cuspidatum* which has a much longer leaf acumens. Fleischer (1908) correctly reduced it to a variety of *D. nigricaula*.

The var. *cirratum* has not been clearly distinguished, in the past, from the typical form of *D. nigricaula*. The differences between the two taxa are discussed above under *D. nigricaula* var. *nigricaula*. In addition, the leaf acumens of var. *cirratum*, measuring 60–105 μm long, are longer than those of var. *nigricaula*, which measure about 30–60 μm long. The description of *D. nigricaula* in Fleischer (1908) better fits the present variety.

Distichophyllum perundulatum (Dixon, 1935) from Borneo is identical with this variety.

***Distichophyllum nigricaula* var. *elmeri* (Brotherus) Tan & Robinson, new combination**

FIGURES 25, 26

Distichophyllum elmeri Brotherus, *Leaflets Philipp. Bot.*, 2:656, 1909, basionym. [Type: Philippines, Luzon, Baguio, Benguet Prov., *Elmer 10453* (holotype, H-BR1).]

Distichophyllum sinuosulum Dixon, *J. Siam Soc., Nat. Hist., Suppl.* 10 (1):15, 1935, syn. nov. [Type: Malaysia, Perak, Binch's Hill, *Burkill 12606* (holotype, BM).]

Plants similar to var. *cirratum* in habit, size and leaf shape. Like var. *cirratum*, the submarginal cells are 9–15 μm in diameter, and are markedly smaller than the 21–27 μm paracostal cells; the leaf borders are as broad, consisting of 3–4 rows of linear cells (Figure 25). However, in var. *elmeri*, the leaf apices are mucous or very shortly mucronate (6–9 μm) and the costae never reach the leaf tips (Figure 26).

SPECIMENS STUDIED.—PHILIPPINES. Luzon: Baguio, *Elmer 8716* (FH); Mt. Makiling, *Hadden 137* (FH), *Tan 82-52* (CAHP). Basilan: UP Land Grant, Zamboanga Prov., *Ebalo 964* (FH).

REMARKS.—Brotherus (1909) distinguished *D. elmeri* from *D. nigricaula* by its different leaf form and its broader leaf border. Later, this species was reduced to a synonym of *D. nigricaula* by Bartram (1939), who did not examine the original material. The species was described by Brotherus (1909:656) as having leaves narrowly oblong, about 2.5 mm long and 0.9 mm wide, with undulate margins consisting of strong borders of 3–4 rows of cells and marginal leaf cells much smaller than

the inner ones, and this compares well with *D. nigricaula* var. *cirratum*. Our examination of the type of *D. elmeri* confirms their close relationship.

Typical plants of var. *elmeri* are easily separated from var. *cirratum* and var. *nigricaula*. This led Noguchi and Iwatsuki (1972) to resurrect *D. elmeri*. The presence, however, of intermediate collections, e.g., *Touw 11709* from Khao Luang, Thailand (NY, L), indicate to us that the taxon should be recognized at the varietal level.

Distichophyllum obtusifolium

Distichophyllum obtusifolium Thériot, *Le Monde des Plantes*, sér. 2, 9:22, 1907. [Type: Japan, Amami-oshima, Naze, *J. Ferrie s.n.*, Nov. 1899 (holotype, PC), not seen.]

Plants small to medium size, in thin mats. Stems procumbent, branched, often becoming ascending, to 3 cm long and 4 mm wide including the leaves. Leaves crisp when dry, narrowly oblanceolate to broadly obovate and spatulate. Leaf borders narrow, consisting of 1–2 rows of linear cells, weakly differentiated into one narrow row of short rectangular cells near the round apex, the margins plane, finely denticulate by the prominent cell angles near the apex. Costae reaching $\frac{1}{2}$ – $\frac{2}{3}$ of the leaf length. Leaf cells mostly large, round-hexagonal, thin-walled, not collenchymatous, with several rows of submarginal cells, about 12–24 μm wide, clearly smaller than the 30–48 μm inner paracostal cells. Sporophytes not seen.

REMARKS.—Like *D. maibarae*, this species was first collected in the Philippines from the Batan Islands (Shin, 1965). Its leaves are distinctive in having a broadly obovate to spatulate outline with rounded, denticulate apices. The peculiarly toothed leaf apices were accurately illustrated by Noguchi (1956). It has yet to be re-collected in the Philippines.

The Malayan taxon, *D. denticulatum* Dixon, is closely related to the present species in having similarly rounded and toothed leaf apices. The two taxa differ from each other in the more narrowly obovate to oblanceolate leaves with fewer rows of smaller submarginal cells in *D. denticulatum*. Perhaps more collections of both taxa in tropical Southeast Asia will bridge this observed morphological gap and prove their synonymy.

Distichophyllum undulatum Bosch & Lacoste from Java and Borneo is also similar in having weakly toothed leaf apices. Nevertheless, *D. undulatum* has an apiculate leaf tip, the apical marginal teeth of the leaf are fewer and irregularly positioned, and the leaf cells are more or less homogeneously small (12–21 μm) in the upper half of the leaf. Another pronounced difference between the two species is in the width of the median leaf cells. In *D. undulatum*, the paracostal leaf cells are 18–27 μm wide, whereas those of *D. obtusifolium* are 30–48 μm wide. Lastly, the leaf borders of *D. undulatum*, like those of *D. mittenii*, are made up of a single row of linear cells in the upper half of the leaf.

Compared to *D. obtusifolium*, *D. osterwaldii* can be distinguished by its total lack of a differentiated border in the

leaf apex. *Distichophyllum osterwaldii* is also a larger plant with entire leaf margins. These differences are best seen in fresh specimens where the leaf border cells are still fully turgid. In rehydrated specimens of *D. osterwaldii*, some leaf border cells may stay collapsed, thereby creating a false appearance of having a faintly toothed leaf margin.

Distichophyllum osterwaldii

Distichophyllum osterwaldii Fleischer, Musci Fl. Buitenzorg, 3:994, 1908. [Type: West Java, Gedehgebirge bei Tjibodas, *Fleischer s.n.* (FH), not seen.]

Plants large, loosely tufted. Stems ascending, to 8 cm long, laxly foliate, flat, 4 cm long and 8 mm wide with leaves. Leaves strongly undulate-crispate when dry, lingulate to spatulate from a narrow leaf base, 4 mm long and 3 mm wide, broadly rounded above and mucous. Leaf borders distinct only in the lower half, narrow, 1–2 rows of linear cells. Costae slender, reaching more than $\frac{3}{4}$ up the leaf length. Leaf cells small, round-hexagonal, 6–10 rows of submarginal cells, 12–21 μm in diameter, distinctly smaller than the 24–36 μm paracostal cells. Setae 5–7 mm long, papillose. Capsules ovoid-oblong, 1 mm long.

SPECIMENS STUDIED.—PHILIPPINES, Luzon: Mt. Makiling, *Tan 81-426* (CAHP), *Nishimura 6989* (HIRO); National Botanic Garden, Real, Quezon Prov., *Tan 81-452* (CAHP). Leyte: Mt. Pangasugan, Baybay, *Tan & Navarez 84-253* (CAHP).

REMARKS.—This is the largest and one of the more commonly seen species of *Distichophyllum* in the Philippines. The large, spatulate leaves with an undifferentiated upper leaf border are unique among the Philippine species.

Distichophyllum tortile has comparably large leaves, but its leaf cells are large and relatively homogenous in the upper half of the leaf. Some forms of *D. obtusifolium* with weakly differentiated apical leaf borders may be confused with *D. osterwaldii*, but the former is a small plant about half the size of the present species. Also, in *D. obtusifolium* the leaf apices always have some trace of a differentiated border.

Distichophyllum osterwaldii is also known from Java, Borneo, Taiwan, mainland China, and Japan.

Distichophyllum santosii

Distichophyllum santosii Bartram, Philipp. J. Sci., 68:259, 1939. [Type: Philippines, Luzon, Baler, Tayabas Prov., *Santos 231* (holotype, FH!).]

Plants small, in dense mats. Stems creeping, much branched, reaching 2 cm long. Leaves not contorted when dry, very complanate, narrowly spatulate-lingulate from a long narrow base, 2–3 mm long, rounded at apex, bluntly toothed by the protruding apical marginal cells. Leaf borders narrow and indistinct, both at the apex and base. Costae faint, short, reaching only midleaf. Leaf cells very lax, hexagonal, nearly homogenous throughout. Setae 5–6 mm long, papillose. Capsules ovoid-oblong, the exothecial cells mamillate and

collenchymatous.

SPECIMENS STUDIED.—PHILIPPINES, Samar: Bagacay, *Tan s.n.*, June 29, 1975 (CAHP).

REMARKS.—This is the only endemic *Distichophyllum* in the country. Its strongly toothed apical leaf margins have no match among local congeners, although its leaf shape and leaf border differentiation suggest a relationship with *D. obtusifolium*. In the Philippines, *D. santosii* seems to occupy only the wet eastern part of the archipelago that faces the Pacific Ocean.

The report of *D. aff. santosii* from Seram Island (Akiyama, 1988) is based on a specimen (*Akiyama 16268*, CAHP) that proves to be *D. denticulatum* Dixon.

Distichophyllum subcuspidatum

FIGURES 15, 16

Distichophyllum subcuspidatum Noguchi & Iwatsuki, J. Hattori Bot. Lab., 36:476, 1972. [Type: North Borneo, Mt. Kinabalu, below Paka Cave, *Iwatsuki NICH 838* (holotype, NICH).]

