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A developmental, phylogenetic and taxonomic study on the moss genus Taxithelium Mitt. (Pylaisiadelphaceae)

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A developmental, phylogenetic and taxonomic study on the moss genus *Taxithelium* Mitt. (Pylaisiadelphaceae)

By

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General Abstract

Mosses are the second largest group of land plants. Hypnales, an order of pleurocarpous mosses, include ca. 50% of all mosses. The family Sematophyllaceae is probably the most diverse Hypnales in the tropics and one of the most complex and taxonomically confused. Traditionally variation in characters of the sporophyte have been used to distinguish genera and even species, but in this study characters of the gametophyte have been found to provide valuable distinctions. This thesis comprises three parts: 1, a micromorphological study of papilla development in *Taxithelium* and relatives; 2, a phylogenetic study of *Taxithelium*; and 3, a revision of *Taxithelium* subgenus *Vernieri*.

1. Micro-morphological studies on mosses are not common, but can illuminate the nature of taxonomic characters. I present data on the structure and development of leaf cell papillae in different Sematophyllaceae to assess their developmental similarity and also the congruence between papilla morphology and taxonomy. Two kinds of papillae are recognized. One is dome-shaped to conical tapering to a firmly rounded apex ("conical"), whereas the other presents a more flaccid, baggy appearance, and is often flat-topped and wider at the apex than at the base ("baggy"). The two types of papillae are also developmentally distinct: Conical papillae first appear as slight protrusions that gradually increase in height, whereas baggy papillae change shape as they develop. Conical papillae occur in most papillose taxa, whereas baggy papillae are present only on *Taxithelium* subgenus *Taxithelium*.

2. In order to test infrageneric classifications and species delimitation within *Taxithelium*, I constructed a molecular phylogeny using three chloroplast DNA loci (*trn*L, *psb*T and

*rps*4), three mitochondrial DNA loci (*rps*3, *nad*5 and *nad*4–5) and a nuclear gene (*ho*1). Analyses of the loci separately and in various combinations all support the monophyly of *Taxithelium*, which is probably of SE Asian origin. Two major clades corresponding to subgenera (see below) were resolved within the genus. The first clade is composed of at least four smaller clades, three of which include only SE Asian plants and one is from the Americas; the latter is nested within the SE Asian clades. The second clade appears to have a Southeast Asia origin and shows two dispersal events to America. Data show that *T. merrillii, T. concavum, T. pluripunctatum, T. planissimum* and *T. isocladum* are each demonstrably monophyletic units. On the other hand, *T. planum, T. nepalense* and *T. instratum* as circumscribed today are polyphyletic. *Taxithelium lindbergii* can be considered monophyletic only with the inclusion of *T. alare*. The *ho*1 nuclear locus is used for the first time in bryological studies, and with promising results.

3. *Taxithelium* is highly variable morphologically and includes plants with pluripapillose leaf cells as well as plants that lack papillae. Based on the results above *Taxithelium* is newly re-circumscribed and includes two subgenera, *Taxithelium* and *Vernieri*, that differ in papilla morphology. Detailed morphometric studies were carried out in subgenus *Vernieri*, individual analyses including different subsets of provisionally recognized groups. Based on these studies, eleven species could be recognized, one from Africa, two from the Americas, and the rest from Southeast Asia and Pacific Islands. A key to identify all the species recognized is provided, as well as full descriptions, nomenclature, distribution maps, etc., of each species. One species, *T. damanhurianum*, is new to science and is described from Seram, Indonesia.

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"…por ser de lá, do sertão, lá do cerrado, lá do interior do mato, da caatinga do roçado…eu não sei ficar na cidade sem viver contrariado…"

Gilberto Gil

R+C

CHAPTER 1

MORPHOLOGY AND DEVELOPMENT OF LEAF PAPILLAE IN SEMATOPHYLLACEAE (BRYOPHYTA)

This chapter will be submitted to the Journal "The Bryologist".

ABSTRACT. Micro-morphological studies on mosses are not common, but have the potential to illuminate the nature of taxonomic characters. Here we present data on the structure and development of leaf cell papillae in Sematophyllaceae, to assess developmental similarity and congruence with taxonomy. Two morphological kinds are recognized. One is dome-shaped to conical, tapering to a firmly rounded apex ("conical"), whereas the other presents a more flaccid, baggy appearance, and is often flat-topped and wider distally than proximally ("baggy"). Conical papillae occur in most papillose taxa, whereas baggy papillae are present only on *Taxithelium* subgenus *Taxithelium*. The two types of papillae are also developmentally distinct. Conical papillae first appear as slight protrusions that gradually increase in height, whereas baggy papillae progress through a series of developmental sizes and forms.

A detailed understanding of morphology is essential for good taxonomic work; also, when associated with phylogenetic studies, it can provide a unique view of evolution of form. Taxonomists are always searching for new characters to help understand better the relationships among organisms. The bryophytes are among the groups that need better exploration of their morphology. Lack of detailed morphological study has often led to misinterpretations and taxonomic confusion.

Morphological characters often show parallelisms, reversals and environmental plasticity. Unrelated taxa can come to look more similar during development, whereas in closely related taxa that differ strongly in morphology, the differences may be due simply to a few changes in developmental patterns. Developmental studies are thus a powerful tool for understanding morphology and addressing questions like parallelism and homoplasy, but are rarely conducted in mosses (but see Mishler 1986, 1987, 1988).

The moss gametophyte is a promising source of morphological characters, but gametophytic characters have often been overlooked by moss taxonomists. However, Buck (1991) suggested that the gametophyte might exhibit more independent characters than the sporophyte, which has been traditionally and widely used to delimit hierarchical groups. Indeed, molecular data may show better correspondence with gametophytic than with sporophytic characters (Huttunen et al. 2004, Gardiner et al. 2005, Câmara 2006). Among the gametophytic characters, leaf morphology has been one of the most used.

Many mosses develop papillae on the cells in their leaves. Papillae are outgrowths of the cell wall or cuticle, visible as “cell ornamentation[s], a solid microscopic protuberance” (Magill, 1990). The presence or absence, number, and distribution of papillae have been widely used in moss taxonomy to define boundaries at the generic

level in many groups (Magill 1977, Boudier 1990, Ireland 1991, Guerra et al. 1992, Werner et al. 2003, Gallego 2005). Papillae appear in unrelated genera throughout the mosses, occurring in both acrocarpous (e.g., Pottiaceae, Fissidentaceae, Rachitheciaceae) and pleurocarpous (e.g., Sematophyllaceae) species. The function of papillae is unclear, although many theories have been proposed, from control of light and temperature to adaptations to xerophytic conditions (see Patterson 1964).

The location, shape and size of papillae are difficult to see under the light microscope (Cano 1994, Robinson 1971), their small size making their observation potentially distorted (e.g. the so-called "C-shaped" papillae that Robinson (1971) and others recognized as being artifacts). This has led to different names being used for the same structure, or different structures being given the same name. The use of Scanning Electronic Microscopy (SEM) can help minimize such problems. It also makes it possible to see structures below the limits of resolution of the light microscope.

Paolilo & Reighard (1967) when studying lamellae in Polytrichaceae were the first to apply SEM techniques in the investigation of moss morphology; later Mozingo et al. (1969) studied leaf architecture of *Sphagnum*. Robinson (1971) was the first to use the SEM to study leaf papillae in mosses; he looked at five unrelated species of mosses and noted four different shapes of leaf papillae. He classified these on the basis of their location (middle or end of the cell), and as "grouped or seriate papillae". He also mentioned "cuticular papillae" referring probably to bulging cells. Unfortunately the study was carried out without the use of a critical point dryer and therefore the cells collapsed; the results are thus difficult to interpret.

Studies of papillae morphology (Robinson 1971, Casas De Puig & Molinas 1974, Werner et al. 2003, Gallego 2005) and development (Mishler 1987) are restricted to acrocarpous mosses; there are no studies of papillae micromorphology and development in pleurocarpous mosses. However, leaf papillae have been considered diagnostic at the generic level, with many taxa being recognized on the basis of papillae presence and number per cell (e.g., *Hypnella, Trichosteleum, Taxithelium, Radulina* and *Acanthorrhynchium*).

Pleurocarpous mosses (as defined by La Farge-England 1996) comprise around 50% of all mosses (Shaw & Renzaglia 2004). Hypnales, which have radiated extensively throughout the tropics, are almost exclusively epiphytic in angiosperm-dominated tropical forests. They are by far the most speciose pleurocarp clade, with around 4418 species or approximately 80% of all pleurocarpous mosses (Buck & Goffinet 2000). Their monophyly has been well established (De Luna et al. 2000, Newton et al. 2000, Goffinet et al. 2001, Cox et al. 2004, Buck et al. 2005). However, family level relationships within the Hypnales are still poorly understood perhaps because of the apparent rapid evolution of the group (Shaw et al. 2003), resulting in poorly defined lineages and very short internal branches on phylogenetic trees, especially at the basal nodes. Large amounts of nucleotide data will likely to be needed to obtain good resolution of such nodes (Shaw & Renzaglia 2004).

Groups within the Hypnales are poorly differentiated morphologically, although this may simply reflect the lack of basic morphological and micromorphological studies. Sporophyte morphology of the Hypnales is relatively constant, and gametophyte morphology has not been studied in depth. Even widely used gametophytic characters

such as pseudoparaphyllia (structures restricted to the areas of the stem around branch primordia) lack the developmental studies needed to safely differentiate foliose pseudoparaphyllia from undeveloped or immature primordial leaves (Akyama & Nishimura 1993, Ignatov & Hedenäs 2007).

Within Hypnales, Sematophyllaceae *sensu lato* (including Sematophyllaceae s.s. plus Pylaisiadelphaceae) are one of the largest and most diverse families (Buck & Tan 1989, Tsubota et al. 2001a,b); their monophyly was established by Tsubota (2001a,b). Taxonomists "dread" Sematophyllaceae (Buck & Tan 1989), considering it one of the "most difficult families of mosses" (Seki 1968). Tan and Jia (1999), when revising the family for China, stated that more than 70% of herbarium specimens they saw were incorrectly identified. More than two-thirds of the genera are mono- or oligotypic (Buck & Tan 1989, Tan & Jia 1999). Estimates of number of genera in the Sematophyllaceae (*sensu lato*) range from 50 (Vitt 1984) to 30 (Tan & Jia 1999) and probably more than 200 species. The numbers remain uncertain as the family is in need of revision.

Sporophyte characters have long been used to delimit genera within the family (Brotherus 1925), but the gametophyte remains a possible source of new morphological characters. Genera within the Sematophyllaceae s.l. vary in the presence or absence of papillae on leaf cells, papillae, when present, are usually one per cell, but species of *Taxithelium* and *Radulina* have multiple papillae per cell borne in a line along the proximo-distal axis.

Although *Taxithelium* has long been recognized as having multiple papillae serially disposed over the lumen of each leaf cell, Brotherus (1925) included some species lacking papillae in the genus; these species have been largely ignored in

subsequent treatments of the genus (Tan et al. 1996, Ramsay et al. 2002). Câmara and Shaw (unpublished) have shown, based on molecular evidence, that *Radulina* and *Taxithelium* are not closely related and that *Taxithelium* is clearly monophyletic. The serial papillae are a synapomorphy for the genus, although they have been lost in some taxa.

Some species of *Acroporium* and *Wijkia* are reported to have papillae (although it is possible that neither is monophyletic). Most species of *Acroporium* have smooth leaf cells; in those species that have papillae, they usually occur only in the upper half of the leaf. *Acroporium* appeared to be monophyletic in analyses using the *rbc*L gene (Tan & Ying 2004, Hedenäs et al. 2007), but ongoing studies using different markers (Goffinet et al. unpublished.) seem to demonstrate the opposite. Species of *Wijkia* have been reported as having leaves with cells that range from smooth to pluripapillose although most species examined here have either smooth or prorulose leaves. *Wijkia* is polyphyletic according to Tsubota et al. (2001a,b).

The published phylogeny for the family Sematophyllaceae (Tsubota et al. 2001a,b) does not include all taxa bearing papillae, making it impossible to assess precisely their phylogenetic relationships. However, a new phylogenetic study of Sematophyllaceae with broader taxon sampling and using molecular data from different genes and genomes, in underway (Goffinet et al. unpublished). Based on unpublished results from this study (**Fig. 1**), there have been at least three independent origins of papillae in the family. The papillose species of *Acroporium* were not available for inclusion in the phylogeny, so their position is unknown.

In this study we investigated the morphology and development of leaf cell papillae in the family Sematophyllaceae s.l. We identify a novel form of papillae that is synapomorphic for one clade within the genus *Taxithelium,* and confirm the developmental similarity of other papillae found elsewhere within the family.

METHODS

At least one species of each papilla-bearing genus in the Sematophyllaceae (sensu Buck & Goffinet 2000) was sampled; in addition we included a species of the non-papillose genus *Isopterygium* for comparison. A total of 23 species was studied. We included one species each of *Acanthorrhynchium, Clastobryophylum, Isocladiella, Isopterygium, Papillidiopsis,* and *Radulina*, and two each of *Acroporium,* and *Trichosteleum.* The two *Acroporium* species differ in presence of papillae; *A. adspersum* is papillose whereas *A. pungens* is non-papillose. We included multiple species of *Taxithelium* because preliminary studies had indicated variation in papilla morphology in the genus. In addition, we included several non-papillose species placed in *Taxithelium* based on molecular data. Because these species have apparently lost the generic synapomorphy (Câmara & Shaw, unpublished), we were particularly interested to see if they retained vestiges of papillae at any stage of development. Reports of papillae in *Wijkia* were determined to be erroneous, so this species was not included. Voucher information is listed in Appendix I.

Preparation - For each plant, a developmental series was studied, with leaves taken from a single individual progressively from the topmost position (younger) towards the base (older) on a single branch.

Samples were prepared according to the protocol suggested by Bozzola and Russel (1998). Fresh material was collected in the field in Southeast Asia. Samples were put in Eppendorf tubes containing 70% ethanol. Plants were dissected under a dissecting microscope and leaves in different stages of development were kept in vials containing 70% ethanol. For herbarium samples, specimens were first re-hydrated in boiling water for five minutes prior to fixation in 70% ethanol. In both cases, material was dehydrated in an ethanol series (70%, 85%, 95%, 100%, 100% and 100%) with changes every two hours. A critical point dryer was used to avoid cell wall collapse: for this procedure 100% ethanol and liquid CO_2 was used (Magill et al. 1974, Bozzola & Russel 1998). Samples were then mounted on stubs, sputter-covered with gold-palladium (Bozzola & Russel 1998), and kept in a container with silica gel under vacuum until used.

Specimens were observed with an SEM Hitachi S-2600H, at a voltage of 20kv and a working distance of 41.3 mm. Digital micrographic pictures were taken. All measurements were made from adult leaves at the middle of stem. At least three measurements were made for each individual, using a compass and a ruler.

RESULTS

We identified two distinct forms of papillae, which differed both in development and in adult morphology. The more common form, which we call here "conical," appears in all taxa except for *Taxithelium* subg. *Taxithelium*. Papillae in the latter group are distinctive and may constitute a morphological novelty.

Papillae appear early in leaf development, and are always present on the youngest leaves examined (ca. 145 µm long). Within a leaf, maturation is basipetal, with young papillae at the base of the leaf and the mature ones at the apex.

Conical papillae- These papillae are more or less cone-shaped, 2.5–3 µm in diameter at the base, and approximately 6 µm high; the apices are usually round and smooth (**Fig. 2A, B**). Most plants investigated have a single papilla per cell, usually on the geometric center of the lumen, but the pluripapillose taxa have three to five. Papillae arise as small outgrowths of the cell wall and grow continually until they reach maturity (**Fig. 2A, B and Fig. 4C**). Young papillae have approximately the same diameter as the adults but protrude less from the surface of the cell.

Conical papillae are found in all unipapillose taxa investigated: *Acroporium*, *Acanthorrhynchium*, *Papillidiopsis*, *Isocladiella*, *Clastobryophylum* and *Trichosteleum*, and also in the pluripapillose *Radulina* and species of *Taxithelium* other than subgenus *Taxithelium.*

Baggy papillae - These are hemispheric outgrowths of the cell wall, 2– 4 µm in diameter at base, and approximately 2 – 3 µm high (**Fig. 2C, D**). Usually three to five papillae form per cell, and are linearly distributed over the lumen. Papillae are almost as wide as the cell. Mature papillae sometimes appear to be divided (**Fig. 3**), or they may have a stem-like structure ca 0.75 – 1 µm long (**Fig. 4D**). Young papillae have a slightly smaller diameter (2 µm) than adult ones. This form occurs only on the pluripapillose species of *Taxithelium* subgenus *Taxithelium*.

During development the baggy papillae change not only in size, but also in shape. The young papillae appear initially as small lines across the whole width of the cell surface (**Fig. 5A, B**). Subsequently the cell wall appears to expand so that the papillae form ellipse-like structures (**Fig. 5C, D**). Finally, the papillae expand laterally, often developing a stalk and in some cases resulting in two paired protuberances (**Fig. 3 and Fig. 4D**).

Papillae absence- We investigated several species that apparently lack papillae, for comparison. In *Isopterygium minutirameum* (Müll. Hal.) A. Jaeger, no trace of papillae was found at any stage of development (**Fig. 6C, D**). However, in species of *Taxithelium* that lack obvious papillae when viewed with the light microscope, we found small, undeveloped papillae at the apex of some leaves. They resemble young conical papillae (**Fig. 6A, B**), although they were rare and difficult to find even under SEM.

A closer look at the sizes of cells with each kind of papillae (baggy and conical) showed that the cells with baggy papillae are only slightly wider on average (see Table 1) than the ones with conical papillae. However, cells with conical papillae are three times longer, resulting in dramatically different length to width ratios.

DISCUSSION

As suspected, the general term "papillae" is inadequate to describe the morphological variation observed. We document here variation in papilla morphology and development within the family Sematophyllaceae s.l. The papillae are easily distinguished from those in other groups of mosses, in which papillae appear to be

independently derived. The morphological distinctions that we find are consistent with the hypothesis of independent origins.

Previous SEM studies on papillae have been restricted to acrocarpous mosses (Robinson 1971, Magill 1977, Guerra & Carrion 1992, Werner et al. 2003, Gallego 2005), particularly on Pottiaceae. These studies have documented differences between taxa in the morphology of adult papillae, but have generally provided no description or discussion of the structures seen. Papillae in the acrocarpous mosses are elaborate, usually big and branched.

Papillae of species in the genus *Syntrichia* (Pottiaceae) have been studied in considerable detail (Gallego 2005). Leaves may be unipapillose or pluripapillose with one to 12 papillae per cell. Pottiaceae have short broad leaf cells, and the papillae may be arranged in two or more longitudinal rows. Papillae may be on either or both sides of the leaves depending on the species. Gallego (2005) classifies them as unbranched, bifurcate and pedicellate, with a range in length from 2.5 – 22.5 µm.

Papillae in Sematophyllaceae are very simple when compared with the large and usually branched papillae found in Pottiaceae. They differ from those of *Syntrichia* in many aspects: the papillae are not branched and their average size is much smaller (ca. 6 µm high). Also there are no papillae on the adaxial surface of the leaves in Sematophyllaceae, there are never more than seven per cell and they are borne in a single row. We could not conform the claim that *Radulina* has two rows of papillae (Ramsay et al. 2004) (**Fig. 4**); the original observation may have been an artifact of light distortion.

There are indeed some similarities between *Syntrichia* and Sematophyllaceae; some papillae in Pottiaceae resemble the conical shape described here, but the majority of

mature forms are definitely quite distinct; unfortunately developmental studies on *Syntrichia* are unavailable for comparison.

Developmental studies on leaf papillae are even more restricted. Mishler (1987) studied leaf development of *Tortula papillosissima* (Pottiaceae), including data on whole leaf development as well as on the papillae. He concluded that the shape of the papillae is not related to the number of branches, or the degree of branching. Early development of papillae in *T. papillosissima* resembles the continuous development of conical papillae described here.

Recent studies on the genus *Taxithelium* (Câmara unpublished, Câmara & Shaw unpublished) show that the genus is comprised of two sister clades, morphologically and genetically distinct, ranked as subgenera. The first group is subgenus *Taxithelium* (or "*Planum* clade") and is characterized by "baggy" papillae, which appear to be synapomorphic for the clade. Both the development and adult morphology of these papillae is unique within Sematophyllaceae s.l., and is also unknown outside the family. The second group ("*Vernieri* clade") is characterized by the more common conical type of papillae. However, some species in the "*planum* clade" appear to have lost papillae. We find that these species retain vestiges of papillae, supporting the phylogenetic inference of papilla loss (Câmara & Shaw unpublished). Our morphological data thus provide further evidence that these species should be retained in *Taxithelium,* and help to shed light on an old taxonomic confusion.

The vestigial papillae present in some species of the "*Planum* clade" resemble the conical papillae present in the "*Vernieri* clade, which might be expected since they are sister groups.

The correlation between leaf cell dimensions and papilla morphology is intriguing, and suggests that cell wall construction and/or cell expansion may lead to the observed differences in form. It would be of interest in future studies to look at cytoskeleton dynamics in *Taxithelium* species to determine whether papilla development is correlated with cell wall formation.

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Table 1, measurements of cells with different kind of papillae. Measurements were taken from six different leaves in two distinct plants

baggy width	baggy length	baggy l:w
4	18.1	4.52
4	16.7	4.17
6.25	17.8	2.84
3.9	25.6	6.56
6	22.6	3.76
4	19	4.75

conic width	conic length	conic l:w
3.6	50	13.88
3.7	44	11.89
2.4	55	22.91
3.9	70	17.94
3.6	80	22.22
3.9	65	16.66

Appendix I. Voucher information

Species	Collector number and herbaria	Locality
Acanthorrhynchium papillatum (Harv.) M. Fleisch.	Câmara 1418 (MO)	Singapore
Acroporium adspersum (Hampe) Broth.	Town 20619 (MO)	Sarawak
A. pungens (Hedw.) Broth.	Câmara 864 (MO)	Malaysia
Clastobryophilum bogoricum (Bosch & Sande Lac.) M. Fleisch.	Town 11979 (MO)	Sarawak
Isocladiella surcularis (Dixon) B. C. Tan & Mohamed	Tan 95- 1368 (MO)	Brunei
Isopterygium minutirameum (Müll. Hal.) A. Jaeger	Câmara et al. 1421	Singapore
Papillidiopsis bruchii (Dozy & Molk.) W. R. Buck & B. C. Tan	B. C. Ho 01-035 (MO)	Malaysia
P. complanata (Dixon) W. R. Buck & B. C. Tan	Tan 2001-04 (MO)	Malaysia
Taxithelium planum (Brid.) Mitt.	Delgadillo 6605 (MO)	Mexico
T. concavum (Hook.) Spruce ex J. Florsch.	Allen 25137 (MO)	Surinam
T. friedense D. H. Norris & T. J. Koponen	Koponen 35136 (NY)	Papua New Guinea
T. juruense (Broth.) Broth.	Prance et al. 12541 (NY)	Brazil
T. kerianum (Broth.) Broth.	Streimann 45708 (MO)	Australia
T. merrillii Broth.	Streimann & Pocs 64500 (MO)	Australia
T. muscicola (Broth.) B. C. Tan, H. P. Ramsay &	Watts 419 (NSW)	Lord Howe Island

W. B. Schofield		
T. nepalense (Schwägr.) Broth.	Câmara et al. 1417 (MO)	Singapore
T. perglabrum Broth. & Paris	Heras 888/93	Equatorial Guinea
T. portoricense R.S. Williams	Buck 4101 (NY)	Puerto Rico
T. pluripunctatum (Renauld & Cardot) W. R. Buck	Buck 32904 (MO)	French Guiana
T. vernieri (Duby) Besch.	Vernier 1316 (G)	Tahiti
Trichosteleum fleischeri B. C. Tan, B. C. Ho & B. K.-B. Seah	Câmara et al. 1411 (MO)	Singapore
T. papillosum (Hornsch.) A. Jaeger	Fuentes et al. 4249 (MO)	Bolivia
Radulina hamata (Dozy & Molk.) W. R. Buck & B. C. Tan	Streimann 21901 (MO)	Papua New Guinea

Fig.1) Backbone of phylogeny in Sematophyllaceae according to Goffinet et al. (unpubl.). Numbers within triangles represents the number of taxa bearing papillae present in each clade (numerator) and the approximate total number of taxa (denominator). Pluripapillose taxa are marked with asterisk (*); papillose *Acroporium* were not included. Reproduced with permission from the authors.

Fig. 2) Mature papillae. A. Conical papillae in *Trichosteleum singapurense*. B. Conical papillae in *Radulina hamata*. C, D. *Baggy* papillae from *Taxithelium nepalense*.

Fig. 3) Baggy papillae forming twins in *Taxithelium planum.*

Fig. 4) A and B: Young stages of conical papilla development in *Radulina hamata.* C. Adult conical papillae in *R. hamata.* D. Baggy papillae with stalk in *Taxithelium nepalense*.

Fig. 5) Development in stages in *Taxithelium nepalense.* A) Uppermost leaves. B) Phase I. C, D) Phase II.

Fig. 6) A and B; Undeveloped papillae in *Taxithelium merrillii*. C and D: Smooth leaves on *Isopterygium minuterameum*

FIG. 1

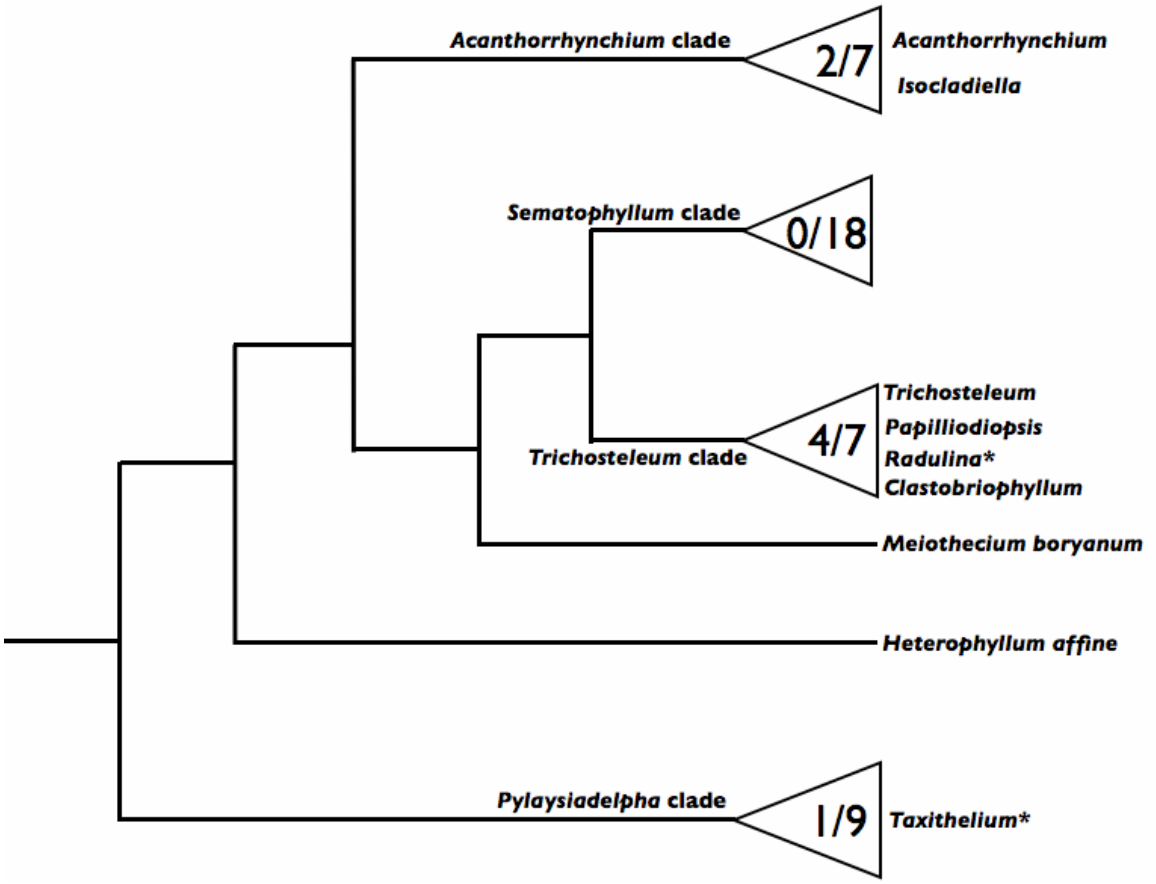

Acanthorrhynchium clade
2/7
Acanthorrhynchium
Isocladiella
Sematophyllum clade
0/18
Trichosteleum
Papilliodiopsis
Radulina*
Clastobriophyllum
Trichosteleum clade
4/7
Meiothecium boryanum
Heterophyllum affine
Pylaysiadelpha clade
1/9
Taxithelium*

