TAXITHELIUM

Helen P. Ramsay

Taxithelium Spruce ex Mitt., J. Linn. Soc., Bot. 12: 21, 496 (1869); from the Greek taxis (from tasso, to arrange) and thele (a teat or nipple), in reference to the rows of papillae over the lumina of laminal cells.

Lecto: T. planum (Brid.) Mitt.

Autoicous or dioicous. Plants small to medium-sized, dull yellow-green to brownish green, forming thin or dense and often extensive mats. Main stems long, creeping, ±regularly pinnate, lacking a central strand (T.S.). Ultimate branches short, usually complanate-foliolate, occasionally with lateral rows of leaves spreading and asymmetrical; dorsal and ventral rows slightly smaller and more appressed, contracted at the clasping base. Pseudoparaphyllia foliose, rarely filamentous. Rhizoids smooth. Branch leaves narrowly to broadly ovate or ovate-lanceolate, similar when dry, ecostate or with a short double costa; apex blunt, acute or acuminate; apical cell smooth, coronate-papillose in a few species; margin erect, occasionally serrulate towards the apex; marginal teeth usually binate. Laminal cells linear-rhomboidal, faintly or strongly seriate-papillose in a single row of no more than 7 over the lumina; alar region usually differentiated; basal cells occasionally inflated, hyaline or coloured; supra-alar cells few to many, subquadrate in 1 or 2 rows, occasionally extending up the margin. Gemmae usually absent, rarely filamentous.

Perichaetial leaves are a good diagnostic character for distinguishing species (Câmara, 2011a, b). Taxithelium can be readily distinguished from other genera with seriately papillose laminal cells such as Rudulina (Sematophyllaceae) which is non-complanate, has divergent or falcate-secund leaves and a long rostrate operculum, and Wijkia extenuata (Pylaisiadelphaceae) which, when papillose, has the papillae over the cell lumen and walls (Ramsay et al., 2002a). The marginal teeth in Wijkia extenuata appear doubled (binate) because the distal end of one cell and the proximal end of an adjacent cell contribute to each tooth. Furthermore, marginal cells in Wijkia extenuata can also be papillose, giving the impression of additional marginal serrations.

More than 200 species of Taxithelium have been described, and the sections of the genus recognised previously, for example by Renaud & Cardot (1901), Fleischer (1923) and Norris & Koponen (1985) have been superseded by recent morphological and molecular studies (Câmara, 2011a, b). Numerous names have been reduced to synonymy, and some species have been transferred to other genera. Unpublished molecular studies by Câmara & Shaw

1 cl- National Herbarium of New South Wales, Mrs Macquaries Road, Sydney, New South Wales 2000.

(see Câmara, 2011b) demonstrate that Taxithelium is monophyletic and consists of two clades. Pluripapillose cells are synapomorph for the genus, even though some taxa have only vestigial papillae or appear to have lost them completely. Thus, in apparently smooth cells, Câmara & Kellogg (2010) found that undeveloped papillae can be seen, but only under the SEM. The worldwide revision provided by Câmara (2011a, b) has reduced the number of accepted species to 19 and identified two subgenera of Taxithelium, as follows:

Plants complanate with ovate acute leaves, foliose pseudoparaphyllia and ‘baggy’ papillae . subg. Taxithelium
8 species; T. instratum, T. leptosigmatum, T. kerianum, T. nepalense in Australia

Plants with spreading lanceolate acuminate leaves, filamentous pseudoparaphyllia and conical papillae .........

As regards the Australian taxa, the new subgeneric classification differs from the interpretation of Ramsay et al. (2002) who placed T. muscicola close to T. kerianum. Câmara (2011a) separates T. muscicola from other species of subg. Vernieri by the non-collenchymatous exothecial cells, linear-lanceolate leaves and perichaetial leaves that are not serrulate at the apex.

The pantropical Taxithelium occurs in North, Central and South America, Africa and Asia, especially Indo-Malesia, with some species extending into northern Australia and New Caledonia. Most are corticolous on tree trunks and branches, while others can be found on rotting logs and, occasionally, on rock, including limestone. Five species are known from Australia, one of which, T. muscicola, is apparently endemic (Ramsay et al., 2002; Câmara, 2011a). Most Australian species, are confined to coastal monsoon forests in the Northern Territory and/or closed forests in north-eastern Queensland. However, T. leptosigmatum occurs on lowland silty sediment and in mangrove communities bathed by brackish water at least during extreme high tides.

References


Hedenäs, L. (1996), A cladistic evaluation of the relationships of the Hookeriales, the Sematophyllaceae and some other taxa, Lindbergia 21: 49–82.


