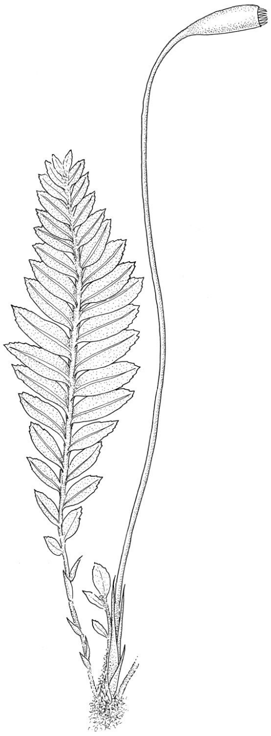
FLORA OF NEW ZEALAND

MOSSES

RHIZOGONIACEAE



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Cover image: *Rhizogonium distichum*, habit with capsule. Drawn by Rebecca Wagstaff from *L. Visch 679*, CHR 267027.

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Introduction

The Rhizogoniaceae are a moderately large family distributed mainly in tropical regions and subtropical to cool parts of the southern hemisphere and are well represented in New Zealand by members of five genera. Species of the core genus, *Rhizogonium*, are particularly attractive and often conspicuous terrestrial or epiphytic plants. Their leaves are inserted in two ranks and the shoots flattened; three species of this genus are widespread in N.Z. Our one species of *Cryptopodium*, an endemic genus often growing on tree-ferns, is one of the largest mosses in our flora. The less conspicuous but highly attractive *Goniobryum* exhibits a classic disjunction between N.Z., eastern Australia (including Tasmania) and the southern tip of South America.

The circumscription of the family and of some of its genera, especially *Rhizogonium* in its broadest sense, has been in a state of flux for decades. For example, the genus *Pyrrhobryum*, represented by three species in N.Z., has been segregated from the traditionally defined *Rhizogonium*. Further “splitting” of *Pyrrhobryum* has been proposed by some workers, but is rejected here.

The Rhizogoniaceae and allied families are considered to occupy a critical evolutionary position relative to pleurocarpous mosses, and they have recently attracted considerable attention from molecular systematists. Some but not all of the taxonomic changes derived from the molecular studies have been accepted here. The enigmatic and gymnostomous genus *Calomnion*, a conspicuous occupant of N.Z. tree fern caudices, is here accepted as a member of the family. Many studies, by contrast, retain *Calomnion* in its own family, with historically controversial affinities. *Calomnion* is represented in N.Z. by a single species, with segregate described species rejected here. Two other small but ecologically important genera in N.Z. (*Leptotheca* and *Hymenodon*), sometimes placed here, have been excluded from the family in part because of published molecular studies.

Typification

The following lectotypifications are made in accordance with the International Code of Nomenclature for Plants, Algae and Fungi.

Rhizogonium pennatum **Hook.f. & Wilson in Wilson, Bot. Antarct. Voy. II (Fl. Nov.-Zel.) Part II 116 (1854)**
Lectotype (designated here): N.Z., Dusky Bay, *A. Menzies 90*, 1791, BM-Wilson! Isolectotype (designated here): BM-Hooker 2544!

Rhizogonium sinuatum **Müll.Hal., Hedwigia 36: 333 (1897)**
Lectotype (designated here): N.Z., Westland, Greymouth, herb. R. Helms, 1885, BM-Bescherelle! Isolectotype (designated here): CHR 494774!

Rhizogoniaceae

Plants small to robust, epiphytic or terrestrial. **Stems** erect, simple or much branched, in cross-section angular in outline, with a central strand. **Shoots** often complanate. **Leaves** either uniform or dimorphic, distichous, tristichous, or inserted in many rows; those of branches similar or rarely differentiated from stem leaves, often bordered, mostly sharply toothed (with teeth either single or paired), less often denticulate or entire; **laminal cells** oblong, rounded-hexagonal or rarely oblong-hexagonal, usually thick-walled and compact, rarely lax (in *Goniobryum*), smooth; **alar cells** not differentiated. **Costa** strong, ending below the apex to excurrent.

Perichaetia mostly basal or lateral, occasionally terminal (in *Calomnion* and *Cryptogonium*). **Setae** single or rarely aggregated, mostly elongate; **capsules** horizontal, inclined or erect, exserted or rarely immersed (in *Cryptogonium*), oblong-cylindric to cylindric; **peristome** mostly double and well-developed, rarely absent (in *Calomnion*); **annulus** differentiated; **operculum** conic or stoutly rostrate. **Calyptra** cucullate and smooth.

Taxonomy: Perichaetia in this family are usually borne at the stem base or low on the stem. However, the perichaetia in *Calomnion* and *Cryptogonium* (the former gymnostomous and often placed in its own family) are terminal, and in *Cryptogonium* the perichaetia are overtopped by innovations.

The difficulty of circumscribing the Rhizogoniaceae and its allies is reflected by its complicated history. Allied (or purportedly allied) genera for many decades have been moved between the present family, the Aulacomniaceae, the Calomniaceae, and, more recently, the Orthodontiaceae.

The Rhizogoniaceae were proposed by Brotherus (1901–1909); in his subsequent (Brotherus 1924) family outline he recognised seven genera occurring mostly in tropical to temperate parts of the southern hemisphere and placed the family in the Bryales (“Eubryales”). Brotherus (1924) recognised four sections within his broadly defined *Rhizogonium*. Dixon (1926), in his discussion for N.Z., accepted the four N.Z. genera (*Cryptopodium, Goniobryum,* and *Rhizogonium,* plus *Hymenodon*) included there by Brotherus, and added *Leptotheca* and *Aulacomnium*. Sainsbury (1955), without comment, followed the placements of Brotherus. In their moss flora of southern Australia, Scott & Stone (1976) also essentially followed a Brotherean concept of the family.

All the treatments above took a broad view of the core genus *Rhizogonium* Brid. Manuel (1980) took a more restricted view of that genus, resurrecting the long-standing but little-known *Pyrrhobryum* Mitt. to accommodate species dispersed by Brotherus among three of his four sections of *Rhizogonium*. The genus *Pyrrhobryum* (based on the widespread *P. spiniforme* (Hedw.) Mitt.) has subsequently been accepted by Koponen et al. (1986) in their treatment for the Huon Peninsula, P.N.G. and by Gilmore (2006) in his treatment for Australia.

Churchill & Buck (1982) argued for the transfer of *Leptotheca* from the Aulacomniaceae to the Rhizogoniaceae. Vitt (1995) presented arguments for the placement of the gymnostomous and problematic *Calomnion* both “near *Rhizogonium*” and in the distantly related Tetraphidales, but ultimately retained it in a monogeneric Calomniaceae.

The family Rhizogoniaceae and its allies remain very much in a state of flux. Modern workers have continued to modify the family, anchored by *Rhizogonium* Brid. (holotype: *R. novae-hollandiae* (Brid.) Brid.). In a large-scale phylogenetic analysis of “early-diverging” pleurocarpous lineages using both chloroplast and mitochondrial genes, Bell et al. (2007) presented strict consensus trees that demand further reassessment of the Rhizogoniaceae and allies.

Many of the realignments suggested by Bell et al. (2007) are identical to those adopted by Goffinet et al. (2009). Most, albeit not all, of the realignments adopted by the latter are followed here. Those accepted here include the inclusion of *Calomnion* in the Rhizogoniaceae (rather than in a monogeneric Calomniaceae) and the movement of both *Leptotheca* and *Hymenodon* to the Orthodontiaceae.

The assignments, suggested by Bell and co-authors, of two N.Z. taxa (*Pyrrhobryum mnioides s.l.* and *P. bifarium*) to the Malesian genus *Hymenodontopsis* Herzog are rejected here, for reasons outlined under the genus *Pyrrhobryum*. Given the uncertainty concerning the circumscription and the relationships of *Pyrrhobryum*, a conservative treatment (a broad interpretation of the genus and its retention in the Rhizogoniaceae) of the genus is adopted here. The family placement of *Hymenodontopsis* is beyond the scope of this Flora. However, the capsule morphology of the type of the genus, *H. steresmannii* from Malesia, differs markedly in many ways (capsule shape, its lack of sulci when dry, operculum form, nature of the annulus, and peristome structure) from that of most species of *Aulacomnium*, a genus to which the analysis of Bell et al. (2007) showed it to be allied.

Key to the genera (N.B.: *Hymenodon* is included in this key, since it has traditionally been placed in this family and many students will seek it here; in this Flora it is treated in the Orthodontiaceae.)

1 **Laminal cells** thin-walled and lax, oblong-hexagonal, 3–5:1; **autoicous (**perigonia scattered amongst perichaetia, brown & bud-like) .... *Goniobryum*

1' **Laminal cells** firm- or thick-walled, not lax, variable in shape but <2:1; **dioicous** (in N.Z. taxa) 2

2 **Leaves** inserted in three distinct ranks (except at shoot apices), with one rank clearly reduced in size; **peristome** lacking; **protonema** persistent .... *Calomnion*

2' **Leaves** not in three ranks and lacking a rank of clearly reduced leaves; **peristome** present, mostly well-developed and double, rarely single; **protonema** not persistent 3

3 **Leaves** piliferous, with costa ending well below the base of the hair-point, unbordered, crenulate at margins; **laminal cells** mammillose; **peristome** single .... *Hymenodon* [Orthodontiaceae]

3' **Leaves** not piliferous, sometimes aristate (due to excurrent costae), bordered or otherwise, serrate to dentate at margins; **laminal cells** not mammillose; **peristome** double and well-developed 4

4 **Plants** very robust, mostly epiphytic on tree ferns; **stems** c. 50–200 mm; **leaves** mostly >7 mm and linear-lanceolate; **setae** <3 mm; **capsules** immersed and often clustered (to four per perichaetium); **perichaetia** terminal, but often overtopped by subperichaetial innovations .... *Cryptopodium*

4' **Plants** less robust, terrestrial or epiphytic; **stems** <70 mm (only rarely >50 mm); **leaves** <6 mm and not linear-lanceolate; **setae** >10 mm, **capsules** exserted and single; **perichaetia** in basal clusters or lateral 5

5 **Stem leaves** distichous; **leaf margins** singly toothed; **costa** smooth abaxially; **perichaetia** basal .... *Rhizogonium*

5' **Stem leaves** not distichous (branch leaves may be); **leaf margins** doubly toothed; **costa** toothed abaxially; **perichaetia** scattered on lower stems or basal (in *P. paramattense*) .... *Pyrrhobryum*

Calomnion Hook.f. & Wilson in Wilson, *Bot. Antarct. Voy. II (Fl. Nov.-Zel.) Part II* 97 (1854)

Type taxon: *Calomnion complanatum* (Hook.f. & Wilson) Lindb.

Plants shiny, small, olive-green to light green, with an extensive and persistent protonema, usually on tree-fern caudices. **Stems** simple, beset at base with papillose brown rhizoids, in cross-section with 2–3 layers of thick-walled cells surrounding several layers of larger thin-walled cortical cells and a small central strand (often collapsed in older stems). **Leaves** tristichous, dimorphic, often caducous; **lateral leaves** in two ranks, ovate to elliptic-lanceolate, entire or denticulate, reduced in size at stem base; **ventral leaves** in a single rank, smaller, and usually broadly elliptic; **upper laminal cells** polygonal, ± isodiametric, smooth, flat to slightly bulging; **basal laminal cells** and **alar cells** not differentiated. **Costa** single, robust, subpercurrent, percurrent, or excurrent.

Dioicous. **Perichaetia** terminal and with leaves much longer than the vegetative, erect and sometimes sheathing. **Perigonia** terminal. **Setae** erect or ± flexuose, elongate; **capsules** cylindric, erect, gymnostomous, ellipsoid or cylindric, smooth or wrinkled when dry; **stomata** restricted to capsule base; **annulus** well-differentiated or absent; **peristome** absent. Spores papillose. **Calyptra** cucullate, ± scabrous above.

Taxonomy: The number of species in *Calomnion* requires reconsideration in a monographic context. Vitt (1995) considered the genus to include nine species distributed in the South Pacific, from Malesia south to Tasmania and N.Z., and east to Tahiti, and attempted to correlate speciation and dispersal with tectonic events in the South Pacific. However, one of his species (*C. brownseyi*) is rejected here for the reasons stated below. The morphological features used to differentiate some species (e.g., what Vitt termed *C. brownseyi* and *C. melanesicum*) likewise need re-evaluation. Only one species of *Calomnion* is accepted for N.Z.

Calomnion laetum is an illegitimate name (Article 52, McNeill et al. 2011) because the epithet of an earlier legitimate name is cited in synonymy in its protologue, as noted by Vitt (1995). Therefore, in accordance with Article 7.5, the type of the genus is *C. complanatum* (Hook.f. & Wilson) Lindb. (*Gymnostomum complanatum* Hook.f. & Wilson).

The relationships of *Calomnion* have been problematic since its description, largely because of its lack of a peristome. Brotherus (1924) placed it in its own family in the general relationship of the Rhizogoniaceae and the Mitteniaceae. Dixon (1932) retained the Calomniaceae but considered it to be allied to nematodontous groups and placed it close to the Georgiaceae (=Tetraphidaceae) and Schistostegaceae. Sainsbury (1955) seemed to have accepted Brotherus' earlier view. Vitt (1995) reached no firm conclusion as to the familial relationships of the *Calomnion*. He cited reasons for following its "more traditional Bryalean placement near *Rhizogonium*" but also noted that its "capsules, seta, and protonema are at least superficially similar to those of the Tetraphidaceae." In their more recent and influential analysis using multiple molecular markers, Bell et al. (2007) found *Calomnion* to be nested within the Rhizogoniaceae. Goffinet et al. (2009) also placed *Calomnion* in the Rhizogoniaceae, and this placement is accepted here.

There is some confusion concerning the interpretation of the position (i.e. "ventral" vs "dorsal") of the rank of reduced leaves in *Calomnion*. Their position is interpreted here as fundamentally similar to those in such genera as *Hypopterygium* and can justifiably be labelled "ventral" as done by Vitt (1995).

The orientation in *C. complanatum* of the reduced rank of leaves in a skyward position is likely an orientation for increased light gathering in a deeply shaded forest habitat. Developmental torsion of the stems is probably involved, but confirmation of this would involve detailed morphogenetic study.

Etymology: The generic name means beautiful moss.

Calomnion complanatum (Hook.f. & Wilson) Lindb., *Contr. Fl. Crypt. As.*, 240 (1872)

≡ *Gymnostomum complanatum* Hook.f. & Wilson, *London J. Bot.* 3: 538 (1844)
Lectotype: N.Z., "On the stem of a tree-fern", BM-Wilson. (Designated by Vitt 1995.) Not seen.

= *Calomnion laetum* Hook.f. & Wilson in Hooker & Wilson, *London J. Bot.* 3: 97 (1844) nom. illeg.
Syntypes: N.Z., North Island, Bay of Islands, *J.D. Hooker* and Waikehi [Waiheke?], *A. Sinclair*. (Cited by Vitt 1995.) Not seen.

= *Calomnion brownseyi* Vitt & H.A.Mill. in Vitt, *Bryologist* 98: 346 (1995)
Holotype: N.Z., Westland, Camp Creek, Nov. 1982, *R.B. Allen s.n.*, CHR 405458A! Isotypes: CHR 405458B!, WELT M034117!

Plants shiny, small, olive-green to light-green or red-brown, mostly on tree-fern caudices. **Stems** c. 7–12 mm, beset at base with papillose brown rhizoids, often arising from a mass of persistent protonema, sometimes becoming nearly naked because of caducous leaves, in cross-section as per genus. **Shoots** c. 1.3–1.8 mm wide. **Lateral leaves** elliptic to ovate-elliptic, acute, bluntly mucronate to short acuminate, entire, crenulate or irregularly denticulate above, asymmetric at base, scarcely altered when dry, mostly 0.7–1.1 mm, but becoming smaller towards stem base; **ventral leaves** broadly elliptic, acute to weakly acuminate, entire to irregularly toothed; **upper laminal cells** irregularly polygonal, firm-walled, mostly 6–11 µm in greater diam., unistratose, when dry with the cell contents occasionally contracted to form a primordial utricle; **basal cells** and **alar cells** not differentiated. **Costa** stout, subpercurrent, percurrent, to long-excurrent, often forming a mucro. **Protonema** persistent, extensive, highly branched, rust-brown, with a rhizome-like, red-brown, and warty caulonema bearing densely bipinnate branches or short, bulging, and chlorophyllose cells.