FIG.2

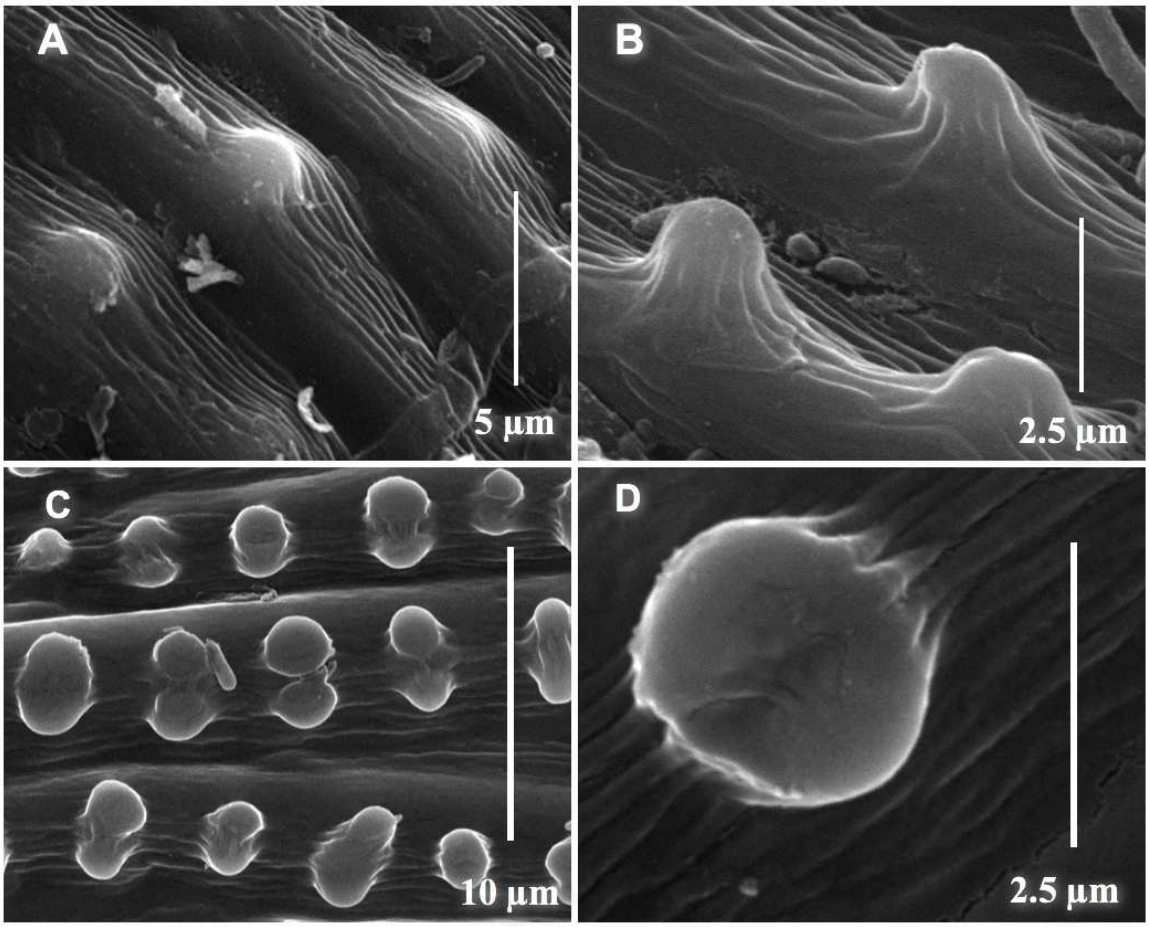


FIG. 3

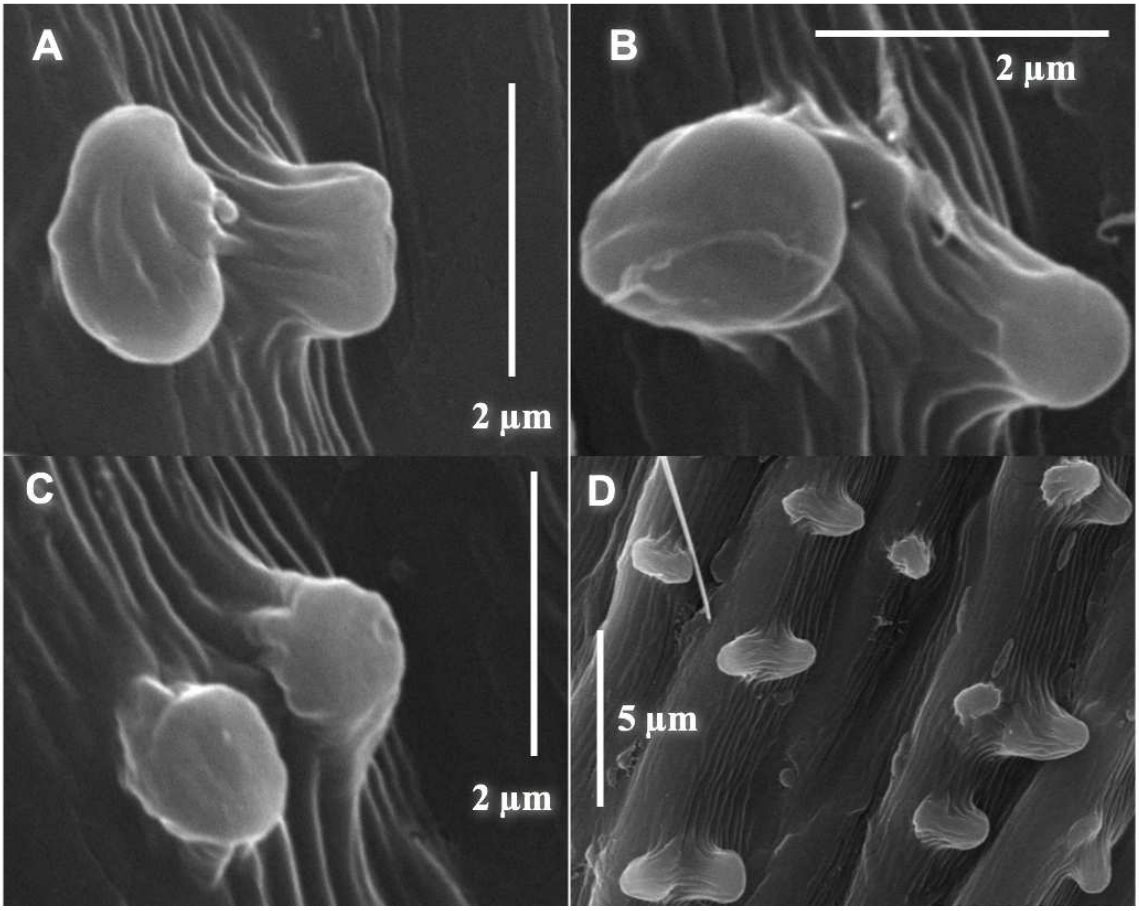


FIG. 4

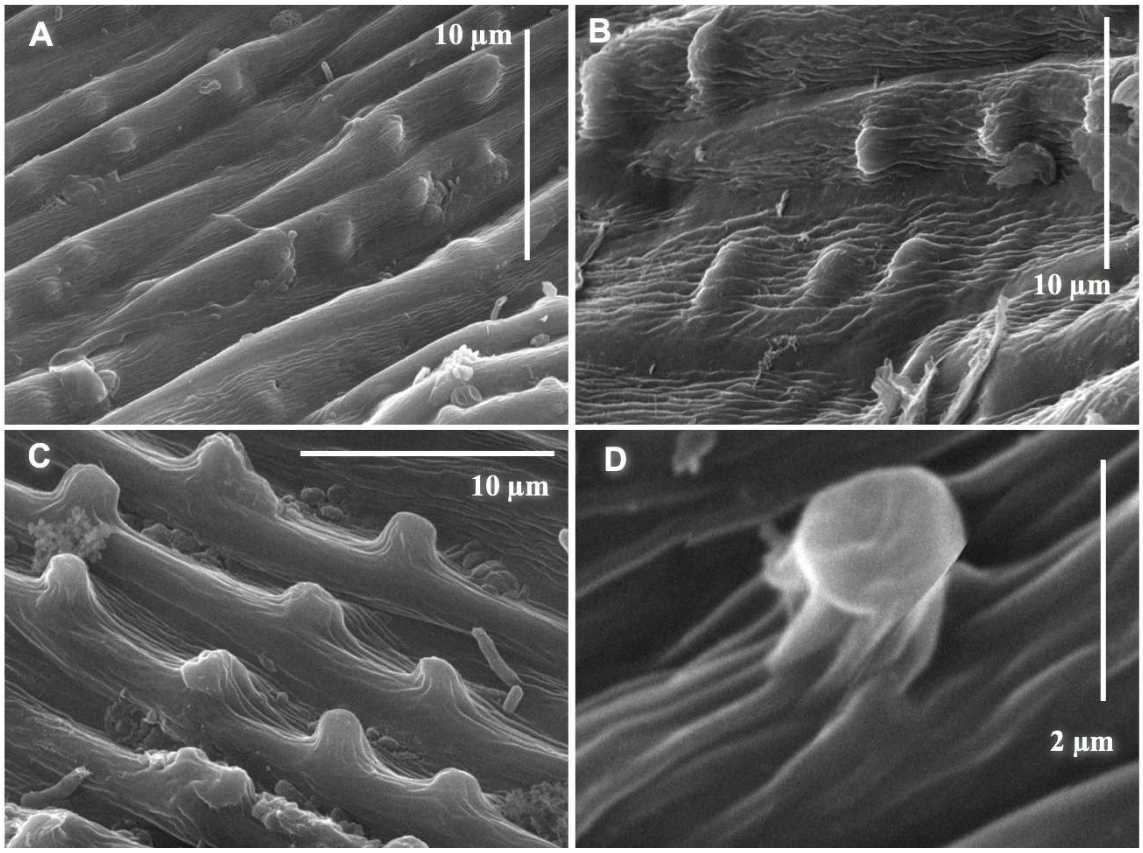


FIG. 5

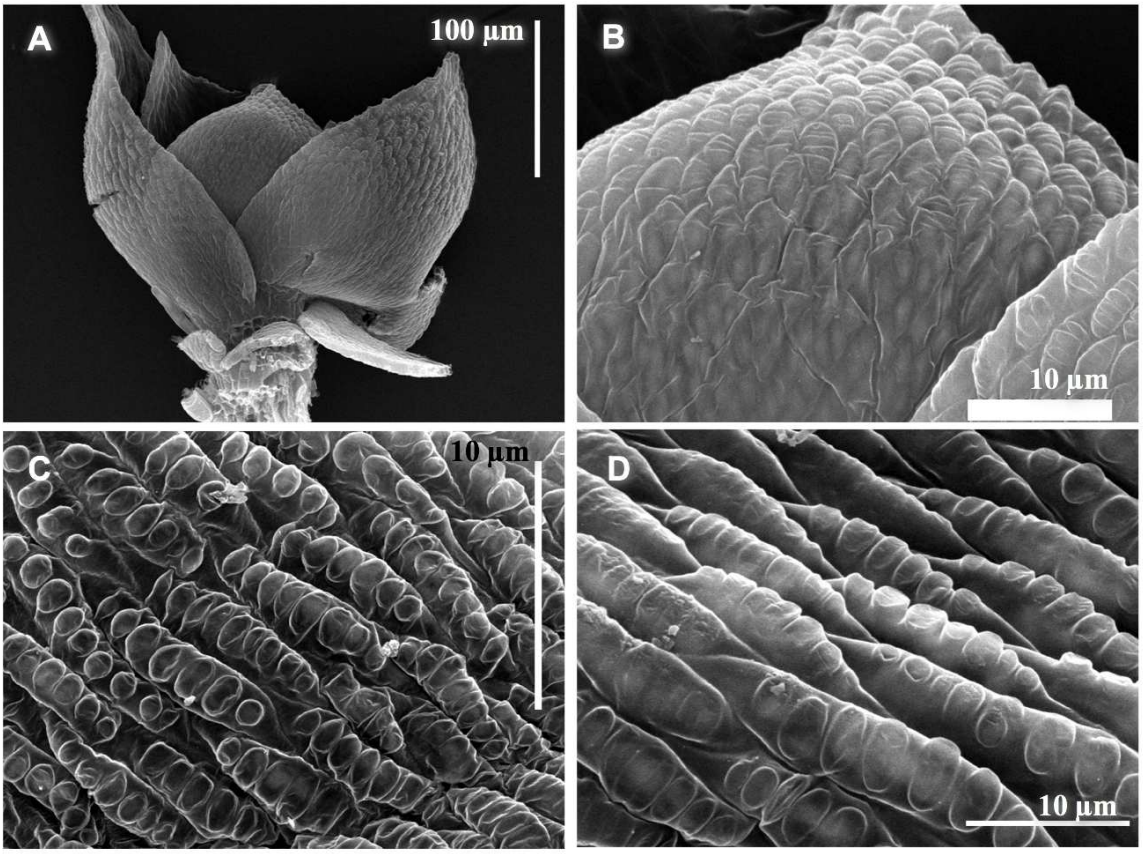
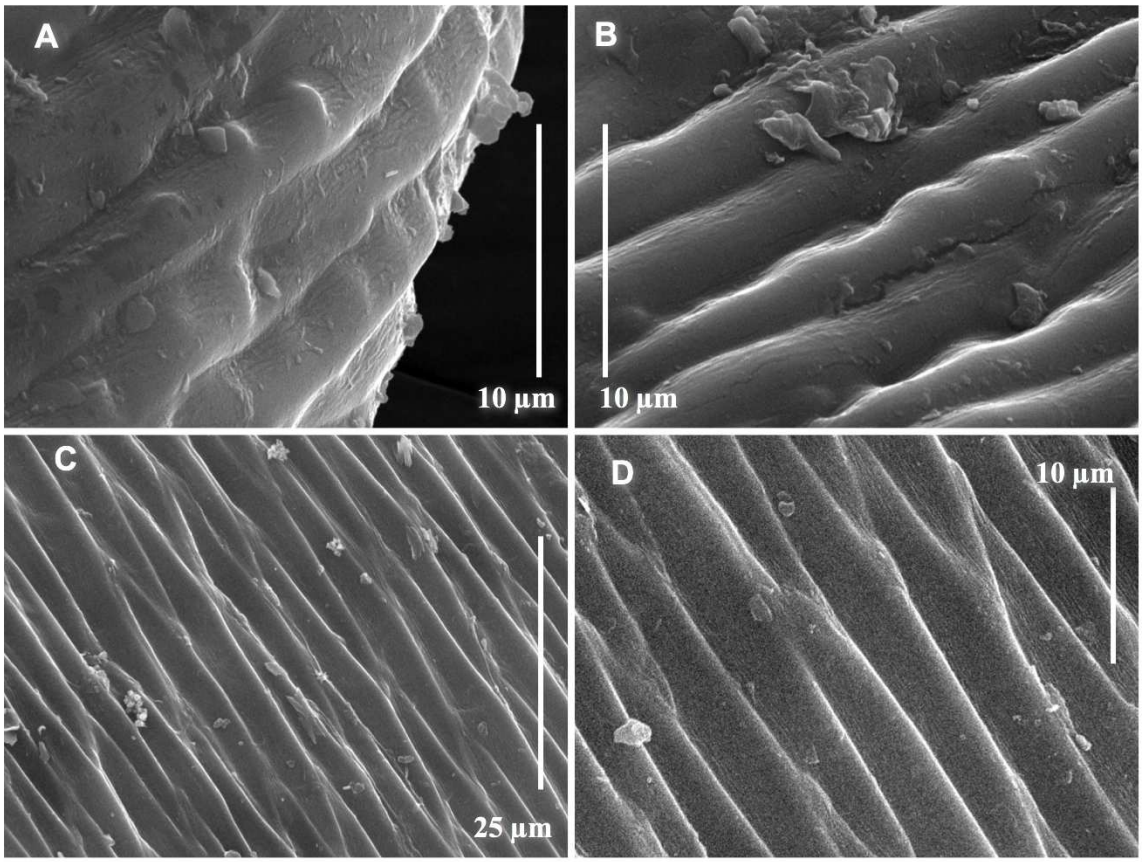


FIG. 6



CHAPTER 2

A MOLECULAR PHYLOGENY OF THE MOSS GENUS *TAXITHELIUM* SPRUCE EX MITT. (PYLAISIADELPHACEAE) BASED ON PLASTID, MITHOCHONDRIAL AND NUCLEAR MARKERS

This chapter has been submitted to the Journal "Systematic Botany".

Abstract– In order to test infrageneric classification and species delimitation within the pantropical moss genus *Taxithelium*, we constructed a molecular phylogeny using three cpDNA loci (*trn*L, *psb*T and *rps*4), three mtDNA loci (*rps*3, *nad*5 and *nad*4–5) and the nuclear gene *ho*1. Analyses of each locus separately and in various combinations support the monophyly of *Taxithelium*. Two major clades corresponding to taxonomically recognized subgenera were resolved within the genus. The first clade is composed of at least four smaller clades, three of which include only SE Asian plants and one is from the Americas; the latter is nested within the SE Asian clades. The second clade appears to have a Southeast Asia origin with two dispersal events to America. *Taxithelium* is highly variable morphologically and includes plants with pluripapillose leaf cells as well as plants that lack papillae. Our data show that *T. merrillii*, *T. concavum*, *T. pluripunctatum*, *T. planissimum* and *T. isocladum* are each demonstrably monophyletic units. On the other hand, *T. planum, T. nepalense* and *T. instratum* as circumscribed today are polyphyletic. *Taxithelium lindbergii* can be considered monophyletic only with the inclusion of *T. alare*. The *ho*1 nuclear locus is used for the first time, with promising results.

Keywords– ho1, nad5, psbT, nad4–5, rps3, rps4, trnG, Sematophyllaceae, papillae

The genus *Taxithelium* belongs to the large and speciose order Hypnales, a group of mosses in which gametangia are borne on lateral branches (pleurocarpous). Species of this genus are found throughout the tropics between 30°N and 20°S, with most species occurring in Southeast Asia, especially the Malesian region (Damanhuri and Longton 1996, Ramsay et al. 2002).

The order Hypnales comprises 80 percent of pleurocarpous moss species but phylogenetic relationships within the order are poorly resolved. The Hypnales apparently underwent a period of rapid diversification early in their history (Shaw et al. 2003), leading to a phylogenetic tree with very short internal branches connecting morphologically similar groups. Nevertheless, some hypnalean families have been shown to be monophyletic; for example: Lembophyllaceae (Quandt et al. 2000), Plagiotheciaceae (Pedersen and Hedenäs 2002), Hylocomiaceae (Chiang and Schaal 2000), Brachytheciaceae (Vanderpoorten et al. 2005), Meteoriaceae (Quandt et al. 2004) and Sematophyllaceae (Tsubota et al. 2001a,b).

Many taxonomists have placed *Taxithelium* in the Sematophyllaceae (Brotherus 1925; Vitt 1984; Buck and Vitt 1986; Tan and But 1997; Buck and Goffinet 2000; Ramsay et al. 2002). However, *Taxithelium* lacks the collenchymatous exothecial cells, long rostrate operculum, and inflated alar cells that are otherwise diagnostic for Sematophyllaceae, leading Seki (1969) to suggest exclusion of the genus from that family. Cladistic analyses of morphological characters (Hedenäs 1996; Tan and Jia 1998; Hedenäs and Buck 1999) also suggested that *Taxithelium* might not, in fact, belong to the Sematophyllaceae.

Recent molecular studies (Buck et al. 2000; Tsubota et al. 2001 a, b) showed that Sematophyllaceae s.l. includes two sister clades: the core sematophyllaceous taxa (e.g., *Sematophyllum* Mitt., *Acroporium* Mitt., and *Trichosteleum* Mitt.), and a clade that includes *Taxithelium, Pylaisiadelpha* Cardot, *Platygyrium* Schimp., *Isopterygium* Mitt. and *Brotherella* Loeske *ex* M. Fleisch. Tsubota et al. (2001a) called the latter group "the *Brotherella* lineage." Based on these results, Goffinet and Buck (2004) described the new family Pylaisiadelphaceae encompassing the "*Brotherella* lineage." However, the family lacks any obvious morphological synapomorphy. We follow the treatment of Goffinet and Buck (2004) and here consider *Taxithelium* to be a member of the Pylaisiadelphaceae; this study is focused on the delimitation of *Taxithelium* and on relationships among species within it rather than on its placement within the broader Hypnales. Relationships within the Sematophyllaceae s.s. and Pylaisiadelphaceae remain unclear.

Relationships between species of *Taxithelium* are also unclear. Renauld and Cardot (1901) divided *Taxithelium* into three subgenera: *Polystigma* (with several papillae disposed serially per cell), *Oligostigma* (with one or few papillae per cell, not disposed serially) and *Monostigma* (with only one papilla per cell). The subgenus *Polystigma* was divided into three Sections: *Vera* (non aquatic plants with vesiculose alar cells), *Aptera* (non aquatic plants with quadrate alar cells) and *Limnobiella* (aquatic plants). Cardot (1905) created section *Anastigma* for a single species that is now placed in *Phyllodon* (Buck 1987), and Brotherus (1909) created the subgenus *Pseudohypnella* also for a single species now placed in the Hookeriales (Buck et al. 2005).

Brotherus (1925) further broadened the boundaries of *Taxithelium* by including within the genus plants with smooth leaf cells, obscuring its limits and thus making it difficult now to differentiate morphologically from genera such as *Isopterygium*, *Chaetomitrium* Dozy & Molk., *Radulina* W. R. Buck & B. C. Tan and *Trichosteleum*. Ramsay et al. (2002) thought that, because *Taxithelium* was so variable, it was probably not monophyletic, and that most taxa should be transferred to other genera or even families. *Taxithelium* has received little attention since 1901; only Damanhuri and Longton (1996) presented a discussion of its characters. The genus has more than 230 accepted names associated with it and is in great need of revision. An ongoing study by Câmara (unpubl. data) will propose a re-circumscription of the genus and present a taxonomic treatment for one of its subgenera.

Papillae– The main characters used for recognizing *Taxithelium* are the presence of multiple papillae arranged in lines over the lumina (hence, Tax- "*taso*"= arranged and "*thelion"* = nipple), lack of long rostrate operculum, and a poorly developed alar region.

The location and size of papillae have been traditionally and widely used to define groups in mosses. In *Taxithelium* and *Radulina*, each cell produces multiple papillae in a line along the proximo-distal axis, but their location, shape and size are difficult to see under the light microscope. Other taxa in Sematophyllaceae have but a single papilla per cell.

As noted above, Brotherus (1925) included some species in *Taxithelium* that completely lacked papillae because of similarities to seriately papillose species in leaf shape, alar cell development, and sporophyte features (lack of collenchymatous

exothecial cells and lack of long rostrate opercula). Most taxonomists largely rejected a concept of a *Taxithelium* without papillae and some authors (e.g., Tan et al. 1996; Ramsay et al. 2002) have excluded these species from local treatments of *Taxithelium*. These "papilla-lacking" *Taxthelium* have remained mostly ignored and unplaced over the years.

Câmara and Kellogg (unpubl. data) have described in detail the development and micromorphology of papillae in Sematophyllaceae using scanning electronic microscopy (SEM). There are two distinct developmental pathways leading to two morphologically distinct kinds of mature papillae: "conical" (Fig. 1A) and "baggy" (Fig. 1B). In addition, some species lack obvious papillae when viewed with the light microscope, but under the SEM they may show small, undeveloped papillae at the apex of some leaves, resembling young conical papillae (Fig.1C, D). However, such young papillae were rare and difficult to find even under the SEM.

This study aims to 1) test the monophyly and assess the circumscription of *Taxithelium*, and investigate relationships within it, 2) reevaluate the current system of classification for the genus, 3) investigate the distribution of papillae within the genus, especially the papilla-lacking taxa, and 4) provide a framework for new classifications that better reflects evolution in the group.

MATERIAL AND METHODS

A phylogenetic hypothesis was constructed using data from chloroplast, mitochondrial and nuclear genomes. The use of different genomes allows greater

confidence in the results, since they are not likely to be subject to lateral transfer at the same time and are not subject to the same functional constraints.

Plant Materials—Specimens were selected to reflect the morphological variation observed within the genus in the ongoing revision by Câmara (unpubl. data), as well as to represent different geographic regions. More than one accession was included whenever possible to assess the monophyly of species and to reflect morphological and geographic variation.

Fresh material was collected in Southeast Asia; herbarium material was used when fresh material was unavailable. We used representatives of Pylaisiadelphaceae as outgroups.

DNA Extraction, Amplification —Total genomic DNA was extracted using the mini-CTAB protocol (Doyle and Doyle 1987). We amplified markers from all three genomes of each plant. From the plastid genome we used the gene coding for transfer RNA for glycine and its intron (hereafter, *trn*G), ribosomal protein 4 (*rps*4), and photosystem II protein T (*psb*T). From mitochondrial genome we used NADH-dehydrogenase subunit 5 (*nad*5), the spacer region between NADH-dehydrogenase subunits 4 and 5 (*nad*4–5), and ribosomal protein 3 (*rps*3). From the nucleus we amplified the single-copy gene for heme oxygenase I (*ho*1). Genes were amplified using the polymerase chain reaction (PCR); primer sequences for the seven loci are provided in Table1.

For *ho*1 we initially used the primers *ho*1F and R (Table 1), designed by Stuart McDaniel (unpubl. data); few taxa were successfully amplified, but we were able to obtain enough sequences to design new primers. Multiple combinations of forward and

reverse primers were then tested; the best results for *Taxithelium* were obtained using *ho*1aF and *ho*1R.

Single amplicons were produced for all markers except *nad*5, which was amplified as two overlapping fragments (Fig. 2): *nad*5K–*nad*5Li and *nad*5L–*nad*5Ki (Bell and Newton 2005). When amplification failed (which happened almost half the time), we used a nested PCR approach, beginning with the primers *nad*5_4F and *nad*5_2220R, followed by *nad*5_4F and *nad*5_3R. Amplification primers were used for sequencing, but for *nad*5 we also used internal primers *nad*5_IR1_pleuro and *nad*5_IF1.

The PCR amplification mix had a total volume of 20 µl and contained 2µl of 10× Thermophilic Buffer, 0.8µl of 50mM $MgCl_2$, 0.4 µl Taq (Promega), 1.5 µl BSA (10mg/ml), 3.2 µl 1mM dNTP, 1µl of each primer (10µM), and 3.0 µl of DNA. For *ho*1 amplifications, 1µl dimethyl sulfoxide (DMSO) was added when amplification initially failed. Genomic DNA was diluted 1:10 prior to use. The PCR profile for *ho*1, *trn*G, *psb*T, *rps*4, *nad*5-4, *nad*5 and *rps*3 was: 94°C (1min), 50–52°C (1 min), 72°C (1 min) for 35 cycles, always preceded by an initial melting step of 2 min at 94°C and a final extension of 72°C for 7 minutes. For nested PCR of *nad*5 the profile was: 96°C (45 sec), 55°C (1 min), 72°C (1min) for 35 cycles, also preceded by an initial melting step of 1.5 min at 96°C and with final extension of 72°C for 7 minutes.

Sequencing and Phylogenetic analyses — PCR products were cleaned using 3 µl of ExoSap mixture (0.2 µl of Exonuclease I plus 0.2 µlof Alkaline Shrimp Phosphatase and 0.6 µl dH_2O), heated at 36°C (30 min) and then at 85°C (15 min). Clean PCR products were used in cycle-sequencing reactions with the Big-Dye terminator kit (Applied

Biosystems). The resulting products were purified by ethanol precipitation and analyzed in an ABI 3100 (Applied Biosystems). Forward and reverse strands were sequenced. In some cases, clean PCR products were sequenced by MACROGEN Inc. (Seoul, Korea). Sequences were assembled using SEQMAN II (version 5.05; DNAStar, Madison, WI). All sequences have been submitted to GenBank.

All datasets were initially aligned using Clustal X (Higgins and Sharp 1988), then adjusted by eye, and the alignments checked at the amino acid level, using MacClade 4.08 (Maddison and Maddison 2000), and exported as Nexus files. Independent searches of trees were made as follows: 1) each gene alone, 2) all mitochondrial genes, 3) all plastid genes, 4) plastid and mitochondrial genes together, 5) all markers together.

A second set of analyses including only individuals corresponding to the *Vernieri* clade was carried out to assess the monophyly of species and relationships within the group. For this analysis, the mtDNA dataset was used because it had the most accessions for the clade; species from the *Planum* clade were used as outgroup.

Phylogenetic analyses were carried out using maximum parsimony (MP), maximum likelihood (ML), and Bayesian inference (BI) using PAUP* v. 4.0b10 for Macintosh (Swofford 2002), GARLI v. 0951 for Macintosh (Zwickl 2006) and Mr Bayes v. 3.1.2 (Ronquist and Huelsenbeck 2003), respectively. Heuristic MP searches were done with 100 random addition replicates, and tree-bisection -reconnection (TBR) branch swapping, saving a maximum of 10,000 trees; all characters were unordered and equally weighted, and gaps were treated as missing data.

For ML and BI analyses the best-fit model of evolution for each locus was obtained using Modeltest 3.06 (Posada and Crandall 1998); for combined analyses a single model was used for combined matrixes (tables 2 and 3).

Clade support was evaluated using the non-parametric bootstrap (Felsenstein 1985), with 1,000 replicates for MP and a 100 replicates for ML. BI support was evaluated using posterior probabilities, estimated using Markov Chain Monte Carlo simulations with four chains, each for 5,000,000 generations, sampled every 1,000 generations, starting with a random tree. For each run the first 1,000 trees were discarded as "burnin."

Shimodaira-Hasegawa test — SH tests (Shimodaira and Hasegawa 1999, Goldman et al. 2000) were performed to statistically compare alternative hypotheses for the phylogeny. Constraint trees were constructed in MacClade, then loaded in PAUP* and a maximum likelihood search was done to find the optimal tree given the constraint. The new values were compared with the score of the original best tree using the SH test as implemented in PAUP* using 1000 replicates and under resampling estimated log likelihood (RELL).

RESULTS

Phylogenetic analyses —A total of 359 new sequences were obtained for this study. Trees from individual markers differed only in degree of resolution, but did not otherwise present strong conflict in topology; the few conflicts were present only in nodes with very low support, so topologies were considered congruent whatever analytical method was

used. The new nuclear marker, *ho*1, provided good resolution of most nodes (Fig. 3). Tree statistics are presented in Tables 2 and 3. Likewise, the trees for the different genomes (plastid, mitochondrion, nuclear) did not show conflict under any analytical method. Accordingly, the datasets were combined into a matrix of 5320 aligned base pairs; 812 sites were variable and 389 parsimony informative.

To illustrate the utility of the *ho*1 locus, we show a reconstruction based on this marker alone (Fig. 3). *Taxithelium* is resolved as monophyletic and contains two main clades (here named *Planum* and *Vernieri*), which are formally being recognized as subgenera by Câmara (unpubl. data). The *Vernieri* clade is characterized by the presence of conical papillae, whereas the *Planum* clade is characterized by the presence of "baggy" papillae (Câmara and Kellogg unpubl. data); papillae have been lost in one clade within the *Planum* group (Fig. 3). Also these results show that the only New World species are in a clade sister to all other clades in *Planum* but without support.

The combined tree from all seven loci (Fig. 4) shows that the *Planum* clade includes four subclades. Clade I is composed of specimens of *T. merrillii*, which are the only members of *Taxithelium* that lack papillae, and are found only in SE Asia and Australia.

Clade II (Fig. 4) is the only one within the *Planum* clade that has representatives in the Americas, and includes *T. planum*, *T. concavum* and *T. perglabrum*. The only available African specimen (*T. perglabrum*) is nested within the American ones, but more sampling is needed for African representatives of *Taxithelium*. *Taxithelium concavum* is monophyletic (see also Fig. 3), but not *T. planum*; the latter could be considered monophyletic only with the inclusion of the rest of clade II.

The third clade (clade III), which is exclusively Southeast Asian (Fig. 4), is composed of *T. nepalense* and *T. instratum* (and *T. ramicola*; see Fig. 3). *Taxithelium instratum* is clearly polyphyletic as other accessions are also present in clade IV.

A fourth group (clade IV) contains *T. kerianum* and *T. instratum* (Fig. 4). *Taxithelium kerianum* is monophyletic but the representatives of *T. instratum* in this clade form a basal paraphyletic complex. This clade (IV) is restricted to SE Asia and Australia.

Relationships within the *Planum* clade differ between the *ho*1 and the combined datasets. The phylogeny of *ho*1 sequences (Fig. 3) places the New World clade as sister to all other (Old World) clades, but support is weak (52% bootstrap). The combined dataset (Fig. 4) places the New World clade nested within the SE Asian clades with much better support (88% bootstrap).

We also investigated the relationships within the *Vernieri* clade in more detail as part of an ongoing taxonomic revision of the group (Fig. 5). Additional accessions were sampled for mitochondrial markers which provided 2644 aligned based pairs, with 132 sites that were variable and 65 potentially parsimony informative (Table 3). For the five taxa represented by more than one accession, four are monophyletic, the exception being *T. lindbergii*.

Taxithelium pluripunctatum and *T. kaernbachii* are sister taxa (Fig. 5), and together these are sister to *T. vernieri*, although neither relationship has support. *Taxithelium pluripunctatum* is a New World species, whereas *T. kaernbachii* is from SE Asia and Africa and *T. vernieri* is from the Pacific Islands. *Taxithelium portoricense*, another New World taxon, is sister to *T. planissimum* from SE Asia; this relationship is

strongly supported. They are both sister to *T. isocladum* (also from SE Asia) but without support. *Taxithelium levieri* appears as sister to a larger clade composed by *T. lindbergii* and *T. alare*, but also without support; they are all from SE Asia. *Taxithelium alare* is a monophyletic unit within *T. lindbergii*.

It is important to note that the names within the "*Planum* clade" were adopted based on the study of the corresponding vouchers and the type collections, but this group has not yet been taxonomically revised. The *Vernieri* clade in currently under revision (Câmara unpubl. data).

DISCUSSION

DNA sequences — This study has used several standard markers as well as novel ones. Chloroplast markers are by far the most widely used for phylogenetic reconstruction in bryophytes, whereas mitochondrial markers are less common. *nad*5 has been used increasingly (Bell and Newton, 2004; Bell and Newton 2005; Buck et al. 2005; Shaw et al. 2005), and Groth-Malonek et al. (2007) have demonstrated the value of the *nad*4–5 spacer. Our data represent the second application of this marker, and confirm its utility. To our knowledge, this is the first study to use the mitochondrial *rps*3 marker in mosses.

Low copy nuclear markers have not been widely used for moss phylogeny. Previously used nuclear markers include mostly those in the ribosomal complex (18s, 5.8s, 26s and ITSI and II), which exist in tandem arrays and have their own complex patterns of evolution. The few exceptions include Wall (2002), Shaw et al. (2005b) and Szovenyi et al. (2006). We show that the nuclear gene *ho*1 is highly promising. This

marker alone has provided a highly supported phylogeny of closely related species (Fig. 3).

Monophyly and circumscription — Our results strongly support *Taxithelium* as monophyletic. Within the genus are two well-supported clades, each of which corresponds to subgenera in Câmara (unpubl. data).

There are two kinds of papillae within *Taxithelium*: the baggy papillae are found only in the *Planum* clade and consitute a synapomorphy for the group. Conical papillae are present in the *Vernieri* clade but also in all other papillose Sematophyllaceae (Câmara and Kellogg unpubl. data). The published phylogeny for the family Sematophyllaceae (Tsubota et al. 2001a,b) does not include all taxa bearing papillae, making it impossible to assess precisely the phylogenetic relations between them and to infer the number of origins of papillae in the family.

Renauld and Cardot (1901) had recognized a subgenus *Polystigma* divided into sections *Vera*, *Aptera* and *Limnobiella*. The section *Limnobiella* does not contain any species currently included in *Taxithelium* but is made up of a heterogeneous mix of species representing distinct genera, mostly *Acanthorrhynchium* M. Fleisch. and *Phyllodon* Bruch & Schimp., (Buck 1987). The remaining sections (*Vera* and *Aptera*) are not monophyletic, and representatives are scattered between the two major clades (*Planum* and *Vernieri*) recognized here (Fig. 6). Renauld and Cardot's subgenera *Monostigma* and *Oligostigma* also do not contain any representatives of *Taxithelium*, and include species from other genera such as *Trichosteleum*, *Taxiphyllum* M. Fleisch. and *Acanthorrhynchium* (Buck 1987).

The subgenera and sections of Renauld and Cardot (1901) are clearly polyphyletic and should be abandoned (Fig. 6). Some names cannot be used, since an autonymic subgenus is required by the International Code of Botanical Nomencalture. This issue is being addressed by the ongoing re- circumscription of the genus by Câmara.

The presence of serially disposed papillae over the lumen of each leaf cell is a synapomorphy for *Taxithelium*, although the papillae are lost in one species, here recognized as *T. merrillii* (Fig. 3), thus supporting Brotherus' (1925) views. The only other taxon within Sematophyllaceae that has a similar pattern of leaf papillation is the genus *Radulina*, but it falls well outside *Taxithelium* in our analyses (Fig. 3). An SH test that constrained *Radulina* and *Taxithelium* to be sister taxa was significantly less likely than the unconstrained ML tree, rejecting a sister group relationship between the two (Table 4). *Radulina* is easily distinguished from *Taxithelium* by the distally verrucose seta, collenchymatous exothecial cells, and inflated, colored alar cells, which are lacking in *Taxithelium*. Thus pluripapillose leaves have arisen at least twice in Sematophyllaceae. A phylogeny for Sematophyllaceae with broader sampling would improve our understanding of the evolution of morphological characters within the family.

Taxonomic implications—The present study clearly suggests the polyphyletic nature of some species within these subgenera, and consequently the need to review the genus.

Within the "*Planum* clade", clade II in the combined analyses (Fig. 4) shows *T. perglabrum* nested within *T. planum*; in the *ho*1 tree (Fig. 3) the situation persists, but a sister relationship between *T. perglabrum* and *T. planum* 4 is suggested. *Taxithelium*

planum 4 is morphologically quite distinct and is from the Andes region; it will probably be recognized as distinct species when the group is taxonomically revised.

Also in the combined tree (Fig. 4), *T. nepalense* and *T. instratum* are nested together (and also with *T. ramicola* in the *ho*1 tree (Fig. 3)). Much confusion on the morphological limits of these three taxa exists and a taxonomic revision is needed. The alar regions of all the species mentioned above have similarities, but leaf shape and apex is highly variable.

In clade IV (Fig. 4), *T. instratum* and *T. kerianum* are nested together. Characters such as perichaetial leaves are very helpful in separating these species but have not been much used. This again shows the need of revision for this group and a better understanding of its morphology.

The relationship between the common species included in the "*Planum* clade" from SE Asia and those of tropical America has been a source of disagreement in the literature. For example, Buck (1998) synonymized *T. nepalense* (SE Asia) with *T. planum* (Americas), based on morphological similarities (complanate branches with ovate leaves and quadrate alar cells). Our molecular data, however, show that the two species are not closely related. They can be distinguished morphologically since leaf apices and supra alar cells differ between the two. Similarly, the identity of *T. concavum* has been controversial; Buck (1998) synonymized it with *T. planum*. A series of SH tests (Table 4) was performed to test these relationships. The following constraint trees were built and tested: *T. planum* + *T. nepalense* and *T. planum* + *T. concavum* + *T. nepalense*. The results rejected the monophyletic association of these (Table 4). For these reasons we suggest that *T. planum* and *T. nepalense* be recognized as different species.

On the other hand, *Taxithelium concavum* is a monophyletic unit nested within *T. planum*. In the *ho*1 tree (Fig. 3), *T. concavum* is well supported as sister group to a larger clade containing *T. planum* and *T. perglabrum*. In the combined tree (Fig. 4), *T. concavum* is a monophyletic unit embedded in the *T. planum* + *T. perglabrum* clade, but most sister relationships within that clade lack support. Therefore *T. concavum* could be recognized either as a distinct species or as part of a broader *T. planum* (plus *T. perglabrum*). The question should be solved when the *Planum* clade is taxonomically revised. It is our hope that this phylogeny will shed some light upon the taxonomic problems that have plagued this genus.

The *Vernieri* clade is being revised; it includes 11 species, of which eight are included in the phylogeny presented here. Of these eight, we were able to study multiple accessions of five putative species. The molecular data confirm the monophyly of the specimens assigned to *T. alare*, *T. pluripunctatum*, *T. planissimum*, *T. isocladum* and *T. vernieri*. It was not possible to obtain DNA from the remaining species (*T. ramivagum*, *T. muscicola*, and an undescribed one).

Taxithelium alare and *T. lindbergii* have overlapping geographical distributions and many morphological similarities (alar cells, leaf shape, leaf margins, perichaetial leaves, seta length), differing mostly in size. *Taxithelium alare* is larger and grows mostly at high elevations (but is not restricted to them). *Taxithelium lindbergii* is smaller and is mostly from lowlands (but is not restricted to them). In the morphometric study by Câmara (unpubl. data) they were indistinguishable. Our results (Fig. 5) show that *T. alare* comprises a monophyletic unit within *T. lindbergii* and consequently a monophyletic *T.*

lindbergii would have to include *T. alare.* Assuming that species should be monophyletic, we suggest that only one species should be recognized (*T. lindbergii*).

Biogeographic considerations—Many mosses show a biogeographic pattern of "everything is everywhere" (Shaw et al. 2005a), with most species being widely dispersed over several continents. In contrast, we have found here a biogeographically distinct pattern, with monophyletic units restricted to smaller geographical areas.

The *Planum* clade may have originated in SE Asia, with one dispersal event to the Americas. As can be inferred by the combined tree (Fig. 4), of the four clades, only clade II has representatives in the New World and this clade is nested within the SE Asian species. Thus the ancestral state is more likely to be SE Asian, and the New World species may be the result of one dispersal event to the Americas.

Within the *Vernieri* clade, the two species from the Americas (*T. pluripunctatum* and *T. portoricense*) are not sister taxa. We tested the monophyly of the New World taxa with an SH test, and a sister relationship between the two was rejected (Table 4). In this clade all other species are from Southeast Asia. (Fig. 5), again, the ancestral distribution state is more likely to be SE Asian, in this case with two dispersal events to the Americas.

As noted above, when the SE Asia taxon *T. nepalense* was considered a synonym of the American *T. planum*, the latter appeared to be a widespread species. However our data demonstrate that the distribution of each is in fact narrower (Fig. 3, 4 and Table 4), and revealed a signficant biogeographic pattern that had been hidden by taxonomic confusion. This shows the importance of investigating species level relationships,

especially using molecular markers, and the need of finding markers with the necessary variation, such as *ho*1.

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TABLE 1. Primers used in this study.

