

## TOWARDS A REVISION OF THE MOSS GENUS *TAXITHELIUM* (SEMATOPHYLLACEAE)

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### RESUMEN

Está en progreso la evaluación de la distribución y de los caracteres que circunscriben al género esencialmente tropical *Taxithelium* Spruce ex Mitt. Tradicionalmente, éste ha sido caracterizado por papilas arregladas en serie sobre el lumen de las células laminares y por células alares más o menos cuadradas. Sin embargo, las observaciones críticas de la morfología, incluyendo las del Microscopio Electrónico de Barrido (MEB), muestran varios caracteres que no se habían usado previamente entre los que están el tipo de desarrollo de las ramas, los márgenes foliares papilosamente serrados y las papilas de las hojas periqueciales. Estos caracteres han sido útiles para distinguir *Taxithelium* de géneros cercanamente relacionados en tanto que los caracteres de los rizoides, caliptra, vaginula y de las células exoteciales han servido para separar las especies dentro del género. El género *Taxithelium* se distribuye en todas las regiones tropicales y en ciertas partes subtropicales, aproximadamente entre los 30° N and 20° S. Su amplia distribución es debida en mucho a *T. planum* (Brid.) Mitt., una especie muy variable que crece desde la punta sur de Florida, hacia el sur a través de Centromérica y en las Antillas hasta Bolivia; en África se conoce del Congo, Angola, Cameroon, Gabon, Guinea y Liberia; se extiende por toda el Asia tropical y el Territorio Norte de Australia. La concentración más alta de especies se encuentra en Malesia.

Palabras clave: taxonomía, musgos, Sematophyllaceae, *Taxithelium*.

### ABSTRACT

In relation to an ongoing taxonomic revision of the essentially tropical moss genus *Taxithelium* Spruce ex Mitt., the characters used to circumscribe the genus and those used to separate the species are being evaluated. The distribution of the genus is also being assessed. Traditionally, *Taxithelium* has been charac-

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terised by the serially arranged papillae over the lumen of the laminal cells and the more or less quadrate alar cells. However, critical observations on morphology, including those made with scanning electron microscopy (SEM), reveal several new characters not used previously, such as type of branch development, the papillose-serrate margins of the leaves and the papillosity of the perichaetial leaves. These characters have proved to be useful in distinguishing *Taxithelium* from closely related genera, whereas characters of the rhizoids, calyptra, vaginula, and exothecial cells are found to be helpful in separating some of the species within the genus. The genus *Taxithelium* extends all over tropical regions, with a slight intrusion into the subtropics, occurring between approximately 30° N and 20° S lat. The wide distribution of this genus is largely due to the very variable species *T. planum* (Brid.) Mitt. which occurs from the southern tip of Florida southwards through Central America and the West Indies to Bolivia; on the African Continent in Congo, Angola, Cameroon, Gabon, Guinea and Liberia; throughout tropical Asia and in the Northern Territory of Australia. The largest concentration of species is found in Malesia.

Key words: taxonomy, mosses, Sematophyllaceae, *Taxithelium*.

## INTRODUCTION

The tropical genus *Taxithelium* Spruce ex Mitt. is one of the largest genera in the family Sematophyllaceae. It is also one of the most difficult and poorly understood moss genera. Species of *Taxithelium* are small to medium-sized plants, typically complanate-foliate with creeping stems, growing in thin, but often extensive mats on rotten wood and other substrata. There are 121 valid specific names in *Index Muscorum* (Wijk, Margadant and Florschütz, 1969) and *Index of Mosses 1963-1989* (Crosby, Magill and Bauer, 1992).

The genus extends throughout the tropical regions between approximately 30° N and 20° S lat. (Fig. 1). The highly variable species *T. planum* has a pantropical distribution (Fig. 2), while some other species are restricted to Africa and the Americas. However, most species are centred in the Malesian region, with one, *T. planissimum*, extending from Malaysia to Sri Lanka (Fig. 3).

The occurrence of *T. novae-zeelandiae* Bartr. & Dix. from New Zealand is reported in *Index Muscorum*. However, Sainsbury (1955) suggested, on the basis of the original description, that this plant is a form of *Camptochaete gracilis*. Sainsbury was unable to locate the specimen, but we have examined what appears to be the original material at BM (New Zealand, Wellington, 1874, S. Berggren in Herb. Dixon) and confirm that it is not a species of *Taxithelium*.

A revision of the genus *Taxithelium* is currently being undertaken at Reading, based on an examination of material representing as many as possible of the named taxa. Specimens of approximately 80 taxa have so far been examined. Types are available of about 60 % of these taxa, but those of species described by

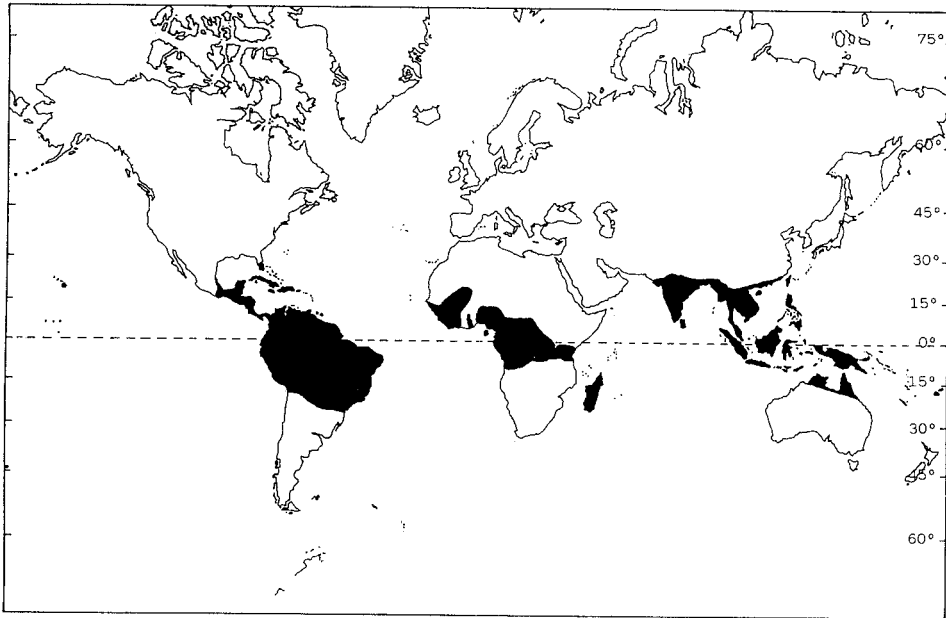


Fig. 1. Distribution of the genus *Taxithelium* Spruce ex Mitt.

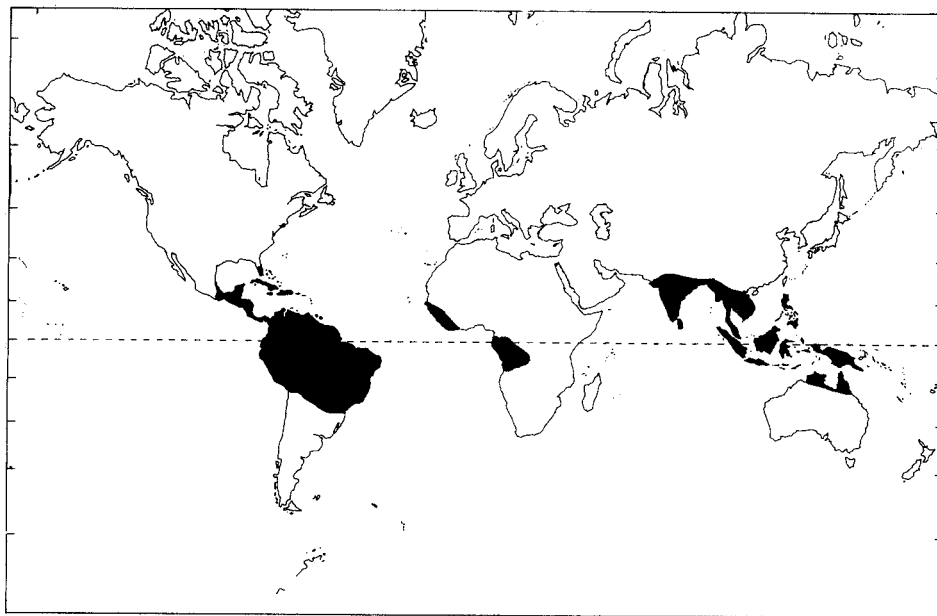


Fig. 2. Distribution of *T. planum* (Brid.) Mitt.

Carl Müller have been destroyed, and types of some other taxa have not yet been located. The material is being systematically scored for over 40 gametophytic and sporophytic characters. This will enable a numerical study of critical taxa, and a cladistic analysis of the genus, to be undertaken. In the present paper we discuss new characters that appear to be useful in circumscribing the genus, and in distinguishing some of the species.

### CHARACTERS OF VALUE IN DELIMITING THE GENUS

Features traditionally used to characterise the genus *Taxithelium* are the ecostate leaves, the more or less quadrate alar cells, and the linear laminal cells each with a row of papillae over the lumen. Indeed the name *Taxithelium* is taken from "tax-" which is derived from the Greek word "taso" (=arrange) and "thelion" (=diminutive teat or nipple), in reference to the papillae arranged in rows over the laminal cells. However, critical observations have revealed several additional characters that appear to be useful in defining the genus.

**Leaf Margin.** The leaf margin in most species of *Taxithelium* is plane (Fig. 4 e, g). The margin is often serrulate nearly to the base (Fig. 4 h). The teeth are sometimes quite strong, especially in the upper part of the leaf (Fig. 4 f, g). In some species, e.g., *T. instratum*, the marginal teeth appear double. Such teeth are formed of two cells, which are fused at their proximal ends and separated distally.

