

A Re-circumscription of the Moss Genus *Taxithelium* (Pylaisiadelphaceae) with a Taxonomic Revision of Subgenus *Vernieri*

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Abstract—The moss genus *Taxithelium* is reclassified into two subgenera: *Taxithelium* and *Vernieri*. The subgenus *Vernieri* can be distinguished from subgenus *Taxithelium* by the lanceolate leaves and filamentous pseudoparaphyllia in the former and ovate leaves plus foliose pseudoparaphyllia in the latter. The subgenus *Vernieri* is revised here and comprises eleven species; one from Africa, two from the Americas, and the remaining from Southeast Asia and Oceania. Keys, illustrations, and descriptions are provided.

Keywords—Bryophyta, classification, Hypnales, Sematophyllaceae, Pylaisiadelphaceae, Southeast Asia, America, Africa, taxonomy.

Taxithelium, a genus of pleurocarpous mosses (sensu La Farge-England 1996) is probably one of the most widespread moss genera in the tropics. The genus is best represented 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 genus has been traditionally associated with the Sematophyllaceae (Hypnales), from its original description until 2004, when Goffinet and Buck (2004) described a new family Pylaisiadelphaceae as a segregate from Sematophyllaceae.

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 the Hypnales and has been described only twice in the 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 differentiated as in most Sematophyllaceae s. l.

Even though the most common species (e.g. *T. planum* (Brid.) Mitt. and *T. nepalense* (Schwägr.) Broth.) are abundant 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 has been no worldwide treatment published for the genus and no systematic treatment at all for the African or Asian species.

Taxonomic History—*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 included only *T. planum* in the genus.

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 exothelial cells, long rostrate operculum, and inflated alar cells that are otherwise diagnostic for the 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 the 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. 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 an obvious morphological synapomorphy, Goffinet and Buck (2004) are followed here and *Taxithelium* is included in the Pylaisiadelphaceae. As the relationships within Sematophyllaceae s. s. and Pylaisiadelphaceae still remain unclear, I refer here to Sematophyllaceae s. l. for the Sematophyllaceae plus Pylaisiadelphaceae.

Since it was first described, the generic boundaries of *Taxithelium* have been stretched to fit a great variety of plant morphologies. Renault 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* (nonaquatic plants with vesiculose alar cells), *Aptera* (nonaquatic 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* for a single species now placed in Pilotrichaceae within Hookeriales (Buck et al. 2005). However, some of the subgeneric names created by Renault and Cardot are synonyms because they failed to identify subg. *Taxithelium* (an autonymic subgenus).

Later, Brotherus (1925) included plants without papillae within *Taxithelium* based on similarities in leaf shape, alar cell organization, and sporophyte features such as the lack of collenchymatous exothelial cells and lack of long rostrate opercula. This further broadened the generic boundaries of *Taxithelium* and made it more difficult to differentiate it morphologically from a broad range of genera such as *Radulina* W. R. Buck & B. C. Tan, *Isopterygium*, and *Trichosteleum*. Most taxonomists have largely rejected the concept of a *Taxithelium* without papillae and some authors (e.g. Tan et al. 1996; Ramsay et al. 2002) have excluded species without papillae from local treatments of *Taxithelium*. Consequently these “papillae-free” *Taxithelium* species have remained mostly ignored and unplaced over the years. Not surprisingly, *Taxithelium* has simultaneously grown to more than 230 accepted species names and is in great need of revision.

Even detailed studies on smaller parts of the genus are few. Buck (1985) reviewed *Taxithelium* for Brazil, and recognized only three species (*T. planum*, *T. pluripunctatum* (Renault & Cardot) W. R. Buck, and *T. juruense* (Broth.) Broth.). Although the genus was under worldwide revision in the 1990s, only preliminary results were published (Damanhuri and Longton 1996) and the effort was halted. Ramsay et al. (2002) provided a local revision of six Australian species, two species were included by Sharp et al. (1994) and three species by Buck (1998). *Taxithelium* has not been treated in recent floras for Southeast Asia and Africa.

Molecular phylogenetic data (Câmara and Shaw, unpubl. data) show that, 1) *Taxithelium* is monophyletic and is composed of 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 placed species with smooth leaf cells in the genus. Detailed study of micromorphology of papillae (Câmara and Kellogg 2010) showed that such smooth leaf cells might have small, undeveloped papillae, only visible under the SEM.

Circumscription—Detailed studies of the morphological characters of species included in *Taxithelium* led to the rejection of the currently accepted circumscription of *Taxithelium*, which was proposed by Renault and Cardot (1901). Most of the species they included in *Taxithelium* belong to other genera such as *Phyllodon* Bruch & Schimp., *Trichosteleum*, *Acanthorrhynchium* M. Fleisch., and *Taxiphyllum* M. Fleisch. Many species of *Taxithelium* described after 1901 would not fit at all into Renault 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 Renault and Cardot (1901) is not supported. The molecular study of Câmara and Shaw (unpublished) showed that Renault and Cardot's groups are polyphyletic and provides support for the new circumscription and infrageneric classification of *Taxithelium* presented here.

Objectives—The goals of this paper are to provide: 1) a new circumscription for *Taxithelium* and 2) a taxonomic revision of the subgenus *Vernieri*. A revision of subgenus *Taxithelium* will be published later.

METHODS

Taxonomy—Loans totaling 6,200 specimens were 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 rehydrated in boiling water and then mounted in Hoyer's solution (Anderson 1954). All observations and measurements were made from mounted material.

Species were recognized on the basis of morphological differences. Even though the taxonomic results presented here are also supported by molecular studies (unpublished results, available upon request) and by using multivariate methods (available upon request), the morphological data presented here are sufficient as the basis for these taxonomic decisions.

Typifications are provided for all names and information from protocols are presented when needed to securely identify the type material and facilitate its location.

The morphological terms used were defined and illustrated in Gradstein et al. (2001) and Magill (1990). All measurements were made from leaves taken from the middle of the stem or branch and viewed under a Nikon Labophot-2 light microscope. All illustrations were made from type material.

Abbreviation of authors follows Brummitt and Powell (1992). Abbreviation of journals follows BPH. The representative materials reported here represents one specimen per locality.

RESULTS

Circumscription of Subgenera—Based on detailed study of the morphology of papillae (Câmara and Kellogg 2010) and careful study of discrete morphological characters, two main groups can be recognized within *Taxithelium* (these clades were also recognized using molecular evidence).

Subgenus *Taxithelium* 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. Species of this subgenus can be recognized by their 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" type (Câmara and Kellogg 2010) and undergo changes in 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 a later evolutionary loss or reversal of a character. In general, there is little morphological variation within this group.

The second subgenus *Vernieri* comprises plants with more variation in morphology, yet it is represented by fewer specimens in herbaria. Its members can be recognized by the presence of spiral, patently disposed, lanceolate leaves and filamentous pseudoparaphyllia. Numerous or few papillae seriatly disposed over the cell lumina always occur in this group, and the papillae have a conical shape throughout their development (Câmara and Kellogg 2010).

Morphology of Subgenus Vernieri Species—The stem anatomy shows no variation within the genus. The complete absence of a central strand is the only feature of interest (Fig. 1F).

Branching patterns show little or no intraspecific variation. Branches are mostly creeping, but sometimes long-ascending. Branching patterns vary from irregular to subpinnate. The presence of filamentous pseudoparaphyllia is constant and diagnostic feature of the subgenus.

Leaves are highly variable within subgenus *Vernieri*. A diagnostic feature of all species of subgenus *Vernieri* is the presence of seriatly arranged papillae over the lumina of the laminal cells. Even though the number of papillae can vary, no leaf lacks 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 Sematophyllaceae (s. l.) genus with pluripapillose leaf cells is *Radulina*, but this genus is distinguished from *Taxithelium* by its distally verrucose seta, collenchymatous exothelial cells, and inflated and colored alar cells, all of which are lacking in *Taxithelium*. The phylogenetic studies of Câmara and Shaw (unpubl. data) show that *Radulina* is not closely related to *Taxithelium*.

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 to always have a distinct double costa (unfortunately, the sampling for this species was poor; see taxonomy section).