Dioicous. **Perichaetial leaves** strongly differentiated, much longer than vegetative leaves, variable in shape, narrowly panduriform, oblanceolate, or narrowly spathulate, acute, acuminate, or rarely obtuse at apex, entire, crenulate, or irregularly denticulate at margins, unistratose throughout or rarely with small bistratose marginal areas, 1.6–2.5 mm, with costa mostly ending a few cells below apex. **Perigonia** terminal, the inner leaves broadly ovate or panduriform, surrounding up to 15 antheridia and few filiform paraphyses. **Setae** (2–)3–4.5(–6) mm, slender and flexuose; **capsules** erect, gymnostomous, ellipsoid or cylindric, (0.8–)1.0–1.4(–1.5) mm, pale brown and ± red at mouth at maturity, weakly sulcate when dry; **exothecial cells** thin-walled, rounded-oblong or rounded-quadrate; **stomata** restricted to neck, superficial; **annulus** well-differentiated, vesicular. **Calyptra** cucullate, ± scabrous above. **Spores** 12–14 µm, papillose.

Illustrations: Plate 1. Sainsbury 1955, pl. 43, fig. 3 (as *C. laetum*); Vitt 1995, figs 8–14; figs 44–47 (as *C. brownseyi*); Malcolm & Malcolm 2003, p. 10; Catcheside & Bell 2006, pls 54–55.

Distribution: K; NI: N Auckland, including offshore islands (GB, LB), S Auckland, Gisborne, Hawke's Bay, Taranaki, Wellington (including KA); SI: Nelson, Marlborough, Canterbury (Banks Peninsula), Westland, Otago, Southland; St; Ch.

Australasian. Mainland Australia*. Reported from Tasmania by Stone (1990) and Catcheside & Bell (2006). Adventive in Ireland*.

Habitat: Mainly on tree-fern caudices, commonly on *Cyathea smithii, C. dealbata*, *Dicksonia squarrosa,* and rarely on *C. medullaris*. In N Auckland L.D. also occurring on *Blechnum fraseri*. Less frequently on trunks of *Rhopalostylis sapida* (nīkau), *Elaeocarpus dentatus* or *Dracophyllum arborea*. Rarely on vertical or overhanging rock faces or vertical clay banks. From near sea level to c. 780 m elevation (Mt Hauhungatahi, Wellington L.D.) on North I. and to at least 460 m (Fyffe-Palmer Scenic Reserve, Marlborough L.D. and near Bruce Bay, Westland L.D.) on South I. Commonly associated species include *Hymenodon pilifer*, *Leptotheca gaudichaudii*, *Rhizogonium novae-hollandiae, R. pennatum,* and *Zoopsis argentea*. Beever (1984) made a detailed study of tree-fern epiphytes in the Waitakere Ranges (N Auckland L.D.) and noted the occurrence of *C. complanatum* on 93% of sampled *Cyathea dealbata*, 100% of *Dicksonia squarrosa*, but only 2% of *Cyathea medullaris*.

Notes: The status of *C. brownseyi* Vitt & H.A.Mill. has been problematic in N.Z. from its description in 1995. Careful reading of the paper in which this taxon was described (Vitt 1995) suggests that the characters considered most significant by the describing authors are the nature of the upper margins of the lateral vegetative leaves and of the inner perichaetial leaves. These two characters seem unlikely to vary independently.

The presence of leaf margin denticulations indeed appears to be a feature restricted to material from the western coast of the South and Stewart Is. However, individual collections from that region are highly variable with respect to vegetative and perichaetial toothing, with variation occurring both within a single plant and between plants. The differentiation of material with and without marginal teeth seems to have been made arbitrarily in naming material in N.Z. herbaria. Both *C. complanatum* and *C. brownseyi* were described by Vitt (1995, in his key to species) as having a percurrent costa in the vegetative leaves. The variation of the vegetative leaf costa in N.Z. material is more variable than allowed by him and ranges from predominantly subpercurrent to short- or long-excurrent, often in the same plant.

Other features cited by Vitt in distinguishing *C. brownseyi* were the shape of the inner perichaetial leaves, their apical shape, and the thickness of their upper margins (unistratose vs partially bistratose). Perichaetial leaf characters in *Calomnion* are often particularly difficult to observe since many collections have few or no perichaetia. When present and intact, the shape of the inner perichaetial leaves is extremely variable and ranges from narrowly panduriform to narrowly spathulate to what Vitt usefully described as oblanceolate. There is no discernible pattern in this variation and it is here interpreted to be either developmental or environmentally induced and of little taxonomic value.

Vitt also cited the presence of partially bistratose perichaetial leaf margins as a character differentiating between the N.Z. "*C. brownseyi*" (unistratose) and *C. melanesicum* H.A.Mill. (partially bistratose). Some collections of N.Z. "*C. brownseyi*" develop small marginal bistratose patches, however, particularly at the base of marginal teeth.

After a study of a range of specimens in the herbarium (including the holotype and some paratypes of *C. brownseyi*) and in the field, N.Z. material of *Calomnion* is viewed here as a single variable species for which the oldest name is *C. complanatum*. *Calomnion brownseyi* is not recognised here. Material of *C. melanesicum*, the species most closely allied to *C. brownseyi* according to Vitt's (1995) trees, has not been available for comparison.

Recognition: In a N.Z. context *C. complanatum* is most likely to be confused with *Rhizogonium pennatum* or *R. novae-hollandiae.* While often growing on tree-ferns, both species of *Rhizogonium* are more robust plants with basal rather than terminal perichaetia. They lack the reduced ventral leaves of *C. complanatum*; both have stoutly excurrent costae and horizontal to pendent capsules with well-developed peristomes. *R. pennatum* also has a well-developed leaf marginal border. Aberrant material of *C. complanatum* could possibly be confused with *Leptotheca gaudichaudii*, but that species differs by regularly producing dark brown, filamentous axillary gemmae, and having longer (1.6–3.1 vs 0.7–1.1 mm) vegetative leaves with sinuose rather than straight costae. *Leptotheca gaudichaudii* also lacks reduced ventral leaves and its capsules are longer and peristomate.

Etymology: The epithet *complanatum* refers to the flattened or complanate nature of the shoots.

Cryptopodium Brid., *Bryol. Univ. 2,* 30 (1827), nom. cons.

Type taxon: *Cryptopodium bartramioides* (Hook.) Brid.

Taxonomy: *Cryptopodium* is a monotypic genus documented only from N.Z.; it has the characteristics of its sole species, described below.

Etymology: The generic name alludes to the hidden capsules, which are immersed among the perichaetial and vegetative leaves.

Cryptopodium bartramioides (Hook.) Brid., *Bryol. Univ. 2,* 31 (1827)

≡ *Bryum bartramioides* Hook., *Musci Exot. 1,* pl. 18 (1818)

> Holotype: N.Z., Dusky Bay, 1791, *A. Menzies 91*, BM-Hooker! There are three duplicates of the type collection in the Hooker herbarium; collectively they constitute the holotype.

= *Rhizogonium helmsii* Müll.Hal., *Hedwigia* 36: 333 (1897)

> Type: N.Z., Greymouth, *R. Helms* (herb. Beckett NZ 807 ex herb. Helms 50), CHR 635980!

Plants very robust, loosely pendent, forming loose tufts or extensive turves, on tree-ferns, bark, or rock, yellow- or red-brown or brown-green, dull, often appearing ± dendroid. **Stems** very long, 50–200(–250 mm) mm, mostly unbranched below and with many, often short branches near apex, loosely pendent, curved or flexuose, with very sparse brown papillose rhizoids nearly restricted to base, densely foliose above, dichotomously branched or less often unbranched above, stiff and wiry, in cross-section with a distinct central strand and angular in outline. **Leaves** in many rows, densely inserted and somewhat more crowded near stem apex, weakly flexuose-secund when dry, erect-spreading and ± straight or weakly secund when moist, narrowly lanceolate (but often appearing weakly ovate at base), carinate nearly throughout, unistratose except for margins and scattered bistratose streaks, doubly toothed, c. 7–12 × 0.75–0.9 mm, those at stem base much smaller, ± ovate-lanceolate, and closely appressed; **margins** bistratose and much thickened above (the thickening apparent under the hand-lens), closely and doubly serrate nearly throughout, reflexed on one or both sides below; **upper laminal cells** irregular in shape, but many ± quadrate, thick-walled, smooth, 1–1.5:1 and 10–15 µm in greater dimension, becoming longer and more rectangular and strongly porose near leaf base; **basal cells** very incrassate and orange-brown in several rows; **alar cells** not differentiated. **Costa** strong, c. 105–120 µm at mid leaf, percurrent or sometimes excurrent, protruding strongly and doubly toothed on abaxial surface, in cross-section (at mid leaf) triangular, with median guide cells and large abaxial and adaxial stereid bands, the cells on the adaxial surface rectangular and mostly 2–4:1.

Dioicous. **Perichaetia** terminal, but often overtopped by subperichaetial innovation, the leaves scarcely differentiated, the archegonia numerous and mixed with filiform paraphyses. **Perigonia** gemmiform, c. 1.2 mm diam. (excluding outer bracts), often produced serially on one branch and subtended by innovations, the inner bracts mostly broadly ovate, concave, and pigmented, surrounding numerous antheridia and filiform paraphyses. **Setae** often aggregated, 1–3(–4) per perichaetium, 1–2 mm (excluding ocrea), stout, pale brown; **capsules** immersed, erect, broadly elliptic and ± symmetric, smooth, c. 2 mm, pale brown at maturity; **mouth** transverse; **exothecial cells** mostly oblong-hexagonal, firm-walled; **stomata** not seen**; annulus** strongly differentiated, apparently persistent at rim when operculum falls; **operculum** bluntly conic. **Peristome** double; **exostome teeth** yellow-brown, lanceolate and weakly shouldered, c. 650 µm, with a zig-zag median dorsal line, bordered, transversely striate below, becoming ± baculate above, with numerous ventral lamellae; **endostome** with a high basal membrane and segments nearly the height of the teeth, with 2–3 nodose cilia. **Calyptra** cucullate, smooth, and naked. **Spores** 12–15 µm, nearly smooth.

Illustrations: Plate 2. Brotherus 1924, fig. 381; Sainsbury 1955, pl. 44, fig. 1.

Distribution: NI: N Auckland including offshore islands (LB), S Auckland, Gisborne, Hawke’s Bay, Taranaki, Wellington; SI: Nelson, Marlborough (Mt Stokes, Grants Pass, Pelorus Bridge Scenic Reserve, Bryant Range), Westland, Otago, Southland; St.

Endemic.

Habitat: Most often occurring on tree ferns caudices and stumps (especially *Cyathea smithii* and *C. dealbata*, occasionally on *Dicksonia squarrosa*) where it forms dense and usually pure turves that sometimes completely obscure the fern caudex. It is also very common on rotten tree stumps in a wide range of forest types and occurs on the bark of angiosperm trees (including *Elaeocarpus dentatus, Lophozonia menziesii,* and *Metrosideros umbellata*) and probably on some podocarps, on thin humus over rock faces (including conglomerate, gneiss, schist, granite, and sandstone), and steep clay banks. This endemic species is most frequent in N Auckland and the West Coast of South I. Eastern

North I. records are largely confined to the Lake Waikaremoana region; Hawke's Bay records are entirely pre-1900. The species is rare in Marlborough and has not been collected in Canterbury (but its eventual discovery near the Main Divide seems likely).

When epiphytic, *C. bartramioides* has few bryophyte associates, apart from trailing hepatics (mostly *Bazzania* spp., and Lejeuneaceae) growing among the stems. Occurring on North I. from c. 125 m to at least 800 m (Lake Waikaremoana, Gisborne L.D.) in the east and to c. 1070 m (Mt Taranaki, Taranaki L.D.) in the west; on South I. occurring from near sea level (Pororari River, Nelson L.D.) to at least 1230 m (Scarlett Range, Nelson L.D.). The upper elevation occurrences are usually terrestrial rather than epiphytic.

Notes: The species is morphologically quite uniform throughout its N.Z. range and differs primarily in stature.

Dixon (1926, p. 223) rejected an early record of *C. bartramioides* from Hawai‘i by Gaudichaud, suggesting that the mounted leaves he saw were from "*Rhizogonium*" *spiniforme*; Dixon's conclusions were for the most part accepted by subsequent workers on Hawai‘ian mosses (e.g., Bartram 1933), thus reinforcing Sainsbury's (1955) conclusions that it is both a N.Z. endemic genus and species.

Recognition: *Cryptopodium bartramioides* is sometimes confused with *Cyrtopus setosus*, which is also a robust and epiphytic plant. However, *C. bartramioides* is generally a larger plant with longer and narrower (7–12 × c. 0.75 mm vs c. 5–7 × 1.2–1.4 mm) and more evenly tapered and linear-lanceolate leaves. The marginal teeth in *C. bartramioides* are paired and readily seen with a hand-lens while those in *Cyrtopus setosus* are single and difficult to observe under a hand-lens. In *Cryptopodium* the cells of the leaf base are uniformly short-rectangular and smooth, while in *Cyrtopus* the laminal cells of the leaf base are dimorphic and have cuticular striations (observable under the compound microscope). The two genera also differ by several sporophytic features and by their host preferences; *Cryptopodium bartramioides* grows mostly on tree ferns, while *Cyrtopus setosus* favours smooth-barked trees, especially tawa (*Beilschmiedia tawa*).

Cryptopodium bartramioides could possibly be confused with *Echinodium hispidum* but that species is primarily terrestrial, normally dark green in colour, and has shorter, entire leaves that are subulate from an ovate or triangular base and with a long subula completely filled by the costa.

The aggregated and short setae and the elongate and strongly porose basal laminal cells are among the features that distinguish *C. bartramioides* from members of *Pyrrhobryum*. The leaves of *C. bartramioides* are larger (7–12 × 0.75–0.9 mm) and not as strongly reduced in size on the lower stems as are those of *P. paramattense* (4.5–6.0 × 0.3 mm and much reduced below). *Cryptopodium bartramioides* is also a more robust plant with stems nearly always in excess of 50 mm.

Etymology: The epithet *bartramioides* refers to a resemblance to the genus *Bartramia*, that was named after the American colonial botanist John Bartram (1699–1777). The similarity is perhaps greatest to members of the subgenus *Bartramia*, to which the Australasian *B. mossmaniana* belongs.

Goniobryum Lindb., *Öfvers. Kongl. Vetensk.-Akad. Förh.* 21: 606 (1865)

Type taxon: *Goniobryum subbasilare* (Hook.) Lindb.

Taxonomy: The type (and probably only) species is described below.

Goniobryum is an exclusively austral genus of one or possibly two species, with one occurring in N.Z.

Etymology: The name means "angled moss". According to Meagher (2011), the name is "presumably alluding to the pendulous capsule, bent down at a sharp angle".

Goniobryum subbasilare (Hook.) Lindb., *Öfvers. Kongl. Vetensk.-Akad. Förh.* 21: 607 (1865)

≡ *Hypnum subbasilare* Hook., *Musci Exot. 1,* pl. 10 (1818)
Holotype: Argentina, Staten Land, near Cape Horn, *A. Menzies 24*, 1787, ("Hooker 3314"), BM-Hooker! Isotype: BM-Wilson!

= *Photinophyllum pellucidum* Mitt., *J. Linn. Soc., Bot.* 10: 175 (1868)
Syntype: N.Z., *C. Knight 139*, BM-Hooker!

Plants medium-sized, yellow-green or bright green, lustrous, forming loose and usually terrestrial turves. **Stems** erect, unbranched, yellow-brown below, green above, c. 15–25 mm, in cross-section ± angled, with 2 layers of firm-walled, pigmented cells surrounding a parenchymatous cortex and a distinct central strand, sparsely beset below with red to red-brown, smooth rhizoids. **Leaves** spreading, symmetric, oblong-lanceolate, narrowly acute, not concave, weakly decurrent (especially the base of the costa), scarcely bordered, strongly spinulose-serrate (with teeth either single or ± paired) in upper ⅔, 2.2–3.5 × c. 0.6–0.7 mm, smaller but not scale-like towards the stem base; **upper laminal cells** lax, oblong-hexagonal, c. 75–120(–150) × 21–30 µm; mostly 3–5:1, with chloroplasts aggregating at cell extremities in dry material, bulging in cross-section, not differentiated below or in alar angles; **marginal cells** narrower in 1(–2) rows but not forming a distinct border. **Costa** c. 45 µm wide near base, extending 0.75–0.9 the leaf length, not toothed abaxially, in cross-section (at mid leaf) plano-convex, with few (usually 2) central guide cells, small (≤6-celled) abaxial and adaxial stereid bands and enlarged superficial cells that are similar in shape to the juxtacostal laminal cells.