The teeth are often obscured by the presence of papillae on the margins which look like additional serrations (Fig. 4 e, i). These papillose-serrate margins can be used to recognise as members of *Taxithelium* those species with very low papillae on the cell lumen. The presence of marginal papillae can also be used to distinguish *Taxithelium* from other genera in the Sematophyllaceae such as *Trichosteleum* where the marginal cells of the leaves may be serrulate or unipapillose, but never pluripapillose. The significance of the papillose-serrate margins in *Taxithelium* was noted by Norris and Koponen (1985).

**Perichaetium.** The perichaetial leaves (Fig. 5) are gradually to more or less abruptly subulate from an ovate to ovate-lanceolate base. They are often slightly concave and have more or less serrate to serrulate margins. The margin on the shoulder of the perichaetial leaves is sometimes notched or lacinate (Fig. 5 a), a feature which is often more developed on one side of the leaf.

As with the vegetative leaves, the margins of the perichaetial leaves may bear papillae that resemble additional serrations (Fig. 5 a, b). The laminal cells of the perichaetial leaves are also papillose. The papillae are best developed in the upper part of the leaf, especially on the subula (Fig. 5 a, b, e). The median and basal cells are usually smooth. In some species, e.g., *T. alare*, *T. sematophylloides* and *T. werneri*, the upper cells are almost smooth but a few papillae can always be detected, especially in the upper portion of the subula (Fig. 5 c, d, f), or at the end of the apical cell where they are often coronate (Fig. 5 a-d, f).

The presence of papillae on the perichaetial leaves has seldom been mentioned in previous work on *Taxithelium* (Brotherus, 1909, 1925; Fleischer, 1923; Bartram, 1939; Gangulee, 1980; Crum and Anderson, 1981; Buck, 1985; Crum, 1994), and the papillae have not previously been used as a source of taxonomic characters. In the present study the shape and papillosity of the perichaetial leaves are found to be very useful in distinguishing *Taxithelium* from related genera where the perichaetial leaves are smooth to irregularly pluripapillose, but with the leaf margin and apical cell always lacking papillae.

*Taxithelium* can also be separated from *Glossadelphus* by the perichaetial leaves, which are gradually to abruptly subulate from an ovate or ovate-lanceolate base in *Taxithelium* as opposed to lanceolate and more strongly acuminate in *Glossadelphus*. Variation in perichaetial leaves can also be used to distinguish some species within *Taxithelium*.

#### CHARACTERS OF VALUE IN DELIMITING THE SPECIES

**Leaf posture and shape.** In the majority of species of *Taxithelium*, the branch leaves are erect-spreading to spreading with the apices straight (Fig. 4 a, b) whereas in the epiphyllous species *T. werneri* the apices of the leaves are often strongly deflexed toward the substratum (Fig. 4 c). This character can be used to distinguish *T. werneri* from *T. capillarisetum*, the other common epiphyllous species, because the leaves are always straight in the latter.

Leaf shape in *Taxithelium* varies from narrowly to broadly ovate-lanceolate, or rarely ovate. The base is often gradually to abruptly narrowed to the insertion. The apex is usually acute to acuminate (Fig. 6 b-k), or rarely rounded-obtuse as in *T. planum* (Fig. 6 a). Leaf shape is variable in some species, e.g., *T. planum*, but is useful in distinguishing between some taxa.

**Branch development and pseudoparaphyllia.** Akiyama (1990) reported two basic types of branch development in mosses, i.e., the *Climacium*-type and the *Bryum*-type. In the *Climacium*-type the apical cell of the branch primordium produces tiny leaves, called scaly leaves by Akiyama and Nishimura (1993), from the very first stage of development. These branch primordia then develop into branch buds before entering dormancy. In the *Bryum*-type, the apical cell of the branch primordium only produces leaves, thus becoming transformed into a branch bud, after its release from dormancy. In the *Bryum*-type development, however, the branch primordium, and later the base of the branch, may be surrounded by filamentous trichomes (= pseudoparaphyllia of earlier authors).

Both types of branch development have been observed in *Taxithelium* during this study. In the majority of species with the *Climacium*-type development the dormant branch buds usually consist of tight clusters of tiny, more or less rounded and strongly concave scaly leaves. The laminal and marginal cells of these leaves are papillose in some species, e.g., *T. planum* (Fig. 7 a). Less typically the scaly

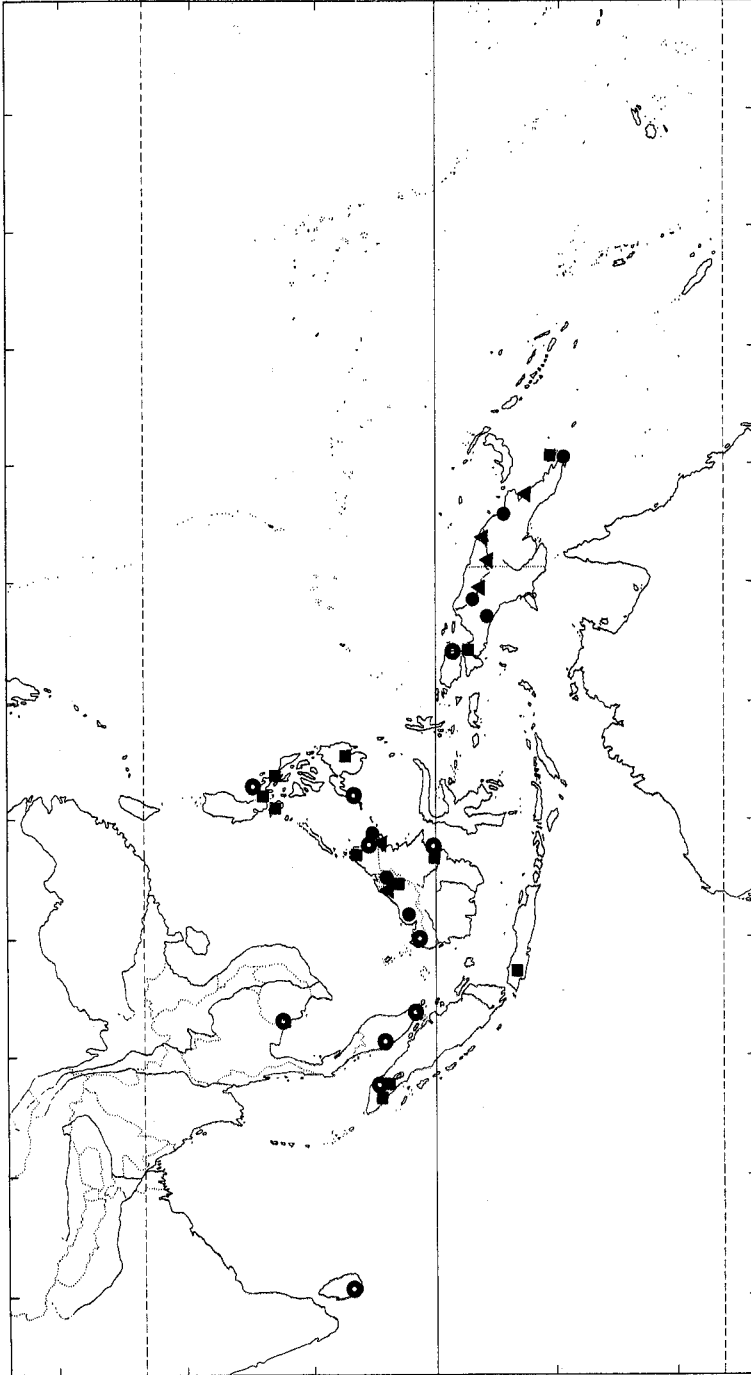


Fig. 3. Distribution of *T. capillarisetum* (Dix.) Broth. (●); *T. alare* Broth. (■); *T. werneri* (Herz.) Broth. (▲), *T. planissimum* Broth. (◆)