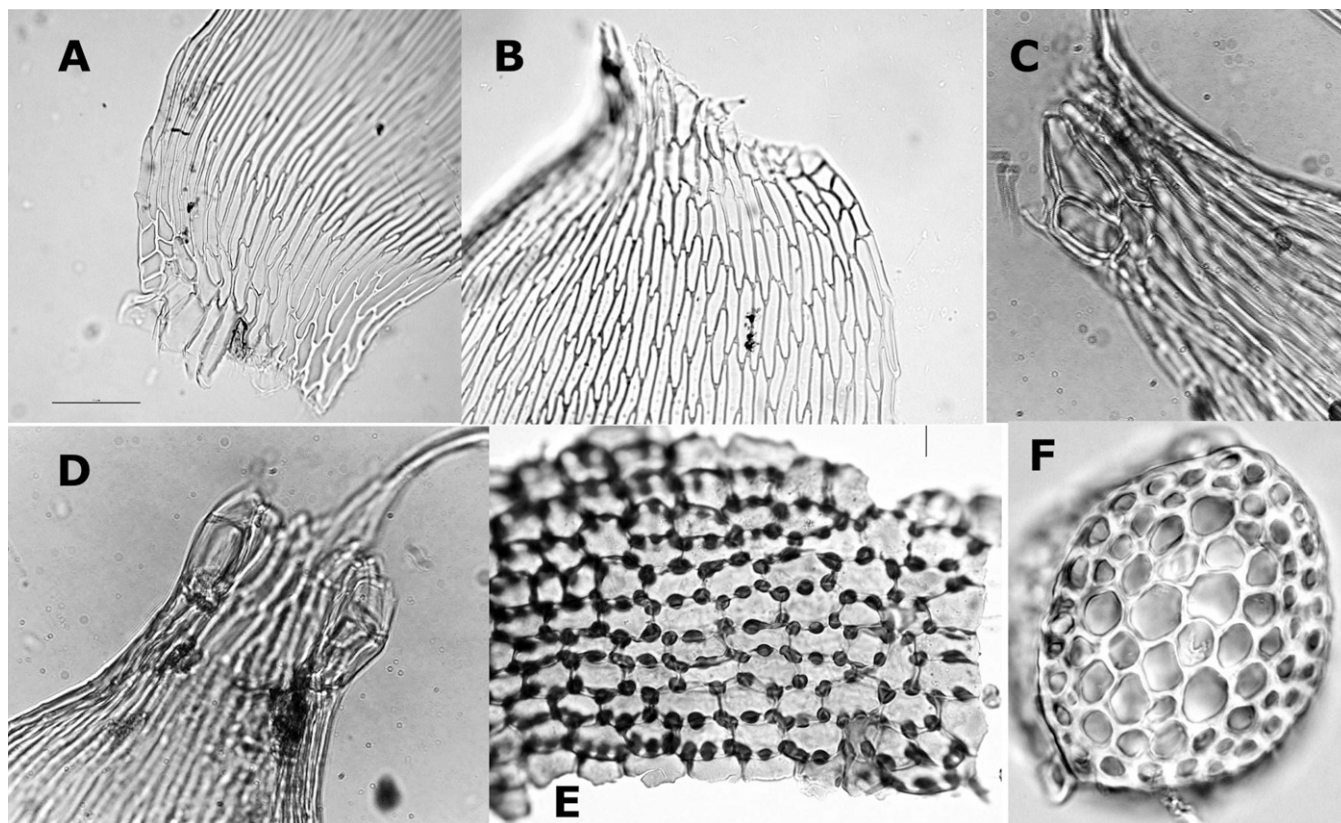


FIG. 1. A. Poorly developed alar cells in *T. planissimum* (400×). B. Poorly developed alar cells in *T. ramivagum* (400×). C. Well-developed alar cells in *T. damanhurii* (400×). D. Well-developed alar cells in *T. lindbergii* (400×). E. Collenchymatous exothelial cells in *T. damanhurianum*. F. Cross section of stem in *Taxithelium* (400×).

Alar cells are always present, but usually not well developed. They resemble the alar cells of some members of the 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. damanhurianum*, *T. levieri*, *T. lindbergii* and *T. muscicola*), the alar cells are well developed (Fig. 1C, D), sometimes resembling those typical of Sematophyllaceae (s.l.) members, although always much smaller. Such developed alar cells are not traditionally associated with *Taxithelium*.

The leaves vary considerably in shape and size. 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. Leaf size ranges from 0.30–2.00 mm long and 0.08–0.40 mm wide, but within a species there is less variation, with some species having 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.

Leaf Cells 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* has more rhombic cells close to the margins, and this is an exception.

The variation in perichaetial leaves is extensive. They can be triangular, lanceolate, or ovate, with size ranging from 0.40–1.85 mm long and 0.15–0.8 mm across; the apex is usually distinct, being long to long-acuminate or setaceous. The margins can be entire or serrulate; sometimes they are serrulate only near 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 the laminal and apical cells are either pluripapillose or smooth. There is little infraspecific variation in these perichaetial features but perichaetial leaves can be very useful in distinguishing between species.

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

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 the subgenus *Vernieri* in *T. planissimum* and *T. levieri*. Similarly, collenchymatous exothelial cells are generally absent, but are known from *T. damanhurianum* alone (Fig. 1E), although weakly collenchymatous cells are seen in some New World taxa. The spores vary from 10–20 μm in diameter.

TAXONOMIC TREATMENT

TAXITHELIUM Spruce ex Mitt., J. Linn. Soc., Bot. 12: 496. 1869.
Taxithelium Spruce, Cat. Musc. 14. 1867, nom. nud. *Hypnum* Hedw. 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. Gallischen-Naturwiss. Ges. 1876–77: 411. 1878; *Sigmatella* (Müll. Hal.) Müll. Hal., Bot. Jahrb Syst. 3: 328. 1896. —TYPE: *T. planum* (Brid.) Mitt., J. Linn. Soc., Bot. 12: 496. 1869. = *Hypnum planum* Brid. Musc. Recent. Suppl. 2: 97. 1812.

Plants small to medium-sized, forming mats. Stems creeping, irregularly branched to subpinnate, shoots long-ascending or not; central strand absent; pseudoparaphyllia foliose or filamentous; branches complanate or terete. Stem and branch leaves usually similar, straight, 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, seriatly papillose over the lumina, sometimes smooth, never unipapillose, thin- or thick-walled; differentiated 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, 4.8–25.0 mm long. Capsules inclined or erect, asymmetric, ovoid or cylindrical, constricted below mouth when deoperculate, 0.5–1.2 mm long; exothelial 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, well-developed, exostome teeth narrowly triangular, with zig-zag dorsal 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 in diameter. Calyptrae cucullate, naked, smooth.

Species of *Taxithelium* are yellowish-green to dull green creeping plants with sporophytes on lateral perichaetial branches. 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 (s. l.) genera, the cells are rarely inflated and often not colored. The diplolepidous sporophyte is well developed; 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 constant. Also in *Taxithelium*, the alar group appearance is more similar to that in Hypnaceae and does not fit into the classification of alar cells for Sematophyllaceae by Tan and Jia (1999).

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*

TAXITHELIUM subgenus *TAXITHELIUM*— TYPE: *Hypnum planum*, Hispaniola. Axes complanate, pseudoparaphyllia foliose, leaves ovate to orbicular.

TAXITHELIUM subgenus *Vernieri* P. S. Câmara subg. nov.
—TYPE: *T. vernieri* (Duby) Besch.

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.

Etymology—*Vernieri* refers to the collector of the type of the subgenus, the missionary Vernier.

KEY TO THE SPECIES OF SUBGENUS *VERNIERI*

1. Exothelial cells slightly collenchymatous, plants from the Americas 2
1. Exothelial cells not or strongly collenchymatous, plants from the Old World 3
2. Leaves falcate; perichaetial leaf cells pluripapillose; leaf margin serrulate 8. *T. pluripunctatum*
2. Leaves symmetric; perichaetial leaf cells smooth; leaf margin entire 9. *T. portoricense*
3. Alar cells well developed 4
3. Alar cells not present or poorly developed 7
4. Leaves with margins serrulate at apex 5. *T. lindbergii*
4. Leaves with entire margins 5
5. Exothelial cells collenchymatous; perichaetial leaves less than 1 mm long 1. *T. damanhurianum*
5. Exothelial cells not collenchymatous; perichaetial leaves more than 1 mm 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; Africa 10. *T. ramiogagum*
9. Leaves strongly papillose, 0.6–1.2 mm long; 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. isocladium*

1. *TAXITHELIUM DAMANHURIANUM* P. S. Câmara. The Bryologist 112(3): 589–592. 2009. —TYPE: INDONESIA. Seram. Manusela National Park, Sawai, *H. Akiyama* 9329 (holotype: HYO!; isotype: NY!).

Plants small, forming golden-yellow mats. Stem creeping, long-ascending, branched. Stem and branch leaves similar, erect-spreading, concave, 0.52–0.88 × 0.10–0.20 mm, linear-lanceolate; margins serrulate; apex acuminate; laminal cells

linear, $70\text{--}74 \times \text{ca. } 2 \mu\text{m}$, thick-walled, basal cells sometimes smooth; costae absent; alar cells well differentiated, consisting of 1–2 rows, 1 row of inflated, vesiculose and not colored cells. Rhizoids evenly distributed along the stem. Perichaetial leaves $0.4\text{--}0.6 \times 0.14\text{--}0.25 \text{ mm}$, ovate; margins entire; apex setaceous; laminal cells linear at midleaf, $40\text{--}46 \times \text{ca. } 2 \mu\text{m}$, pluripapillose at apex; costae absent; alar cells well developed in a single row. Setae $7\text{--}10 \text{ mm}$ long. Capsules inclined, asymmetric, ovoid, $0.5\text{--}0.8 \text{ mm}$ long, not constricted below mouth; exothecial cells quadrate, strongly collenchymatous. Operculum not seen. Spores smooth, $16\text{--}20 \mu\text{m}$ diameter. Figure 2.

Distribution and Habitat—*Taxithelium damanhurianum* is restricted to the forests of the Island of Seram, Indonesia (Fig. 3), where it is epiphyllous and occurs at altitudes of $100\text{--}650 \text{ m}$.

Discussion—This species resembles *T. muscicola*, but the leaves are smaller and narrower. The spores are also different; in *T. muscicola* they are finely papillose and only $12\text{--}16 \mu\text{m}$ across, while in *T. damanhurianum* they are $16\text{--}20 \mu\text{m}$ 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 similar to genus *Radulina*, but *T. damanhurianum* is a much smaller plant. *Taxithelium*

damanhurianum also has a smooth seta (*Radulina* has distally prorate setae), and the alar cells are less developed and neither inflated nor colored like the ones found in *Radulina*. No phylogenetic data is available at the moment to verify the placement of this species and therefore it is here retained in *Taxithelium*. Unfortunately, few collections of this plant are known and molecular data are so far unavailable for this species.

2. *TAXITHELIUM ISOCLADUM* (Bosch & Sande Lac.) Renauld & Cardot, Rev. Bryol. 28: 111. 1901; *Hypnum isocladum* Bosch & Sande Lac., Bryol. Jav. 2: 173. 272. 1867.—TYPE: INDONESIA. Sumatra, Bangka. *Kurz s. n.* (holotype: L!; isotype: H!).

Trichosteleum wernerii Herzog, Hedwigia 49: 126. 1909. *Taxithelium wernerii* (Herzog) Broth., Nat. Pflanzenfam. (II) 11: 443. 1925.—TYPE: PAPUA NEW GUINEA. Finisterre Range. *E. Werner s. n.* (holotype: JE!).

Taxithelium deningeri Herzog, Hedwigia 61: 298. 1919.—TYPE: MALAYSIA: Malacca. *E. Stresemann* 89 (holotype: JE!; isotypes: BM!, S!).

