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Revised keys and additions to the Australian Bryaceae (Bryopsida)

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Abstract

Revised keys to the Bryaceae for the Flora of Australia and its offshore islands are presented, including new keys to genera and to species within each genus following recent molecular studies on the family. Fifty-nine named species and two undetermined taxa are included in the treatments. The first record of *Leptostomopsis pulchra* (Hook.) Ochyra & Bedn.-Ochyra is reported from near Melbourne, Victoria as a new genus and species for Australia. Explanatory notes for each species are included, and comparisons made with the closely similar Bryaceae of New Zealand where relevant.

Introduction

The family Bryaceae was revised for the Bryophyte Flora of Australia by Spence and Ramsay (2006) and later updated in Australian Mosses Online (Spence and Ramsay 2012). Numerous changes in the taxonomy of the family have been published based on both morphological and molecular studies (Pedersen *et al.* 2007; Holyoak and Pedersen 2007; Spence 2005, 2007, 2009, 2014; Spence and Ramsay 2005; Wang and Zhao 2009). Although results from morphological and genetic studies are not entirely consistent, particularly within terminal clades, they do agree in several important ways. There is a deep split in the family into two major sister clades, one exemplified by *Ptychostomum* Hornsch. and related genera including *Rhodobryum* (Schimp.) Limpr. and *Rosulabryum* J.R.Spence, while the second clade is resolved with *Anomobryum* Schimp. *Bryum* Hedw., *Gemmabryum* J.R.Spence & H.P.Ramsay and *Imbribryum* N.Pedersen. Although sporophytes are often essential for identification, leaf areolation and types of asexual gemmae can often place the specimen in the appropriate genus (Spence and Ramsay 2012). For example the two clades mentioned above differ in details of their specialized asexual gemmae as well as leaf characters. The most recent treatment dealing with changes in taxonomic concepts is discussed in Spence (2014).

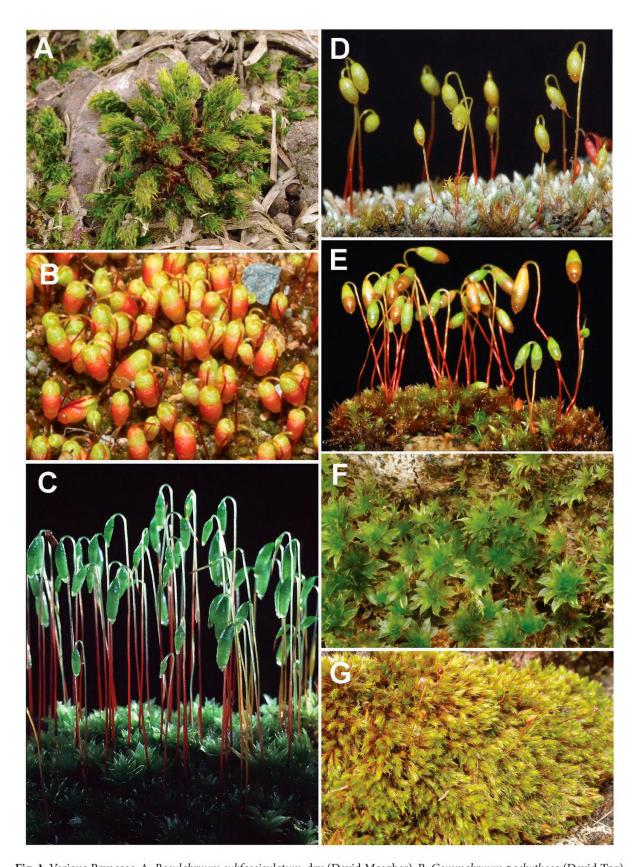


Fig. 1. Various Bryaceae. A: Rosulabryum subfasciculatum, dry (David Meagher). B: Gemmabryum pachytheca (David Tng) C: Rosulabryum torquescens (Ron Oldfield). D: Bryum argenteum (David Tng). E: Gemmabryum dichotomum (David Tng). F: Rosulabryum albolimbatum (David Meagher). G: Gemmabryum coronatum (David Meagher). Photos used with permission.

