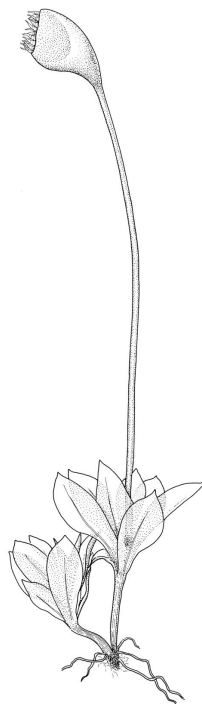




# FLORA OF NEW ZEALAND

## MOSSES

### FUNARIACEAE



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**A.J. FIFE**

Fascicle 45 – APRIL 2019

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## Introduction

The Funariaceae are a family of soil-inhabiting “weeds”. Six genera and 12 species are accepted in the New Zealand flora. Collectively the family is cosmopolitan in distribution, with most tropical species occurring at higher elevations. *Funaria hygrometrica*, which thrives on burnt mineral soils, is one of the most widely recognised mosses worldwide, in part because of its weedy nature, and in part because it is often used as an example of a “typical” moss in introductory botany textbooks and classes. The largest genera in the family, however, are *Entosthodon* (c. 60–70 species worldwide, six in N.Z.) and the very poorly understood genus *Physcomitrium* (probably more than 50 species worldwide, only two in N.Z.).

The Funariaceae are unusual among mosses in having a relatively uniform gametophyte morphology and a comparatively high degree of sporophytic variability. The gametophytes are usually autoicous and have large, thin-walled, and smooth laminal cells, and characteristic perigonal paraphyses with globose to pyriform terminal cells. Sporophytically, some members have morphologically complex double peristomes, while others have extremely small, globose capsules that lack both peristomes and differentiated opercula. All capsules, however, possess unique stomata consisting of an elongate pore in a single guard cell (termed “funariaceous” here). In species where it occurs, the double peristome is distinctive in having endostome segments opposite the exostome teeth, rather than alternating with them.

The morphologically highly reduced *Physcomitrella patens* (which probably does not occur in N.Z.) has been the subject of a large research effort and a very large specialised literature over the past 25 or more years because of its value in the study of gene expression.

For much of the 20th century the prevailing view of the evolution of the Funariaceae was one of progressive simplification of the sporophyte. More recent molecular studies suggest that evolutionary patterns in the family are more complex, with hybridisation (often at the inter-generic level) and homoplasy (or “convergent evolution”) in the sporophyte playing important roles. This has greatly modified both generic and species concepts, and such taxonomic changes are likely to continue into the future.

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## New Names

The following new name is made in accordance with the International Code of Nomenclature for Plants, Algae and Fungi.

***Entosthodon jamesonii* subsp. *productus* (Mitt. in Wilson) Fife, comb. nov.**

Holotype: Tasmania, behind Cumming’s Head, Western Mountains, *Archer*, NY-Mitten! Isotype: BM-Hooker!

≡ *Entosthodon productus* Mitt. in Wilson, Bot. Antarct. Voy. III. (Fl. Tasman.) Part II: 197 (1859).

≡ *Funaria producta* (Mitt. in Wilson) Broth., Nat. Pflanzenfam. [Engler & Prantl] 1(3): 522 (1903).

## Typification

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

***Goniomitrium acuminatum* Hook. & Wilson in Wilson, London J. Bot. 5: 143 (1846)**

Lectotype (designated here): Australia, Swan River, *J. Drummond 6b*, Herb. Wilson, BM 000983172! Isotype: CHR 620699! There are several duplicates of the Drummond collection in BM, thus making the selection of a lectotype desirable, contrary to the statement by Fife & Seppelt (2001) that a holotype is present in that herbarium.

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## Funariaceae

**Plants** minute to medium-sized, mostly pale green, lacking a persistent protonema, gregarious on soil. **Stems** branching by subperichaetial innovation, occasionally unbranched, or forked, not forming “rhizomes”, usually red-brown, in cross-section with a central strand, 1–4 thick-walled cortical cell layers and a hyaloderm, beset with smooth, usually red-brown rhizoids; rarely with tubers. **Leaves** usually larger and more crowded above, lax, concave or less commonly plane, erect-spreading or rarely erect, usually obovate, less often elliptic, lanceolate, or subulate, entire or serrate by projecting cells, or very rarely ciliate, acuminate to obtuse; **laminal cells** large, thin-walled, and smooth, oblong-hexagonal or oblong, usually thinner-walled and more oblong in lower portion of leaf, occasionally elongate at margins to form a border; **costa** single, usually strong, protruding on abaxial surface, nearly always with a small (rarely large) central stereid group surrounded by one abaxial and one or two adaxial layers of larger cells. **Axillary hairs** always present, with long-cylindric terminal cells.

**Mostly autoicous**, less commonly paroiicous, synoiicous, or polygamous. **Perigonia** terminal, usually single, with multicellular paraphyses with globose or pyriform yellow terminal cells (“funariaceous”). **Perichaetial shoot** usually arising by subperigonal innovation and overtopping the perigonium; **perichaetia** terminal, lacking differentiated paraphyses. **Capsules** immersed to long-exserted, erect or curved, often strongly asymmetric, operculate or inoperculate, usually with a distinct neck; **setae** elongate or very short; **stomata** restricted to neck, consisting of an elongate pore in a single guard cell (“funariaceous”), immersed or superficial; **exothelial cells** thick- or thin-walled, the radial walls sometimes cuneate in cross-section; **annulus** present or absent. **Peristome** double, single, rudimentary, or absent; **exostome teeth**, if present, sigmoid or straight, sometimes apically fused as a latticed disc, papillose-striolate or striate, trabeculate on adaxial surface; **endostome** if present coherent at base, with or without a basal membrane, segments (if present) opposite the teeth, acute or irregular, papillose-striolate or papillose; cilia lacking. **Calyptra** deciduous or persistent, usually smooth, papillose; mitrate or cucullate, usually long-rostrate and inflated at base, rarely angled or pleated. **Spores** small to very large.

**Taxonomy:** The Funariaceae are a medium-sized family of cosmopolitan distribution. Six genera and 12 species are accepted from New Zealand. Fife (1985) recognised 13 genera worldwide, of which *Entosthodon* is the largest. Virtually without exception its members occupy bare soil, usually but not always with little humic material. In tropical regions they predominantly occur at higher elevations, although a few genera (mostly those of simple sporophyte morphology) occur in periodically flooded lowland tropical areas. The plants are short-lived, but often overwintering in temperate regions. New Zealand representatives often over-winter in the “spear” stage.

The Australian species were reviewed by Fife & Seppelt (2001).

The family is characterised by having large, thin-walled, and smooth, mostly oblong-hexagonal laminal cells, which are clearly visible under a hand-lens. The gametophytes in the family exhibit only modest variability, while the sporophytes are highly variable and provide most of the morphological features traditionally used to define genera and, in some instances, species. The family includes genera with long-exserted capsules with highly developed double peristomes, reduced peristomes, gymnostomous and operculate capsules, and inoperculate and sessile capsules.

Since von Wettstein’s (1932) pioneering studies on hybridisation in the family, the members of the Funariaceae, particularly *Funaria hygrometrica* and *Physcomitrella patens*, have been important experimental organisms. More recently the family has been the object of intense molecular and developmental study, and its members, particularly *Physcomitrella patens*, have been widely used in studies of gene expression; these studies have given rise to a large body of specialised literature (Rensing et al. 2008; Lang et al. 2008; McDaniel et al. 2010). *Physcomitrella patens* is the first bryophyte to have its genome completely sequenced and can legitimately be considered the *Arabidopsis* of the bryophytes.

The traditional interpretation of the family as a reduction series (in terms of sporophyte complexity) has been recently challenged by gene sequencing techniques and attempts at phylogenetic reconstruction. Homoplasy (convergent evolution) has been convincingly shown to play a major role in the evolution of the funariaceous sporophyte (Liu et al. 2012) and at least three genera (*sensu*Fife 1985) (*Physcomitrium*, *Entosthodon*, and *Physcomitrella*) have been hypothesised as polyphyletic.

The resurrection of the genus *Physcomitridium* (Goffinet & Buck 2011; Hooper et al. 2010) was initially argued for using data derived from four nuclear gene loci (McDaniel et al. (2010)) and has subsequently received extremely strong corroboration by Liu et al. (2012), who used 10 gene loci from nuclear, chloroplast, and mitochondrial genomes to outline relationships in the Funariaceae. The genus *Physcomitridium* is accepted here. Accordingly, *Physcomitrella* is excluded from the N.Z. flora.

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The generic circumscriptions of *Entosthodon* and *Physcomitrium* presented in this Flora are likely to be modified in future when consensus is reached concerning the “backbone” phylogenetic structure of the Funariaceae.

Material of Funariaceae is rarely collected without sporophytes, and this is reflected in the strong emphasis on sporophyte characters in the following key to genera. Indeed there are few, if any, reliable gametophytic features, even at a regional level, that permit the confident distinction of genera as they are circumscribed here. Because of the high level of autoicy, capsules are rarely completely absent from collections. Several species of N.Z. Funariaceae, however, do have distinctive gametophyte features (e.g., overall leaf shape, the nature of the leaf apex, the strength of the costa, the presence of differentiated margin cells and tothing, rhizoid colour), which would permit their recognition if sterile. Ironically, the two most widespread and frequent genera, *Funaria* and *Physcomitrium*, are perhaps the most difficult to confidently separate using gametophyte characters. The preference of *Funaria hygrometrica* for a burnt soil substrate can sometimes help to distinguish them if the plants are completely sterile, but it also often grows on unburnt soils.

- 1       **Capsules** clearly immersed, lacking a peristome; a functional **operculum** either present or absent; **plants** extremely rare and known only from North I. (N & S Auckland and Hawke’s Bay L.D.) ..... 2
- 1'       **Capsules** exserted (either weakly or strongly), with or without a peristome; a functional **operculum** present (except in *Bryobeckettia* and then capsules only weakly exserted); **plants** more common and often widespread ..... 4
- 2       **Capsules** lacking a functional operculum; **capsules** globose, lacking a neck, often disintegrating due to extreme delicacy of the exothecium (and then leaving an exposed mass of spores); **exothecial cells** at mid urn extremely thin-walled, hyaline, not collenchymatous ..... *Physcomitridium*
- 2'       **Capsules** with a functional operculum; **capsules** neither globose nor disintegrating due to the delicacy of the exothecium; **exothecial cells** firmer-walled, pigmented or hyaline, sometimes weakly collenchymatous ..... 3
- 3       **Calyptra** mitrate, with 8 conspicuous radial pleats; **mouth** equal or slightly less than the diameter of capsule; **spores** ellipsoid, 40–110 µm in greater diam., yellow-brown, often appearing smooth under light microscope, becoming reticulate at maturity; **plants** known from a single Hawke’s Bay L.D. locality ..... *Goniomitrium*
- 3'       **Calyptra** mitrate but lacking 8 radial pleats; **mouth** c. 1/3 the diameter of the capsule; **spores** spherical to subreniform, <50 µm in greater diam., red-brown, conspicuously spinose; **plants** known from N & S Auckland L.D. ....  
..... *Physcomitrium (pusillum)*
- 4       **Setae** 0.8–1.5 mm; **capsules** weakly exserted, ellipsoid with a distinct and often somewhat inflated neck; **operculum** not clearly differentiated or weakly differentiated and non-functional; **peristome** absent ..... *Bryobeckettia*
- 4'       **Setae** longer; **capsules** clearly exserted, not ellipsoid; **operculum** well differentiated and functional; **peristome** absent (in *Physcomitrium*) or more often well developed ..... 5
- 5       **Annulus** strongly differentiated, compound, revoluble, composed of 1–4 rows of vesicular cells; **exostome teeth** fused at their apices by a lattice disc; **capsules** strongly sulcate at maturity; **exothecial cells** in alternating bands of thin- and thick-walled cells ..... *Funaria*
- 5'       **Annulus** absent or rudimentary (in N.Z. species); **exostome teeth** either absent or not fused apically; **capsules** not sulcate; **exothecial cells** not in alternating bands of thin- and thick-walled cells ..... 6
- 6       **Peristome** absent; **calyptra** mitrate; exothecial **cell** walls uniformly thickened when viewed in cross-section; **spores** spinose ....  
..... *Physcomitrium (pyriforme)*
- 6'       **Peristome** present or sometimes absent; **calyptra** mostly cucullate (mitrate in *E. laxus*, but then a double peristome present); **exothecial cell walls** cuneate when viewed in cross-section (but uniformly thickened in *E. laxus*); **spores** variously ornamented ..... *Entosthodon*

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## ***Bryobeckettia* Fife, *J. Hattori Bot. Lab.* 58: 191 (1985)**

= *Physcomitrella* subgen. *Exsertofructus* Fife, *Lindbergia* 8: 103 (1982) nom. inval.

**Type taxon:** *Bryobeckettia bartlettii* (Fife) Fife

**Taxonomy:** *Bryobeckettia* is a monotypic genus with characters of the type species.

*Bryobeckettia* has been interpreted as a member of both the genera *Physcomitrella* and *Physcomitridium*. Part of this considerable (and continuing) confusion has been the result of misinterpretation of *Physcomitridium readeri* (Müll. Hal.) G.Roth. Sainsbury's (1955) description of what he incorrectly termed *P. readeri* is based mainly on *Bryobeckettia bartlettii*, but further complicated by the presence of inter-generic hybrid sporophytes in some of the material he used while drafting his description. An attempt to clarify this confusion is given below and based in part on Goffinet & Buck (2011), in the discussion of *P. readeri*.

**Etymology:** The generic name honours the remarkable amateur bryologist T.W.N. Beckett (1839–1906), who for many years lived at Ilam, Christchurch. Beckett collected N.Z. bryophytes mainly in Canterbury, Nelson, and the West Coast, corresponded and exchanged specimens with many of the leading bryologists of his day, and amassed a large herbarium and library, which are today an important part of the Allan Herbarium (CHR) at Lincoln.

## ***Bryobeckettia bartlettii* (Fife) Fife, *J. Hattori Bot. Lab.* 58: 191 (1985)**

≡ *Physcomitrella bartlettii* Fife, *Lindbergia* 8: 103 (1982)

Holotype: N.Z.: junction of Whangamarino R. and Waikato R., *J.K. Bartlett s.n.*, 17 March 1980, MICH! Isotypes: AK!, CHR 499617!, UBC!, WELT M007529!

**Misapplications:** *Physcomitridium readeri sensu* Sainsbury (1955)

**Plants** small, gregarious, yellow-green. **Stems** commonly c. 2–4 mm, unbranched, branched once by subperigonal innovation or rarely branching repeatedly by innovations, red-brown, in cross-section with a small central strand, a parenchymatous medulla, and 1–2 cortical layers of firm-walled cells, beset below with smooth, red-brown rhizoids. **Leaves** obovate to oblong-obovate, obtuse or broadly rounded at apex, 1.5–2.8 × 0.6–1.6 mm, erect-spreading, weakly concave, contorted when dry, plane at margins, entire or weakly and bluntly toothed above by projecting cell ends; **upper laminal cells** oblong-hexagonal (some ± irregular), thin-walled, (25–)45–60(–80) × c. 20–36 µm, becoming larger and more oblong near leaf base, and slightly smaller near apex; **marginal cells** not or weakly differentiated; **alar cells** scarcely differentiated. **Costa** yellow-brown, c. 40 µm wide near base, ending 3–10 cells below leaf apex, in cross-section with a small central stereid group and large abaxial and adaxial cells. **Axillary hairs** as per family.

**Autoicous** or perigonia not observable. **Perigonia** commonly terminal and overtopped by a perichaetial innovation. **Setae** red-brown, straight, weakly dextrorse, 0.8–1.5 mm (excluding the vaginula, which is c. 0.3 mm long); **capsules** erect, weakly exserted, ellipsoid, 0.8–1.5(–1.8) mm, broadly obtuse, with a distinct and often somewhat inflated neck ( $\frac{1}{5}$ – $\frac{1}{4}$ – $\frac{1}{3}$  the total length of the capsule (not well illustrated here), splitting irregularly at maturity and/or rarely splitting transversely ± at equator; **columella** not seen (presumably resorbed); **exothecial cells** oblong or ± irregular, thin-walled, not thickened at corners, mostly c. 45–55 in greater diam., moderately differentiated and thicker-walled at capsule apex; rarely forming a ± functional operculum; **peristome** nil; **stomata** numerous (c. >40) and weakly immersed; **operculum** absent or sometimes poorly differentiated and not functional. **Calyptra** mitrate or becoming split on one side, c. 1 mm long and covering only the capsule apex, deciduous or persistent. **Spores** spherical or subreniform, 28–38 µm, red-brown, uniformly spinose, lacking a trilete scar and not persisting in tetrads.

**Illustrations:** Plate 1. Fife 1982b, figs 11–21 (as *Physcomitrella bartlettii*).

**Distribution:** NI: N Auckland (Whangārei), S Auckland, Hawke's Bay (Wairoa), Wellington (Somes I., Taihape, Carterton, Paekākāriki Hill Road, Petone); SI: Nelson (Wakefield, Westport), Canterbury (Christchurch vicinity, Banks Peninsula), Otago (Blueskin Bay, Evansdale, Kelso), Southland (Riverton). Ch (Pitt I.)

Endemic.

**Habitat:** On damp, often recently disturbed silt or clay, often at the margins of streams or drainage ditches. Sometimes on recently deposited alluvium and tolerant of some coastal salt spray. Associated taxa include *Eurhynchium praelongum*, *Funaria hygrometrica*, *Hennediella macrophylla*, *Physcomitridium readeri*, *Physcomitrium pusillum*, *P. pyriforme*, *Pseudephemerum nitidum*, *Tortula*

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*truncata*, and *Weissia controversa*. Collections have been made throughout the year, but capsules are most frequently mature in early summer. Known only from low elevation (<100 m) sites, with the exception of the Kelso collection, probably made at c. 200 m elevation.

**Notes:** Sexuality, although sometimes clearly autoicous (and with the stem branching by subperigonal innovation), is often unclear and in many collections antheridia cannot be demonstrated.

Mature capsules of representative *B. bartlettii* usually have a weakly defined area of thicker-walled cells at the capsule apex (suggestive of an incipient operculum and rarely  $\pm$  functional), but spore escape is most often by irregular fragmentation of the capsule wall. The spore sac readily separates from the exothecial cells in dissected capsules. The degree of differentiation of the exothecial cells near the capsule apex varies greatly between populations and even between plants in a population. In some, but probably not all, instances the differentiation of a small and  $\pm$  functional operculum may be the result of hybridisation with *Physcomitrium pyriforme* (as in the Kelso material discussed below).

The absence of material of the relatively widespread *B. bartlettii* in the Sainsbury herbarium (at WELT) is perplexing.

Sainsbury's (1955, p. 248) description of *Physcomitridium readeri sensu* Sainsbury is partly based on *Bryobeckettia bartlettii* collections made by E.A. Hodgson at Wairoa, Hawke's Bay L.D. These are currently not present in the WELT-Sainsbury herbarium, but are represented by four duplicates in CHR, including CHR 548148. No identifiable *Physcomitrium* is present in the Hodgson collection.

Sainsbury also used collections by W. Martin, including *Martin 807* of 29 Dec. 1948 from Kelso (Otago L.D.) when drafting his *Physcomitridium readeri* description. A part of this collection is preserved as CHR 266335 and it is a mixture of *B. bartlettii*, *Physcomitrium pyriforme*, and plants with inter-generic hybrid sporophytes. The hybrid capsules are mostly *B. bartlettii* ♀  $\times$  *P. pyriforme* ♂, borne on *Bryobeckettia* gametophytes. The resultant capsules are exserted, ellipsoid, with a well defined neck and an umbonate operculum, which in at least one plant was functional. In other capsules the umbonate operculum is not fallen. The spores in some of these capsules are highly malformed, with a considerable fraction persistent as tetrads. In one immature capsule with an apparently functional but attached operculum, the spores are well formed, uniformly spinose, and neither in tetrads nor trilete scarred. One example of an apparent *P. pyriforme* ♀  $\times$  *B. bartlettii* ♂ is also present; the spores here are variable in diameter (c. 18–33  $\mu$ m) and the larger spores well developed, while some of the smaller spores are poorly formed. This Martin collection from Kelso material provides the most convincing N.Z. example of funariaceous inter-generic hybrids. No hybrid sporophytes have been seen in a scant duplicate (CHR 548151) of a Martin collection from the same locality gathered three days later (on 1 Jan 1949). No other collections of *B. bartlettii* have been seen with hybrid capsules.

Inter-generic hybrid capsules involving other genera in the Funariaceae (including the North American genus *Aphanorhegma*) have been documented (e.g., by Fife 1982a) and are well documented in culture experiments since the classic studies of von Wettstein (1932).

**Recognition:** Features that distinguish *B. bartlettii* from the rarer *Physcomitrium pusillum* and *Physcomitridium readeri* are discussed under those species.

**Etymology:** The species epithet *bartlettii* honours the highly observant and indefatigable N.Z. plant collector J.K. Bartlett (1945–1986), who gathered the type specimen.