Taxithelium isocladoides Dixon, Bull. Torrey Bot. Club 51: 243. 1924.—TYPE: MALAYSIA: Malacca. *Ridley* 737 (holotype: BM!).

Taxithelium epiphyllum Broth., Mitt. Inst. Allg. Bot. Hamburg. 7(2): 136. 1928.—TYPE: INDONESIA. Kalimantan. *H. Winkler* 3145 (holotype: H!).

Taxithelium magnum M. Fleisch. var. *laticuspis* Zanten, Nova Guinea, Bot. 10(16): 343, plate. 31, Fig. 4. 1964.—TYPE: PAPUA NEW GUINEA, Mt. Antares, *Zanten* 440 (holotype: L!; isotypes: BM!, NICH!).

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, $1.0\text{--}1.5 \times 0.28\text{--}0.45 \text{ mm}$, oblong-lanceolate; margins entire; apex entire, slightly acuminate; laminal cells linear, $40\text{--}50 \times \text{ca. } 2 \mu\text{m}$, 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 $1.5\text{--}2.5 \times 0.30\text{--}0.40 \text{ mm}$, narrow-lanceolate; margins entire at base, serrulate at

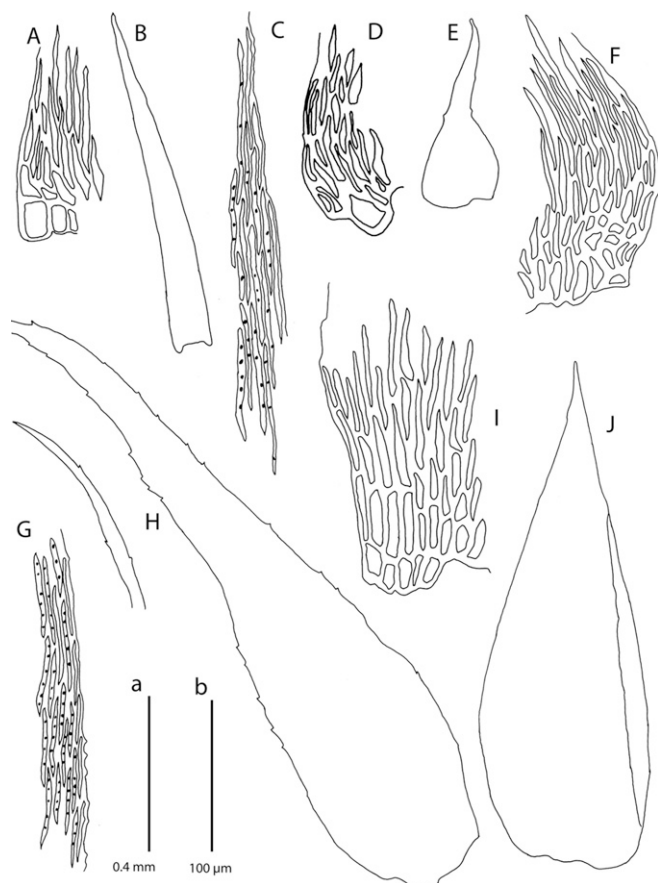


FIG. 2. A–E: *Taxithelium damanhurianum*. A. Alar cells, B. Branch leaf, C. Leaf margin cells, D. Perichaetial alar region, E. Perichaetial leaf. B and E scale a; and A, C, D, scale b. *Akiyama* 9329 (HYO). F–G: *Taxithelium isocladum*. F. Alar cells, G. Leaf margin cells, H. Perichaetial alar region, I. Perichaetial leaf, J. Branch leaf, H and J scale a; and F, G, I, scale b. *Kurz s. n.* (L!).

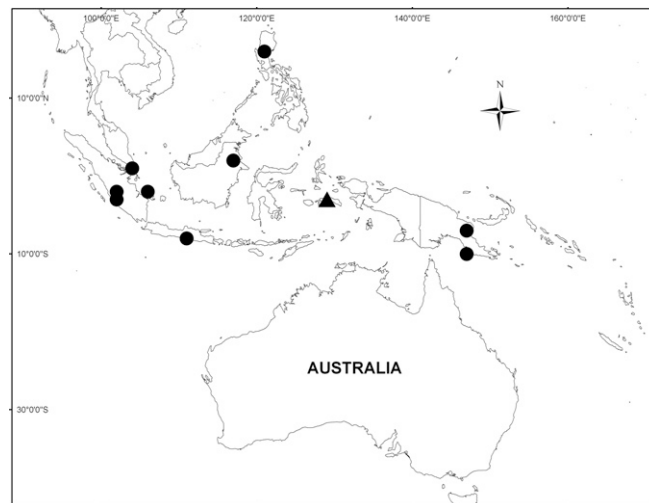


FIG. 3. Distribution map for *T. damanhurianum* (triangle) and *T. isocladum* (circles).

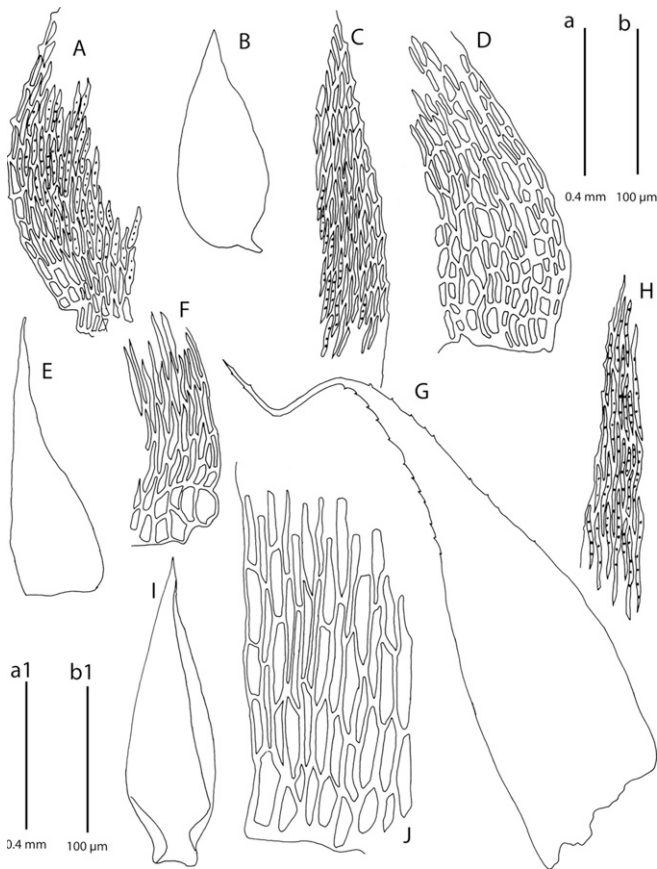


FIG. 4. A–E: *Taxithelium kaernbachii*. A. Alar cells, B. Branch leaf, C. Leaf margin cells, D. Perichaetial alar region, E. Perichaetial leaf. B and E scale a; and A, C, D, scale b. *Kaernbach s. n.* (BM). F–G: *Taxithelium levieri* F. Alar cells, G. Perichaetial leaf, H. Leaf margin cells, I. Branch leaf, J. Perichaetial alar region, I and G scale a1; and F, H, J, scale b1. Beccari 147 (H).

apex; apex setaceous; laminal cells linear, $50\text{--}65 \times \text{ca. } 2 \mu\text{m}$, thick-walled, pluripapillose only at apex; costae absent or single; alar cells poorly differentiated with 2 rows, not inflated. Setae $5\text{--}10 \text{ mm}$ long. Capsules erect, asymmetric, ovoid, $0.6\text{--}0.8 \text{ mm}$ long, constricted below mouth; exothelial cells subquadrate, not collenchymatous. Operculum short, conic or obliquely conic-rostrate, ca. 0.3 mm long. Spores finely papillose, $15\text{--}20 \mu\text{m}$ in diameter. Figure 2.

Distribution and Habitat—This species occurs only in Southeast Asia, in Malesia (Fig. 3). It grows on tree trunks, twigs, and as an epiphyll, from sea level to $1,500 \text{ m}$.

Discussion—Its large leaves with entire margins and poorly differentiated alar cells distinguish it from other species 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 under *T. ramivagum*).

Nomenclatural Notes—Even though the Mitten herbarium is at NY, the type of *Taxithelium isocladoides* was found at BM.

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). MALAYSIA. Genting Highlands, Câmara 870 (MO); Sarawak, Eerett s. n. (M); Selangor, Câmara 974 (MO). PAPUA NEW GUINEA. 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.—TYPE: PAPUA NEW GUINEA. Sine loco. *L. Kaernbach s. n.* (holotype: H? (not seen); isotypes: BM!, FH!).

Taxithelium perminutum Broth., Bot. Jahrb. Syst. 24: 267. 1897.—TYPE: CAMEROON. Mokundange, Dusén 1030 (holotype: H!; isotypes: BR!, PC!, S!).

Taxithelium petrophilum R. S. Williams, Bull. New York Bot. Gard. 8(31): 370. 1914.—TYPE: PHILIPPINES. Batan, Lamao River, R. Williams 865 (holotype: NY? (not seen); isotypes: FH!, H!, US!).

Taxithelium bakeri Broth., Philipp. J. Sci. 13: 218. 1918.—TYPE: PHILIPPINES, Luzon, Laguna Province, Baker 2379, (lectotype H!, designated here).

Taxithelium meiothecioides Broth., Mitt. Inst. Allg. Bot. Hamb. 7(2): 136. 1928.—TYPE: INDONESIA. Serawei, H. Winkler 3009 (holotype: H!; isotype: BM!).

Taxithelium archboldii E. B. Bartram, Brittonia 9: 53. 1957.—TYPE: PAPUA NEW GUINEA. Baiawa, Brass 22175 (holotype: FH!; isotypes: H!, NICH!).