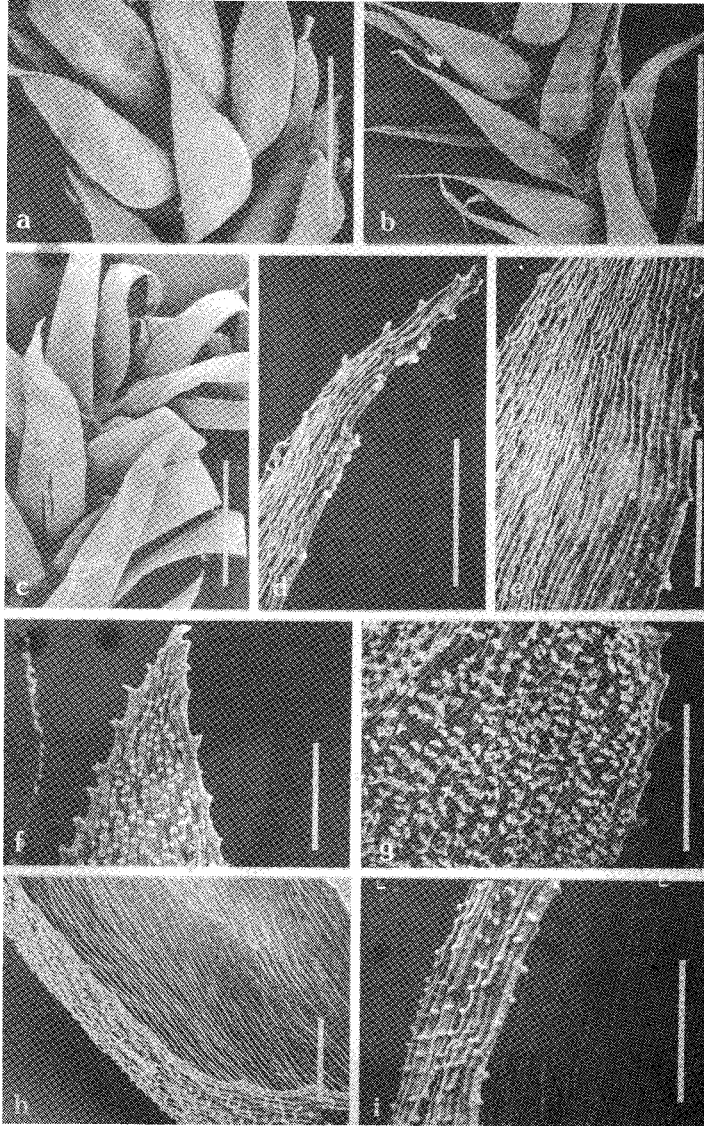


Fig. 4. Scanning electron micrographs of part of branches and various parts of leaves showing papillae. a, f-h. *T. instratum* (Brid.) Broth. in Ren. & Card. a. Part of a branch. f. Apical part of branch leaf. g. Upper margin of branch leaf. h. Basal part of branch leaf. b. *T. anandii* Broth. & Watts, part of a branch. c-e. *T. weneri* (Herz.) Broth. c. Part of a branch. d. Apical part of branch leaf. e. Upper part of branch leaf. i. *T. capillarisetum* (Dix.) Broth., upper part of branch leaf. Figs. a, f-h from *Damanhuri s.n.* (UKMB); b, from syntype of *T. anandii*, *Watts 17* (NSW); c-e, from *Damanhuri s.n.* (UKMB); i, from *Damanhuri s.n.* (UKMB). Scale bars: a-c=0.5mm; d-i = 50  $\mu$ m.

leaves are lanceolate, and not or only slightly concave, as in *T. wernerii*. Branch buds indicating the *Climacium*-type of development can easily be observed as tiny round structures on the younger portion of the stem, especially towards the shoot tip (Fig. 7 b).

Branch primordia in species of *Taxithelium* showing the *Bryum*-type of development are usually surrounded by several filamentous trichomes, as shown in figure 7 d. These trichomes can also be observed at the base of mature branches, as in *T. sematophylloides* (Fig. 7 c).

In general the larger species of *Taxithelium* tend to show *Climacium*-type branch development, e.g., *T. planum* and *T. merillii*, whereas smaller species such as *T. alare* and *T. kerianum* show the *Bryum*-type. The *Climacium*-type and *Bryum*-type of branch development in *Taxithelium* correspond respectively with type I-1-A and II-2 in the classification of Akiyama and Nishimura (1993).

**Rhizoids.** The rhizoids in most species are yellowish- to reddish-brown in colour and arise from the ventral side of the creeping stem, typically just below the points of insertion of the leaves. Two kinds of rhizoid have been observed. In the first, clusters of rhizoids are distributed irregularly along the stem, occurring principally where the stem is in contact with the substrate. These rhizoids vary in length within species dependent on the nature of the substrate, grow into the substrate, and branch only at the tip (Fig. 8 a-b). In the second, the rhizoids are profusely branched and the branches become aggregated into disc-shaped or star shaped units which tend to occur at more or less regular intervals along the stem. These rhizoidal discs adhere to the surface of the substrate (Fig. 8 c, d). The surface of both types of rhizoid is smooth (Fig. 8 e, f).

Rhizoid discs were observed only in *T. capillarisetum* and *T. wernerii*, both of which normally grow on the surface of angiosperm leaves. The remaining species grow on other types of substrate, and develop the first type of rhizoid.

**Operculum.** The operculum in most species of *Taxithelium* is conic with a short, blunt beak (Fig. 9 a), but *T. capillarisetum* and *T. planissimum* have long-rostrate opercula (Fig. 9 b). Before this study only the conic operculum was reported in *Taxithelium*, and this feature had been used to separate *Taxithelium* from related genera (Brotherus, 1925; Fleischer, 1923; Bartram, 1939; Manuel, 1981).

**Exothecial cells.** Exothecial cells in *Taxithelium* have generally been described as not, or slightly collenchymatous (Seki, 1968; Crum, 1994), and most species examined during the present study had exothecial cells of this type (Fig. 10 a, b). However, the two epiphyllous species, *T. capillarisetum* and *T. wernerii*, were found to have strongly collenchymatous exothecial cells with prominent trigones but otherwise thin walls (Fig. 10 c, d).

**Peristome.** The peristome in *Taxithelium* consists of two concentric series of 16 radially alternating teeth. The exostome teeth are inserted near the mouth of the capsule (Fig. 11 b, d, f). They are lance-subulate and usually gradually tapering as in *T. planum* (Fig. 11 a, b) but they are more abruptly tapered in *T. capillarisetum* (Fig. 11 d). The outer surface of the exostome teeth is distinctly papillose in the



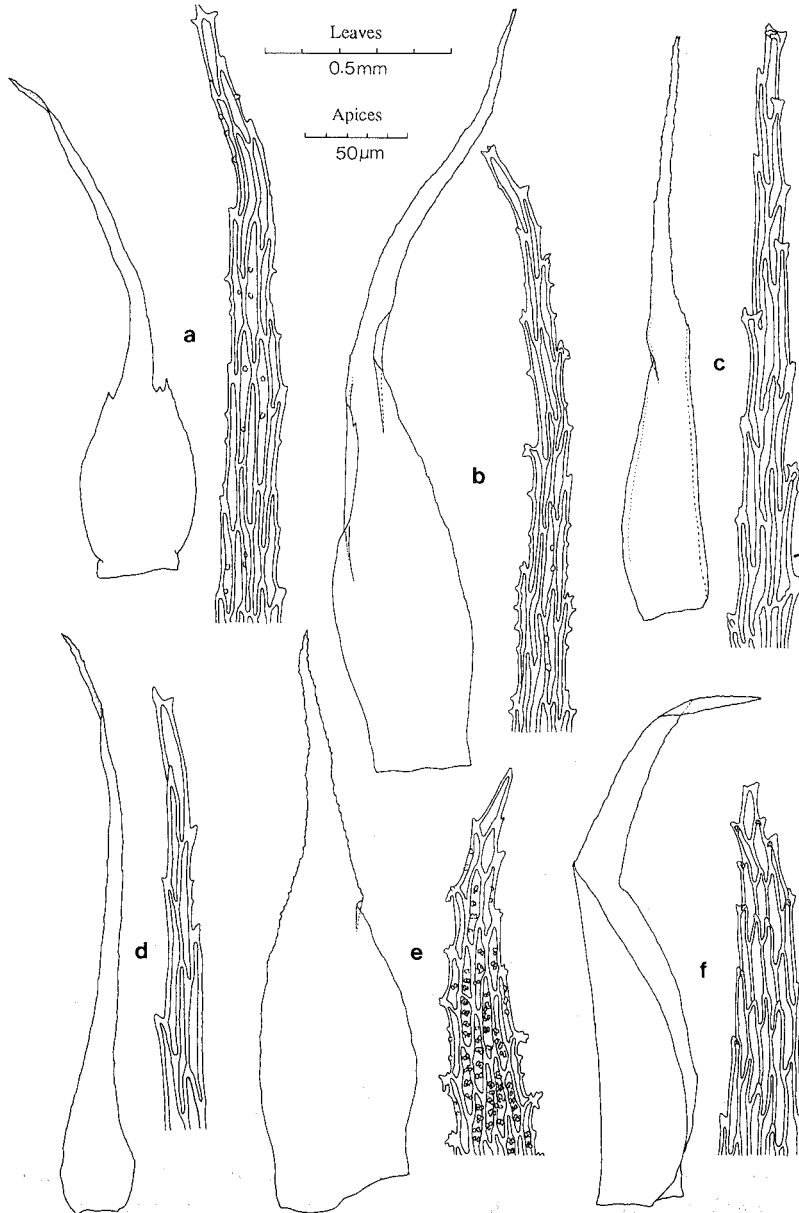


Fig. 5. Perichaetial leaves. a. *T. capillarisetum* (Dix.) Broth. b. *T. planissimum* Broth. c. *T. alare* Broth. d. *T. sematophylloides* Card. & Herz. ex A. Damanhuri. e. *T. nepalense* (Schwaegr.) Broth. f. *T. weneri* (Herz.) Broth. Fig. a was drawn from *Touw 19267* (L); b, from *Ridley 213* (H-BR) - as *T. perakense* Broth. in Dix. nom. nud. in synonym. c, from *McGregor 19919* (NY); d, from holotype of *T. sematophylloides* (JE); e, from *Touw 8346* (BM); f, from holotype of *T. weneri* (JE).