## ***Entosthodon* Schwägr., *Sp. Musc. Frond. Suppl. 2(1)*, 44 (1823)**

**Type taxon:** *Entosthodon attenuatus* (Dicks.) Bryhn

**Plants** medium-sized to robust, gregarious, yellow-, brown- or bright green. **Stems** red-brown, rarely pale, usually branched once by a subperigonal innovation, rarely branched by forking or repeated innovation, in cross-section with a central strand, a parenchymatous medulla, a cortex of 1–3 layers of thick-walled cells, and a  $\pm$  developed hyalodermis, beset with smooth rhizoids. **Leaves** larger and more crowded near stem apices, erect-spreading or rarely erect and imbricate, oblong-obovate, spatulate, or rarely ovate-lanceolate, acute, obtuse, or acuminate at apex, rarely cuspidate, concave or plane, serrate at margins by projecting cells or entire; **upper laminal cells** thin-walled and lax, oblong-hexagonal or oblong, becoming longer and laxer below, a few cells often somewhat inflated at alar angles; **marginal cells** mostly not differentiated, rarely elongate to form a weak border. **Costa** single, mostly ending below the leaf apex, rarely excurrent to form a cusp, in cross-section as per family. **Axillary hairs** present, as per family.

**Autoicous**, rarely paroicous or polygamous. **Perigonia** usually single, terminating a shoot from which the perichaetial shoot arises by innovation, with funariaceous paraphyses among the antheridia. **Setae** straight, weakly or rarely strongly hygroscopic, smooth in N.Z. species, very rarely verrucose;

**capsules** erect or inclined, strongly exerted, symmetric or asymmetric, obovoid, pyriform to narrowly cylindrical-pyriform, or rarely ovoid, red-brown at maturity, usually wrinkled at neck and constricted below the mouth when dry, with a neck c. ¼ to ½ the capsule length; **mouth** equal the capsule diameter, rarely smaller, transverse or oblique; **exothecial cells** oblong to elongate, 2–8:1 in N.Z. species, not forming vertical bands, in cross-section with thick, cuneate or rarely non-cuneate walls, several rows oblate at mouth; **stomata** immersed or rarely superficial; **annulus** absent or rudimentary; **operculum** plano-convex, rarely mammillate or conic. **Peristome** double, single, or absent, persistent or fugacious; **exostome teeth** variably developed, straight or sigmoid, free at apices, not or weakly appendiculate, papillose-striolate to strongly striate; **endostome segments** variably developed, papillose, coherent at base. **Calyptra** cucullate-rostrate. **Spores** subreniform, variously ornamented.

**Taxonomy:** A genus of c. 60–70 species with a nearly cosmopolitan distribution. Six species of *Entosthodon* occur in N.Z.

The influential treatment of Brotherus (1924) included *Entosthodon* within a broadly circumscribed *Funaria*. This broad definition of *Funaria* was accepted by Dixon (1926), by Sainsbury (1955), and by other workers on the Australasian Funariaceae.

The generic concepts for both *Entosthodon* and *Funaria* utilised here are the same as presented for Andean species by Fife (1987b). According to these sporophytically defined concepts, the capsules in *Entosthodon* can be either erect and symmetric with transverse mouths, or inclined and asymmetric with oblique mouths. The peristomes can be variably developed (double, single, rudimentary, or absent) with the exostome teeth (if present) either straight or sigmoid. In all cases, however, the exostome teeth are free at their apices and lack a fused apical lattice, such as found in *Funaria*. The exothecial cells in *Entosthodon* usually have, in cross-section, cuneate and thick walls (only rarely non-cuneate) and lack alternating longitudinal bands of thick- and thinner-cell walls. *Entosthodon* spp. also lack a revoluble annulus. An apical lattice, alternating longitudinal bands of exothecial cells, and a revoluble annulus all characterise *Funaria s.s.*

No attempt is made here to distinguish at the subgeneric level those *Entosthodon* species with markedly asymmetric capsules and sigmoid exostome teeth. Such species were placed by Fife (1985, 1987b) in a sporophyte-defined *Entosthodon* subgenus *Plagiodus*.

Liu et al. (2012) have presented convincing evidence, using 10 molecular markers, that *Entosthodon* is polyphyletic. Their conclusions are accepted here, and substantial taxonomic and nomenclatural change to *Entosthodon*, following from their conclusions, seem inevitable. Liu et al. hypothesised that homoplasy is a pervasive feature of sporophyte evolution of *Entosthodon* and its allies. Consensus concerning the relationships within *Entosthodon sensu* Fife is unlikely to be reached easily or quickly, even by the use of molecular methods.

As in other genera of Funariaceae, material of *Entosthodon* with fragmentary sporophytes and/or tattered gametophytes can be difficult or impossible to determine with confidence. A small number of collections, putatively allied to *E. apophysatus*, exhibit strongly aberrant sporophytes. These collections are discussed under *E. apophysatus* and their taxonomic status cannot be fully resolved.

**Etymology:** The generic name refers to the exostome teeth that are inserted below the rim of the capsule mouth. This is a feature of the generitype, but is not universal in the genus.

- |    |  |   |
|----|--|---|
| 1  | <b>Capsules</b> symmetric or nearly so, ± erect; <b>peristome teeth</b> ± straight in outline or absent; <b>spores</b> variously ornamented but not baculate-insulate; <b>marginal leaf cells</b> not differentiated; <b>leaves</b> entire or toothed ..... 2  | 2 |
| 1' | <b>Capsules</b> markedly asymmetric, inclined to horizontal; <b>peristome teeth</b> sigmoid in outline; <b>spores</b> coarsely baculate-insulate; <b>marginal leaf cells</b> mostly differentiated, often forming a ± distinct border (sometimes not obviously differentiated in <i>E. muhlenbergii</i> ); <b>leaves</b> toothed at least in upper ⅓ ..... 5       | 5 |
| 2  | <b>Leaves</b> widest in lowest third, ovate-lanceolate, erect and appressed to stem both dry and moist; <b>setae</b> sinistrorse throughout; <b>capsules</b> <1.5 mm long, gymnostomous; <b>spores</b> usually with obvious trilete scar; <b>plants</b> restricted to northern N.Z. .... <i>E. jamesonii</i> subsp. <i>productus</i>                               |   |
| 2' | <b>Leaves</b> widest at or above mid leaf, ± oblong-obovate to lingulate, erect-spreading when moist; <b>setae</b> dextrorse above or throughout; <b>capsules</b> >1.5 mm long (except in small forms of <i>E. subnudus</i> var. <i>gracilis</i> ), with or without peristome; <b>spores</b> with or without trilete scar; <b>plants</b> widespread in N.Z. .... 3 | 3 |

- 3 **Rhizoids** cerise; **exothecial cells** in cross-section with longitudinal walls not or weakly cuneate, in surface view with distinct lumina; **peristome** present, cerise; **operculum** mammillate or strongly convex; **leaves** lingulate, broadly acute or obtuse at apices; subalpine or alpine plants ..... *E. laxus*
- 3' **Rhizoids** red-brown; **exothecial cells** in cross-section with longitudinal walls distinctly cuneate, in surface view with obscure lumina; **peristome** absent or red-brown; **operculum** plano-convex; **leaves** ± obovate, aristate, cuspidate, or less often acute at apices; lowland plants ..... 4
- 4 **Capsules** 1.5–2.0 mm, obovate or rarely oblong-cylindric, with necks c.  $\frac{1}{3}$  the capsule length; **peristome** double (with endostome segments rudimentary, to c.  $\frac{1}{3}$  height of teeth); **setae** 9–22 mm; **spores** finely lirate, lacking trilete scar and not persisting in tetrads, not collapsed when dry ....  
..... *E. subnudus* var. *gracilis*
- 4' **Capsules** averaging >2.5 mm long, oblong-cylindric, with necks c.  $\frac{1}{2}$  the capsule length; **peristome** mostly absent or very rarely double; **setae** 2–4 (rarely–7) mm; **spores** nearly smooth or sometimes insulate, often with trilete scars or persisting in tetrads, often collapsed when dry ....  
..... *E. apophysatus*
- 5 **Leaves** acute or short-apiculate at apex; **apical cell** 30–90 µm long; **capsules** averaging <2.0 mm, with a weakly defined neck c.  $\frac{1}{3}$  the capsule length; common in N Auckland L.D. and scattered elsewhere ..... *E. radians*
- 5' **Leaves** acuminate at apex; **apical cell** mostly c. 150 µm long; **capsules** oblong-obovoid, averaging 2.3–2.8 mm, with a well-defined neck c.  $\frac{1}{2}$  the capsule length; rare, known from Canterbury and Otago L.D. ....  
..... *E. muhlenbergii*

**Excluded Taxa:** *E. subnudus* var. *subcuspidatus* (Broth.) Fife [Bryologist 98: 315, 1995] [Basionym: *Funaria subcuspidata* Broth., Öfvers. Finska Vetensk.-Soc. Förh. 40: 171, 1898]. The type of this taxon (*T.W.N. Beckett NZ64*, Holotype: H-Brotherus! Isotype: CHR 500758!) was collected in 1887 from the Bridle Path in the Lyttelton Hills (Canterbury L.D.). The type collection has both tattered gametophytes and immature capsules. The former have elongate apical cells and are suggestive of both *E. apophysatus* and *E. subnudus* s.l. However, a few of the more intact leaves have differentiated and projecting marginal cells suggestive of *E. muhlenbergii*. The sporophytes are immature, but in form and dimension (setae 5–7 mm, weakly dextrorse; capsules oblong-cylindric, 2.5–3.2 mm, with a neck c.  $\frac{1}{2}$  the total capsule length) are most suggestive of *E. apophysatus*. The few opercula seen are conic, but this may be a function of immaturity or desiccation. The spores, mostly 33–36 µm, are immature but appear to lack a trilete scar. Confusingly, however, one dissected capsule showed a double peristome with well-developed, weakly sigmoid, striate, and trabeculate teeth c. 385 µm long, and well developed endostome segments c.  $\frac{2}{3}$  the height of the teeth. The peristome characters are suggestive of *E. muhlenbergii*. Both *E. apophysatus* and the rarer *E. muhlenbergii* occur on the South I. It is best to consider *Entosthodon subnudus* var. *subcuspidatus* and its basionym as *nomina confusa* and to exclude them from further consideration.

### ***Entosthodon apophysatus* (Taylor) Mitt., J. Proc. Linn. Soc., Bot. 4: 80 (1859)**

- ≡ *Gymnostomum apophysatum* Taylor, *London J. Bot.* 5: 43 (1846)
- ≡ *Physcomitrium apophysatum* (Taylor) Hook.f. & Wilson in Wilson, *Bot. Antarct. Voy. II (Fl. Nov.-Zel.) Part II*, 91 (1854)
- ≡ *Funaria apophysata* (Taylor) Broth., *Nat. Pflanzenfam. [Engler & Prantl]* 1(3), 523 (1903)  
Lectotype: Western Australia, Swan River, 1843, *J. Drummond* s.n., FH-Taylor!  
Isolectotypes: BM-Wilson!, H-Brotherus!, NY-Mitten! (Designated by Fife and Seppelt 2001.)

**Plants** yellow-green. **Stems** red-brown, 2–5(–7) mm high, branching once by subperigonal innovation, beset with red-brown rhizoids. **Leaves** erect-spreading, broadly obovate to oblong-spathulate, 1.5–3.5 × 0.75–0.9 mm (including arista), concave, entire, tapered in upper  $\frac{1}{3}$  to a slender, ± yellow arista or very rarely with arista absent (see below); **upper laminal cells** oblong-hexagonal, (24–)30–60 × 17–30 µm, longer and more oblong below; **marginal cells** not differentiated; **apical cell** (150–)180–300(–400) µm; **alar cells** 2–4, moderately inflated. **Costa** c. 30–50 µm wide near base,

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failing a few to several cells below base of the arista or fusing with it and appearing long excurrent. **Axillary hairs** present.

**Autoicous. Perigonia and perichaetia** as per genus. **Setae** 2–4 (rarely–7) mm, weakly dextrorse, weakly hygroscopic, pale red-brown; **capsules** erect or rarely inclined, symmetric, oblong-cylindric, constricted below mouth when dry, (2.0–)3.0–4.5 mm, with a well differentiated, tapered neck c. ½ the capsule length, red-brown; **mouth** ⅔ to equal the capsule diameter, transverse; **exothecial cells** c. 5–8:1, 50–90 µm long, with thick, strongly cuneate cell walls, c. 6–8 rows quadrate to oblate and strongly pigmented at mouth; **operculum** plano-convex. **Peristome** absent or very rarely double and weakly developed (see below). **Spores** (27–)30–43 µm, nearly smooth or sometimes insulate, often with trilete scars or persisting in tetrads, often collapsed when dry.

**Illustrations:** Plate 2. Brotherus 1924, fig. 274 (as *Funaria apophysata*); Catcheside 1980, fig. 122 (as *Funaria apophysata*); Meagher & Fuhrer 2003, p. 151.

**Distribution:** NI: N Auckland (near Cascades, Erin Point, Remuera, Wiri, near Mangōnui), S Auckland (near Huntly (aberrant)), Hawke's Bay (Te Awanga, Havelock North, near Waipukurau (aberrant), Napier); SI: Nelson (Pūponga), Canterbury (Port Hills, Quail I.), Otago (Glendhu Bluff at Lake Wānaka).

Austral. Tasmania\*, Australia (all states)\*, Uruguay\*, Chile\*.

**Habitat:** On damp mineral silt or clay soil, in natural or highly modified grassland or scrub; sometimes in horticultural sites (e.g. vineyards). Frequent associates include *Ceratodon purpureus*, *E. radicans*, *E. subnudus* var. *gracilis*, *Physcomitrium pyriforme*, *Pleuridium nervosum*, *Schizymerium bryoides*, *Tortula truncata*, *Weissia austro-crispa*, and *W. controversa*. Ranging in elevation from sea level (Wiri) to c. 300 m (Lake Wānaka).

The long, oblong-cylindric, gymnostomous capsules, short setae, and markedly aristate comal leaves in most instances set this species apart from all other N.Z. species in the genus. However, *E. apophysatus* in N.Z. is variable in both sporophyte and gametophyte features and a small number of aberrant collections have been seen. The sporophytic variability here is consistent with high levels of plasticity in other *Entosthodon* species and is arguably consistent with the high levels of variability and evolutionary homoplasy hypothesised for the genus as a whole by Liu et al. (2012).

**Notes:** In aberrant material from near Huntly, S Auckland L.D. (*J.K. Bartlett 5169*; CHR 413349), some sporophytes are gymnostomous while others are peristomate. The gymnostomous plants have setae to 5 mm (slightly longer than usual for *E. apophysatus*), aristate leaves, ± tetrahedral spores, and are thus representative of the species. However, other plants in the same collection have weakly developed double peristomes, longer than usual setae (to 7 mm), comal leaves mostly acute or with a very short aristae, and costae ending below the base of the aristae. The peristome teeth here are highly irregular, striate, mostly broadly rounded apically, and c. 75–150 µm high, and the endostome segments are irregular and to c. 90 µm high. Spores throughout the collection appear to be normally developed for *E. apophysatus*, mostly 27–36 µm, weakly tetrahedral (with three ± flat surfaces), apparently insulate, occasionally trilete and with a few persisting as tetrads.

Aberrant material from near Waipukurau, Hawke's Bay L.D. (*R.E. Beever s.n.*, 19 Oct. 2009, CHR 604767) has consistently non-cuspidate comal leaves but representative and entirely gymnostomous capsules. The unusual form of the leaves here may be a result of herbicide spraying in a vineyard.

A single collection from eastern Spirits Bay, N Auckland L.D. (*J.K. Bartlett 22431*, CHR 91832), at the northern extremity of the North I., tentatively referred to *E. apophysatus*, has setae much longer than typical (9–11 mm), and may deserve varietal status. However, the obovate-aristate, entire leaves, the nearly smooth, trilete spores, and long oblong-cylindric capsule indicate its affinity to this species. A very rudimentary (or possibly fragmentary) peristome has been noted in one capsule of this collection. No other material of Australasian *E. apophysatus* has been seen with such elongate setae.

At this stage in our understanding of *E. apophysatus* there seems no alternative but to record aberrant material and to acknowledge the puzzling variability of this taxon.

*Entosthodon clavaeformis* Müll.Hal. & Hampe (South Australia), *Funaria aristata* Broth. (N.S.W.), and *E. clavellatus* Mitt. (Uruguay) are synonymous with *E. apophysatus*.

**Recognition:** In its most representative form, *E. apophysatus* has leaves similar in shape to those of *E. mühlenbergii*, but that species has toothed leaf margins, more markedly differentiated marginal cells, and asymmetric, peristomate capsules. *Entosthodon apophysatus* differs from the Australian *E. subnudus* var. *subnudus* in leaf form and in apical cell, seta, and capsule lengths, peristome development, and spore ornamentation.

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**Etymology:** The epithet *apophysatus* refers to the elongate stomata-bearing neck of this species.

***Entosthodon jamesonii* (Taylor) Mitt., *Hooker's J. Bot. Kew Gard. Misc. 3: 354 (1851)***

as "Jamesoni"

≡ *Physcomitrium jamesonii* Taylor, *London J. Bot.* 6: 329 (1847) – as Jamesoni

**Etymology:** The species epithet honours the 19th century botanist William Jameson, who collected extensively in present-day Ecuador. Jameson's mosses were in-part described by T. Taylor (1846) and subsequently incorporated into Mitten's monumental *Musci Austro-Americani* (1869).

***Entosthodon jamesonii* subsp. *productus* (Mitt. in Wilson) Fife, comb. nov.**

≡ *Entosthodon productus* Mitt. in Wilson, *Bot. Antarct. Voy. III. (Fl. Tasman.) Part II*, 197 (1859)

≡ *Funaria producta* (Mitt. in Wilson) Broth., *Nat. Pflanzenfam. [Engler & Prantl] 1(3)*, 522 (1903)

Holotype: Tasmania, behind Cumming's Head, Western Mountains, Archer, NY-Mitten!

Isotype: BM-Hooker!

**Plants** yellow-green. **Stems** red-brown, to 4 mm, branching once by subperigonal innovation or with multiple perigonia, hyalodermis faint (usually only a thin outer wall of otherwise thick-walled epidermal cells), beset with red-brown rhizoids. **Leaves** erect, ovate-lanceolate, 0.7–1.7(–2.2) × 0.2–0.4(–0.6) mm (including comal leaves), concave to subtubulose, gradually or abruptly tapered to a subulate apex, entire; **upper laminal cells** oblong, 25–70 × 12–15 µm, becoming longer (to c. 105 µm), laxer and more hexagonal below; **marginal cells** not differentiated; **apical cell** 30–48 µm; **alar cells** not differentiated. **Costa** 25–37 µm wide near base, failing in the subula. **Axillary hairs** not seen.

**Autoicous.** **Perigonia** single or multiple, but **perigonia** and **perichaetia** otherwise as per genus.

**Setae** 2.5–9 mm, sinistrorse throughout, red-brown, weakly hygroscopic; **capsules** erect, symmetric, oblong-pyriform, not or very weakly constricted below mouth when dry, 1.0–1.3 × 0.5–0.7 mm, with a gradually tapered, irregularly wrinkled neck c. ½ the capsule length, red-brown at maturity; **mouth** c. ¾ the capsule diameter (at dehiscence), transverse, gymnostomous; **exothecial cells** c. 30–60 µm, 3–6:1, in cross-section with thick, cuneate anticlinal walls, 6–8 rows oblate and more pigmented at mouth; **operculum** plano-convex, c. 325–350 µm diameter. **Peristome** absent. **Spores** 30–36 µm, verrucate-bullate and usually irregularly wrinkled, usually with obvious trilete scar.

**Illustrations:** Plate 2. Catcheside 1980, fig. 121 (as *Funaria producta*).

**Distribution:** NI: N Auckland (Te Paki, Mōkaikai Scenic Reserve, Ahipara Plateau, Takapuna, Henderson, Glen Eden), Hawke's Bay (Wairoa). This subspecies remains poorly documented in N.Z., with several of its documented localities in (now) urban sites.

Australasian. Tasmania\*, mainland Australia\* (Vic., S.A., W.A.).

**Habitat:** On damp, often shaded soil in *Leptospermum scoparium* scrub or in grassland (including mown grassland). Material from Takapuna is from shaded grass in a golf course. A well-documented collection from Te Paki occurred on "ferricrete" soil. Ranging from near sea level to c. 250 m (Te Paki).