Plants small, forming dark-green mats. Stems creeping, freely branched. Stem and branch leaves slightly differentiated, stem leaves slightly bigger, erect-spreading, complanate, $0.30\text{--}0.55 \times 0.12\text{--}0.26 \text{ mm}$, lanceolate-ovate; margins entire; apex acute; laminal cells linear, $28\text{--}36 \times \text{ca. } 2 \mu\text{m}$, thick-walled; basal cells smooth; costae absent; alar cells not differentiated. Rhizoids clustered beneath the stem. Perichaetial leaves $0.4\text{--}0.8 \times 0.16\text{--}0.30 \text{ mm}$, triangular; margins entire; apex long-aristate; laminal cells linear, $24\text{--}30 \times \text{ca. } 2 \mu\text{m}$, thick-walled, smooth; costae absent; alar cells not differentiated. Setae $4\text{--}7 \text{ mm}$ long. Capsules inclined, asymmetric, long-ovoid, $0.6\text{--}0.8 \text{ mm}$ long, constricted below mouth; exothelial cells subquadrate, not collenchymatous. Operculum long, obliquely conic-rostrate, ca. 0.3 mm long. Spores smooth, $7\text{--}8 \mu\text{m}$ diameter. Figure 4.

Distribution and Habitat—*Taxithelium kaernbachii* is known only from a few collections but from a wide area, including Malesia, Cameroon, and the Seychelles (Fig. 5). It is most likely undercollected due to its small size (leaves are less than

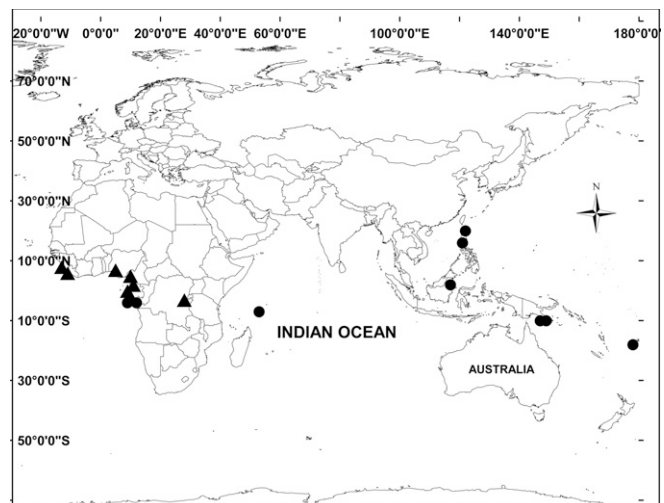


FIG. 5. Distribution map for *T. kaernbachii* (circles) and *T. ramivagum* (triangles).

0.5 mm long). It grows on rocks and rarely on tree trunks at low elevations.

Discussion—This species can be easily identified by its small size in comparison with all other *Taxithelium* species. Sometimes the strong papillosity 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 places this species in subg. *Vernieri*.

Nomenclatural Notes—No type of *Taxithelium kaernbachii* was found in the Brotherus herbarium in H, but during my stay at H, I was informed that the specimen was probably on loan, so in this particular case I am assuming that the holotype is not lost and may still be in H.

Representative Specimens Examined—CAMEROON. N'Dian, *Dusén* 1030 (H, PC). FIJI. Viti Levu, *Buck* 7108 (NY); Koro, *Smith* 1024 (NY). MALAYSIA. Selangor, Gombak, *Câmara* 963 (MO). PAPUA NEW GUINEA. Simbong, *Nyman* 73 (NY). PHILIPPINES. Luzon, *Penecilla* 10347 (PNH). SEYCHELLES. Vallée 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. —TYPE: [INDONESIA]: Kalimantan: *Beccari* 147 (holotype: H!; isotypes: JE!, FH!).

Taxithelium horridulum Broth., Philipp. J. Sci. 8: 90. 1913. —TYPE: PHILIPPINES. Luzon, Province of Laguna, Mount Banajao, *Bur. Sci. Robinson* 9773 (holotype: 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; apex acute; laminal cells linear, 60–65 × ca. 2 µm, 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 × 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 diameter. Figure 4.

Distribution and Habitat—*Taxithelium levieri* is restricted to Southeast Asia (Fig. 6), Malesia, and some Pacific islands (Fiji, Tonga, and Niue). It grows on tree trunks, rotten tree stumps and on volcanic blocks, between 270 and 1,170 m.

Discussion—The convolute margins of the leaves in this species resemble those of *Taxithelium portoricense*. *T. levieri* has well-developed alar cells, smaller leaves and more strongly papillose cells, whereas *T. portoricense* has poorly developed alar cells and larger leaves. The two species do not overlap in geographical range.

Representative Specimens Examined—INDONESIA. Bali, *Touw* 24745 (L); Irian Jaya, *Brass* 13764 (MICH); Java, *Nyman* 8752 (W); Seram, *Akyama* 9409 (NY). PHILIPPINES. Mindanao, *Bartlett* 15933 (MICH). NIUE. sine loco, *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.

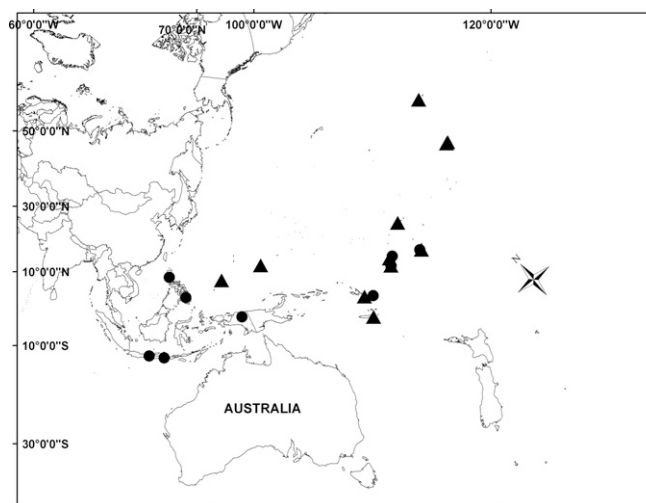


FIG. 6. Distribution map for *T. levieri* (circles) and *T. vernieri* (triangles).

pl. 271. 1867, nom. illegit.—TYPE: INDONESIA. Java, *Teysmann s. n.* (lectotype H!; isoelectotype: BM!, designated here).

Taxithelium nossianum Besch., Ann. Sci. Nat., Bot. sér. 6, 10: 310. 1880.—TYPE: MADAGASCAR. Nossi-Bé, *Perville s. n.* (holotype: BM? (not seen); isotypes: PC!, BR!).

Taxithelium argyrophyllum Renauld & Cardot, Bull. Soc. Roy. Bot. Belgique. 33(2): 131. 1895.—TYPE: MADAGASCAR. Antsiranana, *Chenagon s. n.* (holotype: PC!; isotypes: BM!, BR!, H!, FH!, S!).

Trichosteleum parvulum Broth. & Paris, Bull. Herb. Boissier, sér. 2, 2: 988. 1902. *Taxithelium parvulum* (Broth. & Paris) Broth., Nat. Pflanzenfam. I (3): 1092. 1908.—TYPE: JAPAN. Tsurugi-zan, *Faurie* 1400 (holotype: H!; isotype: PC!).

Taxithelium falciculatum Broth. & Paris, Oefvers. Förh. Finska Vetensk.-Soc. 48(15): 22. 1906.—TYPE: NEW CALEDONIA. Mont Koghi, *Le Rat s. n.* (holotype: H!; isotypes: FH!, M!, PC!, S!).

Taxithelium voeltzkowii Broth., Reise Ostafri., Syst. Arbeit. 3: 63, f. 9: 14. 1908.—TYPE: MAURITIUS, sine loco, *Voeltzkow s. n.* (holotype: H!; isotypes: BR!, PC!, S!).

Taxithelium alare Broth., Philipp. J. Sci. 3: 28. 1908.—TYPE: PHILIPPINES. Mindoro, *For. Bur.* 4476 *Merritt*. (holotype: H!; isotypes: FH!, PC!).

Taxithelium ludovicae Broth. & Paris, Öefvers. Förh. Finska Vetensk.-Soc. 51A (17): 28. 1909.—TYPE: NEW CALEDONIA. Negropo forest, A. *Le Rat s. n.* (holotype: H!; isotypes: M!, PC!).

Taxithelium benguetiae Broth., Philipp. J. Sci. 8: 90. 1913.—TYPE: PHILIPPINES. Luzon, Province of Benguet, *Sanchez B. S.* 10 (holotype: H!; isotypes: BM! E!, FH!, NY!, US!, S!).

Taxithelium robinsonii Broth., Philipp. J. Sci. 13: 218. 1918.—TYPE: PHILIPPINES. Laguna province, Mount Banahao, *Robinson Bur. Sci.* 9864 (lectotype: H!; isoelectotypes: BM!, FH!, NY!, US!, designated here).

Trichosteleum capillarisetum Dixon, J. Linn. Soc., Bot. 45: 494. 1922. *Taxithelium capillarisetum* (Dixon) Broth., Nat. Pflanzenfam. (II) 11: 443. 1925.—TYPE: INDONESIA. Kalimantan. C. B. *Kloss* 34, (holotype: BM!).

Taxithelium clastobryoides Dixon, J. Siam Soc., Nat. Hist. Suppl. 10(1): 26. 1935.—TYPE: THAILAND. Puket, Kerr 512b (holotype: BM!).

Taxithelium convolutum Dixon, J. Linn. Soc., Bot. 50: 130. 41. 1935. —TYPE: MALAYSIA. Sarawak, Everett s. n. (holotype: BM!).

Taxithelium brassii E. B. Bartram, Lloydia 5: 288. 56. 1942.—TYPE: INDONESIA. Irian Jaya, Lake Habbema, Brass 10977 (holotype: FH!; isotypes: L!, MICH!).