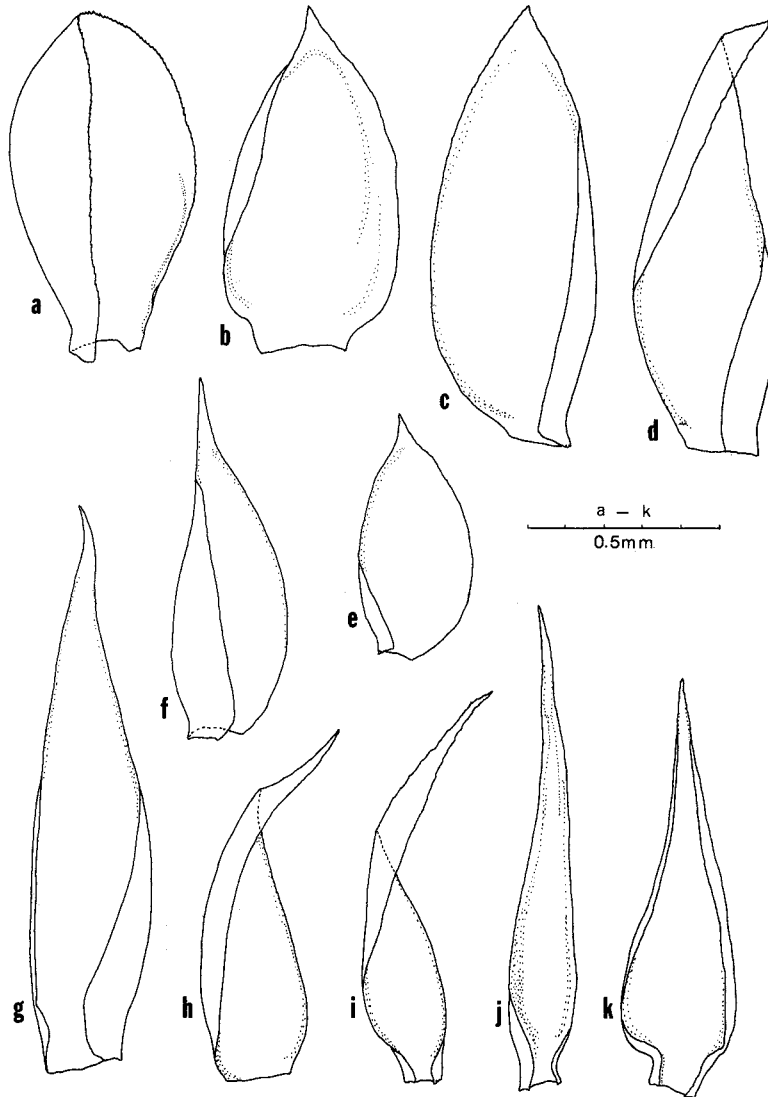


Fig. 6. Leaf morphology. a, b. *T. planum* (Brid.) Mitt. c. *T. merillii* Broth. d. *T. weneri* (Herz.) Broth. e. *T. archboldii* Bartr. f. *T. annandii* Broth. & Watts. g. *T. planissimum* Broth. h. *T. falcifolium* Bartr. i. *T. alare* Broth. j. *T. sematophylloides* Card. & Herz. ex Damanhuri. k. *T. capillarisetum* (Dix.) Broth. Fig. a was drawn from Churchill *et al.* 17646 (NY); b, from Small 5221 (NY); e, from isotype of *T. novae-guineae* Dix. (CANB); d, from holotype of *T. weneri* (JE); e, from holotype of *T. archboldii* (FH-BARTR); f, from syntype of *T. annandii*, Watts 17 (NSW); g, from holotype of *T. planissimum* (H-BR); h, from holotype of *T. falcifolium* (FH); i, from holotype of *T. alare* (H-BR); j, from holotype of *T. sematophylloides* (JE); k, from isoparatype of *T. convolutum* Dix., Richards 2563 (BM).

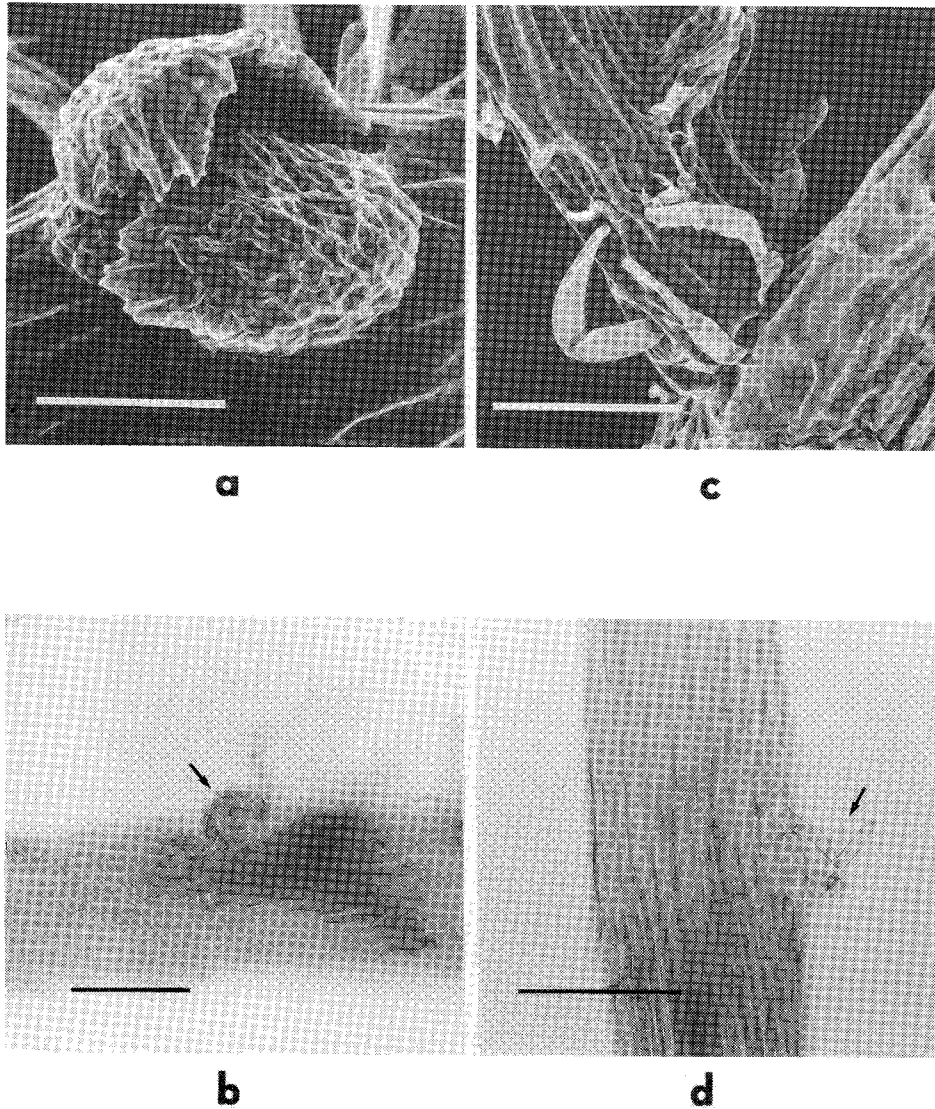


Fig. 7. Scanning electron micrographs and photomicrographs of branch bud and pseudoparaphyllia. a, b. *T. planum* (Brid.) Mitt. a. Arrangement of scaly leaves of a branch bud. b. Branch bud on stem (arrow indicates branch bud). c, d. *T. sematophylloides* Card. & Herz. ex Damanhuri. c. Filamentous pseudoparaphyllia at the base of a branch. d. Filamentous pseudoparaphyllia surrounding a branch primordium on the stem (arrow indicates the filamentous pseudoparaphyllia). Fig. a from *Small et al. 3683* (NY); b, from *Smith 5728* (NY); c, d, from holotype of *T. sematophylloides* (JE). Scale bars: a, c = 50  $\mu$ m; b, d = 100  $\mu$ m.