Autoicous. Perichaetia scattered on lowermost stem, with leaves acuminate from an oblong and yellow base, widely spreading in upper half, costate, to c. 1.8 mm. **Perigonia** scattered among the perichaetia, brown and bud-like, c. 1 mm long, with bracts c. 0.8 mm, ecostate, and acute from an ovate base, with filiform, 5-celled paraphyses. **Setae** 24–50 mm, straight, smooth, twisted weakly to the left, pale yellow-brown; **capsules** horizontal or weakly pendent, oblong-cylindric from an asymmetric and strongly curved base, c. 2.5–3.5 mm, wrinkled below, contracted below the mouth when dry, yellow-brown; **exothecial cells** mostly oblong-hexagonal, firm- and smooth-walled, mostly 75–105 × 24–30 µm; **annulus** vesicular, persistent; **operculum** conic. **Peristome** double; **exostome teeth** pale yellow-brown, narrowly lanceolate, inserted close to rim, c. 500–580 µm, bordered, with the outer surface finely and densely papillose (non-striolate) below, more coarsely so above, with the inner surface lamellate; **endostome** from a high membrane, with keeled and perforate segments nearly as long as the teeth and very long (but fragile) and weakly nodose cilia in groups of 3. **Calyptra** cucullate, c. 3 mm. **Spores** ± spherical, 13–16 µm, pale brown, reticulate.

Illustrations: Plate 3. Brotherus 1924, fig. 379 a–e (as *G. subbasilare* and *G. pellucidum*); Scott & Stone 1976, pl. 58; Beever et al. 1992, pl. 54; Malcolm & Malcolm 2003, p. 31.

Distribution: NI: S Auckland, Gisborne, Taranaki (Mt Egmont), Wellington. SI: Nelson (Travers Valley, Mt Arthur, Reefton, Paparoa Range), Marlborough (Mt Stokes), Canterbury (49 Mile Peg near Arthur's Pass), Westland (Camp Creek, Ōtira, Ross), Otago, Southland; St.

Australasian. Tasmania*, mainland Australia*, Argentina*. Reported from Chile by Matteri & Piñero (1987). Reported from Samoa by Mitten (1868), but its occurrence there seems unlikely and was doubted by Schultze-Motel (1974).

Habitat: On humic soil, rotten wood, and tree fern trunks; less commonly on alluvial silt and often sheltered by overhanging rocks or vegetation. Forming pure turves or mixed with other bryophytes. Although the majority of N.Z. collections are from South I. south of 45º, there is a curious absence of records from Fiordland and the subantarctic islands. Records from the northern half of South I. are mostly from humic soil sheltered by overhanging rocks or vegetation, and nearly (excepting one or two from Marlborough L.D.) all are from areas near to or west of the Main Divide. There are a large number of collections known from the Dunedin region and it is most frequent in the southern portions of South I. and on Stewart I. On North I. ranging from c. 350 (Stubb's Farm, S Auckland L.D.) to c. 760 m (Mt Kapakapanui, Wellington L.D.). On South I ranging from near sea level (in Otago and Southland L.D.) to c. 1100 m (Paparoa Range, Nelson L.D.); on Stewart I. found up to c. 300 m.

Recognition: The large, thin-walled laminal cells are easily observed under the hand-lens. The lax areolation, the sharply toothed leaf margins, and the basal perichaetia make this species easily recognisable. In herbarium material the chloroplasts aggregate at both ends of the laminal cells.

Confusion between this species and other members of the Rhizogoniaceae seems unlikely. In the field its habit is suggestive of a *Pohlia*, but its lax and large laminal cells should prevent confusion with that genus.

Etymology: The epithet refers to the location of the perichaetia.

Pyrrhobryum Mitt., *J. Linn. Soc., Bot.* 10: 174 (1868)

Type taxon: *Hypnum spiniforme* Hedw. ≡ *Pyrrhobryum spiniforme* (Hedw.) Mitt.

Plants medium-sized to robust, tufted or forming turves. **Stems** erect, in cross-section ± angled, simple or much branched, in cross-section with a central strand and thick-walled cortical cells. **Leaves** uniform or sometimes dimorphic (in *P. bifarium*). **Stem leaves** distributed around stem, spreading, linear-lanceolate, linear, or ovate-lanceolate, often acuminate, often decurrent, bistratose and mostly plane at margins, sometimes becoming scale-like near stem base. **Branch leaves** differing in some species (in *P. bifarium*), then more ovate-lanceolate and shorter than stem leaves, bifarious, somewhat asymmetric at base. **Upper laminal cells** of stem and branch leaves smooth, firm-walled, mostly oblong, ± isodiametric, or oblate, often somewhat irregular; **marginal cells** bistratose and often forming wings (best viewed in cross-section), not elongate; **alar cells** not differentiated. **Costa** fading in acumen or excurrent, bearing abaxial spines above, in cross-section with median guide cells and abaxial and adaxial stereids.

Dioicous (in N.Z. species) or autoicous. **Perichaetia** lateral and scattered on stems or in basal clusters. **Perigonia** budlike, mostly scattered on lower stems, with filiform paraphyses. **Setae** elongate, straight or flexuose; **capsules** inclined or horizontal, oblong-cylindric or obovate, asymmetric, with a weakly defined neck, constricted below the mouth when dry; **exothecial cells** mostly irregular, with firm or thin walls; **annulus** vesicular and persistent in N.Z. species; **operculum** conic, often rostrate. **Peristome** double and well-developed; **exostome teeth** yellow-brown, narrowly lanceolate, bordered, outer surface transversely striate in lower half, baculate above, inner surface lamellate; **endostome** from a high membrane; segments as long as teeth, keeled, widely or weakly perforate; cilia in groups of 1–3, nodose. **Calyptra** cucullate. **Spores** spherical, finely papillose.

Taxonomy: Mitten's concept of *Pyrrhobryum* received little application until 1980 when Manuel (1980) focused attention on the heterogeneity of Brotherus' concept of *Rhizogonium*. Manuel amended Mitten's concept of *Pyrrhobryum* to include only species with radially disposed leaves, multistratose, doubly-toothed margins, abaxially spined costae, and distinctly necked capsules. Koponen et al. (1986) noted that some species included within Manuel's concept of *Pyrrhobryum* (e.g., *P. bifarium*) can have distichous leaves, and proposed that a more meaningful classification would utilise the length of the marginal cells (short in *Pyrrhobryum* vs elongate in those species of *Rhizogonium* in which a border occurs) and de-emphasise the insertion pattern of the leaves.

Manuel's generic concept is adopted here. *Pyrrhobryum paramattense* was placed by Manuel in section *Pyrrhobryum* (characterised by basal perichaetia). It is clearly closely allied to the generitype. *Pyrrhobryum bifarium* and *P. mnioides s.l.* were placed by him in the section *Bifariella* (characterised by lateral perichaetia).

Alternative generic and family placements for two of the *Pyrrhobryum* species occurring in N.Z. have recently been proposed. Bell et al. (2007) transferred *P. bifarium* and *P. mnioides* to the genus *Hymenodontopsis* Herzog, which is founded on the Malesian *H. stresemannii* Herzog. The species occurs in New Guinea and was treated for the Huon Peninsula by Koponen et al. (1986). In addition to the transfer of N.Z. species to *Hymenodontopsis*, the molecular phylogeny presented by Bell et al. places the genus in a clade with *Aulacomnium androgynum* (only the type species of *Aulacomnium* was sampled) and two species of the Australian genus *Mesochaete*. They treat this clade as the Aulacomniaceae. Their phylogeny is based on four genes derived from both chloroplast and mitochondrial genomes and is presented as a strict consensus tree based on 16 most probable topologies.

There is a lack of congruence between their molecular data and morphology. Considering the transfer of N.Z. taxa to *Hymenodontopis*: *H. stresemannii* from Malesia (CHR 352062) has erect, symmetric, cupulate, and very short (c. 1.0 × 0.8 mm) capsules with very long (c. 2.0 mm) and slenderly rostrate opercula (c. two to three times the urn). The peristome is single and consists of a low endostomal membrane with short and irregular projecting segments. There is no annulus. The endostomal nature of the *H. stresemannii* peristome was confirmed by Shaw & Anderson (1986). The capsules of the two N.Z. species allegedly congeneric with this species differ strongly from it in their sporophyte morphology. *P. bifarium* has horizontal, asymmetric, and obovate capsules, with a conic operculum. The peristome is well-developed and double with a high endostomal membrane, keeled segments, and nodose cilia; there is a differentiated vesicular annulus. New Zealand material of *P. mnioides* subsp. *contortum* likewise has horizontal, asymmetric, and obovate capsules albeit with a stoutly rostrate operculum that is c. half the urn in length. The peristome here is well-developed and double with a high endostomal membrane, well-developed keeled segments and nodose cilia. Its annulus is also vesicular and persistent. These two N.Z. taxa differ markedly in capsule morphology from *H. steresmannii* and the proposed transfer of these species to *Hymenodontopsis* is therefore not accepted here. Material of the South African *P. vallis-gratiae* (Müll.Hal.) Manuel (also transferred to *Hymenodontopsis* by Bell et al. 2007) has not been seen. While *Pyrrhobryum* as presently circumscribed is probably heterogeneous (polyphyletic), further study is required to clarify the relationships of its component species. The conservative generic assignments advocated here accord with those of Gilmore (2006) and are similar to those of Koponen et al. (1986).

Etymology: According to Meagher (2011), the name *Pyrrhobryum* probably alludes to fire-coloured peristome teeth, but Mitten (1868) did not indicate the etymology.

1 **Stems** freely branched above and dendroid; **leaves** dimorphic, those of stems <2.2 mm; **branch leaves** clearly differentiated (more ovate, shorter, and non-decurrent) and distinctly bifarious; **exothecial cells** in longitudinal ranks (clearly visible under stereoscope), with thin transverse walls and strongly thickened longitudinal walls; **perichaetia** scattered on stems .... *P. bifarium*

1' **Stems** not or sparsely branched, not dendroid; **leaves** not dimorphic, rarely less than 3.0 mm; **exothecial cells** not in clear longitudinal ranks, with uniformly thickened walls; **perichaetia** basal or scattered on stems 2

2 **Perichaetia** basal; **leaves** flexuose (but not crisped) when dry and much reduced in size on lower stem, when well-developed 4.5–5.5 × c. 0.3 mm, not decurrent; **laminal cells** not or scarcely differentiated at leaf base .... *P. paramattense*

2' **Perichaetia** lateral; **leaves** crisped when dry and not obviously reduced on lower stem, when well-developed 2.0–4.5 × 0.5–0.8 mm, narrowly decurrent; **laminal cells** becoming elongate (to 5:1) and sometimes weakly porose at base of leaf .... *P. mnioides* subsp. *contortum*

Pyrrhobryum bifarium (Hook.) Manuel, *Cryptog. Bryol. Lichénol.* 1: 70 (1980)

≡ *Hypnum bifarium* Hook., *Musci Exot. 1,* 57 (1818)
≡ *Rhizogonium bifarium* (Hook.) Schimp. in Müller, *Bot. Zeitung (Berlin)* 5: 803 (1847)
≡ *Hymenodontopsis bifaria* (Hook.) N.E.Bell, A.E.Newton & D.Quandt, *Bryologist* 110: 555 (2007)
Holotype: N. Z., Dusky Bay, *A. Menzies 87*, 1791 (“Hooker 3309”) BM-Hooker! Isotypes: BM-Wilson!, BM-Turner!

Plants small or medium-sized, 12–22 mm high, dark green, dendroid, forming turves. **Stems** erect, unbranched below and densely branched above (occasionally unbranched), red-brown below, becoming green above, c. 5–10 mm high (to the base of branching), not complanate, in cross-section five-angled, with 2–4 layers of small, thick-walled cells (the outermost strongly pigmented) gradually merging with the cortex and surrounding a small, distinct central strand, appearing zig-zag when leaves are removed, beset at base with brown, smooth, much branched rhizoids. **Branches** mostly 4–5 mm, with leaves distinctly 2-ranked and ± complanate. **Stem leaves** spreading, little crisped when dry, symmetric, ovate-lanceolate or lanceolate with an acuminate apex, not concave, narrowly but long-decurrent, bistratose and winged at margins, plane or narrowly recurved below, serrate nearly to base by 5–10 pairs of single-celled teeth, 1.6–2.0(–2.2) × 0.4–0.5 mm, becoming smaller and scale-like at stem base. **Branch leaves** more ovate and shorter than stem leaves, 1.0–1.8 × 0.3–0.4 mm, bifarious, somewhat asymmetric at base, not decurrent, with paired, single-celled teeth nearly to base and a subpercurrent costa. **Upper laminal cells** (of stem leaves) firm walled, irregular in outline but mostly ± isodiametric or oblong, a few longer and to 2:1, nearly all ≤15 µm in greater diam., becoming more oblate below, a small group at insertion obscure in outline and partially ± bistratose, sometimes more elongate (to 4:1); **laminal cells of branch leaves** similar; **marginal cells** (of stem and branch leaves) bistratose and forming 2 distinct wings (best viewed in cross-section), but not otherwise differentiated; **alar cells** not differentiated (both stem and branch leaves). **Costa** (of stem leaf) concolorous, c. 75–90 µm wide at base and evenly tapered, c. 30 µm wide at mid leaf, ending in the acumen, bearing several abaxial serrations near the apex, in cross section (at mid leaf) biconvex, with few median guide cells and 2 small stereid bands.

Dioicous. Perichaetia scattered on stems, with perichaetial leaves lanceolate and long acuminate, costate, c. 1.5 mm. **Perigonia** scattered on stem and branches, with bracts c. 2 mm, costate, long acuminate from an obovate, concave, and strongly pigmented base, with numerous antheridia and filiform, 6–8-celled paraphyses. **Setae** 14–35 mm, straight, smooth, twisting weakly to the left, bright red or red-brown. **Capsules** horizontal, obovoid, asymmetric, c. 1.5–1.8 mm, smooth, moderately constricted below the mouth when dry, pale brown, red-brown at mouth; **exothecial cells** in distinct longitudinal ranks (clearly visible under stereoscope), irregular oblong or quadrate, with thin transverse walls and strongly thickened longitudinal walls, mostly 30–54 × 30–39 µm, not striate; **annulus** vesicular and persistent; **operculum** high-conic, not rostrate, c. 0.8 mm long. **Exostome teeth** pale yellowish-brown, narrowly lanceolate, inserted c. 60 µm beneath the rim (exclusive of annulus), c. 460 µm long, bordered, outer surface transversely striate in lower half, baculate above, inner surface lamellate; **endostome** from a high membrane; segments as long as teeth, keeled, not or scarcely perforate; cilia single, nodose. **Calyptra** cucullate, covering only the operculum and upper portion of the capsule, c. 2.5 mm. **Spores** ± spherical, 15 µm, pale brown, very finely papillose.

Illustrations: Plate 4. Brotherus 1924, fig. 376 A–C (as *Rhizogonium bifarium*); Scott & Stone 1976, pl. 54 (as *Rhizogonium bifarium*); Beever et al. 1992, fig. 45 a–d.

Distribution: NI: N Auckland, including offshore islands (LB), S Auckland, Gisborne, Hawke's Bay, Taranaki, Wellington. SI: Nelson, Marlborough, Canterbury, Westland, Otago, Southland; St; Ch; Sol; Sn; A; C.

Australasian. Tasmania*, mainland Australia*.

Habitat: On rotten logs and stumps, also on tree bases, exposed roots, humic soil, and rarely on sandy soil. Rarely epiphytic on tree or tree fern trunks, or rock. Occurring in a variety of forest types but apparently absent from grasslands, and rare in peatlands. From c. 60 m (Logue's Bush Scenic Reserve, N Auckland L.D.) to at least 950 m (near Lake Waikareiti, Gisborne L.D.) on North I; from near sea level (Dusky Sound, Southland L.D.) to 1095 m (near Flora Saddle, Nelson L.D.) on South I.

Notes: This is an exceedingly common and widespread species in N.Z. The dendroid habit and dimorphic leaves with the thickened margins and paired teeth, and scattered (non-basal) sex organs make this species unmistakable. Well-developed plants can look like minute palm trees in the field.