**Notes:** Australasian material of *E. jamesonii* s.l. is comparable with Andean (and Central American) material in the critical characters of erect ovate-lanceolate leaves, oblong-pyriform capsules with well-defined necks, poorly developed peristomes, and spores with trilete scars (or persisting in tetrads). Australasian material generally differs by its smaller stature relative to Andean material (including the species type). The stems in Australasian material are ≤4 mm while those of Andean material are ≤8 mm (or ≤20 mm in non-Andean material), the perichaetial leaves are smaller, to 2.2 mm vs to 3.0 mm. The setae (2.5–9 mm vs 12–20 mm), and the capsules (1.0–1.3 mm vs 1.5–2.5) are nearly always shorter. Andean material frequently has dichotomously branched stems, a feature not noted in Australasian material and a rare feature in the genus. One Andean specimen from Peru (*P. & E. Hegewald 9174*, CHR 609123) is comparable to Australasian material in stature, but has more branched shoots. The nearly constant (but rarely overlapping) difference in plant stature alone is insufficient to maintain the Australasian and Andean / Central American taxa distinct at the species level, and the reduction of the Australasian material to subspecies rank is therefore proposed. Only a single Malesian collection of *E. jamesonii* has been available at the time of writing, but I have earlier

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(Fife 1987b) considered it synonymous with the Andean taxon, using a broader range of Malesian collections.

*Entosthodon jamesonii* subsp. *jamesonii* ranges widely in the northern Andes, Central America, and the Caribbean island of Dominica (Fife 1987b). In the northern Andes it occurs primarily in páramos habitats at elevations of >3000 m, but in Central America and Dominica it occurs at lower elevations. Heterotypic synonyms from Victoria, cited by Fife & Seppelt (2001), include *Funaria perpusilla* Broth. (Holotype: Heyington, *W.W. Watts 196*, H-Brotherus!) and *Entosthodon minuticaulis* Müll.Hal. ex Geh. (Holotype: Moyston, *D. Sullivan*, H-Brotherus!).

**Recognition:** The narrowly ovate-lanceolate leaves make this taxon nearly unmistakable in a regional context. Confusion could conceivably occur with erect-capsuled members of the Bryaceae. However, the distinctive cucullate-rostrate calyptra, the perigonal paraphyses (with globose or pyriform terminal cells), and the single-celled stomata preclude confusion there.

**Etymology:** The epithet *productus* means extended or elongated. Its meaning in the context of this taxon is unclear, although it may refer to the phrase “acumen lanceolatum angustatus” in the basionym protologue.

### ***Entosthodon laxus* (Hook.f. & Wilson) Mitt., *Hooker's J. Bot. Kew Gard. Misc.* 8: 259 (1856)**

- ≡ *Gymnostomum laxum* Hook.f. & Wilson, *Bot. Antarct. Voy. I. (Fl. Antarct.) Part II*, 399 (1847) – as *Gymnostomum* (*Physcomitrium*) *laxum*
- ≡ *Physcomitrium laxum* (Hook.f. & Wilson) Müll.Hal., *Syn. Musc. Frond.* 2, 546 (1851)
- ≡ *Funaria laxa* (Hook.f. & Wilson) Broth., *Deutsche Sudpolar-Exped. 1901–1903*, 8, 88 (1906)  
Lectotype: Kerguelen, Antarctic Expedition 1839–1843, *J.D. Hooker 744* (“Wilson no. 257”), BM-Hooker! Isolectotypes: BM-Hooker!, NY-Mitten! (Designated by Fife 1987a.)
- = *Funaria subattenuata* Broth., *Öfvers. Finska Vetensk.-Soc. Förh.* 40: 173 (1898) – as *Funaria* (*Entosthodon*) *subattenuata*  
Holotype: N.Z., Canterbury, swamp at top of Arthur's Pass, 3013 ft., Jan. 1888, *T.W.N. Beckett 93*, H-Brotherus! Isotypes: CHR 500808!, CHR 527857!
- = *Meesia craigieburnensis* R.Br.bis, *Trans. & Proc. New Zealand Inst.* 31: 464 (1899)  
Lectotype: N.Z., Broken River, 1887, *R. Brown s.n.*, BM-Dixon! Isolectotype: CHR 335686! (Designated by Fife 1987a.)
- = *Tayloria maidenii* Broth., *Proc. Linn. Soc. New South Wales* 41: 583 (1916)  
Type material: Australia, Mt. Kosciusko, Merrit's Camp, *Maiden & Forsyth 184*, FH!

**Plants** yellow- or bright green, gregarious. **Stems** pale to red-brown, to 15 mm, branching once by subperigonal innovation, or forking beneath soil surface and producing subperigonal innovations above, beset with cerise rhizoids. **Leaves** erect-spreading, lingulate, 1.5–3.0(–4.0) × 0.6–1.0 mm, plane to weakly concave, entire or weakly crenulate above, tapered in upper 1/3, broadly acute or obtuse; **upper laminal cells** oblong-hexagonal, c. 70–100(–130) × 24–30(–45) µm, longer and more oblong below but not thinner-walled; **marginal cells** not differentiated or rarely weakly differentiated above; **apical cell** 25–55 µm (rarely to 100 µm); **alar cells** not differentiated or slightly more pigmented than adjacent cells. **Costa** rather thin and weak, c. 30–40(–50) µm wide near base, failing c. 5–10 cells (rarely more) below leaf apex. **Axillary hairs** present.

**Autoicous.** **Perigonia** and **perichaetia** as per genus. **Setae** (5–)10–20(–23) mm, dextrorse above, pale brown, weakly hygroscopic; **capsules** erect, symmetric, oblong-obovoid or oblong-pyriform, scarcely constricted below mouth when dry, 1.5–2.5(–3.0) mm, with a well-differentiated neck 1/3 to 1/2 the capsule length, red-brown at maturity; **mouth** c. 3/4 the capsule diameter, transverse; **exothecial cells** with distinct lumina, c. 2–3:1, averaging 30–40 µm, in cross-section with anticlinal walls not or very weakly cuneate, c. 6–8 rows isodiametric to oblate and darker at capsule mouth; **operculum** mammillate or strongly convex. **Peristome** double; **exostome teeth** straight, cerise, often fugacious, to 300 × 50–75 µm but often shorter and irregular, acute or rounded, baculate-papillose, not or weakly striate, weakly nodulose (lacking marginal appendiculae), inner surface scarcely trabeculate; **endostome** rudimentary and fugacious, with segments irregular and hyaline, to 120 µm, gemmate to lowly insulate. **Calyptra** mitrate or splitting on one side to become cucullate, rostrate. **Spores** 25–35 µm, gemmate to lowly insulate.

**Illustrations:** Plate 4. Fife 1987a, figs 1–21; Fife 1987b, figs 91–116; Malcolm & Malcolm 2003, p. 26.

**Distribution:** NI: Gisborne (near Lake Waikareiti), Wellington (Mt Ruapehu, Mt Ngāuruhoe, Northwest Ruahine Range); SI: Nelson, Canterbury, Westland, Otago, Southland (Eyre Range); A; M. No indisputable collections from St or C have been confirmed, but it almost certainly occurs on those islands.

Austral-Andean. Tasmania\*, mainland Australia (Australian Alps)\*, Kerguelen\*, Marion I.\*, Crozet Is\*, Chile\*, Bolivia\*, Peru\*, Ecuador\*, Venezuela\*.

**Habitat:** On waterlogged to sometimes mesic and usually shaded humic soil (usually with sand or gravel fragments). Often at the margins of small subalpine or alpine streams; also on wet outcrops or in seepages. Occurring in areas with various bedrock types, including greywacke, schist, granite, limestone, and ultra-mafics. It is frequently shaded by overhanging snow tussocks. From c. 900 (Tongariro National Park, Wellington L.D.) to c. 1900 m (Makatote River headwaters, Mt Ruapehu, Wellington L.D.) on the North I. and from c. 730 (Broken River Basin, Canterbury L.D.) to at least 1650 m (Mt Arthur, Nelson L.D.) on the South I. On Auckland I. it grows to near sea level. Frequently associated flowering plants include *Nertera depressa*, *Pratia angulata*, and *Drosera* spp. (especially *D. arcturi*), while associated bryophytes can include *Breutelia pendula*, *Blindia robusta*, aquatic growth forms of *Distichophyllum pulchellum*, *Isotachis montana*, *Jamesoniella tasmanica*, and members of the Aneuraceae.

The broadly acute or obtuse, lingulate leaves, the ± mammillate opercula, and oblong-obovoid capsules, and the bright cerise (cherry-coloured) rhizoids and exostome teeth facilitate recognition of this species, as does its predominantly subalpine to alpine distribution. Microscopically, the short exothecial cells with distinct lumina and non-cuneate anticlinal cell walls are very distinctive.

The only other regional *Entosthodon* with which *E. laxus* could be confused is *E. subnudus* var. *gracilis*, which is a much smaller lowland plant with plano-convex opercula. A review of the ecology, world distribution, and extensive synonymy of *E. laxus* was provided by Fife (1987a).

**Etymology:** The epithet *laxus* roughly translates as flaccid or loose and presumably is derived from Hooker and Wilson's descriptive phrase (in the protologue) "*foliis erect-patentibus laxe imbricatis elliptico-lanceolatis...*" The description of the loosely imbricate leaves is probably drawn in comparison to other taxa placed in the (then) larger genus *Gymnostomum*.

## ***Entosthodon muhlenbergii* (Turner) Fife, *J. Hattori Bot. Lab.* 58: 192 (1985)**

as "*Entosthodon* (*Plagiodus*) *muehlenbergii*"

≡ *Funaria muhlenbergii* Turner, *Ann. Bot. [König & Sims]* 2: 198 (1805)

Type material: England, Yorkshire, Copgrove, *Rev. J. Dalton*, BM-Turner!

= *Funaria glabra* Taylor, *London J. Bot.* 5: 57 (1846)

Holotype: Western Australia, Swan River, 1843, *J. Drummond*, FH-Taylor! Isotype: H-Lindberg! [*Non Funaria glabra sensu* Sainsbury 1955].

= *Funaria tasmanica* Müll.Hal. & Hampe, *Linnaea* 26: 490 (1855)

Lectotype: Tasmania, *F. Mueller* 6, BM-Hampe! (Designated by Fife and Seppelt, 2001.)

The following description is based on type material of *Funaria glabra* Taylor, and altered using N.Z. specimens.

**Plants** yellow-green. **Stems** red-brown, c. 2–4 mm, usually branching once by subperigonal innovation, beset below with smooth, red-brown rhizoids. **Leaves** erect-spreading, oblong-obovate, 2.0–2.9 × 0.7–1.0 mm, concave, bluntly toothed in upper 1/3 by projecting cells, tapered in upper 1/3 to an acuminate apex; **upper laminal cells** oblong-hexagonal, (45–)60–90 × c. 30 µm, more oblong and to c. 120 µm long below; **marginal cells** mostly ± differentiated (but sometimes scarcely differentiated in N.Z. material); **apical cell** elongate, 125–180(–300) µm, often ± yellow; **alar cells** not or weakly differentiated. **Costa** c. 45–60 µm wide near base, failing below the base of the acumen. **Axillary hairs** present.

**Autoicous. Perigonia** and **perichaetia** as per genus. **Setae** c. 5–7 mm in N.Z. material, pale red-brown, weakly dextrorse and weakly hygroscopic; **capsules** weakly inclined, asymmetric, oblong-obovoid and curved, (2.3–)2.5–3.2 mm, constricted below the mouth when dry, with a well-defined, strongly wrinkled neck c. 1/2 the capsule length; **mouth** equal the capsule diameter, oblique; **exothecial cells** with indistinct lumina in surface view, c. 60 µm long, in cross-section with strongly cuneate walls; **operculum** plano-convex. **Peristome** double; **exostome teeth** sigmoid, c. 300–330 × 75–90 µm, acute, vertically striate nearly throughout, coarsely baculate near apices, with weak marginal appendiculae upper 1/2, with trabeculae well developed on inner surface, not fused at apices;

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**endostome** well developed, segments as wide as and c.  $\frac{3}{4}$  the height of the exostome teeth, striate-baculate below, baculate above. **Spores** 29–32  $\mu\text{m}$ , coarsely baculate-insulate, apparently lacking trilete scars.

**Illustrations:** Plate 2. Smith 2004, fig. 164, 9–13.

**Distribution:** NI: *sine loc.*; SI: Canterbury (Godley Head, Castle Hill Basin?), Otago (Arrow River, Mātukituki River).

Nearly cosmopolitan. Tasmania\*, mainland Australia\*, Africa\* western North America\*, Europe\* including Great Britain\*, Middle East\*.

**Habitat:** The collection from Godley Head was made from a silt bank associated with basalt bedrock at 120 m elevation; that from the Mātukituki River was collected from soil in a schist crevice at c. 300 m elevation. The Arrow River collection (*D. Petrie*, WELT M001297) bears no habitat details. There are two Colenso collections from an unknown North I. locality or localities; one was apparently segregated from a collection of *Gigaspermum repens* (suggesting an association with limestone).

**Notes:** The narrowly acuminate comal leaves with strongly elongate and yellow terminal cells, as well as the longer and more strongly defined capsule necks, distinguish this species from the much commoner *E. radians*. Poor specimens might be confused with the widespread *E. apophysatus* (where the comal leaf shape is very similar), but the present species has nearly entire leaf margins, asymmetric and peristomate capsules, and baculate-insulate and non-trilete spores. The probable record from the Castle Hill Basin is very scant and poor, but has perigonal leaves with narrowly acuminate apices, terminal cells c. 250  $\mu\text{m}$  long, and a few capsules in the size range of the present species.

The South American *Entosthodon laevis* (Mitt.) Fife is closely allied (Fife 1987b) and may eventually prove to be synonymous.

**Etymology:** The epithet *muhlenbergii* honours the German-American Lutheran clergyman and botanist G.H.E. Muhlenberg (1753–1815). Crundwell & Nyholm (1974) clarified the complicated early nomenclatural history of this plant, which, although named in honour of an American botanist, was first described using plants collected by Rev. James Dalton in Yorkshire, England.

## ***Entosthodon radians* (Hedw.) Müll.Hal., *Syn. Musc. Frond.* 1, 122 (1848)**

≡ *Weissia radians* Hedw., *Sp. Musc. Frond.* 73 (1801)

≡ *Bryum radians* (Hedw.) P.Beauv., *Prodr. Aethéogam.* 49 (1805)

≡ *Eremodon radians* (Hedw.) Brid., *Bryol. Univ.* 1, 236 (1826)

≡ *Funaria radians* (Hedw.) Müll.Hal., *Linnaea* 18: 692 (1845)

≡ *Funaria crispula* Hook.f. & Wilson in Wilson, *Bot. Antarct. Voy. III. (Fl. Tasman.) Part II*, 198 (1859) nom. superfl.

Lectotype: N.Z., “*Insulae australes*,” *s. loc.*, 1769–70, J. Banks, BM-Turner! (Designated by Fife 1996.)

= *Funaria acaulis* Hampe, *Linnaea* 30: 624 (1860)

≡ *Entosthodon acaulis* (Hampe) Fife, *J. Hattori Bot. Lab.* 58: 192 (1985) – as *Entosthodon* (*Plagiopus*) *acaulis*

Holotype: Victoria, Gippsland, 1855, *F. Mueller 119*, BM-Hampe! Isotypes: BM-Hooker!, H-Lindberg!

**Misapplications:** *Funaria glabra sensu* Sainsbury (1955), *non Funaria glabra* Taylor (1846)

**Plants** yellow- or brown-green. **Stems** red-brown, most 3–5 mm and usually branching once by subperigonal innovation (occasionally elongate to c. 25 mm, but this probably when subject to deposition), beset below with smooth red-brown rhizoids. **Leaves** erect-spreading, broadly obovate to spatulate, 1.5–3.5(–4.0) mm × 1.0–1.8 mm, ± concave, weakly toothed above, tapered in upper  $\frac{1}{3}$  to an acute or shortly apiculate apex; **upper laminal cells** oblong-hexagonal, 45–90(–105) × 30–36  $\mu\text{m}$ , longer and more oblong below; **marginal cells** longer and firmer-walled to form an indistinct border of 1–3 rows (most obvious at shoulder), often ± yellow, with ends weakly projecting to form short and blunt marginal teeth; **apical cell** short, 30–90  $\mu\text{m}$ . **Costa** concolourous or red-brown, c. 45  $\mu\text{m}$  wide near base, failing (5–)7–10 cells below base of the apiculus. **Axillary hairs** present.

**Autoicous. Perigonia** and **perichaetia** as per genus. **Setae** 5–12(–14) mm, pale- or red-brown, dextrorse, weakly hygroscopic; **capsules** inclined to nearly horizontal, asymmetric, obovoid,



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constricted below the mouth when dry, 1.5–2.0(–2.3) mm, with a weakly defined neck c.  $\frac{1}{3}$  (occasionally  $-\frac{1}{2}$ ) the capsule length, red-brown (but often dehiscent when lower portion of capsule is still green), strongly wrinkled below when dry; **mouth** equal the capsule diameter,  $\pm$  oblique; **exothecial cells** with indistinct lumina in surface view, mostly 39–60  $\mu\text{m}$  long and c. 2–4:1, in cross-section with anticlinal walls strongly cuneate, c. 6 rows isodiametric to oblate at mouth; **operculum** plano-convex. **Peristome** double; **exostome teeth** sigmoid, (225–)250–300(–475)  $\times$  (60–)75–90  $\mu\text{m}$ , acute, vertically striate nearly throughout, coarsely baculate near apices, with marginal appendiculae weak in upper  $\frac{1}{2}$  or lacking, with well-developed trabeculae on inner surface, not fused at apices; **endostome segments** variable, c. 90  $\mu\text{m}$  wide, acute, and c.  $\frac{3}{4}$  height of the exostome teeth or irregular and shorter, striate-baculate below, baculate above. **Spores** (24–)27–33(–35)  $\mu\text{m}$ , insulate-baculate, lacking trilete scars.

**Illustrations:** Plate 3. Wilson 1859, pl. 175, fig. 2 (as *Funaria crispula*); Catcheside 1980, fig. 127 (as *F. glabra*); Fife 1987b, figs 1–23 (as *E. acaulis*).

**Distribution:** NI: N Auckland (widespread), including offshore islands (LB, GB), S Auckland, (Moehau, Mercury Bay, near Katikati, Huntly, near Ātiāmuri, near Pureora, Te Aroha, near Waimiha), Gisborne (Waiotahi River), Taranaki (Ōmata), Wellington (near Chateau Tongariro, Tawhai Falls, Mangahao Lower Dam, Kaitoke Waterworks); SI: Nelson (Pūponga, Parapara, Little Wanganui, Ōpārara Valley), Marlborough (Pelorus Bridge Scenic Reserve), Otago (Horse Range, Dunedin); A. Austral-Andean. Tasmania\*, mainland Australia\*, New Caledonia\*, Ecuador\*, Venezuela\*.

**Habitat:** *Entosthodon radians* occurs mostly on steep clay/silt banks at low elevations. On the North I. it frequently occurs under scrub of *Leptospermum scoparium*, *Sophora microphylla*, *Geniostoma ligustrifolium*, *Leucopogon fasciculatus*, and *Piper excelsum*. It is occasionally associated with *Drosera auriculata*, indicating a tolerance of acidic soils. Associated bryophytes include species of *Breutelia*, *Bryum*, *Campylopodium*, *Dicranella*, *Ditrichum*, *Fissidens*, *Philonotis*, *Polytrichastrum*, and *Fossombronia*. *Entosthodon radians* is a very common species in N Auckland L.D., but is more scattered south of 38° south latitude. On the North I. ranging from near sea level to at least 1150 m (near Chateau Tongariro, Wellington L.D.) and to c. 210 m (Ōpārara River, Nelson L.D.) on the South I. A single collection made “near the summit of Mt Hauhungatahi,” Wellington L.D., from a subalpine site at 5000 feet (=1525 m) elevation (*J.K. Bartlett s.n.*, CHR 499633) has also been confirmed.

**Notes:** Degree of endostome development varies within populations and even within single capsules. The complicated nomenclatural history and typification of *E. radians* Hedw., including an explanation of why the widely applied *Funaria glabra sensu* Sainsbury (1955) should not be used for this species, and *Funaria crispula* Hook.f. & Wilson should be considered a homotypic synonym, was detailed by Fife (1996).

Sainsbury's (1955, p. 246) report of what he termed *Funaria glabra* from the Arrow River (Otago L.D.) is based on a misidentification of *E. muhlenbergii*. The shorter capsule with a weaker neck and the shorter leaf apical cell of *E. radians* preclude its confusion with the much rarer *E. muhlenbergii*.

**Etymology:** The specific epithet *radians* means radiating, but Hedwig's (1801, p. 73) protologue provides no indication of the applicability of the epithet to this species.

## ***Entosthodon subnudus* (Taylor) Fife, *J. Hattori Bot. Lab.* 58: 192 (1985)**

≡ *Funaria subnuda* Taylor, *London J. Bot.* 5: 57 (1846)

Holotype: Western Australia, Swan River, 1843, *J. Drummond s.n.*, FH-Taylor! Isotype: BM-Wilson!