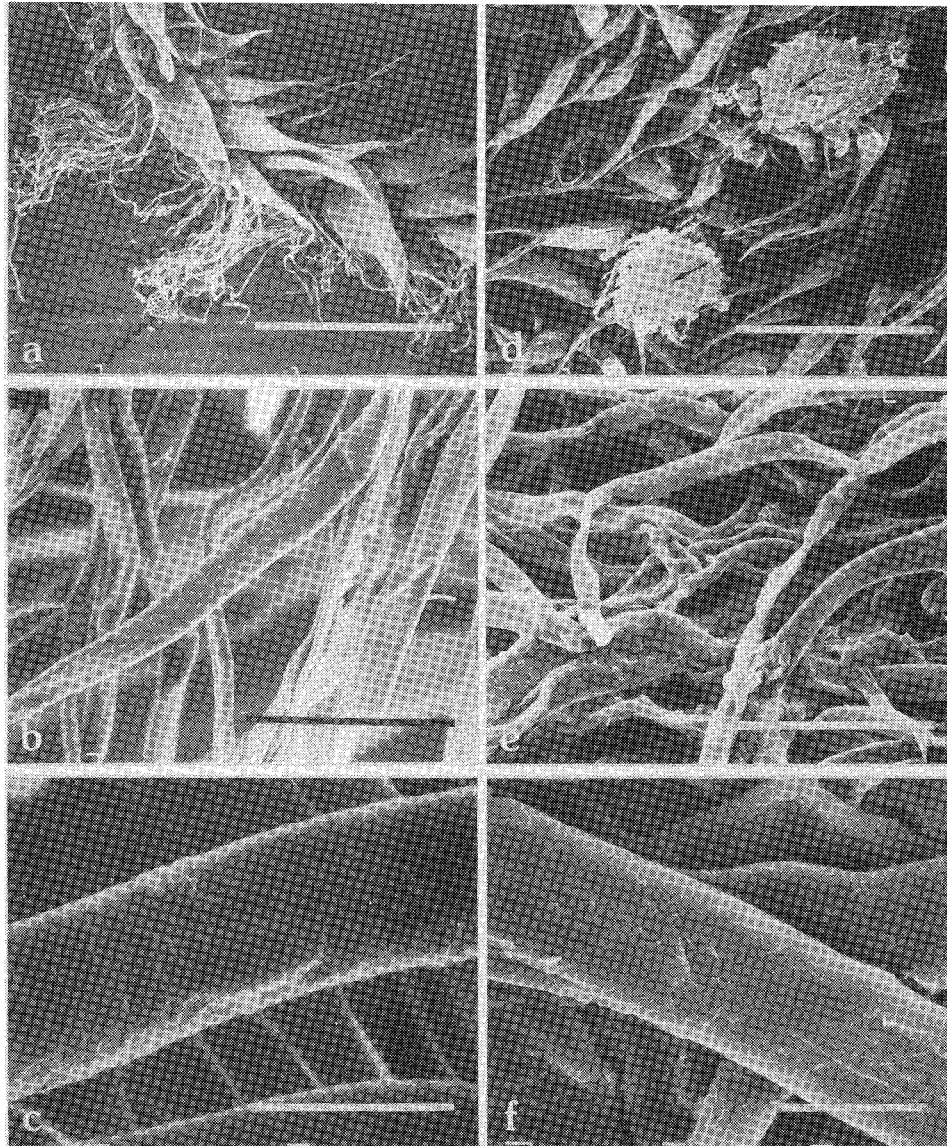


Fig. 8. Scanning electron micrographs of rhizoids. a-c. *T. instratum* (Brid.) Broth. in Ren. & Card. a. Distribution of rhizoids along the stem. b. Branched rhizoids growing towards the substratum. c. Detail of the surface of rhizoid. d-f. *T. capillarisetum* (Dix.) Broth. d. Disc-shaped rhizoid patches (arrow indicates detached cuticle layer of host leaf stuck to the lower surface of rhizoidal disc). e. Profusely branched rhizoids growing along the surface of the substratum. f. Detail of the surface of rhizoid. Figs. a-c from Damanhuri s.n. (UKMB); d-f from Damanhuri s.n. (UKMB). Scale bars: a, d = 1  $\mu\text{m}$ ; b, e = 50  $\mu\text{m}$ ; c, f = 10  $\mu\text{m}$ .

slender apical portion, and cross-striolate below with the cross-striolation plates densely papillose (Fig. 11 b, c, d). The inner surface of the exostome teeth is trabeculate, with the trabeculae in the apical parts of the teeth also distinctly papillose (Fig. 11 e, f, i).

The endostome has a high basal membrane, the segments are usually strongly keeled, and the inner surface of the endostome is papillose (Fig. 11 g, h). The cilia are appendiculate and occur singly or sometimes in pairs. They are brittle, easily broken in mature capsules, and are not shown in figure 11.

The peristome has proved to be rather uniform within the genus, but the abruptly tapering exostome teeth in *T. capillarisetum* are distinctive.

**Spores.** Spore diameter ranges from 12 - 22  $\mu\text{m}$  and the spore surface is finely papillose. The papillae are more widely spaced in *T. capillarisetum* (Fig. 12 b) than in most other species (Fig. 12 a). Otherwise, spore ornamentation appear to be of little taxonomic significance within *Taxithelium*, as is generally the case in pleurocarpous mosses.

**Calyptrae and vaginulae.** The calyptra is cucullate in all species so far examined. It is usually smooth (Fig. 13 a), except in *T. planissimum* where it is distinctly pilose (Fig. 13 c). Similarly, the vaginula in most species is naked or bears a few, short hairs (Fig. 13 b), but in *T. planissimum* the hairs are long and numerous (Fig. 13 d).

The hairs on the vaginula in *T. planissimum* are uniseriate, or often biseriate below (Fig. 13 e), and are composed of thick-walled cells. They clearly arise in the same manner as the hairs on the calyptra, and the same term should therefore be applied in each case. The vaginula may carry unfertilized archegonia on its surface (Fig. 13 b, d). Thus the vaginula, and possibly also the calyptra, arise in part from upward growth of the stem, and not entirely from the fertilized archegonium. In *T. planissimum* long paraphyses are present in the perichaetium before fertilization. It is not yet clear whether they persist on the vaginula and calyptra, in which case the term paraphyses should be applied, or whether the hairs on the calyptra and vaginula are new structures, developing after fertilization, in which case they should be called trichomes.

The presence of numerous long hairs on the vaginula and calyptra helps to distinguish *T. planissimum* from other members of the genus.

### PRELIMINARY CONCLUSIONS

The observations to date suggest that several species included within *Taxithelium* in *Index Muscorum* should be transferred to other genera, and that many other names should be reduced to synonymy. We anticipate that this will leave about 40 good species in *Taxithelium*. Examples of taxa to be transferred to other genera include:

*Taxithelium latitruncatum*

This species differs from species of *Taxithelium* in its truncate to emarginate leaf

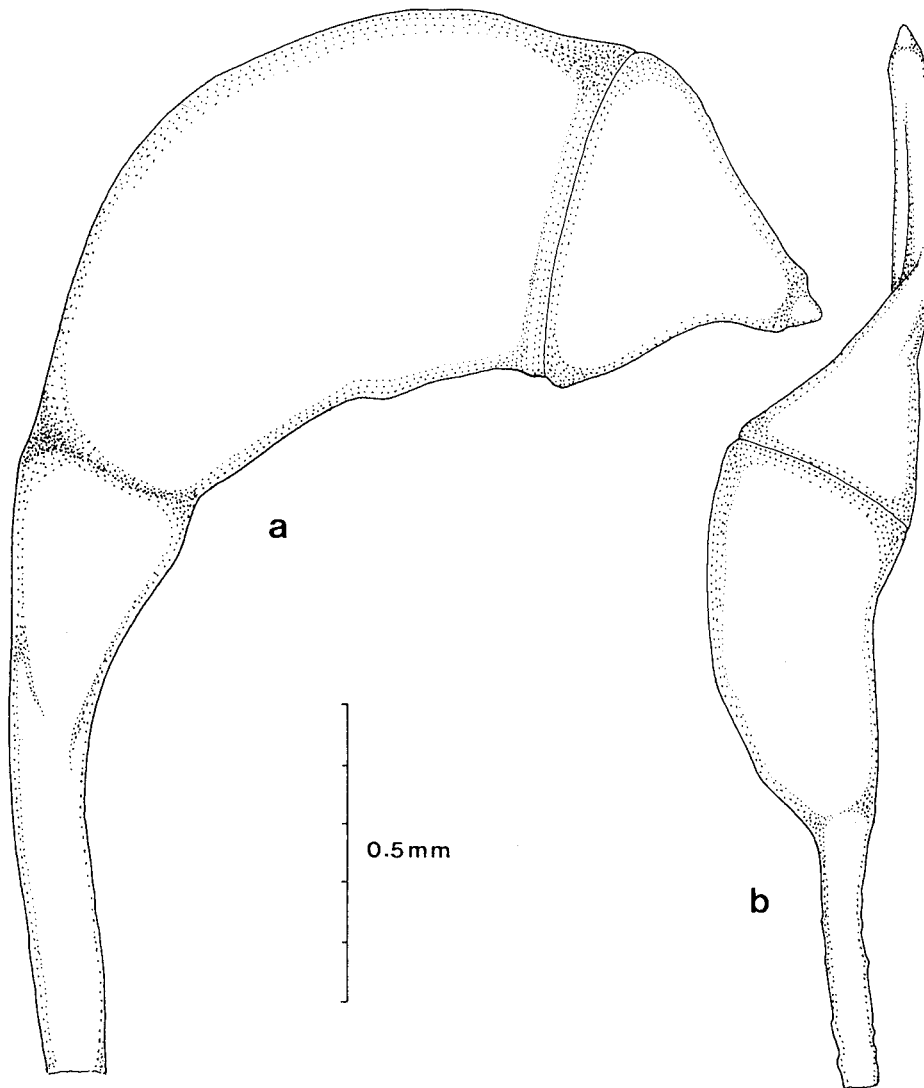


Fig. 9. Capsules. a. *T. instratum* (Brid.) Broth. in Ren. & Card., b. *T. capillarisetum* (Dix.) Broth. a, b. Capsule with operculum intact. Fig. a, from *Damanhuri s.n.* (UKMB); b, from *Damanhuri s.n.* (UKMB).