Rosario, R.M. del (1979), *Moss Flora of the National Botanic Garden, Philippines* 1–133.


Rosario, R.M. del (1979), *Moss Flora of the National Botanic Garden, Philippines* 1–133.


**Key**

1. Leaves lanceolate to narrowly lanceolate, with acuminate apices; margin entire; perichaetial leaves acuminate, with the apical cell coronate-papillose .............................................. 4. *T. muscicola*

1'. Leaves ovate or ovate-lanceolate, with acute apices, only occasionally short-acuminate; margin serrulate; perichaetial leaves acuminate, with the cell usually smooth ................................. 2

2. Laminal cells only faintly seriately papillose to smooth, short, c. 4–5:1; plants growing on mangrove roots ........................................................................................................ 3. *T. leptosigmatum*

2'. Laminal cells strongly seriately papillose, short or long; growing on stems and logs in rainforest and monsoon forest, rarely on rock ........................................................................ 3

3. Leaves ovate-lanceolate, gradually narrowing to a short acumens; mid-laminal cells short, c. 5–6:1; perichaetial leaves lanceolate, abruptly narrowing to long narrow subulate apex ............. 2. *T. kerianum*

3'. Leaves ovate; apices acute; mid-laminal cells c. 10:1; leaf margins entire to minutely crenulate or serrulate near the apex; perichaetial leaves lanceolate, gradually narrowing to the apex ....................... 4

4. Leaf margins sharply serrate towards the apex, serrulate towards the base; basal alar cells usually 2, slightly enlarged and pigmented; supra-alar cells in a small triangular group .......... 1. *T. instratum*

4'. Leaf margins entire to serrulate at the apex, smooth below; basal alar cells 3 or 4, scarcely enlarged and thick-walled, yellowish or hyaline; supra-alar cells numerous ........................................... 5. *T. nepalense*


Illustrations: E.B.Bartram, *Philipp. J. Sci.* 68: 345, pl. 26, fig. 443 (1939); R.M. del Rosario, *op. cit.* 106, fig. 81; A.Damanhuri & R.Longton, *op. cit.* 41, fig. 4a, f–h; 46, fig. 8a–c; 48, fig. 9a; 50, fig. 11a–c; H.P.Ramsay, W.B.Schofield & B.C.Tan, *op. cit.* 586, fig. 1; P.E.A.S.Câmara, *op. cit.* 825, fig. 2B (2011b).

Autoicous. Plants slender, dull yellowish green, forming dense flat mats. Stems elongate, creeping, regularly and sparsely pinate; branches short, widely spreading, to 3 mm long, complanately foliate. Stem and branch leaves ovate from a contracted clasping base, concave, acute to short acuminate, c. 1 mm long and 0.4 mm wide; margins erect, sharply serrate above, serrulate to the base. Upper laminal cells short-rhomboïd, c. 25–35 × c. 5–6 μm; median laminal cells narrowly linear, thin-walled, 40–80 × c. 3 μm, strongly seriate-papillose, the papillae irregularly shaped; alar region, small; enlarged basal alar cells usually 2, occasionally 3, oval, slightly inflated, often yellowish; supra-alar cells irregularly quadrate, forming a small triangular group.
Perichaeta on stems; perichaetial leaves lanceolate, acumenate with papillose cells; upper margin serrate; laminar cells shorter and less papillose than those of other leaves. Seta slender, 12–18 mm long, smooth. Capsules small, erect c. 1 mm long and 0.3 mm wide; exothelial cells subquadrate to rectangular, non-collenchymatous, the longitudinal walls thickened. Peristome with exostome teeth and endostome segments of similar length; ciliolum 1, as long as the segments; operculum to 0.4 mm long. Spores small, 10–15 μm diam.

Occurs on the bark of trees and on decayed wood in Sri Lanka, Malesia, Papua New Guinea, the Solomon Islands and China. In Australia, rare in northern N.T. and common in north-eastern Qld.

N.T.: ‘Black Jungle’, 10 km E of Humpty Doo, J. Russell Smith 139 (DNA, CANB). Qld: Stoney Cr, Cardwell, J.G.Stone 18743, 14891 (MEL); Seaview Ra., J.G.Stone 16813, 21294 (MEL); Gordon Cr, SW of Cape Weymouth, H.Streimann 56598, 56539 (CANB); Tozers Gap, Iron Range Natl Park, H.Streimann 56412, 56421 (CANB); Sullivans Track, W.B.Schofield 90393 (NSW); Cape Tribulation beach, W.B.Schofield 79951 (NSW).