**Plants** yellow- or brown-green. **Stems** red-brown, 2–5 mm, branching once by subperigonal innovation, beset with red-brown rhizoids. **Leaves** erect-spreading, obovate to oblong-obovate, occasionally widest below mid leaf and  $\pm$  oblong-ovate, tapered in upper  $\frac{1}{3}$  to a broadly acute, acuminate, cuspidate, aristate, or rarely obtuse apex, (1.3–)1.5–2.5  $\times$  0.6–0.8 mm, variably concave, entire or rarely bluntly dentate in upper  $\frac{1}{2}$ ; **upper laminal cells** oblong-hexagonal, (24–)30–69(–80)  $\times$  15–18(–25)  $\mu\text{m}$ , becoming larger, more oblong, and laxer below; **marginal cells** not differentiated; **apical cell** length variable, (45–)60–165 (rarely –210)  $\mu\text{m}$ ; **alar cells** few, moderately inflated. **Costa** highly variable, ending below apex, percurrent to long excurrent (often variable within a population or even a single plant), (30–)36–45(–60)  $\mu\text{m}$  wide near base. **Axillary hairs** present.

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**Autoicous. Perigonia** and **perichaetia** as per genus. **Setae** variable in length, 4–22(–30) mm, weakly dextrorse throughout, pale red-brown, weakly hygroscopic; **capsules** erect, symmetric, obovoid-cylindric or obovoid (in var. *gracilis*), or occasionally narrowly pyriform (in var. *subnudus*), (1.3–)1.5–2.0 mm (in var. *gracilis*; to 2.5 mm in var. *subnudus*) with a neck c.  $\frac{1}{3}$  the capsule length (to c.  $\frac{1}{2}$  in var. *subnudus*), usually strongly constricted below mouth when dry; **mouth** equal the capsule diameter, transverse; **exothecial cells** elongate, 45–55(–75)  $\mu\text{m}$ , with obscure lumina in surface view, in cross-section with anticlinal walls strongly cuneate, c. 6–8 rows oblate at mouth; **operculum** plano-convex. **Peristome** double; **exostome teeth** variably developed, straight, red-brown, usually  $\pm$  irregular in outline and with sinuose margins, (150–)180–225  $\times$  45–60  $\mu\text{m}$ , tapered to a slender or bilobed and often  $\pm$  perforate apex, striate, weakly trabeculate, not appendiculate; **endostome** variable, rudimentary to well developed, rarely with fragments adhering to the upper inner surface of teeth or seemingly absent. **Spores** (27–)31–39(–41)  $\mu\text{m}$ , finely verrucate or liriate-murate (rarely gemmate), lacking a trilete scar.

**Notes:** The var. *subnudus* is accepted only from Australia; the report of this variety in N.Z. by Fife & Seppelt (2001) is based on a misidentification. Only the single (but variable) variety, var. *gracilis*, occurs in N.Z.

Too many intermediate specimens in Australian material occur between the typical variety and var. *gracilis* to permit the latter's recognition at the specific level. The features noted in the key should allow placement for all but a small fraction of intermediate and/or aberrant specimens.

**Etymology:** The specific epithet *subnudus* means somewhat or almost naked; the reference is unclear.

### ***Entosthodon subnudus* var. *gracilis* (Hook.f. & Wilson) Fife, J. Hattori Bot. Lab. 58: 192 (1985)**

$\equiv$  *Entosthodon gracilis* Hook.f. & Wilson in Wilson, *Bot. Antarct. Voy. II (Fl. Nov.-Zel.) Part II*, 91 (1854)

$\equiv$  *Funaria gracilis* (Hook.f. & Wilson) Broth., *Nat. Pflanzenfam. [Engler & Prantl] 1(3)*, 524 (1903)

Lectotype: N.Z., Bay of Islands, *J.D. Hooker s.n.* ("Wilson no. 348b"), BM-Wilson!

Isolectotypes: BM-Wilson!, BM-Hooker!, BM-Bescherelle! (Designated by Fife & Seppelt 2001.)

= *Funaria cuspidata* Hook.f. & Wilson in Wilson, *Bot. Antarct. Voy. II (Fl. Nov.-Zel.) Part II*, 91 (1854)

Lectotype: N.Z., Bay of Islands, *J.D. Hooker s.n.* ("Wilson no. 348" or "348a"), BM-Wilson!

Isolectotypes: BM-Wilson!, H-Lindberg! (Designated by Fife & Seppelt 2001.)

**Plants** yellow- or brown-green. **Stems** red-brown, 2–5 mm, branching once by subperigonal innovation, beset with red-brown rhizoids. **Leaves** erect-spreading when moist, oblong-obovate, tapered in upper  $\frac{1}{3}$  to an acute, obtuse, or slender and aristate or cuspidate apex, (1.3–)1.5–2.1  $\times$  0.6–0.8 mm, concave, entire; **upper laminal cells** (24–)33–69  $\times$  15–18  $\mu\text{m}$ ; **apical cell** variable in length, 60–110(–165)  $\mu\text{m}$ ; **alar cells** few, moderately inflated. **Costa** highly variable in length (often variable within a population or even a single plant), failing below leaf apices, percurrent to long excurrent as a cusp, c. 36–45  $\mu\text{m}$  wide near base. **Axillary hairs** present.

**Autoicous. Perigonia** and **perichaetia** as per genus. **Setae** slender, 9–22 mm, weakly dextrorse throughout, pale red-brown, weakly hygroscopic; **capsules** erect and symmetric, obovoid-cylindric or obovoid, 1.5–1.8(–2.0) mm with a neck c.  $\frac{1}{3}$  the capsule length, strongly constricted below mouth when dry; **mouth** transverse, equal to the capsule diameter; **exothecial cells** elongate, in surface view with obscure lumina, in cross-section with anticlinal walls strongly cuneate, c. 6–8 rows oblate at mouth; **operculum** plano-convex. **Peristome** double; **exostome teeth** variably developed and usually  $\pm$  irregular in outline and with sinuose margins, striate, tapered to an acute or irregular and often  $\pm$  perforate apex; **endostome** variable, rudimentary to c.  $\frac{1}{3}$  height of teeth. **Spores** 32–39(–45)  $\mu\text{m}$ , finely liriate, lacking a trilete scar.

**Illustrations:** Plate 4. Wilson 1854, pl. 86, fig. 3 (as *Funaria cuspidata*); fig. 7 (as *Entosthodon gracilis*); Catcheside 1980, figs 123–125 (as *Funaria gracilis*, *F. bullata*, and *F. cuspidata*); Meagher & Fuhrer 2003, p. 153.

**Distribution:** NI: N Auckland (numerous localities), S Auckland (Coromandel Peninsula, Waerenga, Cambridge, Ātiāmuri, Waiotapu Valley), Hawke's Bay (Wairoa, Māhia Peninsula, near Whakamahi Lagoon); SI: Marlborough (Kenepuru), Canterbury (Black Range), Otago (Trotters Gorge).

Australasian. Tasmania\*, mainland Australia\*, New Caledonia\*.

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**Habitat:** On finely grained (clay or silt) soil in relatively open vegetation. Often associated with *Leptospermum* or *Kunzea* scrub, and sometimes occurring in areas with impeded drainage. Frequent associates include *Campylopus clavatus*, *Eccremidium pulchellum*, *Entosthodon radians*, and *Pleuridium* spp. This taxon is widespread and commonly collected in N Auckland L.D. but known from only three localities on the South I. Occurring mostly from near sea level to c. 520 m (Waioapu Valley); found once at c. 1000 m in the Black Range.

**Notes:** Populations showing the intergradation between the "*gracilis* growth form" and the "*cuspidatus* growth form" occur very frequently, and usually include morphologically intermediate plants in respect to leaf form and costa length. The frequency with which intermediate forms occur precludes the taxonomic recognition of these forms, although their frequent co-occurrence in a population suggests that the variation is genetic rather than environmentally induced. Linzey (*in herb.*) correctly noted that pure populations of the "*cuspidatus* growth form" (with excurrent costae and cuspidate leaves) are frequently seen, but that pure populations of the "*gracilis* growth form" rarely if ever occur. An example of the variability of the var. *gracilis* is provided by the Hooker collection from the Bay of Islands. Collections from the Waitakere Ranges (N Auckland L.D.) by J.K. Bartlett (11 Nov. 1978, CHR 429600) and J.T. Linzey (1 Oct. 1972, CHR 433059) are also of highly variable populations. Similarly, variable populations occur in Tasmania and in Victoria.

Sainsbury's (1955, p. 244) observations concerning the degree of endostome development do not agree with my own; material with broadly acute or obtuse leaf apices and short costae (assignable to "*Funaria gracilis*" by his criteria) nearly always have at least rudimentary segments, contrary to Sainsbury's observations.

Both leaf apical forms are found in J.D. Hooker's Bay of Islands collection, from which Wilson segregated the types of both *Funaria cuspidata* Wilson ("W.348a") and *Entosthodon gracilis* Wilson ("W.348b"). Wilson second-guessed himself as to the identity of at least one of the segregates of "W.348b", labelling one initially *Funaria cuspidata*, then crossing this out and naming the segregate *Entosthodon gracilis*. This renamed segregate of "W.348b" shows clearly the variable nature of the collection and corroborates the interpretation that a single variable taxon is present.

Heterotypic synonyms include *Funaria bullata* Broth. (Victoria, Heyington, *W.W. Watts 208*, H-Br!), *Entosthodon varius* Mitt. (Victoria, *s.loc.*, *F.M. Adamson s.n.*, NY-Mitt!), and *Entosthodon noumeanus* Besch. (New Caledonia: *Balansa 2534*, BM-Bescherelle!).

**Etymology:** The varietal epithet *gracilis* means slender and is a reference to the long and slender setae of the taxon.

## ***Funaria* Hedw., Sp. Musc. Frond. 172 (1801)**

**Type taxon:** *Funaria hygrometrica* Hedw.

**Plants** medium-sized to robust, gregarious, usually yellow-green. **Stems** red-brown, rarely pale, usually branched once by subperigonal innovation which overtops the perigonium, in cross-section with a central strand and parenchymatous medulla, a cortex of 2–4 layers of thick-walled, red-brown cells, and a hyalodermis, beset below with smooth, red-brown rhizoids. **Leaves** erect or erect-spreading, both moist and dry, concave, oblong-ovate to obovate, tapered to an acute, acuminate, or obtuse apex, entire or weakly serrulate above; **upper laminal cells** oblong-hexagonal, rarely more or less quadrate, in lower portion longer and more oblong, usually 4–6 cells at alar angles inflated; **marginal cells** not or very weakly differentiated, never forming a distinct border; **costa** subpercurrent, percurrent, or rarely excurrent to form an awn. **Axillary hairs** as per family.

**Autoicous** or rarely polygamous. **Perichaetia** lacking paraphyses. **Perigonia** usually single, terminating a shoot from which the perichaetial branch arises by innovation, with numerous antheridia and paraphyses with globose terminal cells. **Setae** yellow- or red-brown, dextrorse below, and sinistrorse or dextrorse above, from less than 8 to >50 mm, smooth, curved (sometimes only in uppermost portion) or rarely geniculate when moist, strongly or weakly hygroscopic; **capsules** strongly asymmetric to symmetric, inclined, erect, or pendent (when moist), broadly ovoid-pyriform, narrowly pyriform or ovoid, red-brown at maturity, sulcate, with a neck  $\frac{1}{3}$  to  $\frac{1}{2}$  capsule length; **mouth** from c.  $\frac{1}{3}$  to equal the diameter of the capsule, oblique, or transverse; **exothecial cells** oblong to oblong-hexagonal, mostly 2–5:1, in cross-section with cuneate walls and forming alternating bands of thicker and thin-walled cells, c. 5–8 rows oblate at mouth; **operculum** plano-convex or low conic, composed of firm-walled, oblong cells in sigmoid files, bordered by radially elongate red-brown cells; **stomata** immersed, single-celled, numerous and restricted to neck; **annulus** compound, strongly revoluble, composed of 1–3 rows of isodiametric, usually yellowish cells and one row of larger, more or less ellipsoid, vesicular and nearly hyaline cells. **Peristome** double; **exostome teeth** inserted at mouth,

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sigmoid, fused at their apices by a lattice disc, marginally appendiculate nearly throughout or merely at apex, papillose-striolate below, papillose above (most, if not all ornamentation on the outer surface), outer surface with a median zig-zag line; inner surface strongly trabeculate; **endostome segments** opposite and wider than the teeth, coherent at base, from  $\frac{1}{3}$  to equal the height of the teeth, acuminate or truncate and retuse, free or adherent (especially in lower portions) to teeth, papillose-striolate; **cilia** absent. **Calyptra** inflated at base, cucullate, and rostrate. **Spores** spherical or subreniform, mostly 10–30  $\mu\text{m}$ , uniformly verrucate or verrucate-lirate (often appearing nearly smooth under the light microscope), lacking trilete scars.

**Taxonomy:** *Funaria*, in the narrow sense that it is accepted here (excluding *Entosthodon*), is a genus of fewer than 20 species. It is of nearly cosmopolitan distribution, but in the tropics it is largely restricted to higher elevations. Species of *Funaria* are usually associated with disturbed and often nutrient- or mineral-enriched soils. *Funaria calvescens* Schwägr. (often treated as a variety of *F. hygrometrica*) is widely distributed from mostly high altitude sites in tropical areas. The genus extends into high arctic regions as *F. polaris* Bryhn (which is usually associated with lemming burrows), and *F. arctica* (Berggr.) Kindb. *Funaria flavicans* Michx. is widely distributed in eastern North America. *Funaria microstoma* is widely distributed world-wide, but is mostly rare throughout its range and is associated with salt spray or saline springs or lakes; it extends to high northern latitudes and also occurs in Australia. Only *F. hygrometrica* is documented from N.Z.

**Excluded Taxa:** *Funaria microstoma* Bruch ex Schimp. [Flora 23: 850, 1840] was recorded from the Māhia Peninsula (Hawke's Bay L.D.) by Sainsbury (1955). This record is rejected. The collection on which the report is founded (*G.O.K. Sainsbury 4047*; WELT M016982!; CHR 454724!; FH!) has strongly oblique mouths, which appear, in the dry material, to be relatively small in relation to the capsule and spores (c. 27–30  $\mu\text{m}$  diam.), near the upper limit of continuous variation for *F. hygrometrica*. However, the endostome in the Sainsbury collection is well developed, with the segments acute and nearly the length of the exostome teeth (rather than short and clearly bilobed apically as in *F. microstoma*). *Funaria microstoma* is associated with saline habitats throughout its range and is recorded from a small number of mainland Australian sites (sometimes named there as *F. salsicola* Müll.Hal. [Hedwigia 41: 120, 1902]), but to date no verifiable material has been found in N.Z.

## ***Funaria hygrometrica* Hedw., Sp. Musc. Frond. 172 (1801)**

Type specimen: Germany. Not seen.

**Plants** medium-sized, comose, often with sporophytes large relative to the gametophytes, gregarious, usually yellow-green. **Stems** as per genus, with one or sometimes more innovative branches, in cross-section as per genus. **Leaves** erect, both moist and dry, strongly comose and clasping the base of the sporophyte, strongly concave, oblong-ovate or obovate, tapered to an acute, sometimes mucronate, apex, entire, mostly 2.0–3.8  $\times$  c. 1.6 (difficult to flatten); **upper laminal cells** oblong-hexagonal, lax, and smooth, mostly 36–70(–90)  $\times$  30–36  $\mu\text{m}$ , but some usually smaller and  $\pm$  irregular, becoming smaller near apex, and larger and more oblong near base; **marginal cells** not differentiated; **alar cells** not or scarcely differentiated. **Costa** red- or yellow-brown, percurrent or short-excurrent to form a mucro, c. 45–60  $\mu\text{m}$  wide in lower leaf, in cross-section with a conspicuous central stereid group. **Axillary hairs** few, with cylindric terminal cells.

**Autoicous. Perigonia** and **perichaetia** as per genus. **Setae** red- or pale orange-brown at maturity, highly variable in length (to at least 50 mm), dextrorse below, sinistrorse above, smooth, strongly hygroscopic, nearly straight when dry, strongly sinuose when moist; **capsules** strongly asymmetric, strongly inclined when moist, semi-erect or inclined when dry, broadly ovoid-pyriform, sulcate both moist and dry, yellow-brown and becoming red-brown at maturity, with an ill-defined neck c.  $\frac{1}{3}$  to  $\frac{1}{2}$  the total capsule length, mostly c. 2.5–3  $\times$  c. 1.5 mm (at maturity, prior to dehiscence), with spore sac c.  $\frac{1}{2}$  the total capsule length; **mouth** oblique; **exothecial cells**, **stomata**, and **annulus** as per genus; **operculum** plano-convex, otherwise as per genus. **Peristome** double; **exostome** teeth as per genus; **endostome segments** from  $\frac{3}{4}$  to equal the height of the teeth, pale, acuminate at apex, papillose-striolate, otherwise as per genus. **Calyptra** as per genus. **Spores** slightly subreniform, c. 10–30(–38)  $\mu\text{m}$ , appearing nearly smooth under the light microscope, lacking trilete scars.

**Illustrations:** Plate 5. Brotherus 1924, fig. 282; Flowers 1973, pl. 62, 1–8; Crum & Anderson 1981, fig. 216, A–F; Beaver et al. 1992, fig. 37; Malcolm & Malcolm 2003, p. 30; Meagher & Fuhrer 2003, p. 155; Malcolm & Malcolm 2006, numerous illustrations.

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**Distribution:** K; NI: N Auckland including offshore islands (PK, HC, LB, RT), S Auckland, Gisborne, Hawke's Bay, Taranaki, Wellington; SI: Nelson, Marlborough, Canterbury, Westland, Otago, Southland; St; Ch; A; C. Reported from M by Seppelt (2004).

Cosmopolitan. Tasmania\*, mainland Australia\* (W.A.\*, S.A.\*, N.S.W.\* A.C.T.\*, Vic.\* Qld\* and N.T.\*). This species is virtually ubiquitous in temperate regions worldwide.

**Habitat:** This is an extremely weedy species and listing all its potential habitats is difficult. It occurs most abundantly on mineral soil after fire. However, it occurs in a wide range of terrestrial habitats with a wide range of disturbance levels. Frequent habitats include soil heated by fire, ash piles, margins of roadside and trackside drains (with or without some saline influence), earth/clay soil banks, agricultural soils, mortar, paving stones or bricks, and nutrient-enriched soil in bird colonies. It can occupy areas of many square metres and it tolerates a wide range of soil textures. It can even rarely occur as an epiphyte, but then it is almost always associated with bird perches. On the North I. it ranges from near sea level to 2135 m (Mt Ruapehu, Wellington L.D.); on the South I. it ranges from sea level to at least 1085 m (Crown Range, Otago L.D.). *Ceratodon purpureus* and a range of weedy *Bryum* spp. are frequent associates in N.Z.

*Funaria hygrometrica* is a serious greenhouse weed (like *Marchantia polymorpha* and *Leptobryum pyriforme*). It has been observed growing, if not actually thriving, on commercial potting soil inside a translucent sealed plastic bag. It often survives on disturbed soil where herbicides have been applied.

**Notes:** Large colonies of *F. hygrometrica* can often be recognised from a distance by the distinctive orange-brown colour of its capsules. Fully mature capsules that have shed their spores also have a distinctive dark red-brown colour that can likewise be recognised at distance.

Much has been written about the nutrient requirements of *F. hygrometrica*. Hoffman (1966) found in the western U.S. that elevated levels of nitrogen and phosphorous and circum-neutral pH were the most significant factors promoting *F. hygrometrica* invasion of burn sites. He found that calcium, magnesium, and potassium concentrations had little influence on its growth. Southorn (1977) found that elevated ammonium concentration immediately after bonfires could be toxic to *F. hygrometrica* protonema, and that some leaching is required before successful colonisation can occur. He found high levels of calcium promoted growth (seemingly conflicting with the results of Hoffman), and also that *F. hygrometrica* might be tolerant of levels of "specific nutrients such as manganese" that are toxic to angiosperms. Such tolerances, an abbreviated life cycle, and high nutrient requirements help to explain the domination of early stages of post-fire succession by *F. hygrometrica*, both in N.Z. and in other parts of its range. In natural conditions in N.Z. *F. hygrometrica* normally completes its life cycle in less than a year, with plants observed in winter months frequently in the "spear" stage of sporophyte development.

*Funaria hygrometrica* also tolerates saline soils. It often occurs (often as only a small number of plants) on soil among seaside rocks subject to some salt spray. It has been collected from silt at the margin on an ephemeral inland saline lake (Salt Lake, near Sutton, Otago L.D.) by J. Child (CHR 644305). The species exhibits a wide variation in stature. Natural populations from various parts of its worldwide range have been recorded as having various ploidy levels, with  $n=14$ , 28, and 56 (Crum & Anderson 1981) and possibly other numbers;  $n=28$  was recorded from three Australian populations (Ramsay in Löve 1967). The possibility of chromosome races being present in N.Z. has not been explored, nor has the distinct possibility that both indigenous and adventive races occur here.

This is one of the most widely recognised mosses, in part because of its weedy nature, and because it is often used as an example of a "typical" moss in introductory botany textbooks, where it is often used to illustrate a representative moss life cycle. In English it is often given the common name "Cord Moss", which alludes to the strongly twisted (like a cord or rope) setae. Another widely used common name is "Cinderella Moss", which alludes to its occurrence on ashes or cinders. This is also one of very few N.Z. mosses with a Māori name: wairua (Beever 1991).