In addition to these taxonomic changes, new species that have come to light in Australia based on field and herbarium studies include three new species records for the family (Spence and Ramsay 2013). More recent discoveries include the first record of the genus *Leptostomopsis* (Müll. Hal. ex Broth.) J.R.Spence & H.P.Ramsay for Australia. In the light of these taxonomic changes and additions, we present newly revised keys to the genera and species of the Bryaceae for Australia and its offshore islands. The keys include two distinct but unnamed collections: one in *Gemmabryum* J.R.Spence & H.P.Ramsay and one in *Plagiobryoides* J.R.Spence. Included in the keys are two New Zealand species that may be found with additional field work in Tasmania and southeastern Australia. Where relevant, comparisons are made with the recent treatment of the Bryaceae of New Zealand (Fife 2015). Notes on each species, including changes in status and distribution, are included. The following 11 genera are presently accepted – *Anomobryum* Schimp., *Brachymenium* Schwägr., *Bryum* Hedw., *Gemmabryum* J.R.Spence & H.P.Ramsay, *Imbribryum* N.Pedersen, *Leptostomopsis* (Müll. Hal. ex Broth.) J.R.Spence & H.P.Ramsay, *Ochiobryum* J.R.Spence & H.P.Ramsay, *Plagiobryoides* J.R.Spence, *Ptychostomum* Hornsch., *Rhodobryum* (Schimp.) Limpr., and *Rosulabryum* J.R.Spence. Figure 1 shows colour photographs of selected species.

New Record

An Australian herbarium specimen distinguished by its small size, densely compact cushions, silver-green colouration, extremely long spinose awn and numerous small leafy bulbils in the upper leaf axils is here attributed to *Leptostomopsis pulchra* (Hook.) Ochyra & Bedn.-Ochra, which is the first report of the genus for Australia. The specimen, although sterile, agrees well with named African material of *L. pulchra* that we have examined.

Specimen examined: Australia, Victoria: Cape Schank, Mornington Peninsula, woody debris on light sandy soil under *Leptospermum laevigatum* and *Melaleuca pubescens*, 16 Feb 1952, *JH Willis 191W* (MEL 1031404).

Key to the Genera of the Bryaceae in Australia

Useful illustrations and photographs of species and especially gemmae can be found in Malcolm and Malcolm (2000), Preussel *et al.* (2007), Hallingbäck *et al.* (2008), and Porley (2008). Additional images for many species can also be found online.

5:	Capsules patent to nodding; peristome generally well developed, basal membrane at least ½ height of exostome, cilia present; plants mostly saxicolous or terricolous
6.	Stems evenly foliate; stolons present; leaves large, often >5 mm, costal stereid band reduced, gemmae lacking (1 species from E Australia)
6:	Stems rosulate or rarely evenly foliate; stolons absent; leaves typically <5 mm; costal stereid band well developed; rhizoidal tubers and leaf axil filiform gemmae often present (widespread, 15 species)
7.	Laminal cells elongate, uniform throughout leaf except at base and alar region, many cells >80 to 120 µm
7:	Laminal cells various, rhomboidal to hexagonal or rectangular, mostly $< 60(-80) \mu m$ long, areolation often heterogeneous, with distal and proximal cells of different lengths and shapes10
8.	Laminal cells thin-walled, $20-30~\mu m$ wide, irregularly rhomboidal distally; leaf apex obtuse (2 species from subtropical and tropical regions)
8:	Laminal cells narrow, mostly $<15~\mu m$ wide, regularly hexagonal distally; leaf apex obtuse, broadly acute to acuminate
9.	Plants often complanate, laminal cells strongly incrassate, distinct limbidium present; alar cells not differentiated; leaf apex obtuse to broadly acute; rhizoidal tubers absent (1 species from cold-climate/montane regions)
9:	Plants evenly foliate but never complanate; laminal cells mostly thin-walled, limbidium absent or weak; alar cells often differentiated as small quadrate group; leaf apex acute to acuminate; rhizoidal tubers present (widespread, 23 species)
10.	Distal laminal cells elongate, (3–)4–6:1, often incrassate, longer than the quadrate or short-rectangular proximal cells; stems gemmiform (short and bud-like) or elongate and evenly foliate; leaves imbricate, not strongly contorted or twisted when dry; limbidium absent or rarely present; rhizoidal tubers and leaf axil bulbils often present; capsule erect to nodding
10:	Distal laminal cells mostly 2–4:1, the same length or shorter than the rectangular to long-rectangular proximal cells; stems comose to evenly foliate; leaves generally twisted to strongly contorted when dry; limbidium usually present, often strong; rhizoidal tubers and leaf axil filiform gemmae sometimes present, bulbils absent; capsules mostly nodding
11.	Plants small, stems mostly <1 cm, gemmiform to evenly foliate; leaves 0.5–2.5 mm, not stiff or rigid; leaf axil bulbils often present, tubers if present on long rhizioids in substratum or at base of stem, often abundant; capsules ovate to pyriform, apophysis sometimes thickened and rugose; plants of soil or rock, sometimes seasonally wet (widespread; 23 species)
11:	Plants medium-sized or large, stems 1–5(–10) cm, rarely comose to more often evenly foliate; leaves 2.0–3.5 mm, often stiff and rigid; tubers if present on micronemata or macronemata on stem, usually arising out of leaf axils, scarce, sometimes absent; capsules pyriform to clavate, apophysis slender; plants of waterfalls, springs, wet rocks and soil (widespread, 5 species)
12.	Leaves ovate to obovate, distal margins mostly serrulate or rarely nearly smooth; filiform leaf axil gemmae sometimes present, rhizoidal tubers usually present, dioicous (widespread, 15 species)
12:	Leaves ovate-lanceolate to ovate; distal leaf margins predominantly smooth or rarely serrulate; rhizoidal tubers absent, leaf axil filiform gemmae rarely present; dioicous or monoicous
13.	Plants evenly foliate; leaves ovate, costa percurrent to excurrent in short awn; distal laminal cells very short and wide, often nearly quadrate to 2:1, proximal cells longer, irregularly rhomboidal to rectangular; capsule short, ovate, with widely flaring mouth; spores $>$ 30 μ m; peristome somewhat reduced (cilia short or absent); dioicous (2 species from tropical-subtropical regions)
13:	Plants comose, tufted to evenly foliate; leaves ovate to ovate-lanceolate, costa excurrent in short to long awn; distal laminal cells mostly rhomboidal, 3–4:1, proximal cells the same length or often longer, more regularly rectangular; capsule pyriform to cylindrical; spores <30 µm; peristome well developed to variously reduced; autoicous, synoicous, or dioicous (widespread, 7 species)