Taxithelium instratum is characterised by its closely and regularly complanate appearance, with short, dull yellowish green branches, ovate leaves with strongly serratulate, acute to acumenate apices, and conspicuous alar cells, usually paired and zinflated. The laminar cells are strongly seriately papillate, with irregularly shaped papillae.

2. Taxithelium kerianum (Broth.) Broth., Nat. Pflanzenfam. I, 3: 1091 (1908)


Illustrations: E.B.Bartram, Philipp. J. Sci. 68: pl. 26, fig. 452 (1939); R.M. del Rosario, op. cit. 107, fig. 82; H.C.Gangulee, Mosses of Eastern India and Adjacent Regions 3: 1922, fig. 984 (1980); A.Noguchi, Illustrated Moss Fl. Japan 5: 1088, fig. 479c (1994); H.P.Ramsay, W.B.Schofield & B.C.Tan, op. cit. 588, fig. 4; P.E.A.S Câmara, op. cit. 825, fig. 2A; 826, fig. 6 (2011b).

Autoicous. Plants small, usually dull, pale golden yellow, forming dense feathery mats. Main stems elongate, to 20–30 mm long, creeping, sparsely pinnate; branches 1–3 mm long, spreading, loosely complanate-foliolate. Stem and branch leaves erect-patent to spreading horizontally, more appressed when dry, ovate-lanceolate, gradually narrowing to the acumen, concave, 0.8–1.0 mm long, 0.2–0.3 mm wide, ecostate or with a short double costa; margin usually involute, entire; apical cell short, usually coronate-papillate, with 1–3 papillae, occasionally smooth. Laminal cells spindle-shaped, 48–90 × 3–6 μm, distinctly seriately-papillate, with 3–5 simple papillae along the cell lumen (except at the extreme tip and lower margins); basal alar cells few and small, occasionally slightly enlarged at the corners, hyaline; supra-alar cells quadrate, in 2 or 3 rows.

Perichaetia on main stems; perichaetial leaves filiform-acuminate, subentire; apical cell elongate [L:W c. 4:1], coronate-papillate; margin smooth. Calyptra cucullate, smooth. Seta slender, erect, 5–10 mm long, slightly rugulose distally. Capsules small, c. 0.8–1.5 mm long, suberect-inclined and cernuate-ovate; exothelial cells rectangular. Peristome with endostome segments slightly shorter than the exostome teeth. Spores 15–20 μm diam.

Rather rare in tropical N.T., also in north-eastern Qld; usually on twiggy branches or small logs in closed riverine forest. Also in India, Thailand, Cambodia, Vietnam, Malaysia, the Philippines, Papua New Guinea and Fiji.

N.T.: Berry Springs, 30 km S of Darwin, H.Streimann 8833 (CANB). Qld: near Majors Falls, Ravenshoe, W.W.Watts Q597 (NSW); Lower Tully, Sept. 1937, E.Henry (BM, CANB); The Boulders, Babinda, W.B.Schofield 90149, J.G.Stone & M.I.Schofield (NSW); Davies Cr, P.I.Forster 3913 (BRI); Butcher Creek School, road to Mt Bartle Frere, P.I.Forster 4562 (BRI); Cape Tribulation, H.Streimann 45764 (CANB, NY).

Taxithelium kerianum is characterised by the densely pinnate stems with short and somewhat complanate branches and comparatively small leaves with a short-acuminate apex, a coronate-papillate apical cell, elongate multipapillose laminar cells and scarcely inflated alar cells. According to Renauld & Cardot (1901), the coronate-papillate apical cell was diagnostic for their sect. Aptera, and while Ramsay et al. (2002) noted its occurrence in two


Autoicous. Plants forming dense robust dull brownish green mats. Stems creeping, closely pinnate; branches 1–5 mm long, complanately foliate. Stem and branch leaves slightly differentiated; stem leaves larger and longer, erect-spreading, oblong-lanceolate, concave, obtuse or broadly acute, 0.8–1.0 mm long, 0.3–0.4 mm wide; margin erose, serrulate near the apex. Laminal cells linear, 24–40 × 3–4 μm, minutely seriate-papillose; alar region somewhat differentiated, small, with a single row of non-inflated cells at the base and a triangular group of a few supra-alar cells.