Material from tropical parts of the range is usually referred to *F. hygrometrica* var. *calvescens* (Schwägr.) Mont., distinguished by its very long setae and longer and narrower capsules. No N.Z. collections, including the few seen from the Kermadec Is, are referable to this variety, and it is not considered further here.

**Recognition:** There is no species in the N.Z. flora that could be confused with *F. hygrometrica* when fruiting. Even when non-fruiting, the large and lax laminal cells distinguish it from other taxa, except other members of Funariaceae. Sterile plants of *Physcomitrium pyriforme* can be difficult to distinguish from the present species.

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**Etymology:** The epithet *hygrometrica* is derived from Greek roots *hygro-* (moisture) and *metricus* (measuring) and alludes to the manner in which the setae twist dramatically in response to changes of humidity.

## ***Goniomitrium* Hook. & Wilson in Wilson, *London J. Bot.* 5: 142 (1846)**

**Type taxon:** *Goniomitrium acuminatum* Hook. & Wilson

**Plants** small, brown-green to bright green. **Stems** red-brown or pale, unbranched or rarely forked, to c. 2 mm high, in cross-section with weakly differentiated, firmer-walled cortical layers and a weak central strand, beset below with red-brown or cerise rhizoids that rarely bear ovoid tubers. **Leaves** erect-spreading to spreading, concave to somewhat keeled, ovate to obovate-spathulate, acute to acuminate-aristate; margins plane and entire; **upper lamina cells** quite variable, often hexagonal to oblong and frequently with some cells oblate, not differentiated at margins; those in lower portion of lamina more oblong or quadrate and often laxer, sometimes with walls undulate and weakly thickened at corners, a row of yellow-brown cells frequently present at the insertion; **alar cells** not differentiated. **Costa** weakly to well developed (rarely  $\pm$  absent), usually percurrent to excurrent. **Axillary hairs** present, difficult to observe.

**Paroicous**, but with antheridia not present in all perichaetia. **Setae** yellow, 0.2–1.0 mm long, smooth, straight, untwisted; **capsules** erect, symmetric, ellipsoid to globose (before dehiscence), globose to somewhat pyriform (after dehiscence), c. 1 mm long, operculate, gymnostomous, yellow-brown, strongly and irregularly wrinkled when dry, with a weakly differentiated neck  $\frac{1}{5}$  or less the length of the capsule; **mouth** transverse, equal or slightly less than the diameter of capsule; **exothecial cells** irregularly polygonal, c. 30–50  $\mu\text{m}$  diam., with thin, radially non-cuneate walls, several suboral rows oblate and firmer-walled; **operculum** plano-convex, not rostrate, falling with a portion of the columella attached, composed of irregularly arranged, thin-walled cells; **annulus** weakly differentiated, composed of a single row of small, firm-walled, isodiametric to oblong cells, persistent; **stomata** numerous, superficial or weakly immersed, single-celled. **Calyptra** broadly mitrate, with a short, stout rostrum, with 8 radial pleats, 8-lobed at base, completely covering the immature capsule and often persisting after dehiscence. **Spores** ellipsoid, yellow-brown, minutely verrucate and often appearing smooth under light microscope, usually reticulate at maturity, (40–)60–110  $\mu\text{m}$  in greater diam.

**Taxonomy:** A small genus of between one and five species, distributed mainly in Australia, southern Africa, and Spain. Taxa occurring in southern Africa, Australia, and Spain could justifiably be reduced to subspecies within *G. acuminatum*. *Goniomitrium* has been traditionally (Brotherus 1924) placed in the Funariaceae. A molecular study by Goffinet & Cox (2000) presented the surprising conclusion that *Goniomitrium* should be shifted to the Pottiaceae. However, a more recent molecular study (Werner et al. 2007) concluded that Goffinet & Cox used incorrectly determined material in their study, and, using chloroplast DNA (*rps4* and *trnL-trnF* sequences), corroborated the traditional view that *Goniomitrium* is best placed in the Funariaceae. Further, they concluded that the present genus belongs to a well-supported clade together with the monotypic northern hemisphere *Pyramidula* Brid., and formally proposed the subfamily Pyramiduloideae to accommodate these two genera.

*Goniomitrium* and the allied *Pyramidula* are unique in the Funariaceae in having relatively large (mostly 50–90  $\mu\text{m}$ ) spores, which often appear smooth under the light microscope but become reticulate with maturity. The spores are pale to gold-brown in both genera (Fife 1985). Stone (1981) examined Australian *Goniomitrium* taxa in detail, including their spore morphology, and compared the Australian and Africa taxa.

All species of *Goniomitrium* occur on soil and probably develop after heavy seasonal rains.

**Etymology:** The generic name refers to the angled nature of the mitrate calyptra, which is unique in the Funariaceae.

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***Goniomitrium acuminatum* Hook. & Wilson in Wilson, *London J. Bot.* 5: 143 (1846)**

Lectotype: Australia, Swan River, *J. Drummond 6b*, Herb. Wilson, BM000983172! Isotype: CHR 620699! There are several duplicates of the Drummond collection in BM, thus making the selection of a lectotype desirable, contrary to the statement by Fife & Seppelt (2001) that a holotype is present in that herbarium.

The following description is based mainly on material from Western Australia and Queensland.

**Plants** pale green to brown, on mineral soil. **Stems** red-brown, erect, unbranched or branched, beset with red-brown, smooth rhizoids below, c. 2 mm, with no distinct cortical layer and a weak central strand. **Leaves** erect to weakly erect-spreading when moist, moderately contorted when dry, ovate to ovate-lanceolate, gradually tapered to an acuminate apex, (1.0–)1.6–2.0(–2.2) × (0.3–)0.5(–0.8) mm, including the acumen, which is 1/3 to 1/2 the length of the leaf, concave; **margins** plane, entire, and unbordered; **upper laminal cells** rather firm-walled, quadrate to oblong to weakly hexagonal, variable in size, (20–)52–65(–100) × (15–)21–24(–27) μm, becoming more regularly oblong in mid leaf but not differing in size, nearer insertion larger and oblong, (53–)75–95 × 27–32 μm, with a band of yellow-brown cells at insertion. **Costa** yellow, narrow, c. 50 μm wide at mid leaf and excurrent to fill a slender acumen in well-developed leaves (in N.Z. material), sometimes fading in lower portion of leaf (in Australian material) and in small leaves often ± absent. **Axillary hairs** present, 4-celled, c. 140 μm long; with terminal cell c. 60 × 12 μm (only one seen).

**Paroicus** but with antheridia not associated with all perichaetia. **Antheridia** often associated with reduced, ecostate leaves; paraphyses with inflated terminal cells usually present. **Setae** pale yellow, c. 1 mm, in cross-section with a single cortical layer and lacking a central strand; **capsule** broadly ellipsoid to globose, c. 1.0 × 0.8 mm, yellow-brown, operculate, gymnostomous, strongly and irregularly wrinkled when dry; **exothecial cells** irregularly oblong to polygonal, c. 27–40 μm in greater dimension, thin-walled, c. 8 rows of cells transversely elongate and thick-walled below the mouth; **mouth** transverse, slightly smaller in diameter than the mature capsule; **operculum** yellow at maturity, convex, composed of irregularly arranged, thin-walled cells; **annulus** as per genus; **stomata** numerous, superficial, funariaceous, restricted to capsule base. **Calyptra** broadly mitrate, 1–1.2 mm long, 1 mm diam., with a short (<0.2 mm long) rostrum, with eight radial pleats and eight-lobed at base, completely covering the immature capsule and often persisting after dehiscence. **Spores** yellow-brown in mass, ± ellipsoid, appearing minutely verrucate or smooth under light microscope, becoming reticulate at maturity, in polar view oval to isodiametric, in lateral view convex distally, flat to slightly concave proximally, with a long, narrow, monolete aperture, mostly (60–)70–80(–110) μm in greater diam.

**Illustrations:** Plate 6. Catcheside 1980, figs 133–134; Stone 1981, pl. 1, a–d, fig. 1, a–e, i–t; Fife 1985, pl. 9, fig. 88, pl. 11, fig. b (as *G. acuminatum* subsp. *africanum*). The subsp. *enerve* is illustrated by Wilson 1846 (pl. 3).

**Distribution:** NI: Hawke's Bay (Napier).

Australasian. Mainland Australia (W.A.\*, S.A.\*, N.S.W.\*, Qld\*, N.T.\*).

**Habitat:** All members of the genus occur on bare soil, mostly following periods of heavy rain. No habitat details are known from the single 19th century N.Z. collection, which was associated with *Microbryum starckeanum*.

**Notes:** The occurrence of this species in N.Z. is based on *S. Berggren 1405*, a collection made at Napier in Aug. 1873 and preserved in NY. A small number of fruiting stems (CHR 573733) have also been isolated from another Berggren collection of *Microbryum starckeanum* from the same locality.

It is probable that this species dispersed naturally from Australia and temporarily established. Following its 1873 collection by the gifted collector S. Berggren, no further populations have been discovered in nearly 150 years. In the most recent report on the conservation status of N.Z. mosses (Rolfe et al. 2016), *G. acuminatum* is treated as a vagrant species.

In Fife & Seppelt (2001) the describing authors of *G. acuminatum* were given incorrectly as Hook.f. et Wilson, whereas the first author is W.J. Hooker ("Hook.") rather than "Hook.f."

In Australian material examined the development of the costa in *G. acuminatum* is variable, even within single populations. The types of both *G. acuminatum* and *G. enerve* Hook. & Wilson in Wilson [London J. Bot. 5: 142, 1846] were segregated from one James Drummond collection from Swan River, Western Australia. Other Australian herbarium specimens of *Goniomitrium* have been seen in which costal development is variable and from which more or less ecostate plants have been

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segregated and named as *G. enerve*. Fife & Seppelt (2001) treated the latter as a subspecies of *G. acuminatum*. The subspecific epithet *acuminatum* is not employed here.

**Recognition:** Confusion in N.Z. would be most likely with the relatively widespread *Gigaspermum repens*. However, *Goniomitrium* can be easily distinguished from that species by, *inter alia*, lack of fleshy subterranean stems, the presence of a single excurrent costa, the pleated nature of the calyptra, and much smaller (mostly 70–80 vs 150–190 µm) spores. The fleshy subterranean primary stems in *Gigaspermum repens* can be difficult to observe in herbarium material and are often overlooked.

**Etymology:** The epithet *acuminatum* refers to the apical form of the leaves.

## ***Physcomitridium* G.Roth., *Aussereur. Laubm.* 250 (1911)**

**Type taxon:** *Physcomitridium readeri* (Müll.Hal.) G.Roth.

The species description below is applicable to this monotypic genus.

**Taxonomy:** Much confusion surrounds the relationships and the consequent nomenclature of N.Z. material treated here as *Physcomitridium readeri*. Much of this confusion is due to the near impossibility of distinguishing *Physcomitridium* from *Physcomitrella* Bruch & Schimp. without using genetic markers.

The sole species of *Physcomitridium* was originally described as *Ephemerella readeri* Müll.Hal. However, the type species of *Ephemerella* Müll.Hal. [Syn. Musc. Frond. 1: 34, 1848] is the European *Ephemerella pachycarpa* (Schwägr.) Müll.Hal., which is conspecific with *Ephemerum recurvifolium* (Dicks.) Boulay (Goffinet & Buck 2011). Thus, the generic name *Ephemerella* is nomenclaturally synonymous with *Ephemerum*.

Since its description, the minute *Physcomitridium readeri* has been shifted between the genera *Physcomitridium* (where it was treated by Sainsbury 1955) and *Physcomitrella* (where it was treated by Stone & Scott 1973; Tan 1979; and Fife & Seppelt 2001). *Physcomitridium readeri* has also been recognised as both a species (Stone & Scott 1973, as *Physcomitrella readeri*) and as a subspecies (Tan 1979, as *Physcomitrella patens* subsp. *readeri*). Fife & Seppelt (2001) accepted the last placement and ranking in their discussion of Australian representatives of the Funariaceae.

Regionally the confusion surrounding *Physcomitridium* and *Physcomitrella* was partly caused by Sainsbury's (1955, p. 248) description of what he termed *Physcomitridium readeri*. Sainsbury's description of alleged *P. readeri* was written using *Bryobeckettia bartlettii* from Wairoa and Kelso, collected by E.A. Hodgson and W. Martin, respectively. The Kelso material, in addition to representative *B. bartlettii*, also includes numerous inter-generic hybrid [*Bryobartlettia bartlettii* ♀ × *Physcomitrium pyriforme* ♂] sporophytes, which generated further confusion. In short, the plants named and described by Sainsbury as *Physcomitridium readeri* (Müll.Hal.) Roth belong to neither that species nor that genus.

An enormous literature has grown up around the northern hemisphere *Physcomitrella patens* (Hedw.) Bruch & Schimp. because of its widespread use in the study of gene expression (e.g., Rensing et al. 2008). Consequently, the morphologically similar *Physcomitridium readeri* has also become the object of molecular investigations (McDaniel et al. 2010; Hooper et al. 2010). Liu et al. (2012) used 10 gene loci from nuclear, chloroplast, and mitochondrial genomes to present an impressive outline of relationships in the Funariaceae, including members of *Physcomitrella s.s.* and *Physcomitridium*. The collective results of these three molecular studies demonstrate that *Physcomitrella s.l.* is polyphyletic and argue persuasively for the recognition of *Physcomitridium* as a distinct genus. The remarkable similarity of their sporophytes is thus a result of convergent evolution or homoplasy.

N.Z. material of the taxon “*readeri*” is best treated in *Physcomitridium* rather than in *Physcomitrella*, where it has often been placed.

**Etymology:** The generic name *Physcomitridium* alludes to a similarity to *Physcomitrium*. However, since the name *Physcomitrium* in turn refers to inflated and mitrate calyptrae, the name of the present genus, which has minute calyptrae of indeterminate form, seems particularly inappropriate.



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## ***Physcomitridium readeri* (Müll.Hal.) G.Roth., *Aussereur. Laubm.* 250 (1911)**

≡ *Ephemerella readeri* Müll.Hal., *Hedwigia* 41: 120 (1902)

≡ *Physcomitrella readeri* (Müll.Hal.) I.G.Stone & G.A.M.Scott, *J. Bryol.* 7: 604 (1973)

≡ *Physcomitrella patens* subsp. *readeri* (Müll.Hal.) B.C.Tan, *J. Hattori Bot. Lab.* 46: 334 (1979)

Type: Australia, Victoria, Dimboola, Sep. 1897, *F.M. Reader*, CHR 626904! See discussion below.

= *Physcomitrella austropatens* Broth. in Roth, *Hedwigia* 54: 273 (1914) – as austro-patens

Type: Australia, Victoria, Yarra Bay (“Yarraback-Bucht”), *F.M. Reader*, 1902. (Type not seen; see discussion below.)

**Plants** very small, gregarious, dark green. **Stems** 0.5–1.5 mm, red-brown, unbranched, cross-section anatomy not clearly seen, beset near base with smooth, red-brown rhizoids. **Leaves** incurved around the capsule when dry, spreading when moist, oblong-lanceolate, moderately concave, those of coma c. 1.5 × 0.4–0.5 mm, smaller below (to c. 2 mm in Australian material), acute, **margins** plane, entire or weakly and bluntly toothed near apex; **upper laminal cells** oblong-hexagonal, thin-walled, mostly 39–60 × 18–27 µm (some more irregular), becoming larger and more oblong near leaf base, and more compact near apex; **marginal cells** not differentiated; **alar cells** slightly inflated but not distinct; **costa** ½ to ¾ the leaf length, red-brown, mostly unbranched but sometimes weakly bifurcate, in cross-section atypical of the family and lacking stereids. **Axillary hairs** not seen.

**Sexuality uncertain.** **Perichaetia** terminal. **Perigonia** not differentiated. **Setae** dark, c. 100 µm (vaginula c. 300 µm long); **capsule** erect, globose, inoperculate, disintegrating irregularly, 400–500 µm diam. (excluding rostrum), stoutly rostrate, lacking an obvious air space beneath the exothecium, dark red at maturity due to the colour of the enclosed spores, with columella absent at maturity; **rostrum** straight or oblique, longer than wide, c. 150–200 × c. 50 µm; **exothecial cells** very thin-walled, oblong-hexagonal, hyaline, at mid urn mostly c. 60 × 30 µm; **stomata** few and obscure, single-celled, restricted to base of the capsule. **Calyptra** minute, neither clearly mitrate nor cucullate, c. 0.4 mm, lobed at base covering only the rostrum. **Spores** spherical to slightly tetragonal, red-brown, uniformly spinose, 30–39 µm diam., a few with weak trilete scars.

**Illustrations:** Plate 7. Roth 1910–1911, pl. XXI, fig. 4 (as *Ephemerella readeri*, from type specimen); Roth 1914, pl. X, fig. 4 (as *Physcomitrella austro-patens*); Scott & Stone 1976, pl. 48 (as *Physcomitrella readeri*); Catcheside 1980, fig. 136 (as *Physcomitrella readeri*). The illustrations of Hooper et al. 2010 (figs 4–5, as *Physcomitrella readeri*) may or may not represent this species.

**Distribution:** NI: N Auckland (Lower Huia Dam in the Waitakere Ranges), S Auckland (near the confluence of the Whangamarino & Waikato Rivers, Meremere, near Kōpuku).

Australasian. Mainland Australia (Vic.\*, N.S.W.\*). Reported from Tasmania by Fife & Seppelt (2001, as *Physcomitrella patens* subsp. *readeri*). Reported as *Physcomitrella readeri* from the “silt by the Murray River and edges of billabongs” in S.A. by Catcheside (1980), while Scott & Stone (1976) considered *P. readeri* occurred in “S.A., Vic., and probably other states”. Also reported as a possible adventive in Britain by Hooper et al. (2010), but their claims of occurrence there are beyond the ambit of this Flora. Their suggestion (p. 260) that the present taxon can be “immediately distinguish[ed]” from true *Physcomitrella* using morphological features is an over-simplification. Because of the afore-mentioned near impossibility of distinguishing *Physcomitridium* from *Physcomitrella* Bruch & Schimp. without using genetic markers, all published distribution records of *P. readeri* should be regarded with caution.

**Habitat:** The Waikato River material was all collected from alluvial sandy-silt or clay soil near the river margin and at low elevation. All the collections from this site were made between 1980 and 1983 (the earliest by J.K. Bartlett) and the best documented were made from very near the confluence with the Whangamarino River. There is also one collection (AK 179821) labelled as from “Meremere”, which is c. 2 km from this confluence, and one (CHR 351334), from near Kōpuku, some 15 km distant. The single well-developed and ample collection, made by R.O. Gardner, from the Lower Huia Dam, grew on exposed clay in the draw-down zone of a drinking-water reservoir. Associated species at the Waikato River site included *Bryobeckettia bartlettii* and *Physcomitrium pusillum*, and, at the Kōpuku site, *P. pusillum*. No associates were recorded at the Lower Huia Dam site. *Physcomitridium readeri* is an ephemeral species, and all N.Z. collections were made either in the spring or autumn. Disturbance by invertebrates may play a role in the irregular fragmentation of the capsule exothecium and subsequent spore dispersal.

**Notes:** The material from the Waikato River sites (three or four collections) is morphologically uniform (and as described above). The Waikato River material (including *J.K. Bartlett s.n.*, 17 Mar. 1980,

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CHR 449103) is clearly the same species as both the type collected by Reader (see below) and Victorian material distributed as *H. Inoue's Bryophyta Selecta Exsiccata* 341.

Given the great confusion surrounding this species, it is necessary to be precise about some details of the type collection and publication details of *Ephemerella readeri* Müll.Hal. and associated names. The protologue states it to be from “Dimboola, Victoria, solo humida, Septembri 1897, *Fr. Reader*”). Nine years later Roth (1910–1911, p. 251) cited the type as from “bei Dimboola” with otherwise identical collection details. Roth (1910–1911) also provided a valuable illustration (pl. XXI, fig. 4) based on the Reader type collection. Apart from this illustration, type material has only been found in the Beckett collection at CHR (626904!). This specimen is labelled “*Ephemerella (Physcomitridium) Readeri* C.M., sp. nov., Basin of old sheep wash, Upper Region Station, 3/9 1897, leg. *F.M. Reader*”. All the collection data, except the precise locality, agrees with the protologue. Moreover “Upper Region(s) Station” is cited (Wikipedia, accessed 19 July 2017) as an earlier name for the Dimboola area. This specimen is confidently asserted to be original material.

A few years later Roth (1914) published another illustration, as *Physcomitrella austro-patens* Broth. in Roth (Hedwigia 54: 273, pl. X, fig. 3 a, b, & d). This illustration was based on a second *F.M. Reader* Victorian collection, made from the Yarra Bay (“Yarraback-Bucht”) on 27 Jul. 1902. This collection, not seen, can be taken as the type of *Physcomitrella austro-patens*, and Roth’s (1914) illustration corroborates Scott & Stone’s (1976, p. 262) suggestion that *P. austro-patens* is synonymous with *Physcomitridium readeri*. Scott & Stone are also correct in noting that “New Zealand ‘*Physcomitridium readeri*’ is not the same species” (see discussion of *Bryobeckettia bartlettii*, above).