Sequence	Source
*trn*G	Pacak et al., 2000
*rps*4	Nadot et al., 1994
*psb*T	Krellwitz et al., 2001
*nad*4–5	Groth-Malonek et al. 2007
*nad*5K	Beckert et al. 1999
*nad*5Li	Beckert et al. 1999
*nad*5L	Beckert et al. 1999
*nad*5Ki	Beckert et al. 1999
*nad*5_4F	Buck et al. 2005
*nad*5_3R	Buck et al. 2005
*nad*5_2220R (5’ ATATTCCAGTGGTTGCCGCG 3’)	Quandt, unpublished
*nad*5_IR1_pleuro (5’ GATTCAATACAAGGTTTTCTACA 3’)	Quandt, unpublished
*nad*5_IF1 (5’ GATTTAACTAAGATACGAAGCATT 3’)	Quandt, unpublished
*ho*1F (5’ CTTTGCTCATTCAG 3’)	McDaniel, unpublished
*ho*1R (5’ CAAGATCTTGCCAGAGTAC 3’)	McDaniel, unpublished
*ho*1aF (5’ TGCTCATTCAGCTGGTGGTA 3’)	This study
*ho*1aR (5’ TGGACCTTGGATGACAGTAGG 3’)	This study
*ho*1bF (5’ TCAGCTGGTGGTAGATTCAT 3’)	This study
*ho*1bR (5’ ATGAGAACTGGACCTTGGAT 3’)	This study
*rps*3F*2* (5’ CATTTTCCTAAAAGGACATTCA 3’)	Boles, unpublished
*rps*3R3 (5’ TTTTTCMAATAATAATAACGACTG 3’)	Boles, unpublished

TABLE 2. Characteristics of individual markers. CI= consistency index; RI= Retention index.

DNA region	***rps***4	***trn***G	***psb***T	***nad***5	***nad***4–5	***rps***3	***ho***1
Taxa included	59	50	59	59	43	50	39
Matrix length	687	676	540	1177	1056	411	773
Variable sites	194	170	92	193	128	27	411
Parsimony informative sites	104	100	62	81	63	20	240
N^{o} trees	10,000	10,000	10,000	10,000	128	10,000	10,000
Tree length	329	280	135	234	159	34	695
CI	0.699	0.7	0.77	0.787	0.811	0.794	0.777
RI	0.806	0.815	0.893	0.837	0.908	0.933	0.818
Model	K81uf+G	K81uf+G	K81uf+G	GTR+G	HKG+G	HKY+G	HKY+G
Log. Likelihood	-2727.113	-2365.998	-1442.227	-3255.538	-2516.325	-751.012	-4381.127

TABLE 3. Characteristics of combined datasets and of subgenus *Vernieri*. CI= consistency index; RI= Retention index.

DNA region	**All mitochondrial**	**All Plastid**	**Combined (all regions)**	***Vernieri***
Taxa included	47	44	32	19
Matrix length	2644	1903	5320	2644
Variable sites	276	387	812	132
Parsimony informative sites	136	213	389	65
No. trees	10,000	10,000	432	14
Tree length	367	609	1211	159
CI	0.768	0.726	0.757	0.836
RI	0.841	0.791	0.737	0.814
Model	HKY+I+G	K81uf+I+G	HKY+I+G	HKY+G
Log. Likelihood	-5959.697	-5992.954	-13896.096	-4587.918

TABLE 4. Results from the SH tests. Statistically worse trees at P< 0.05 are marked with asterisk (*).

Constrained topology	Tree used	-ln L	Diff –ln L	P
T. portoricense + *T. pluripuncatum*	mt	4531.58633	26.79690	0.016*
Radulina + *Taxithelium*	*ho*1	4582.688247	48.45221	0.0001*
T. planum + *T. concavum* + *T. nepalense*	Combined	12018.57370	26.29557	0.038*
T. planum + *T. nepalense*	Combined	12018.57370	26.29557	0.046*

Fig. 1. SEM pictures of papillae in *Taxithelium*. A. Conical papillae, B. Baggy papillae, C and D, undeveloped papillae from *T. merrillii*.

Fig. 2. The *nad*5 region in mosses.

Fig. 3. Maximum likelihood cladogram obtained from *ho*1. Numbers at the branches are bootstrap values and Bayesian posterior probabilities respectively. Only values above 50% and 95 are shown for bootstrap and posterior probabilities. Numbers after taxa represent different accessions.

Fig. 4. Maximum likelihood phylogram obtained from combined dataset (all markers). Numbers at the branches are bootstrap values and Bayesian posterior probabilities respectively. Only values above 50% and 95 are shown for bootstrap and posterior probabilities. Numbers after taxa represent different accessions.

Fig. 5. Maximum Likelihood cladogram obtained from mtDNA dataset. Numbers above the branches are bootstrap and posterior probabilities values respectively. Only values above 50% and 95 are shown for bootstrap and posterior probabilities. New World taxa are marked with an asterisk (*). Numbers after taxa represent different accessions.

Fig. 6. Overview of Renauld and Cardot's (1901) system of classification. Continuous line represents taxa in section *Vera* and dashed line the section *Aptera*

FIG. 1

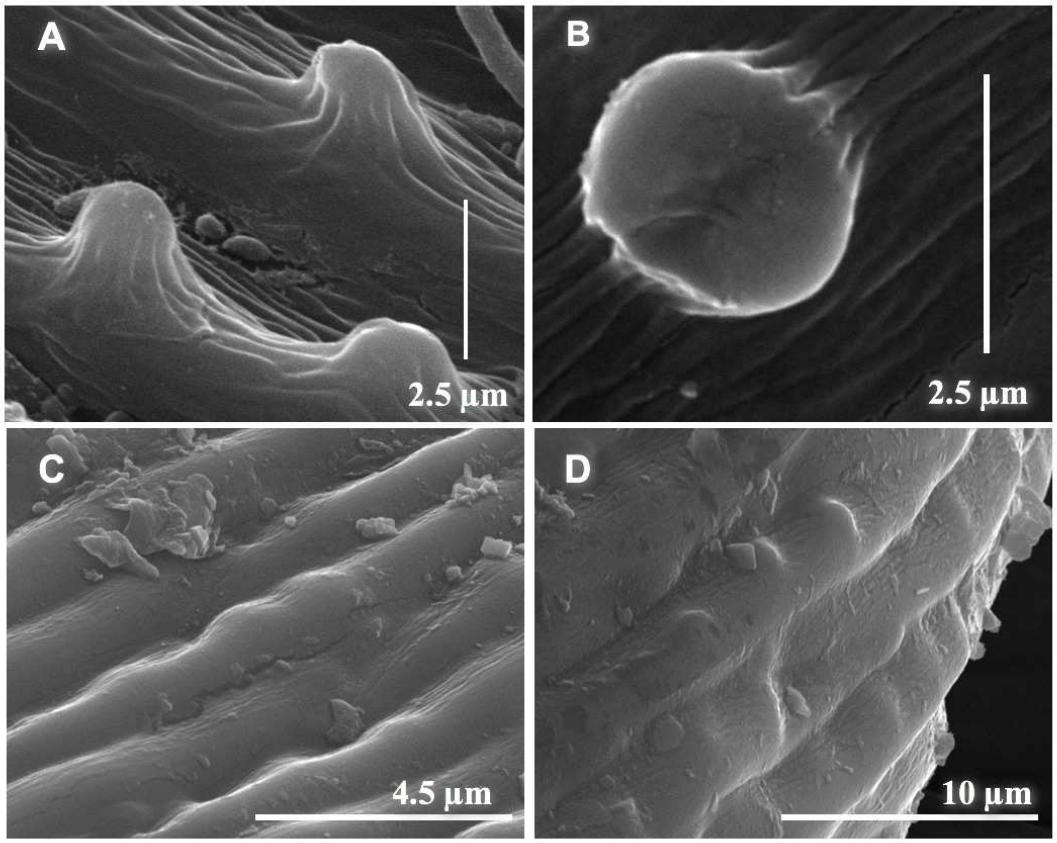


FIG 2

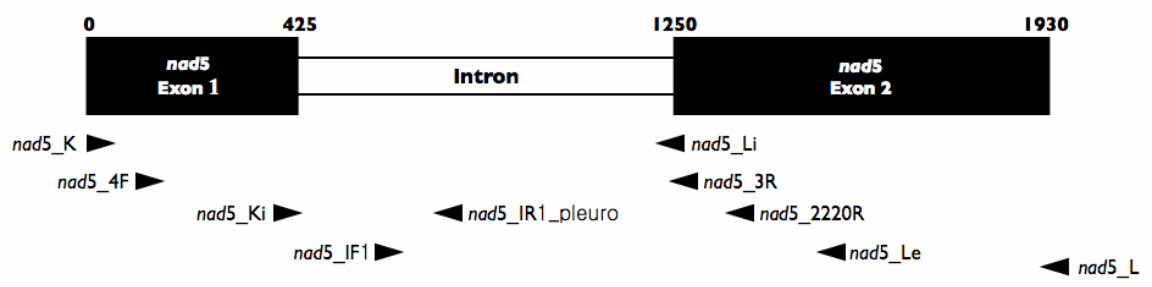

0
425
1250
1930
nad5 Exon 1
Intron
nad5 Exon 2
nad5_K
nad5_4F
nad5_Ki
nad5_IF1
nad5_IR1_pleuro
nad5_Li
nad5_3R
nad5_2220R
nad5_Le
nad5_L

FIG. 3

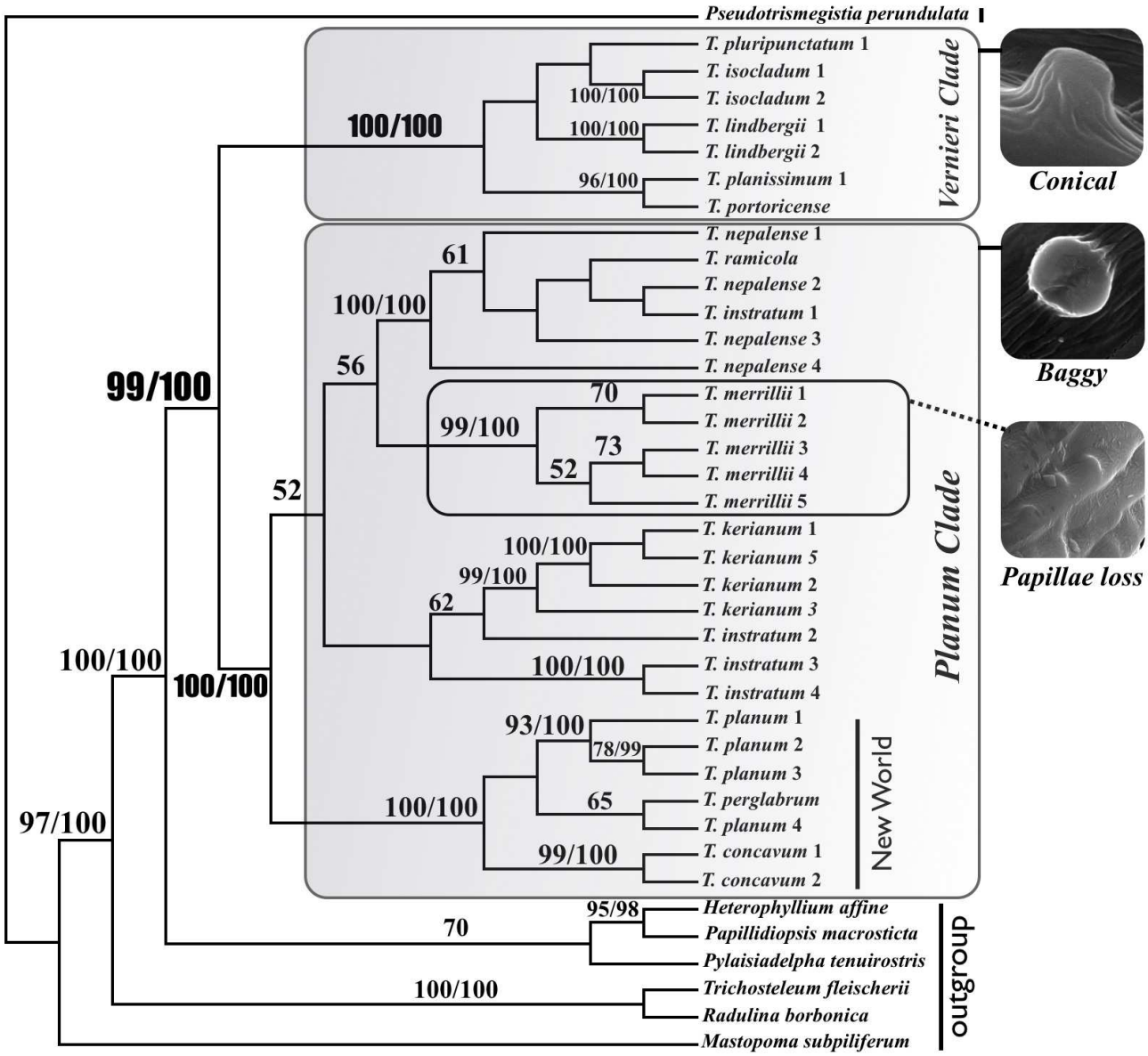

Pseudotrismegistia perundulata
T. pluripunctatum 1
T. isocladum 1
T. isocladum 2
T. lindbergii 1
T. lindbergii 2
T. planissimum 1
T. portoricense
Vernieri Clade
Conical
T. nepalense 1
T. ramicola
T. nepalense 2
T. instratum 1
T. nepalense 3
T. nepalense 4
T. merrillii 1
T. merrillii 2
T. merrillii 3
T. merrillii 4
T. merrillii 5
Baggy
Papillae loss
T. kerianum 1
T. kerianum 5
T. kerianum 2
T. kerianum 3
T. instratum 2
T. instratum 3
T. instratum 4
T. planum 1
T. planum 2
T. planum 3
T. perglabrum
T. planum 4
T. concavum 1
T. concavum 2
Planum Clade
New World
Heterophyllium affine
Papillidiopsis macrosticta
Pylaisiadelpha tenuirostris
Trichosteleum fleischerii
Radulina borbonica
Mastopoma subpiliferum
outgroup
100/100
100/100
100/100
96/100
61
100/100
56
99/100
70
99/100
73
52
52
100/100
99/100
62
100/100
100/100
93/100
78/99
65
100/100
99/100
97/100
95/98
70
100/100

FIG. 4

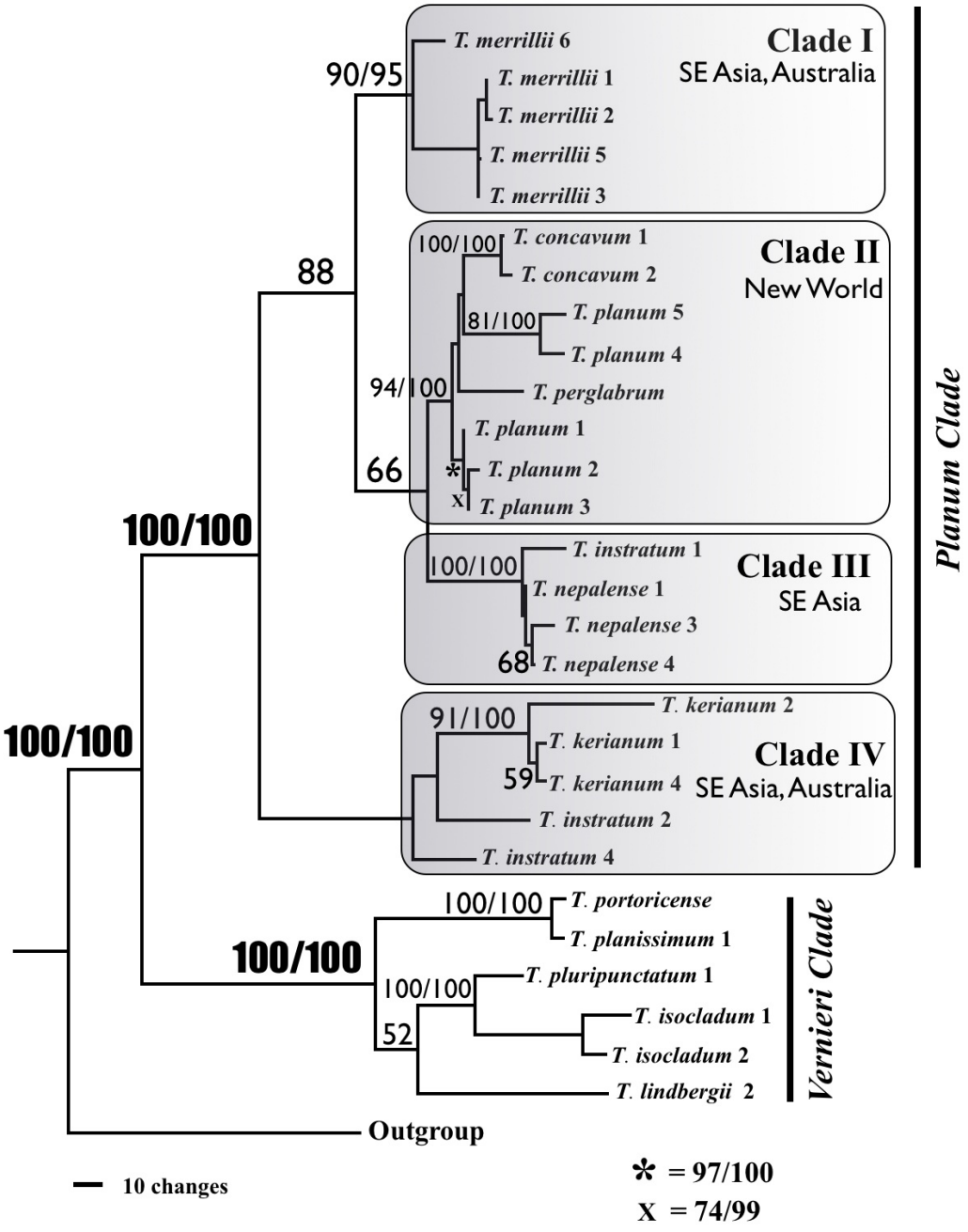

Clade I
SE Asia, Australia
T. merrillii 6
T. merrillii 1
T. merrillii 2
T. merrillii 5
T. merrillii 3
90/95
Clade II
New World
T. concavum 1
T. concavum 2
T. planum 5
T. planum 4
T. perglabrum
T. planum 1
T. planum 2
T. planum 3
100/100
81/100
94/100
66
88
Clade III
SE Asia
T. instratum 1
T. nepalense 1
T. nepalense 3
T. nepalense 4
100/100
68
Clade IV
SE Asia, Australia
T. kerianum 2
T. kerianum 1
T. kerianum 4
T. instratum 2
T. instratum 4
91/100
59
100/100
Planum Clade
Vernieri Clade
T. portoricense
T. planissimum 1
T. pluripunctatum 1
T. isocladum 1
T. isocladum 2
T. lindbergii 2
100/100
100/100
52
Outgroup
10 changes
= 97/100
X = 74/99

Fig. 5

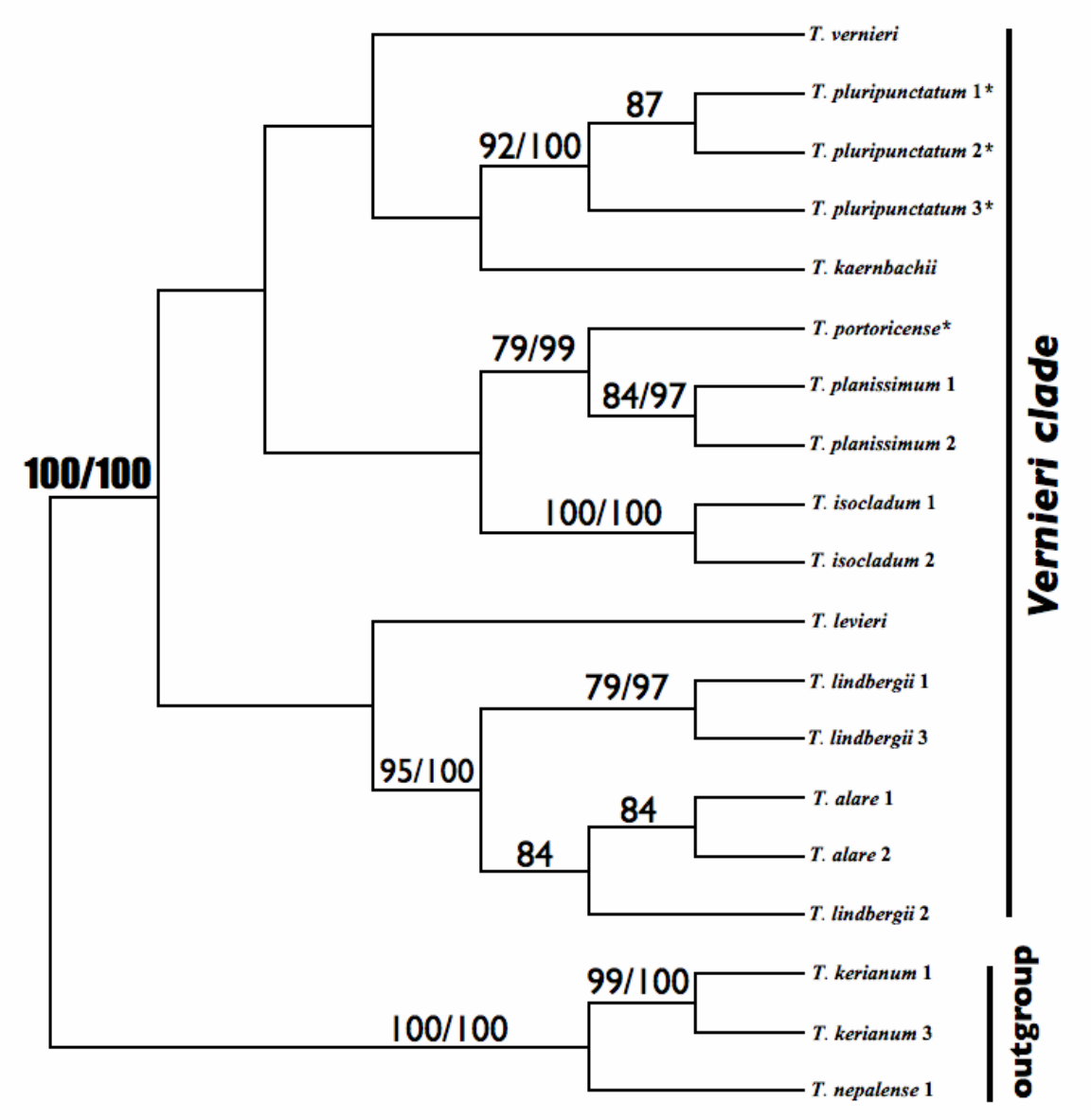
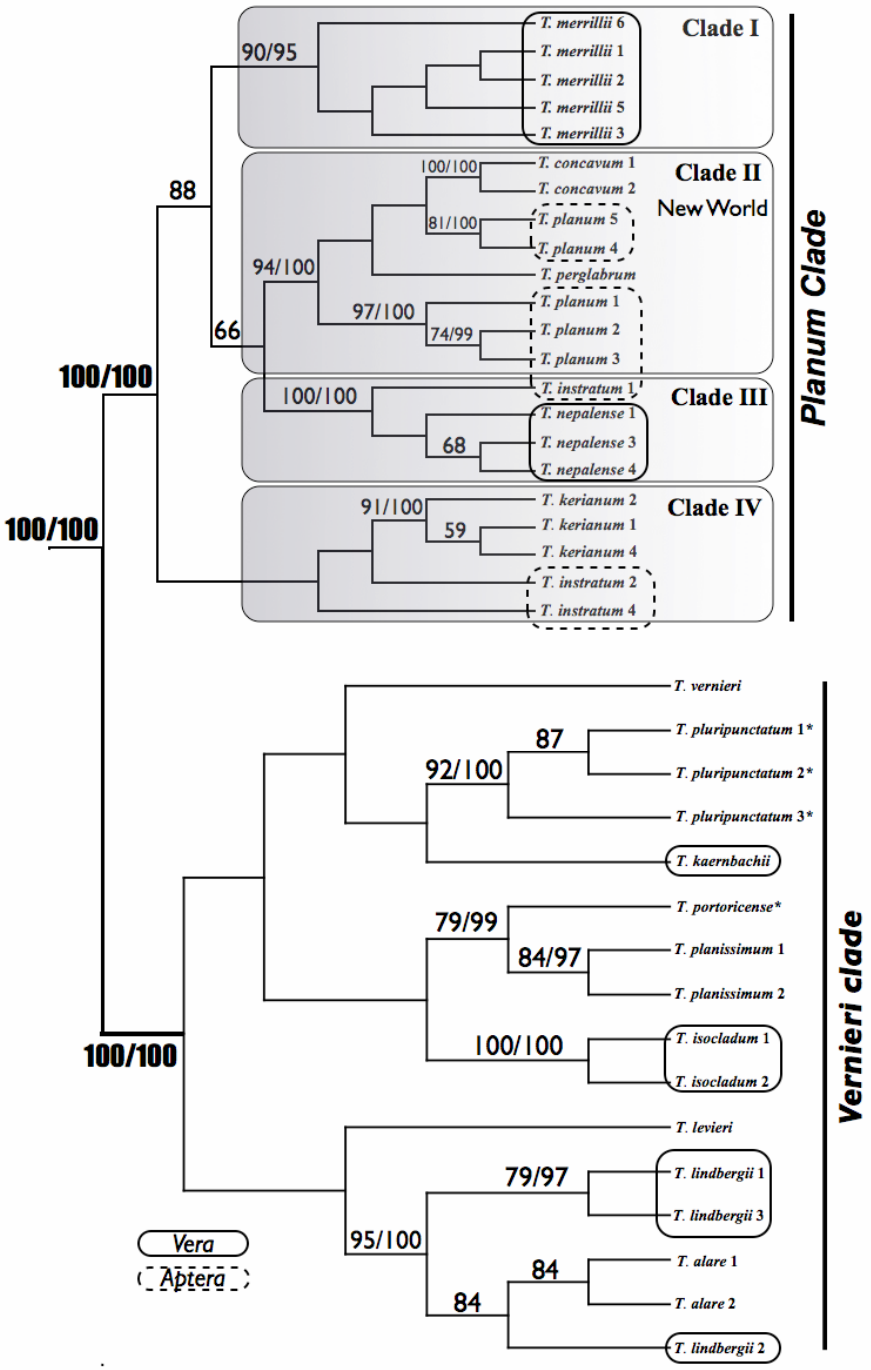

T. vernieri
T. pluripunctatum 1*
T. pluripunctatum 2*
T. pluripunctatum 3*
T. kaernbachii
T. portoricense*
T. planissimum 1
T. planissimum 2
T. isocladum 1
T. isocladum 2
T. levieri
T. lindbergii 1
T. lindbergii 3
T. alare 1
T. alare 2
T. lindbergii 2
T. kerianum 1
T. kerianum 3
T. nepalense 1
87
92/100
79/99
84/97
100/100
79/97
95/100
84
84
99/100
100/100
100/100
Vernieri clade
outgroup

FIG. 6


Clade I
T. merrillii 6
T. merrillii 1
T. merrillii 2
T. merrillii 5
T. merrillii 3
90/95
Clade II
New World
T. concavum 1
T. concavum 2
T. planum 5
T. planum 4
T. perglabrum
T. planum 1
T. planum 2
T. planum 3
T. instratum 1
100/100
81/100
94/100
97/100
74/99
88
66
Clade III
T. nepalense 1
T. nepalense 3
T. nepalense 4
100/100
68
Clade IV
T. kerianum 2
T. kerianum 1
T. kerianum 4
T. instratum 2
T. instratum 4
91/100
59
Planum Clade
100/100
100/100
T. vernieri
T. pluripunctatum 1*
T. pluripunctatum 2*
T. pluripunctatum 3*
T. kaernbachii
87
92/100
T. portoricense*
T. planissimum 1
T. planissimum 2
T. isocladum 1
T. isocladum 2
79/99
84/97
100/100
T. levieri
T. lindbergii 1
T. lindbergii 3
79/97
95/100
T. alare 1
T. alare 2
T. lindbergii 2
84
84
Vera
Aptera
Vernieri clade

CHAPTER 3

A RE-CIRCUMSCRIPTION OF THE MOSS GENUS *TAXITHELIUM* SPRUCE EX MITT. (PYLAISIADELPHACEAE) WITH A TAXONOMIC REVISION OF SUBGENUS *VERNIERI*

This chapter will be submitted to the Journal "Systematic Botany".

Abstract: *Taxithelium* is newly circumscribed with two subgenera: *Taxithelium* and *Vernieri*. The subgenus *Vernieri* is revised and comprises eleven species; one from Africa, two from the Americas and the rest from Southeast Asia and Pacific Islands. A new species, *T. damanhurianum* is described from Seram, Indonesia. Morphometric analyses were used to test species limits.

Keywords– Morphometrics, Sematophyllaceae, Southeast Asia, America

Taxithelium, a genus of pleurocarpous mosses (sensu La Farge-England 1996) traditionally associated with Sematophyllaceae, is probably one of the most widespread moss genera in the tropics, occurring mostly between 30° N and 20° S, with most species occurring in Southeast Asia, especially the Malesian region (Damanhuri and Longton 1996; Ramsay et al. 2002a).

The main character that defines *Taxithelium* is the presence of multiple papillae disposed in series on the lumina of leaf cells (hence, Tax- "*taso*"= arranged and *thelion* = nipple). This is a rare character in Hypnales that has been described only twice in Sematophyllaceae. Other characters that are useful in recognizing the genus are the complanate branches with leaves having an alar region with cells not nearly as well developed as in most Sematophyllaceae.

Even though the most common species (e.g., *T. planum* and *T. nepalense*) are very common mosses in the tropics, there are a number of poorly known and less common species of *Taxithelium* and many names within the group. To date there is no worldwide treatment for the genus and no systematic treatment for the African or Asian species at all.

Taxonomic history– The genus *Taxithelium* was first recognized by Spruce (1867), but the name was only later validly published by Mitten (1869) in the tribe Sematophylleae. Mitten provided a brief diagnosis and described only one species, *T. planum* (Brid.) Mitt.

Brotherus (1925) placed the genus in the family Sematophyllaceae, and many taxonomists have subsequently followed this treatment (Vitt 1984; Buck and Vitt 1986; Tan and But 1997; Buck and Goffinet 2000; Ramsay et al. 2002). However, *Taxithelium*

lacks the collenchymatous exothecial cells, long rostrate operculum, and inflated alar cells that are otherwise diagnostic for Sematophyllaceae. Seki (1969) suggested the exclusion of the genus from the family, and morphological cladistic analyses (Hedenäs 1996; Tan and Jia 1998; Hedenäs and Buck 1999) also suggested that *Taxithelium* might not belong there.

Recent molecular studies (Buck et al. 2000; Tsubota et al. 2001a, b) show that Sematophyllaceae s.l. includes two sister clades: the core sematophyllaceous taxa (e.g., *Sematophyllum* Mitt., *Acroporium* Mitt., and *Trichosteleum* Mitt.), and a clade that includes *Taxithelium*, *Pylasiadelpha* Cardot, *Platygyrium* Schimp., *Isopterygium* Mitt. and *Brotherella* Loeske. Tsubota et al. (2001a) called the latter group "the *Brotherella* lineage". Based on these results, Goffinet and Buck (2004) described the new family Pylaisiadelphaceae for the "*Brotherella* lineage". Although this group lacks any obvious morphological synapomorphy, Goffinet and Buck (2004) are followed here and *Taxithelium* is included in Pylaisiadelphaceae. Relationships within Sematophyllaceae s.s. and Pylaisiadelphaceae still remain unclear.

Since it was first described, the generic boundaries of *Taxithelium* have been stretched to fit a great variety of plants. Renauld and Cardot (1901) divided *Taxithelium* into three subgenera: *Polystigma* (with several papillae disposed serially per cell), *Oligostigma* (with one or few papillae per cell, not serially disposed) and *Monostigma* (with only one papilla per cell). The subgenus *Polystigma* was divided into three Sections: *Vera* (non aquatic plants with vesiculose alar cells), *Aptera* (non aquatic plants with quadrate alar cells) and *Limnobiella* (aquatic plants). Cardot (1905) created section *Anastigma* for a single species that is now placed in *Phyllodon* (Buck 1987) and

Brotherus (1909) created the subgenus *Pseudohypnella* also for a single species now placed in Hookeriales (Buck et al. 2005). However some of the names created by Renauld and Cardot cannot be used, because they failed to define subg. *Taxithelium* (an autonymic section).

Later, Brotherus (1925) included plants without papillae within *Taxithelium* based on similarities in leaf shape, alar cell development, and sporophyte features such as the lack of collenchymatous exothecial cells and lack of long rostrate opercula. This further broadened the generic boundaries of *Taxithelium* and now makes it difficult to differentiate morphologically from genera such as *Radulina* W. R. Buck and B. C. Tan, *Isopterygium* and *Trichosteleum.* Most taxonomists have largely rejected a concept of a *Taxithelium* without papillae and some authors (e.g., Tan et al. 1996; Ramsay et al. 2000) have excluded species without papillae from local treatments of *Taxithelium*. Consequently these "papillae-free" *Taxthelium* species have remained mostly ignored and unplaced over the years. Not surprisingly, *Taxithelium* has grown to more than 230 accepted names and is in great need of revision.

Detailed studies on even parts of the genus are few. Buck (1985) reviewed *Taxithelium* for Brazil, and recognized only three species (*T. planum* (Brid.) Mitt., *T. pluripunctatum* (Renauld and Cardot) W. R. Buck and *T. juruense* (Broth.) Broth.). Although the genus was being revised worldwide in the 1990s, only preliminary results were published (Damanhuri and Longton 1996) and the effort was halted. Ramsay et al. (2002a) provided a local revision of six Australian species, two species were included by Sharp et al. (1994) in the "Moss Flora of Mexico" and three species in "Pleurocarpous

Mosses of West Indies" by Buck (1998). *Taxithelium* has not been treated in floras for SE Asia and Africa.

Molecular phylogenetic data (Câmara and Shaw, unpubl. data) show that 1) *Taxithelium* is monophyletic and is composed by two strongly supported clades, each of which can be recognized by a particular papilla morphology, 2) pluripapillose leaf cells are synapomorphic for *Taxithelium* and 3) some species of *Taxithelium* have lost the papillae. The latter conclusion supports the views of Brotherus (1925), who recognized within the genus species with smooth leaf cells. Detailed study of micro-morphology of papillae (Câmara and Kellogg unpubl. data) showed that such smooth leaf cells might have small, undeveloped papillae, only visible under the SEM.

Circumscription– Detailed study of the morphological characters of species included in *Taxithelium* led to the rejection of the currently accepted circumscription of *Taxithelium* proposed by Renauld and Cardot (1901). Most of the species they included in *Taxithelium* belong to other genera such as *Phyllodon* Bruch and Schimp., *Trichosteleum*, *Acanthorrhynchium* M. Fleisch. and *Taxiphyllum* M. Fleisch. Many species of *Taxithelium* described after 1901 would not fit at all into Renauld and Cardot's concepts, and many characters considered important in generic placement today, such as pseudoparaphyllia and perichaetial leaves, were either ignored or were not known at that time. In addition, the subgeneric classification of Renauld and Cardot (1901) is not supported. The molecular study of Câmara and Shaw (unpulished) showed that Renauld and Cardot's groups are polyphyletic and provides support for the new circumscription and infrageneric classification of *Taxithelium* presented here.

Objectives– In this paper I will: 1) provide a new circumscription for *Taxithelium* 2) evaluate the distinctiveness of proposed taxa using quantitative data and statistical analyses as well as discrete qualitative characters and 3) provide a taxonomic revision of the subgenus *Vernieri*. A revision of subgenus *Taxithelium* will be presented elsewhere.

METHODS

Taxonomy– Loans totaling 6,200 specimens have been obtained from 29 herbaria (B, BM, BR, CANB, DUKE, E, FH, G, H, JE, L, M, MG, MICH, MO, NICH, NY, NSW, PC, PHS, S, SING, SINU, SP, TSN, UB, UPS, US, W). Specimens were re-hydrated in boiling water and then mounted in Hoyer's solution (Anderson 1954). All observations and measurements were made from mounted material, and species were evaluated on the basis of morphological differences.

Typifications are provided for all species and consist of two parts: a) Protologue, which contains the exact information "verbatim" from the protologue; information within brackets indicates relevant information given in the original paper, but absent from the description, and b) citation of the type, but with minimum information obtained from the specimen (usually only collector and number) in order to facilitate its location.

The morphological terms used are defined and illustrated in Gradstein et al. (2001) and Magill et al. (1990). All measurements were made from leaves taken from the middle of the stem or branch using specimens prepared in Hoyer's solution, and viewed under a Nikon Labophot-2 light microscope. Abbreviation of authors follows Brummitt

and Powell (1992). Abbreviation of journals follows BPH. The selected material represents one plant per locality.

Species are recognized on the basis of their morphological differences, using both qualitative and discrete characters. Molecular evidence, when available, is used to support the species circumscription, assuming that species are monophyletic units.