Perichaetia on stems; perichaetal leaves smaller than vegetative leaves, oblong-linear, short-acute-margined; margins entire. Calyptra narrowly conical–concave. Seta to 17 mm long, smooth. Capsules erect, ovoid, slightly asymmetrical c. 1.2 mm long and 0.5 mm wide; exothecal cells reddish gold, subquadrate, not or only slightly thickened at the corners; stomata small; operculum conical-short-rostrate, with a curved beak. Peristome well developed; exostome teeth papillose, with lamellae on the inner surface and hyaline apices; endostome segments with a high basal membrane, only slightly papillose; cilia not seen. Spores 12–30 μm diam.

Known from a few localities in north-eastern Qld; also in Malesia (including Papua New Guinea), SE Asia and the Philippines. Occurs on brackish soil and mud among mangrove roots in a zone covered at least at very high tides.

Qld: Mosquito Hill, Tully, J. Galeano & I. G. Stone 21370 (MEL, AD); Noah Head, Cape Tribulation Natl Park, H. Streimann 4577 (CANB). Mulligans Ck, Mulligans Bay, SE Hinchinbrook Is., June 1999, A. Cairns s.n. (JCU); Russell River landing, June 2000, A. Cairns s.n. (JCU).

Originally considered to ne endemic to the Philippines (Bartram, 1939) as *T. merrillii*, this species is now known from other parts of SE Asia (Tan & Iwatsuki, 1993; Câmara 2011b) as well as north-eastern Australia (Stone, 1982; Ramsay et al., 2002). Câmara (2011b) placed *T. merrillii* into synonymy with *T. leptosigmatum*.


Illustrations: B.C. Tan, H. P. Ramsay & W. B. Schofield, *op. cit.* 325, fig. 2; H. P. Ramsay, W. B. Schofield & B. C. Tan, *op. cit.* 592, fig. 6, as *T. merrillii*; P.E.A.S. Câmara, *op. cit.* 15, fig. 7A, D, F, I (2011a).

Dicoccous. Plants scarcely branched, irregularly pinnate, dull, forming flat pale yellowish green complanate mats. Stems 2–5 cm long. Stem leaves narrowly lanceolate, 1–2 mm long, concave, slightly falcate-cuspidate; mid-laminal cells linear, 30–60 × 2–4 μm; basal alar cells several, thin-walled and slightly inflated. Pseudoparaphyllia absent or sparse, filamentous and curved. Branches erect, 1–3 mm long; branch leaves complanate, narrowly lanceolate, gradually long-acuminate, falcate, 0.8–1.0 mm long (including the apex); apex slightly twisted when dry; margin serrulate above, entire below; apical cell coronate-papillose; laminal cells of branch leaves linear, thick-walled, weakly and seriately papillose over the lumina; alar region multi-tiered, basal alars a row of 3 or 4 small vesiculose or rectangular thick-walled hyaline or yellowish cells; supra-alaras 2–5, forming a quadrato to triangular group.
Perichaeta on main stems; inner perichaetal leaves ovate, long-acuminate, with a serrulate acumen. Seta long-exserted, 10–25 mm long, orange-red, straight, smooth. Capsules narrowly ovate c. 1 mm long and 0.5 mm wide, with a slightly mammillose base; exothecial cells thickened longitudinally; operculum curved-roststrate from a conical base. Peristome with strongly papillose exostome teeth; endostome segments narrow, papillose; basal membrane low, a quarter the length of the teeth; cilium 1, narrow, nodulose. Spores 12–18 µm diam.

Known from Lord Howe Island in the south-western Pacific Ocean and from the Atherton and Windsor Tablelands in north-eastern Qld. Grows on bark and over other mosses.

Qld: National Forest Reserve No. 198, Atherton, B. de Winter 985 (NSW); Windsor Tableland, I.G. Stone 16049b (MEL).

*Taxithelium muscicola* is very similar to *T. damanhurianum* P.S. Câmara from Malesia (Câmara, 2011a), differing in its larger size, smaller and narrower leaves, and smaller spores. Well-developed alar cells and narrowly lanceolate leaves with entire margins are a distinctive combination for *T. muscicola*.

5. *Taxithelium nepalense* (Schwägr.) Broth., *Monsunia* 1: 51 (1900)


Autoicous. Plants robust, dull yellowish green, forming dense flat mats. Stems to 2 cm long; branches slightly complanate to almost terete, 2–3 mm long. Stem and branch leaves similar, tightly imbricate, broadly ovate, deeply concave, 0.8–1.2 mm long, 0.2–0.5 mm wide; apex serrulate, obtuse or bluntly acute; margins minutely crenulate above, entire below. Median laminal cells narrowly rhomboidal, thin-walled, 40–80 × 4 µm, strongly seriate-papillose; the apical cells papillose; alar cells small, oval, scarcely inflated, with a row of 3 or 4 yellowish or hyaline rectangular cells across the base; supra-alar numerous, irregularly quadrate, extending obliquely a few cells up the margin.