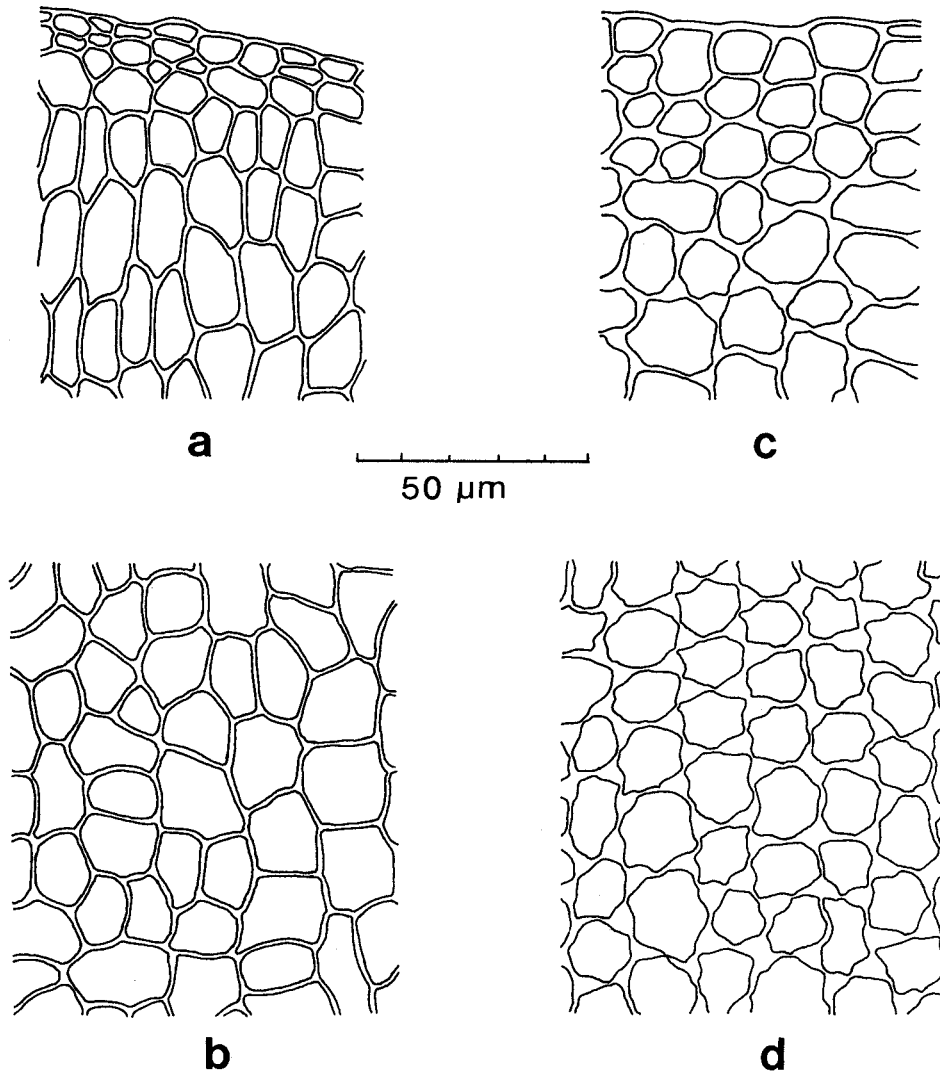


Fig. 10. Exothecial cells. a, b. *T. nepalense* (Schwaegr.) Broth. a. Cells below mouth of capsule. b. Cells in middle of capsule. c, d. *T. capillarisetum* (Dix.) Broth. c. Cells below mouth of capsule. d. Cells in middle of capsule. Figs. a, b were drawn from *Touw 8346* (BM); c, d, from isoparatype of *T. convolutum* Dix., *Richards 2563* (BM).

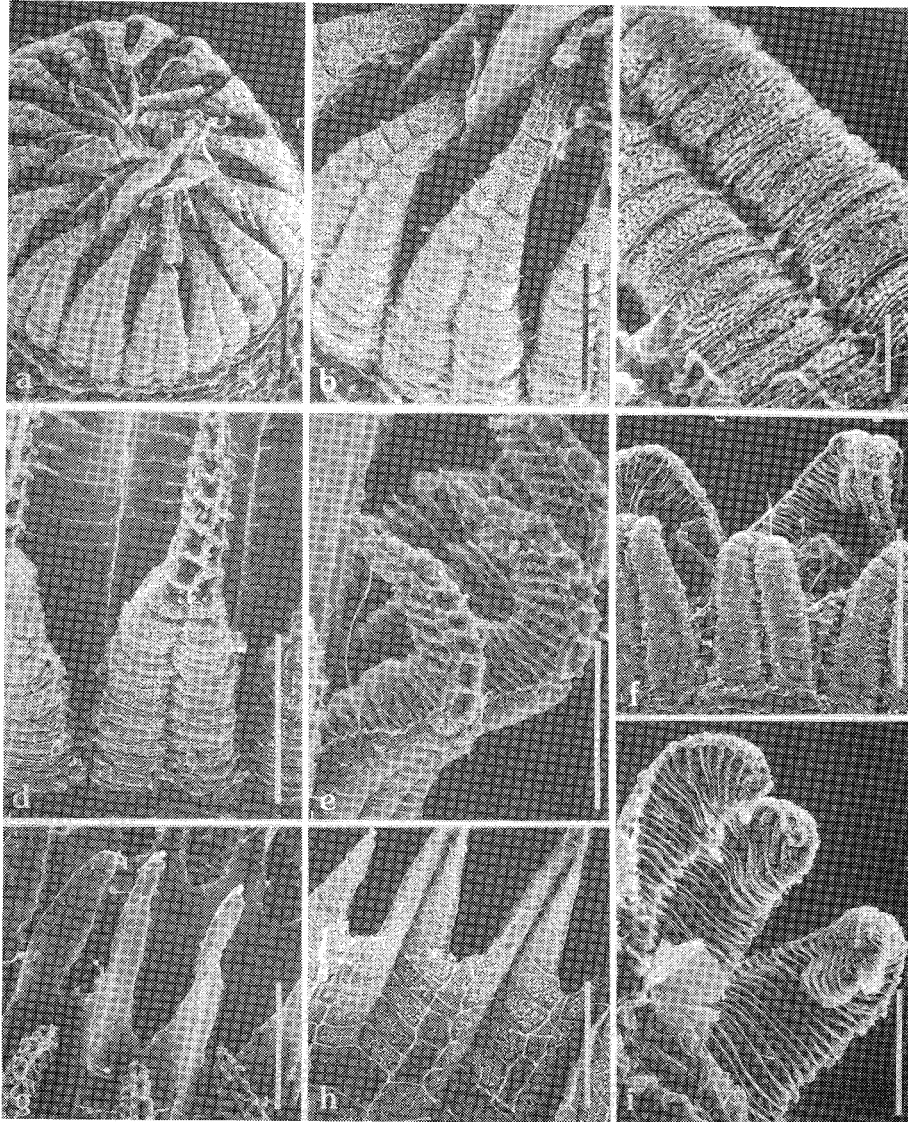


Fig. 11. Peristomes teeth. a-c. *T. instratum* (Brid.) Broth. in Ren. & Card. a. Arrangement of peristome teeth around capsule mouth. b. Exostome teeth. c. Detail of outer surface of exostome. d, e, g, h. *T. capillarisetum* (Dix.) Broth. d. Exostome teeth. e. Exostome teeth showing trabeculae on the inner surface. g. Endostome teeth. h. Endostome teeth showing high basal membrane and papillose inner surface. f, i. *T. wernerii* (Herz.) Broth. f. Exostome teeth. i. Exostome teeth showing trabeculae on the inner surface. Figs. a-c from *Damanhuri s. n.* (UKMB); d, e, g, h, from isoparatype of *T. convolutum* Dix., *Richards 2563* (BM); f, i, from *Damanhuri s.n.* (UKMB). Scale bars: a, f = 100  $\mu$ m; b-e, g-i = 50  $\mu$ m.



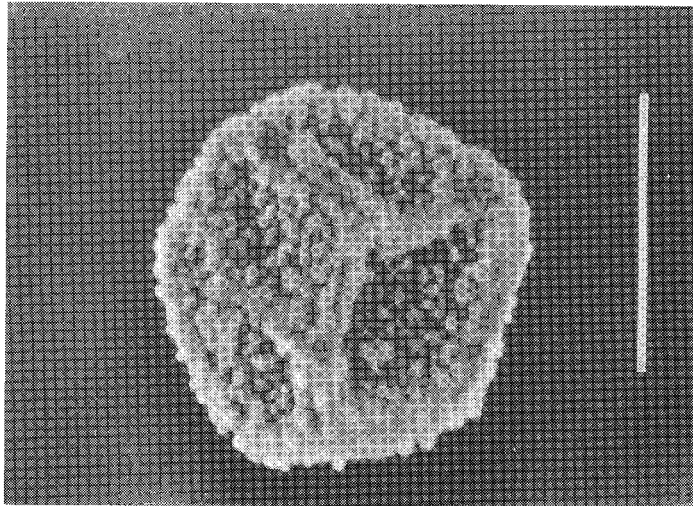
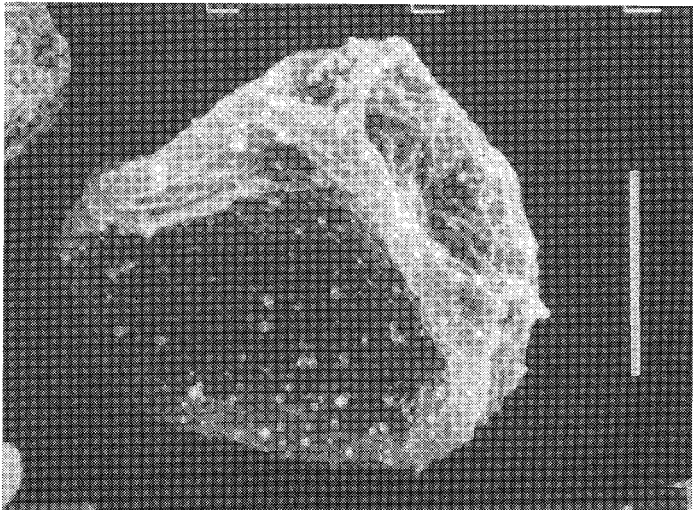
**a****b**

Fig. 12. Spores. a. *T. planum* (Brid.) Mitt. b. *T. capillarisetum* (Dix.) Broth. Fig. a from *Breen* 3244 (NY); b, from isoparatype of *T. convolutum* Dix., *Richards* 2563 (BM). Scale bars: a, b = 10  $\mu$ m.