Morphometric analysis– Of the 6,200 specimens seen, about 900 belonged to the subgenus *Vernieri*. These were separated into groups on the basis of gross morphological similarities; twelve of these groups were recognized as "morphogroups" and are numbered from 1 to 12.

A set of 100 herbarium specimens (including all types) was sampled across all morphotypes including the extent of geographic and morphological variation encompassed by the subgenus. Measurements were taken and analyses were performed using SPSS (version 16.0 for Macintosh).

Initially 11 morphological quantitative characters were selected for study: 1) leaf length, 2) leaf width, 3) leaf cell length, 4) leaf cell width, 5) perichaetial leaf length, 6) perichaetial leaf width, 7) perichaetial leaf cell length, 8) perichaetial leaf cell width, 9) seta length, 10) rhizoid length and 11) spore diameter. Some characters (4, 8, 10) were later discarded due to low eigenvalues in PCA or because they showed no variation, so eight characters were included in the final analyses. Principal Component Analyses (PCA) and Discriminant Analyses (DA) were used to detect morphological groups and to check the validity of these groups respectively.

RESULTS

1. Circumscription

Based on molecular evidence (Câmara and Shaw, unpubl. data), detailed study of the morphology of papillae (Câmara and Kellogg, unpubl. data), morphometric analyses, and careful study of discrete morphological characters, two main groups can be recognized within the genus *Taxithelium*.

The first is subgenus *Taxithelium*; it comprises some of the most common and widespread moss species in the tropics (e.g., *T. planum* and *T. nepalense*) and includes about 85% of all *Taxithelium* specimens deposited in herbaria. It corresponds to the "*Planum* clade" of the molecular study of Câmara and Shaw (unpubl. data).

It can be recognized by its oblong, dorsiventrally complanate branches and leaves alternately disposed along the stem and the presence of foliose pseudoparaphyllia. Papillae within this group are of the "baggy" shape (Câmara and Kellogg, unpubl. data) and undergo changes of shape during development. Baggy papillae only occur in *Taxithelium* subgen. *Taxithelium* and constitute a synapomorphy for the group. A few species in this subgenus may lack papillae, as an evolutionary loss. In general, there is little morphological variation within this group.

The second is subgenus *Vernieri* and comprises plants with much more variation in morphology, yet is represented by fewer specimens in herbaria. It corresponds to the "*Vernieri* clade" cited in Câmara and Shaw (unpubl. data). It can be recognized by the presence of spiral, patently disposed, lanceolate leaves and filamentous pseudoparaphyllia. Numerous or few papillae seriately disposed over the cell lumina

always occur in this group; the papillae are of conical shape throughout development (Câmara and Kellogg, unpubl. data).

2. Morphology

Stem anatomy– The stem anatomy shows no variation within the whole genus. The total absence of a central strand is the only feature of interest (Fig. 1F)

Branching– Branching patterns show little or no intraspecific variation. Branches are mostly creeping, sometimes long-ascending. Branching varies from having no particular arrangement to being subpinnate. The presence of filamentous pseudoparaphyllia is constant and a diagnostic feature of the subgenus.

Leaves– These are highly variable within subgenus *Vernieri*.

1) Papillae: A diagnostic feature present in all species of *Vernieri* is the presence of seriately arranged papillae over the lumina of the laminal cells. Even though the number of papillae can vary, no leaf cells lack papillae (as opposed to some taxa in subgenus *Taxithelium*). The papillae may be very obvious and sometimes make the leaf appear dark (e.g., *T. levieri*), or they may be few and difficult to see (e.g., *T. ramivagum*).

The only other Sematophyllaceous genus with pluripapillose leaf cells is *Radulina*, but *Radulina* is easily distinguished from *Taxithelium* by the distally verrucose seta, collenchymatous exothecial cells, and inflated and colored alar cells, all which are lacking in *Taxithelium*. The phylogenetic studies of Câmara and Shaw (unpubl. data) show that *Radulina* is not immediately related to *Taxithelium*.

2) Costae: The costae are highly variable. They are usually absent, but when present they are always double and short. This feature may vary within the same individual, although *T. muscicola* appears always to have a distinct double costa. Unfortunately, the sampling for this taxon was very poor (see taxonomy section).

3) Alar cells: Always present, but usually not well developed. They resemble alar cells of Hypnaceae (Fig. 1A, B), and usually consist of only one or two rows of cells that are neither colored nor inflated. However in a few species (*T. lindbergii, T. muscicola, T. levieri* and *T. damanhurianum*) the alar cells are well developed (Fig. 1C, D), sometimes resembling those typical of Sematophyllaceae, although always much smaller. Such developed alar cells are not traditionally associated with *Taxithelium*.

4) Leaf shape and size: Leaves vary considerably in shape. They are usually concave and lanceolate, or more rarely ovate to oblong. The margins can be entire or serrulate; the apex is mostly acuminate or acute, and it too, can be entire or serrulate. Leaf size ranges from 0.3–2 mm long and 0.08–0.40 mm wide, but within a species there is much less variation, with plants tending to have smaller (*T. damanhurianum* and *T. kaernbachii*) or larger (*T. muscicola* and *T. ramivagum*) leaves. The branch and stem leaves usually do not differ in size, but when they do, the stem leaves are usually slightly larger than the branch ones.

5) Leaf cells: These are usually linear (or long-linear), varying from 30–85 µm in length but with little variation in width (ca. 2 µm wide). *Taxithelium kaernbachii*, having more rhombic cells close to the margins, is an exception.

Perichaetia– Variation in perichaetial leaves is extensive. They can be triangular, lanceolate or ovate, with size ranging from 0.4–1.85 mm long and 0.15–0.8 mm across;

the apex is usually distinct, being long-aristate, to long acuminate or setaceous. The margins can be entire or serrulate; and sometimes they are serrulate only at the apex. Costae are mostly absent but when present they are short and double; *T. isocladum*, which has single costa (when present), is an exception. Both laminal and apical cells are either pluripapillose or smooth. There is little infraespecific variation in any of these perichaetial features but perichaetial leaves can be very useful in distinguishing between species.

Rhizoids– Rhizoids are usually yellowish to reddish; they can be either clustered or evenly distributed on the ventral surface of the stem.

Sporophyte– Most sporophyte structures show little or no variation. One character that does vary within the subgenus is seta length, and although *Taxithelium* has been thought to lack a long-rostrate operculum, this feature is present in *T. planissimum* and *T. levieri* (in subgenus *Vernieri*). Similarly, collenchymatous exothecial cells are generally absent, but are known from *T. damanhurianum* (Fig. 1E) alone, although weakly collenchymatous cells are seen in some New World taxa. Spores vary from 10–20 µm in diameter.

2.1 Morphometric analyses

Three different PCA analyses were performed: a) including all taxa, b) excluding taxa from the New World, and c) excluding all the well defined groups present in the previous two analyses.

Analyses with all taxa– A total of 69.8% of the variation was explained by the first three components. Component 1 explains 32.6 % of the variation, and mostly reflects variation

in perichaetial leaf length, leaf length and perichaetial cell width. Component 2 explains 20.4% of the variation and reflects variation mostly in perichaetial leaf width, leaf width and seta length. Component 3 explains 16.7% of the variation and reflects variation mostly in leaf cell length, seta length and perichaetial leaf width.

Five distinct groups can be recognized (Fig. 2) The first is formed by morphogroups 4, 6 and 9, the second by morphogroup 5, the third by morphogroup 10, a fourth one by morphogroups 1, 3, 7, 8, 11, 12 plus some from 2, and a fifth and last group is composed by the remaining members of morphogroup 2.

Analyses of Old World taxa– New World taxa were excluded to allow a better resolution on a geographical scale.

A total of 72.6 % of the variation was explained by first three components. Component 1 explains 39.1 % of the variation, and mostly reflects variation in leaf width, leaf length and seta length. Component 2 represents 19.2 % of the variation and reflects variation mostly in leaf width, leaf cell length and seta length. Component 3 represents 14.2 % of the variation and reflects variation mostly in leaf cell length, leaf length and seta length.

Four groups can be recognized, one composed by morphogroups 4, 6 and 9 (also present in the previous analyses), the second by morphogroup 5, a third by morphogroup 10 and the last by morphogroups 3, 7, 8, 11 and 12 (Fig. 3)

The last group is a little more distinct than in the previous analyses. This was expected because the New World species that were removed were intermediate between

it and the other major unresolved group. Nonetheless, the cluster of morphogroups 3, 7, 8, 11 and 12 it is still very diffuse.

Analyses excluding well-defined groups– With the exclusion of well-defined groups I expected to increase resolution of unresolved groups, by decreasing the distance between the remaining points.

A total of 73.1 % of the variation was explained by three components. Component 1 represents 27.5 % of the variation, and reflects mostly variation in leaf width, perichaetial leaf length and perichaetial cell length. Component 2 represents 26% of the variation and reflects variation mostly in perichaetial leaf width, leaf length and leaf cell length. Component 3 represents 19.5% of the variation and reflects variation mostly in leaf length, perichaetial leaf width and leaf width.

Like the previous analyses, morphogroups 4, 6, and 9 formed a cloud in morphological space. Groups 3 and 11 are distinguished from this cloud by factor 1 (Fig. 4). Morphogroups 8 and 12 are separated by factor 3 (Fig. 5).

Discriminant analyses– The same data used in the third PCA (analyses without distinctive groups) were used here. Results show that morphogroups 7, 8, 9 and 11 can be differentiated (Fig. 6), but morphogroups 3 + 12 and 4 + 6 could not be separated.

Discussion of multivariate analyses– Morphogroups 1 and 2 are the only ones from the Americas, and although diffuse in the analyses of the whole group (Fig. 2) they can also be differentiated from each other by qualitative morphological characters, such as the

presence of falcate leaves and smooth perichaetial leaf cells in morphogroup 1 versus symmetric leaves and papillose perichaetal leaf cells in 2. They were also shown to be distinct (boostrap support > 80%) from each other and from the rest of the morphogroups in the molecular studies of Câmara and Shaw (unpubl. data). Therefore, both groups are recognized as separate species.

Morphogroups 5 and 10 were recognized as distinct in analyses A and B (Figs. 2 and 3). Plants in morphogroup 10 have collenchymatous exothecial cells, a unique feature within *Taxithelium*. Plants in morphogroup 5 were distinct in the molecular study of Câmara and Shaw (unpubl. data). Both are recognized as distinct species.

Morphogroups 4 and 6 were frequently associated with 9 in the PCA. They all (4, 6 and 9) share well developed alar cells, but morphogroup 9 has entire leaf margins, whereas both morphogroups 4 and 6 have serrate leaf margins. Also plants in morphogroup 9 are endemic to Australia while morphogroups 4 and 6 have overlapping geographical distributions in Southeast Asia. The combination of well-developed alar cells and large, lanceolate leaves with entire margins in morphogroup 9 is very distinct; I recognize morphogroup 9 as a distinct species.

Morphogroups 4 and 6 on the other hand lack any qualitative characters that distinguish them. Furthermore, they were inseparable both in the PCA analyses and in the molecular study of Câmara and Shaw (unpubl. data). Together they constitute a monophyletic unit. I infer that morphogroups 4 and 6 are two forms of the same species. Morphogroup 4, rather larger, is mostly from high altitudes, and morphogroup 6 is smaller and mostly from the lowlands. These differences in habitat may be related to the differences in size between the two groups.

Morphogroup 11 can be recognized as distinct in most analyses (Figs 2, 3 and 4), particularly in analyses of Old World taxa alone (Fig. 4). Plants within this morphogroup have been shown to be distinct also in the molecular studies of Câmara and Shaw (unpubl. data), and are recognized here as a distinct species.

Morphogroup 3 also is recognizable in some analyses (Fig. 3 and 4), but in analyses with well-defined groups excluded (Fig. 5) it is nested with morphogroup 7. The two are easily separated by the well-developed alar cells of morphogroup 3 that are absent in 7; also both are distinct (bootstrap > 80%) in the molecular study. The two are recognized as distinct species.

The last two morphogroups (8 and 12) are distinguishable only in the analysis with well-defined groups excluded (Fig. 5). However the two have distinct geographic distributions, 12 being endemic to mainland Tropical Africa and 8 occurring only on the Pacific islands. They also differ in papillosity, morphogroup 8 being strongly papillose and 12 scarcely papillose. The leaves on morphogroup 8 are constricted at the base with a narrower apex. The two morphogroups represent distinct species.

Discussion on DA– Discriminant analyses are mostly congruent with PCA, with morphogroups 7, 9, 8 and 11 recognized as distinct. Also in the DA morphogroups 4 and 6 were inseparable (as in the PCA); they also lack any qualitative differential characters and molecular evidence to distinguish them, supporting the argument above that they should be recognized as single species.

The only difference in results between the PCA and DA is that groups 3 and 12 could not be separated in the latter (Fig. 6). However plants in morphogroups 3 (distinct

in Figs. 3 and 4) and 12 (distinct in Fig. 5), can be easily distinguished from each other by the well-developed alar cells present in morphogroup 3 (and absent in 12), and plants in morphogroup 12 have perichaetial leaves with serrulate apex (entire in 3). They also have very different geographical range, with morphogroup 3 being found only in the Pacific Islands whereas 12 is found only in Africa.

Conclusions on morphometrics– Based on these results eleven of the twelve provisional morphogroups are recognized taxonomically in this study and are treated as distinct species. The results of the morphometric study largely complement the molecular data showed by Câmara and Shaw (unpubl. data).

TAXONOMIC TREATMENT

Taxithelium Spruce ex Mitt., J. Linn. Soc., Bot. 12: 496. 1869.

Type: *Taxithelium planum* (Brid.) Mitt., J. Linn. Soc., Bot. 12: 496. 1869.

Taxithelium Spruce, Cat. Musc. 14. 1867, *nom. nud.*; *Hypnum* Hedw. sect *Omalia* Müll. Hal. subsect. *Sigmatella* Müll. Hal., Syn. Musc. Frond 2: 263. 1851; *Hypnum* sect. *Sigmatella* (Müll. Hal.) Müll. Hal., J. Mus. Godeffroy 3(6): 86. 1874; *Trichosteleum* sect. *Sigmatella* (Müll. Hal.) A. Jaeger, Ber. Thätigk. St. Gall. Nat. Gess. 1876-77: 411. 1878; *Sigmatella* (Müll. Hal.) Müll. Hal., Bot. Jahrb Syst. 3: 328. 1896.

Type: *Hypnum planum* Brid., Musc. Recent. Suppl. 2: 97. 1812.

Plants small to medium sized, forming mats. **Stems** creeping, branching without order to subpinnate, long ascending or not; central strand absent; pseudoparaphyllia foliose or filamentose, branches complanate or terete. **Stem and branch leaves** usually similar, sometimes falcate-secund, erect to wide-spreading, broadly oblong-ovate to lanceolate, 0.3–2 × 0.08–0.70 mm; margins entire or serrulate; apex obtuse to acuminate; costa double and short or absent; laminal cells linear, 30–85 × ca. 2 µm, seriately papillose over the lumina, sometimes smooth, never unipapillose, thin- or thick-walled; alar cells few, quadrate in basal angles, sometimes inflated and colored. **Asexual propagula** absent. **Autoicous**. **Perigonia** lateral; paraphyses present; antheridia 3–5; perigonial leaves lanceolate to oblong, concave; costae absent; laminal cells linear, lax, usually pluripapillose; alar cells not differentiated. **Perichaetia** lateral; paraphyses present; archegonia 3–5; perichaetial leaves lanceolate or ovate, 0.4–1.8 × 0.15–0.8 mm; apex acuminate or aristate; costae absent, single or short and double; laminal cells linear, 24–95 × ca. 2 µm, lax, pluripapillose or smooth; alar cells not or rarely differentiated. **Setae** elongate, slender, smooth, 4.8–25 mm long. **Capsules** inclined or erect, asymmetric, ovoid or cilindric, constricted below mouth when deoperculate; 0.5–1.2 mm long; exothecial cells subquadrate, thick-walled, slightly collenchymatous or not; annulus not differentiated. **Operculum** short, rarely long, conic or obliquely conic-rostrate, 0.3–0.8 mm long. **Peristome** double, hypnoid, exostome teeth narrowly triangular, with ziz-zag median line, cross-striolate below, papillose above, trabeculate at back; endostome with a high basal membrane, segments keeled, papillose, broad, keeled, perforate, as long as the teeth; cilia single, narrow, nodulose. **Spores** spherical, smooth or finely papillose, 7–20 µm across. **Calyptrae** cucullate, naked, smooth.

Species of *Taxithelium* are yellowish-green to dull green creeping plants with lateral sporophytes. The leaves vary from complanate-foliate to spirally disposed and ovate to lanceolate, sometimes falcate. The cells are linear or rhomboid; in many species each cell bears multiple papillae arranged in lines over the lumina. A differentiated alar region is present, but is not as well developed as in other sematophyllaceous genera, the cells rarely being inflated and often not colored. The diplolepideous sporophyte is hypnalean; it has a conic or apiculate (rarely long rostrate) operculum and the calyptra is usually cucullate. Most variation in morphology is found in the gametophyte, the sporophyte characters being very constant.

Taxithelium alar development is more similar to that in Hypnaceae and does not fit into the classification of alar cells for Sematophyllaceae by Tan and Jia (1999).

Taxithelum subgenus *Taxithelium*

Type: *Hypnum planum*, Hispaniola, *Poiteau s.n.* (B!).

Axes complanate, pseudoparaphyllia foliose, leaves ovate to orbicular.

Taxithelum subgenus *Vernieri subgenus novum*

A subgenus Taxithelium in foliis lanceolatis, spiralis (haud complanatis) dispositis et pseudoparaphyllis filamentosis (haud foliosis) differt.

Axes with spreading leaves, pseudoparaphyllia filamentose, leaves lanceolate to oblong-lanceolate

Type: *Taxithelium vernieri* (Duby) Besch., *Hypnum vernieri* Duby, Flora 58: 285. 1875.

Etymology: *Vernieri* refers to the collector, the missionary *Vernier*.

Key to the subgenera of *Taxithelium*

1. Plants complanate with ovate leaves; pseudoparaphyllia foliose…….Subg. *Taxithelium*

1. Plants with spreading and lanceolate leaves; pseudoparaphyllia filamentous.…….Subg. *Vernieri*

Key to the species in subgenus *Vernieri*

1. Plants from the Americas……..…….…..….2
1. Plants from elsewhere……...…….……..3
2. Leaf falcate; perichaetial leaves pluripapillose and serrulate…8. *T. pluripunctatum*
2. Leaf symmetric; perichaetial leaves smooth and entire.……..…..9. *T. portoricense*
3. Alar cells well developed……...…….……...……..4
3. Alar cells not or poorly developed…….……..…….....7
4. Leaves with margins serrulate at apex…….…...…...….. 5. .*T. lindbergii*
4. Leaves with entire margins ……...……...……..…….……..5
5. Exothecial cells collenchymatous, perichaetial leaves less than 1mm long…....1. *T. damanhurianum*
5. Exothecial cells not collenchymatous, perichaetial leaves more than 1mm long……..……6

6. Leaves linear-lanceolate, perichaetial leaves not serrulate at apex….6. *T. muscicola*

6. Leaves oblong-lanceolate, perichaetial leaves strongly serrulate at apex.4. *T. levieri*

7. Leaves less than 0.6 mm long, oblong to elliptical……..….3. *T. kaernbachii*

7. Leaves more than 0.6 mm long, oblong to lanceolate…….……..8

8. Perichaetial leaves with entire margins……..9

8. Perichaetial leaves with serrate margins……..10

9. Leaves scarcely papillose, 1–1.6 mm long, from Africa…..……10. *T. ramivagum*

9. Leaves strongly papillose, 0.6 –1.2 mm long, from Pacific islands….11. *T. vernieri*

10. Operculum long rostrate, perichaetial leaves with most cells pluripapillose….7. *T. planissimum*

10. Operculum shortly rostrate, perichaetial leaves with pluripapillose cells only at apex…….……2. *T. isocladum*

1. Taxithelium damanhurianum P. S. Câmara. The Bryologist 111. 2008. *In press*

Holotype: INDONESIA, Seram, Manusela National Park, Sawai, *Akiyama 9329* (NY!). Fig. 7.

Plants small, forming golden-yellow mats. **Stem** creeping, long-ascending branched. **Stem and branch leaves** same, erect-spreading, concave, 0.52–0.88 × 0.10–0.20 mm, linear-lanceolate, margins serrulate; apex acuminate; laminal cells linear, 70–74 × ca. 2 µm, seriately papillose over the lumina, thick-walled, basal cells sometimes smooth; costae absent; alar cells well differentiated, consisting of 1–2 rows, 1 of inflated, vesiculose and not colored cells, supra alar cells not inflated. **Rhizoids** evenly distributed along the stem. **Perichaetial leaves** 0.4–0.6 × 0.14–0.25 mm, ovate, margins entire; apex

setaceous; laminal cells linear at mid-leaf, 40–46 × ca. 2 µm, thick-walled, quadrate and smooth at base, pluripapillose at apex; costae absent; alar cells well developed. **Setae** 7–10 mm long. **Capsules** inclined, asymmetric, ovoid, 0.5–0.8 mm long; exothecial cells quadrate, strongly collenchymatous. **Operculum** not seen. **Spores** smooth, 16–20 µm across.

Notes: This new species resembles *T. muscicola*, but is much smaller and narrower. The spores are also different; in *T. muscicola* they are finely papillose and only 12–16 µm across, while in *T. damanhurianum* they are 16–20 µm across and smooth. Although the plants of *T. damanhurianum* are smaller than those of *T. muscicola* they have larger spores.

Unique to *T. damanhurianum* are the strongly collenchymatous exothecial cells (Fig. 1E). These, along with the relatively well-developed alar cells, make it look like *Radulina*, but *T. damanhurianum* is a much smaller plant. *Taxithelium damanhurianum* also lacks any papillae on the seta (*Radulina* has distally papillose setae), and the alar cells are much less developed and neither inflated nor colored like the ones found in *Radulina*. No phylogenetic data are available at the moment to verify the placement of this species and therefore it is more appropriate to keep it in *Taxithelium*. Unfortunately, few collections of this plant are known and molecular data are unavailable.

Taxithelium damanhurianum is restricted to the Island of Seram, Indonesia (Fig. 8), where it is ephyphyllous and occurs between 100–650 m of altitude.

Representative Specimens Examined (paratypes)– INDONESIA**.** Seram, Manusela National Park, *Akiyama 9409, 9923* (NY).

2. Taxithelium isocladum (Bosch & Sande Lac.) Renauld & Cardot, Rev. Bryol. 28: 111. 1901; *Hypnum isocladum* Bosch & Sande Lac., Bryol. Jav. 2: 173. 272. 1867. Protologue: [Indonesia], Habitat insulam *Banca*; in sylvis *Batoeroesak* m. Jul. 1858 legit KURZ. Holotype: *Kurz s.n.* (L!). Isotype: H! Fig. 9.

Taxithelium deningeri Herzog, Hedwigia 61: 298. 1919, *syn. nov.* Protologue: [Malacca, Malay Peninsula], "Batang Padang Tal", leg. E. Stresemann, Nr. 89. Holotype: *Stresemann s.n.* (JE!). Isotypes: S!, BM!

Taxithelium isocladioides Dixon, Bull. Torrey Bot. Club 51: 243, 4 f. 1. 1924, *syn. nov*. Protologue: [Malay Peninsula], Hab. Bujong Malacca, Perak, 1898; Ridley (737) in herb. Mitten. Holotype: *Ridley 737* (BM!).

Taxithelium werneri (Herzog) Broth., Nat. Pflanzenfam. (II) 11: 443. 1925; *Trichosteleum werneri* Herzog, Hedwigia 49: 126. 1909, *syn. nov*. Protologue: New Guinea. Hab. Auf abgefallenen Blättern bei Gelustation (Finisterregebirge), ca 800m; August 1907, leg. Dr. E. Werner. Holotype: *Werner s.n.* (JE!).

Taxithelium epiphyllum Broth., Mitt. Inst. Allg. Bot. Hamburg. 7(2): 136. 1928, *syn. nov*. Protologue: West Borneo: Am oberen Serawei, um 400 m, auf Blättern. (Hans Winkler n. 3145). Holotype: *Winkler 3145* (H!).

Taxithelium magnum M. Fleisch. var. *laticuspis* Zanten, Nova Guinea, Bot. 10(16): 343, pl. 31, f. 4. 1964, *syn. nov*. Protologue: [New Guinea], Mt. Antares, Camp 39a, 1500 m, July 4 No 440. [*Zanten*]. Holotype: *Zanten 440* (L!). Isotypes: BM!, NICH!

Nomenclatural note:

1. Even though the Mitten herbarium is at NY the type of this species was found at BM.

Plants large, forming golden-yellow mats. **Stems** creeping, long–ascending branched. **Stem and branch leaves** slightly differentiated; stem leaves larger and longer, erect-spreading, concave, 1.0–1.5 × 0.28–0.45 mm, oblong-lanceolate, margins entire; apex entire, slighlty acuminate; laminal cells linear, 40–50 × ca. 2 µm, seriately papillose over the lumina, thick-walled, basal cells sometimes smooth; costae short and double or absent; alar cells poorly differentiated, consisting of 2 rows, not inflated. **Rhizoids** evenly distributed along the stem. **Perichaetial leaves** 1.5–2.5 × 0.30–0.40 mm, narrow-lanceolate, margins entire at base, serrulate at apex; apex setaceous; laminal cells linear, 50–65 × ca. 2 µm, thick-walled, pluripapillose only at apex; costae absent or single; alar cells poorly differentiated with 2 rows, not inflated. **Setae** 5–10 mm long. **Capsules** erect, asymmetric, ovoid, 0.6–0.8 mm long, constricted below mouth; exothecial cells subquadrate, not collenchymatous. **Operculum** short, conic or obliquely conic-rostrate, ca. 0.3 mm long. **Spores** finely papillose, 15–20 µm across.

Notes: Molecular data show this species to be monophyletic (Câmara and Shaw, unpubl. data). Its large leaves with entire margins and poorly differentiated alar cells distinguish it from others in subgenus *Vernieri*. The perichaetial leaves are unusually long and often ecostate but sometimes they have a single subpercurrent costa, a unique feature within the subgenus. Some specimens of *Taxithelium isocladum* may resemble *T. ramivagum* (see notes on *T. ramivagum*).

The species occurs only in Southeast Asia, in Malesia (Fig. 10). It grows on tree trunks, twigs and as an epiphyll, from sea level to 1,500 m.

Representative Specimens Examined– INDONESIA**.** Kalimantan, Pontianak, *Ledrui 2332* (G); Kalimantan, Serawei, *Winkler 3145* (H); Irian Jaya, *Brass 13634* (MICH); Java, Tijibodas, *Fleisher s.n.* (JE); Sumatra, Bangka, *Kurz s.n.* (L, H).

MALAYSIA**.** Malacca: *Stresemann 89* (JE, S*), Ridley 737* (BM); Genting Highlands: *Câmara 870* (MO); Sarawak: *Everett s.n.* (M); Selangor, *Câmara 974* (MO).

PAPUA NEW GUINEA**.** Mt. Antares, *Zanten 440* (L, BM, NICH); Morobe, *Werner s.n*. (JE).

PHILIPPINES**.** Luzon, *Ramos 22166* (NY).

SINGAPORE**.** *sine loco, Ridley 37* (H).

3. Taxithelium kaernbachii (Broth.) Broth., Nat. Pflanzenfam. I(3): 1091. 1908; *Trichosteleum kaernbachii* Broth. Bot. Jahrb. Syst. 17: 480. 1893. Protologue: Nova Guinea, Gogolexpedition (L. Kaernbach). Isotypes: *Kaernbach s.n.* (BM!, FH!). Fig. 11.

Taxithelium perminutum Broth., Bot. Jahrb. Syst. 24: 267. 1897, *syn. nov*. Protologue: Kamerun: Mokundange und N'dian, an Steinen (Dusén n.1030). Holotype: *Dusén 1030* (H!). Isotypes: PC!, S!, BR!

Taxithelium petrophilum R. S. Williams, Bull. New York Bot. Gard. 8(31): 370. 1914, *syn. nov*. Type: [Philippines], Lamao River, 75 meters, on rock, Dec. 1903 [Robert Williams 865]. Isotypes: *Williams 865* (US!, FH!, H!).

Taxithelium bakeri Broth., Philipp. J. Sci. 13: 218. 1918, *syn. nov*. Protologue: [Philippines], LUZON, Laguna Province, Los Baños, *Baker 2379, 2400*. Lectotype (designated here): *Baker 2379* (H!). Syntype: *Baker 2400* (FH!).

Taxithelium archboldii E. B. Bartram, Brittonia 9: 53. 1957, *syn. nov*. Type: [Papua New Guinea], Baiawa, Moi Biri Bay, 60m, on rocks in rain forest, 22175 (type). [Brass]. Holotype: *Brass 22175* (FH!). Isotypes: NICH!, H!

Nomenclatural notes:

1) No type of *Taxithelium kaernbachii* was found in Brotherus herbarium in H.

Plants very small, forming dark-green mats. **Stems** creeping, freely branched. **Stem and branch leaves** slightly differentiated, stem leaves slightly bigger, erect-spreading, complanate, 0.30–0.55 × 0.12–0.26 mm, lanceolate-ovate, margins entire; apex acute;

laminal cells linear, 28–36 × ca. 2 µm, seriately papillose over the lumina, thick-walled; costae absent; alar cells not differentiated. **Rhizoids** clustered beneath the stem. **Perichaetial leaves** 0.4–0.8 × 0.16–0.30 mm, triangular, margins entire; apex long-aristate; laminal cells linear, 24–30 × ca. 2 µm, thick-walled, smooth; costae absent; alar cells not differentiated. **Setae** 4–7 mm long. **Capsules** inclined, asymmetric, long-ovoid, 0.6–0.8 mm long, constricted below mouth; exothecial cells subquadrate, not collenchymatous. **Operculum** long, obliquely conic-rostrate, ca. 0.3 mm long. **Spores** smooth, 7–8 µm across.

Notes: This species can be easily identified by its small size in comparison with all other *Taxithelium* species. Sometimes the strong papillation of the leaf cells can give the false impression of a serrate leaf margin. *Taxithelium kaernbachii* also has the smallest spores observed in the group. It resembles plants in subgenus *Taxithelium* in its leaf shape and more rhombic leaf cells. However, the presence of filamentous pseudoparaphyllia, as well as molecular data (Câmara and Shaw, unpubl. data), place this species in subg. *Vernieri*.

Taxithelium kaernbachii is known only from a few collections but from a very wide area, having been collected in Malesia, Cameroon and the Seychelles (Fig. 12). It is most likely to be undercollected due to its very small size (leaves are less than 0.5 mm). It grows on rocks and rarely on tree trunks at lowland elevations.

Representative Specimens Examined– CAMERUN. N'Dian, *Dusén 1030* (PC, H).

FIJI. Viti Levu, *Buck 7108* (NY); Koro, *Smith 1024* (NY).

MALAYSIA. Selangor, Gombak, *Câmara 963* (MO).

PAPUA NEW GUINEA. Baiawa**,** *Brass 22175* (FH, H, NICH); Simbong, *Nyman 73* (NY).

PHILIPPINES. Lamao river, *Williams 865* (FH, H, US); Luzon, *Penecilla 10347* (PNH).

SEYCHELLES. Vallè de Mai**,** *Onraedt 157* (BR).

4. Taxithelium levieri (Broth. & Geh.) Broth., Nat. Pflanzenfam. ed. 2, 11: 443. 1925; *Trichosteleum levieri* Broth. & Geh. Biblioth. Bot. 44: 23. 19. 1898. Protologue: Papua Onin, Tangion Bair, sub No 147, 9 april 1872 [Beccari]. Holotype: *Beccari 147* (H!). Isotypes: JE!, FH! Fig. 13.

Taxithelium horridulum Broth., Philipp. J. Sci. 8: 90. 1913, *syn. nov.* Protologue: [Philippines], Luzon, Province of Laguna, Mount Banajao, on dead trees, altitude 800m, *Bur. Sci. Robinson 9773.* Holotype: *Robinson B. S. 9973* (H!). Isotypes: BM!, FH!, NY!

Plants medium sized, forming lax, yellow-opaque mats. **Stem** creeping, freely branched. **Stem and branch leaves** similar, wide-spreading, concave, 0.74–0.90 × 0.16–0.25 mm, lanceolate, margins entire, convolute; apex acute; laminal cells linear, 60–65 × ca. 2 µm, strongly seriately papillose over the lumina, thick-walled; apical cells papillose; costae absent; alar cells well differentiated, consisting of 1–2 rows, sometimes colored. **Rhizoids** clustered beneath the stem. **Perichaetial leaves** 1.2–1.6 × 0.2–0.3 mm, lanceolate, margins entire; apex aristate; laminal cells linear, 60–86 v ca. 2 µm, thick-

walled, smooth; costae absent; alar cells not differentiated. **Setae** ca. 5.0 mm long. **Capsules** inclined, asymmetric, ovoid, 0.6–0.8 mm long, constricted below mouth; exothecial cells subquadrate, not collenchymatous. **Operculum** long, obliquely conic-rostrate, ca. 0.8 mm long. **Spores** finely papillose, 15–20 µm across.

Notes: The convolute margins of the leaves in this species resemble those of *T. portoricense*, but *T. levieri* has well-developed alar cells, smaller leaves and stronger papillation whereas *T. portoricense* has poorly developed alar cells and larger leaves. The two species do not overlap in geographical range.

Taxithelium levieri is restricted to Southeast Asia (Fig. 14), Malesia, and some Pacific islands (Fiji, Tonga, Niue). It grows on tree trunks, rotten tree stumps and on volcanic blocks, between 270–1170 m of altitude.

Representative Specimens Examined– INDONESIA. Bali, *Touw 24745* (L); Irian Jaya, *Brass 13764* (MICH); Java, *Nyman 8752* (W); Seram, *Akyiama 9409* (NY).

PHILIPPINES. Mindanao, *Bartlett 15933* (MICH); Luzon, *Robinson B. S. 9773* (H, BM, FH, NY).

NIUE. *sin. loc., Yuncker 10251* (NY, MICH).

FIJI. Taveuni, *A. C. Smith 793* (NY); Viti Levu, *Buck 7338* (NY).

SAMOA. *sine loco, Vaupel 152* (JE).

TONGA. *sine loco, Yuncker 16175* (NY).

5. Taxithelium lindbergii (A. Jaeger) Renauld & Cardot, Rev. Bryol. 28:111. 1901; *Trichosteleum lindbergii* A. Jaeger, Ber. Thätigk. St. Gallischen Naturwiss. Ges.

1876–77: 412. 1878; *Hypnum lindbergii* Sande Lac., Bryol. Jav. 2: 172. pl. 271. 1867, *nom. illegit.* Protologue: Patria: Insul. Java (*Blume*) in montibus Gédé et Salak (*Teysmann*), Ceram (*de Vriese*). Lectotype (designated here): *Teysmann s.n.* (H!). Isolectotype: BM! Fig. 15.

Taxithelium nossianum Besch., Ann. Sci. Nat., Bot. sér. 6, 10: 310. 1880, *syn. nov*. Protologue: Nossi-Bé, sur les vieux troncs d'arbres, Perville (Herb. Mus. Par). Isotypes: *Perville s.n.* (PC!, BR!).

Taxithelium argyrophyllum Renauld & Cardot, Bull. Soc. Roy. Bot. Belgique. 33(2): 131. 1895, *syn. nov*. Protologue: Hab. Madagascar: Diego Suarez, ad truncus putridos (Chenagon). Holotype: *Chenagon s.n.* (PC!). Isotypes: BM!, BR!, S!, H!, FH!

Taxithelium falcatulum Broth. & Paris, Oefvers. Förh. Finska Vetensk.-Soc. 48(15): 22. 1906, *syn. nov*. Protologue: [New Caledonia], Mont Koghi, ad arbores in silvaticis, alt 400–500m (Le Rat). Holotype: *Le Rat s.n.* (H!). Isotypes: PC!, M!, S!, FH!