Perichaetia on stems between branches; inner perichaetal leaves lanceolate, long-acuminate; laminal cells strongly seriatly papillose; margins smooth above, serrulate to the base. Seta 10–20 mm long, smooth. Capsules inclined, strongly constricted under the mouth when dry; urn ovoid, 1.0–1.4 mm long. Peristome well developed; exostome teeth papillose, with short lamellae; endostome segments narrow, papillose; basal membrane low; cilia not seen. Spores 15–20 µm diam.

This widespread Palaeotropical species is known from Africa, Madagascar, India, Sri Lanka, Bangladesh, Malesia, SE Asia, China, New Zealand and tropical Australia. Occurs in northern N.T., where it is it is common on decaying logs, the bases and roots of large trees and on rock faces in lowland monsoon rainforest, riparian rainforest or regrowth forest on river flats; also in north-eastern Qld.


nepalense in synonymy with T. planum. The leaves of T. nepalense are narrower, margins are serrulate only distally, laminal cells are shorter, and supra-alar cells are fewer. Taxithelium nepalense is similar in colour to T. instratum, but it is more robust, has densely foliate, terete branches, with broader and more abruptly pointed concave leaves, non-inflated alar cells and almost smooth margins.

Having examined the holotype of the New Zealand species T. polystictum Mitt. (NY), Câmara (2011b) placed it in synonymy with T. nepalense. A specimen supposedly of T. polystictum in BM and labelled “type” is Wijkia extenuata (Ramsay et al., 2002).

Among the specimens listed above, L.J.Brass 18170, 18646 and 19795 were identified by Ramsay et al. (2002) as T. planum (but see below).

**Doubtful Records**

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


The recent revision of *Taxithelium* subg. *Taxithelium* by Câmara (2011b) confirmed *T. planum* to be one of the most common and widespread species in the Neotropics, being found in south-eastern U.S.A. (Florida), Central America and the Caribbean, tropical South America, as well as West Africa. Having examined more than 6,000 specimens of *Taxithelium*, Câmara (2011b) rejected Buck’s (1998) merger of *T. nepalense* with *T. planum*, treating them as distinct species. This separation is supported by morphological (Câmara, 2011b) and molecular data (Câmara & Shaw, in prep.).

Ramsay et al. (2002) reported *T. planum* from India, SE Asia and Malesia, based mainly on literature sources. However, Câmara (2011b) limited its Palaeotropical distribution to West Africa, and maintained that all other reports from Africa, southern Asia, as well as Australia, were almost certainly referable to other taxa (Câmara, pers. comm.). Unfortunately, Câmara has been unable to examine Australian specimens held in MEL (I.G.Stone) and FH (L.J.Brass). However, based on his thorough worldwide revision, it is unlikely that *T. planum* occurs in Australia.

Câmara (2011b) noted that *T. planum* was an extremely variable species distinguished from other species of *Taxithelium* by its ovate, concave leaves (0.5–1.2 mm long), pluripapillose cells in both vegetative and perichaetial leaves, acute leaf apices (not obtuse or acuminate) and margins that are slightly serrulate below the apex. *Taxithelium nepalense* differs especially in the alar region, with the basal cells not being inflated or enlarged, and with rows of supra-alar, while leaf margins are serrulate only at the apex.

A re-examination of the original data and the illustration of the specimens Stone 14735, Stone 23474 (see below) named as *T. planum* (Ramsay et al., 2002) suggest that they may have been misidentified. Characters that agree with *T. nepalense* include leaf shape, acute leaf apices, margins serrulate near the apex and the appearance of the alar region. Differences from *T. nepalense* (fig. 7) are the larger leaves (fig. 8a), longer mid-laminal cells (fig. 8c), the peristome (fig. 8j) and larger spores (fig. 8i). As *T. nepalense* is a variable species, this variation might fall within an acceptable range. In view of Câmara’s (2011b) investigations that *T. planum* is a Northern Hemisphere and non-Asian species, these specimens should be renamed as *T. nepalense*.


The Bartram (1952) specimens [Brass 18170, 18646, 19061, 19795 (FH)] were originally labelled as *T. selenithecium*, which is a synonym of *T. nepalense* (Câmara, 2011b), not *T. planum* as reported in Ramsay et al. (2002). These have been listed under *T. nepalense* in the current treatment.