Occasional herbarium material of *Leptotheca gaudichaudii* is misnamed as this species, but the lack of double serrations, and the unbranched habit of *Leptotheca* permit ready differentiation.

The specimen (in herb. Hooker) interpreted here as the holotype consists of five tufts of one to five stems each, with mature, intact capsules and is labelled “No. 87. Dusky Bay New Zealand 1791” in Menzies' script.

Etymology: The species epithet *bifarium* refers to the two-ranked (bifarious) insertion of the branch leaves.

Pyrrhobryum mnioides (Hook.) Manuel, *Cryptog. Bryol. Lichénol.* 1: 70 (1980)

≡ *Hypnum mnioides* Hook., *Musci Exot. 1,* 77 (1818)
≡ *Rhizogonium mnioides* (Hook.) Hook.f. & Wilson in Wilson, *Bot. Antarct. Voy. II (Fl. Nov.-Zel.) Part II* 116 (1854)
≡ *Hymenodontopsis mnioides* N.E.Bell, A.E.Newton & D.Quandt, *Bryologist* 110: 555 (2007)
Holotype: Argentina, “Staten Island prope Cape Horn,” *A. Menzies, 1787*, BM-Hooker!

Notes: South American populations of *P. mnioides* have longer (3.8–7.2 mm) and broader (0.7–1.0 mm) leaves than Australasian populations. There is also a strong tendency for leaves in South American material to be less concave and less crisped when dry, for the leaves on the lower stems to be reduced, and for the stems to be less densely covered with rhizoids. The differences in leaf dimensions are the most consistent differences; collectively, the differences result in a quite marked difference in habit between South American and Australasian populations. A small fraction of South American specimens have dry leaves contorted in a manner suggestive of Australasian specimens, but in all such material the leaf dimensions are consistently larger. Perichaetia in both South American and Australasian material are borne in vegetative leaf axils. The morphologic differences and isolation of the two entities dictate the recognition of the Australasian material at the subspecific rank. The interpretation of South American and Australasian populations as distinct subspecies is broadly supported by molecular studies published by McDaniel & Shaw (2003).

Etymology: The species epithet alludes to a resemblance to members of the genus *Mnium*, typified by the widespread *M. hornum* Hedw.

Pyrrhobryum mnioides subsp. *contortum* (Hook.f. & Wilson) Fife, *Bryologist* 98: 315 (1995)

≡ *Rhizogonium mnioides* var. *contortum* Hook.f. & Wilson in Wilson, *Bot. Antarct. Voy. III. (Fl. Tasman.) Part II* 216 (1859)
Lectotype: Tasmania, Back River Gully, *Oldfield 114*, BM-K! (Designated by Fife 1995, p. 315.)

= *Mnium hookeri* Müll.Hal., *Syn. Musc. Frond. 2,* 555 (1851)
≡ *Rhizogonium hookeri* (Müll.Hal.) Mitt., *J. Proc. Linn. Soc., Bot.* 4: 95 (1859)
Holotype: N.Z., Lord Auckland's Islands, *J.D. Hooker s.n.*, 1840 (“Wilson 74”), BM!

= *Mnium mossmanianum* Müll.Hal., *Bot. Zeitung (Berlin)* 9: 547 (1851)
≡ *Rhizogonium mossmanianum* (Müll.Hal.) A.Jaeger, *Ber. Thätigk. St. Gallischen Naturwiss. Ges.*1873–1874: 221 (1875)
Type material: Tasmania, Mt. Wellington, on moist trees and rocks in water courses, *S. Mossman 53*, 1850, BM!

Plants medium-sized, bright yellow-green to dark green or black (when submerged), forming turves. **Stems** erect, not or sparsely and irregularly branched, dark brown below, green above, 30–70 mm high, in cross-section five-angled, with c. 4 layers of small, thick-walled cortical cells (the outermost strongly pigmented) gradually merging with parenchyma and surrounding a small central strand, densely beset below with dark brown, much-branched, and smooth rhizoids. **Leaves** erect-spreading when moist, not complanate, strongly crisped and tubular when dry, symmetric, narrowly lanceolate, weakly auriculate and decurrent at base, bistratose and plane at margins, serrate nearly to base by c. 25–30 pairs of single-celled teeth, (2.0–)3.0–3.9(–4.5) × 0.5–0.8 mm, not conspicuously reduced in size near stem base; **upper laminal cells** firm walled, irregular in outline (oblong, ± isodiametric or oblate), mostly 0.5–2:1 and 9–15 µm in greater diam., becoming more oblong and/or oblate below and often elongate (to 5:1) and weakly porose near insertion; **marginal cells** similar in shape, mostly bistratose and adjacent to teeth forming 2 distinct wings (best viewed in cross-section); **alar cells** not differentiated. **Costa** concolorous, c. 100–140 µm wide near base and evenly tapered, c. 70 µm wide at mid leaf, subpercurrent, bearing numerous abaxial spines in upper half or more, in cross-section biconvex (more strongly on abaxial surface), with c. 4 median guide cells and abaxial and adaxial stereid bands.

Dioicous. Perichaetia lateral on stem, with leaves slenderly acuminate from an oblong base, to c. 3 mm long (apparently enlarging after fertilisation to c. 5 mm). **Perigonia** budlike, axillary on lower stem or branches, rarely terminating a lateral branch, with bracts c. 1.5 mm, spreading, costate, acuminate from an obovate, concave, and strongly pigmented base, with numerous antheridia and 5–8 celled filiform paraphyses. **Setae** 30–50 mm, flexuose, smooth, twisting to the left, orange; **capsules** horizontal, obovoid from a moderately differentiated neck, asymmetric, 2.0–2.5 mm, smooth, constricted below the mouth when dry, red-brown (darker at mouth); **exothecial cells** not in longitudinal ranks, irregular (± isodiametric, shortly oblong or oblate), smooth, with uniformly thickened walls, mostly <30 µm in greater diam.; **annulus** vesicular and persistent; **operculum** rostrate from a conic base, c. 1 mm. **Exostome teeth** pale yellow-brown, narrowly lanceolate, inserted c. 50 µm beneath the rim, c. 700 µm long, bordered, outer surface finely papillose (not transversely striate) in lower half, baculate above, inner surface lamellate; **endostome** with a high membrane; segments ± equal the teeth, keeled, and widely perforate; cilia in groups of 1–3, nodose. **Calyptra** cucullate, covering the operculum and upper portion of the capsule, c. 3.3 mm. **Spores** ± spherical, 18–21 µm, pale brown, finely papillose.

Illustrations: Plate 5. Scott & Stone 1976, pl. 56 (as *Rhizogonium mnioides*); Malcolm & Malcolm 2003, p. 57 (as *Pyrrhobryum mnioides*); Meagher & Fuhrer 2003, p. 167; Seppelt 2004, fig. 97 (as *P. mnioides*).

Distribution: NI: N Auckland, S Auckland, Gisborne, Hawke's Bay, Taranaki, Wellington. SI: Nelson, Marlborough, Canterbury, Westland, Otago, Southland; St; Ch; A; M. Reported from C by Vitt (1974, as *Rhizogonium mnioides*).

Australasian. Tasmania*, mainland Australia*. The subsp. *mnioides* is restricted to South America.

Habitat: On fine or coarse, humic or mineral soil, on rotten logs, tree bases, in lightly to densely shaded forest, subalpine scrub, and occasionally in alpine tussock grassland. It occurs most commonly and is best developed in moist and shaded situations in forest, but also occurs in well-lit habitats. It is often associated with stream margins and when subject to submergence it can be nearly black in colour. Apparently tolerant of a wide range of nutrient availability. It is widespread, frequent, and morphologically variable in N.Z. On North I. from c. 30 (Warawara Forest, N Auckland L.D.) to c. 1200 m (Kaweka Range, Hawke's Bay L.D.); on South I. from near sea level (Nydia Bay, Marlborough L.D.) to at least 1340 m (Lake Peel and Mt Owen Range, Nelson L.D).

Notes: The single published record of *P. mnioides* from the Kermadecs (Sykes 1977, p. 58) is based on a misidentification of *P. paramattense* and it was excluded from the flora of that archipelago by both Beever et al. (1996) and by de Lange & Beever (2015).

Paradoxically, perigonia in this dioicous species are difficult to locate despite the common occurrence of capsules. The perigonia are axillary on the lower portion of stems and branches, often partially obscured by rhizoids. Occasionally they occur on rather short (5–10 mm) lateral branches. Scott & Stone (1976, p. 314) quoted from an unknown source that the perigonia (which Scott & Stone had not seen) were “terminal at the apex of main stems”, but this is not the usual position.

The type of *Hypnum spiniforme* var. β Hook.f. & Wilson from the Auckland Islands has not been seen.

Etymology: The subspecies epithet refers to its contorted dry leaves.

Pyrrhobryum paramattense (Müll.Hal.) Manuel, *Cryptog. Bryol. Lichénol.* 1: 69 (1980)

≡ *Mnium paramattense* Müll.Hal., *Syn. Musc. Frond. 2,* 555 (1851)
≡ *Rhizogonium paramattense* (Müll.Hal.) Reichardt, *Reise Novara 1,* 180 (1870)
Type specimen: Australia (Nova Hollandia). Not seen.

Misapplications: *Rhizogonium spiniforme sensu* Sykes (1977, p. 58)

Plants robust, brown- or dark green, unbranched or forked near base, forming dense tufts. **Stems** erect, unbranched, red-brown below, green above, c. 15–50 mm high, not complanate, in cross-section ± three-angled, with 2–3 layers of small, thick-walled cortical cells (the outermost strongly pigmented) surrounding a medulla of larger, firm-walled cells and a weak central strand, beset at base with red-brown, strongly papillose rhizoids. **Leaves** wide-spreading below (excluding the reduced basal leaves) and progressively more erect towards the stem apex, flexuous when dry, symmetric, linear-lanceolate with an acuminate apex, not concave, not decurrent, partially bistratose and plane at margins, serrate nearly to base by up to 25 pairs of single-celled teeth, 4.5–6.0 × 0.3 mm, becoming progressively reduced and scale-like near stem base. **Upper laminal cells** firm-walled, irregular in shape (mostly rounded-oblong, isodiametric, or oblate), not exceeding 1.5:1, 15 µm or less in greater diam., scarcely differentiated in lower part of leaf, usually with a few rows of cells at insertion ± longer (to 4:1); **marginal cells** partially bistratose (forming in parts distinct wings that are best viewed in cross-section) but otherwise not differentiated; **alar cells** not differentiated. **Costa** concolorous, c. 120 µm wide near leaf base (flaring to 150 µm or more at extreme base), evenly tapered, c. 60–75 µm at mid leaf, excurrent, bearing numerous single or paired abaxial spines for ⅓–½ its length, in cross-section plano-convex, with c. 8 median guide cells, and large abaxial and adaxial stereid bands.

Dioicous. Perichaetia single or in clusters at base of stem, with leaves linear-lanceolate, costate, c. 2 mm. **Perigonia** scattered on lower stem (to 7 or more per stem, and extending at least 8 mm above stem base), with bracts c. 1.5 mm, costate, acuminate from an obovate, concave, and pigmented base, with numerous antheridia and filiform, 6–8-celled paraphyses. **Setae** 20–42 mm, straight, smooth, c. 180 µm diam., twisting weakly to the left, red-brown; **capsules** inclined, oblong-cylindric, asymmetric, 2.3–2.6 mm, smooth, moderately constricted below the mouth when dry, pale brown; **exothecial cells** not in distinct longitudinal ranks, oblong, with uniformly thickened walls, smooth, mostly 45–60 × 18–21 µm; **annulus** vesicular and persistent; **operculum** rostrate from a conic base, c. 1 mm. **Exostome teeth** pale yellow-brown, narrowly lanceolate, inserted close to rim, c. 700 µm long, bordered, outer surface transversely striate in lower half, baculate above, inner surface lamellate; **endostome** from a high membrane; segments as long as teeth, keeled, variably perforate; cilia in groups of 3, well-developed and nodose. **Calyptra** not seen. **Spores** ± spherical, 15–18 µm, very finely papillose.

Illustrations: Plate 6. Scott & Stone 1976, pl. 57 (as *Rhizogonium parramattense*); Streimann 2002, fig. 62, 1–2; pl. 29.

Distribution: K; NI: N Auckland (Maungaraho Rock Scenic Reserve, Puketi State Forest, Waipoua Forest), S Auckland (Mayor I.); Ch (Tuku-a-Tamatea Reserve).

Australasian. Mainland Australia*, Norfolk I.*, Lord Howe I.*

Habitat: According to Sykes (1977, p. 58) this species, which he cited as *Rhizogonium spiniforme* (Hedw.) Bruch, is a “common and locally abundant epiphyte and common terrestrial of the wet and dry forest” on Raoul I. in the Kermadecs. In N Auckland it occurs on rotten wood, tree trunks (*Elaeocarpus* and *Weinmannia*), and on rock in warm temperate forest of varying species composition. The single documented Chatham I. collection grew on silty peat at the margin of a small stream which was “evidently frequently flooded”. Occurring from c. 40–520 m in the Kermadec Is, and recorded from c. 140–305 m on North I.

Notes: *Pyrrhobryum paramattense* is known in the North I. by at least six well-documented collections (three being from Waipoua Forest). Sainsbury (1955, p. 299) excluded *Rhizogonium spiniforme* from the flora as a “doubtful species”. My interpretation of Sainsbury’s comments is that he did not see either of the Cunningham collections he mentioned. Presumably the two specimens cited by Dixon (1926, p. 222) are Cunningham collections. I have not seen the Cunningham material. Whittier’s

(1976, p. 174) claim that *R. spiniforme* occurs in New Zealand is presumably founded on Dixon's comments.

At least 16 collections are known from the Kermadec Is., and the dioicous sexuality of several of these collections can be readily demonstrated. Repeated efforts to locate antheridia in North I. material have failed.

Material has been seen in BM (herb. Hampe) which is labelled in Müller's script: "*Mnium (Rhizogonium) paramattense mihi*"; it was collected from the Brisbane River by Dietrich in 1864. If original material (collected by Hügel) cannot be located, this material would be a suitable neotype.

Recognition: *Pyrrhobryum paramattense* can be distinguished from *P. mnioides* subsp*. contortum* (both are dioicous) by having flexuose (not crisped) dry leaves that are much reduced in size toward the stem base, differently positioned sex organs, shorter basal leaf cells and no leaf decurrencies. At least in the herbarium, the overall aspect of the two species is quite different.

Pyrrhobryum paramattense is a dioicous segregate of the synoicous and pantropical *P. spiniforme*. Inoue & Iwatsuki (1976) studied the cytotaxonomy of the "*Rhizogonium spiniforme* complex" and noted that the synoicous and autoicous conditions are correlated with the chromosome number n=12 and the dioicous condition with n=6. They considered synoicy to be "one of the most important characters" for the recognition of "*R. spiniforme* var. *spiniforme*" and suggested that varietal status may be more appropriate for its dioicous allies.

Etymology: The species epithet refers to a river in Sydney, N.S.W. The epithet is here spelt "*paramattense*" in accordance with the protologue of the basionym, although the modern spelling of the river is usually given as Parramatta.

Rhizogonium Brid., *Bryol. Univ. 2,* 663 (1827)

Plants small or medium-sized, tufted or forming turves. **Stems** prostrate or erect, unbranched, with upper leaves distichous and lower leaves scale-like and unranked, in cross-section with a central strand and thick-walled cortical cells. **Leaves** uniform in shape, distichous, spreading, ovate, oblong-ovate, or ovate-lanceolate, plane at margins, with or without a border of elongate cells, moderately or strongly asymmetric at base, not or rarely decurrent, serrate or dentate above by single or rarely multicellular teeth. **Upper laminal cells** ± oblong-hexagonal and rounded, <2:1, firm-walled, smooth or rarely with fine cuticular striations, becoming ± more elongate in lower leaf; **marginal cells** not differentiated or elongate and forming a unistratose or rarely bistratose border; **alar cells** not differentiated. **Costa** excurrent (often strongly) or ending below the leaf apex, lacking abaxial teeth.