Taxithelium parvulum (Broth. & Paris) Broth., Nat. Pflanzenfam. I(3): 1092. 1908. *Trichosteleum parvulum* Broth. & Paris, Bull. Herb. Boissier, sér. 2, 2: 988. 1902, *syn. nov*. Protologue: [Japan], Tsurugi-zan, n. 1400. [Faurie]. Holotype: *Faurie s.n.* (H!). Isotype: PC!

Taxithelium voeltzkowii Broth., Reise Ostafr., Syst. Arbeit. 3: 63, f. 9: 14. 1908, *syn. nov*. Type: Mauritius [*Voeltzkow s.n.*]. Holotype: *Voeltzkow s.n* (H!). Isotypes: S!, PC!, BR!

Taxithelium alare Broth., Philipp. J. Sci. 3: 28. 1908, *syn. nov*. Protologue: [Philippines] Mindoro, Mount Halcon (For. Bur. 4476 *Merritt*). Holotype: *Merritt F. B. 4476* (H!). Isotypes: PC!, FH!

Taxithelium ludovicae Broth. & Paris, Oefvers. Förh. Finska Vetensk.-Soc. 51A (17): 28. 1909, *syn. nov*. Protologue: Nouvelle Calèdonie. Inter Col d'Annieu et fl. Negropo, ad ramos arborum (A. Le Rat). Holotype: *Le Rat s.n.* (H!). Isotypes: PC!, M!

Taxithelium benguetiae Broth., Philipp. J. Sci. 8: 90. 1913, *syn. nov*. Protologue: [Philippines], LUZON, Province of Benguet, on tree trunks, *Sanchez B. S. 10*. Holotype: H! Isotypes: E!, US!, FH!, S!, BM!, NY!

Taxithelium robinsonii Broth., Philipp. J. Sci. 13: 218. 1918, *syn. nov*. Protologue: Phillipines, Laguna province, Mount Banahao, Bur Sci. 9820, 9864 Robinson. Lectotype (designated here): *Robinson B. S. 9864* (H!). Isolectotypes: US!, FH!, NY!, BM! Syntype: *Robinson B. S. 9820* (H!, NY!).

Taxithelium capillarisetum (Dixon) Broth., Nat. Pflanzenfam. (II)11: 443. 1925. *Trichosteleum capillarisetum* Dixon, J. Linn. Soc., Bot. 45: 494. 1922, *syn. nov*. Protologue: Dutch New Guinea collected by C. B. Kloss, Canoe Camp, Oct.-Nov. 1912 (No 34). Holotype: *Kloss 34* (BM!).

Taxithelium clastobryoides Dixon, J. Siam Soc., Nat. Hist. Suppl. 10(1): 26. 1935, *syn. nov*. Protologue: [Thailand], Hab. Puket. Krabi, Panom Bencha, circa 1100 m., on trees in evergreen forest, 28 Mar., 1930; coll. Kerr (512b). Holotype: *Kerr 512b* (BM!).

Taxithelium convolutum Dixon, J. Linn. Soc., Bot. 50: 130. 41. 1935, *syn. nov*. Protologue: Upper Sarawak; coll. Everett; Herb. Mitten, type. Holotype: *Everett s.n.* (BM!).

Taxithelium brassii E. B. Bartram, Lloydia 5: 288. 56. 1942, *syn. nov*. Protologue: [Indonesia, Irian Jaya], Forest Undergrowth, 9km, NE of Lake Habbema, 2800 m., no 10977. Protologue: [Brass]. Holotype: *Brass 10977* (FH!). Isotypes: MICH!, L!

Nomenclatural notes

1. The type specimens of *T. lindbergii*, *T. falcatulum*, *T. nossianum* and *T. argyrophyllum* have no collection numbers either in the protologue or on the specimens; however the information on the specimens matches that in the protologue.

2. The syntype specimen of *T. lindbergii* was not found.

3. Even though the Mitten herbarium is at NY, the type of this species was found in BM.

Plants medium to large, forming golden-yellow mats. **Stem** creeping, branches long ascending. **Stem and branch leaves** slightly differentiated; stem leaves larger and longer; erect-spreading, 0.95–1.5 × 0.18–0.30 mm, concave, lanceolate, margins entire at base, serrulate at apex; apex acuminate; laminal cells linear, 50 – 55 × ca. 2 µm, seriately papillose over the lumina, basal cells sometimes smooth, thick-walled; costae short and double or absent; alar cells well differentiated, consisting of 2 rows, the lower with inflated colored cells and the upper not inflated. **Rhizoids** evenly distributed along the stem. **Perichaetial leaves** 1.0–1.8 × 0.25–0.30 mm, lanceolate, margins entire at base, serrulate at apex; apex long-aristate; laminal cells linear, 60–90 × ca. 2 µm, thick-walled, smooth; costae absent; alar cells differentiated, with 3–4 rows of usually inflated cells. **Setae** 20–22 mm long. **Capsules** erect, asymmetric, ovoid, 0.8–1.1 mm long, constricted below mouth; exothecial cells subquadrate, not collenchymatous. **Operculum** short, conic-rostrate, ca. 0.5 mm long. **Spores** finely papillose, 15–20 µm across.

Notes: There has been confusion over the correct identification of *T. lindbergii* due to its considerable variation (see morphometrics section). Plants that occur at high elevation (between 1000 and 2000 m) on Mt. Kinabalu (Borneo), Mt. Halcon (Philippines), Mt. Luang (Thailand), Mt. Konghis (New Caledonia) and elsewhere, are larger plants. Lowland specimens are usually much smaller and have leaves that can be slightly falcate. The type specimen of *T. parvulum*, from Japan, is included in *T. lindbergii* until more

collections can be gathered; however, the plants are somewhat distinct, being slightly smaller but wider.

The variability of this taxon has resulted in many names being proposed that are now synonymized. The morphometric data presented here show that no quantitative morphological separate species, nor are there any qualitative (discrete) characters. The molecular data presented by Câmara and Shaw (unpubl. data) are the basis for the wide circumscription of *T. lindbergii* proposed here; in that study specimens assigned to *T. alare* were embedded in a paraphyletic *T. lindbergii* s.l. This species can be recognized by its developed alar cells, serrate leaves, long seta, and smooth perichaetial leaf cells.

This species is widely distributed (Fig. 16), from Sri-Lanka to Malesia, New Caledonia, Fiji, Samoa, and Pacific Islands. Is also present in the Mascarenes, Seychelles, Madagascar, Vietnam and Japan.

Representative Specimens Examined–FIJI. Viti Levu, *Whitehouse 29980* (DUKE); Ovalau (Mt. Tana), *Smith 7719* (DUKE); Taveuni, *Smith 756* (NY).

INDONESIA. Bangka, *Kurz s.n.* (L); Java, *Schif. 12105* (S); Sumatra, *Touw & Snoek 25306* (L). Irian Jaya, *sine legit* (BM).

JAPAN. Shikoku, *Faurie 1400* (H, PC).

MADAGASCAR. Nossi-Be, *Perville s.n.* (PC, BR); Diego Suarez (Antsiranana), *Chenagon s.n.* (PC, BM, BR, S, H, FH)**.**

MALAYSIA. Genting Highlands, *Câmara 878* (MO); Selangor, *HBR 4022* (NY); Sabah, *Holtman 1931* (NY); Sarawak, *Richards 2563* (BM).

MAURICE. Le Pouce, *Onraedt 272* (BR), *sine loco*., *Voeltzkow s.n* (H, PC, S, BR).

NEW CALEDONIA. Negropo, *Le Rat s.n.* (M); Mt. Koghis, *Le Rat s.n*. (M).

PHILIPPINES. Mindoro, *Salgado Edw, 12360* (BR); Mindanao, *Ramos B. S. 14894* (NY); Luzon, *Sanchez B. S. 10* (NY), *MacGregor B. S. 19919* (NY); Laguna, *Robinson B. S. 17077* (NY), *Robinson B. S. 9864* (H, US, FH, NY, BM); Silipan, *Phillips 16* (MICH).

REUNION. Tremblet, *Arts 92/18,* (BR), St. Phillippe, *Arts 11/59* (BR).

SEYCHELLES. Ile Mahé, *Decorié s.n.* (BR).

SRI LANKA. *Sine Loco, Thwaites 217* (G).

THAILAND. Mt. Luang, *Touw 11800* (MICH, NY); Puket, *Kerr 512b* (BM).

VIETNAM. Bao Loc. *Tixier s.n*. (PC)

6. Taxithelium muscicola (Broth.) B. C. Tan, H. P. Ramsay & W. B. Schofield, Austral. Syst. Bot. 9: 324. 1996; *Trichosteleum muscicola* Broth., Öefvers. Förh. Finska Vetensk.–Soc. 42: 117. 1900. Protologue: Patria, Lord Howe Island, Mt. Gower, ubi supra muscos crescens m. Sept. 1887 detexit amicissimus Th. Whitelegge et mihi sub n. 11 misit. Anno 1898 eandem speciem legit J. H. Maiden (n. 218). Syntype: *Whitelegge 11* (H!). Fig. 17.

Nomenclatural notes:

1. The epithet was first spelled *Trichosteleum muscicolum*; however, because it is a noun in apposition the correct name is *T. muscicola.*

2. The syntype *Maiden 218* was not found; therefore I have not lectotypified the name.

Plants medium sized, forming pale-yellow mats. **Stems** creeping, pinnately branched. **Stem and branch leaves** slightly differentiated; stem leaves larger and longer, erect-spreading, concave, 1–2 × 0.15–0.18 mm, narrow-lanceolate, slightly falcate-cuspidate, margins entire; apex long acuminate; laminal cells linear, 60–70 × ca. 2 µm, seriately papillose over the lumina, thick-walled, basal cells sometimes smooth; costae short and double or absent; alar cells differentiated, consisting of 1–4 rows, vesiculose, yellowish or hyaline. **Rhizoids** evenly distributed along the stem. **Perichaetial leaves** 1.5–2.0 × 0.18–0.3 mm, ovate; margins entire at base, serrulate at apex; apex filiform; laminal cells linear, 72–74 × ca. 2 µm, thick-walled, smooth at base, papillose at apex; costae absent; alar cells poorly differentiated. **Setae** 10–25 mm long. **Capsules** erect, asymmetric, ovoid, 0.6–0.8 mm long, constricted below mouth; exothecial cells subquadrate, not collenchymatous. **Operculum** not seen. **Spores** finely papillose, 12–16 µm across.

Notes: This very distinct plant was once considered to be endemic to Lord Howe Island; however, it was later found in Queensland (Fig. 18). Unfortunately, I was unable to study specimens from mainland Australia but Ramsay et al. (2002a) and Tan et al. (1996) studied this species for the Flora of Australia.

Taxithelium muscicola resembles *T. damanhurianum*, but it is much larger (see notes on *T. damanhurianum*). The well-developed alar cells, along with large and narrowly lanceolate leaves with entire margins make a very distinctive combination.

Taxithelium muscicola is epiphytic or epiphyllous in montane rain forest.

Representative Specimens Examined –AUSTRALIA. Lord Howe Island, *Whitelegge 11* (H, NSW), *Watts 419* (NSW), *Watts 403* (PC).

7. Taxithelium planissimum Broth., Hedwigia 50: 141. 1910. Protologue: Ceylon. Auf faulem Holz im Urwald des Hayocock-Hill (Hiniduma) c. 300m [*Herzog*]. Holotype: *Herzog 20* (H!). Isotypes: JE!, S!, BR! Fig. 19.

Taxithelium ramicola Broth., Philipp. J. Sci. 8: 91. 1913, *syn. nov*. Protologue: Polillo, on branches of trees, *Bur. Sci. 10509 McGregor*. Holotype: *McGregor B. S. 10509* (H!). Isotypes: BM!, NY!, S!, FH!, US!

Taxithelium wewakense E. B. Bartram, Brittonia 13: 378. 1961, *syn. nov*. Protologue: [New Guinea], Sepik District: Wewak-Angoram Area, Prince Alexander Ranges, Maprik-But track, on leaf, rain forest, 2500 ft, 30 July 1959, *2026*, type; Keram River near Chuimundo, levee-bank forest, *2515*, robust form. [Robbins]. Holotype: *Robbins 2026* (FH!). Isotype: L!

Plants medium sized, forming pale-yellow mats. **Stems** creeping, long ascending branched. **Stem and branch leaves** slightly differentiated; stem leaves larger and longer, erect-spreading, concave, 0.75–1.5 × 0.20–0.40 mm, oblong-lanceolate, margins entire; apex acuminate; laminal cells linear, 60–65 × ca. 2 µm, seriately papillose over the

lumina, thick-walled, basal cells sometimes smooth; costae short and double or absent; alar cells poorly differentiated, consisting of 1 row, not inflated **Rhizoids** evenly distributed along the stem. **Perichaetial leaves** 1.2–2.0 × 0.30–0.45 mm, lanceolate, margins serrulate; apex acuminate; laminal cells linear, 35–40 × ca. 2 µm, thick-walled, pluripapillose; costae absent; alar cells poorly differentiated in 2 rows, not inflated. **Setae** 5–7 mm long. **Capsules** inclined, asymmetric, ovoid, 0.6–0.8 mm long, constricted below mouth; exothecial cells subquadrate, not collenchymatous. **Operculum** long, conic-rostrate, ca. 0.8 mm long. **Spores** finely papillose, 15–20 µm across.

Notes: *Taxithelium planissimum* resembles *T. isocladum* in its leaf shape and size and absence of well developed alar cells, but it can be distinguished by the very distinct long rostrate opercula and much longer seta. Furthermore, the perichaetial leaves of *T. isocladum* have pluripapillose cells at the apex, while the perichaetial leaves of *T. planissimum* have smooth cells.

Taxithelium isocladum occurs in lowlands from Sri Lanka to SE Asia (Malesia), and Vietnam, between sea level and 300 m, but it was collected in Mt. Binohan (Palawan, Philippines) at about 1,000 m (Fig. 20). It grows almost exclusively on twigs and as an epiphyll, rarely on bark.

Representative Specimens Examined – INDONESIA. Sumatra (Brastagi), *Holtamm 25327*, *HBR 437* (NY); Seram, *Akiyama 9906* (NY); Java, *Zollinger 1106* (S).

MALAYSIA. Selangor, *Câmara 960* (MO); Malacca, *Werner s.n.* (JE); Perak, *Ridley 213* (H); Sabah, *Holtmann 1931* (NY).

PAPUA NEW GUINEA. Wewak, *Robbins 2026* (FH, L).

PHILIPPINES. Palawan, *Ebalo 391* (MICH); *MacGregor B. S. 10509* (H, BM, NY, S, FH, US).

SRI – LANKA. Hiniduma, *Herzog 3979* (H), *Herzog s.n.* (JE, S, BR, H); *sine loco, Thwaites 217* (NY).

VIETNAM. Lao Cai. *Moctier s.n.* (S).

8. Taxithelium pluripunctatum (Renauld & Cardot) W. R. Buck, Moscosoa 2: 60. 1983; *Trichosteleum pluripunctatum* Renauld & Cardot, Bull. Soc. Roy. Bot. Belgique 29(1): 184. 1890. Protologue: Hab. Martinique: Ste-Marie (Bordaz). Holotype: *Bordaz 1* (PC!). Isotype : NY! Fig. 21.

Taxithelium thelidiellum Besch., J. Bot. (Morot) 6: 10. 1902.

Protologue: Guadeloupe, sur un arbre, au Trou aux trois Diables (P. Duss, N^{o} 1364). Isotypes: *Père Duss 1364* (NY!, H!).

Taxithelium patulifolium Thér., Ann. Bryol. 7: 160. 1934.

Protologue: Guyane française: Saint-Jean-du-Maroni (leg.?, année 1895). Holotype: *Sine Legit* PC! Isotypes: H!, NY!

Nomenclatural notes:

1. Even though Émile Bescherelle's herbarium is now at BM, no type of *T. thelidiellum* was found there.

2. The type specimens of *T. patulifolium* have no data on the collector, either from the protologue or on the specimen, but the other information on the specimen matches with the protologue.

Plants medium sized, forming lax, golden mats. **Stem** creeping, freely branched. **Stem and branch leaves** slightly differentiated; stem leaves larger and longer, branch leaves more papillose; wide-spreading, 0.70–1.2 × 0.20–0.40 mm, falcate, lanceolate-ovate, margins sub-entire or serrulate at base; apex acuminate to aristate; laminal cells linear, 72–85 × ca. 2 µm, seriately papillose over the lumina, thick-walled; apical cells usually smooth; costae double and short or absent; alar cells poorly differentiated. **Rhizoids** clustered beneath the stem. **Perichaetial leaves** 1.0–1.5 × 0.18–0.30 mm, long-triangular, margins serrulate at apex; apex acuminate to aristate; laminal cells linear, 60–80 × ca. 2 µm, thick-walled, poorly pluripapillose; costae absent; alar cells poorly differentiated. **Setae** 4.9–5.1 mm long. **Capsules** inclined, asymmetric, ovoid, 0.6–0.8 mm long, constricted below mouth; exothecial cells subquadrate, slightly or not collenchymatous. **Operculum** short, conic or obliquely conic-rostrate, ca. 0.3 mm long. **Spores** finely papillose, 15–20 µm across.

Notes: This species, together with *T. portoricense*, is one of the two species that occur in the New World. However *T. portoricense* has involute leaf margins, less papillose leaves, and smooth perichaetial leaf cells, *T. pluripunctatum* also has slightly falcate leaves.

Some species of *Mittenothamnium* Henn. may also resemble *T. pluripunctatum* (Buck 1998), but the latter can be recognized by its pluripapillose leaf cells and poorly

differentiated alar cells, whereas *Mittenothamnium* has smooth leaf cells and well developed alar cells.

Taxithelium pluripunctatum is restricted to the New World, being found from Mexico to South America and the West Indies (Fig. 22). It grows on tree trunks, limestone and humus, at elevations between sea level and 900 m**.**

Representative Specimens Examined– BRAZIL. Amazonas: Rio Uamatã, *Buck 3148* (NY); Bahia: Ilhéus, *Boom & Mori 870* (NY), Uruçuca, *Vital & Buck 20321A* (NY); Roraima: Boca da Mata, *Buck 1948* (NY).

COLOMBIA. Isla Gorgona, *Rudas & Aguirre 130* (NY).

DOMINICA. Four Hunk, *Fishlock 13* (NY, MICH).

FRENCH GUYANA. Dt. Laurent-du- Maroni: Commune de Saül, *Buck 18349A* (NY); Commune de Appropague-Kaw, *Buck 37799* (NY)*;* Commune de Matoury *Buck 32904* (NY, MO).

GUADELOUPE. *sine loco*, *Duss 1364* (NY); Sofaia, *Allorge s.n.* (MICH)

MARTINIQUE. Absalon, *Welch 21336* (NY, MICH).

PUERTO RICO. Luquillo, *Buck 4192* (NY).

TRINIDAD. Aripo, *Djan-Chékar 94-510* (NY).

9. Taxithelium portoricense R. S. Williams, Bryologist 30: 37. 1927. Protologue: Porto Rico near Cidra, no *8390*, growing on twigs in wooded ravine, by Mrs. E. G. Britton, March 1925; also obtained in Isle of Pines, Cuba, March, 1916, by N.L. Britton, P. Wilson and Bro. Leon no. *6119*. Lectotype (designated here): *E. G.*

Britton 8390 (NY!). Isolectotypes: FH!, PC!. MICH! Syntype: *Wilson & León 6119* (NY!). Fig. 23.

Plants medium sized, forming lax, golden mats. **Stem** creeping, freely branched. **Stem and branch leaves** slightly differentiated; stem leaves larger and longer, branch leaves more papillose, wide-spreading, 0.70–1.2 × 0.20–0.35 mm, oblong-lanceolate, margins sub-entire or serrulate only at base; apex acuminate; laminal cells linear, 44–50 × ca. 2 µm, seriately papillose over the lumina, thick-walled; apical cells usually smooth; costae double and short or absent; alar cells poorly differentiated. **Rhizoids** clustered beneath the stem. **Perichaetial leaves** 0.80–1.2 × 0.18–0.45 mm, long-triangular, margins entire, laminal cells linear, 80–90 × ca. 2 µm, thick-walled, smooth; apex acuminate; costae absent; alar cells poorly differentiated. **Setae** 4.9–5.1 mm long. **Capsules** inclined, asymmetric, ovoid, 0.6–0.8 mm long, constricted below mouth; exothecial cells subquadrate, slightly or not collenchymatous. **Operculum** short, conic or obliquely conic-rostrate, ca. 0.3 mm long. **Spores** finely papillose, 15–20 µm across.

Notes: This species is one of two growing in the Americas (the other being *T. pluripunctatum*). Because of its more oblong leaf it has been suggested that *T. portoricense* is close to *T. planum*, of subgenus *Taxithelium* (Buck 1998), but both the key characteristics of subgenus *Vernieri* and molecular evidence (Câmara and Shaw unpubl. data) support its placement here. *Taxithelium portoricense* can be differentiated from *T. pluripunctatum* because of its less papillate and more symmetric leaves with involute margins, and perichaetial leaf cells that lack papillae (see also comments on *T. pluripunctatum*).

Taxithelium portoricense was also recorded from the Brazilian Amazon by Lisboa and Ilkiu Borges (1997), although it was not possible to study the specimen cited there. The description is unclear and the illustration is of *T. pluripunctatum*; therefore I am excluding this record.

It is restricted to Islands in the Caribbean (Fig. 24), and grows on twigs and dead logs, between sea-level and 1,500 m.

Representative Specimens Examined– CUBA. El Yunque, *Underwood & Earle 1054* (NY), Caleta Cocodrilos, *Britton et al. 15281* (NY), Isle de Pines, *E. P. Killip 43735* (FH, S).

DOMINICA. Picard Valley, *W. R. Elliot 961c* (FH!).

DOMINICAN REPUBLIC. Prov. Samará, *Buck 8701* (NY); Repressa Dam, *Allard 17275* (NY).

GUADELOUPE. Sofaia, *Le Gallo 444a* (FH).

JAMAICA. Portland Parish, *Crosby 13743* (NY).

MEXICO. Cozumel Island, *Steere 2767* (NY).

PUERTO RICO. Caribbean National Forest, *Buck 4101* (NY, FH); Las Cruces, *Steere 6361* (MICH, FH).

ST. KITTS. St. Thomas Middle Island Parish, *Buck 29826* (NY).

10. Taxithelium ramivagum Broth., Bot. Jahrb. Syst. 24: 266. 1897. Protologue: Kamerun: Ekundu N'dene, an Baumästen (Dusén n. 797) Lolodorf, Berg Mbanga (Staudt n. 277). Lectotype (designated here): *Staudt 277* (H!). Isolectotype: PC! Syntypes: *Dusén 797* (H!, S!). Fig. 25.

Taxithelium ramivagum Broth. var. ***elongatum*** P. de la Varde, Revue Bryologique et Lichénologique 5: 207. 1933. *Syn. Nov.* Protologue: Foret des echiras, entre Pogha et malongo-mabey leg Le testu. Holotype*: Le Testu 6768* (PC!).

Taxithelium theriotii P. de la Varde Bulletin de la Société Botanique de France 72: 364. f. 16. 1925. *Syn. Nov*. Protologue: Hab. Gabon, pays Apindjí, entre Ghenyonga et Benzé. Leg. Le testu, no 5324. Holotye*: Le Testu 5324* (PC!).

Plants large, forming golden-yellow mats. **Stems** creeping, long ascending branched. **Stem and branch leaves** slightly differentiated (stem leaves larger and longer), erect-spreading, concave, 1.0–1.6 × 0.25–0.40 mm, oblong-lanceolate, margins entire; apex entire or slighlty acuminate; laminal cells linear, 75–80 × ca. 2 µm, seriately papillose over the lumina, thick-walled, basal cells sometimes smooth; costae absent; alar cells poorly differentiated, consisting of 2 rows, not inflated. **Rhizoids** evenly distributed along the stem. **Perichaetial leaves** 1.0–1.5 × 0.24–0.30 mm, narrow-lanceolate, margins entire; apex setaceous; laminal cells linear, 32–40 × ca. 2 µm, thick-walled, smooth; costae absent; alar cells poorly differentiated in 2 rows, not inflated. **Setae** ca. 10 mm long. **Capsules** unknown.

Notes: Known only from few collections (mostly types), this species is restricted to Tropical Africa (Fig. 26); the last collection made was from the 1920s.

Taxithelium ramivagum resembles *T. isocladum* in its leaf size and leaf shape but the leaf cells are about twice as long in *T. ramivagum* and the perichaetial leaf cells are smooth (*T. isocladum* has pluripapillose cells at apex).

It grows on bark from sea level to 875m.

Representative Specimens Examined – CAMEROON. N'Dende, *Dusen 797* (H, S); Mbanga, *Staudt 277* (H).

CÔTE D'IVOIRE. Hourotte, *Jolly s.n.* (S).

DEMOCRATIC REPUBLIC OF CONGO. Kivu, station de recherché de L'IRSAC, pres de la Luhoho, *fzaire s.n.* (BR).

GABON. Mavenga, *Le Testu s.n.* (M); Malongo-Mabey, *Le Testu 6768* (PC).

LIBERIA. Sinoe District, *Baldwin 11337* (PC)

SIERRA LEONE. Freetown, Mt. Oriel. *Arnell 2306* (PC)

11. Taxithelium vernieri (Duby) Besch., Bull. Soc. Bot. France 45: 123. 1898; *Hypnum vernieri* Duby, Flora 58: 285. 1875. Protologue: Ad ligna emortua ins. Tahiti adpressum legit D. Vernier missionarius Aff. *H. tenuiseto* Sull. Holotype: *Vernier s.n.* (G!). Isotypes: PC!, BM!, NY! Fig. 27.

Taxithelium nitidulum Broth. & Paris, Oefvers. Förh. Finska Vetensk.-Soc. 48 (15): 23. 1906, *syn. nov*. Type: [New Caledonia], Ad arbores riparum amnis Thi (Le Rat). Holotype: *Le Rat s.n.* (H!). Isotypes: PC!, M!

Taxithelium francii Thér., Bull. Acad. Int. Géogr. Bot. 20: 103. 1910, *syn. nov*. Type: [New Caledonia], Mont Koghis, 400m. [M. Franc]. Holotype: *Franc s.n.* (PC!). Isotypes*:* FH!, BM!, H!

Taxithelium kuniense Broth. & Paris, Oefvers. Förh. Finska Vetensk.-Soc. 53A(11): 36. 1911, *syn. nov*. Protologue: [New Caledonia], Ile des Pins, forêt de Gadge et forêt de Uapan, ad ligna putrida (Louise Le Rat). Lectotype (designated here): Forêt de Gadge, *L. Le Rat 1372* (H!). Isolectotype: Foret de Gadge, *Louise Le Rat s.n*. (S!, PC!). Syntype: Forêt de Uapan, *L. Le Rat 1403* (H!, M!).

Taxithelium protensum Dixon, Proc. Linn. Soc. New South Wales 55: 297, f. 24. 1930, *syn. nov*. Protologue: Hab. Fiji Is. Coll. Steel: herb. Dixon (4). Holotype: *Steel 4* (BM!).

Taxithelium falcifolium E. B. Bartram, Occas. Pap. Bernice Pauahi Bishop Mus. 10(10): 14. 1933, *syn. nov*. Protologue: Polynesia. Type: Eiao, interior of furas forest, high ridge, elevation 700m., September 20, 1922, W.B. Jones no. 1522. Holotype: *Jones 1522* (FH!). Isotype: L!, US!

Plants small, forming golden-yellow mats. **Stems** creeping, long ascending branched. **Stem and branch leaves** similar, erect-spreading, concave, 0.6–1.2 × 0.15–0.30 mm, oblong-lanceolate, margins entire; apex acuminate or acute; laminal cells linear, 58–60 × ca. 2 µm, seriately papillose over the lumina, thick-walled, basal cells sometimes smooth;

costae short and double or absent; alar cells poorly differentiated, consisting of 1–3 rows, supra alar cells not differentiated. **Rhizoids** evenly distributed along the stem. **Perichaetial leaves** 1.2–1.6 × 0.40–0.50 mm, lanceolate, margins entire at base, serrulate at apex; apex long- aristate; laminal cells linear, 50–70 × ca. 2 µm, thick-walled, smooth; costae absent; alar cells not differentiated. **Setae** 14–16 mm long. **Capsules** inclined, asymmetric, ovoid, 0.6–0.8 mm long, constricted below mouth; exothecial cells subquadrate or rectangular, not collenchymatous. **Operculum** short, conic or obliquely conic-rostrate, ca. 0.3 mm long. **Spores** finely papillose, 15–20 µm across.

Notes: *Taxithelium vernieri* can be recognized by its lanceolate leaves with entire margins and smooth perichaetial leaves. It is by far the most common species of *Taxithelium* in the Pacific. It can resemble species of *T. levieri*, but the alar cells in *T. vernieri* are not well developed as they are in *T. levieri*.

It grows in dense forests, usually on dead logs, sometimes on bark of living trees, between sea level and 700 m ,and is restricted to the islands of the Pacific, New Caledonia, Society Islands (French Polynesia), Micronesia and Marquesas (Fig. 28).

Representative Specimens Examined – MICRONESIA. Etten Island, *Whittier & Miller 797* (NY); Atoll Ulul, *Whittier & Miller 1075* (NY), Atoll Puluwatt, *Whittier & Miller 1108* (NY); Atoll Iruh, *Whittier & Miller 7471* (G).

FIJI. Vanua Levu, *Smith 1618* (NY); Viti Levu, *Smith 8548* (DUKE); Vanua Mbalavu, *Smith 1478* (NY).

FRENCH POLYNESIA. Society Islands, Moorea, *Sloover 20946* (NY); Tahiti, *Vernier s.n.* (G, PC, NY, BM), *Vernier 1316* (G); Marquesas, Nuku Hiva, *Jordan s.n.* (NY).

MARQUESAS. Eiao, *Jones 1522* (L, US, FH).

NEW CALEDONIA. *Sine loco, L. Le Rat 1372* (H!); Mé Aoui, *Guillaumin et Baumann 10519* (PC); Mé Ammeri, *Guillaumin et Baumann 9152* (PC); Mt. Coughi, Balansa 2579b (PC)

SAMOA. Southeast shore, *Yuncker 9517* (NY, MICH).

TONGA. Island of Eua, *Yuncker 15392* (NY).

VANUATU. *Campbell 3* (BM).

Types not seen in genus *Taxithelium*

1. *Taxithelium anderssonii* (Ångstr.) Broth., Nat. Pflanzenfam. I (3): 1237. 1909. *Plagiothecium anderssonii* Ångstr., Öfvers. Förh. Kongl. Svenska Vetensk.-Akad. 29(4): 15. 1872. Protologue: Port Famine vid Magalhaens sund. Andersson.

Even though it was not possible to locate this type, is is probably not *Taxithelium*, since the genus is not known to occur that far south.

2. *Taxithelium aureolum* Cardot, Bull. Soc. Bot. Genève sér. 2, 5: 319. 1913. Protologue: Japon: Hirosaki (n.18).

Probably not *Taxithelium* but *Phyllodon*. According to the original description this plant has a single papilla per cell, therefore it is unlikely to be a *Taxithelium*. Cardot assigned this species to section *Anastigma*, all species of which are now placed in the unrelated genus *Phyllodon*. The description of *T. aureolum* would fit into *Phyllodon* rather than in *Taxithelium*.

3. *Taxithelium bilobatum* var. *scabrifolium* Dixon, Gard. Bull. Straits Settlem. 4: 35. 1926. Protologue: Perak: Bujong Malacca (R. 739); Birrsch's Hill, 3800 ft., on stone in forest (Burkill 13007), nov.var. *scabrifolium* Dixon.

According to the original description, the specimen has bilobate leaves, which are not found in *Taxithelium.*

4. *Taxithelium confusum* Cardot, Hist. Phys. Madagascar, Mousses 39: 471. 1915. Protologue: [Madagascar], Ile a Sainte-Marie. Boivin s.n.

The ilustration provided by Cardot resembles the widespread *Taxithelium lindbergii*.

5. *Taxithelium decrescens* (Sande Lac.) Broth., Nat. Pflanzenfam. I (3): 1092. 1908. *Hypnum decrescens* Sande Lac., Bryol. Jav. 2: 168. 266. 1866. Protologue: Habitat insulam *Celebs*, herb. Ludg. Bat.

The illustration provided in the original description shows unipapillose cells and consequently is probably not a *Taxithelium*. The illustration of the perichaetia also does not resemble those found in *Taxithelium*.

6. *Taxithelium glabrisetum* (Müll. Hal.) Paris, Index Bryol. 1261. 1898. *Sigmatella glabriseta* Müll. Hal., Bot. Jahrb. Syst. 23: 329. 1896. Protologue: Samoa Inseln, Olosina, zwischen Flechten (n.91).

Unfortunately the protologue does not provide a good description and illustration that would allow placement of this type. The specimen was probably destroyed during the bombing of the Berlin herbarium in 1943.

7. *Taxithelium herpetium* (Müll. Hal.) Broth., Nat. Pflanzenfam. I(3): 1091. 1908. *Hypnum herpetium* Müll. Hal., J. Mus. Godeffroy 3(6): 84. 1874. Protologue: Patria: Tutuila, Inter alios muscos.

The original description states that the leaves of the type have single papillae and therefore it is probably not *Taxithelium*; but unfortunately, no illustration of this plant exists. The type was also probably destroyed during the bombing of the Berlin herbarium in 1943.

8. *Taxithelium inerme* Tixier, Rev. Bryol. Lichénol. 38: 159, f. 8. 1971 [1972]. Protologue: Thailand, Chandhaburi, Plew Waterfalls, au sol, 3/6/65 *Tixier 965*, (holotype).

The original description says that this plant has smooth leaf cells, but the illustration provided does not resemble the non-papillose species of *Taxithelium*. I visited the herbarium in Paris (PC) twice and tried unsuccessfully to locate this specimen in Tixier's herbarium.

9. *Taxithelium isocladum* (Bosch. & Sande Lac.) Renauld & Cardot var. *vietnamense* Tixier, Rev. Bryol. Lichénol. 34: 171. 1966. Protologue: Vietnam. Quang-Binh, 50 m *Maunier s.n.*, 1927.

The original description and illustration provided matches with *T. isocladum*, but it is otherwise unknown from Vietnam. I visited the herbarium in Paris (PC) twice and tried unsuccessfully to locate this specimen in Tixier's herbarium.

10. *Taxithelium ivoreanum* (Mitt.) Broth., Nat. Pflanzenfam. I(3): 1093. 1908. *Stereodon ivoreanus* Mitt., J. Proc. Linn. Soc., Bot., Suppl. 2: 105. 1859. Protologue: Hab. In Nepal, *Wallich*! In Mont. Nilghiri, *McIvor*.

This species is probably a *Phyllodon*. Unfortunately the original description is vague. However Brotherus, when transferring *Stereodon ivoreanus* to *Taxithelium* considered it close to *T. glossoides, T. similans* and *T. ligulatum*, all now placed in *Phyllodon*.

Thiers (1992) in the "Indices to the species of mosses and lichens described by William Mitten" (Thiers 1992) to this specimen was listed as *non vide*, so it was already lost when Mitten's herbarium was transferred to NY.

11. *Taxithelium laeve* Cardot, Bull. Soc. Bot. Genève sér. 2, 4: 387. 1912. Protologue: Japon: Tosa, Arakusa (Okamura; herb. Holzinger).

The original description says that the type specimen has smooth leaf cells. As the only *Taxithelium* known from Japan (*T. lindbergii*) is papillose, *T. laeve* may not be a member of the genus. It was not possible to locate this type during my two visits to PC.

12. *Taxithelium liukiuense* Sakurai, Bot. Mag. (Tokyo) 46: 505. 1932. Protologue: Japan, Liukiu: Nishi-Omotejima, auf Felsen (coll. Y. Dor, Typus in Herb. K. Sakurai, Nr. 2170, 6 -Aug-1931).

Sakurai compares this species with *T. nepalense*, considering the two to be closely related. The description would fit species of subgenus *Taxithelium* (in which *T. nepalense* belongs).

Although the type is listed as being at K, there are no moss collections at Kew any longer, since they were sent to the herbarium of the Natural History Museum (BM) on a permanent loan. However, I was unable to locate this specimen during my visit to BM

13. *Taxithelium natans* (Müll. Hal.) Renauld & Cardot, Rev. Bryol. 28: 111. 1901. *Sigmatella natans* Müll. Hal., Hedwigia 40: 70. 1901. Protologue: Habitatio. Brasilia, Rio de Janeiro, Morro da Cintra, in aqua fontis, Aug. 1887: E.Ule, coll. No 161.