Dixon (1926) discussed *Physcomitridium readeri* at length, and it is clear that he saw Victorian material. He quoted an opinion by Brotherus that he was inclined to refer it to *Physcomitrella s.s.* Dixon, however, considered *Physcomitridium readeri* generically distinct from *Physcomitrella* based on differences of stomata morphology; he found the stomata in *P. readeri* to be immersed compared to published illustrations (Limpricht 1885–1889) of those of true *Physcomitrella*. I have found stomata in the present species to be few in number and difficult to observe and hence cannot corroborate Dixon’s opinion. His observations deserve further study.

Although Tan (1979) studied Victorian material, he did not study type material. He made the combination *Physcomitrella patens* (Hedw.) Bruch & Schimp. subsp. *readeri* (Müll.Hal.) B.C.Tan, which is, however, accepted here as a homotypic synonym of both *Physcomitridium readeri* (Müll. Hal.) G.Roth and its basionym *Ephemerella readeri* Müll.Hal.

Dixon (1926) also discussed *Phascum chiltonii* R.Br.bis from the Robert Brown herbarium and collected from the Avon River in Christchurch. Dixon’s observations are confusing as he initially compared the Brown collection favourably to Roth’s illustrations, but then provided a description that seems to be based on material of *Bryobeckettia bartlettii* (which is well documented and relatively common in the Christchurch area). The type of *Phascum chiltonii* has not been seen.

Although most of the N.Z. collections of *Physcomitridium readeri* are more than 30 years old, there is one more recent and well-developed collection from exposed clay in the draw-down zone of a reservoir at Lower Huia Dam in the Waitakere Ranges, N Auckland L.D. (*R.O. Gardner s.n.*, 22 May 2010, CHR 614783) and initially named by J.E. Beever as *Physcomitrella patens* subsp. *readeri*. It is confirmed here as *Physcomitridium readeri*, albeit with reservations. The Lower Huia Dam plants are more yellow-green and softer in appearance than the Waikato plants, with leaves more obovate, considerably wider (to 0.9 mm wide), and apically more obtuse. The margins are entire or bluntly toothed above. Its stem cross-section anatomy is obscure, with no obvious clear central strand seen. The costae are c.  $\frac{2}{3}$  the leaf length and in cross-section lack stereids. The capsules here are larger and nearly globose, to 0.9 mm long and to 0.75 mm diam., have an obvious air space underneath the exothecium, and a shorter and stouter apical rostrum (with its length  $\pm$  equal its width and c.  $100 \times 100 \mu\text{m}$ ). The characteristic one-celled funariaceous stomata, restricted to the extreme capsule base, are much easier to observe here than in the Waikato material. The spores in the Huia material are slightly smaller (mostly 30–33  $\mu\text{m}$ ) than those of the Waikato plants. Some of these observed differences call to mind Dixon’s (1926, p. 192) observations on the stomata of *P. readeri* and those of true *Physcomitrella*. The morphological differences (especially the leaf shape and width, stomata, and other capsule features) suggest that the Lower Huia Dam collection may differ from the Waikato collections. The taxonomic difficulties associated with *Physcomitridium readeri* and taxa closely resembling it cannot be completely resolved here.

*Physcomitridium readeri* remains one of the most poorly documented moss species in N.Z. The few herbarium specimens are mostly sparse and difficult to study. The species is classified as “national critical” in the Department of Conservation’s New Zealand Threat Classification System (Rolfe et al. 2016). Given its ephemeral appearance on recently exposed or deposited silt/clay, it is likely to remain

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poorly documented indefinitely. Its particular habitat requirements make it an unlikely candidate for active management and it may be more frequent than records suggest.

**Recognition:** *Physcomitridium readeri*, while difficult to detect due to its minute size, is recognisable regionally by its minute, globose, inoperculate, and red-brown capsules. The enclosed spores, rather than the very delicate exothecium, provide the colour of the mature capsules. Because of the fragility of the exothecial cells, the capsule walls often fragment irregularly, leaving a mass of red-brown spores only partially contained in the fragmentary capsule. The laminal cells are lax, smooth, and thin-walled.

There are several species that could be confused with *P. readeri*. The pottiaceous *Acaulon integrifolium* has similar immersed and globose inoperculate capsules. It grows on drier sites, has firmer-walled and smaller laminal cells, and usually percurrent to slightly excurrent costae.

*Physcomitridium readeri* is superficially similar to and sometimes grows intermixed with *Physcomitrium pusillum*. The lack of a differentiated operculum and its delicate exothecial cells, its fewer and more obscure stomata, smaller spores, and obscure sexuality serve to differentiate the present species. *Physcomitrium pusillum*, by contrast, has a differentiated operculum, somewhat collenchymatous exothecial cells, more numerous and weakly immersed stomata, and larger spores, and is demonstrably autoicous. The more widespread *Bryobeckettia bartlettii* can also grow mixed with *Physcomitridium*. However, *B. bartlettii* has exserted and ellipsoid capsules with a distinct neck and numerous weakly immersed stomata, and is usually demonstrably autoicous. Both *Physcomitrium pusillum* and *Bryobeckettia bartlettii* grew with *Physcomitridium* at the Waikato River site.

**Etymology:** The specific epithet commemorates Felix Maximilian Franz Reader (1850–1911), a German-born pharmacist and amateur botanist, best known for his Australian collections. Reader lived briefly in Blenheim (N.Z.) in the late 1870s or early 1880s (collecting near Blenheim in 1881) before emigrating from N.Z. to Victoria, where he lived, apparently for many years, at Dimboola. He was an enthusiastic botanist who published many papers in the Victorian Naturalist and established himself as an expert on Victorian grasses. He sent mosses to Brotherus and Carl Müller (Müll.Hal.) and eventually sold his large private herbarium to the National Herbarium of Victoria in 1906.

## ***Physcomitrium* (Brid.) Brid., *Bryol. Univ.* 2, 815 (1827)**

≡ *Gymnostomum* subgen. *Physcomitrium* Brid., *Bryol. Univ.* 1, 97 (1826)

**Type taxon:** *Physcomitrium sphaericum* (Ludw. ex Schkuhr) Fűrnr.

**Plants** small to medium sized, gregarious, pale green. **Stems** red-brown, less commonly brown or pale, usually branched once by subperigonal innovation, very short to 10 mm or more, in cross-section with a parenchymatous medulla and a cortex of 2–3 layers of thick-walled cells, with or without a central strand, beset with red-brown rhizoids, tubers absent in N.Z. species. **Leaves** erect-spreading, rarely somewhat incurved, more or less concave, larger and more crowded near stem apices, obovate to oblong-lanceolate, acuminate, acute or obtuse; **margins** plane, toothed above or rarely entire; **upper laminal cells** thin-walled, oblong-hexagonal, rarely short oblong or more or less quadrate, in lower portion longer and more oblong; **marginal cells** usually longer and narrow, not forming a distinct border in N.Z. species. **Costa** ending well below apex to subpercurrent, rarely shortly excurrent.

**Autoicous** in N.Z. species, rarely paroicous, polygamous, or synoicous. **Perigonia** single, terminating a shoot from which the female branch arises by innovation. **Setae** red-brown or yellow, <0.5 mm to c. 15 mm, smooth, straight; **capsules** erect, pyriform to hemispheric or globose, operculate, gymnostomous, neck variably developed; **mouth** transverse, as wide as the capsule or rarely strongly narrowed; often becoming flared with age; **exothecial cells** isodiametric to shortly oblong, firm- or rarely thin-walled, non-cuneate, weakly to markedly thickened at corners, few to several suboral rows oblate and with thickened transverse walls; **annulus** composed of a single row of thin-walled cells with a thick distal transverse wall, rarely vesicular, or of more than one ring of cells and revoluble; **stomata** variably immersed. **Operculum** plano-convex and rostrate, rarely conic. **Calyptra** mitrate-rostrate, covering less than half the capsule and falling before maturity. **Spores** subreniform, red-brown, spinose.

**Taxonomy:** The spores are consistently spinose in *Physcomitrium*. The non-cuneate exothecial cells are sometimes useful in distinguishing *Physcomitrium* from gymnostomous species of *Entosthodon*, although regionally such confusion is unlikely. Given the absence of peristome characters in this genus, there has been considerable emphasis on capsule form (see Fife 1985, pl. 11), as well as a limited range of gametophytic differences, to differentiate species. As a consequence many

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geographically isolated populations have been unduly dignified with specific rank. Clarification of the relationships within *Physcomitrium* (which is likely not monophyletic) is not possible using morphological features alone.

A genus of probably more than 50 species, widely distributed in temperate and, to a lesser extent, tropical regions. Only two species are accepted for N.Z.

**Etymology:** The generic name refers to the swollen base and the mitrate form of the calyptra.

- 1**        **Setae** 0.1–0.5 mm; **capsules** nearly globose and with a mouth c.  $\frac{1}{3}$  the capsule diameter; **spores**  $\geq 37$   $\mu\text{m}$  diameter; very rare and known only north of 38° S ..... *P. pusillum*
- 1'**       **Setae** 3–6 mm; **capsules** globose-pyriform, with mouth as wide as capsule and usually becoming flared with age; **spores** 27–39  $\mu\text{m}$  diameter; common and widespread ..... *P. pyriforme*

**Excluded Taxa:** *Physcomitrium perrottetii* Mont. was cited from the Bay of Islands by Wilson (1854, p. 92). This species is not listed in Tropicos (Data seen online, TROPICOS, accessed 12 Jul. 2017). Dixon (1926) rejected the inclusion of this apparently Indian species in the N.Z. flora, and this taxon is not considered further here.

*Physcomitrium pyriforme* var. *pumilum* Hook.f. & Wilson [Bot. Antarct. Voy II (Fl. Nov.-Zel.) Part II 92, 1854], was described from the Bay of Islands; type material has not been seen. Dixon (1926, p. 193) reported seeing a scrap collected by C. Knight and labelled as this variety by Mitten at Kew. No useful purpose would be served by questioning Dixon's decision to place it in the synonymy of *P. conicum* (which is considered a synonym of *P. pyriforme* here).

### ***Physcomitrium pusillum* Hook.f. & Wilson in Wilson, Bot. Antarct. Voy. II (Fl. Nov.-Zel.) Part II, 92 (1854)**

Holotype: N.Z.: North Island, s. loc., *Dr Sinclair*, 1850, BM000983165! The holotype is accompanied by Wilson's original drawings that were reproduced as Bot. Antarct. Voy II (Fl. Nov.-Zel.) Part II, pl. 87, fig. 1.

**Plants** very small, yellow- to brown-green. **Stems** branched once by innovation or occasionally with several innovations, to 4 mm, yellowish- or red-brown, in cross-section with a weak central strand, beset below with smooth, red-brown rhizoids, which lack tubers. **Leaves** obovate to oblong-obovate, acute, c. 2.0–3.1 mm, erect-spreading or incurved when damp, incurved when dry, plane at margins, weakly concave, serrulate to serrate above by projecting cell ends; **upper laminal cells** oblong-hexagonal, c. 25–50  $\times$  18–25  $\mu\text{m}$ , becoming longer and more regularly oblong below, c. 4–6 cells somewhat inflated and nearly round at alar angles; **marginal cells** not differentiated. **Costa** yellow-brown, 25–43  $\mu\text{m}$  wide near base, ending 3–8 cells below apex, in cross-section with a central stereid group enclosed by 1 abaxial and 2 adaxial layers of large and thin-walled cells. **Axillary hairs** present, often observable in dried material, with 1 or 2 stalk cells and an oblong terminal cell 100–130  $\mu\text{m}$  long.

**Autoicous. Perigonia** 1 or occasionally 2 per plant, terminal, mostly overtopped by a perichaetial innovation, and c.  $\frac{2}{3}$  the plant height, with numerous paraphyses with globose terminal cells.

**Perichaetia** terminating the innovation. **Setae** 1 or rarely 2 per perichaetium, yellow, 0.1 to 0.5 mm; **capsules** nearly globose, operculate, 1–1.5  $\times$  0.9–1.1 mm, yellow-brown, with a neck c.  $\frac{1}{5}$  the length of the capsule; **mouth** c.  $\frac{1}{3}$  the diameter of the capsule; **exothecial cells** isodiametric to short oblong, thin-walled, weakly thickened at corners, a few rows oblate and red-brown at mouth; **stomata** weakly immersed, c. 20–30 per capsule. **Operculum** conic, obtuse. **Calyptra** covering c. one-third of capsule, 4–5 lobed at base. **Spores** uniformly spinose, 37–49  $\mu\text{m}$ .

**Illustrations:** Plate 8. Wilson 1854, pl. 87, fig. 1; Fife 1982b, figs. 1–9; Fife 1985, pl. 11, f.

**Distribution:** NI: N Auckland (Mercer, junction of Whangamarino & Waikato Rivers); S Auckland (Island Block).

Australasian. Mainland Australia ("near Melbourne")\*. The single Victorian specimen studied (Herb. Mitten, NY 00968163!) was collected by F.M. Reader in July 1884. It is ample and well developed.

**Habitat:** Known only from a very restricted area near the lower Waikato River between Meremere and Mercer and from the nearby "Island Block"; the best-documented collections are from near the mouth of the Whangamarino River. The type specimen is from an unknown North I. locality. This species is

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known only from sites below c. 100 m elevation, where it has been found growing on riparian silt or clay.

**Notes:** This species is considered to be “national critical” in the 2014 version of the Department of Conservation’s assessment of the conservation status of N.Z. mosses (Rolfe et al. 2016). J.E. Beever (pers. comm.) has informed me that the site where *P. pusillum* was last collected (in Oct. 1983) has been modified by the construction of a boat launching ramp. The ephemeral nature of this species and its occupancy of riparian silt suggest that active management of populations would not be possible. The typification and relationships of *P. pusillum* were discussed by Fife (1982b).

**Recognition:** *Physcomitrium pusillum* is most likely to be confused with *Bryobeckettia bartlettii*, a species with which it sometimes grows. The present species differs by capsule form (immersed and globose vs exserted and ellipsoid), the presence of a well-defined and functional operculum, and more acute and toothed leaves. The latter species is more common and more widespread in N.Z.

**Etymology:** The epithet *pusillum* means very small, and is apt for this minute species.

## ***Physcomitrium pyriforme* (Hedw.) Hampe, *Linnaea* 11: 80 (1837)**

≡ *Gymnostomum pyriforme* Hedw., *Sp. Musc. Frond.* 38 (1801)

Type locality: Europe. Not seen. *Gymnostomum pyriforme* Hedw. has apparently never been lectotypified. A lectotype would ideally be chosen from the Hedwigian herbarium at G. Hedwig (1801) gives little information that would facilitate a selection, although he cites literature by several earlier authors. Although this is a very widely distributed species, the selection of a lectotype is essentially a European problem. There is no evidence that Hedwig sighted any of the photographed specimens on JSTOR (accessed 22 Jun 2017).

= *Physcomitrium conicum* Mitt. in Wilson, *Bot. Antarct. Voy. III. (Fl. Tasman.) Part II*, 197 (1859)

Holotype: Tasmania: Leith’s Creek, Mr. Archer, 29 July (year not specified), Herb. Mitten, NY 00968148!

= *Entosthodon physcomitrioides* Müll.Hal., *Gen. Musc. Frond.* 109 (1900) nom. illeg.

Type: N.Z.: North Canterbury, Rockwood, T.W.N. Beckett NZ 367, CHR 500991!

**Plants** medium-sized, gregarious, bright green. **Stems** branched once by subperigonal innovation, c. 4–11 mm, yellow- or red-brown, in cross-section with a well-defined central strand, beset below with smooth, red-brown rhizoids which lack tubers. **Leaves** oblong-obovate, acute, c. 2.0–3.0(–3.8) mm, erect-spreading when damp, inrolled and somewhat contorted when dry, plane, weakly concave, bluntly serrate above by projecting cell ends or occasionally nearly entire; **upper laminal cells** oblong-hexagonal, c. 45–69 × 26–30 µm, becoming longer and more regularly oblong below, c. 4–6 cells inflated but poorly differentiated at alar angles; **marginal cells** narrower and somewhat longer but not forming a distinct border. **Costa** green or yellow-brown, c. 60–75 µm wide near base, subpercurrent. **Axillary hairs** present, with 1 or 2 stalk cells and an oblong terminal cell.

**Autoicous. Perigonia** terminal and overtopped by a perichaetial innovation. **Setae** single, red-brown, c. 3–6 mm; **capsules** globose-pyriform, usually constricted below mouth when dry, 1–1.5(–1.8) × 0.9–1.2 mm, yellow- to red-brown, with a neck to one-third the capsule length; **mouth** equal the capsule in diameter, flaring when dry; **exothecial cells** oblong-hexagonal or irregular, firm-walled, not thickened at corners, several rows isodiametric or oblate at mouth; **stomata** immersed; **annulus** a single row of round, thinner-walled cells that are smaller than adjacent suboral cells, persistent. **Operculum** conic or shortly and obtusely rostrate from a plano-convex base. **Calyptra** often becoming split on one side, covering c. 1/3 of the capsule, falling early. **Spores** uniformly spinose, 27–39 µm.

**Illustrations:** Plate 8. Crum & Anderson 1981, fig. 212; Fife 1985, pl. 11c; Malcolm & Malcolm 2003, p. 49.

**Distribution:** NI: N Auckland, including offshore islands (LB), S Auckland (numerous localities), Hawke’s Bay, Taranaki (Kaitiēke), Wellington (numerous localities). SI: Nelson (Cape Foulwind, Cobden), Marlborough (single collection with no locality given), Canterbury (numerous localities), Otago (numerous localities), Southland (near Riverton).

Probably adventive. Tasmania\*, Australia\*, North America\*, Europe\*.

**Habitat:** On bare, damp soil, especially silt or clay; often in disturbed habitats such as ditch, stream, or pond margins and on spoil; roadsides and in paddocks, sometimes forming extensive turves. Avoiding deeply shaded situations and tolerant of herbicides. Ranging from near sea level to at least c. 375 m

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(Waiotapu, S Auckland L.D.) on the North I. and from sea level to at least 500 (Lake Pūkaki, Canterbury L.D.) m on the South I. Capsules normally mature in late spring or early summer. No material has been seen from Gisborne L.D., but this is probably a collection artefact. The species is also undocumented from Westland L.D. *Bryobeckettia bartlettii*, *Bryum dichotomum* and other weedy *Bryum* species, *Calliergonella cuspidata*, *Ceratodon purpureus*, and *Tortula truncata* are frequently closely associated.

**Notes:** Capsules are often more turbinate and the setae are generally shorter in N.Z. material than in European. However, given the considerable variability of the species in other parts of its range, particularly in North America, the variability in N.Z. material provides insufficient reason to recognise the Tasmanian *P. conicum*. Polyploidy is well documented in *P. pyriforme* in other parts of its range, but ploidy levels have not been investigated here.

Inter-generic hybrids occur between *Bryobeckettia bartlettii* and *P. pyriforme*, and are present in collections of both these species made by W. Martin at Kelso (Otago L.D.). The resultant hybrid capsules seem mainly to be the result of *B. bartlettii* ♀ × *P. pyriforme* ♂ crosses and are discussed in greater detail above, under *Bryobeckettia*.

Wilson (1854) provided the first record of *P. pyriforme* in N.Z., based on both Colenso and Hooker collections from the Bay of Islands (N Auckland L.D.). Despite these very early records, the weedy habitats invariably occupied by this species make it a strong candidate for adventive status.

**Recognition:** *Physcomitrium pyriforme* is easily confused with *Tortula truncata*, a species with which it often grows on disturbed soils. The present species can be distinguished from the *Tortula* by several features, including larger leaf cells (those of *P. pyriforme* are clearly visible under a hand-lens, those of *T. truncata* are not); shorter costae (subpercurrent vs excurrent in *T. truncata*); shorter, less pointed opercula; and larger capsules (1.0–1.8 × 0.9–1.2 mm vs <1 mm long, and c. 0.6 mm diameter).