Dioicous. Perichaetia clustered or single at base of stem. **Perigonia** bud-like, clustered at base or scattered on lower stem, often difficult to observe. **Setae** elongate and straight; **capsules** horizontal or pendent, oblong-cylindric with a poorly defined neck; **operculum** rostrate from a conic base. **Peristome** double and well-developed; **exostome teeth** yellow-brown in N.Z. species, bordered, finely papillose or striolate below; **endostome** with a high basal membrane, segments nearly as long as the teeth, keeled but lacking perforations, cilia 2–3, well-developed or rudimentary. **Calyptra** cucullate. **Spores** small, finely papillose.

Taxonomy: A genus of c. nine species distributed in Australasia, East Asia, Pacific Islands, and South America. Gilmore (2006) reported four species from Australia.

A type has not been designated for this genus.

The genus is here treated in a narrower sense than by Brotherus (1924). Manuel (1980) emended the genus to include only those species placed in section *Rhizogonium* Mitt., and in so doing, elevated section *Pyrrhobryum* (Mitt.) Mitt. to generic rank. Manuel's interpretation of the genus *Rhizogonium* is accepted here. Matteri & Piñero (1987) provided useful notes on the genus in temperate South America.

Koponen et al. (1986) noted that some species retained in *Rhizogonium* by Manuel (e.g., *R. pennatum*) have multistratose leaf borders, but that in such instances the marginal cells were elongate, rather than short as in species of *Pyrrhobryum.* Other discrepancies exist between Manuel's classification summary and N.Z. species, such as the occurrence of decurrent leaves in *R. distichum*.

Etymology: According to Meagher (2011), the generic names alludes "to the fact that the sporophytes appear to arise from the 'root' of the plant… although they are actually borne on specialised branches at the base of the stem". However, Crum & Anderson (1981, p. 657) suggest that *Rhizogonium* "refers to copious paraphyses suggesting a rooted sporophyte."

1 **Costa** ending several cells below the leaf apex, >100 µm wide and rather ill-defined near base; **leaves** decurrent, unbordered, >0.8 mm wide; **margins** dentate with mostly multicellular, broadly acute or obtuse teeth; **endostomal cilia** well-developed .... *R. distichum*

1' **Costa** excurrent to form an arista, <75 µm wide and well-defined near base; **leaves** not decurrent, bordered or not, <0.6 mm wide; **margins** serrate or serrate-spinose with mostly one-celled and acute teeth; **endostome cilia** well-developed or rudimentary 2

2 **Vegetative leaves** bordered by 3–5 rows of elongate cells, usually >1.9 mm long; **stem cross-section** lacking parenchyma, with c. 5 layers of thick-walled cells surrounding a large central strand; **endostomal cilia** well-developed .... *R. pennatum*

2' **Vegetative leaves** unbordered, <1.7 mm long; **stem cross-section** with a layer of thin-walled parenchyma cells between the cortical cells and the central strand; **endostomal cilia** rudimentary .... *R. novae-hollandiae*

Rhizogonium distichum (Sw.) Brid., *Bryol. Univ. 2,* 665 (1827)

≡ *Hypnum distichum* Sw., *J. Bot. (Schrader)* 1800(2): 179, pl. 3, fig. A (1801)
Type material: N.Z., Dusky Bay, *A. Menzies 89*, 1791, BM-Hooker!, BM-Wilson!

Plants medium-sized, dull green, forming turves. **Stems** prostrate, unbranched, dull green above, usually red-brown near base, c. (8–)15–25 mm, in cross-section elliptic, with 3–5 layers of very thick-walled cortical cells surrounding parenchyma cells and a large, flattened central strand, beset at base with bright red-brown, smooth rhizoids. **Shoots** to 4 mm wide, strongly complanate. **Leaves** distichous, spreading, asymmetric at base, oblong-ovate with a broadly acute or obtuse apex, not or very weakly concave, variably decurrent, unbordered, dentate above with few to numerous, broadly acute or obtuse, mostly multicellular teeth, (1.8–)2.2–2.6 × 0.9–1.2 mm, becoming much smaller and scale-like near stem base. **Upper laminal cells** thick-walled, ± hexagonal but ± irregular in shape and size, 0.5–2:1, at least some cells >18 µm in greater dimension, often more regular and ± quadrate or oblate towards margins, becoming elongate at extreme base, **alar cells** and **marginal cells** not differentiated. **Costa** broad (c. 120–200 µm) near base, uniformly tapered (c. 100–125 µm at mid leaf) and terminating several cells below the leaf apex, in cross section (at mid leaf) biconvex, with a central layer of guide cells, and elongate (3–6:1) superficial cells.

Dioicous. Perichaetia in clusters at base of stem, with leaves lanceolate, costate, c. 2 mm (but apparently lengthening after fertilisation to c. 3 mm). **Perigonia** dark brown and budlike, single at base of stem or numerous and scattered on stem, with bracts c. 1.2 mm, ecostate, acute from an ovate and concave base, with filiform, 5–7-celled paraphyses. **Setae** 20–35 mm, straight, smooth, twisting weakly to the left, pale brown; **capsules** horizontal or pendent, oblong-cylindric from a slightly asymmetric base, 2.0–3.5 mm, smooth and not or weakly constricted below the mouth when dry, pale yellow-brown, dark brown at mouth; **exothecial cells** irregular, mostly oblong-hexagonal or quadrate, 1–3:1 with firm walls, finely and irregularly striate; **annulus** not clearly observed; **operculum** rostrate from a conic base, c. 1 mm. **Exostome teeth** pale yellow-brown, narrowly lanceolate, inserted c. 60 µm beneath the rim, c. 500 µm long, bordered, outer surface finely papillose (non-striolate) below, more coarsely so above, inner surface lamellate; **endostome** pale, with high basal membrane; segments nearly as long as the teeth, keeled but not perforate, papillose-baculate; cilia in groups of (2–)3, nodose, finely baculate. **Calyptra** cucullate, c. 3 mm, smooth. **Spores** ± spherical, 15–19 µm, pale brown, finely papillose.

Illustrations: Plate 7. Malcolm & Malcolm 2003, p. 59; Meagher & Fuhrer 2003, p. 47; Gilmore 2006, pl. 53.

Distribution: NI: N Auckland, including offshore islands (LB), S Auckland (including Mayor I.), Gisborne, Hawke’s Bay, Taranaki, Wellington. SI: Nelson, Marlborough, Canterbury, Westland, Otago, Southland; St; Sol; A.

Australasian. Tasmania*, mainland Australia*. A report by Bartram (1945) of this species from P.N.G. was rejected by Koponen et al. (1986). Scott & Stone (1976) recorded this species from southeast Asia, without detail.

Habitat: Primarily on rotten logs, humic soil (occasionally thin and over rock), less commonly on tree or tree-fern trunks in a variety of forest types. Ranging from c. 60 m (Logue’s Bush Scenic Reserve, N Auckland L.D.) to c. 1200 m (Mt Taranaki, Taranaki L.D.) on North I; near sea level (numerous localities including Punakaikī, Nelson L.D. and Papatōwai, Otago L.D.) to at least 1100 m (Mt Mytton and Flora Saddle, both Nelson L.D.) on South I.

Notes: Perigonia are only infrequently observed, which is surprising given the frequent occurrence of capsules.

Holotype material has not been seen, but could be searched for in the Swartz herbarium at UPS. If no appropriate material is present there, one of the duplicates of *A. Menzies 89* in BM would be an appropriate lectotype. One of two duplicates in herb. Hooker bears the more complete collection data; the other bears "New Zealand, Mr Menzies" and a citation of Swartz's protologue. The duplicate in herb. Wilson bears "Dusky Bay, *Menzies 89*" and the herbarium number "H(ooker) 3313".

Recognition: In a N.Z. context, *R. distichum* is unlikely to be mistaken for anything else. *Rhizogonium graeffeanum* of Australia and southeast Asia is similar but differs by having costae that are narrower, not dilated at their base, and percurrent to short excurrent.

It is possible that *R. lamii* Reimers (see Koponen et al. 1986) from P.N.G. is a form of *R. distichum*, but no material from there has been available for comparison. Koponen et al. (1986, p. 21) considered the occurrence of *R. distichum* in P.N.G. to be "highly unlikely". If these names were shown to be taxonomically synonymous, *R. distichum* would have priority.

Etymology: The species epithet refers to the two-rowed insertion of the leaves.

Rhizogonium novae-hollandiae (Brid.) Brid., *Bryol. Univ. 2,* 664 (1827)

≡ *Fissidens novae-hollandiae* Brid., *Bot. Zeitung (Regensburg)* 1: 212, 234 (1802)
Holotype: Australia (Victoria?), comm. La Billardière, B!

Plants small, dull green, forming turves. **Stems** prostrate, unbranched, dull green above, usually red-brown near base, c. (8–)10–15 mm, in cross-section elliptic, with 3–5 layers of very thick-walled cortical cells surrounding well- or ill-defined parenchyma cells and an often flattened central strand, beset at base with bright red-brown, smooth rhizoids. **Shoots** 1.8–2.5 mm wide, complanate when moist, ± conduplicate when dry. **Leaves** distichous, spreading, asymmetric at base, ovate or oblong-ovate with an acute apex, neither concave nor decurrent, unbordered, serrate above by numerous acute, mostly unicellular teeth, 1.0–1.6 × 0.3–0.4 mm, becoming much smaller and scale-like near stem base. **Upper laminal cells** firm walled, rounded and ± hexagonal but irregular in outline and size, 0.5–2:1, <15 µm in greater dimension, smooth or with ± prominent cuticular striolations, often a single row at margin somewhat longer (to 3:1), but not forming a distinct border, becoming somewhat more elongate (to 4:1) at extreme base of leaf; **alar cells** not differentiated. **Costa** variable in width, 30–60(–75) µm near base, uniformly tapered (usually 30–40 µm in mid leaf), excurrent to form a stout arista (90–300 µm long), in cross-section (at mid leaf) plano-convex (projecting more strongly on abaxial surface), with a central layer of guide cells and elongate superficial cells.

Dioicous. Perichaetia in clusters at base of stem, with leaves lanceolate, costate, c. 1.6 mm. **Perigonia** red-brown and budlike, in clusters at base of stem, bracts c. 0.5 mm, ecostate, acute from an ovate and concave base, surrounding c. 5 antheridia and filiform, 5-celled paraphyses.
Setae 11–30 mm, straight, smooth, twisting to the left, pale brown; **capsules** horizontal or pendent, oblong-cylindric from a slightly asymmetric base, 1.8–2.1(–2.5) mm, smooth and not or weakly constricted below the mouth when dry, pale yellow-brown, dark brown at mouth; **exothecial cells** irregular, mostly oblong-hexagonal or quadrate, 1–3:1, with firm, smooth walls; **annulus** not seen; **operculum** rostrate from a conic base, c. 1 mm. **Exostome teeth** pale yellow-brown, narrowly lanceolate, inserted c. 50 µm beneath the rim, c. 500 µm long, bordered, outer surface finely and densely papillose-striolate below, more coarsely papillose-trabeculate above, inner surface lamellate; **endostome** pale, with a basal membrane ⅓–½ the total endostome height; segments nearly as long as the teeth, keeled but not perforate, papillose-baculate; cilia rudimentary. **Calyptra** cucullate, c. 2 mm, smooth. **Spores** ± spherical, 15–18 µm, finely papillose.

Illustrations: Plate 8. Meagher & Fuhrer 2003, p. 47.

Distribution: NI: N Auckland including offshore islands (LB), S Auckland, Gisborne (Lake Waikaremoana), Wellington. SI: Nelson, Marlborough, Canterbury, Westland, Otago (Leith Valley, Mt. Cargill, Tautuku), Southland; St, Ch, Sol, A, C.

Australasian. Tasmania*, mainland Australia*, Chile*.

Habitat: Often on tree fern (*Cyathea dealbata, Dicksonia squarrosa*) caudices and rotten wood, but also occurring on tree bases, exposed roots, rotting logs, and rarely on soil. *Libocedrus*, *Lophozonia*, *Weinmannia*, *Metrosideros*, and *Rhopalostylis* appear to be the most common genera of non-tree-fern hosts. Beever (1984) recorded its presence on 93% of *Cyathea dealbata*, 41% of *Dicksonia squarrosa,* and 12% of *Rhopalostylis sapida* trunks in the Waitakere Ranges (N Auckland L.D.) but did not record it from *Cyathea medullaris* (with 41 trunks examined in detail). Ranging from c. 75 to 1200 m on North

I. and from near sea level (Dusky Sound, Southland L.D.) to c. 1000 m (Mt Arthur, Nelson L.D.) on South I; not growing above tree line. *Calomnion complanatum* and *Rhizogonium pennatum* are frequent associates.

Notes: Populations in the southern parts of the range, growing as epiphytes or on rotten wood and perhaps in drier situations, are often more compact, with stouter costae (to 75 µm wide near leaf base), more striolate cuticles, and shoots more conduplicate (especially when dry) than more northern plants. While such forms viewed in isolation may appear distinctive, they are here considered to fall within the range of variation of the species, and not given taxonomic recognition. A collection by W. Martin from the head of Southwest Arm of Paterson Inlet, Stewart I. exhibits considerable variability with respect to the above characters and also has prominent cuticular striolations. Cuticular striolations were observed for this species by Scott & Stone (1976, p. 312); they appear to be prominent in only a small fraction of N.Z. populations.

There is no type material of *Fissidens novae-hollandiae* Brid. at BM. Although von Bridel-Brideri's original description has not been located, his description in Bryologia Universa (1827) indicates the type to have been collected by La Billardière, a naturalist on the La Pérouse expedition.

Rhizogonium novae-hollandiae is superficially similar to *Calomnion complanatum* and depauperate plants of the two are sometimes confused. In such material the number of rows of leaves (two in *R. novae-hollandiae,* three in *Calomnion*) can be difficult to observe and the stoutly excurrent costae and the coarser toothing of the leaves of the former are more useful differentiating features. When fertile, the larger, horizontal to pendent, and peristomate capsules of *R. novae-hollandiae* readily distinguish it from *C. complanatum*, as does the leaf dispensation. *Leptotheca gaudichaudii* is also sometimes confused with *R. novae-hollandiae*, but it is distinguished by having non-complanate shoots, larger vegetative leaves, filamentous brown brood bodies, and erect and striate capsules.

Etymology: The epithet *novae-hollandiae* is derived from an early name for Australia.

Rhizogonium pennatum Hook.f. & Wilson in Wilson, *Bot. Antarct. Voy. II (Fl. Nov.-Zel.) Part II* 116 (1854)

Lectotype: N.Z., Dusky Bay, *A. Menzies 90*, 1791, BM-Wilson! Isolectotype: BM-Hooker 2544!

= *Rhizogonium aristatum* Hampe, *Linnaea* 40: 314 (1876)
≡ *Rhizogonium pennatum* var. *aristatum* (Hampe) Dixon, *Bull. New Zealand Inst.* 3: 220 (1926)
Holotype: Tasmania, “Mounts toward Lake Pedder”, *Schuster 70*, BM-Hampe!

= *Rhizogonium sinuatum* Müll.Hal., *Hedwigia* 36: 333 (1897)
Lectotype: N.Z., Westland, Greymouth, herb. R. Helms, 1885, BM-Bescherelle! Isolectotype: CHR 494774!

Plants medium-sized, bright green when fresh, turning brown-green in herbarium, forming loose or dense turves. **Stems** erect, unbranched, pale brown- or yellow-green, c. 15–25(–35) mm, in cross-section with c. 5 layers of thick-walled cells surrounding a large central strand (lacking parenchyma), beset at base with sparse, bright red-brown, smooth rhizoids. **Shoots** 3–4 mm wide, complanate. **Leaves** distichous, spreading, asymmetric at base, ovate-lanceolate with an acute apex, neither concave nor decurrent, bordered throughout by 3–5 rows (fewer near apex) of bistratose, elongate cells that are confluent with the excurrent costa, variably serrate in upper half with mostly unicellular teeth, (1.5–)1.9–2.2(–2.5) × 0.3–0.5 mm, becoming smaller and scale-like near stem base. **Upper laminal cells** firm walled, rounded-hexagonal or ± irregular in shape, mostly c. 15 µm in greater dimension, somewhat longer (to c. 30 µm) and narrower near leaf base; **alar cells** not differentiated; **marginal cells** narrow and elongate, mostly 30–90 µm, forming a distinct and bistratose border 3–5 cells wide at mid leaf. **Costa** c. 60–75 µm wide near base, tapering to c. 40–50 µm at mid leaf, long excurrent to form a stout, smooth or toothed arista c. 220–450 µm long, in cross section (at mid leaf) biconvex, with a central layer of guide cells, and elongate (10–15:1) superficial cells.