Plants small, like *D. cuspidatum*. Leaves slightly contorted when dry, oblong to oblanceolate, slightly concave in some, weakly plicate in others, broadly cuspidate, the acumina strong, 210–240 μm long. Leaf margins plane, entire, the borders strong, with 3–4 rows of very thick-walled, linear cells. Costae reaching $\frac{2}{3}$ of the leaf length. Leaf cells hexagonal to round, (9–)12–21(–24) μm , thick-walled, strongly collenchymatous, distinctly porose, more or less homogenous in the upper half. Sporophytes not seen.

SPECIMENS STUDIED.—PHILIPPINES, Sibuyan Is.: Mt. Giting-Giting, *Tan & Hernaez 87-508* (US), *87-468*, *87-518* (CAHP).

REMARKS.—*Distichophyllum subcuspidatum*, which is newly reported from the Philippines, appears to be closely related to *D. cuspidatum*. Both taxa develop long, apical leaf acumina and strong leaf borders. However, the leaf cells of *D. subcuspidatum* have distinctly pitted cell walls and collenchymatous corners. These distinctions may prove erroneous when more collections of the two species are made and compared.

Noguchi and Iwatsuki (1972) reported fusiform and falcate brood bodies for the species from Bornean plants.

The Philippine plants, like the Bornean specimens, came from basic substrates at an elevation between 3500–4000 ft.

Distichophyllum subnigricaule

Distichophyllum subnigricaule Brotherus, Philipp. J. Sci., 31:289, 1926. [Types: Philippines, Mindanao, Zamboanga, *Merrill 8324* (holotype, HI; isotypes, NY!, FH!).]

Distichophyllum laxirete Noguchi & Iwatsuki, J. Hattori Bot. Lab., 36:425, 1972, syn. nov. [Type: North Borneo, Mt. Kinabalu, near Ulu Liwagu, *Mizutani 3604c* (holotype, NICH!).]

Distichophyllum rotundatum Noguchi & Iwatsuki, J. Hattori Bot. Lab., 36:476, 1972. [Type: Sabah: Mt. Kinabalu, between Hot Spring, Poring, and Royal Soc. Bungalow, *Iwatsuki 1711a* (holotype, NICH).]

Plants small to medium size, pale green, in dense mats.

Stems dark brown, 1–3 cm long and 2–2.5 mm wide including the leaves. Leaves slightly contorted when dry, 1–2 mm long, broadly lingulate to obovate, at times nearly orbicular, the apices rounded to broadly obtuse, weakly apiculate in some leaves, the apiculus, if present, 9–15 μm long. Leaf borders very narrow, with one row of linear cells near apex. Costae short, often less than half the leaf length. Leaf cells large, hexagonal, 27–40(–45) μm wide, very thin-walled, laxly arranged. Setae strongly spinose, 6–8 mm long.

SPECIMENS STUDIED.—PHILIPPINES. Luzon: Mt. Makiling, *Tan 84-62* (CAHP). Leyte: Mt. Pangasugan, Baybay, *Tan 84-252b* (CAHP).

REMARKS.—This species is distinctive in its very lax leaf cell areolation. The distinction between this species and *D. catinifolium* has been clarified by Noguchi and Iwatsuki (1972).

Iwatsuki and Tan (1980) reported *D. subnigricaula* for Borneo under the synonym *D. rotundatum* Noguchi & Iwatsuki. In the same publication, they reported *D. laxirete* as a new addition to the Philippine moss flora. According to Noguchi and Iwatsuki (1972) and Iwatsuki and Tan (1980), *D. laxirete* differs from *D. subnigricaula* in leaf shape and costa length. As more Philippine specimens of *D. subnigricaula* have been studied, these differences have become less clear. It seems best to recognize only one species.

Distichophyllum jungermannioides (C. Müller) Bosch & Lacoste, from Borneo and Java, is closely related to the present species. The two share a similarly lax leaf cell areolation, but the leaf costae of *D. jungermannioides* are shorter, often less than $\frac{1}{3}$ the leaf length, and the leaf apiculus stouter, measuring 60–75 μm long. The upper leaf cells of *D. jungermannioides* also appear to be smaller, 12–21 μm wide. Fleischer (1908, fig. 168) elegantly illustrated *D. jungermannioides* showing the characteristically concave, broadly obovate to somewhat rhomboidal leaves with a short base.

Distichophyllum nigricaula differs from the present species in having smaller leaf cells, several rows of submarginal leaf cells distinctly smaller than the paracostal cells, and a well developed leaf costa reaching at least to midleaf. A New Guinean specimen (*Koponen 36044*, FH) distributed as *D. gracilicaule* is instead *D. subnigricaula*, a new record for New Guinea.

The short leaf costae of *D. subnigricaula* are reminiscent of *Distichophyllum* Fleischer. The latter genus is defined as having, among other characters, a papillose peristome. Since the sporophytes of *D. subnigricaula* are unknown, we have maintained it in *Distichophyllum*.

Distichophyllum tortile

Distichophyllum tortile Dozy & Molkenboer ex Bosch & Lacoste, *Bryol. Jav.*, 2:27, 1862. [Types: Java, Gedeh, *Teysmann s.n.*; Banca, sine loco, *Amann s.n.* (L), not seen.]

Plants large, as in *D. osterwaldii*. Stems to 4 cm long and

6–10 mm wide including the leaves. Leaves strongly crisped when dry, oblong-lingulate to slightly obovate, 4–5 mm long and 1–1.5 mm wide, roundly obtuse above, apiculate to mucronate, the acumina 27–60 μm long. Leaf borders strong, with 2–3(–4) rows of linear cells, 30–42 μm wide, somewhat wavy even in fresh state. Costae slender, reaching $\frac{2}{3}$ of the leaf length or shorter. Leaf cells large, 45–60 μm wide, lax, thin-walled. Calyptra smooth above, fringed below. Setae papillose, less than 1 cm long.

SPECIMEN STUDIED.—PHILIPPINES. Luzon: Bataan Prov., Upper Lamao River, *Williams 851* (US).

REMARKS.—This distinctive species has large plants and leaves with large, thin-walled cells in the upper half. It is rather uncommon in the Philippine rainforests, and is also known from Indochina, the Malay Peninsula, Java, and Borneo. It most often occurs on wet rocks in deeply shaded sites.

Genus *Hookeria*

Hookeria S.E. Smith, *Trans. Linn. Soc. London*, 9:275, 1808, nom. cons. [Type: *H. lucens* (Hedwig) Smith.]

This is the type genus of the family Hookeriaceae. It is easy to recognize in the field by its thin, flat, somewhat transparent leaves and its large, net-like areolation. Only one species is known from the Philippines.

Hookeria acutifolia

Hookeria acutifolia Hooker & Greville, *Edinburgh J. Sci.*, 2:225, 1825. [Type: Nepal, *Hooker* (K).]

Plants mat-forming. Stems medium size, 2–3 cm long, pale green, simple or branched, mostly prostrate on ground. Leaves complanate, ovate to lanceolate, broadly acuminate, not bordered, slightly wrinkled when dry. Costa none. Leaf cells oval to rhomboidal, 42–75 μm long and 18–24 μm wide, thin-walled, smooth, becoming short-rectangular on the margin and laxer at base. Leaf apex with a cluster of short oval cells (27–30 μm long) often producing rhizoidal gemmae. Perichaetial leaves small, half the size of the vegetative leaves. Calyptra mitrate, covering the rostrate operculum, slightly torn at base. Seta lateral, smooth, 1–2 cm long. Capsules ovoid-oblong, inclined. Peristome teeth with median furrow on the exostome, cilia on the endostome absent or occasionally with a few cells.

SPECIMENS STUDIED.—PHILIPPINES. Batanes Is.: Mt. Iraya, *Tan 84-162* (CAHP). Luzon: Mt. Pulog, *Tan 82-212* (CAHP); Bicol Region, *A. de Jesus s.n.* (PNOC Herb.). Negros: Mt. Cuernos, *Tan 81-142* (CAHP). Mindanao: Mt. Apo, *Tan 82-246* (CAHP); Mt. Hilong-Hilong, Cabadbaran, *Tan 84-510* (CAHP).

REMARKS.—In the Philippines, this temperate and pantropical species is widespread in both lowland and montane rainforests. Its discovery dates only from 1965, when it was reported by Shin from Batan Island at the northern end of the archipelago.

Genus *Hookeriopsis*

Hookeriopsis (Bescherelle) Jaeger, Ber. S. Gall. Naturw. Ges., 1875-1876:358, 1877.

The genus *Hookeriopsis* is in need of a world monograph. Over the years, its species composition has grown too large and too diverse to represent a natural grouping.

The history of the genus was recently outlined by Buck (1987) who redefined the taxon to include only the two original Lesser Antillean species first proposed by Bescherelle as a section of *Hookeria*. The remaining species have been reassigned by Buck (1987) to three genera: *Thamniopsis*

(Mitten) Fleischer, *Trachyxiphium* Buck, and *Brymela* Crosby & Allen. In our opinion, *Brymela* is a worthwhile segregate. The separation of *Hookeriopsis* from *Thamniopsis*, however, is not convincing, nor is the segregation of the new genus, *Trachyxiphium*.

Because the genus consists of only two species in the study area and a few more in the tropical Asiatic region, we are content to stay with the traditional treatment in the absence of a satisfactory body of evidence to do otherwise. For those who wish to follow the generic revision of Buck (1987), the two Philippine species should be placed in *Thamniopsis*.