**Etymology:** The epithet *pyriforme* means pear-shaped, and refers to the form of the mature capsules.

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# Conventions

## Abbreviations and Latin terms

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

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PK	Poor Knights Islands
P.N.G.	Papua New Guinea
<i>pro parte</i>	in part
Qld	Queensland
q.v.	which see ( <i>quod vide</i> )
RT	Rangitoto Island
S.A.	South Australia
<i>s.coll.</i>	without collector ( <i>sine collectore</i> )
<i>s.d.</i>	without date ( <i>sine die</i> )
sect.	section
SEM	scanning electron microscope/microscopy
<i>sensu</i>	in the taxonomic sense of
SI	South Island
<i>sic</i>	as written
<i>s.l.</i>	in a broad taxonomic sense ( <i>sensu lato</i> )
<i>s.loc.</i>	without location ( <i>sine locus</i> )
Sn	Snares Islands
<i>s.n.</i>	without a collection number ( <i>sine numero</i> )
Sol	Solander Island
sp.	species (singular)
spp.	species (plural)
<i>s.s.</i>	in a narrow taxonomic sense ( <i>sensu stricto</i> )
St	Stewart Island
<i>stat. nov.</i>	new status ( <i>status novus</i> )
subg.	subgenus
subsect.	subsection
subsp.	subspecies (singular)
subsp.	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 ( <i>videlicet</i> )
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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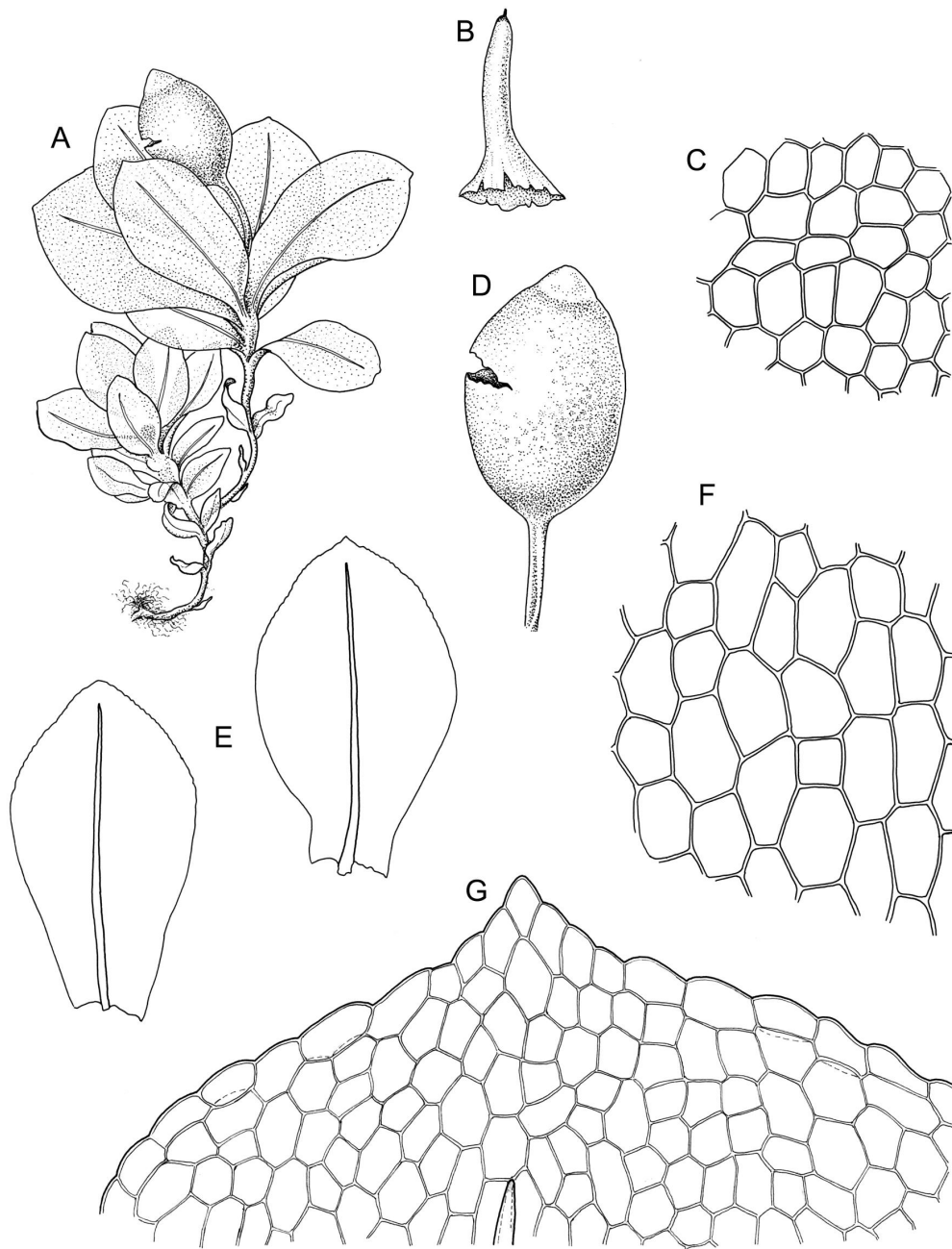
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## Acknowledgements

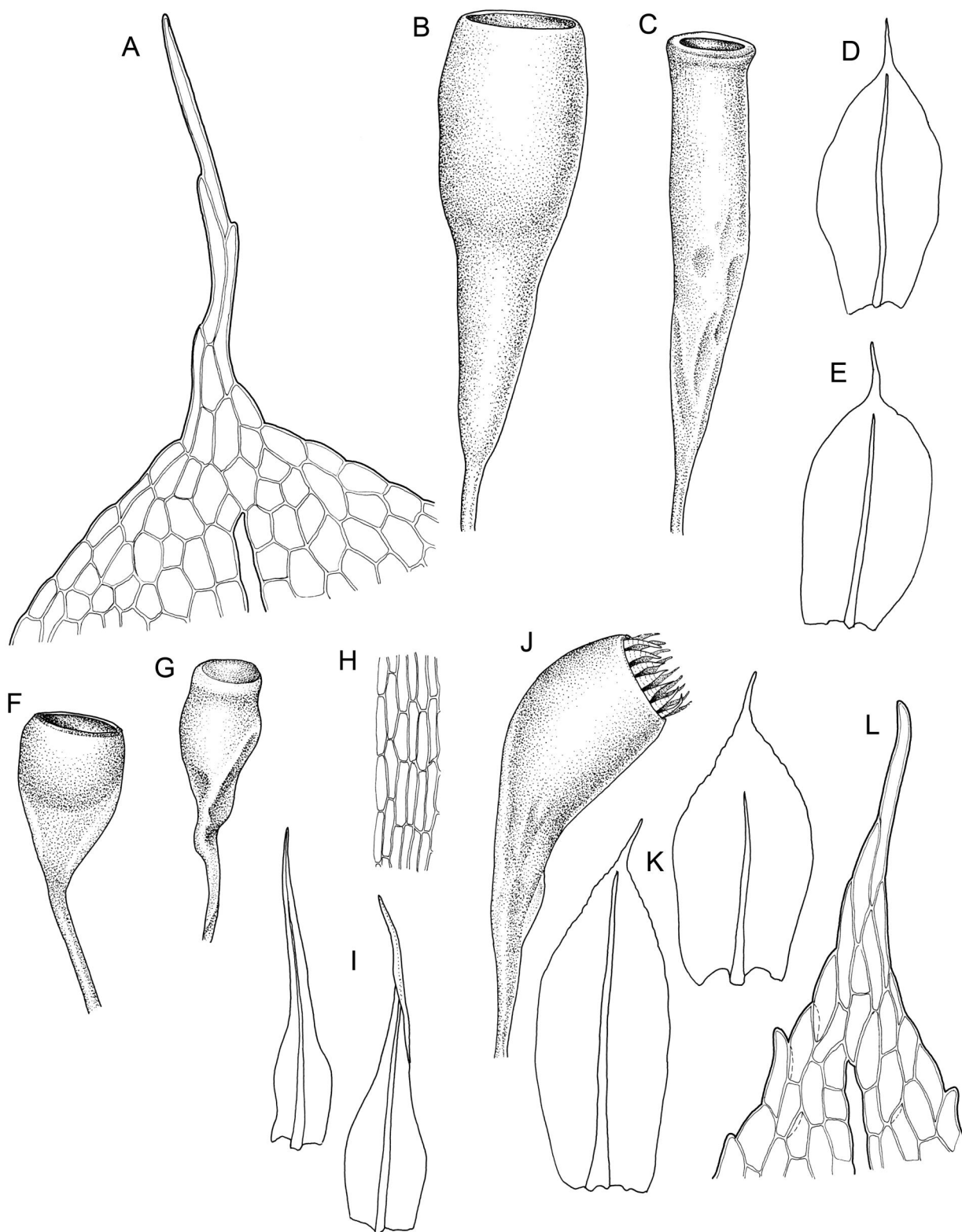
Jessica Beever and Rod Seppelt critically read a draft of this treatment and provided suggestions for its improvement. Rebecca Wagstaff skilfully executed the line drawings. Rhys Gardner allowed me to study his unreported collection of *Physcomitridium readeri*. Supply of loans or access to collections was facilitated by the curators at AK, BM, H, HO, NY, and WELT. Ilse Breitwieser encouraged me to submit this manuscript to the eFlora of New Zealand series. I thank Sue Gibb for her meticulous checking of literature and nomenclatural citations. Aaron Wilton, Katarina Tawiri, and Kate Boardman were instrumental in converting the manuscript into a format suitable for electronic publication. I thank Ray Prebble for his skilled editing. Finally, I thank the participants, over many years, of the John Child Bryological and Lichenological Workshops. The preparation of this revision was supported by Core funding for Crown Research Institutes from the Ministry of Business, Innovation and Employment's Science and Innovation Group.

### **A.J. Fife**

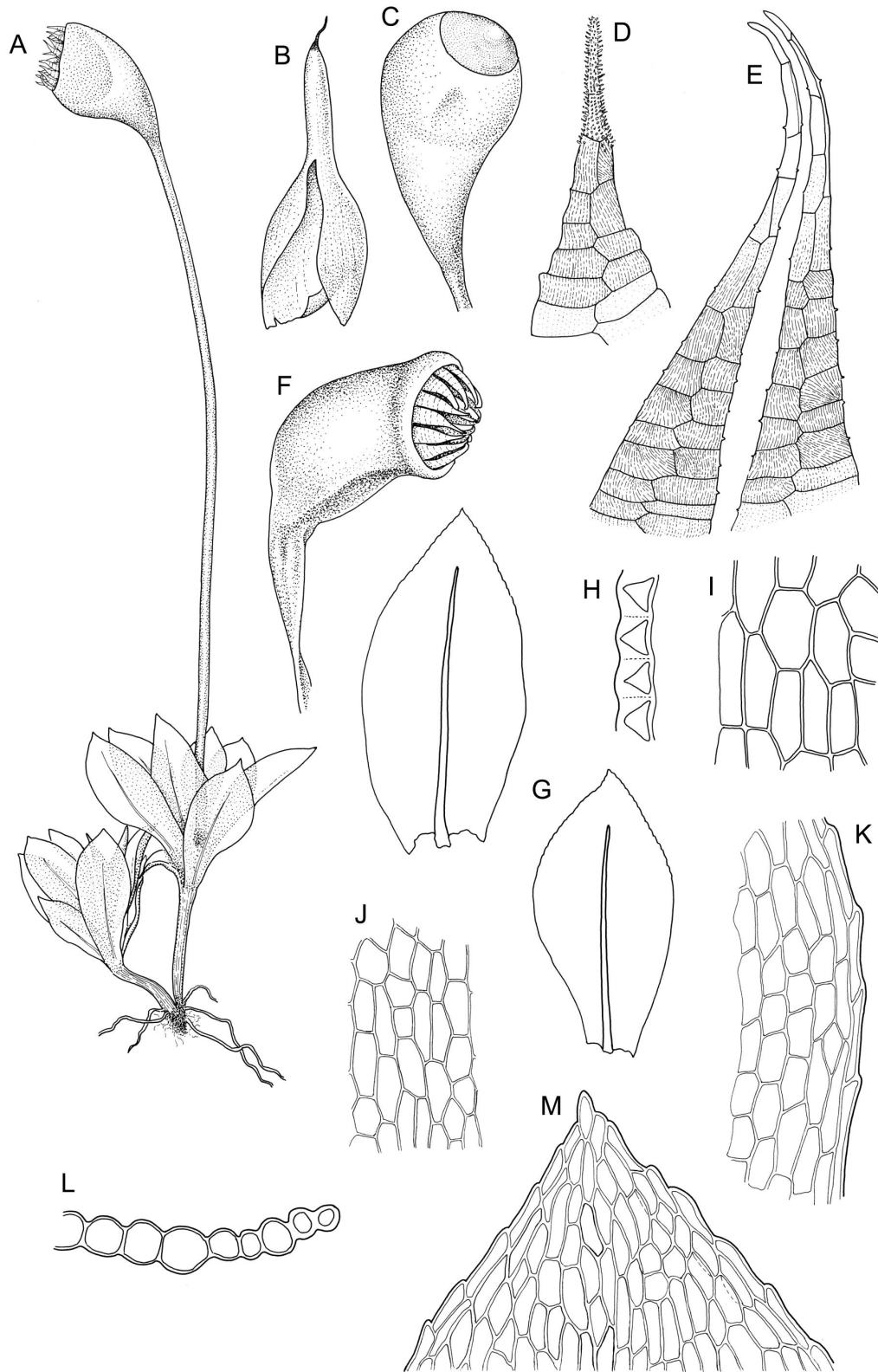
Manaaki Whenua – Landcare Research, PO Box 69040, Lincoln 7640, New Zealand  
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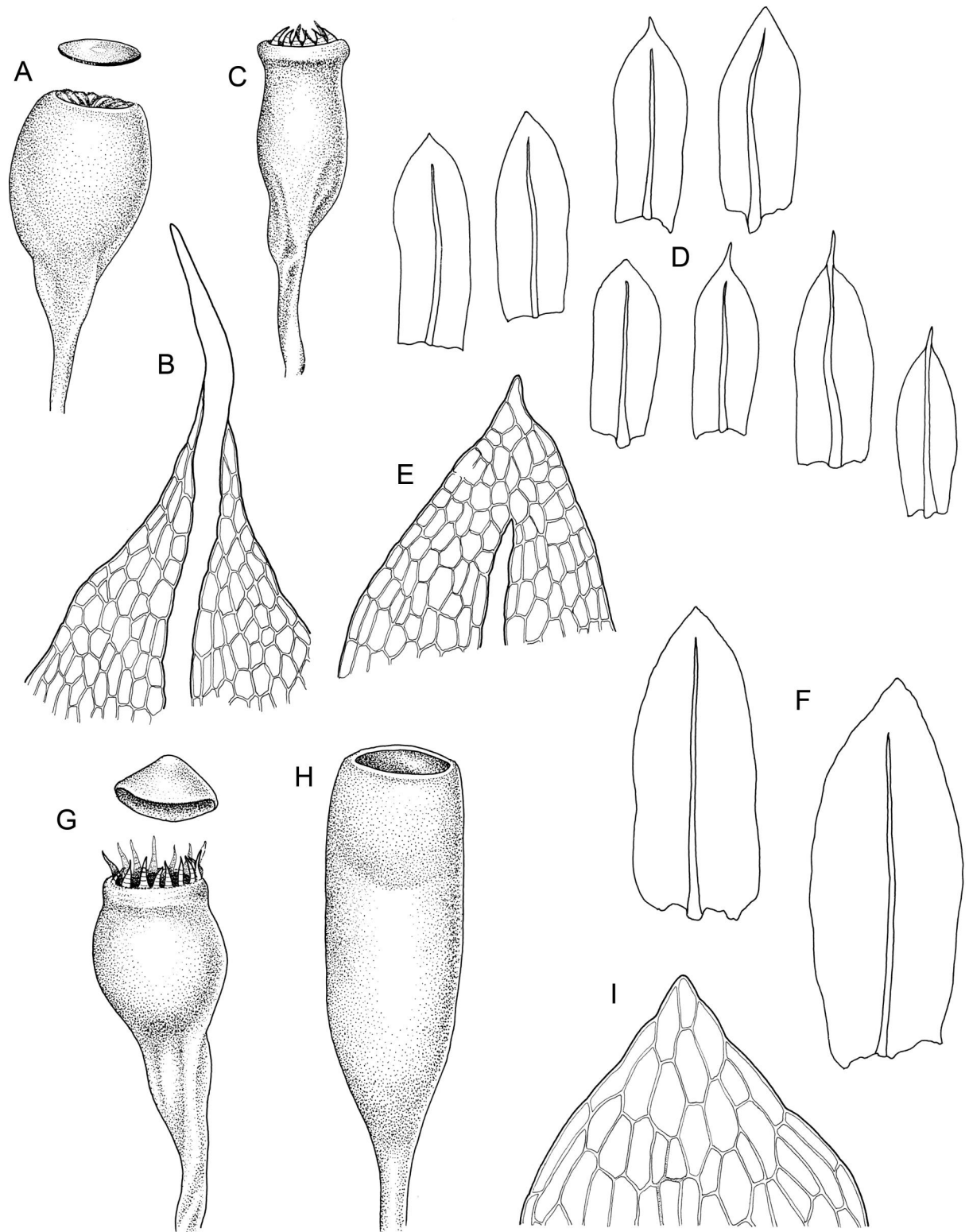
**Plate 1: *Bryobeckettia*. A–G: *B. bartlettii*.** A, habit with capsule, moist. B, calyptra. C, exothecial cells from mid capsule. D, capsule. E, comal leaves. F, upper laminal cells. G, leaf apex. Drawn from *W. Martin* 3419, CHR 266327.



**Plate 2: *Entosthodon*. A–E: *E. apophysatus*. A, leaf apex. B, capsule, moist. C, capsule, dry. D–E, comal leaves. F–I: *E. jamesonii* subsp. *productus*. F, capsule, moist. G, capsule, dry. H, upper laminal cells. I, comal leaves. J–L: *E. muhlenbergii*. J, capsule, moist. K, comal leaves. L, leaf apex. *Entosthodon apophysatus* drawn from K.W. Allison 8364, CHR 454696. *E. jamesonii* subsp. *productus* drawn from G.O.K. Sainsbury s.n., Nov. 1931, CHR 499803. *E. muhlenbergii* drawn from J.T. Linzey 1215, CHR 454702.**

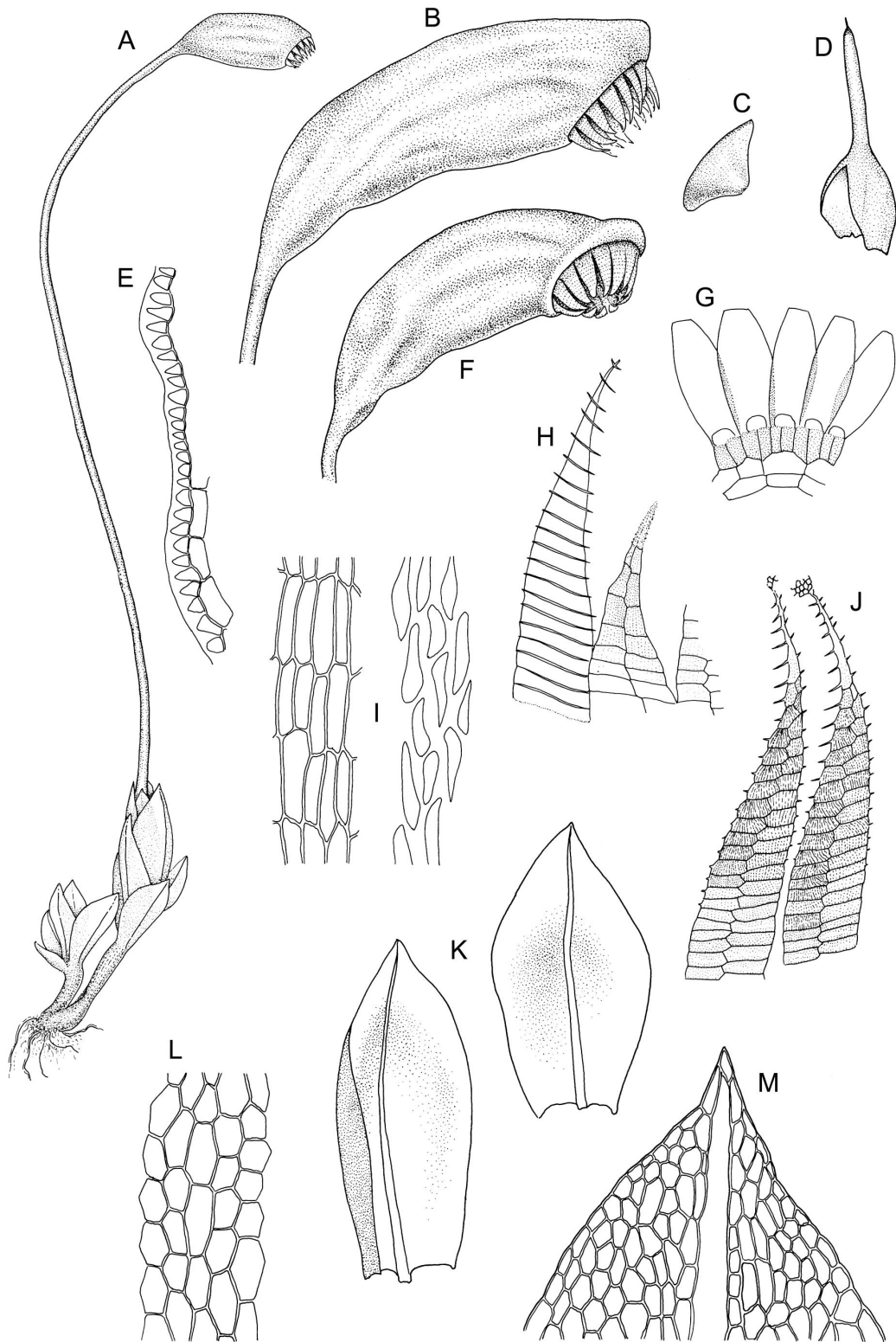


**Plate 3: *Entosthodon*. A–M: *E. radians*.** A, habit with capsule, moist. B, calyptra. C, immature capsule. D, endostome segment. E, exostome teeth, outer surface. F, mature capsule, dry. G, comal leaves. H, cross-section of exothelial cells. I, exothelial cells. J, upper laminal cells. K, laminal cells at marginal shoulder. L, cross section of upper laminal cells, showing margin. M, leaf apex. Drawn from A.J. Fife 5882, CHR 104422.