Plants medium to large, forming golden-yellow mats. Stem creeping, long-ascending branches. Stem and branch leaves slightly differentiated; stem leaves larger and longer; erect-spreading, concave, $0.95\text{--}1.5 \times 0.18\text{--}0.30$ mm, lanceolate; margins entire at base, serrulate at apex; apex acuminate; laminal cells linear, $50\text{--}55 \times \text{ca. } 2$ μm , thick-walled, basal cells sometimes smooth; 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 $1.0\text{--}1.8 \times 0.25\text{--}0.30$ mm, lanceolate; margins entire at base, serrulate at apex; apex long-aristate; laminal cells linear, $60\text{--}90 \times \text{ca. } 2$ 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, $0.8\text{--}1.1$ mm long, constricted below mouth; exothecial cells subquadrate, not colenchymatous. Operculum short, conic-rostrate, ca. 0.5 mm long. Spores finely papillose, $15\text{--}20$ μm diameter. Figure 7.

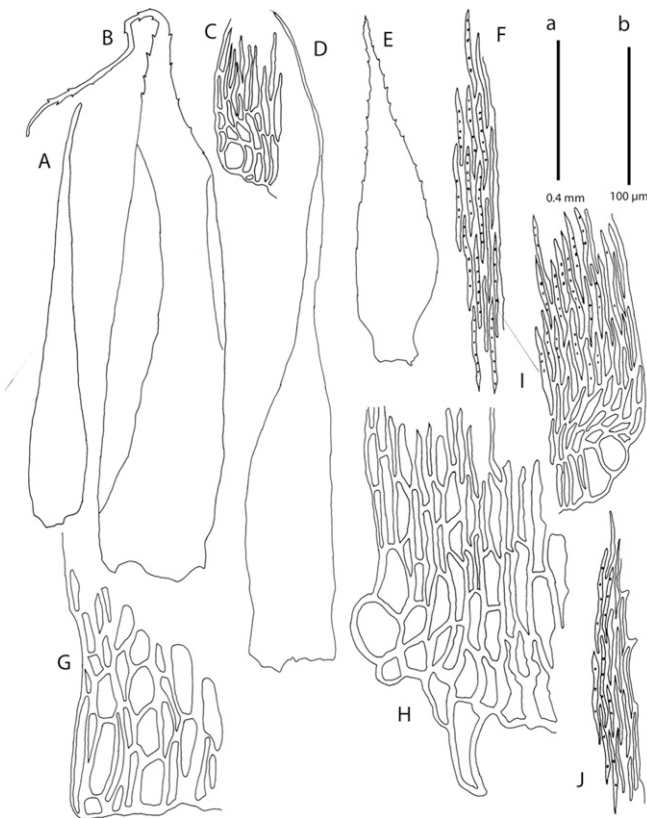


FIG. 7. A, D, E, G, I: *Taxithelium muscicola* A. Branch leaf, D. Perichaetial leaf, F. Leaf margin cells, G. Perichaetial alar region, I. Alar cells.. *Whitelegge 11* (H). B, C, E, H, J: *Taxithelium lindbergii* B. *Taxithelium lindbergii* perichaetial leaf, C. *T. lindbergii* alar cells, E. *T. lindbergii* branch leaf, H. *T. lindbergii* Perichaetial alar region, J. *T. lindbergii* leaf margin cells. *Teyssmann s. n.* (H). A, B, D, E scale a and remaining scale b.

Distribution and Habitat—This species is widely distributed (Fig. 8), from Sri Lanka to Malesia, New Caledonia, Fiji, Samoa, and Pacific Islands. It is also present in the Mascarenes, Seychelles, Madagascar, Vietnam, and Japan.

Discussion—There has been confusion over the correct identification of *T. lindbergii* due to its considerable variation. Plants that occur at high elevation (1,000–2,000 m) on Mt. Kinabalu (Borneo), Mt. Halcon (Philippines), Mt. Luang (Thailand), Mt. Konghis (New Caledonia) and elsewhere, are larger plants. Lowland specimens are usually 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, such plants are slightly smaller but wider.

The variability of this taxon has resulted in many names being proposed that are now synonymized. The morphometric data (available upon request) show that no quantitative morphological trait separates previously recognized species in this complex, nor are there any qualitative (discrete) characters, therefore I decided on the wider circumscription of *T. lindbergii* proposed here. This species can be recognized by its differentiated alar cells, serrate leaves, long seta, and smooth perichaetial leaf cells.

Nomenclatural Notes—The type specimens of *T. lindbergii*, *T. falciculatum*, *T. nossianum*, and *T. argyrophyllum* have no collection numbers, either in the protologue or on the specimens. However, the additional information on the specimens matches that in each protologue. Even though the Mitten herbarium is at NY, the type of *Taxithelium convolutum* was found in BM. The type specimen for *T. nossianum* Besch. was not found in BM (where Emile Bescherelle's herbarium is hosted), but isotypes were found in PC and BR.

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). MALAYSIA. Genting Highlands, *Cámara 878* (MO); Selangor, *HBR 4022* (NY); Sabah, *Holtman 1931* (NY); Sarawak, *Richards 2563* (BM). MAURITIUS. Le Pouce, *Onraedt 272* (BR). PHILIPPINES. Mindoro, *Salgado Edw. 12360* (BR); Mindanao, *Ramos B. S. 14894* (NY); Luzon, *MacGregor B. S. 19919* (NY); Laguna, *Robinson B. S. 17077* (NY); Silipan, *Phillips 16* (MICH). REUNION. Tremblet, *Arts 92/18*, (BR), St. Phillippe, *Arts 11/59* (BR). SEYCHELLES. Ile Mahé, *Decorie 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)

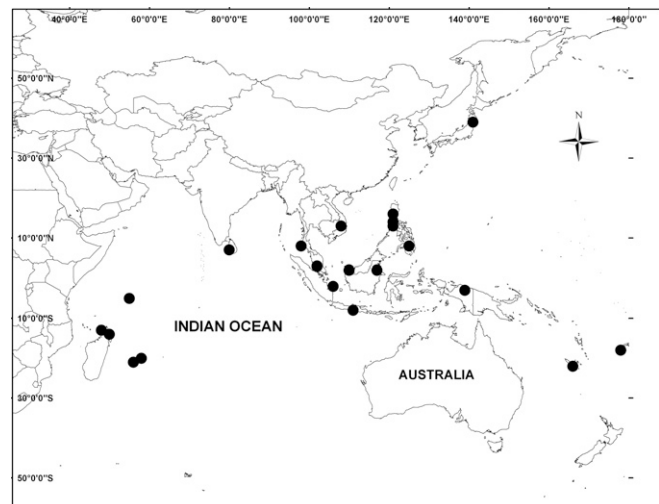


FIG. 8. Distribution map for *T. lindbergii*.

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.—TYPE: AUSTRALIA. Lord Howe Island, Mt. Gower, *T. Whitelegge* 11 (lectotype H!, designated here).

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, $1-2 \times 0.15-0.18$ mm, narrow-lanceolate, slightly falcate-cuspidate; margins entire; apex long acuminate; laminal cells linear, $60-70 \times \text{ca. } 2$ μm , 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 $1.5-2.0 \times 0.18-0.3$ mm, ovate; margins entire at base, serrulate at apex; apex filiform; laminal cells linear, $72-74 \times \text{ca. } 2$ μm , thick-walled, pluripapillose only 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; exothelial cells subquadrate, not collenchymatous. Operculum not seen. Spores finely papillose, 12-16 μm diameter. Figure 7.

Distribution and Habitat—*Taxithelium muscicola* is epiphytic or epiphyllous in montane rain forest. This distinct plant was once considered to be endemic to Lord Howe Island; however, it was later found in Queensland (Fig. 9).

Discussion—Unfortunately, I was unable to study specimens from mainland Australia but Ramsay et al. (2002) and Tan et al. (1996) studied this species for the *Flora of Australia*. *Taxithelium muscicola* resembles *T. damanhurianum*, but it is larger (see notes under *T. damanhurianum*). The well-developed alar cells, along with large and narrowly lanceolate leaves with entire margins, are a distinctive combination.

Nomenclatural Notes—The epithet was first spelled *muscicolum*; however, because it is a noun in apposition, the correct name is *muscicola* (see ICBN Art. 23.5). Unfortunately the syntype *Maiden* 218 was not found in the herbaria visited or in loaned material.

Representative Specimens Examined—AUSTRALIA. Lord Howe Island, *Watts* 419 (NSW), *Watts* 403 (PC).

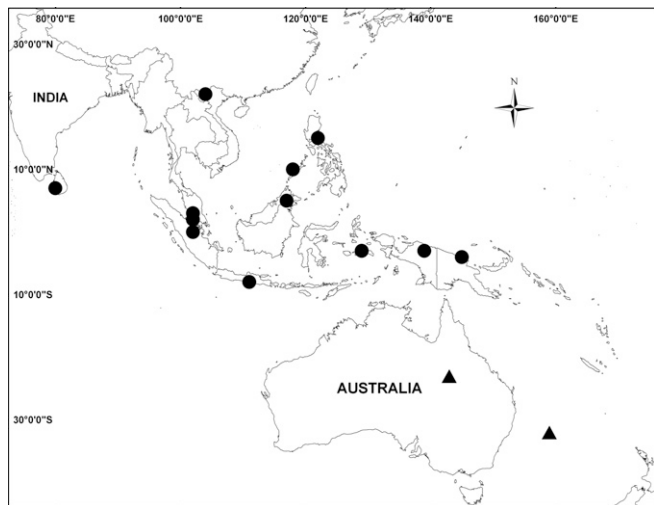


FIG. 9. Distribution map for *T. muscicola* (triangles) and *T. planissimum* (circles).

7. *TAXITHELIUM PLANISSIMUM* Broth., *Hedwigia* 50: 141. 1910.—TYPE: SRI LANKA. Hiniduma, *Herzog* 20 (holotype: H!; isotypes: BR!, JE!, S!).

Taxithelium ramicola Broth., *Philipp. J. Sci.* 8: 91. 1913.—TYPE: PHILIPPINES. Polillo, *McGregor Bur. Sci.* 10509 (holotype: H!; isotypes: BM!, FH!, NY!, S!, US!).