Key to the Philippine Species of *Hookeriopsis*

- Apices of mature, lateral leaves long-acuminate; the upper leaf cells mostly elongate, with a ratio of length to width 6-8:1 *H. wichurae*
- Apices of mature, lateral leaves broadly acute or short-acuminate; the upper leaf cells mostly narrowly rhomboidal to oblong, with a ratio of length to width 3-5:1 *H. utacamundiana*

Hookeriopsis utacamundiana

- Hookeriopsis utacamundiana* (Montagne) Brotherus, Nat. Pfl., 1(3):942, 1907.
- Hookeria utacamundiana* Montagne, Ann. Sc. Nat. Bot., ser. 2, 17:247, 1842. [Type: India, Montibus Nilgheriensibus, Prope Ootacamund, *Perrotet s.n.*, (isotype, NY!).]
- Hookeria secunda* Griffith, Calcutta J. Nat. Hist., 3:280, 1843, syn. nov. [Type: India, Mumbree, *Griffith s.n.* (isotype, NY!).]
- Hookeria purpurea* C. Müller, Flora, 82:459, 1896, fide Buck (1987). [Type: Hawaii, sine loco spec., *Hillebrand s.n.* (B, destroyed), not seen.]
- Hookeriopsis geminidens* Brotherus, Philipp. J. Sci., 5C (Bot.): 156, 1910, syn. nov. [Types: Philippines, Luzon, Benguet, *Bacani s.n.*, *For. Bur. 15929* (holotype, HI; isotypes, NY!, FH!).]
- Lepidopilum sumatranum* Bosch & Lacoste, Bryol. Jav., 2:42, 1862, fide Dixon (1916). [Type: Indonesia, Sumatra, monte Simpai, *Korthals, Herb. Ludg. Bat. 898.20-113-17* (lectotype, L).]

Plants mat-forming, silky green, with deep purplish tinge. Primary stems prostrate, complanate; the secondary stems and branches creeping or erect, to 10 mm tall. Leaves flatly arranged, slightly flexuose when dry, concave when wet. Lateral leaves ovate-oblong, 2-3 mm long, broadly acute; marginal borders not well differentiated, except for the strongly bifid, unicellular teeth along leaf margins near the apex. Costae double, strong, asymmetrically placed at leaf base, reaching mid-leaf, spinose abaxially. Dorsal and ventral leaves like the lateral ones but smaller, the apices sometimes acuminate. Leaf cells narrowly rhomboidal, (36-)45-60(-90) µm long and 12-15 µm wide, smooth or at times slightly prorulose, becoming oval near apex and rectangular at base, thin to thick-walled. All collections studied are sterile.

According to Fleischer (1908) and Gangulee (1977), the calyptrae are mitrate and hairy, the setae smooth, the capsules

ovoid-oblong, horizontal, and the exostome teeth cross-striolate at base, papillose above, with distinct median furrow.

SPECIMENS STUDIED.—PHILIPPINES. Mindanao: Mt. Kitanglad, *Tan & Navarez 84-379* (CAHP, US). Mindoro: Mt. Halcon, *Tan 87-048* (CAHP). SRI LANKA. Hanasgiriya, *Alston 1564*, ex herb. Peradeniya (US). NEW GUINEA. Port Moresby, *Carr 14185* (US).

REMARKS.—*Hookeriopsis utacamundiana* is a widespread species in tropical Asia, reaching Hawaii in the Pacific (Bartram, 1933 as *H. purpurea*). The leaf marginal teeth, the length of the costae, as well as the leaf areolation can be highly variable. Consistent characters include the presence of at least some deep purplish coloration, the broadly acute to obtuse leaf apices, and the bifid marginal teeth near the leaf apex. Dorsal and ventral leaves often assume a variety of shapes and in some cases may develop weak marginal dentation in combination with acuminate apices. Such atypical forms may be confused with *H. wichurae*.

In comparing the species to *H. geminidens*, Brotherus (1910) described *H. utacamundiana* as having only weak dentation on the leaf margins and a dioicous sexuality. However, Fleischer (1908) and Dixon (1916) reported that Javan and Indian populations of the latter are monoicous or autoicous. In addition, the leaf marginal dentation in the type of *H. geminidens* was observed by us to vary significantly. In the case of *Hookeriopsis sumatrana* and *H. utacamundiana*, the two differ only in the extent of their purplish coloration, angle of leaf insertion, and sexuality, characters not good for diagnostic purposes.

Likewise, the differences between the Indian taxon, *H.*

secunda, and the widespread *H. utacamundiana*, as illustrated in Gangulee (1977), and Iwatsuki and Mizutani (1972), involve the above mentioned variable characters. Buck (1987) recently suggested the synonymy of *H. geminidens* and *H. secunda*, but does not consider them synonymous with *H. utacamundiana*. On the other hand, Dixon (1916) proposed that *H. sumatrana* be treated as a synonym of *H. utacamundiana*. We consider all these taxa synonymous.

Although we were not able to study the Hawaiian type of *H. purpurea*, we have seen many collections from Hawaii and agree with Buck (1987) that it is a synonym of *H. utacamundiana*.

Hookeriopsis wichurae

Hookeriopsis wichurae Fleischer, Musci Fl. Buitenzorg, 3:1032, 1908. [Types: Indonesia, West Java, am Berg Malabar bei Bandoeng, *Wichura s.n.* (lectotype, FH!); am Gedeh, oberhalb Tjibodas bei Huis, *Fleischer s.n.* (syntype, FH!)]

Plants mat-forming, often deeply purplish. Stems 1–2.5 cm long, laxly branched. Leaves shrunken when dry, slightly plicate, ovate-lanceolate, long-acuminate, 1–1.75 mm long and less than 1 mm wide. Leaf margins weakly bordered with a row of shorter cells, toothed above, with bigeminate ends. Costae double, strong, asymmetrically placed at leaf base, reaching midleaf or beyond, spinose abaxially. Leaf cells narrowly fusiform to elongate, thick-walled, slightly pitted. Calyptrae mitrate, covering only the upper portion of the capsule, lacinate at base. Setae to 2 cm long. Operculum rostrate.

REMARKS.—The Malesian *Hookeriopsis wichurae* is very similar to *H. utacamundiana*, except that the leaf apices are long-acuminate, the leaf cells more elongate, and the leaf marginal teeth weakly developed and rarely bifid. Thus far, the differences between the two species appear to be consistent in the few specimens examined by us. Fleischer (1908) has illustrated *H. wichurae*.

The first and only Philippine record of this species was reported by Tan and Iwatsuki (1983) from Mt. Cuernos (= Mt. Talinis) on Negros Island in Central Philippines.

Genus *Leskeodon*

Leskeodon Brotherus, Nat. Pfl., 1(3):925, 1907. [Type: not selected. See below re *L. auratus* (C. Müller) Brotherus.]

The genus shows a combination of characters that calls into question the recent redelimitations of the family Hookeriaceae. Its leafy gametophyte closely resembles *Distichophyllum* but the sporophytic characters such as the non-collenchymatous exothecial cells and the papillose exostome without a median furrow are definitely not distichophylloid. Without capsules, specimens of *Leskeodon* can be difficult to place generically.

The enigma of *Distichophyllum* and *Leskeodon* is a good example of the discordant evolution of the gametophyte and sporophyte. A parallel situation exists in another generic pair,

Distichophyllum and *Distichophyllidium*. As mentioned by Norris and Koponen (1985), these related generic pairs, which have almost identical gametophytes but radically different sporophytic designs, cast doubts on the appropriateness of the sporophyte oriented philosophy expressed by Crosby (1974) and Allen et al. (1985) in their familial classification of hookeriaceous genera.

Recently, Norris and Koponen (1985) described a species from Papua New Guinea, *Distichophyllum leskeodontoides*, that has leaves similar to those of *Leskeodon acuminatus*, but has a distichophylloid peristome. The specimen may indicate a plausible intergeneric hybridization between *Distichophyllum* and *Leskeodon*, resulting in the odd combination of gametophytic and sporophytic characters. Already there are a few intergeneric hybrids reported in literature (Andrews and Hermann, 1959; Rushing and Snider, 1985). In all cases, the structure of the diploid sporophytic body is the one affected by the cross-fertilization process. Of course, theoretically, the characters of the gametophytes could also be recombined in the hybrid sporophyte. Indeed, this is one area of cytogenetics and developmental morphology in bryophytes that has not been critically investigated.

In Southeast Asia, species of *Leskeodon* tend to be small to medium-size plants growing to 2 cm long. The somewhat complanately arranged leaves nearly always have a strong and firm border above. When dry, the leaves have a stiff appearance with a wavy marginal contortion. The upper laminal cells of *Leskeodon* are mostly hexagonal to subhexagonal-rhomboidal with sharp angles. They are longer than wide, moderately thick-walled, and arranged in a vertically oriented pattern along the leaf costa. They are never round-hexagonal and thin-walled as in most *Distichophyllum* species. In our opinion, the leaf cell areolation of Asiatic *Leskeodon* is more similar to that of *Calypstrochaeta* than *Distichophyllum*.