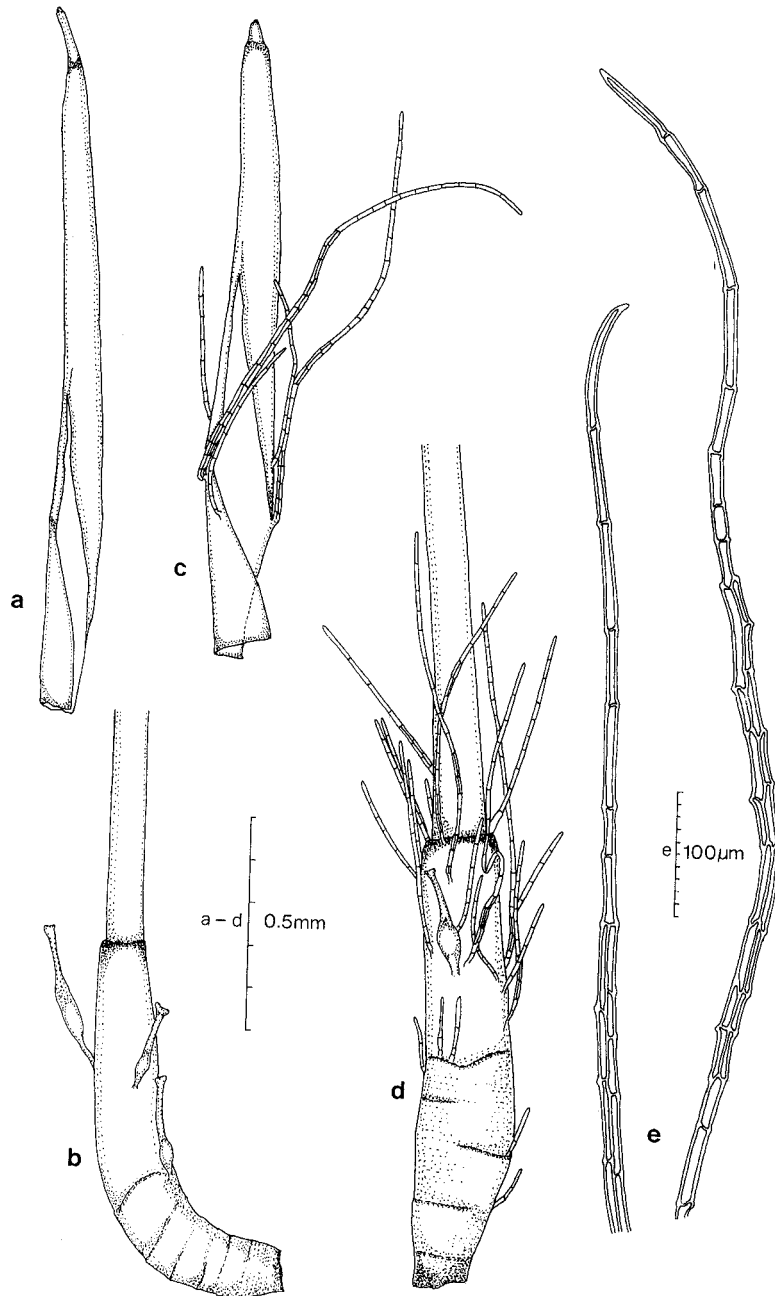


Fig. 13. Calyptrae and vaginulae. a, b. *T. capillarisetum* (Dix.) Broth. a. Calyptra. b. Vaginula. c-e. *T. planissimum* Broth. c. Calyptra. d. Vaginula. e. Paraphyses. Figs. a, b were drawn from *Damanhuri s.n.* (UKMB); c-e, from *Damanhuri s.n.* (UKMB).

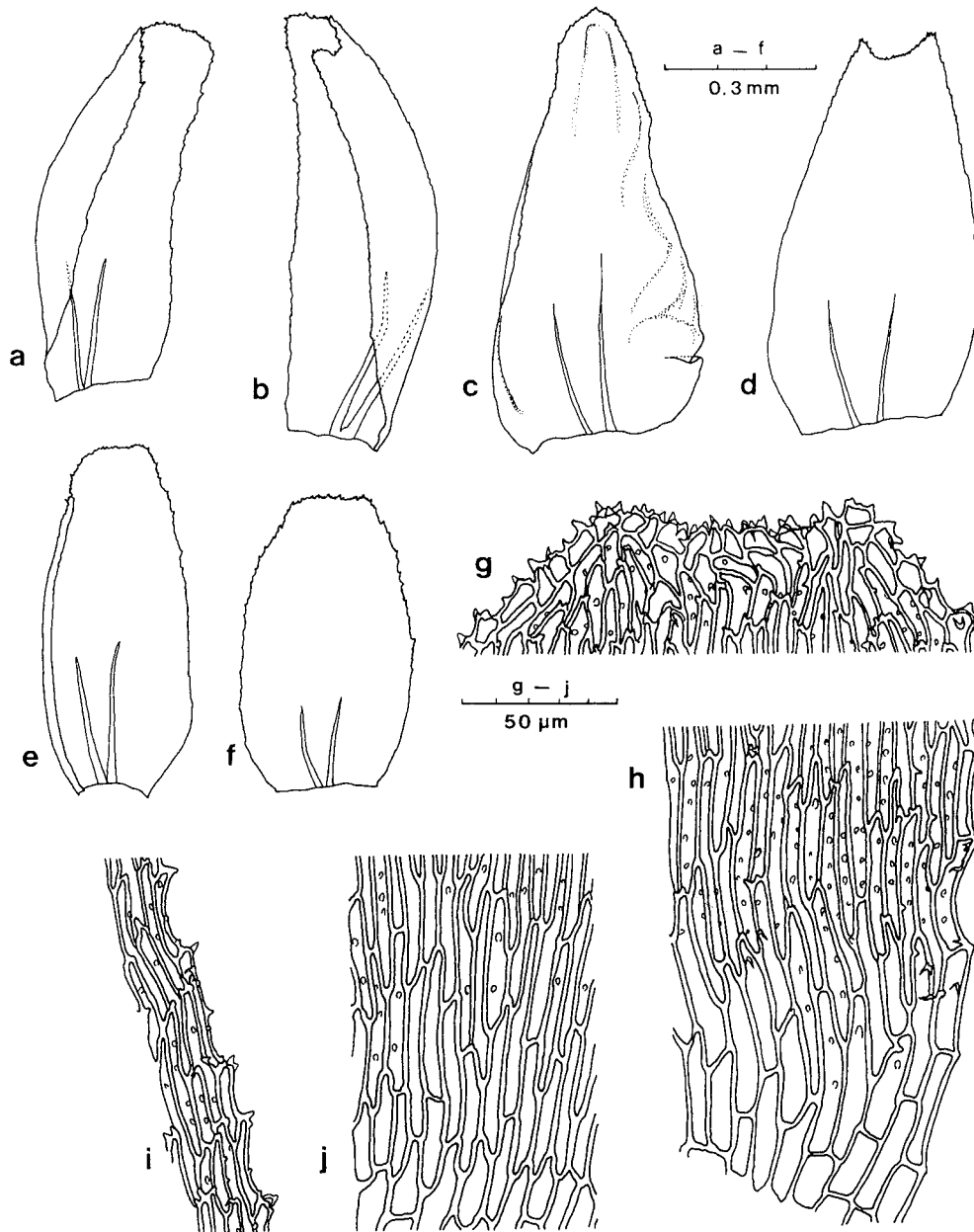


Fig. 14. *Taxithelium latitruncatum* Card. in Grand. a, b, e, f. Branch leaves; c, d. Stem leaves; g. Cells at apex of branch leaf; h. Cells at basal angle of branch leaf; i. Cells at upper margin of branch leaf; j. Cells in middle of leaf base. All were drawn from isotype of *Taxithelium latitruncatum* Card. in Grand. (PCCARDOT).