Taxithelium wewakense E. B. Bartram, *Brittonia* 13: 378. 1961.—TYPE: PAPUA NEW GUINEA. Sepik District, Wewak-Angoram Area, *Robbins* 2026 (holotype: 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, $0.75-1.5 \times 0.20-0.40$ mm, oblong-lanceolate; margins entire; apex acuminate; laminal cells linear, $60-65 \times \text{ca. } 2$ μm , 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 $1.2-2.0 \times 0.30-0.45$ mm, lanceolate; margins serrulate; apex acuminate; laminal cells linear, $35-40 \times \text{ca. } 2$ 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; exothelial cells subquadrate, not collenchymatous. Operculum long, conic-rostrate, ca. 0.8 mm long. Spores finely papillose, 15-20 μm diameter. Figure 10.

Distribution and Habitat—*Taxithelium planissimum* occurs in lowlands from Sri Lanka to SE Asia (Malaysia), and Vietnam, between sea level and 300 m, but it was also collected on Mt. Binohan (Palawan, Philippines) at about 1,000 m (Fig. 9). It grows almost exclusively on twigs or as an epiphyll, rarely on bark.

Discussion—*Taxithelium planissimum* resembles *T. isocladum* in its leaf shape and in size and in the absence of well-developed alar cells, but it can be distinguished by the 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.

Representative Specimens Examined—INDONESIA. Sumatra (Brastagi), *Holtmann* 25327 (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). PHILIPPINES. Palawan, *Ebalo* 391 (MICH). SRI LANKA. Hiniduma, *Herzog* 3979 (H); sine loco, *Thwaites* 217 (NY). VIETNAM. Lao Cai, *Moctier* s. n. (S).

8. *TAXITHELIUM PLURIPUNCTATUM* (Renaud & Cardot) W. R. Buck, *Moscossa* 2: 60. 1983; *Trichosteleum pluripunctatum* Renaud & Cardot, *Bull. Soc. Roy. Bot. Belgique* 29(1): 184. 1890.—TYPE: MARTINIQUE. Ste-Marie, *Bordaz* 1 (holotype: PC!; isotype: NY!).

Taxithelium thelidiellum Besch., *J. Bot. (Morot)* 6: 10. 1902.—TYPE: GUADELOUPE. Trois Diabes, *P. Duss* 1364 (Holotype: BM? (not seen); isotypes: H!, NY!).

Taxithelium patulifolium Thér., *Ann. Bryol.* 7: 160. 1934.—TYPE: FRENCH GUIANA. Saint-Jean-du-Maroni Sine Legit (holotype: PC!; isotypes: H!, NY!).

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 strongly papillose, wide-spreading, $0.70-1.2 \times 0.20-0.40$ mm, falcate, lanceolate-ovate; margins subentire, serrulate at base; apex acuminate to aristate; laminal cells linear, $72-85 \times \text{ca. } 2$ μm ,

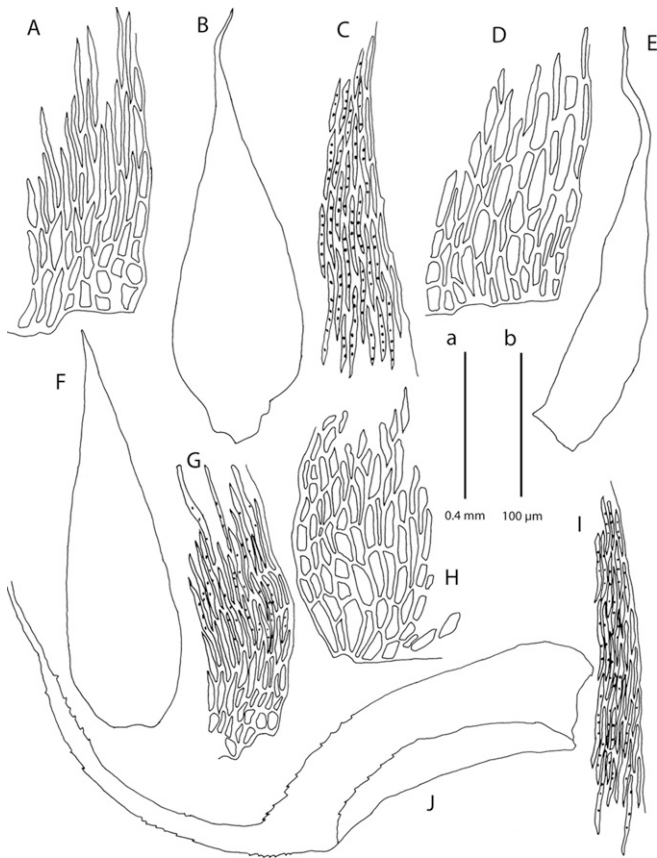


FIG. 10. A–E: *Taxithelium vernieri*. A. Alar cells, B. Branch leaf, C. Leaf margin cells, D. Perichaetial alar region, E. Perichaetial leaf. B and E scale a; and A, C, D, scale b. McGregor B.S. 10509 (H). F–G: *Taxithelium planissimum*. F. Branch leaf, G. Alar cells, H. Perichaetial alar region, I. Leaf margin cells, J. Perichaetial leaf. F and J scale a; and remaining scale b. Vernier s. n. (G).

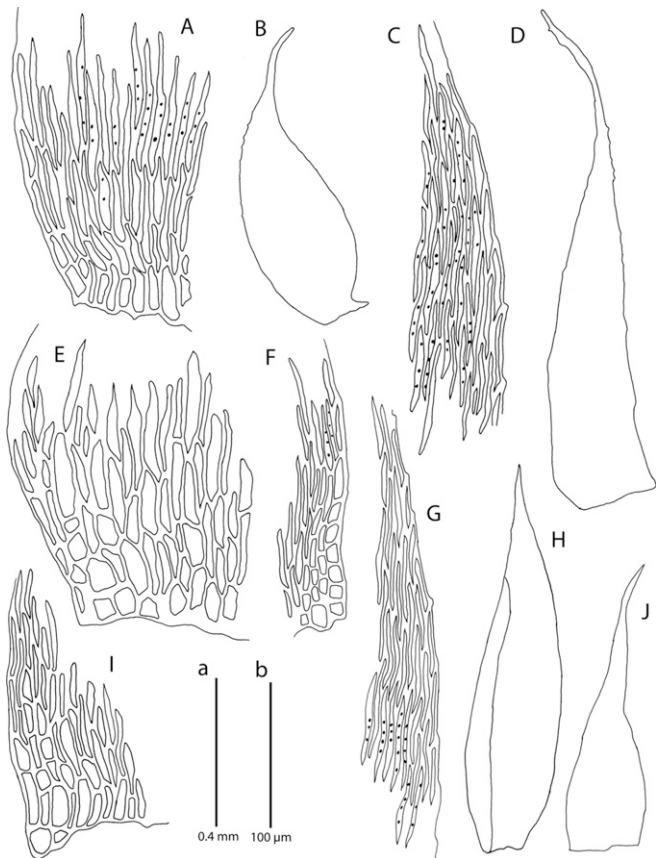


FIG. 11. A–E: *Taxithelium pluripunctatum*. A. Alar cells, B. Branch leaf, C. Leaf margin cells, D. Perichaetial alar region, E. Perichaetial leaf. B and D scale a; and A, C, D, scale b. Bordaz 1 (PC). F–J: *Taxithelium portoricense*. F. Alar cells, G. Leaf margin cells, H. Branch leaf, I. Perichaetial alar region, J. Perichaetial leaf. H and J scale a; and F, G, I, scale b. E. G. Britton 8390 (NY).

thick-walled; apical cells usually smooth; costae short and double or absent; alar cells poorly differentiated in 2 rows, not inflated. Rhizoids clustered on lower stem. Perichaetial leaves $1.0\text{--}1.5 \times 0.18\text{--}0.30$ mm, long-triangular, margins serrulate at apex; apex acuminate to aristate; laminal cells linear, $60\text{--}80 \times \text{ca. } 2$ μm , thick-walled, poorly pluripapillose; costae absent; alar cells poorly differentiated. Setae $4.9\text{--}5.1$ mm long. Capsules inclined, asymmetric, ovoid, $0.6\text{--}0.8$ 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, $15\text{--}20$ μm diameter. Figure 11.

Distribution and Habitat—*Taxithelium pluripunctatum* is restricted to the New World, being found in South America and the West Indies (Fig. 12). It is also reported from Mexico and Central America (Buck 1998; Sharp et al. 1994) but I have not seen specimens from these areas. It grows on tree trunks, limestone and humus, at elevations between sea level and 900 m.

Discussion—This species, together with *T. portoricense*, is one of the two species that occur in the New World. However *T. portoricense* differs in its involute leaf margins, less papillose leaves, and smooth perichaetial leaf cells. *Taxithelium 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* species has smooth or prurilose leaf cells and better developed alar cells.

Nomenclatural Notes—Even though Bescherelle's herbarium is at BM, no type of *T. thelidiellum* was found there. The type specimens of *T. patulifolium* have no data on the collector, either in the protologue or on the specimen, but the other information on the specimen matches that of the protologue.

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 GUIANA. 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. 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. —TYPE: PUERTO RICO. Cidra, E. G. Britton 8390 (lectotype: NY!; isolectotypes: FH!, PC!, MICH!, designated here).