However, when the New World species of *Leskeodon* are studied and compared, two basic patterns of leaf cell areolation emerge. One of which, represented by *L. andicola* (Spruce) Brotherus and *L. mariei* (Bescherelle) Brotherus, approximates the leaf cell areolation of the Old World taxa. The other group, *L. longipilus* (Bescherelle) Bartram and *L. cubensis* (Mitten) Thériot, has basically large, round, thin-walled cells with a weak costa, much more reminiscent of the members of *Distichophyllidium* from Southeast Asia. More strikingly, the weakly collenchymatous exothecial cells and the fragile, papillose peristomes seen in *L. longipilus* (Figures 55–60) also closely resemble those of *Distichophyllidium*, especially when seen under the SEM (Figures 61–63). We have not been able to examine mature capsules of *L. andicola* and its related taxa to decide on the proper disposition of these neotropical taxa in relation to *Distichophyllidium* and the Old World taxa of *Leskeodon*. It appears that a proper typification of the genus will be of critical importance in the light of the above described variations of leaf cell patterns. The species emphasized in the original description of the genus (Brotherus, 1907), *L. auratus*

(C. Müller) Brotherus from Trinidad (also reported from Dominica, Bartram, 1955) is unfortunately not well known. In any case, the genus, as defined today, is doubtless a heterogenous group.

Bartram (1961) described *L. robbinsii* from New Guinea with a rather atypical leaf cell areolation for the genus. The isotype (New Guinea, Wabag area, *Robbins 3191*, B!) has laxly imbricate, ovate-lanceolate leaves with a short apiculate apex. The leaf cells are more or less homogenously rhomboidal to

subrectangular and thin-walled. The leaf costa is percurrent and the leaf margins are revolute, and have a narrowly differentiated border with only two rows of linear cells. We think that the species is best placed in *Daltonia*, *Daltonia robbinsii* (Bartram) Tan & Robinson, comb. nov. (Basionym: *Leskeodon robbinsii* Bartram, Rev. Bryol. Lichénol., 30:200, 1961.)

There are three species of *Leskeodon* known from the Philippines. Two of these, *Leskeodon acuminatus* and *L. brevicuspidatus*, are new additions to the local moss flora.

Key to the Philippine Species of *Leskeodon*

1. Leaf borders narrow, less than 20 µm wide, with 1-2 rows of linear cells; leaf cells large, mostly more than 30 µm in diameter; leaf apices gradually long acuminate *L. philippinensis*
 Leaf borders wide, more than 20 µm wide, with 3-5 rows of linear cells; leaf cells smaller, mostly less than 25 µm in diameter; leaf apices abruptly narrowed into a long acumen 2
2. Leaf costae percurrent or ending 15 or less cells below the apex; leaf borders strong, especially near the base, 30-60 µm wide; leaf acumina stout, 160-280 µm long and 48-72 µm wide at base *L. acuminatus*
 Leaf costae not percurrent, ending well below the apex; leaf borders narrower, not well differentiated at base, 21-33 µm wide; leaf acumina slender, 240-480 µm long and 32-56 µm wide at base *L. brevicuspidatus*

Leskeodon acuminatus

Leskeodon acuminatus (Bosch & Lacoste) Fleischer, Musci Fl. Buitenzorg, 3:971, 1908.

Distichophyllum acuminatum Bosch & Lacoste, Bryol. Jav., 2:26, 1862. [Type: Java, Mt. Gedeh, *Teymann s.n.* (L), not seen.]

Plants large, in dense mats, at times tufted. Stems 2-3 cm long and 4-6 mm wide including the leaves. Leaves complanate and slightly crisped when dry, 3-4 mm long and about 1.5 mm wide, long-acuminate to cuspidate at apex, the acumina stout, semi-twisted, 160-280 µm long and 48-72 µm wide basally. Leaf borders strong throughout, to 60 µm wide, with 2-4(-5) rows of thick-walled linear cells. Costa single, reaching mostly 2/3 of the leaf length, at times percurrent. Leaf cells sharply subhexagonal, (15-)18-24(-30) µm long, slightly longer than wide, becoming isodiametrically hexagonal toward margin and rectangular near base. Perichaetial leaves small, 1 mm long, acute-acuminate, weakly bordered, and shortly costate. Calyptra deeply fringed at base. Setae to 2 mm long, smooth below and scabrous above. Capsules ovoid, to 1 mm long, exothecial cells non-collenchymatous. Operculum conic-rostrate. Exostome teeth papillose.

SPECIMENS STUDIED.—PHILIPPINES. Mindanao: Mt. Hilong-Hilong, Agusan Prov., *Tan & Navarez 84-399* (CAHP, US). MALAYSIA. Borneo: Mt. Kinabalu, *Bryotropica 4937* (B).

REMARKS.—*Leskeodon acuminatus* is a new addition to the

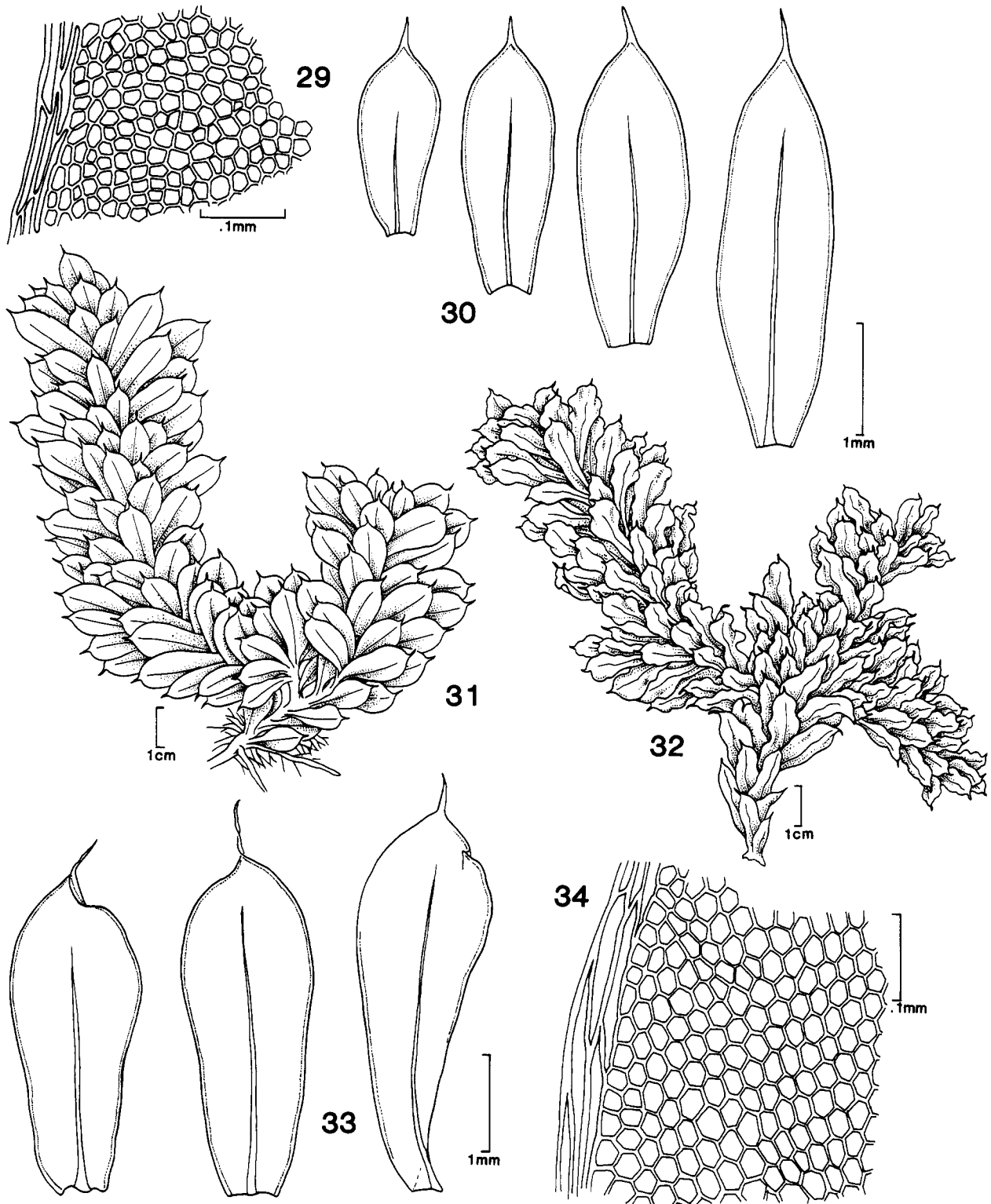
Philippine moss flora. Filiform brood bodies were observed by us on Bornean specimens, but not on the Philippine plants. The species is presently known from all the major islands of Malesia.

***Leskeodon brevicuspidatus* (Bartram) Tan & Robinson, new combination**

FIGURES 31-34, 51-54

Distichophyllum brevicuspidatum Bartram, Brittonia, 9:48, 1957, basionym. [Type: New Guinea, Mt. Dayman, epiphyllous, *Brass 23069* (holotype, FH!).]

Plants large, stems to 2 cm long, densely foliate. Leaves somewhat twisted when dry, erect-spreading when wet, oblong-obovate to broadly spathulate from a short base, 2.5-4.0 mm long and 1-2 mm wide, rounded obtuse above, cuspidate, the acumina slender, often twisted, 240-480 µm long and basally 32-56 µm wide. Leaf borders entire, strong in the upper half, less markedly differentiated near base, with 2-3(-4) rows of thin-walled linear cells, 21-33(-45) µm wide. Costae ending well below the apex. Leaf cells sharply subhexagonal, slightly longer than wide, (12-)15-21(-36) µm long, becoming smaller near the margin and rectangular toward the base. Calyptra fringed at base. Setae 2 mm long, smooth. Capsules erect, ovoid, less than 1 mm long; exothecial cells



FIGURES 29-34.—*Distichophyllum* and *Leskeodon*: 29, 30, *Distichophyllum cuspidatum* (Philippines: Sibuyan Is., Mt. Giting-Giting, Tan & Hernaez 87-528, US): 29, upper leaf cells; 30, whole leaves. 31-34, *Leskeodon brevicuspidatus* (Philippines: Mindanao, Mt. Hilong-Hilong, Tan & Navarez 84-471, US): 31, plant, wet; 32, plant, dry; 33, whole leaves; 34, upper leaf cells.

quadrate, thin-walled, non-collenchymatous.