The original description of of both *T. natans* and *T. oophyllum* matches *T. planum*, which is the only species of *Taxithelium* known to occur in Rio de Janeiro and Minas Gerais. The types of both were probably lost during the fire in the bombing of the Berlin herbarium in 1943.

14. *Taxithelium oophyllum* (Müll. Hal.) Renauld & Cardot, Rev. Bryol. 28: 111. 1901. *Sigmatella oophylla* Müll. Hal., Hedwigia 40: 70. 1901. Protologue: Habitatio. Brasilia, Minas Geraes, ad cataractam prope Uberaba, Junio 1892: E.Ule coll. 1598.

See comments above on *T. natans*.

15. *Taxithelium orthothecium* (A. Jaeger) Broth., Nat. Pflanzenfam. I(3): 1091. 1908. *Trichosteleum orthothecium* A. Jaeger, Ber. Thätigk. St. Gallischen Naturwiss. Ges. 1876–77: 414. 1878. Protologue: Patria. Insula samoan. Tutuila (*Graeffe*)

Unfortunately the original description is mostly useless and there is no illustration available. Brotherus however assigned this plant to the same group as *T. vernieri, T. isocladum* and *T. alare* (=*T. lindbergii*), all belonging now to subgenus *Vernieri*. The most common of the species of *Taxithelium* subgenus *Vernieri* in Samoa is *T. vernieri.*

16. *Taxithelium planum* (Brid.) Mitt. var. *flavescens* (Müll. Hal.) Paris, Index Bryol. 1262. 1898. *Hypnum planum* Brid. var. *flavescens* Müll. Hal., Syn. Musc. Frond. 2: 265. 1851. Protologue: In insula Trinitatis Antillarum prope St. Joseph legit Crüger 14. Febr. 1874.

Unfortunately this species was probably lost during the fire in Berlin's herbarium in 1943. The original descrption matches with *T. planum* (subgenus *Taxithelium*)

17. *Taxithelium planum* (Brid.) Mitt. var. *hookerioides* Bizot & Thér., Bull. Mens. Soc. Linn. Soc. Bot. Lyon 34: 326. 1965. Protologue: Cuba. Loma San Juan *Hioram 11808*, (Holotype: herb. Bizot; isotype: herb. Thériot).

I was unable to locate the type, but *T. planum*, this is the only species of subgenus *Taxithelium* present in Cuba.

18. *Taxithelium plumularia* (Müll. Hal.) Broth., Nat. Pflanzenfam. I(3): 1092. 1908. *Hypnum plumularia* Müll. Hal., Syn. Musc. Frond. 2: 684. 1851. Protologue: Patria. Java: Blume. Hb. Al. Braun.

The original description is vague; it says the cells are "poorly papillose", but no illustration was provided. This type was probably lost due to the bombing of Berlin in 1943.

19. *Taxithelium rhizophoreti* (Müll. Hal.) Broth., Nat. Pflanzenfam. I(3): 1091. 1908. *Hypnum rhizophoreti* Müll. Hal., J. Mus. Godeffroy 3(6): 83. 1874. Protologue: Patria.

Samoa-Insulae. Tutuila, inter alios muscos. Upolu, in rhizophoretis inter *Hypnum cyathothecium.*

There was no illustration accompanying the original description. The protologue is quite broad, but it does fit *Taxithelium*. Brotherus, when tranferring *Hypnum rhizophoreti* into *Taxithelium* considerd it close to species now included in subgenus *Vernieri*. The most common representative of that subgenus in Samoa is *T. vernieri*. The type was presumably lost during the bombing of Berlin in 1943.

20. *Taxithelium spathulifolium* Dixon, J. Siam Soc., Nat. Hist. Suppl. 10: 26. 1935. Protologue: Siam, Hab. Puket. Krabi, Panon Bencha, circa 1300 m., on trees and shrubs in evergreen forest, 28 March, 1930; coll. Kerr (511b).

In the original description the leaf cells are described as being smooth, which is not known in any species of *Taxithelium* from Thailand. I was unable to locate the type during my visit to BM.

21. *Taxithelium subretusum* (Thwaites & Mitt.) Broth., Nat. Pflanzenfam. I(3): 1093. 1908. *Ectropothecium subretusum* Thwaites & Mitt., J. Linn. Soc., Bot. 13: 321. 1873. Protologue: Hab. In Ceylon, *Dr. Thwaites*.

This species is probably a *Phyllodon*. According to the vague protologue, *Ectropothecium subretusum* is a papillose plant. Brotherus, when transferring this name into *Taxithelium* considered it to be close to *T. glossoides* and *T. ligulatum*, both now in *Phyllodon*.

22. *Taxithelium tongense* (Müll. Hal.) Broth., Nat. Pflanzenfam. I(3): 1090. 1908. *Hypnum tongense* Müll. Hal., J. Mus. Godeffroy 3(6): 83. 1874. Protologue: Patria: Tonga-Insulae, Tongatabú: Dr. Ed. Graeffe.

Probably a species in subgenus *Taxithelium*. Brotherus considered it close to *T. planum* and *T. instratum;* both these species are in subgenus *Taxithelium*; which would also agree with the somehow vague original description. The type was probably lost during the bombing of Berlin in 1943.

23. *Taxithelium ventrifolium* (Müll. Hal.) Broth., Nat. Pflanzenfam. I(3): 1090. 1908. *Hypnum ventrifolium* Müll. Hal., J. Mus. Godeffroy 3(6): 84. 1874. Protologue: Patria: Fidschi-Insulae, Ovalau, inter Hypnum rhinophyllum intertextum.

The original description does not mention the papillae, but Brotherus, when he transferred *Hypnum ventrifolium* into *Taxithelium,* considered it to be close to *T. planum* and *T. instratum*, both in subgenus *Taxithelium*. The type was probably lost during the bombing of Berlin in 1943.

There is a reference in *Index Muscorum* and TROPICOS, to "*Taxithelium annandii* Broth. & Watts, Proc. Linn. Soc. New South Wales 40: 152. 1915", I was unable to find the name anywere in the literature.

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Fig. 1) A, B. Poorly developed alar cells in *T. planissimum* and *T. ramivagum* respectively (400x). C, D. Well developed alar cells in *T. damanhurii* and *T. lindbergii* respectively (400 x). E. Collenchymatous exothecial cells in *T. damanhurianum.* F. Cross section of stem in *Taxithelium* (400x).

Fig. 2) Scatter plot for taxa in analyses "A", legend corresponds to groups previously recognized on basis of morphological differences.

Fig. 3) Scatter plot for taxa in analyses "B", legend corresponds to groups previously recognized on basis of morphological differences.

Fig. 4) First scatter plot for taxa in analyses "C", legend corresponds to groups previously recognized on basis of morphological differences.

Fig. 5) Second scatter plot for taxa in analyses "C", legend corresponds to groups previously recognized on basis of morphological differences.

Fig. 6) Scatter plot for discriminant analyses

Fig. 7) *Taxithelium damanhurianum.* A. Alar cells, B. Branch leaf, C. Leaf margin cells, D. Perichaetial alar region, E. Perichaetial leaf. B and E scale a; and A, C, D, scale b.

Fig. 8) Distribution map for *T. damanhurianum.*

Fig. 9) *Taxithelium isocladum*. A. Alar cells, B. Branch leaf, C. Leaf margin cells, D. Perichaetial alar region, E. Perichaetial leaf. B and E scale a; and A, C, D, scale b.

Fig. 10) Distribution map for *T. isocladum.*

Fig. 11) *Taxithelium kaernbachii*. A. Alar cells, B. Branch leaf, C. Leaf margin cells, D. Perichaetial alar region, E. Perichaetial leaf. B and E scale a; and A, C, D, scale b.

Fig. 12) Distribution map for *T. kaernbachii.*

Fig. 13) *Taxithelium levieri*. A. Alar cells, B. Branch leaf, C. Leaf margin cells, D. Perichaetial alar region, E. Perichaetial leaf. B and E scale a; and A, C, D, scale b.

Fig. 14) Distribution map for *T. levieri.*

Fig. 15) *Taxithelium lindbergii*. A. Alar cells, B. Branch leaf, C. Leaf margin cells, D. Perichaetial alar region, E. Perichaetial leaf. B and E scale a; and A, C, D, scale b.

Fig. 16) Distribution map for *T. lindbergii.*

Fig. 17) *Taxithelium muscicola*. A. Alar cells, B. Branch leaf, C. Leaf margin cells, D. Perichaetial alar region, E. Perichaetial leaf. B and E scale a; and A, C, D, scale b.

Fig. 18) Distribution map for *T. muscicola.*

Fig. 19) *Taxithelium planissimum*. A. Alar cells, B. Branch leaf, C. Leaf margin cells, D. Perichaetial alar region, E. Perichaetial leaf. B and E scale a; and A, C, D, scale b.

Fig. 20) Distribution map for *T. planissimum.*

Fig. 21) *Taxithelium pluripunctatum*. A. Alar cells, B. Branch leaf, C. Leaf margin cells, D Perichaetial alar region, E. Perichaetial leaf. B and E scale a; and A, C, D, scale b.

Fig. 22) Distribution map for *T. pluripunctatum.*

Fig. 23) *Taxithelium portoricense*. A. Alar cells, B. Branch leaf, C. Leaf margin cells, D. Perichaetial alar region, E. Perichaetial leaf. B and E scale a; and A, C, D, scale b.

Fig. 24) Distribution map for *T. portoricense.*

Fig. 25) *Taxithelium ramivagum*. A. Alar cells, B. Branch leaf, C. Leaf margin cells, D. Perichaetial alar region, E. Perichaetial leaf. B and E scale a; and A, C, D, scale b.

Fig. 26) Distribution map for *T. ramivagum.*

Fig. 27) *Taxithelium vernieri*. A. Alar cells, B. Branch leaf, C. Leaf margin cells, D. Perichaetial alar region, E. Perichaetial leaf. B and E scale a; and A, C, D, scale b.

Fig. 28) Distribution map for *T. vernieri.*

Fig. 1

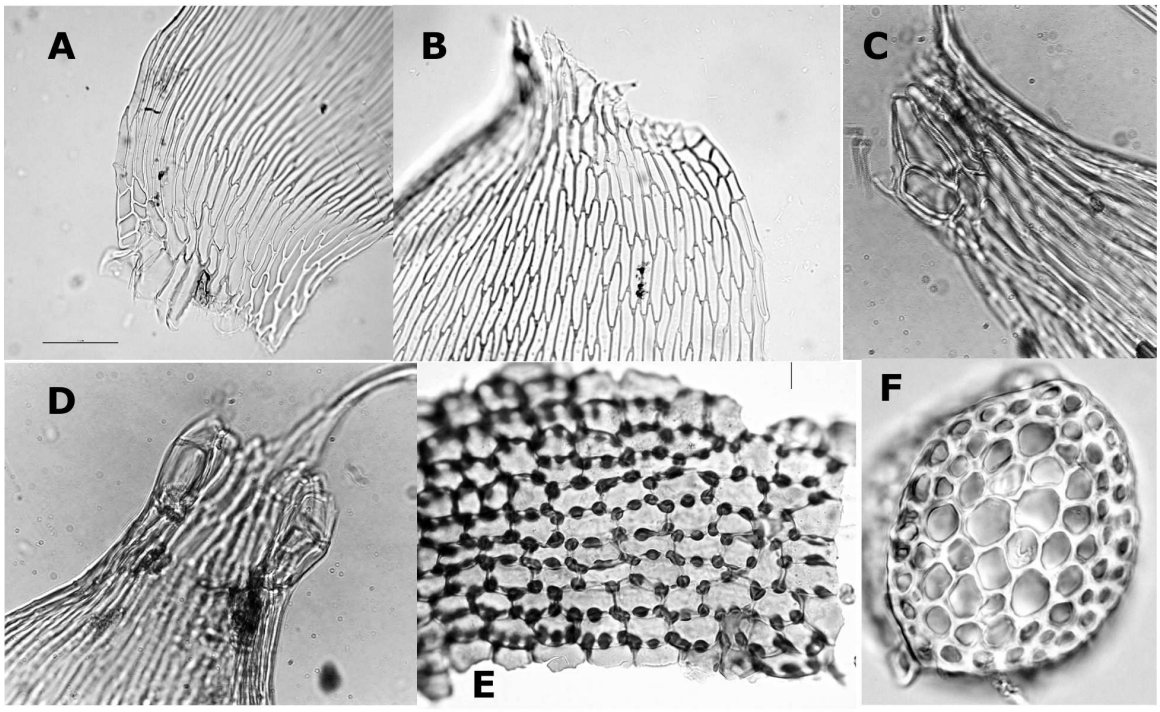
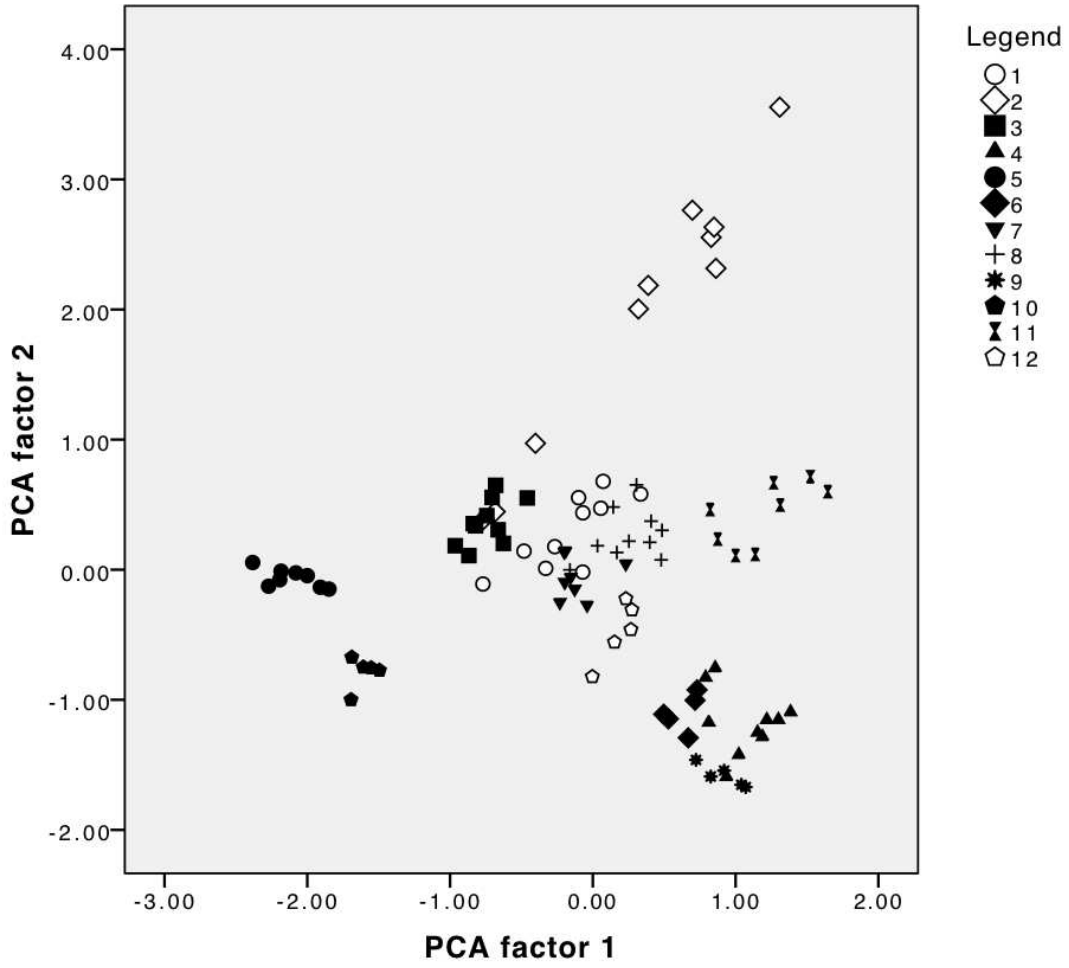


FIG. 2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PCA factor 1

FIG. 3

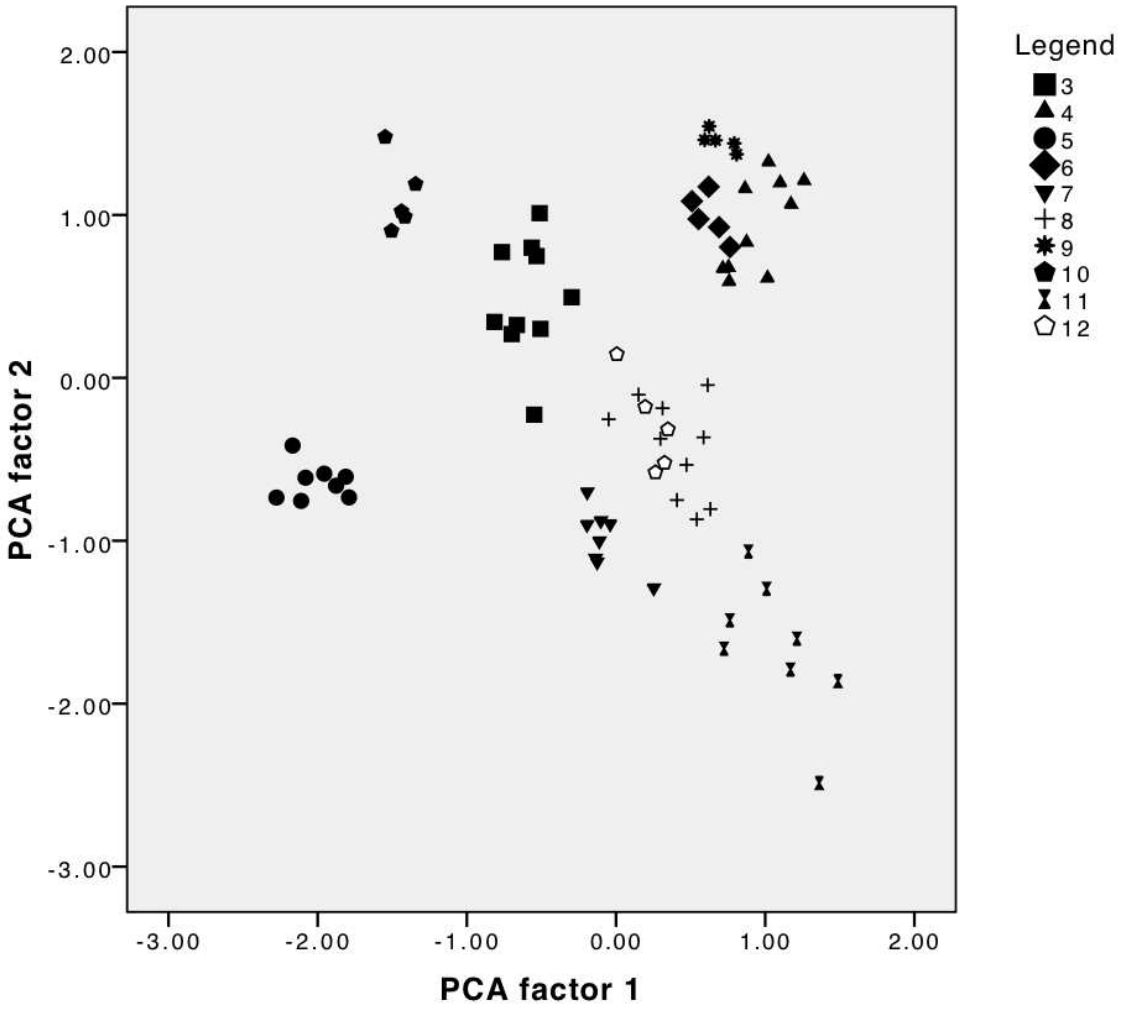
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FIG. 4

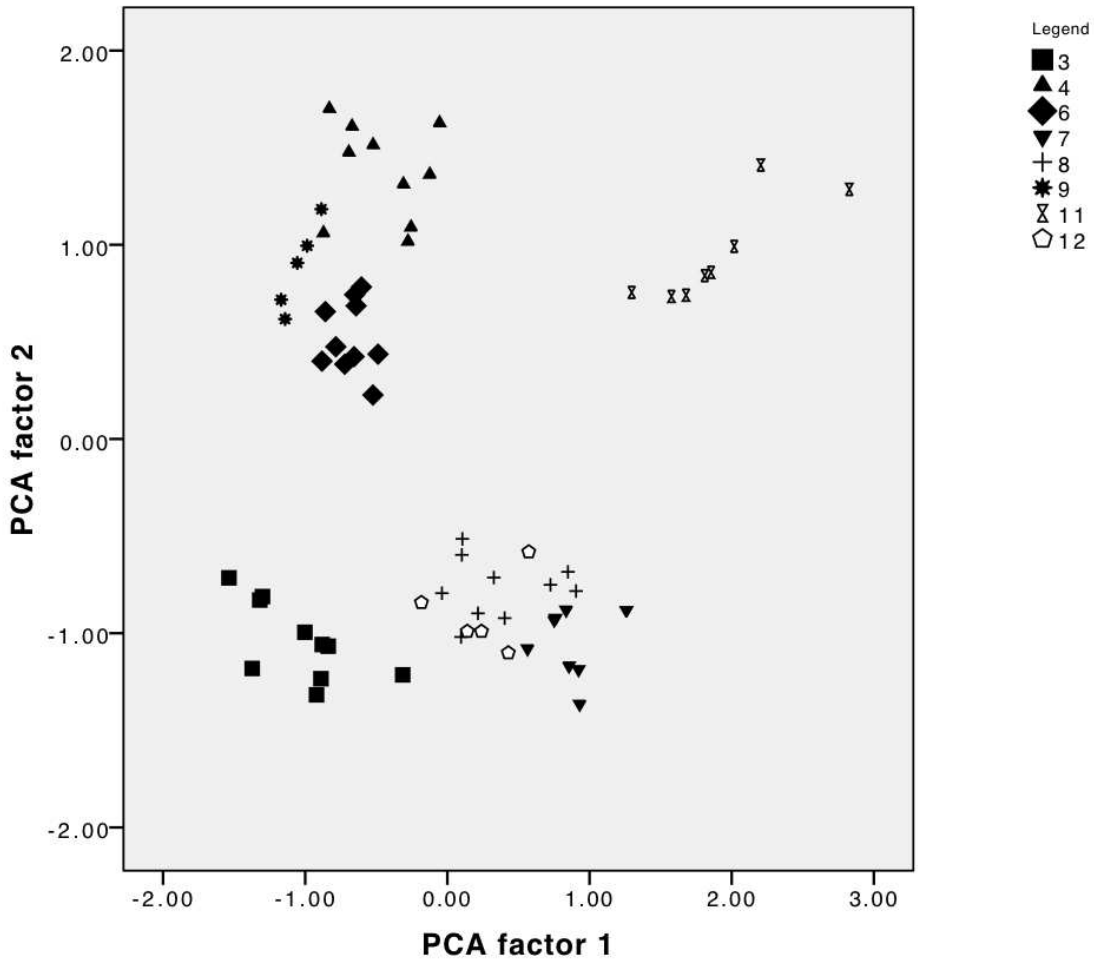
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FIG. 5

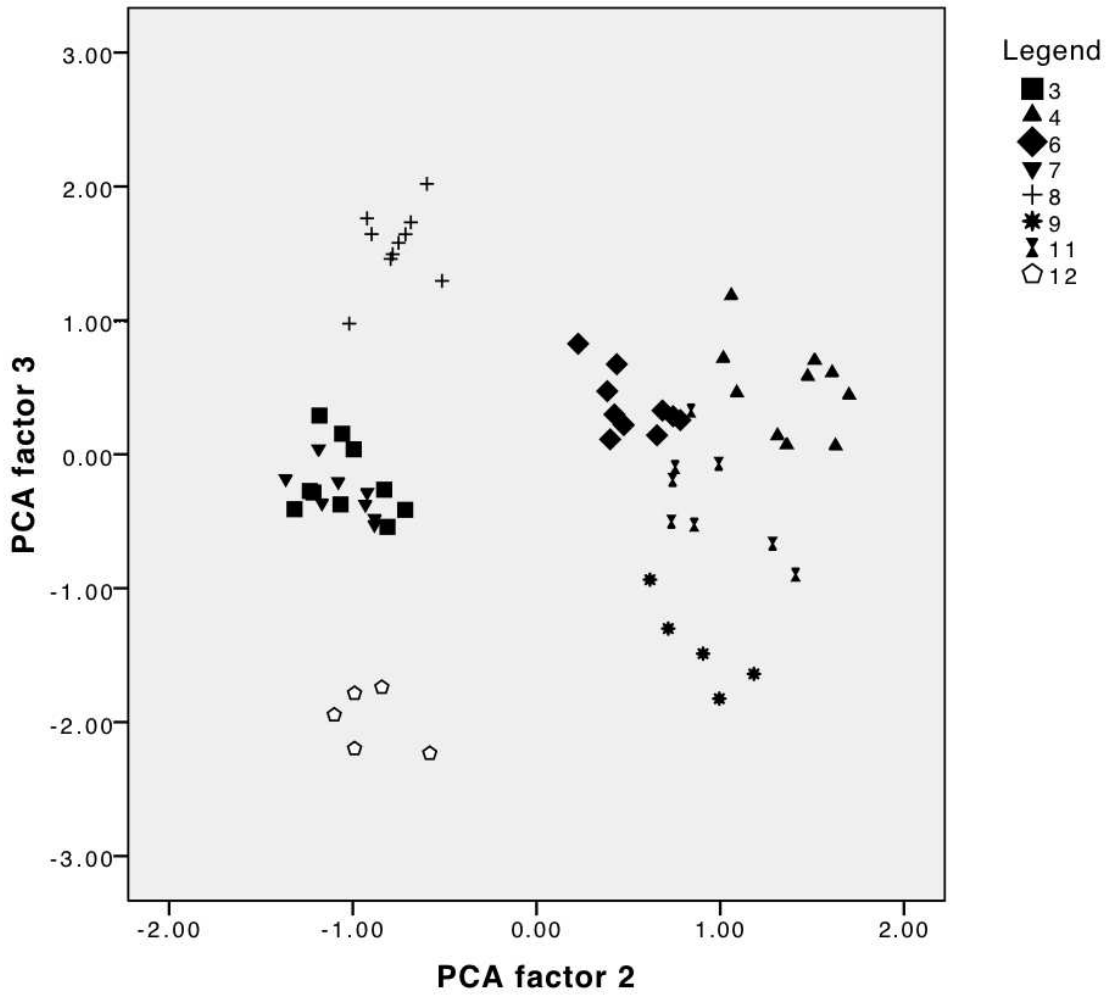
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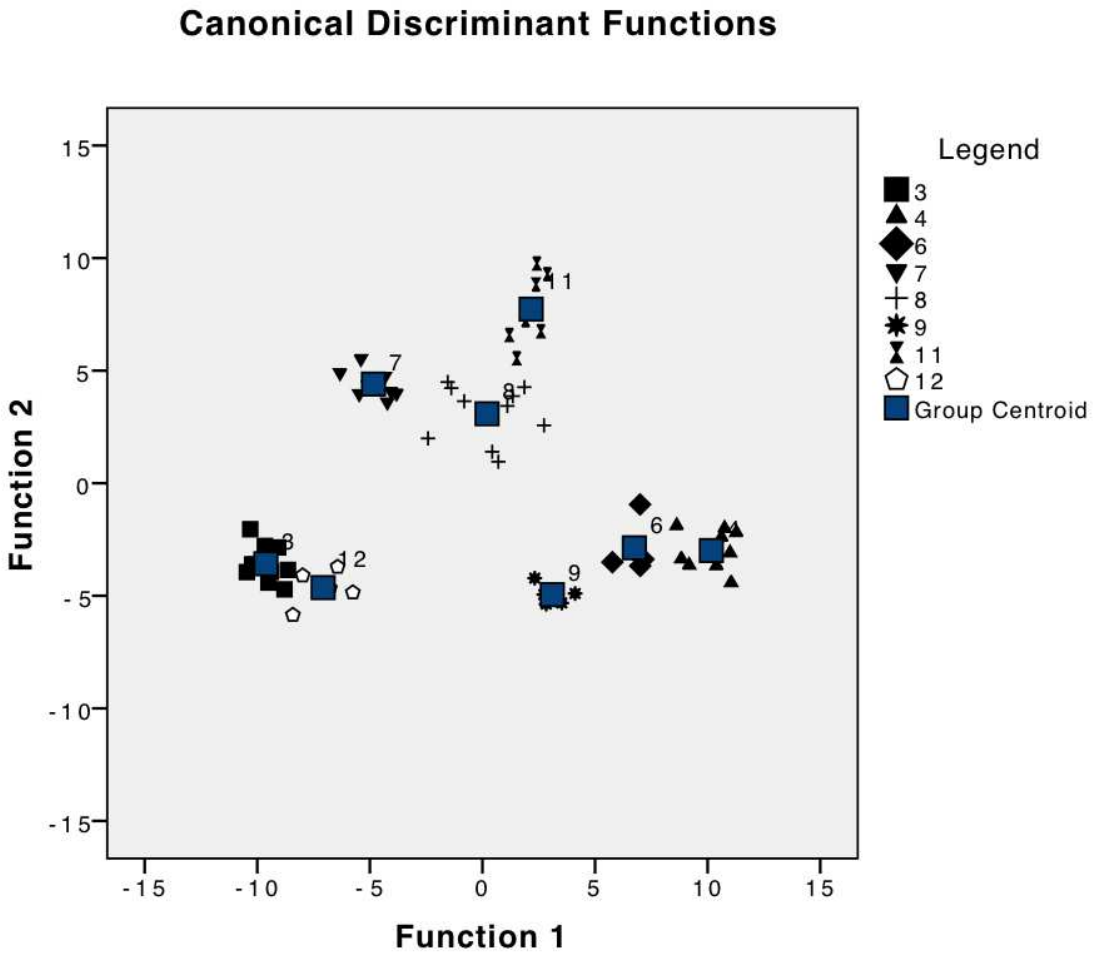
FIG. 6


Canonical Discriminant Functions
Function 2
Function 1
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12
Group Centroid