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 strongly papillose, wide-spreading, $0.70\text{--}1.2 \times 0.20\text{--}0.35$ mm, oblong-lanceolate; margins subentire, serrulate only at base; apex acuminate; laminal cells linear, $44\text{--}50 \times \text{ca. } 2$ μm , thick-walled; apical cells usually smooth; costae double and short or

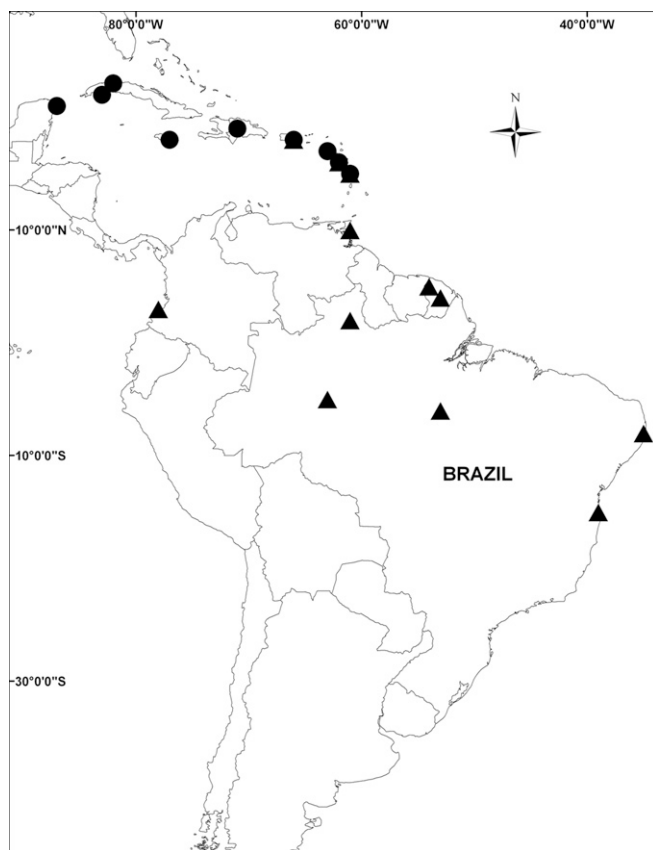


FIG. 12. Distribution map for *T. pluripunctatum* (triangles) and *T. portoricense* (circles).

absent; alar cells poorly differentiated. Rhizoids clustered in lower stem. Perichaetial leaves $0.80\text{--}1.2 \times 0.18\text{--}0.45$ mm, long-triangular; margins entire; apex acuminate; laminal cells linear, $80\text{--}90 \times \text{ca. } 2$ μm , thick-walled, smooth; costae absent; alar cells poorly differentiated in 2 rows, not inflated. Setae $4.9\text{--}5.1$ mm long. Capsules inclined, asymmetric, ovoid, $0.6\text{--}0.8$ 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, $15\text{--}20$ μm . Figure 11.

Distribution and Habitat—This species is restricted to islands in the Caribbean (Fig. 12), and grows on twigs and dead logs, between sea-level and $1,500$ m. It was also cited from the Brazilian Amazon by Lisboa and Ilkiu Borges (1997), although it was not possible for me to study the specimen they cited. Their species description is unclear and the illustration is of *T. pluripunctatum*; therefore I am excluding this record.

Discussion—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 the 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* by its less strongly papillose and more symmetric leaves with involute margins, and perichaetial leaf cells that lack papillae (see also comments under *T. pluripunctatum*).

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 (FH, NY); Las Cruces, Steere 6361 (FH, MICH). ST. KITTS. St. Thomas Middle Island Parish, Buck 29826 (NY).

10. *TAXITHELIUM RAMIVAGUM* Broth., Bot. Jahrb. Syst. 24: 266. 1897.—TYPE: CAMEROON. Mbanga, Staudt 277 (lectotype: H!; isoelectotype: PC!, designated here).

Taxithelium ramivagum Broth. var. *elongatum* P. de la Varde, Rev. Bryol Lichénol. 5: 207. 1933.—TYPE: GABON. Malongomabey, Le testu 6768 (holotype: PC!).

Taxithelium theriotii P. de la Varde, Bull. Soc. Bot. France 72: 364. f. 16. 1925.—TYPE: GABON. Benzé, Le testu 5324 (holotype: 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, $1.0\text{--}1.6 \times 0.25\text{--}0.40$ mm, oblong-lanceolate; margins entire; apex entire or slightly acuminate; laminal cells linear, $75\text{--}80 \times \text{ca. } 2$ μm , 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 $1.0\text{--}1.5 \times 0.24\text{--}0.30$ mm, narrow-lanceolate; margins entire; apex setaceous; laminal cells linear, $32\text{--}40 \times \text{ca. } 2$ μm , thick-walled, smooth; costae absent; alar cells poorly differentiated in 2 rows, not inflated. Setae ca. 10 mm long. Capsules unknown. Figure 13.

Distribution and Habitat—Known from few collections (mostly types), this species is restricted to tropical Africa (Fig. 5); the last collection was made in the 1920s. It grows on bark from sea level to 875 m.

Discussion—*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).

Representative Specimens Examined—CAMEROON. Ekundu, Dusen 797 (PC). CÔTE D'IVOIRE. Hourotte, Jolly s. n. (S). DEMOCRATIC REPUBLIC OF CONGO. Kivu, Luhoho, Fzaire s. n. (BR). GABON. Mavenga, Le Testu s. n. (M). 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.—TYPE: TAHITI. *D. Vernier* s. n. (holotype: G!; isotypes: BM!, NY!, PC!).

Taxithelium nitidulum Broth. & Paris, Öefvers. Förh. Finska Vetensk.-Soc. 48 (15): 23. 1906.—TYPE: NEW CALEDONIA. Thi, *Le Rat* s. n. (holotype: H!; isotypes: M!, PC!).

Taxithelium francii Thér., Bull. Acad. Int. Géogr. Bot. 20: 103. 1910.—TYPE: NEW CALEDONIA. Mont Koghis, *Franc* s. n. (holotype: PC!; isotypes: BM!, FH!, H!).

Taxithelium kuniense Broth. & Paris, Öefvers. Förh. Finska Vetensk.-Soc. 53A(11): 36. 1911.—TYPE: NEW CALEDONIA. Ile des Pins, forêt de Gadge, *Louise Le Rat* 1372 (lectotype: H!; isoelectotypes: PC!, S!, designated here).

Taxithelium protensum Dixon, Proc. Linn. Soc. New South Wales 55: 297, f. 24. 1930.—TYPE: FIJI. Sine loco, *Steel* 4 (holotype: BM!).

Taxithelium falcifolium E. B. Bartram, Occas. Pap. Bernice Pauahi Bishop Mus. 10(10): 14. 1933.—TYPE: [FRENCH

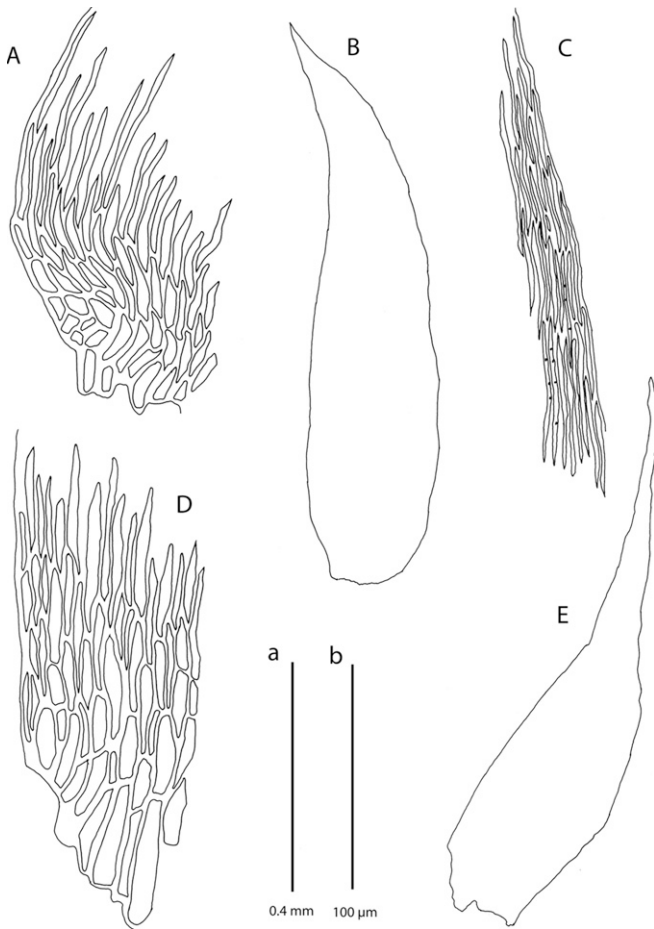


FIG. 13. *Taxithelium ramivagum*. A. Alar cells, B. Branch leaf, C. Leaf margin cells, D. Perichaetial alar region, E. Perichaetial leaf. B and E scale a; and A, C, D, scale b. Staudt 277 (H).

POLYNESIA]. Eiao, furas forest, W. B. Jones 1522 (holotype: FH!; isotypes: L!, US!).

Plants small, forming golden-yellow mats. Stems creeping, long ascending branched. Stem and branch leaves similar, erect-spreading, concave, $0.6\text{--}1.2 \times 0.15\text{--}0.30$ mm, oblong-lanceolate; margins entire; apex acuminate or acute; laminal cells linear, $58\text{--}60 \times \text{ca. } 2$ μm, thick-walled, basal cells sometimes smooth; costae short and double or absent; alar cells poorly differentiated, consisting of 1–3 rows. Rhizoids evenly distributed along the stem. Perichaetial leaves $1.2\text{--}1.6 \times 0.40\text{--}0.50$ mm, lanceolate; margins entire at base, serrulate at apex; apex long-aristate; laminal cells linear, $50\text{--}70 \times \text{ca. } 2$ μm, thick-walled, smooth; costae absent; alar cells not differentiated. Setae 14–16 mm long. Capsules inclined, asymmetric, ovoid, $0.6\text{--}0.8$ 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, $15\text{--}20$ μm. Figure 10.

Distribution and Habitat—This species grows in dense forests, usually on dead logs, sometimes on bark of living trees, between the sea level and 700 m, and is restricted to the islands of the Pacific, New Caledonia, Society Islands (French Polynesia), Micronesia and Marquesas (Fig. 6).

Discussion—*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 specimens of *T. levieri*, but the alar cells in *T. vernieri* are not well developed as they are in *T. levieri*.