SPECIMENS STUDIED.—PHILIPPINES. Mindanao: Mt. Hilong-Hilong, Agusan Prov., *Tan & Navarez 84-471* (CAHP, US). PAPUA NEW GUINEA. Timin River, Sau Valley, *Robbins 2873*, sub *Distichophyllum brevicuspidatum* (B).

REMARKS.—*Leskeodon brevicuspidatus* was described as a *Distichophyllum* by Bartram (1957). In the protologue, the author mentioned the capsule but failed to notice the nature of the exostomial ornamentation. The holotype specimen at FH has two capsules showing the papillose exostome. A second collection from New Guinea (*Robbins 2873*) bears mature capsules having a papillose exostome without a median furrow.

The differences between the present species and *L. acuminatus* are outlined in our diagnostic key. The Philippine specimen collected from Mindanao compares well with the type at FH, except that the leaves are smaller and have longer leaf acumens ranging 153–300 μm long.

Leskeodon brevicuspidatus is a new addition to the Philippine flora. It is known from Papua New Guinea and Mindanao, Philippines.

Leskeodon philippinensis

Leskeodon philippinensis Brotherus, Philipp. J. Sci., 13 C (Bot.):213, 1918. [Type: Southern Philippines, Biliran Island, *MacGregor 18468* (holotype, H!).]

Plants large, light green in color, in flat, dense mats. Stems to 2.5 cm long, densely foliate, about 5 mm wide including the leaves. Lateral leaves elliptic-spathulate, entire, 4–5 mm long and 1.0–1.5 mm wide, gradually long-acuminate at apex, the acumina 90–120 μm long, often twisted. Costae long, nearly percurrent. Leaf borders very narrow for the genus, consisting of 1–2 rows of linear cells, not well differentiated at leaf base. Leaf cells hexagonal, mostly large, 25–30 μm in diameter, thin-walled, with only a few smaller submarginal cells. Calyptra deeply fringed at base. Setae short, 1–2 mm long, smooth below, papillose above. Capsules small, ovoid, about 1 mm long. Peristome teeth papillose.

REMARKS.—Brotherus (1918), when describing *Leskeodon philippinensis* compared the species to *L. acuminatus* and considered them to differ in “foliorum forma cellulisque laxioribus.” Indeed, the leaf cells of *L. philippinensis* are much larger and thinner-walled. Later, Brotherus (1925) reported that *L. philippinensis* was synoicous and *L. acuminatus* was heteroicous or autoicous. This difference in sexuality does not hold true, since we have seen a synoicous specimen of *L. acuminatus* from Mt. Kinabalu, Borneo. We think the two taxa

are best separated by leaf shape. In *L. philippinensis*, the leaves are elliptic-spathulate with both ends gradually becoming narrower. Bartram (1939) provided a good sketch of this peculiar leaf form. The leaves of *L. acuminatus* are typically spathulate with a greatly expanded upper half that becomes abruptly cuspidate.

This Philippine endemic is known only from the type collection in Helsinki. The specimen labelled *L. philippinensis* at the Philippine National Herbarium in Manila is cited from Biliran Island, but no collector is given, and the specimen is apparently not an isotype. The packet contains material of *L. acuminatus*.

Notes on Philippine *Chaetomitrium*

The genus *Chaetomitrium* is unique among the hookeriaceous taxa in the following combined gametophytic features: unbordered leaves with short double costae, narrowly oblong to elongate, thick-walled and prorate leaf cells, and an enlarged perichaetium with often erose or sharply toothed leaf margins. Each of the marginal teeth of the perichaetial leaves consists of a long cell with a bigeminate tip, often projecting perpendicularly from the leaf margin.

The exostome structure of *Chaetomitrium* is also atypical for the Hookeriaceae in which it has traditionally been placed. They appear cross-striolate under the light microscope, but the ornamentation of the outer exostomial plate actually consists of irregularly and incompletely formed folds or ridges studded with papillae (Figures 39–42). This type of ornament is more commonly seen among Hypnalean taxa (Higuchi, 1985).

Dixon (1935) stated that Borneo (13 species) and New Guinea (14 species) represent the two “headquarters” of this remarkable genus. The Philippines, with 17 species, would seem to be a third center of local distribution.

Among the local species, *Chaetomitrium seriatum* Brotherus ex Bartram had been considered by Mohamed (1985) to be a synonym of the Bornean *C. borneense* Mitten. Our study of the types of these two taxa has led us to conclude otherwise. The Philippine specimens differ consistently from *C. borneense* in lacking an acute to shortly acuminate leaf apex. Perichaetial leaves of Philippine specimens are weakly toothed whereas the perichaetial leaves in the Bornean species are strongly toothed. The calyptra of *C. seriatum* is only sparsely fringed at the base, quite unlike that of *C. borneense*. The seta of *C. seriatum* is also longer than that of *C. borneense*. Apparently, Mohamed (1985) was overly influenced by the spirally ranked pilotricheloid foliation shared by the two species.

Key to the Philippine Species of *Chaetomitrium*

In the key, which is based as much as possible on the gametophytic characters, a few couplets lead to two species. This implies that the taxa involved may prove to be synonymous when their respective types are examined.

1. Leaf cells strongly tuberculate or sharply spiculose 2
 Leaf cells smooth, prorate, or at most prorate 5
2. Papillae of leaf cells tuberculate or knob-like; setae more than 1.5 cm in length *C. elmeri*
 Papillae of leaf cells spiculose; setae less than 1.5 cm in length 3
3. Leaf apices broadly rounded, at times with a small apiculus; calyptra cucullate *C. perarmatum*
 Leaf apices acute to acuminate; calyptra mitrate 4
4. Leaves ovate to short-lanceolate, the apices acute, slightly constricted near the tip; setae papillose *C. leptopoma*
 Leaves lanceolate, the apices acuminate, often strongly constricted near the tip; setae setose *C. beccarii/C. orthorrhynchum*
5. Leaf apices mostly truncate, broadly rounded or bluntly obtuse, at times abruptly terminated in a small apiculus 6
 Leaf apices acute to acuminate 9
6. Branch leaves spirally seriate in arrangement 7
 Branch leaves not seriatly arranged 8
7. Leaf apices short apiculate or bluntly obtuse, not recurved *C. schofieldii*
 Leaf apices rounded to broadly obtuse, if apiculate, the apiculus very small, recurved *C. warburgii*
8. Upper half of the leaf margins strongly wavy, entire, or serrate; leaf apices nearly orbicular, often recurved, mucous or apiculate *C. warburgii/C. pseudo-elongatum*
 Upper half of the leaf margins undulate, or constricted, forming a throat-like apex; leaf apices acuminate, strongly armed marginally with long, unicellular, uncinuate teeth *C. everettii*
9. Branches complanate 10
 Branches tumid, not complanate 11
10. Leaves concave when wet, with apices constricted, forming a somewhat flaring throat-like region *C. weberi*
 Leaves flat or slightly concave when wet, without any apical constriction *C. elegans*
11. Upper half of leaf margins undulate, strongly toothed with long, sharp, and uncinuate teeth *C. everettii*
 Upper half of leaf margins plane, or slightly rugose, entire, serrulate or serrate . 12
12. Leaf apices without a constriction, or a flaring throat-like region 13
 Leaf apices constricted, forming a throat-like region 14
13. Plants small, lateral branches to 5 mm long and 1 mm wide; leaf apices acute; leaf margins entire or weakly serrulate; calyptrae mitrate *C. fimbriatulum*
 Plants larger, lateral branches more than 5 mm long and wider than 1 mm; leaf apices long-acuminate; leaf margins slightly irregularly serrate; calyptrae cucullate *C. lanceolatum*
14. Calyptra cucullate, not or scarcely fringed at base *C. lanceolatum*
 Calyptra mitrate, fringed at base 15
15. Leaf apices mostly acuminate to long-acuminate 16
 Leaf apices mostly acute to short-acuminate 17

- 16. Leaf margins irregularly serrate; leaf cells sharply prorate; setae setose above *C. orthorrhynchum*
 Leaf margins regularly serrulate; leaf cells prorulose; setae papillose above *C. papillifolium*
- 17. Leaves oblong-lanceolate, widest at midleaf or below, slightly rugose; leaf cells distinctly prorate 18
 Leaves oblong-oblongeolate, widest above midleaf, strongly rugose; leaf cells smooth 19
- 18. Setae short, less than 10 mm, strongly papillose above *C. philippinense*
 Setae long, more than 10 mm, slightly papillose above *C. weberi*
- 19. Leaf margins regularly toothed; setae papillose above *C. elongatum*
 Leaf margins irregularly toothed, with larger teeth near the throat-like constricted region; setae spinose-hispid above *C. laevifolium*

***Chaetomitrium schofieldii* Tan & Robinson, new name**

FIGURES 39-42

Chaetomitrium seriatum Brotherus ex Bartram, Philipp. J. Sci., 68:271, 1939, hom. illeg. non *C. seriatum* Brotherus, Bot. Jahrb. 1913.