FIG. 7

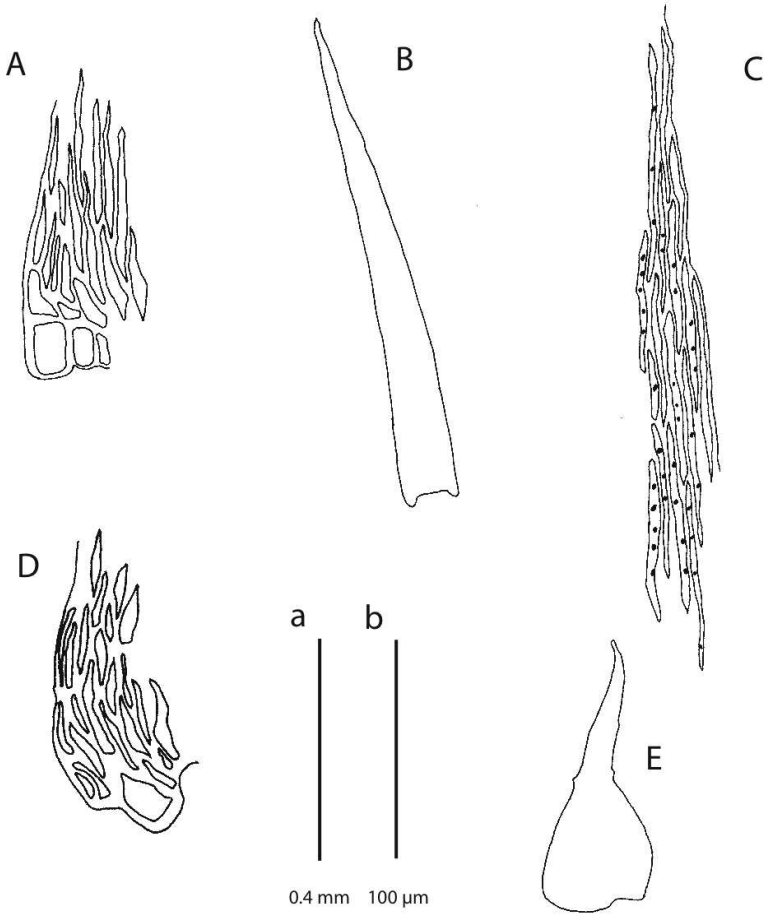


FIG. 8

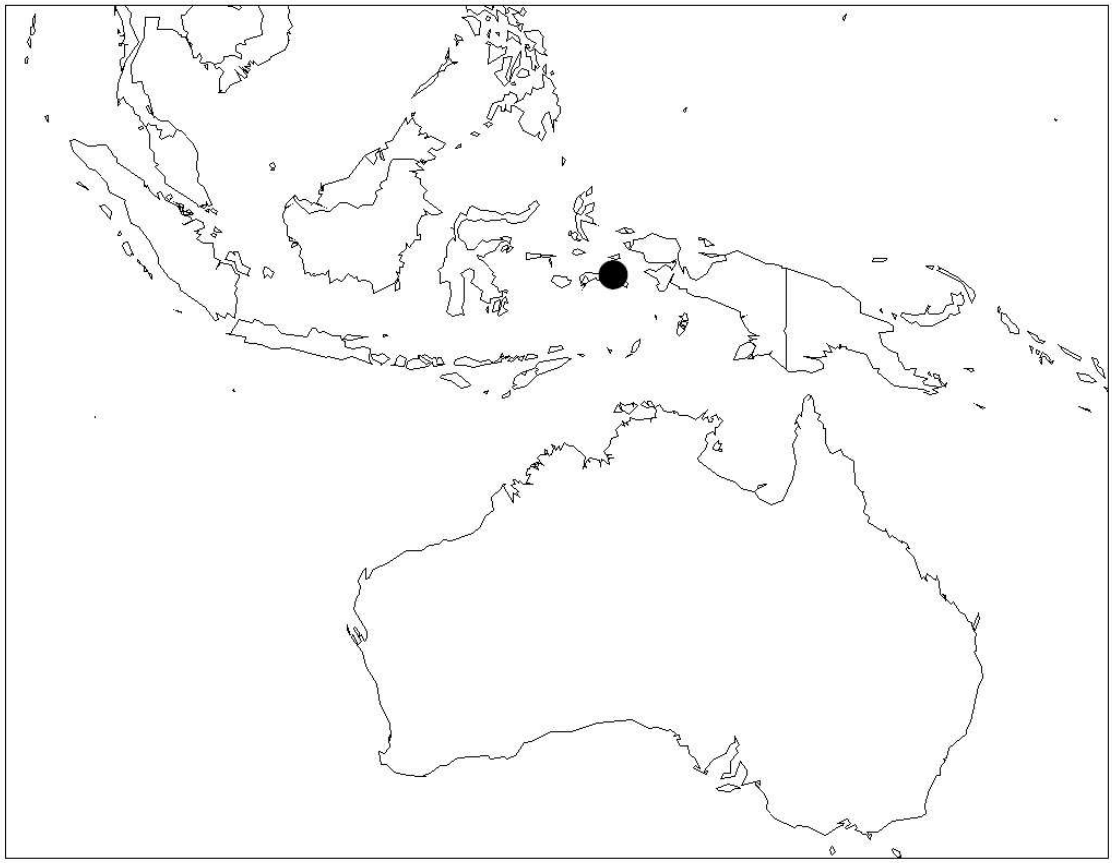


FIG. 9

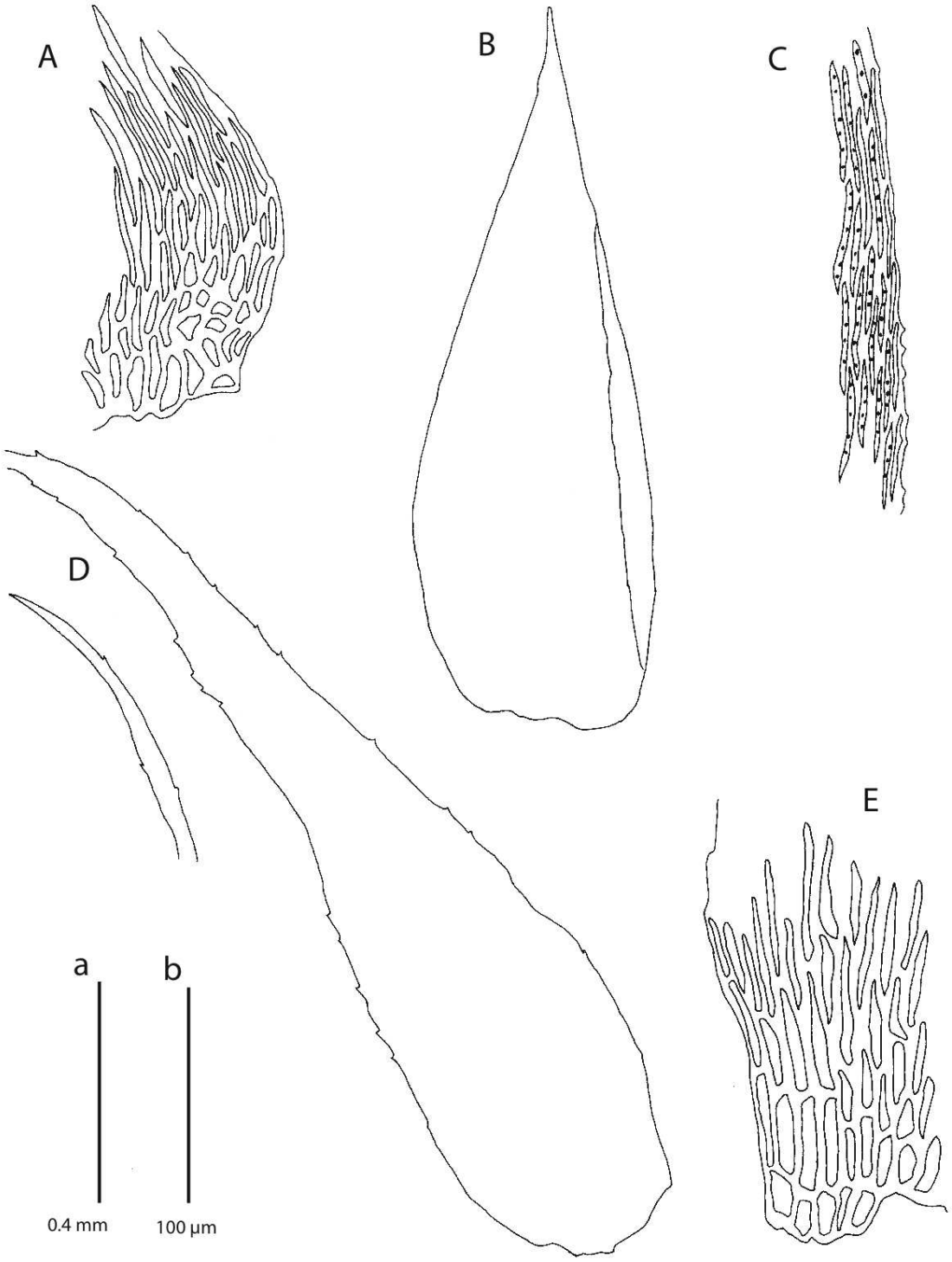


FIG. 10

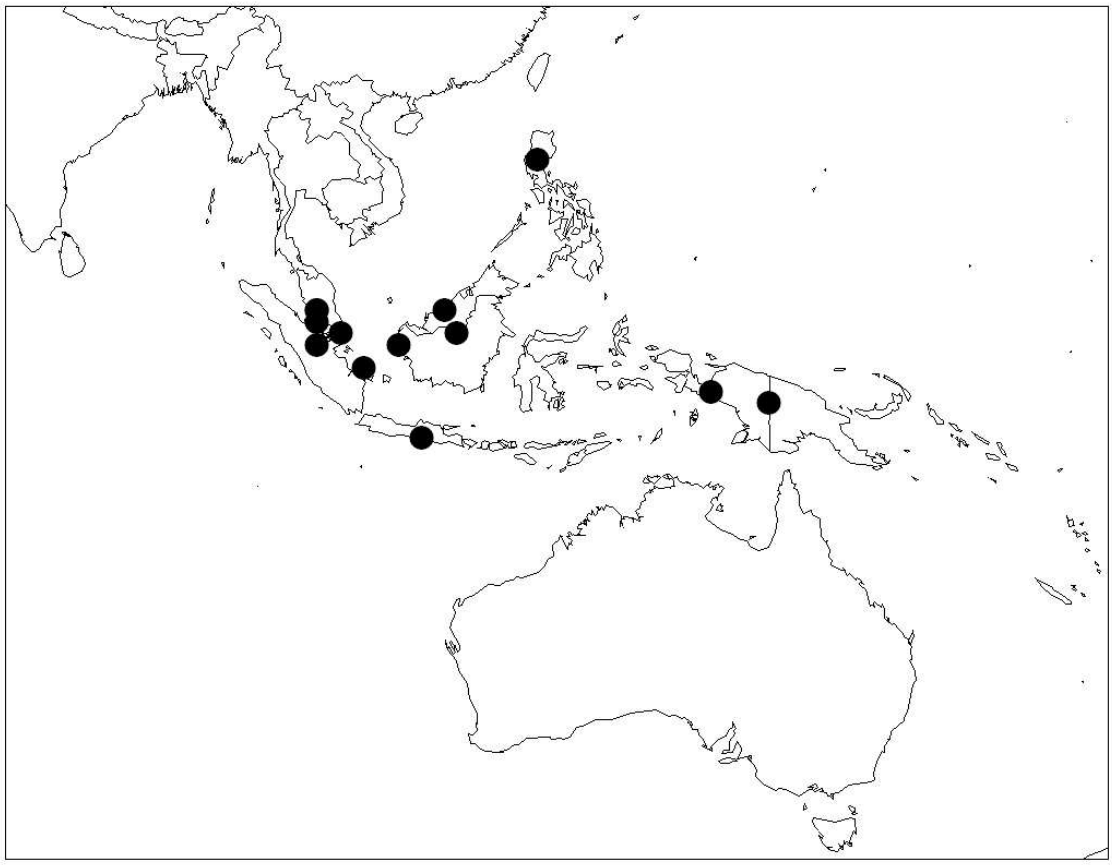


FIG. 11

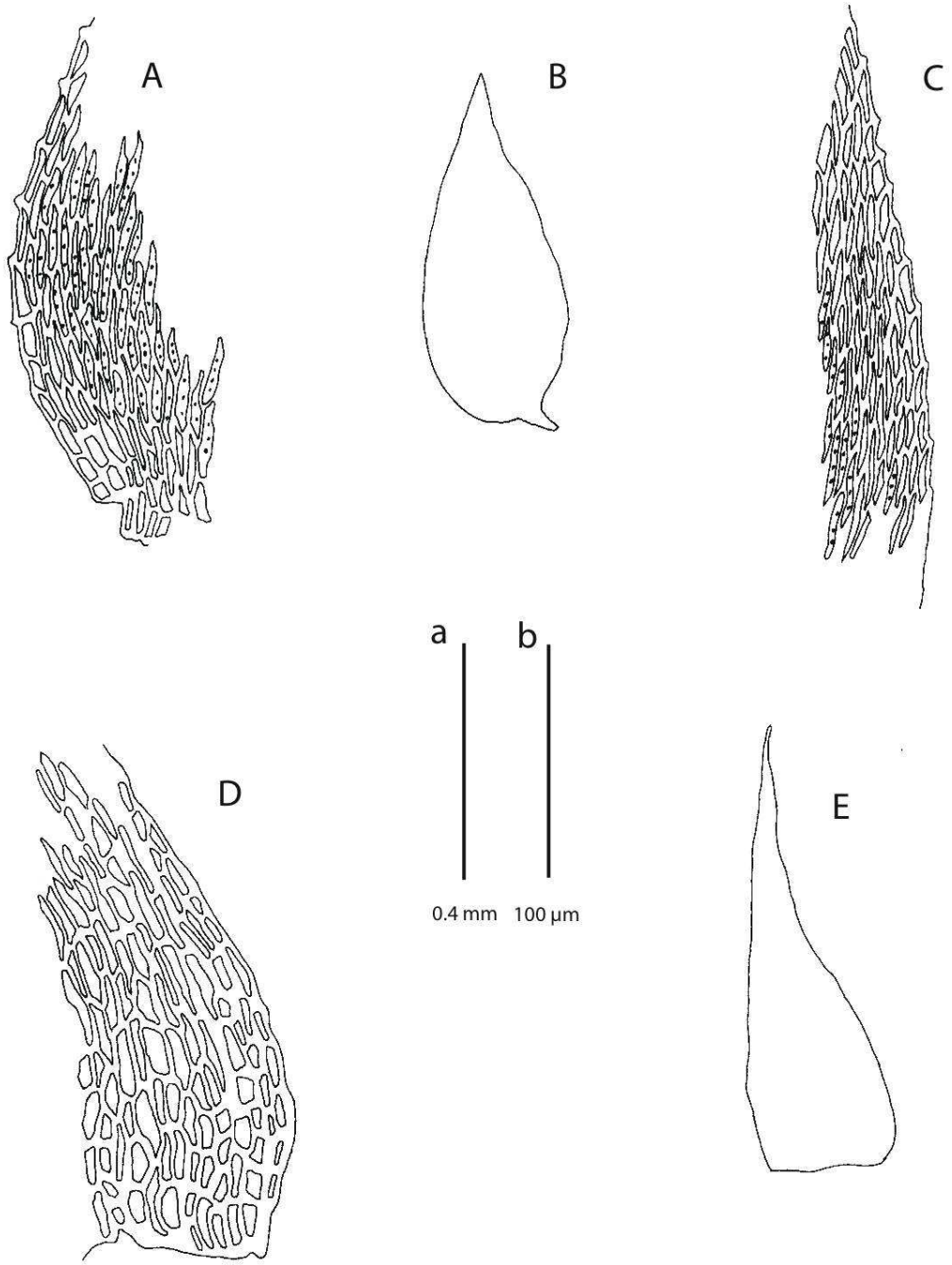


FIG. 12

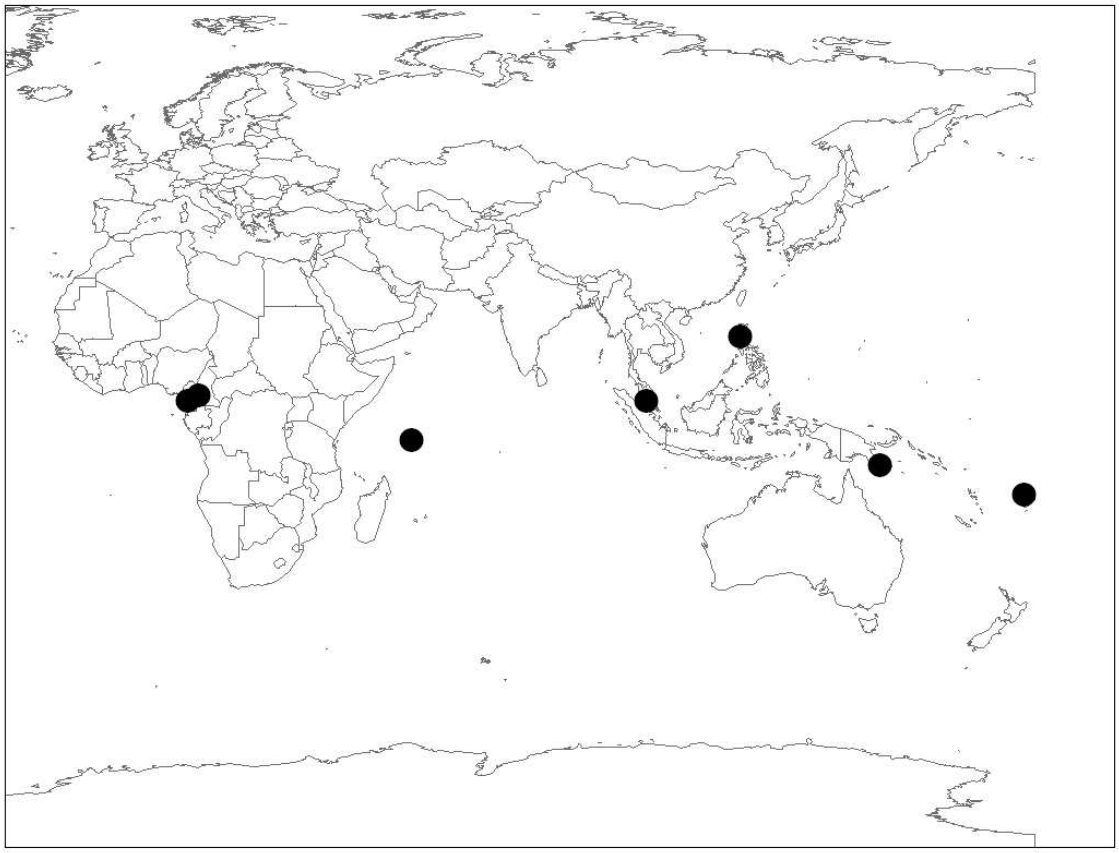


FIG. 13

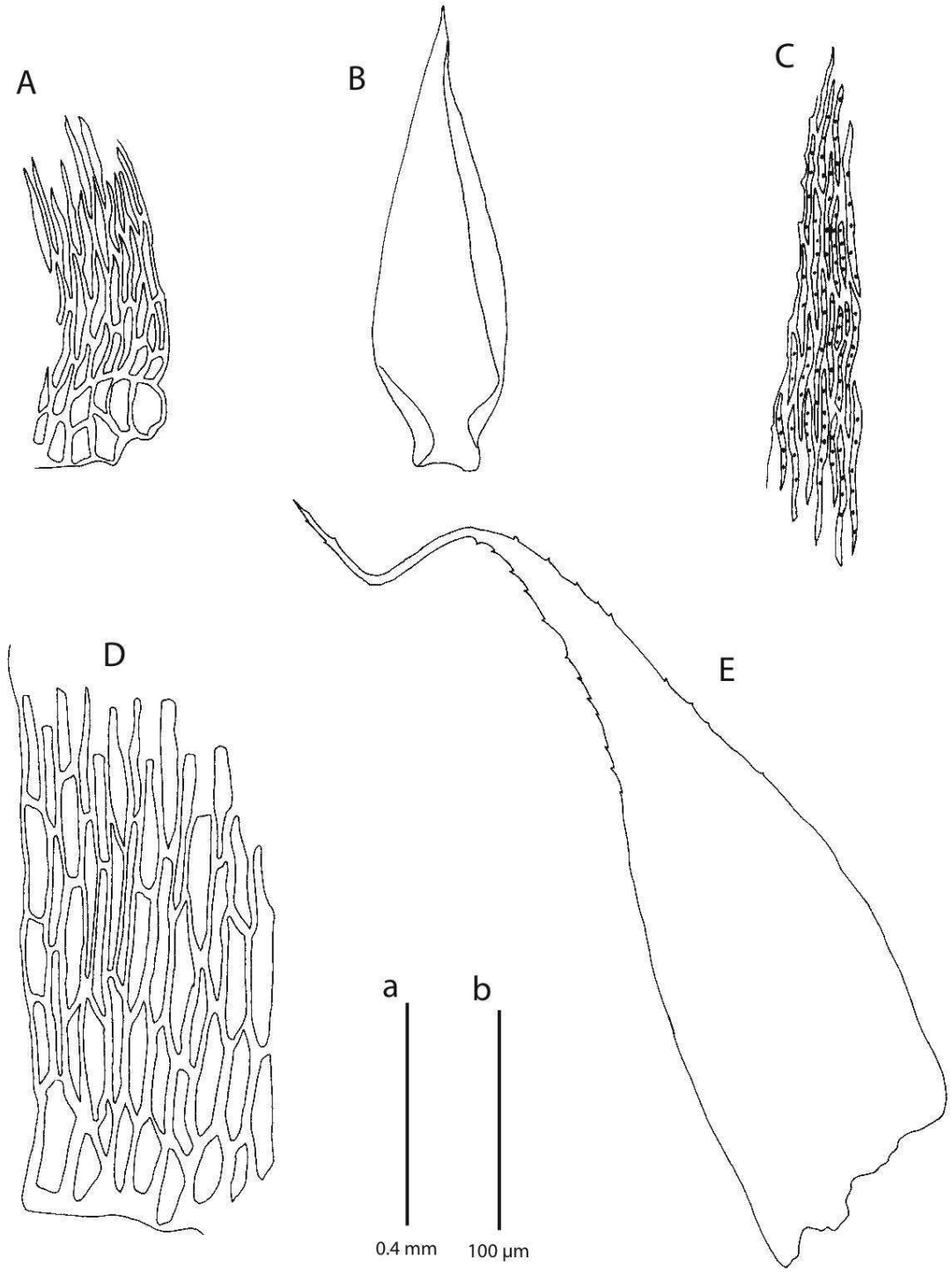


FIG. 14

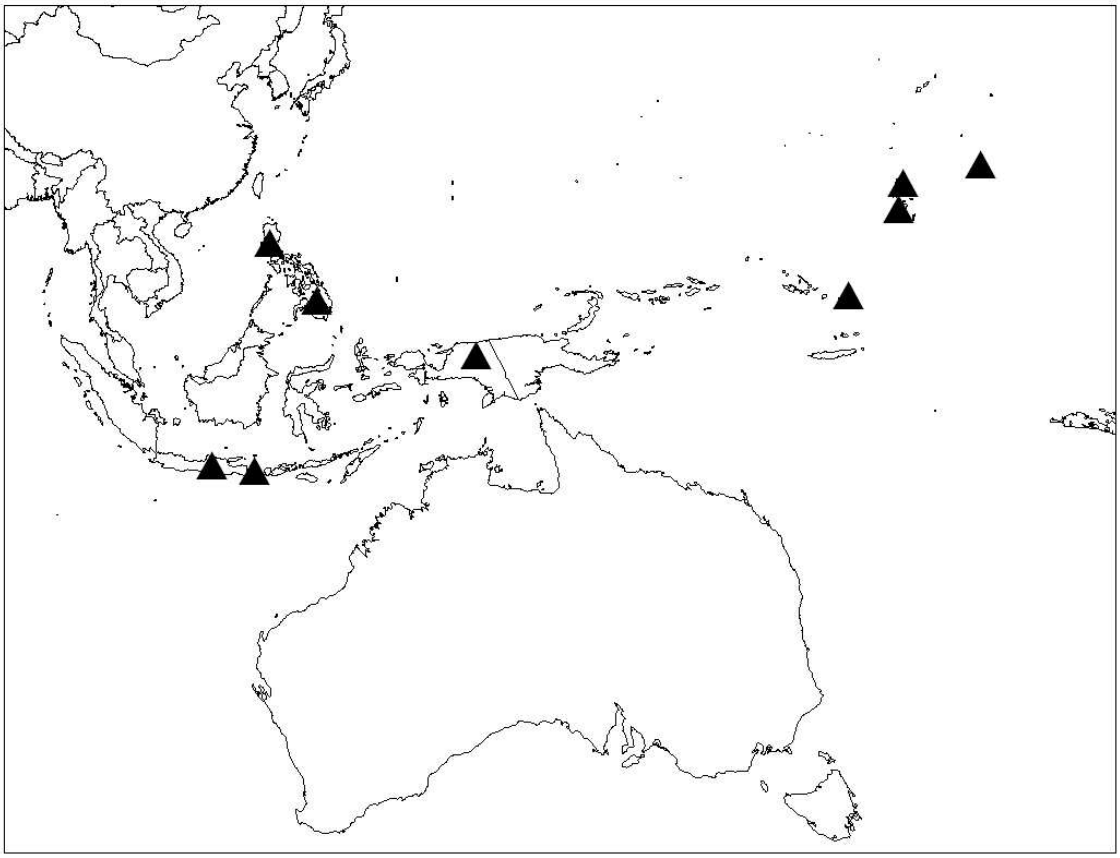


FIG. 15

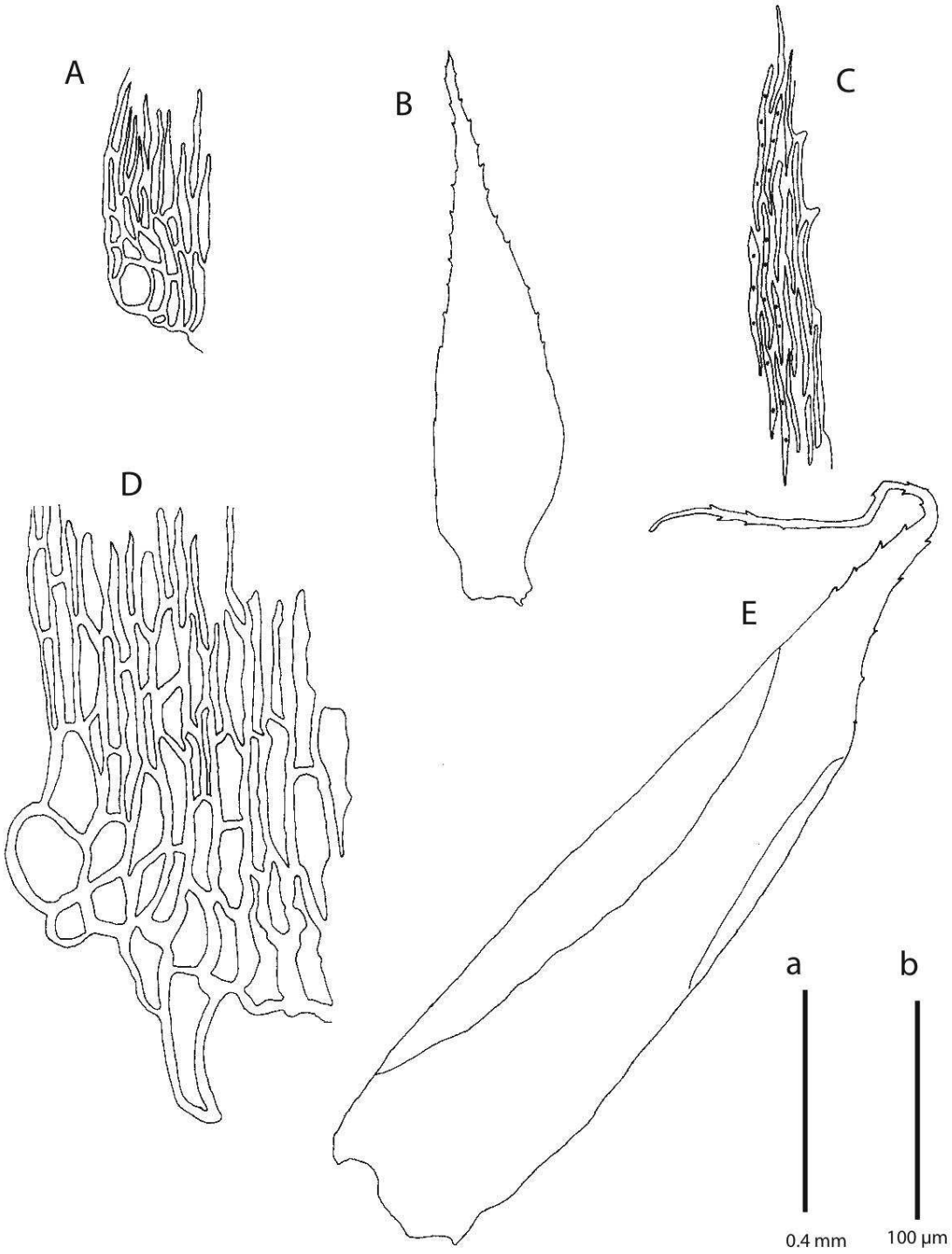


FIG. 16

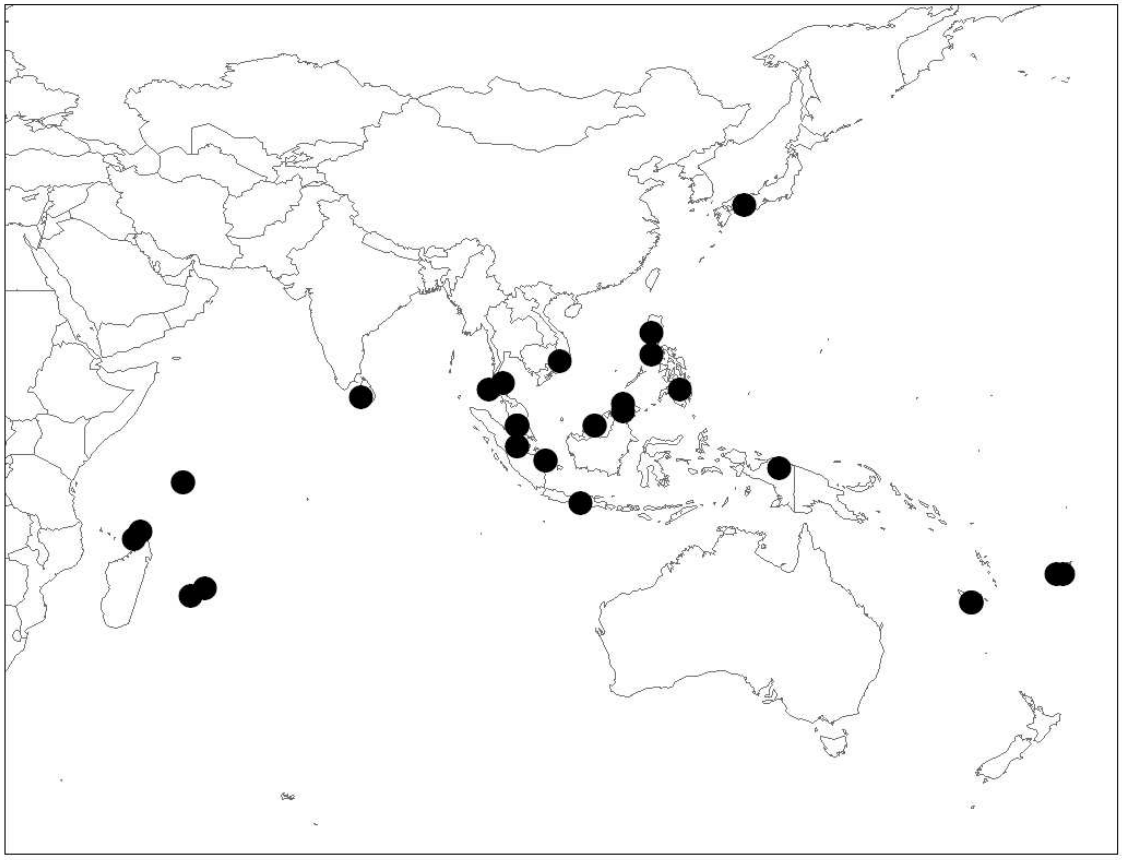


FIG. 17

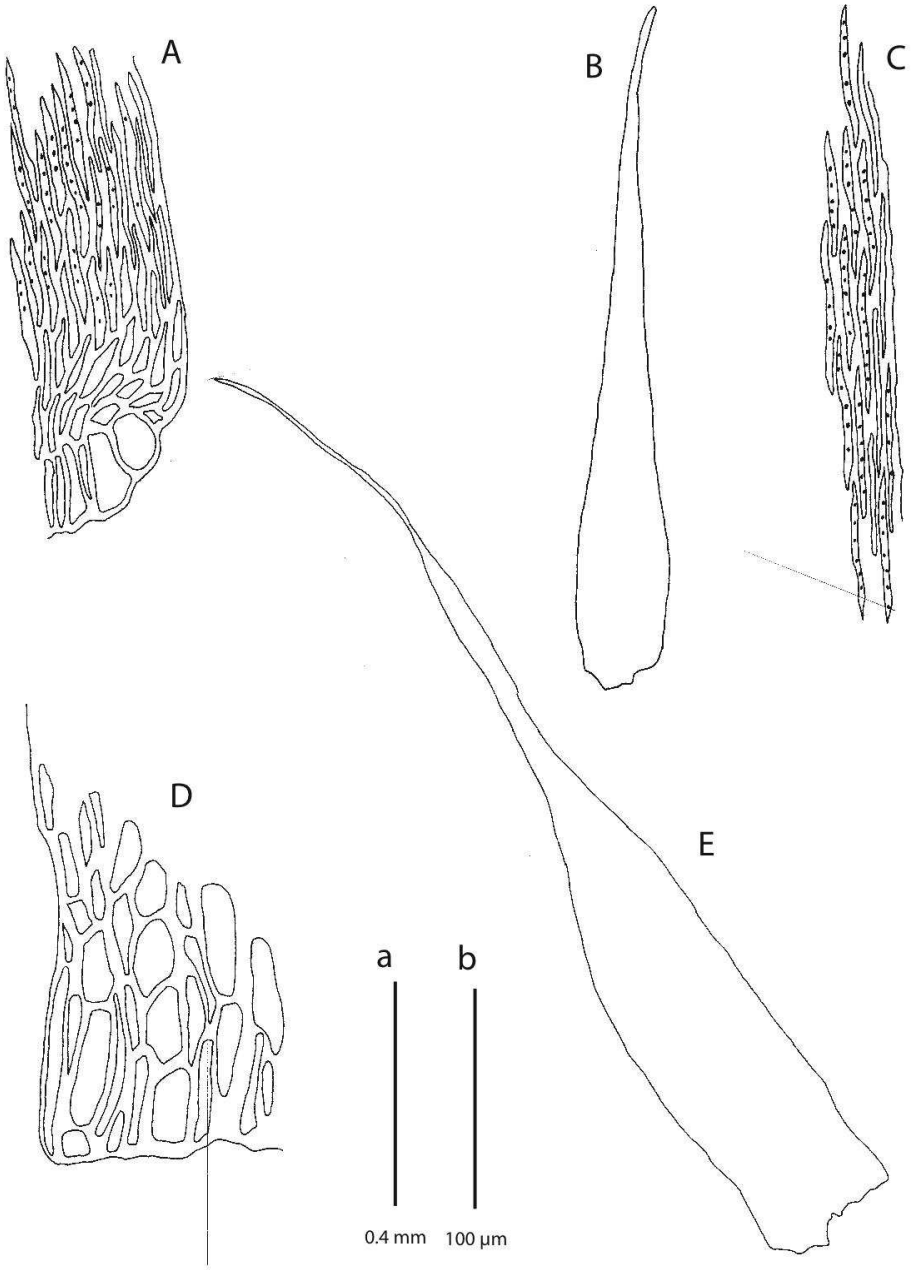


FIG. 18

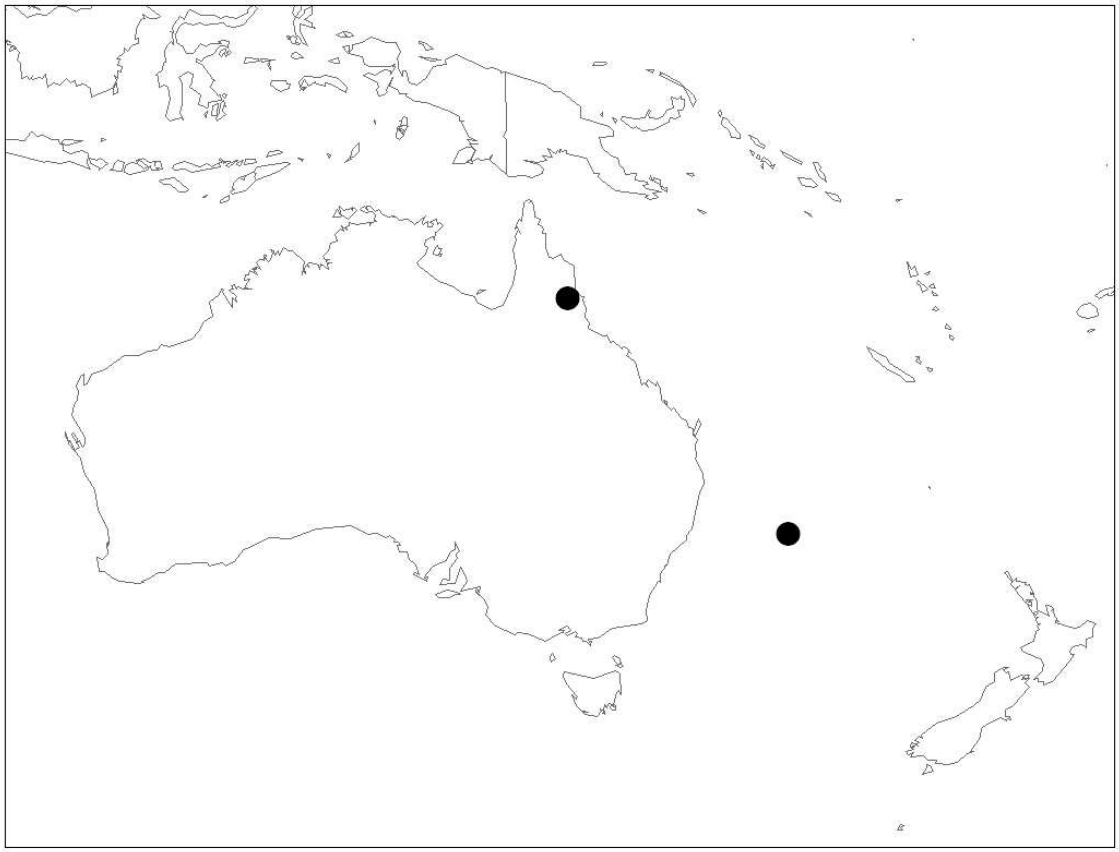


FIG. 19

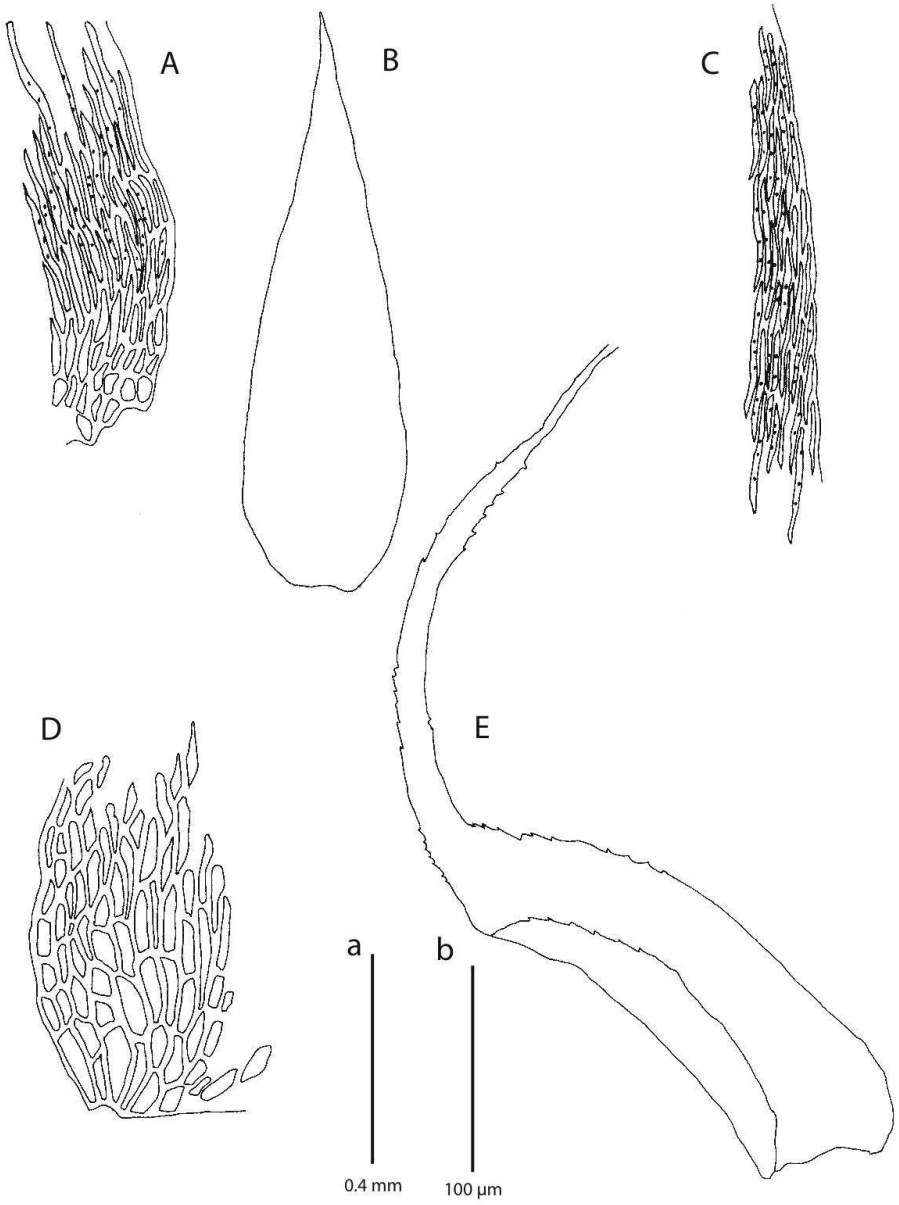


FIG. 20

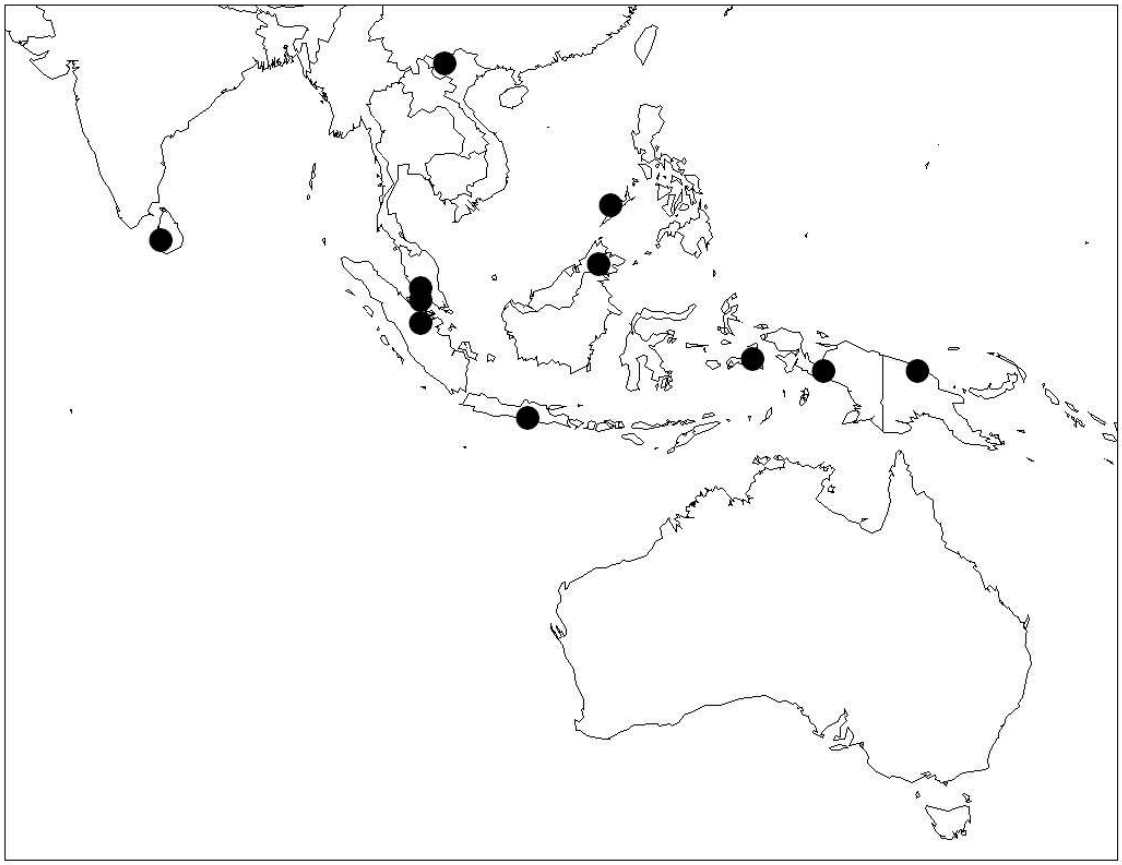


FIG. 21

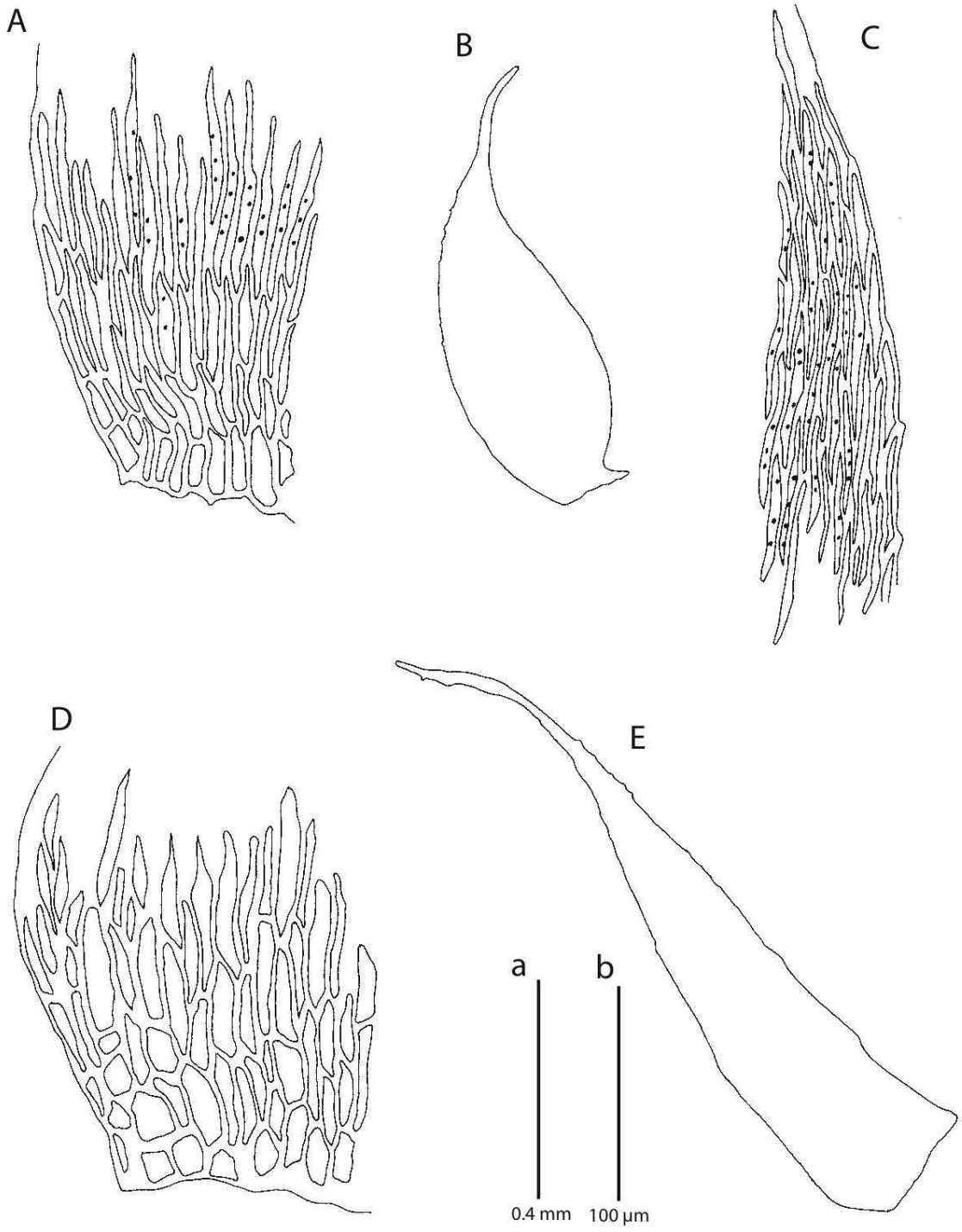


FIG. 22

FIG. 23

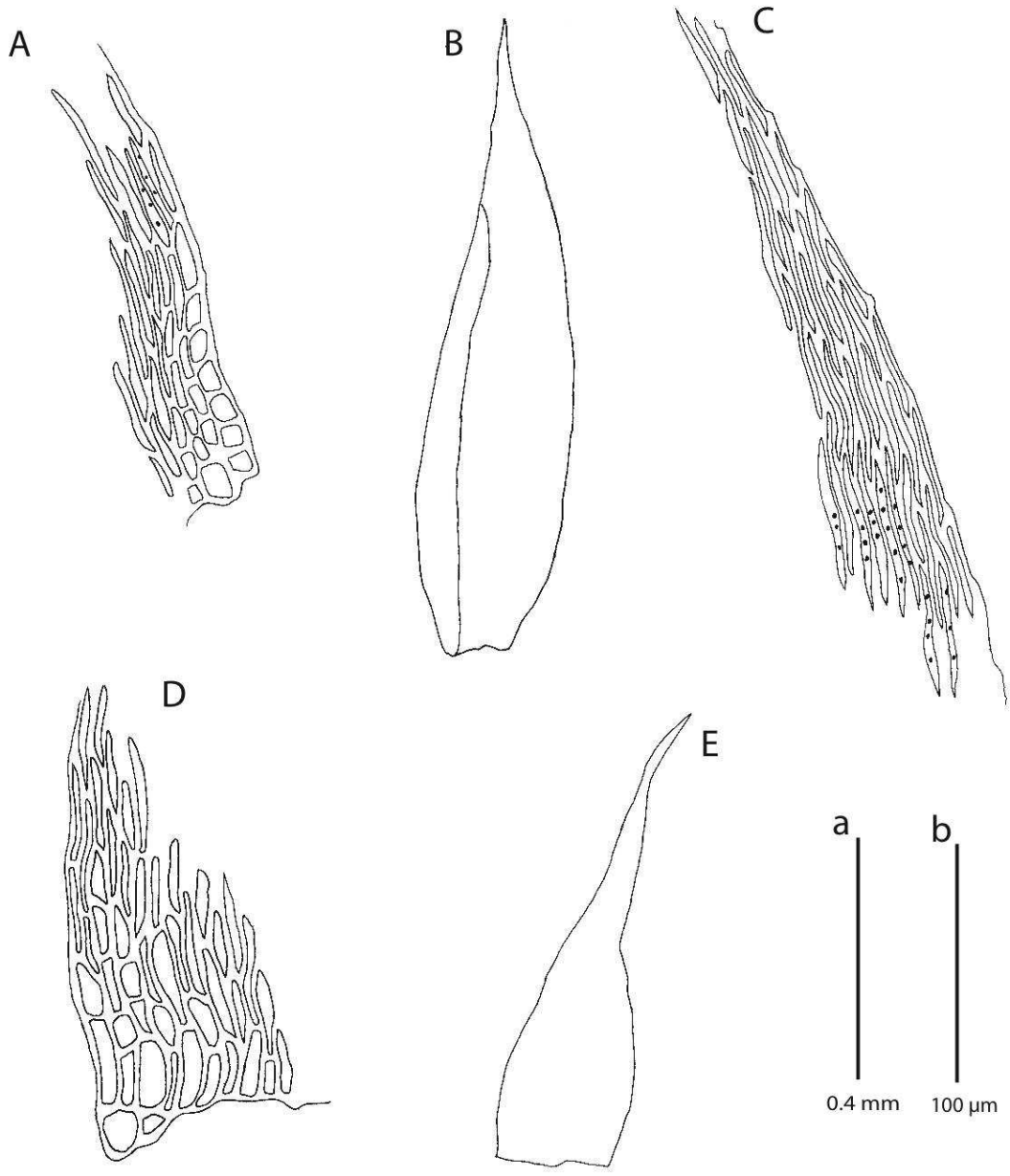


FIG. 24

FIG. 25

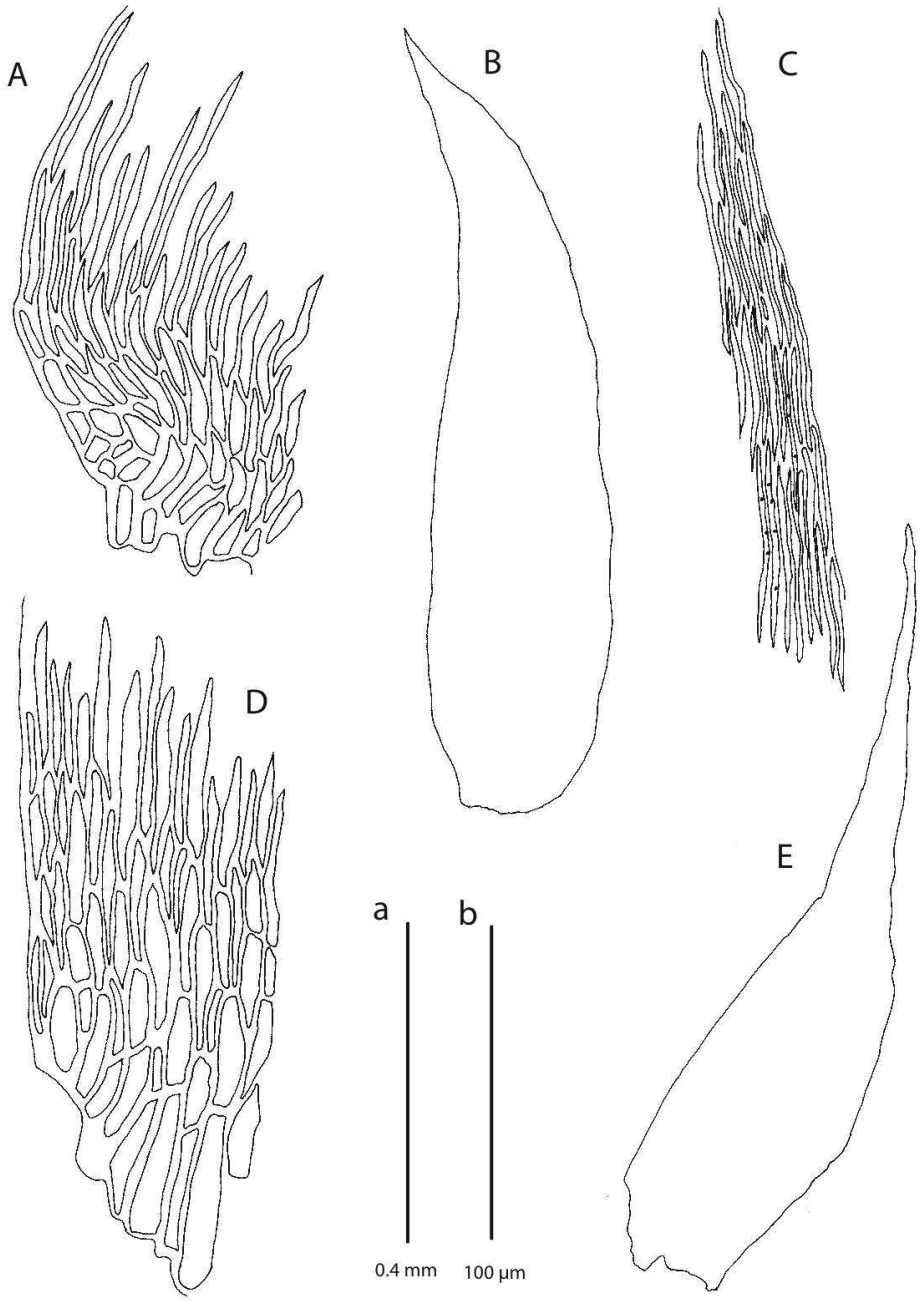


FIG. 26

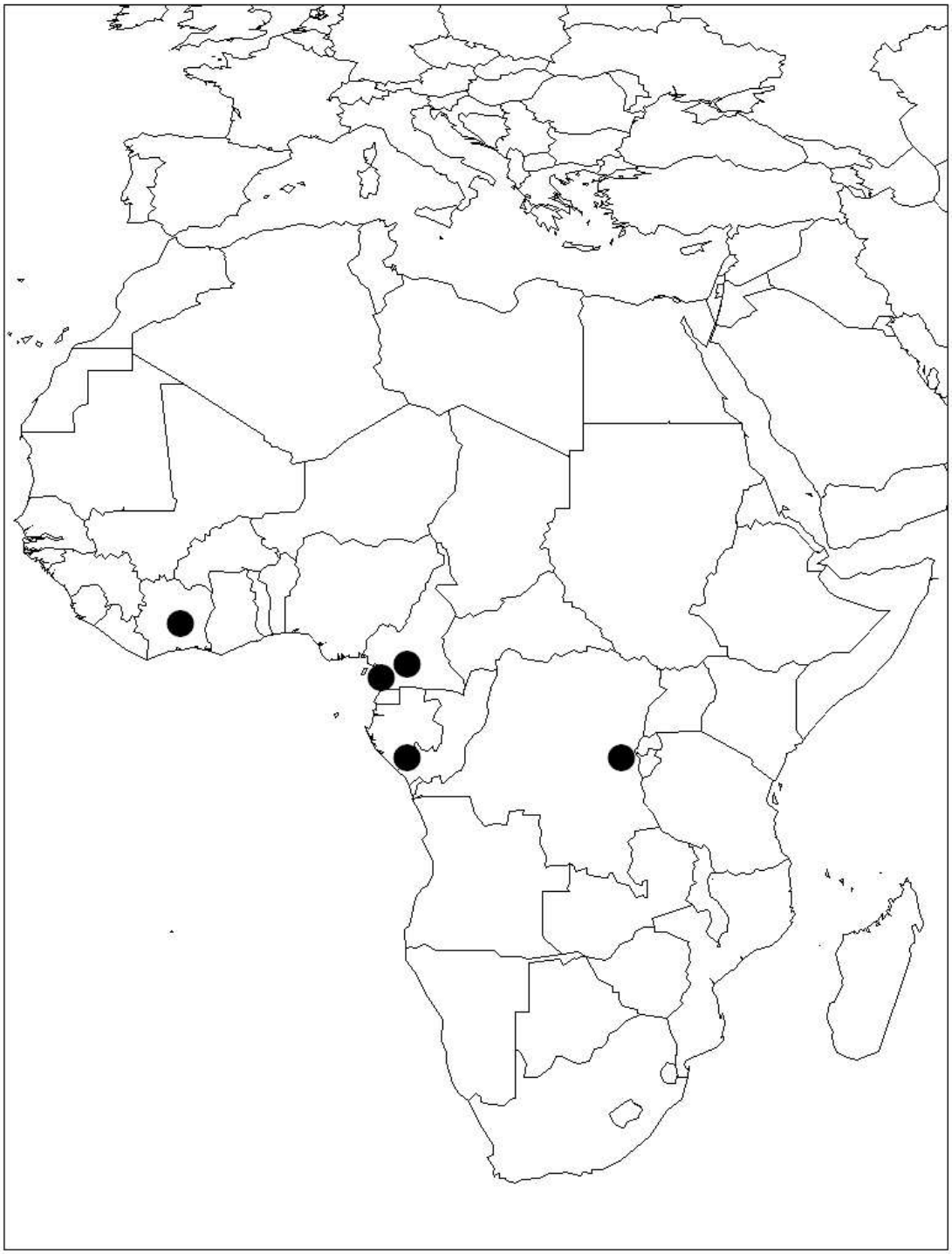


FIG. 27

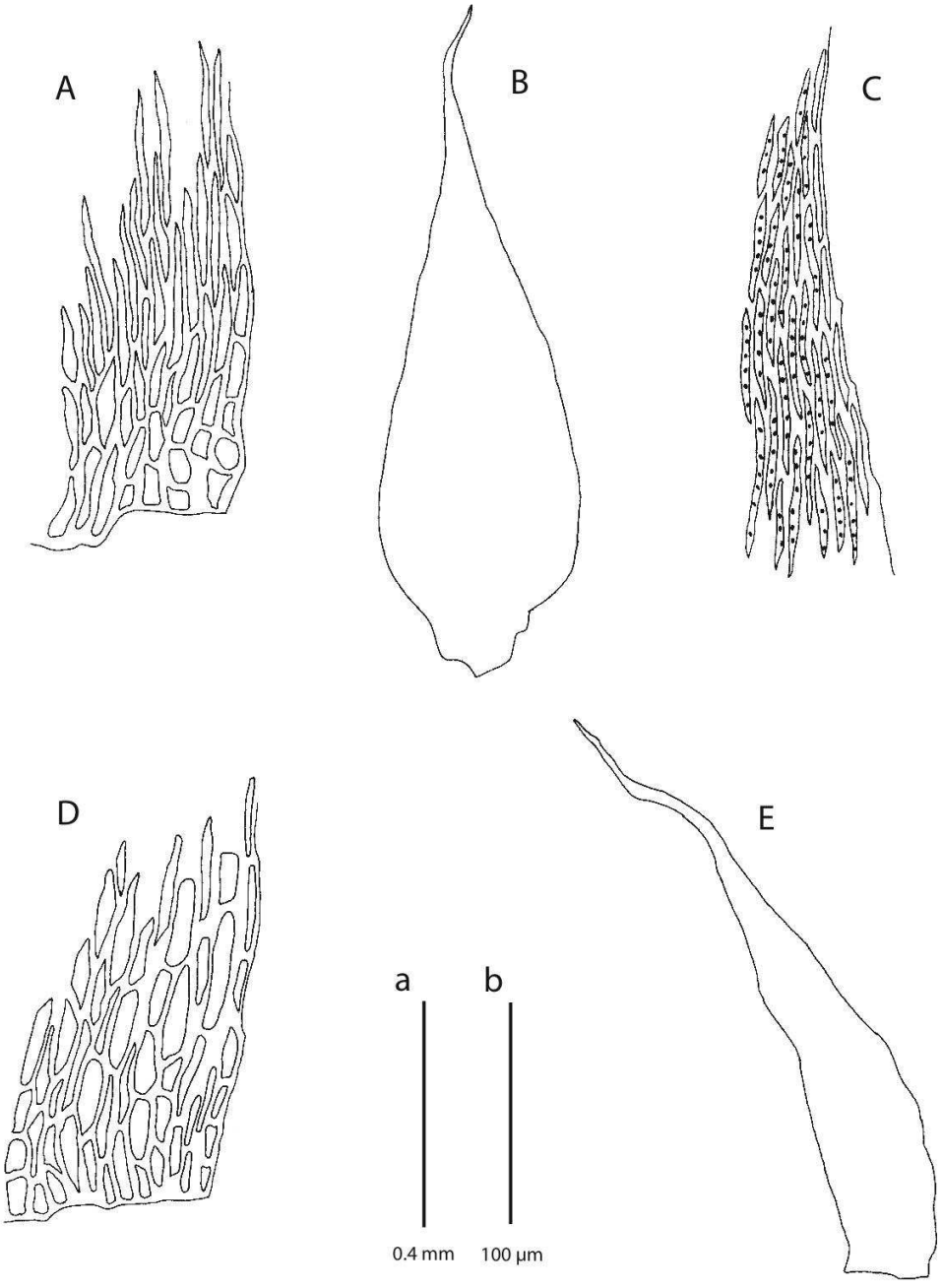
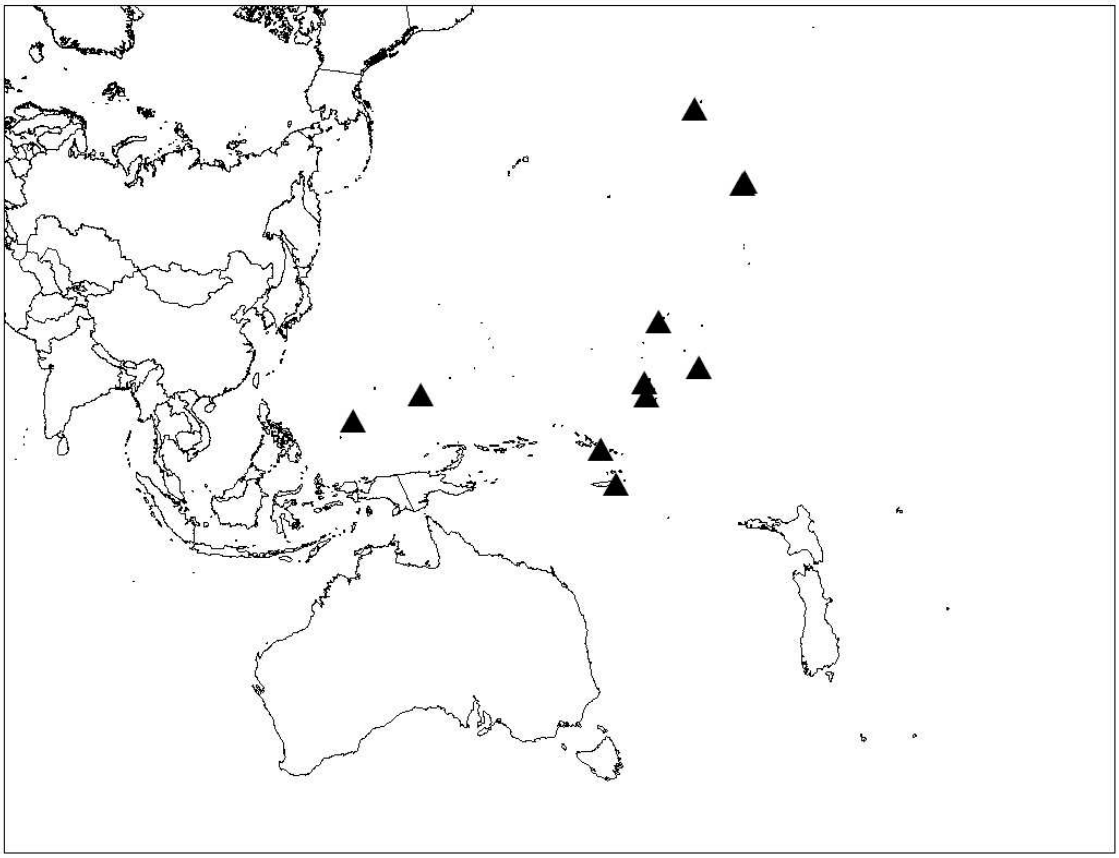


FIG. 28



CHAPTER 4

NEW COMBINATIONS AND ONE NEW NAME FOR THE MOSS GENUS TAXITHELIUM (PYLAISIADELPHACEAE)

This chapter has been submitted to the Journal "Novon".

Abstract. During the taxonomic revision of *Taxithelium*, species previously treated in the genus are excluded and nine new combinations and one new name are presented here: *Camptochaete novae-zeelandiae* (E.B. Bartram & Dixon) P. S. Câmara, *Chaetomitrium spuriosubtile* (Brotherus) P. S. Câmara, *Phyllodon bilobatum* (Dixon) P. S. Câmara, *P. choiropyxis* (Carl Müller) P. S. Câmara, *P. glossoides* (Bosch & Sande Lacoste) P. S. Câmara, *Sematophyllum borneense* (Brotherus) P. S. Câmara, *S. mundulum* (Sullivant) P. S. Câmara, *S. laevigatus* P. S. Câmara, *Trichosteleum friedense* (D. H. Norris & T. J. Koponen.) P. S. Câmara, and *T. subintegrum* (Brotherus & Dixon) P. S. Câmara.

The genus *Taxithelium* Mitten was first described by Mitten (1869) in tribe Sematophylleae and later Brotherus (1925) assigned the genus to the family Sematophyllaceae. However, much controversy has arisen because the lack of sematophyllaceous characters in *Taxithelium*, such as collenchymatous exothecial cells, long rostrate opercula, and well developed and often inflated alar cells (Seki, 1969; Hedenäs, 1996; Tan & Jia, 1998; Hedenäs & Buck, 1999). The molecular phylogenetic works of Tsubota et al. (2001 a,b) have demonstrated that *Taxithelium* is not closely related to the core Sematophyllaceae (*Sematophyllum*, *Trichosteleum* and *Acroporium*) but is more related to *Pylaisiadelpha, Isopterigyum* and *Brotherella.* Therefore Goffinet & Buck (2004) transferred the genus into a newly described family Pylaisiadelphaceae. The absence of above cited features typical of Sematophyllaceae also associates *Taxithelium* more with Pylaisiadelphaceae than with Sematophyllaceae.

Taxithelium is a pantropical genus occurring mainly in Southeast Asia between 30^{o}N and 20^{o}S. Ongoing work by Câmara and Shaw suggests that *Taxithelium* is monophyletic and is characterized by the presence of multiple papillae seriately disposed over the lumina of leaf cells and a poorly developed alar region. The genus is currently being revised by the author, and some taxa clearly do not belong to *Taxithelium*. New combinations are presented here to re-circumscribe the genus. All the taxa presented below lack pluripapillose leaf cells, a diagnostic character for *Taxithelium.* An ongoing morphogloical study addresses this character in more detail.

I. Camptochaete Reichardt, Reise Novara 1(3): 190, 1870. TYPE: *Hookeria arbuscula* J. E. Smith

The genus was revised by Tangney (1997). It occurs in Indonesia, Papua New Guinea, New Caledonia, Vanuatu, Fiji, Australia and New Zealand.

1. Camptochaete novae-zeelandiae (E. B. Bartram & Dixon) P. S. Câmara, comb. nov. Basionym: *Taxithelium novae-zeelandiae* E. B. Bartram & Dixon, Bot. Not. 83:7. 1937. TYPE: New Zealand. Wellington, 1874, *S. Bergren s.n.* (holotype, BM).

The lack of papillae, phyllotaxy, cell shape and size of leaves do not conform with the current circumscription of *Taxithelium*. Sainsbury (1955) suggested that this species was a synonym of *Camptochaete gracilis* (Hook. f. & Wilson) Paris, and Damanhurii & Longton (1996) agreed with the exclusion of this taxon from *Taxithelium* but provided no new combination or further evidence. A closer look at the specimen associates it with the genus *Camptochaete* (Lembophyllaceae); examination of herbaria specimens suggests that it was not conspecific with *Camptochaete gracilis* or with any other other species seen.

II. Chaetomitrium Dozy & Molkenboer, Musci Frond. Ined. Archip. Ind. 117, 1846. TYPE: *Hookeria elongata* Dozy & Molkenboer.

This Southeast Asian genus belongs in Hookeriaceae. Akiyama & Suleiman (2001) studied the genus for Borneo and Streimann (1997) for Australia. The Philippine species have not yet been studied in detail.

1. Chaetomitrium spuriosubtile (Brotherus) P. S. Câmara, comb. nov. Basionym: *Taxithelium spuriosubtile* Brotherus, Philipp. J. Sci. 5: 160. 1910. TYPE:

Philippines. Luzon: Lepanto, 1910, *Bacani For. Bur. 16016* (holotype, H; isotypes, BM, FH, JE, L, NY, PC, PNH, US).

This small specimen (ca. 0.3 mm) is known only from the type collection. Even though it is much smaller than other species of *Chaetomitrium*, the oblong leaf shape, alar cells, leaf papillation pattern and the similar leaf margin clearly associate this specimen with the genus *Chaetomitrium* rather than *Taxithelium.*

III. Phyllodon Bruch & Schimper, Bryol. Europaea 5: 60. 1851. TYPE: *Hookeria retusa* Wilson.

The following three taxa have truncate leaf apexes, serrulate margins and the costae are strongly visible and double; all these are characteristics of the pantropical *Phyllodon*. Also, the pattern of papillae on the leaves provides strong evidence of their generic placement. Buck (1987) studied the Asiatic species, Kis (2002) the African ones and Higuchi & Nishimura (2002) those in the Pacific islands.

1. Phyllodon bilobatum (Dixon) P. S. Câmara, comb. nov. Basionym: *Taxithelium bilobatum* Dixon, Bull. Torrey Bot. Club 51: 244, 1924. *Glossadelphus bilobatus* (Dixon) Brotherus, Nat. Pflanzenfam. (II) 11: 535. 1925. TYPE: Malaysia. Malacca: Perak, *Ridley 739* (holotype, NY; isotype, BM).

2. Phyllodon choiropyxis (Carl Müller) P. S. Câmara, comb. nov. Basionym: *Sigmatella choiropyxis* Carl Müller, Hedwigia 40: 69. 1901. *Taxithelium choiropyxis* (Carl Müller) Renauld & Cardot., Rev. Bryol. 28: 111. 1901. TYPE: Brazil. São Paulo: Iporanga, 1879, *Puiggari s.n*. (isotype, FH).

3. Phyllodon glossoides (Bosch & Sande Lacoste) P. S. Câmara, comb. nov. Basionym: *Hypnum glossoides* Bosch & Sande Lacoste, Bryol. Jav. 2: 146. 243. 1866. *Trichosteleum glossoides* (Bosch & Sande Lacoste) Geheb, Rev. Bryol. 21: 85. 1894. *Taxithelium glossoides* (Bosch & Lacoste) M. Fleischer, Nat. Pflanzenfam. I(3): 1093. 1908. *Glossadelphus glossoides* (Bosch & Lacoste) M. Fleischer, Musci Buitenzorg 4: 1358. 1923. TYPE: Indonesia. Java, *Teysmann s.n.* (isotype: H).

IV. Sematophyllum Brotherus, Nat. Pflanzenfam. I(3): 1098, 1908. TYPE: *Hypnum demissum* Wilson.

The following three taxa all have diagnostic features of the core Sematophyllaceae, such as well developed alar cells, long–linear laminal cells, collenchymatous exothecial cells and absence of costae. Also they lack papillae. All these features occur in the pantropical genus *Sematophyllum.* The genus has not yet been revised.

1. Sematophyllum borneense (Brotherus) P. S. Câmara, comb. nov. Basionym: *Taxithelium borneense* Broth., Mitt. Inst. Allg. Bot. Hamburg 7(2): 135. 1928. TYPE: Indonesia. Kalimantan: Sambas, *Micholitz s.n.* (holotype, H).

2. Sematophyllum laevigatus P. S. Câmara**,** *nom. nov*. Basionym: *Hypnum trachaelocarpum* Ångström., Öfvers. Förh. Kongl. Svenska Vetensk-Akad.

30(5): 127. 1873. *Trichosteleum trachaelocarpum* (Ångström) A. Jaeger, Ber. Thätigk. St. Gallischen Naturwiss Ges. 1876–77: 413 (Gen. Sp. Musc. 2: 479). 1878. *Rhaphidostegium trachaelocarpum* (Ångström) Bescherelle. Ann. Sci. Nat. Bot., sér. 7, 50. 1894. Illegitimate. *Taxithelium trachaelocarpum* (Ångström) Brotherus, Nat. Pflanzenfam. I(3): 1091. 1908, *non Sematophyllum trachaelocarpum* (Kindberg) Brotherus. TYPE: Tahiti. Sine loco, *Anderson s.n*. (isotypes: L, H).

Because of the existence of *S. trachaelocarpum* (Kindberg) Brotherus, a new name for *Hypnum trachaelocarpum* was needed. The epithet refers to the smooth leaf cells.

3. Sematophyllum mundulum (Sullivant) P. S. Câmara, comb. nov. Basionym: *Hypnum mundulum* Sullivant, Proc. Amer. Acad. Arts 3: 75. 1854. *Taxithelium mundulum* (Sullivant) E. B. Bartram., Bernice P. Bishop Mus. Bull. 101: 238. 176. 1933. TYPE: Hawaii. Puna, *Wilkes Expedition s.n.* (holotype: FH).

V. Trichosteleum Mitten, J. Linn. Soc., Bot. 10: 181, 1868. TYPE: *Trichosteleum fissum* Mitten.

The following two taxa all have diagnostic features of the core Sematophyllaceae, such as well developed alar cells, long–linear laminal cells, collenchymatous exothecial cells and absence of costae. In addition they have unipapillose leaf cells (as verified by an SEM

survey as part of the revision of *Taxithelium*). This combination of features clearly associates these plants with *Trichosteleum.* The genus has not yet been revised.

1. Trichosteleum friedense (D. H. Norris & T. J. Koponen) P. S. Câmara, comb. nov. Basionym: *Taxithelium friedense* D. H. Norris & T. J. Koponen, Ann. Bot. Fenn. 22: 383. 1985. TYPE: Papua New Guinea. West Sepik: Frieda River, *Koponen 35136.* (holotype, H; isotypes: PC, NY, L, NICH).

2. Trichosteleum subintegrum (Brotherus & Dixon) P. S. Câmara, *comb. nov*. Basionym: *Taxithelium subintegrum* Brotherus & Dixon, J. Linn. Soc., Bot. 43: 320. 1916. *Acanthorrhynchium subintegrum* (Brotherus & Dixon) Brotherus, Nat. Pflanzenfam. (II)11: 440. 1925. TYPE: Malaysia. Sarawak: Baran. (taken from inside a monkey-skin at the British Museum), *B. Hose 110* (holotype, BM; isotype: PC).

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