Dioicous. Perichaetia at base of stem, with leaves, oblong-lanceolate, costate, not bordered, to c. 2 mm (but apparently lengthening after fertilisation to c. 3 mm). **Perigonia** brown and budlike, single or in pairs at base of stem, with bracts c. 0.6 mm, ecostate, ovate and acute, concave at base, with filiform, 5-celled paraphyses. **Setae** c. 25 mm, straight, smooth, twisting weakly to the left below and to the right above (when dry), red-brown; **capsules** horizontal, oblong-cylindric from a slightly asymmetric base, c. 2.0 mm, smooth and not constricted below the mouth when dry, pale yellow- or red-brown; **exothecial cells** irregular, mostly oblong-hexagonal or quadrate, 1–3:1, thick-walled, not striate; **annulus** well differentiated and persistent; **operculum** rostrate from a conic base, c. 1 mm. **Exostome teeth** pale yellow-brown, narrowly lanceolate, inserted c. 75 µm beneath the rim, c. 530 µm long, faintly bordered, outer surface finely and densely papillose (non-striolate) below, more coarsely so above, inner surface lamellate; **endostome** pale, with a high basal membrane; segments nearly as long as the teeth, keeled but not perforate, papillose-baculate; cilia in groups of (2–)3, not nodose, finely baculate. **Calyptra** not seen. **Spores** ± spherical, 16–19 µm, pale brown, nearly smooth.

Illustrations: Plate 8. Scott & Stone 1976, pl. 55.

Distribution: NI: N Auckland, offshore islands only (LB, GB), S Auckland (Coromandel Peninsula, Kaimai Range). SI: Nelson, Westland, Otago (Mt. Cargill), Southland (Fiordland), St; Ch; A; C. Australasian. Tasmania*, mainland Australia.

Habitat: Occurring on a variety of shaded substrates including rotten logs, vertical soil banks, tree bases, and tree fern caudices as well as non-calcareous rock such as conglomerates, granite, and mudstone. Well-developed colonies occur on overhanging and strongly weathered granite near the eastern terminus of the Croesus Track in Westland L.D. and on thin humus over shaded quartzite boulder faces at Te Kuha in Nelson L.D. Near the southern limit of its range this species occurs more frequently as an epiphyte on tree ferns. On North I. *R. pennatum* is known only from a handful of localities with a restricted elevation range of c. 690–950 m; on South I. it occurs mainly in western parts of the island from near sea level (Pororari River, Nelson L.D. and Resolution I., Southland L.D. to at least 960 m (Mt Euclid, Nelson L.D.).

Notes: The majority of collections consist of sterile female plants. Perichaetia are generally easily found, while perigonia are very difficult to observe. The rarity of male plants is reflected in a paucity of fruiting collections.

Of the two syntypes designated by Hooker & Wilson, only that collected by Menzies is fertile. The majority of Wilson’s notes (in herb. Wilson) are also based on this collection; it is therefore an appropriate choice as the lectotype. The isolectotype in herb. Hooker (BM K) bears (in Menzies’ script): “No. 90 Dusky Bay N. Zeeland 1791”. The lectotype has costae extending 330–380 µm beyond the end of the lamina; the margins are entire except for 1–2 teeth at the base of the arista in approximately half the leaves.

The type material of *R. aristatum* represents an extreme form of *R. pennatum*, albeit one not worthy of taxonomic recognition; this conclusion is prevised by comments made by Dixon (1926, p. 220). The leaves are somewhat smaller (c. 1.5 mm) than typical for the species, with some strongly toothed to spinose (with individual teeth to 55 µm). However, the majority of leaves have 4–6 short, rather blunt teeth on one side of the leaf and only sometimes one or two longer, more spinose teeth; there is considerable variability even within single stems. Both in stature and degree of marginal tooth development, the type falls within the range of continuous variation for the species. The occurrence of representative material in Tasmania also argues against recognition of *R. aristatum* at any taxonomic level.

The Helms collection interpreted here as the type of *R. sinuatum* is unremarkable in the context of *R. pennatum* variability. While neither of the two duplicates is labelled as a type, the associated data support this interpretation; it is unlikely that more suitable material can be located in other herbaria.

Recognition: *Rhizogonium pennatum* could be confused with *Calomnion complanatum*, with which it often grows on tree fern trunks. *Rhizogonium pennatum* is a more robust plant with basal rather than the terminal perichaetia seen in *C. complanatum*. It also lacks the reduced rank of ventral leaves of *C. complanatum* and has larger leaves (1.5–2.5 mm vs 0.7–1.1 mm long) with a well-developed leaf border, and more stoutly excurrent costae. The peristomate capsules are also very different.

Etymology: The epithet *pennatum* means feather-like.

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Conventions

Abbreviations and Latin terms

Abbreviations	**Meaning**
A	Auckland Islands
A.C.T.	Australian Capital Territory
aff.	allied to (*affinis*)
agg.	aggregate
Ant	Antipodes Islands
a.s.l.	above sea level
auct.	of authors (*auctorum*)
B	Bounty Islands
C	Campbell Island
c.	about (*circa*)
cf.	compare with, possibly the species named (*confer*)
c.fr.	with fruit (*cum fructibus*)
Ch	Chatham Islands
comb. nov.	new combination (*combinatio nova*)
D'U	D'Urville Island
et al.	and others (*et alia*)
et seq.	and following pages (*et sequentia*)
ex	from
fasc.	fascicle
fide	according to
GB	Great Barrier Island
HC	Hen and Chicken Islands
Herb.	Herbarium
hom. illeg.	illegitimate homonym
I.	Island
ibid.	in the same place (*ibidem*)
incl.	including
in herb.	in herbarium (*in herbario*)
in litt.	in a letter (*in litteris*)
inter alia	among other things (*inter alia*)
Is	Islands
K	Kermadec Islands
KA	Kapiti Island
LB	Little Barrier Island
L.D.	Land District or Districts
leg.	collected by (*legit*)
loc. cit.	in the same place (*loco citato*)
l:w	length:width ratio
M	Macquarie Island
Mt	Mount
nec	nor
NI	North Island
no.	number
nom. cons.	conserved name (*nomen conservandum*)
nom. dub.	name of doubtful application (*nomen dubium*)
nom. illeg.	name contrary to the rules of nomenclature (*nomen illegitimum*)
nom. inval.	invalid name (*nomen invalidum*)
nom. nud.	name published without a description (*nomen nudum*)
non	not
N.P.	National Park
N.S.W.	New South Wales
N.T.	Northern Territory (Australia)
N.Z.	New Zealand
op. cit.	in the work cited (*opere citato*)
pers. comm.	personal communication
PK	Poor Knights Islands

P.N.G.	Papua New Guinea
pro parte	in part
Qld	Queensland
q.v.	which see (*quod vide*)
RT	Rangitoto Island
S.A.	South Australia
s.coll.	without collector (*sine collectore*)
s.d.	without date (*sine die*)
sect.	section
SEM	scanning electron microscope/microsopy
sensu	in the taxonomic sense of
SI	South Island
sic	as written
s.l.	in a broad taxonomic sense (*sensu lato*)
s.loc.	without location (*sine locus*)
Sn	Snares Islands
s.n.	without a collection number (*sine numero*)
Sol	Solander Island
sp.	species (singular)
spp.	species (plural)
s.s.	in a narrow taxonomic sense (*sensu stricto*)
St	Stewart Island
stat. nov.	new status (*status novus*)
subg.	subgenus
subsect.	subsection
subsp.	subspecies (singular)
subspp.	subspecies (plural)
Tas.	Tasmania
TK	Three Kings Islands
U.S.A.	United States of America
var.	variety
vars	varieties
Vic.	Victoria
viz.	that is to say (*videlicet*)
vs	versus
W.A.	Western Australia

Symbols

Symbol	**Meaning**
µm	micrometre
♂	male
♀	female
±	more or less, somewhat
×	times; dimensions connected by × refer to length times width
>	greater than
<	less than
≥	greater than or equal to
≤	less than or equal to
=	heterotypic synonym of the preceding name
≡	homotypic synonym of the preceding name
!	confirmed by the author
*	in distribution statements, indicates non-N.Z. localities from which material has been confirmed by the author

Technical terms conform to Malcolm, B.; Malcolm, N. 2006: *Mosses and other Bryophytes: an Illustrated Glossary*. Edition 2. Micro-Optics Press, Nelson.

Abbreviations for Herbaria follow the standard abbreviations listed in *Index Herbariorum*.

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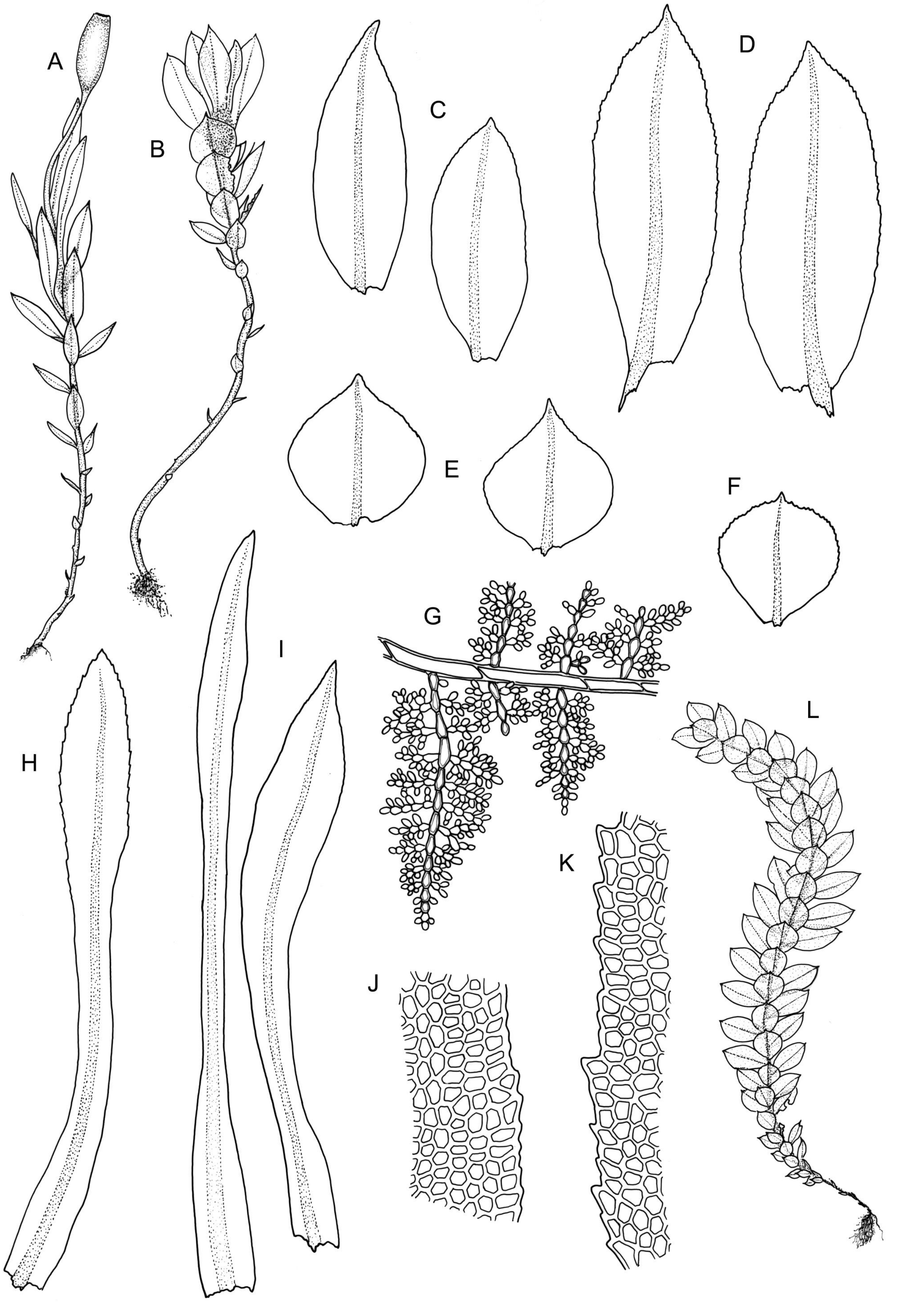


Plate 1: ***Calomnion*. A–L: *C. complanatum*.** A, habit with capsule. B, habit of ♂ shoot. C, two lateral leaves. D, two lateral leaves with denticulate margins. E, two ventral leaves. F, ventral leaf with denticulate margins. G, protonema with bipinnate chlorophyllose branches. H, inner perichaetial leaf with denticulate margins. I, two inner perichaetial leaves. J, upper laminal cells and margin of lateral leaf. K, upper laminal cells and margin of denticulate lateral leaf. L, habit of sterile shoot. A–C; E; I–J; L drawn from *A.J. Fife 11314*, CHR 514642; D; F; H; K drawn from *R.B. Allen s.n.*, CHR 405458; G drawn from *J.H. Tisdall 655*, CHR 433015.

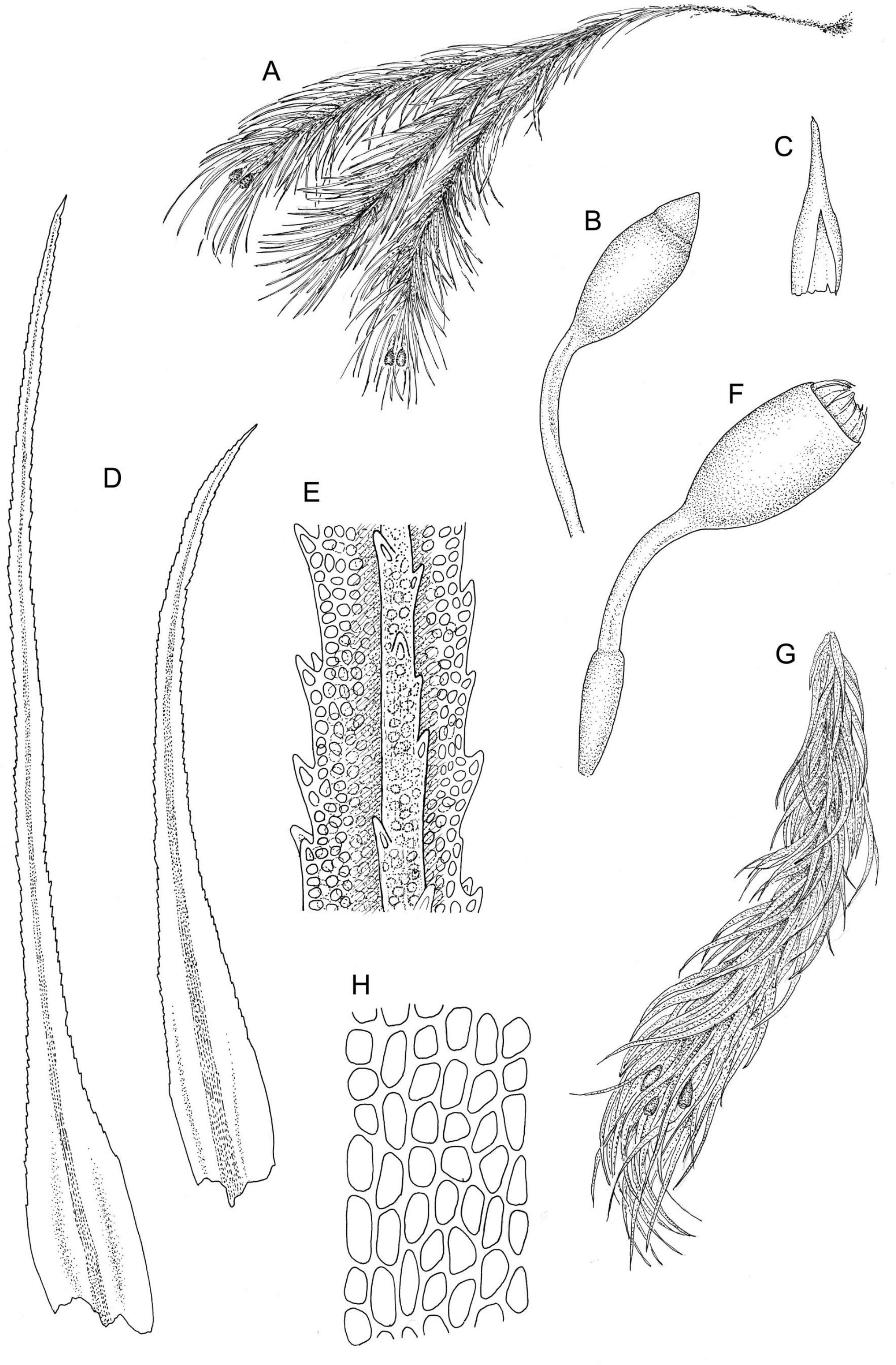


Plate 2: ***Cryptopodium*. A–H: *C. bartramioides*.** A, habit. B, capsule with operculum. C, calyptra. D, vegetative leaves. E, upper laminal cells and costa, abaxial view. F, capsule. G, branch detail, dry. H, lower laminal cells. Drawn from *J.E. Beever 36-49*, CHR 406782.