Because the name *C. seriatum* as applied to the Philippine species is an illegitimate homonym, we propose to replace it with *C. schofieldii*, in honor of Prof. W.B. Schofield, an eminent Canadian bryologist and former professor of the first author at the University of British Columbia.

ACCEPTED NAMES OF PHILIPPINE *Chaetomitrium*

An asterisk (*) indicates a new record for Philippine moss flora.

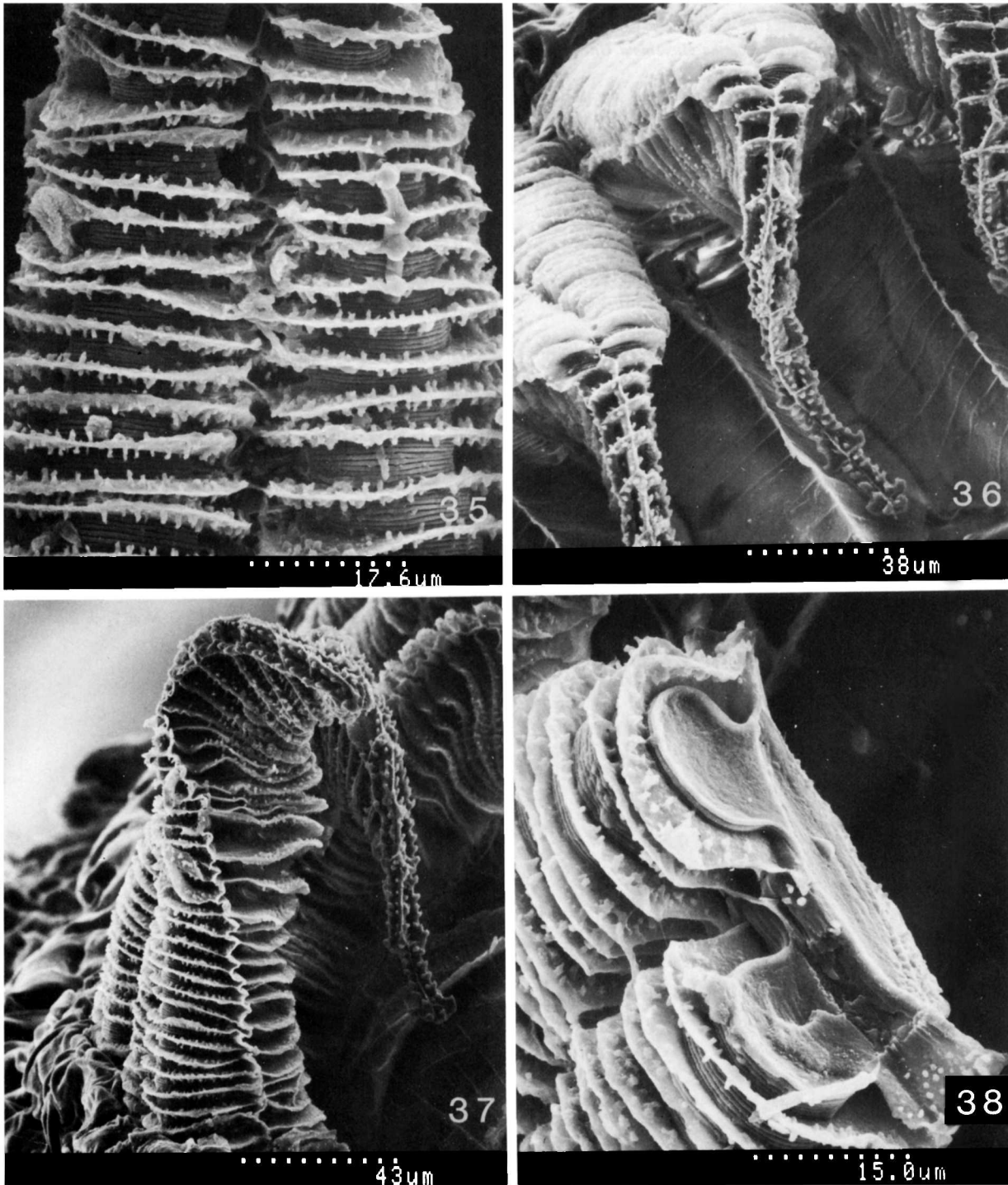
- C. beccarii* Dixon
- **C. elegans* Geheeb
- C. elmeri* Brotherus

- **C. elongatum* (Dozy & Molkenboer) Dozy & Molkenboer
- **C. everettii* Mitten ex Dixon
- **C. fimbriatulum* (Dozy & Molkenboer) Bosch & Lacoste
- C. laevifolium* Dixon ex Bartram
- C. lanceolatum* Bosch & Lacoste
- C. leptopoma* (Schwaegrichen) Bosch & Lacoste
- C. orthorrhynchum* (Dozy & Molkenboer) Bosch & Lacoste
- C. papillifolium* Bosch & Lacoste
- C. perarmatum* Brotherus
- C. philippinense* (Montagne) Bosch & Lacoste
- C. pseudo-elongatum* Brotherus
- C. schofieldii* Tan & Robinson, nom. nov.
- C. warburgii* Brotherus
- C. weberi* Brotherus