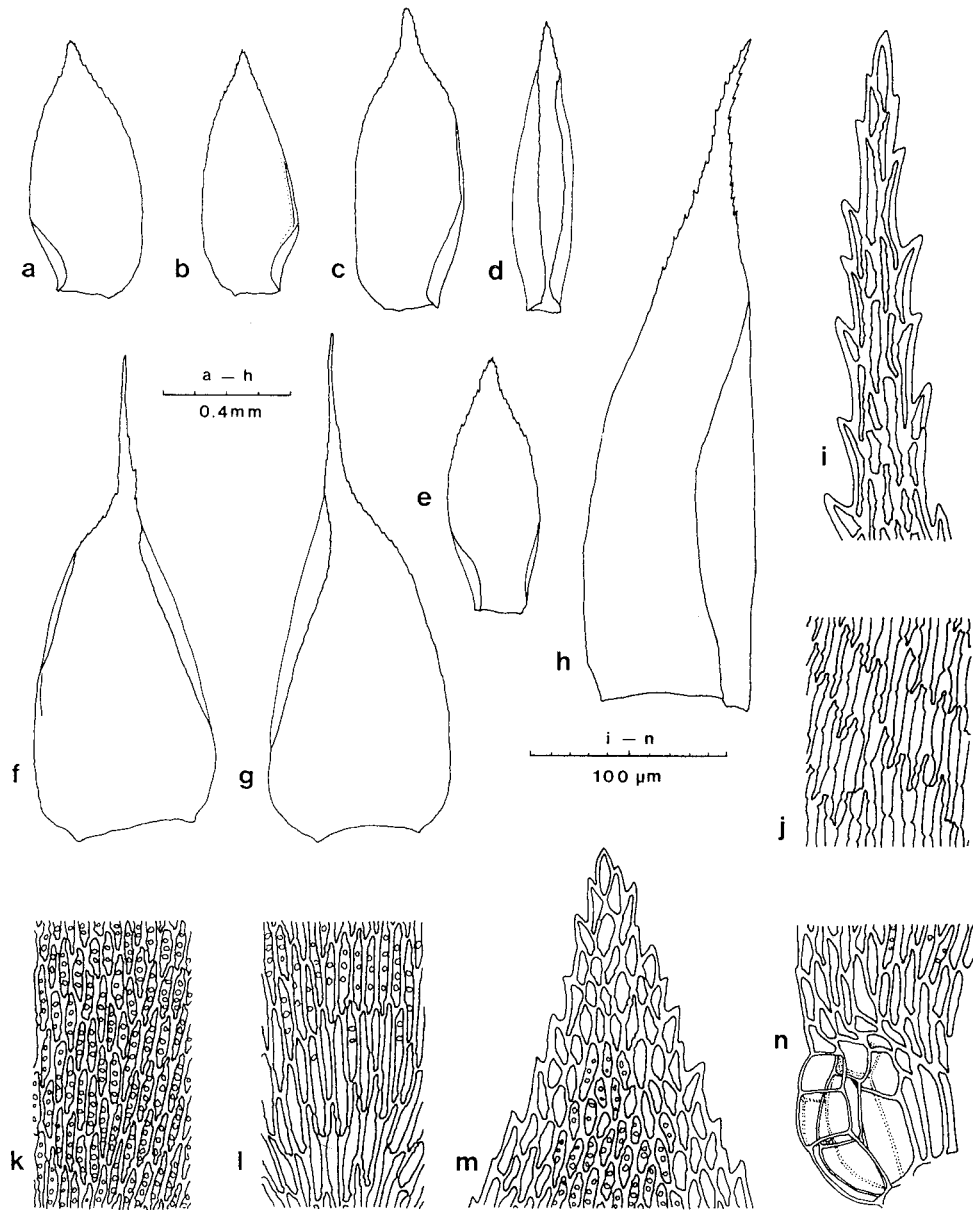


Fig. 15. *Taxithelium zuernianum* Par., *nom. nud.* a-e. Branch leaves; f, g. Stem leaves; h. Perichaetial leaf, i. Cells at apex of perichaetial leaf; j. Cells in middle of perichaetial leaf; k. Cells in middle of branch leaf; l. Cells in middle of leaf base; m. Cells at apex of branch leaf; n. Cells at basal angle of branch leaf. All were drawn from original material of *Taxithelium zuernianum* Par. (JE).

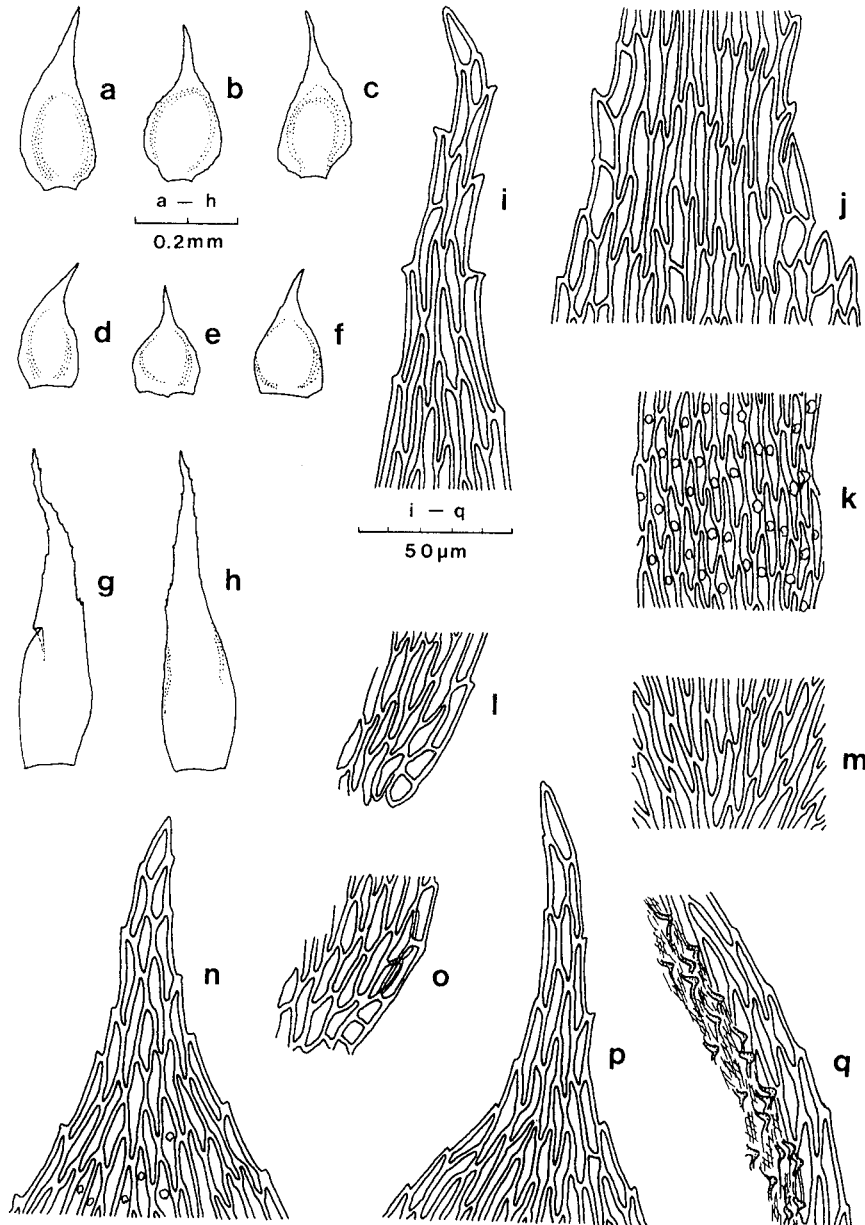


Fig. 16. *Taxithelium spurio-subtile* Broth. a-c. Branch leaves; d-f. Stem leaves; g, h. Perichaetial leaves; i. Cells at apex of perichaetial leaf; j. Cells in middle of perichaetial leaf; k. Cells in middle of branch leaf; l, o. Cells at basal angles of branch leaves; m. Cells in middle of leaf base; n, p. Cells at apices of branch leaves; q. Cells at margin of median part of branch leaf. All were drawn from holotype of *Taxithelium spurio-subtile* Broth. (H-BR).

apices, distinct double costa, more or less undifferentiated alar region, and the presence of papillae over the common wall of adjacent cells as well as over the lumen (Fig. 14). We anticipate transferring it to *Glossadelphus*.

*T. zuernianum*

This species resembles members of the genus *Wijkia* in the strongly dimorphous leaves, the leaf margin more strongly serrate towards the apex than in *Taxithelium*, the short, thick-walled laminal cells, the inflated, coloured alar cells, the perichaetial leaves strongly serrate towards the apex, and the thick-walled, porose, smooth cells of the perichaetial leaf (Fig. 15).

*T. spurio-subtile*

This species is characterized by the short, strongly concave, ovate-acuminate leaves, the short, linear rhomboidal laminal cells with a large single papilla over the cell lumen in median cells, the smooth surface of laminal cells towards the leaf margin, the more or less undifferentiated alar region, and the smooth laminal cells of the perichaetial leaf (Fig. 16). This combination of characters does not correspond to any genus in the Sematophyllaceae or Hypnaceae. Suggestions as to an appropriate treatment would be welcome.

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#### LITERATURE CITED

- AKIYARNA, H. 1990. A morphological study of branch development in mosses with special reference to pseudoparaphyllia. *Bot. Mag. (Tokyo)* 103: 269-282.
- AKIYAMA, H. AND N. NISHIMURA. 1993. Further studies on branch buds in mosses; "pseudoparaphyllia" and "scaly leaves". *J. Pl. Res.* 106: 101-108.
- BARTRAM, E.B. 1939. Mosses of the Philippines. *Philipp. J. Sci.* 68: 1-437.
- BROTHERUS, V.F. 1909. *Taxithelium*. In: A. Engler and K. Prantl (eds.), *Die natürlichen Pflanzenfamilien* 1. Vol. 3: Engelman, Leipzig, pp. 1089-1093.
- BROTHERUS, V.F. 1925. *Taxithelium*. In: A. Engler and K. Prantl (eds.), *Die natürlichen Pflanzenfamilien*, ed. 2, Vol. 2, Engelman, Leipzig, pp. 441-443.
- BUCK, W.R. 1985. A review of *Taxithelium* (Sematophyllaceae) in Brazil. *Acta Amazon.*, Supl. 15(1-2): 43-53.
- CROSBY, M.R., R.E. MAGILL AND C.R. BAUER. 1992. Index of mosses 1963-1989. *Monogr. Syst. Bot. Missouri Bot. Gard.* 42: 1-646.
- CRUM, H. 1994. *Taxithelium* Spruce ex Mitt. In: A.J. Sharp, H. Crum and P.M. Eckel (eds.), *Moss flora of Mexico. Mem. New York Bot. Gard.* 69: 1005-1007.

- CRUM, H.A. AND L.E. ANDERSON. 1981. *Mosses of eastern North America*. 2. Columbia Univ. Press, New York. pp. 665-1328.
- FLEISCHER, M. 1923. *Taxithelium*. In: *Die Musci der Flora von Buitenzorg* 4. E. J. Brill, Leiden, 1335-1351 pp.
- GANGULEE, H.C. 1980. *Mosses of Eastern India and adjacent regions*. 3. Fasc. 7-8: Hypnobryales. Calcutta. pp. 1753-2145.
- MANUEL, M.G. 1981. A generic moss flora of Peninsular Malaysia and Singapore. *Fed. Mus. J., N. S.* 26(2): i-vi + I-163.
- NORRIS, D.H. AND T. KOPONEN. 1985. Bryophytes from Frieda River, East and West Sepik Provinces, Papua New Guinea. 1. Musci. *Ann. Bot. Fenn.* 22: 367-396.
- SAINSBURY, G.O.K. 1955. A handbook of New Zealand mosses. *Bull. Roy. Soc. New Zealand* 5: 1-490.
- SEKI, T. 1968. A revision of the family Sematophyllaceae of Japan with special reference to a statistical demarcation of the family. *J. Sci. Hiroshima Univ., Ser. B, Div. 2, Bot.* 12: 1-80.
- WIJK, R. VAN DER., W.D. MARGADANT AND P.A. FLORSCHÜTZ. 1969. *Taxithelium*. In: *Index Muscorum*, Vol. 5 (T-Z, addenda). *Regnum Veg.* 65: 6-13.