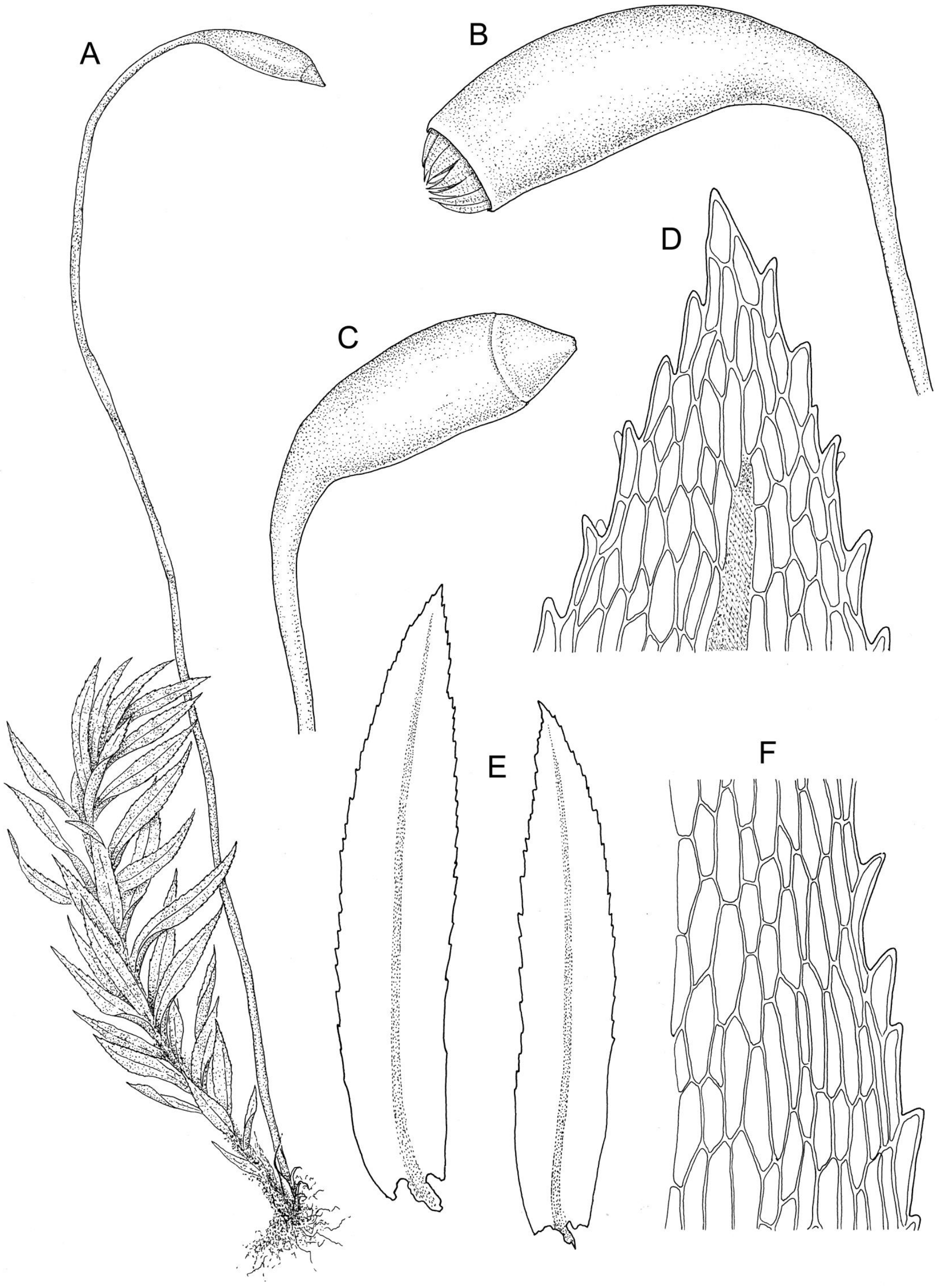


Plate 3: ***Goniobryum*. A–F: *G. subbasilare*.** A, habit. B, capsule. C, capsule with operculum. D, leaf apex. E, leaves. F, mid laminal cells at margin. Drawn from *W. Martin 245.13*, CHR 608307, and *G.O.K. Sainsbury 3223*, CHR 483597.

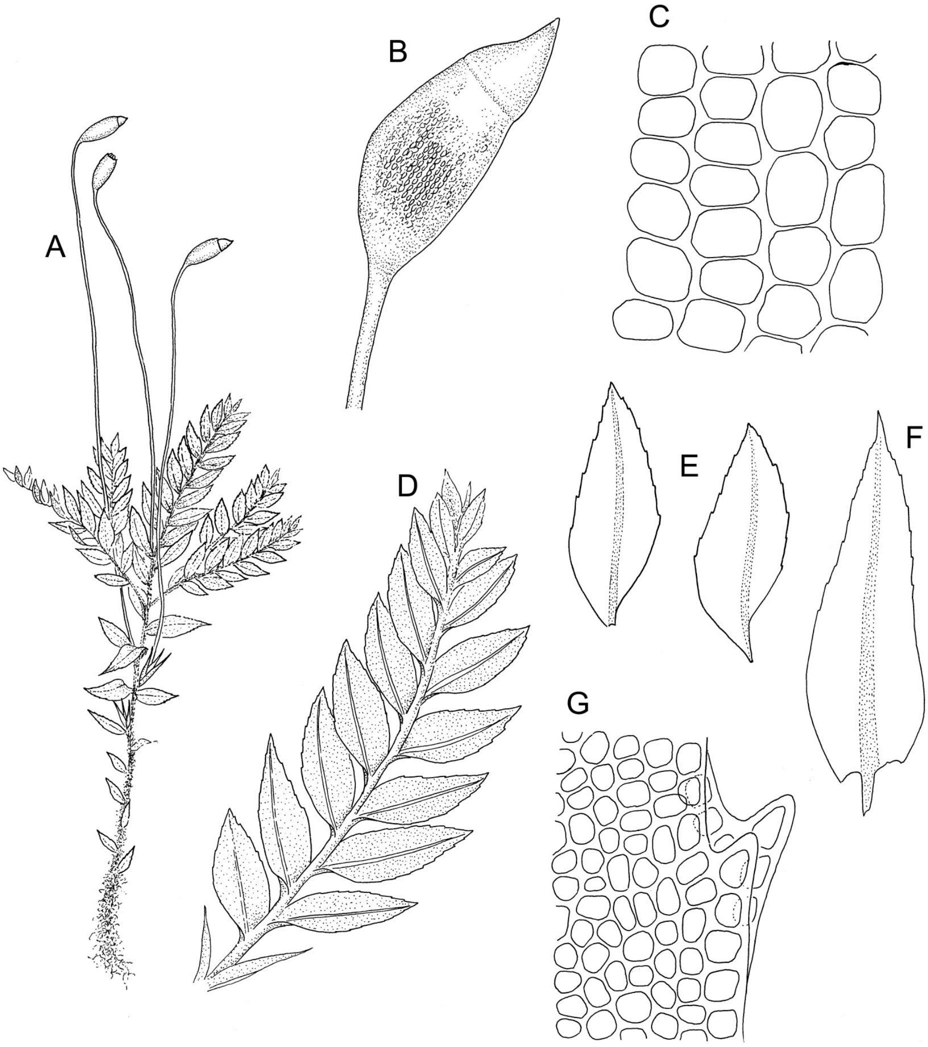


Plate 4: *Pyrrhobryum*. A–G: *P. bifarium*. A, habit with capsules. B, capsule with operculum. C, exothecial cells. D, branch detail. E, branch leaves. F, stem leaf. G, upper laminal cells of branch leaf at margin. Drawn from *K.W. Allison 3216*, CHR 454574.

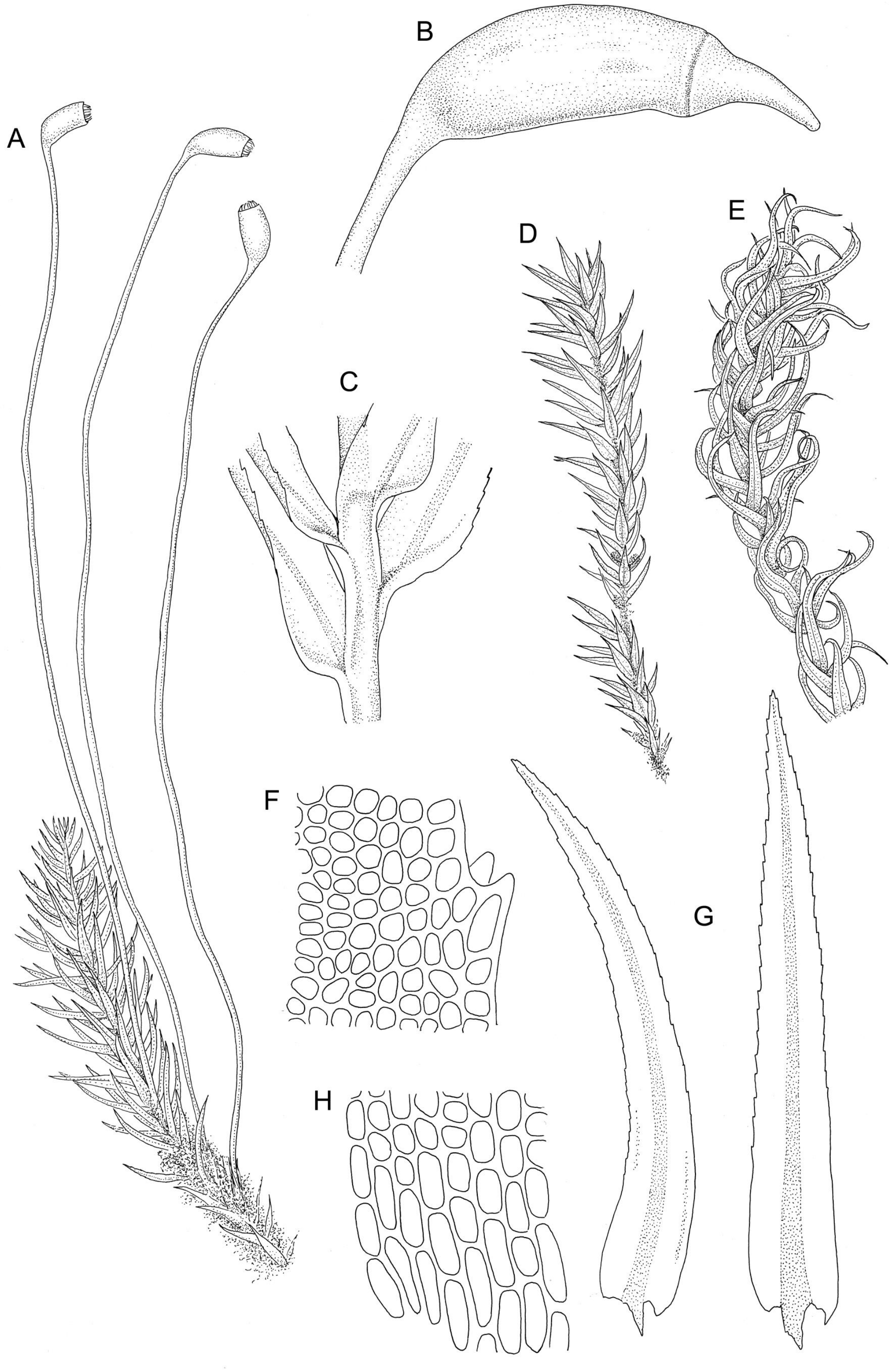


Plate 5: ***Pyrrhobryum*. A–H: *P. mnioides* subsp. *contortum*.** A, habit with capsules. B, capsule with operculum. C, stem detail showing leaf decurrencies. D, habit of male plant. E, portion of shoot, dry. F, upper laminal cells at margin. G, leaves. H, laminal cells at leaf base. Drawn from *T.W.N. Beckett s.n.*, 1900, CHR 517001.

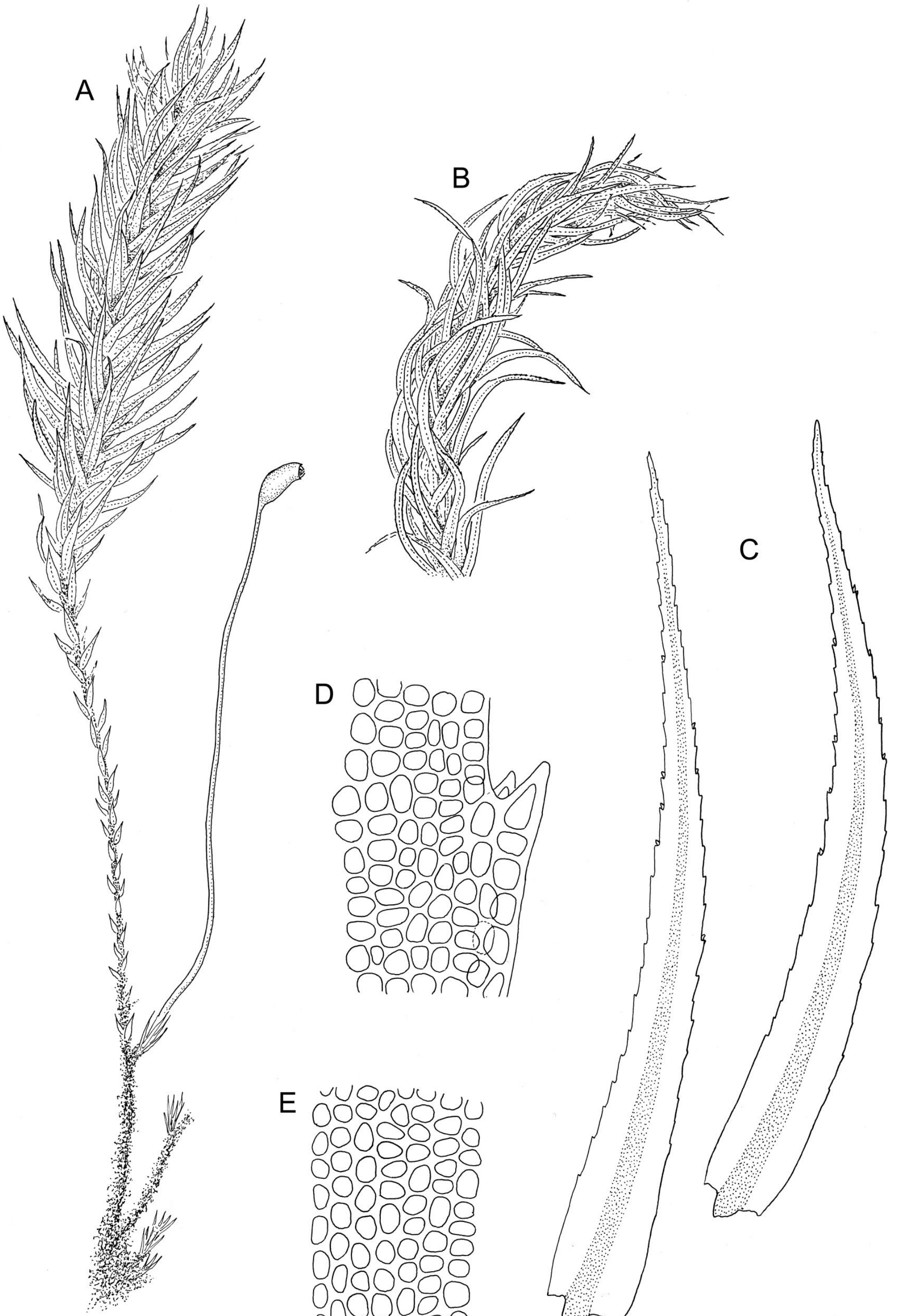


Plate 6: ***Pyrrhobryum*. A–E: *P. paramattense*.** A, habit with capsule. B, portion of shoot, dry. C, leaves. D, upper laminal cells at margin. E, laminal cells at leaf base. Drawn from *W.R. Sykes 738/K*, CHR 161701.