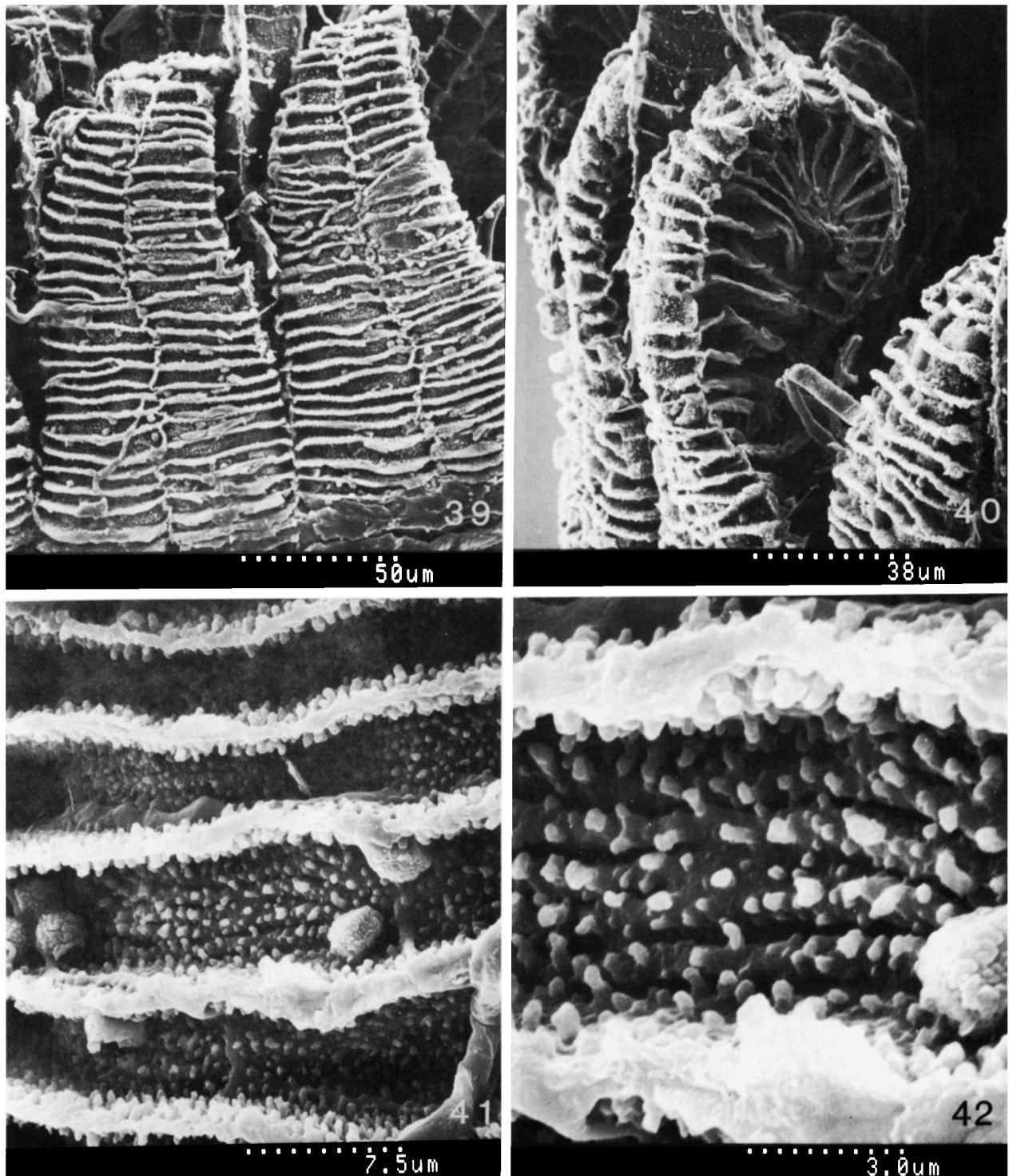
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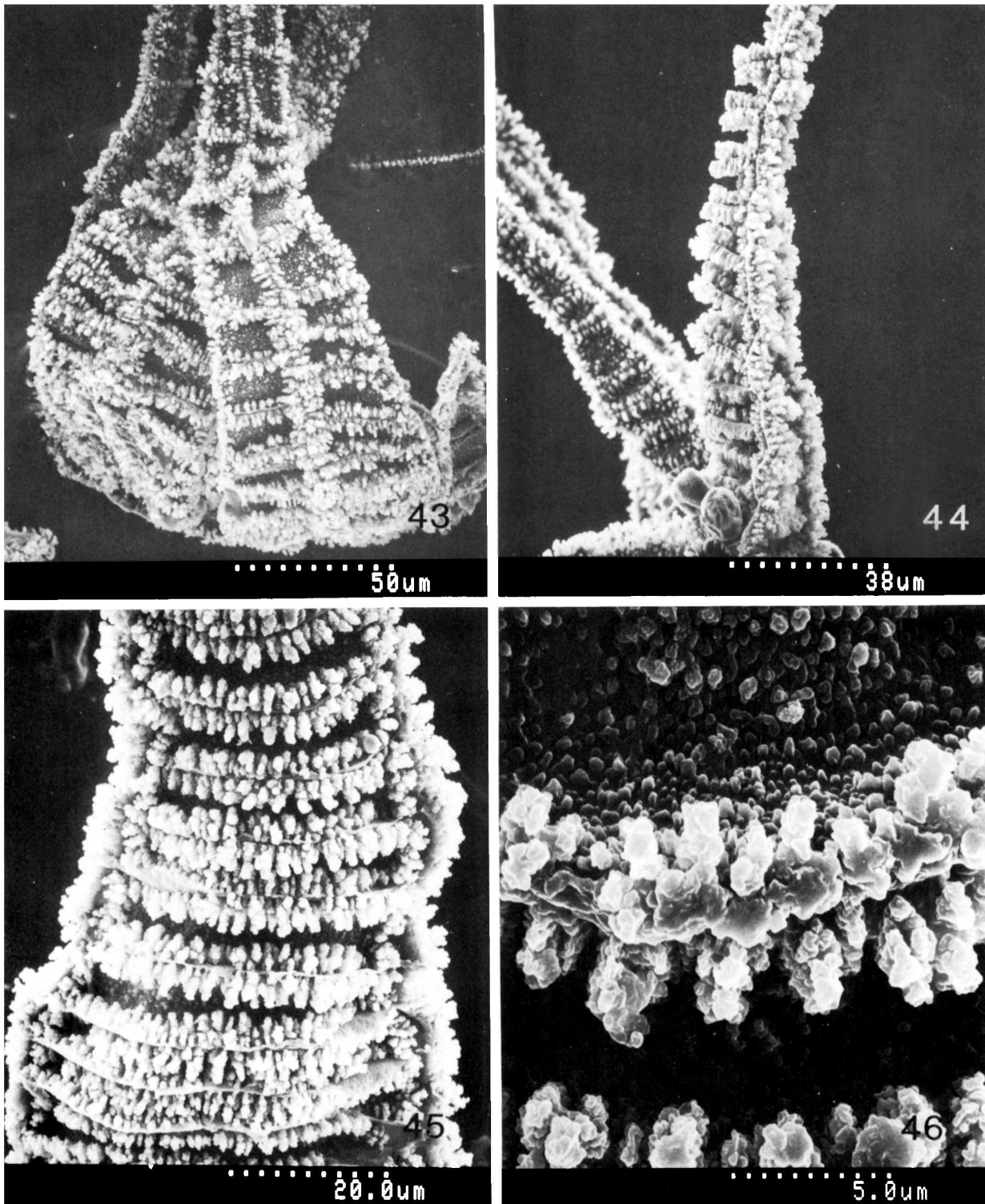
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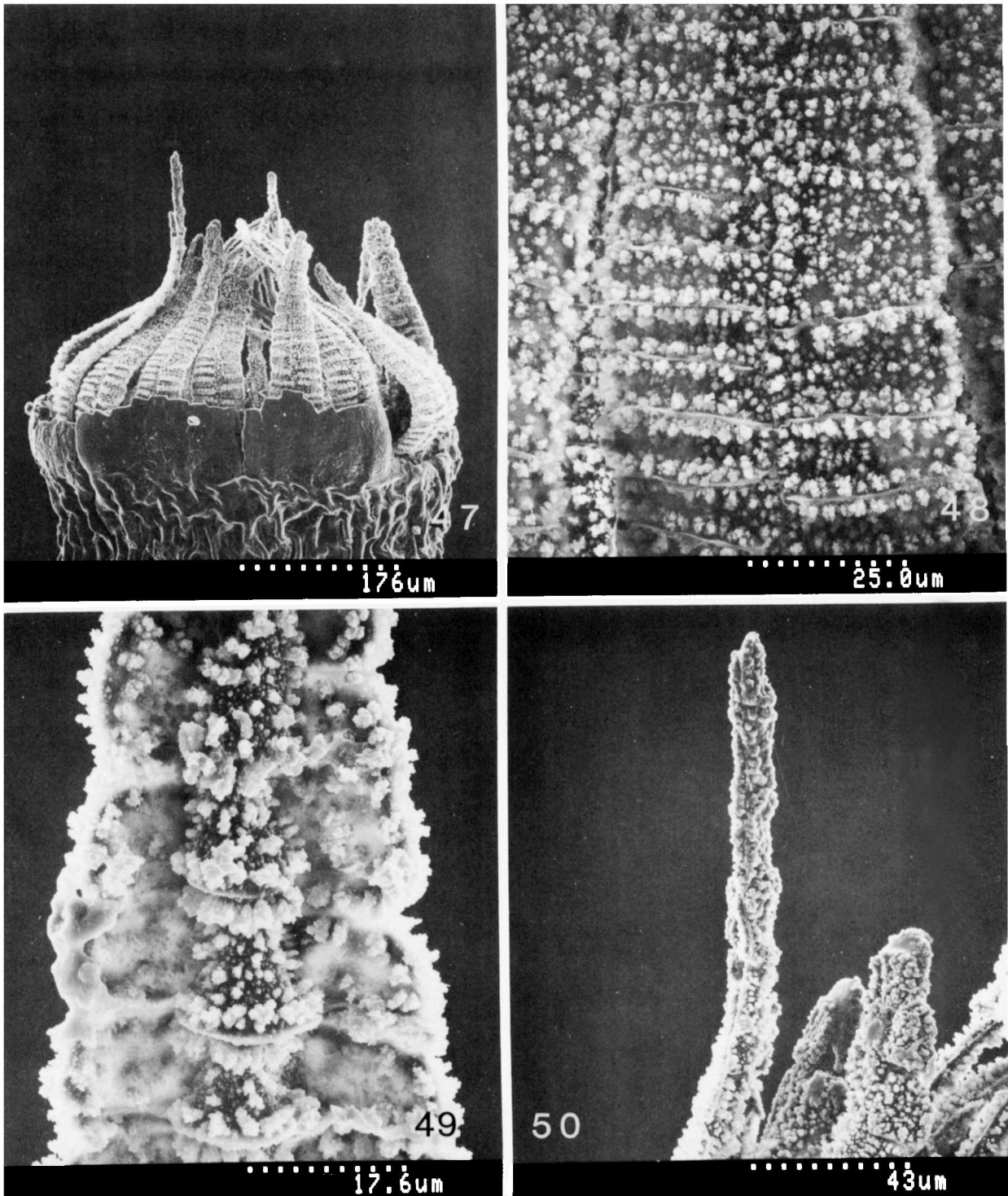
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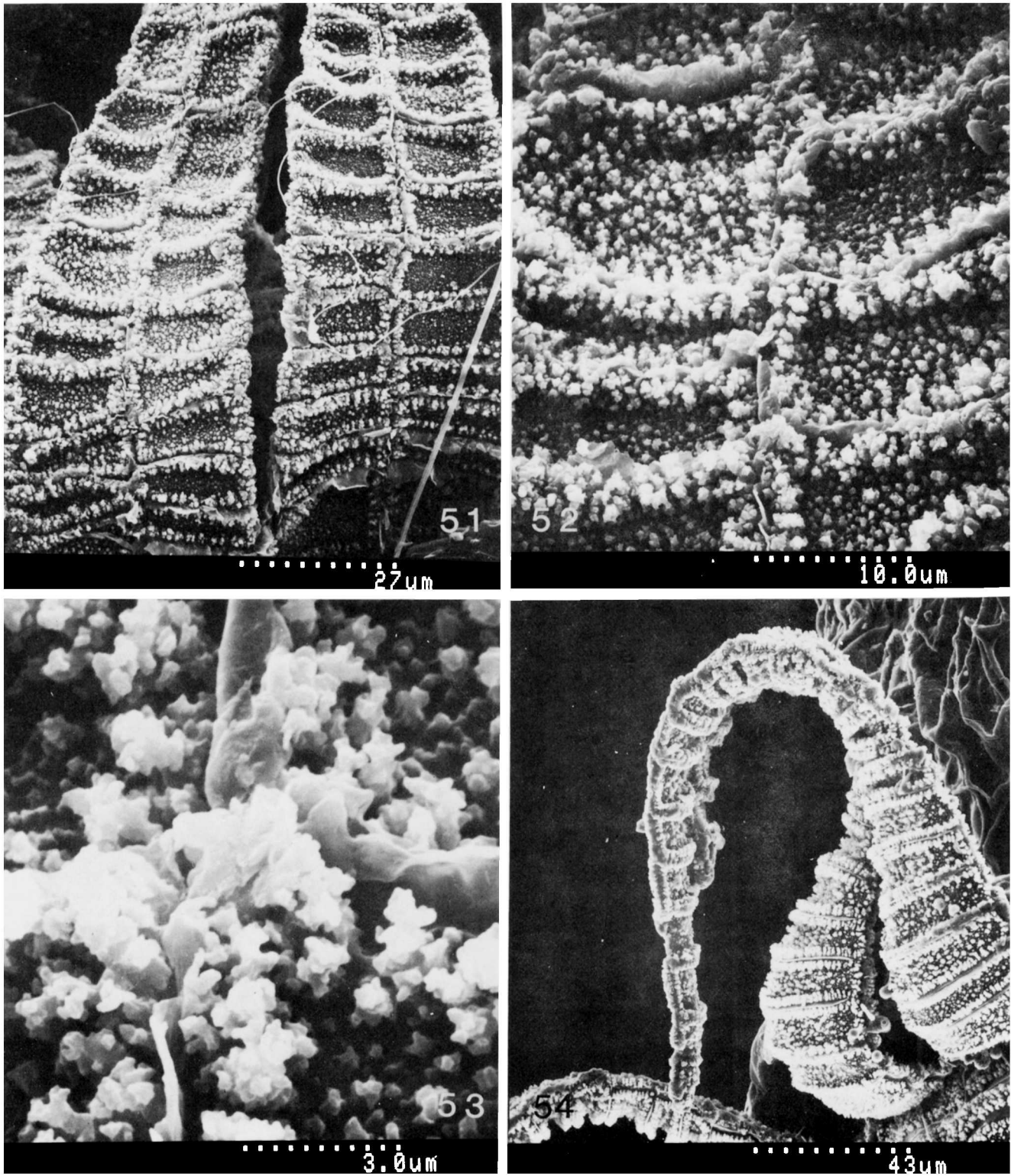