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 1316 (G); Marquesas, Nuku Hiva, Jordan s. n. (NY). NEW CALEDONIA. Sine loco, L. Le Rat 1403 (H, M); 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. Sine loco, Campbell 3 (BM).

Types Not Seen in Genus *Taxithelium*—For the following names it was impossible to locate the type specimens. I looked in all the herbaria cited in the methods. Some are Müller Hallensis names and were most likely destroyed during the bombing of the Berlin herbarium in 1943.

Taxithelium anderssonii (Ångstr.) Broth., Nat. Pflanzenfam. I (3): 1237. 1909. *Plagiothecium anderssonii* Ångstr., Öfvers. Förh. Kongl. Svenska Vetensk.-Akad. 29(4): 15. 1872.—TYPE: CHILE. Port Famine, Magalhaens, Andersson s. n. (holotype S?).

Even though it was not possible to locate the type specimen, it is probably not a *Taxithelium*, since the genus is not known to occur that far south. The description provided in the protologue is uninformative.

Taxithelium aureolum Cardot, Bull. Soc. Bot. Genève sér. 2, 5: 319. 1913.—TYPE: JAPAN. Sine loco. Hiroaki 18. (holotype: PC?).

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*, and the description of *T. aureolum* would fit into *Phyllodon* rather than in *Taxithelium*.

Taxithelium bilobatum var. *scabrifolium* Dixon, Gard. Bull. Straits Settlement. 4: 35. 1926.—TYPE: MALAYSIA. Malacca, Perak, Burkill 13007. (holotype: BM?).

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

Taxithelium confusum Cardot, Hist. Phys. Madagascar, Mousses 39: 471. 1915.—TYPE: MADAGASCAR. Ile a Sainte-Marie, Boivin s. n. (holotype: PC?).

The description and illustration provided by Cardot resembles the widespread *Taxithelium lindbergii*.

Taxithelium decrescens (Sande Lac.) Broth., Nat. Pflanzenfam. I (3): 1092. 1908. *Hypnum decrescens* Sande Lac., Bryol. Jav. 2: 168. 266. 1866.—TYPE: INDONESIA. Sulawesi, Ludwig. Bat. s. n. (holotype: L?).

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*.

Taxithelium glabrisetum (Müll. Hal.) Paris, Index Bryol. 1261. 1898. *Sigmatella glabriseta* Müll. Hal., Bot. Jahrb. Syst. 23: 329. 1896.—TYPE: SAMOA. Olosina, Flechten 91. (holotype B?, probably destroyed).

Unfortunately the protologue does not provide a good description or illustration that would allow placement of this type.

Taxithelium herpetium (Müll. Hal.) Broth., Nat. Pflanzenfam. I(3): 1091. 1908. *Hypnum herpetium* Müll. Hal., J. Mus. Godeffroy 3(6): 84. 1874. —TYPE: SAMOA. Tutuila, sine legit. (holotype: B?, probably destroyed).

The original description states that the leaf cells of the type specimen have single papillae and therefore it is probably not a *Taxithelium*; unfortunately, no illustration of this plant exists.

Taxithelium inerme Tixier, Rev. Bryol. Lichénol. 38: 159, f. 8. 1971 [1972]. —TYPE: THAILAND. Chandhaburi, Plew Waterfalls, Tixier 965. (holotype: PC?).

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

Taxithelium isocladum (Bosch. & Sande Lac.) Renaud & Cardot var. *vietnamense* Tixier, Rev. Bryol. Lichénol. 34: 171. 1966.—TYPE: Vietnam. Quang-Binh, Maunier s. n. (holotype: PC?).

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

Taxithelium ivoreanum (Mitt.) Broth., Nat. Pflanzenfam. I(3): 1093. 1908. *Stereodon ivoreanus* Mitt., J. Proc. Linn. Soc., Bot., Suppl. 2: 105. 1859.—TYPE: NEPAL. Mont. Nilghiri, McIvor s. n. (holotype: NY?).

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*.

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

Taxithelium laeve Cardot, Bull. Soc. Bot. Genève sér. 2, 4: 387. 1912.—TYPE: JAPAN: Tosa, Arakusa, Okamura s. n. (holotype PC?).

The original description says that the type specimen has smooth leaf cells. As the only species of *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.

Taxithelium liukiense Sakurai, Bot. Mag. (Tokyo) 46: 505. 1932.—TYPE: [JAPAN]. Liukiu, Nishi-Omotejima, Y. Dor 2170. (holotype BM?, not seen).

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 information in the protologue states that the type is 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. I was unable to locate this specimen during my visit to BM.

Taxithelium natans (Müll. Hal.) Renaud & Cardot, Rev. Bryol. 28: 111. 1901. *Sigmatella natans* Müll. Hal., Hedwigia 40: 70. 1901.—TYPE: BRAZIL. Rio de Janeiro, Morro da Cintra, E. Ule 161. (holotype B?, probably destroyed).

The original descriptions of both *T. natans* and *T. oophyllum* match *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 bombing of the Berlin herbarium in 1943.

Taxithelium oophyllum (Müll. Hal.) Renaud & Cardot, Rev. Bryol. 28: 111. 1901. *Sigmatella oophylla* Müll. Hal., Hedwigia 40: 70. 1901. —TYPE: BRAZIL. Minas Gerais, Uberaba, E. Ule 1598. (holotype B?, probably destroyed).

See comments under *T. natans*.

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. —TYPE: SAMOA. Tutuila, Graeffe s. n. (holotype B?, probably destroyed).

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 now belonging to subgenus *Vernieri*. The most common of the species of *Taxithelium* subgenus *Vernieri* in Samoa is *T. vernieri*.

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.—TYPE: TRINIDAD and TOBAGO. Trinidad, near St. Joseph, Crüger 14. (holotype B?, probably destroyed).

The original description matches *T. planum* (subgenus *Taxithelium*), which is a common and widespread species. *Taxithelium planum* is also a variable species and therefore many varieties have been described and I believe that they are all synonyms. In this case, unfortunately the type is most likely lost.

Taxithelium planum (Brid.) Mitt. var. *hookerioides* Bizot & Thér., Bull. Mens. Soc. Linn. Soc. Bot. Lyon 34: 326. 1965.—TYPE: CUBA. Loma San Juan, Hioram 11808. (holotype B?, probably destroyed).

I was unable to locate the type, but the description fits the variable *T. planum* (see comments above for *T. planum* var. *flavescens*). *Taxithelium planum* is the only species of subgenus *Taxithelium* known from Cuba.

Taxithelium plumularia (Müll. Hal.) Broth., Nat. Pflanzenfam. I(3): 1092. 1908. *Hypnum plumularia* Müll. Hal., Syn. Musc. Frond. 2: 684. 1851.—TYPE: INDONESIA. Java, Blume s. n. (holotype B?, probably destroyed).

The original description is vague; it says the cells are "indistinctis sparsim tenuiter papilloso," but no illustration was provided.

Taxithelium rhizophoreti (Müll. Hal.) Broth., Nat. Pflanzenfam. I(3): 1091. 1908. *Hypnum rhizophoreti* Müll. Hal., J. Mus. Godeffroy 3(6): 83. 1874. —TYPE: SAMOA. Tutuila, sine legit. (holotype B?, destroyed).

There is no illustration accompanying the original description. The protologue is broad, but it does fit *Taxithelium*. Brotherus, when transferring *Hypnum rhizophoreti* into *Taxithelium* considered it close to species now included in subgenus *Vernieri*. The most common representative of that subgenus in Samoa is *T. vernieri*.

Taxithelium spathulifolium Dixon, J. Siam Soc., Nat. Hist. Suppl. 10: 26. 1935.—TYPE: THAILAND. Puket, Krabi, Kerr 511b. (holotype BM?).

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

Taxithelium subretusum (Thwaites & Mitt.) Broth., Nat. Pflanzenfam. I(3): 1093. 1908. *Ectropothecium subretusum* Thwaites & Mitt., J. Linn. Soc., Bot. 13: 321. 1873. —TYPE: SRI-LANKA. *Thwaites s. n.* (holotype NY?).

This species is probably a *Phyllodon*. According to the vague protologue, *Ectropothecium subretusum* has unipapillose leaf cells. Brotherus, when transferring this name to *Taxithelium*, considered it to be close to *T. glossoides* and *T. ligulatum*, both now in *Phyllodon*. I was unable to locate the type during my visit to NY.

Taxithelium tongense (Müll. Hal.) Broth., Nat. Pflanzenfam. I(3): 1090. 1908. *Hypnum tongense* Müll. Hal., J. Mus. Godeffroy 3(6): 83. 1874.—TYPE: TONGA. Tongatabú, Ed. Graeffe s. n. (holotype B?, probably destroyed).

Probably a species in subgenus *Taxithelium*. Brotherus considered it close to *T. planum* and *T. instratum*; both of these species belong to subgenus *Taxithelium*, which would also agree with the somewhat vague original description.

Taxithelium ventrifolium (Müll. Hal.) Broth., Nat. Pflanzenfam. I(3): 1090. 1908. *Hypnum ventrifolium* Müll. Hal., J. Mus. Godeffroy 3(6): 84. 1874. —TYPE: FIJI. Ovalau, sine legit. (holotype B?, probably destroyed).

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*.

Taxithelium annandii Broth. & Watts, nom. nud.

Taxithelium annandii is cited in *Index Muscorum* and TROPICOS, but I was unable to find the name in the cited journal (Proc. Linn. Soc. New South Wales 40: 152. 1915.) or anywhere else in the literature.

There is one specimen named as such in S, was collected by Dr. Annand in 1903, making it a type candidate, but without the protologue information it is impossible to know whether this is the basis of this illegitimate name.

Excluded Taxa—*Taxithelium latitruncatum* Cardot, Histoire Physique, Naturelle et Politique de Madagascar, Mousses 39: 478. 1915. = *Phyllodon truncatus* (Welw. & Duby) W. R. Buck. Mem New York Bot. Gard. 45: 521. 1987.

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