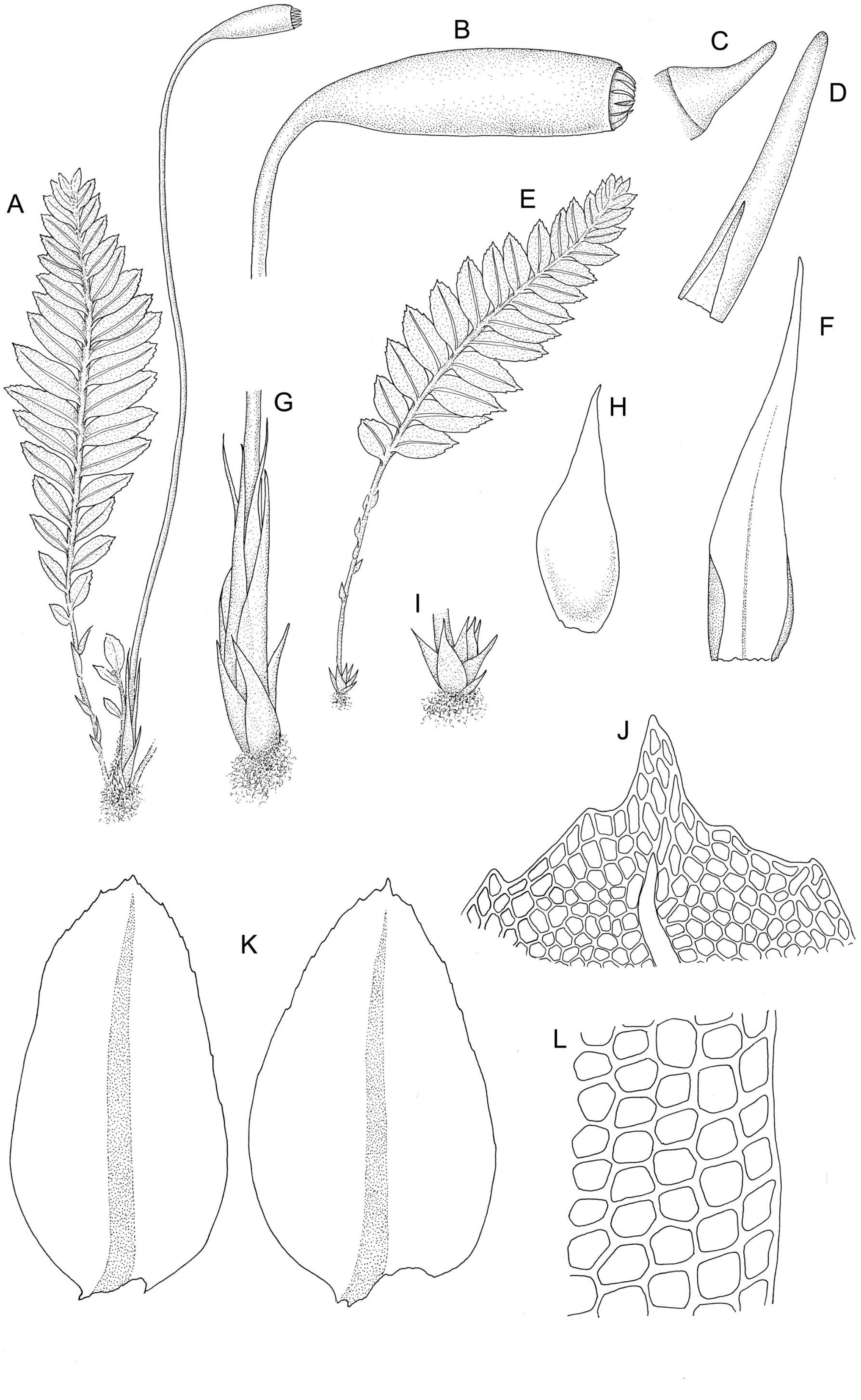


Plate 7: ***Rhizogonium*****. A–L:** ***R. distichum*****.** A, habit with capsule. B, capsule. C, operculum. D, calyptra. E, habit of male plant with basal perigonium. F, perichaetial leaf. G, perichaetium detail. H, perigonial bract. I, perigonium detail. J, leaf apex. K, leaves. L, upper laminal cells at margin. Drawn from *L. Visch 679*, CHR 267027.

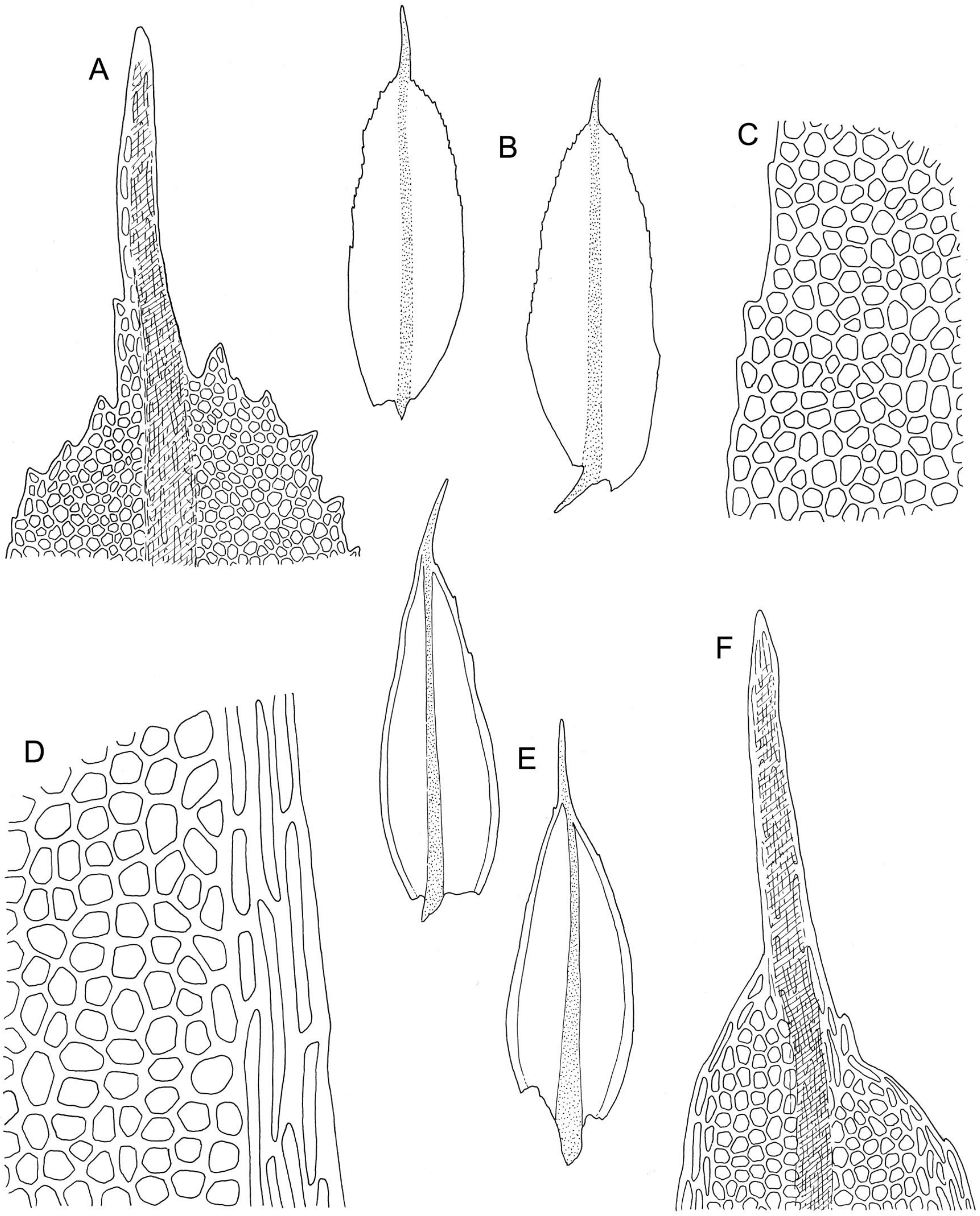
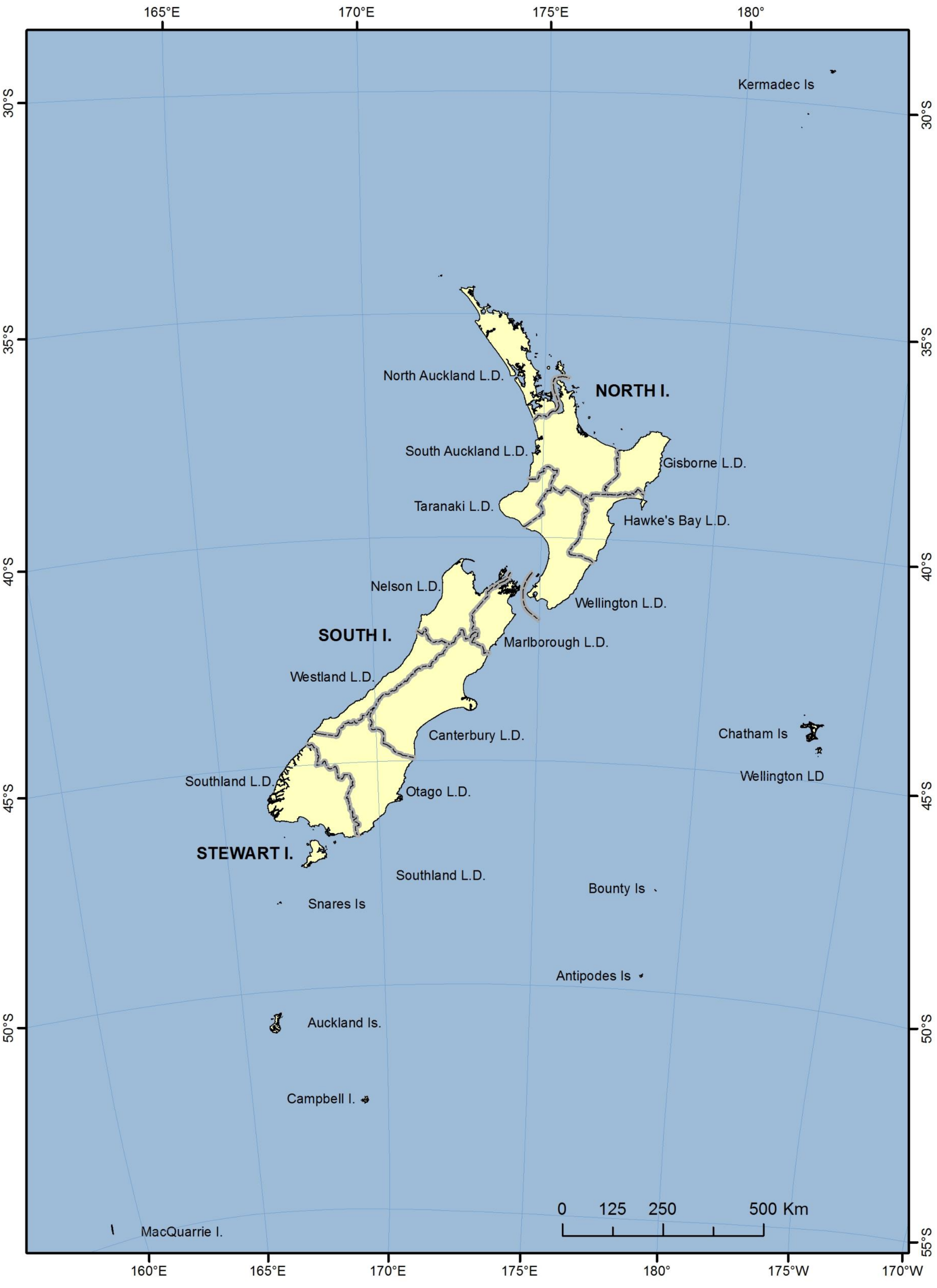
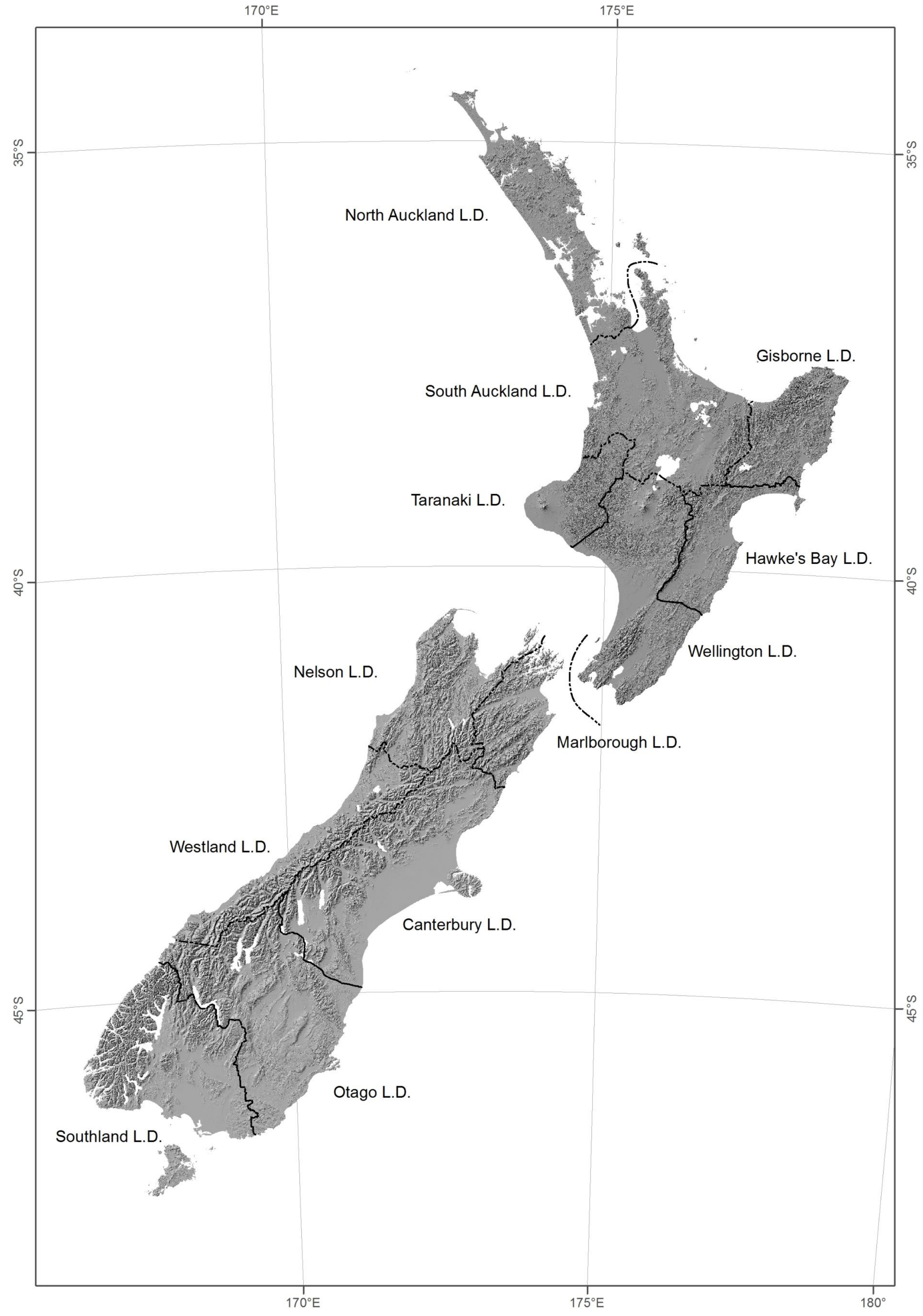


Plate 8: ***Rhizogonium*. A–C: *R. novae-hollandiae*.** A, leaf apex. B, leaves. C, upper laminal cells at margin. **D–F: *R. pennatum*.** D, upper laminal cells at margin. E, leaves. F, leaf apex. *R. novae-hollandiae* drawn from *A.J. Fife 6411*, CHR 104898. *R. pennatum* drawn from *A.J. Fife 6477*, CHR 104901.



Map 1: Map of New Zealand and offshore islands showing Land District boundaries



Map 2: Map of main islands of New Zealand showing Land District boundaries

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Page numbers are in **bold** for the main entry, and *italic* for synonyms.

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