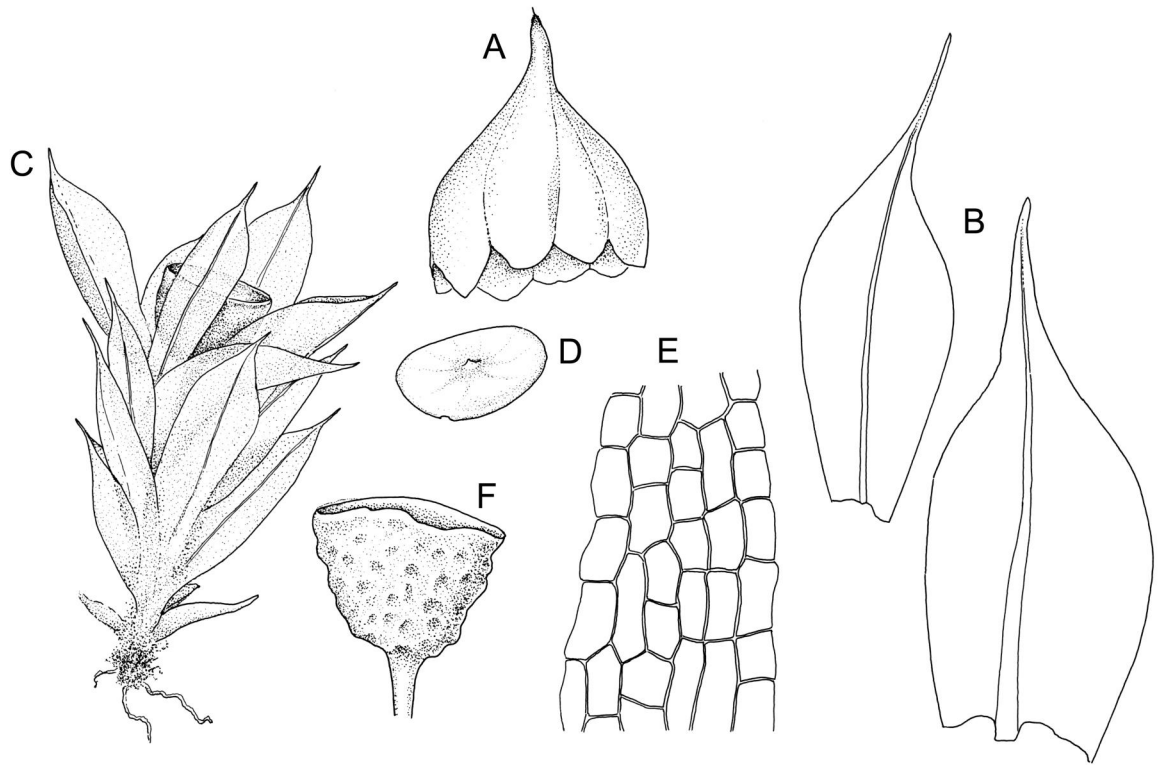


**Plate 4: *Entosthodon*. A–E: *E. subnudus* var. *gracilis*. A, capsule with detached operculum, moist. B, leaf apex of "cuspidatus growth form". C, capsule, dry. D, eight comal leaves, showing variation. E, leaf apex of "gracilis growth form". F–I: *E. laxus*. F, comal leaves. G, capsule with detached operculum, dry. H, capsule, dry (having lost fugacious peristome), moist. I, leaf apex. *Entosthodon subnudus* var. *gracilis* drawn from J.T. Linzey 1531, CHR 566167 and isotype, J. D. Hooker ("Wilson no. 348b"), BM-Wilson; *E. laxus* drawn from A.J. Fife 5910, CHR 104741.**

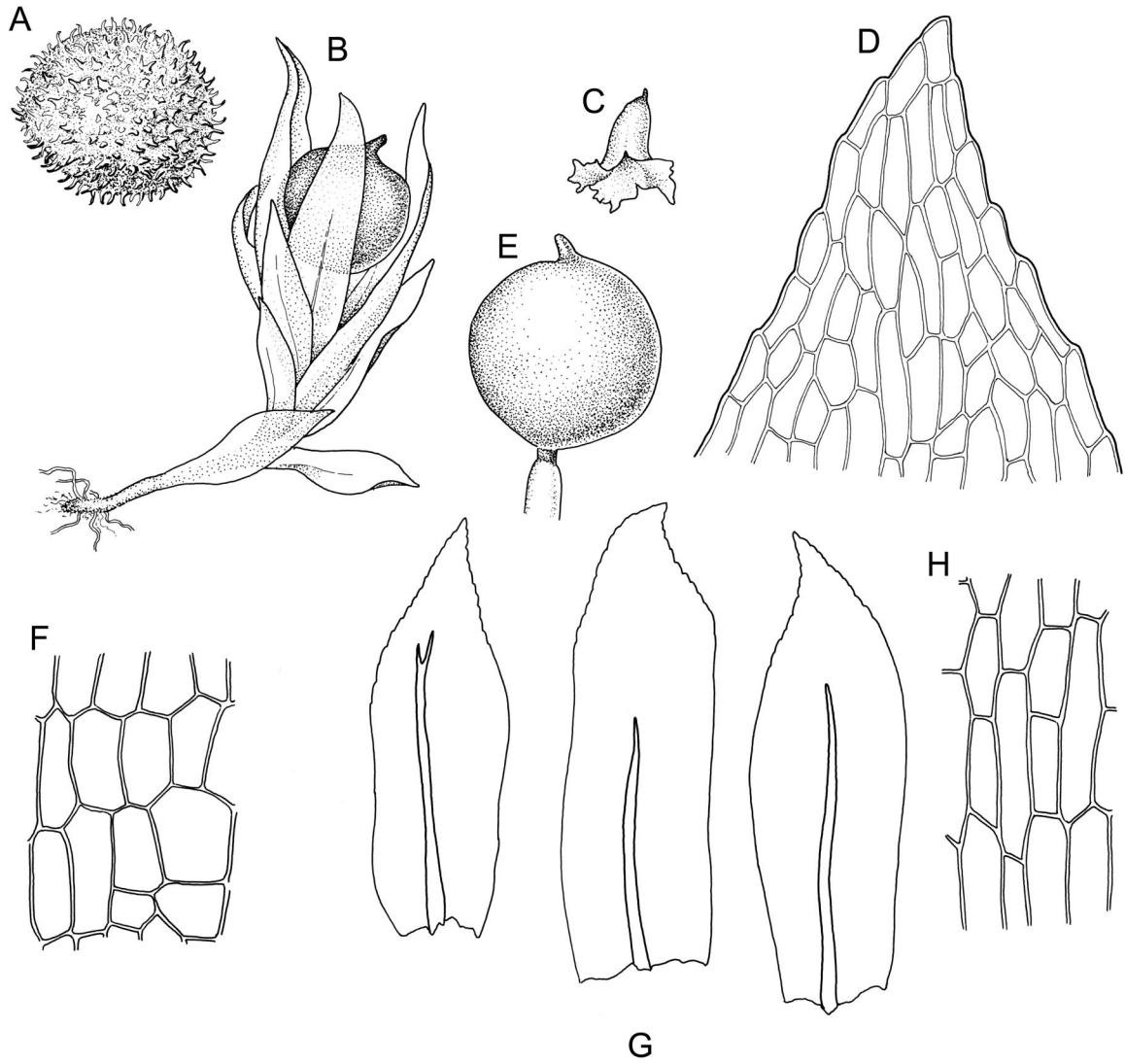




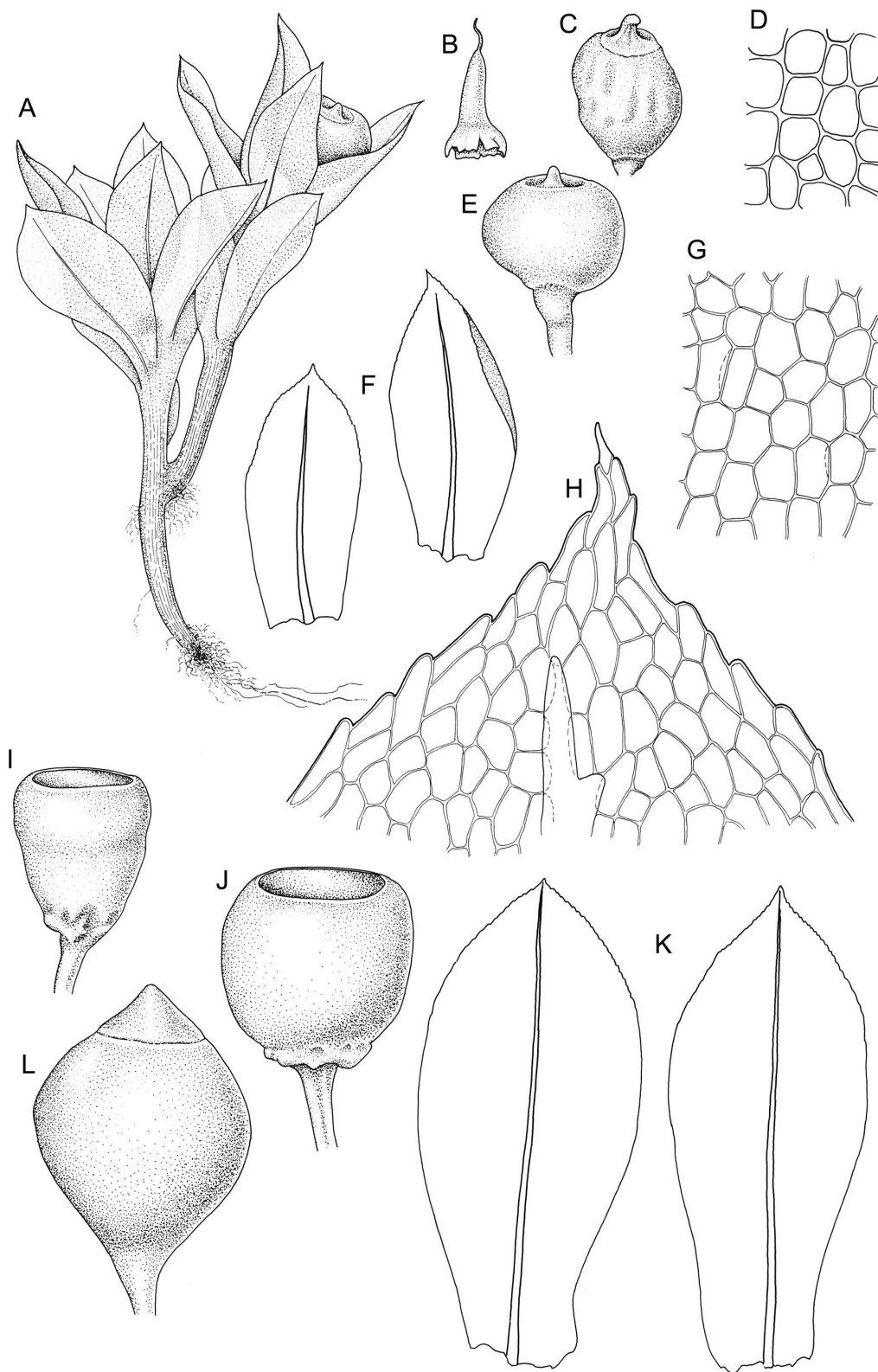
**Plate 5: *Funaria*. A–M: *F. hygrometrica*.** A, habit with capsule, moist. B, capsule, moist. C, operculum. D, calyptra. E, cross-section of exothelial cells. F, capsule, dry. G, annulus fragment. H, exostome tooth inner surface and adjacent endostome segment. I, exothelial cells drawn at two different focal planes. J, exostome teeth outer surface. K, comal leaves. L, upper laminal cells. M, leaf apex. Drawn from A.J. Fife 9733, CHR 477688, and A.J. Fife 6126, CHR 405698.



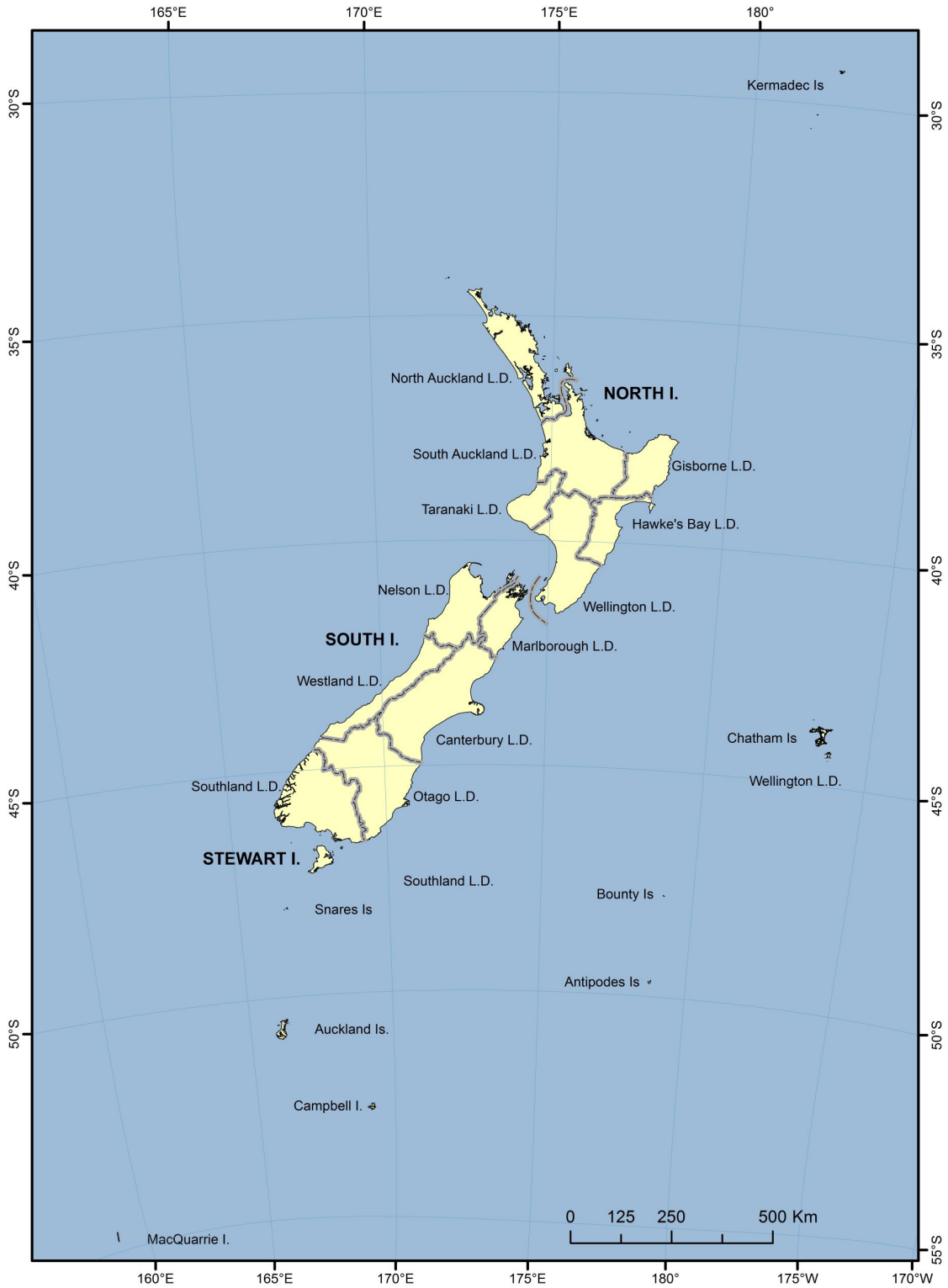
**Plate 6: *Goniomitrium*. A–F: *G. acuminatum*.** A, calyptra. B, comal leaves. C, habit with capsule, moist. D, operculum. E, upper laminal cells. F, capsule, dry. Drawn from *S. Berggren 1405*, CHR 573734, and Australian isotype, *J. Drummond 6*, CHR 620600.



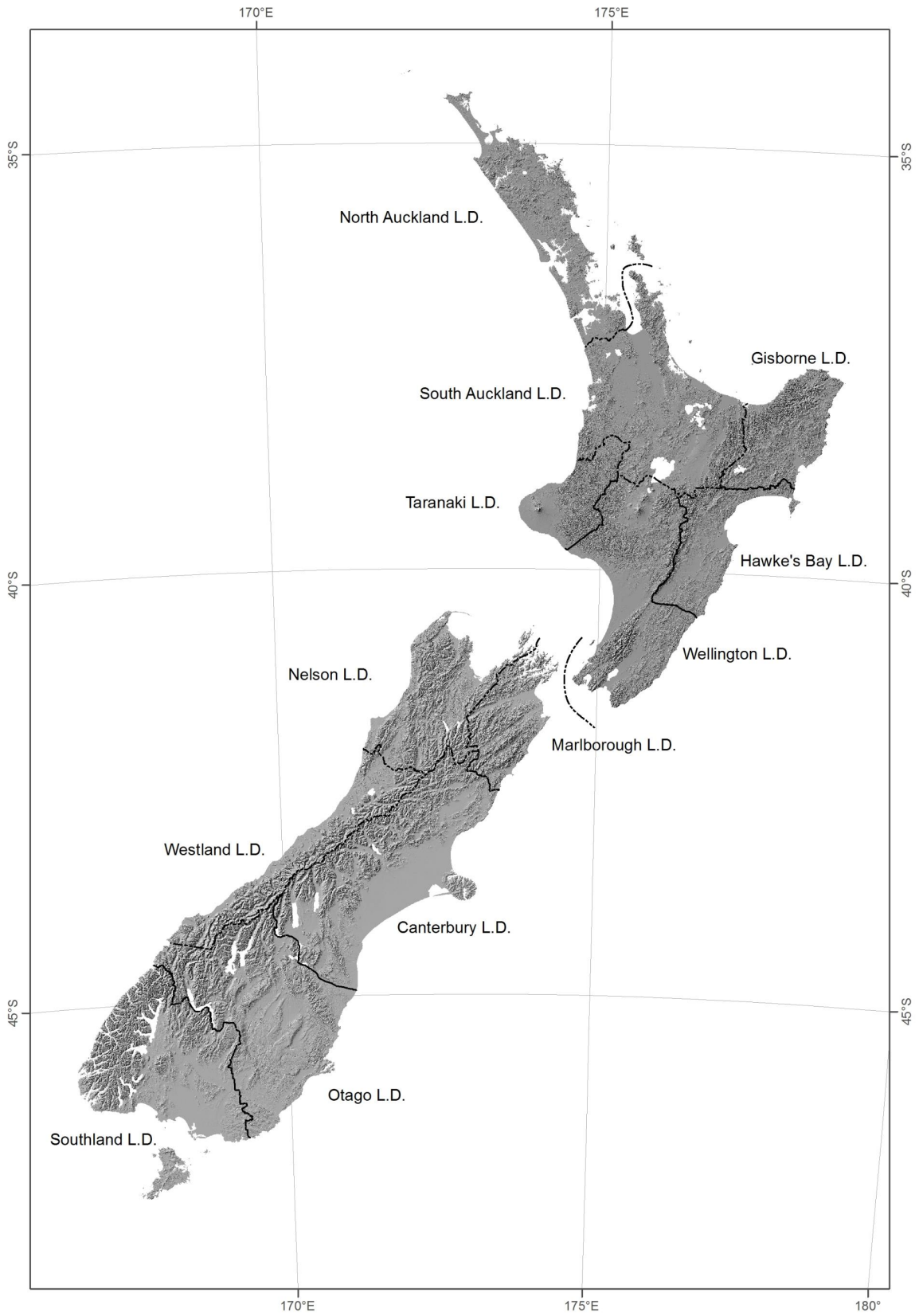
**Plate 7: *Physcomitridium*. A–H: *P. readeri*.** A, spore. B, habit with capsule, moist. C, calyptra. D, leaf apex. E, capsule, moist. F, exothelial cells from mid capsule. G, three leaves. H, upper laminal cells. Drawn from *J.K. Bartlett s.n.*, 19 Mar. 1980, CHR 449103.



**Plate 8: *Physcomitrium*. A–H: *P. pusillum*.** A, habit with capsule, moist. B, calyptra. C, capsule, dry. D, exothecial cells from mid capsule. E, capsule, moist. F, comal leaves. G, upper laminal cells. H, leaf apex. **I–L: *P. pyriforme*:** I, capsule, dry. J, capsule, moist. K, comal leaves. L, immature capsule. *P. pusillum* drawn from J.K. Bartlett 19686, CHR 405917. *P. pyriforme* drawn from K.W. Allison 1548, CHR 578040, and B.H. Macmillan 85/26, CHR 348065.



**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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