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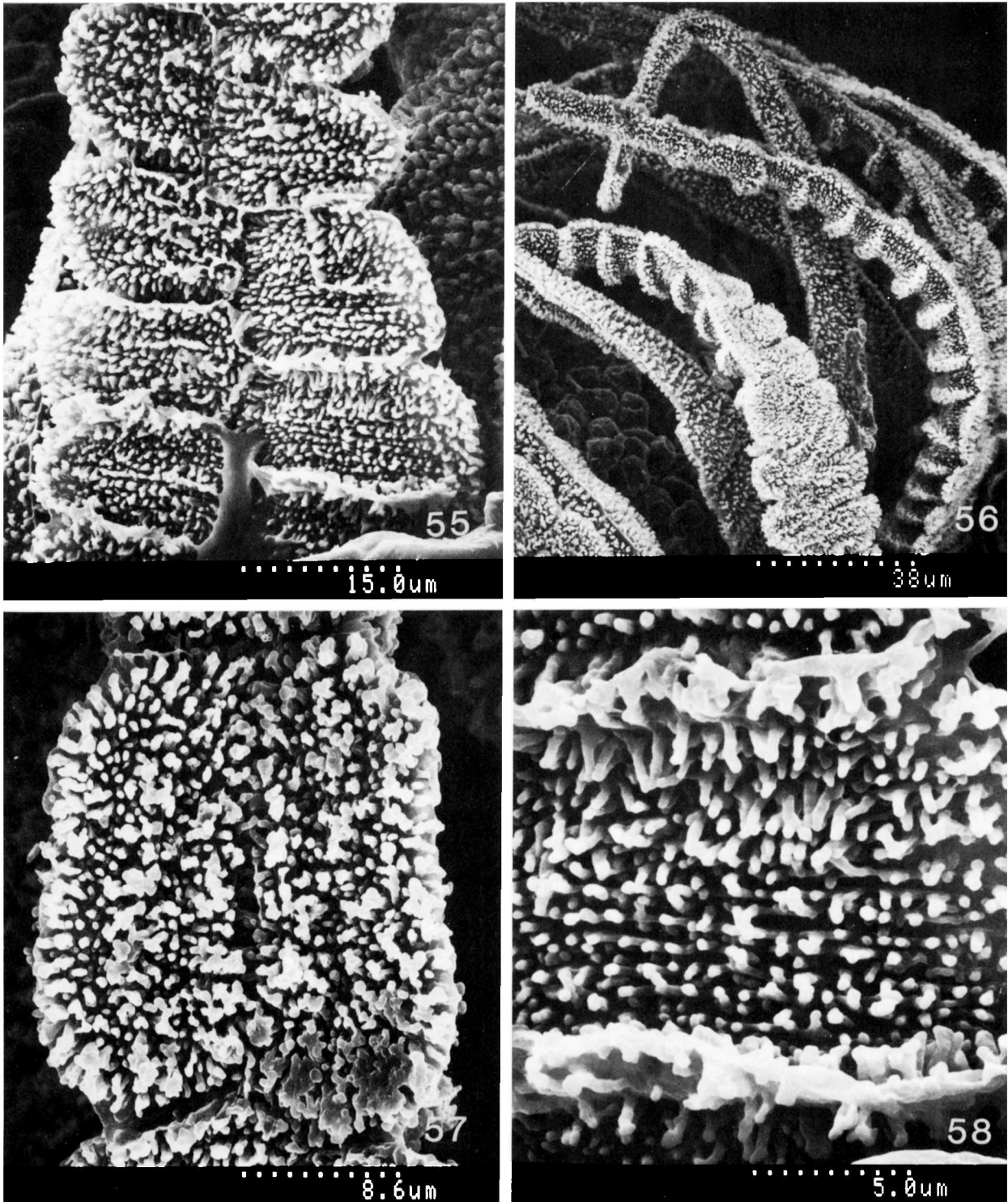
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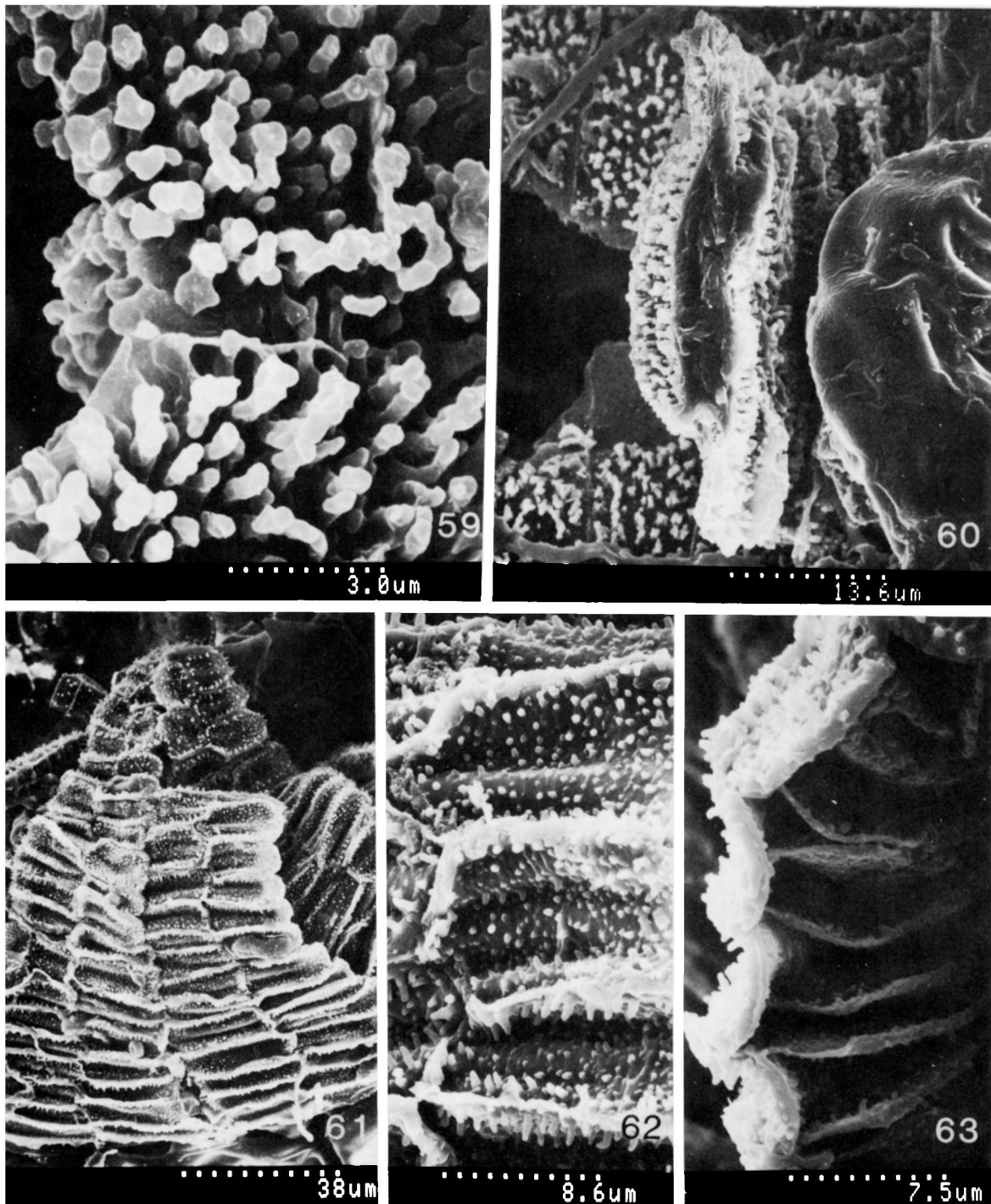
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