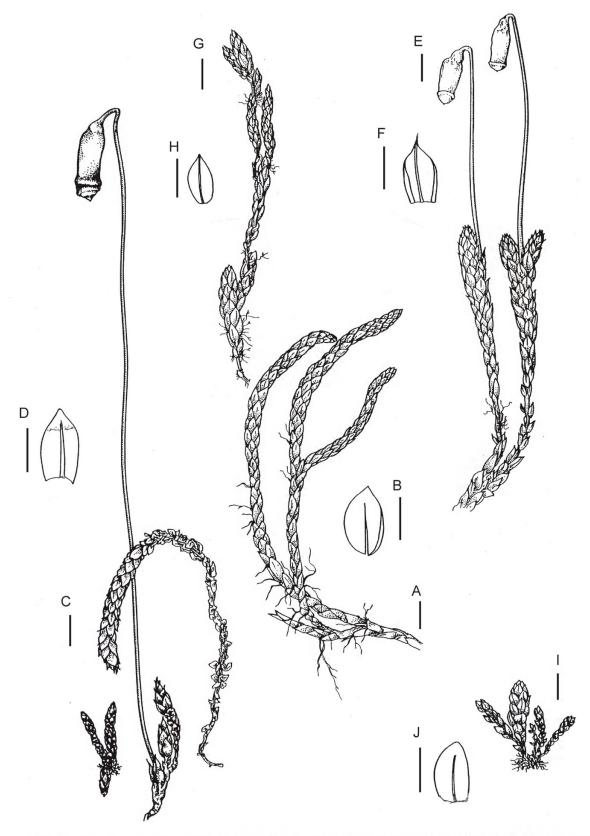


Fig. 2. A-B: *Anomobryum auratum* A: habit of sterile plant. B: leaf (*W.W. Watts* Q532 NSW); C-D: *Bryum argenteum*. C: habits, one with sporophyte. D: leaf (*D. Sullivan s.n.* MEL); E-F: *Bryum lanatum* E: habit with sporophyte. F: leaf (*I.G. Stone* 80214b MEL); G-H: *Bryum harriotii* G: habit sterile. H: leaf (*A.V. Ratkowsky* 7.i.1978 HO. Scale bars 1.0 mm habit; 0.5 mm leaves; 100 μm gemmae.

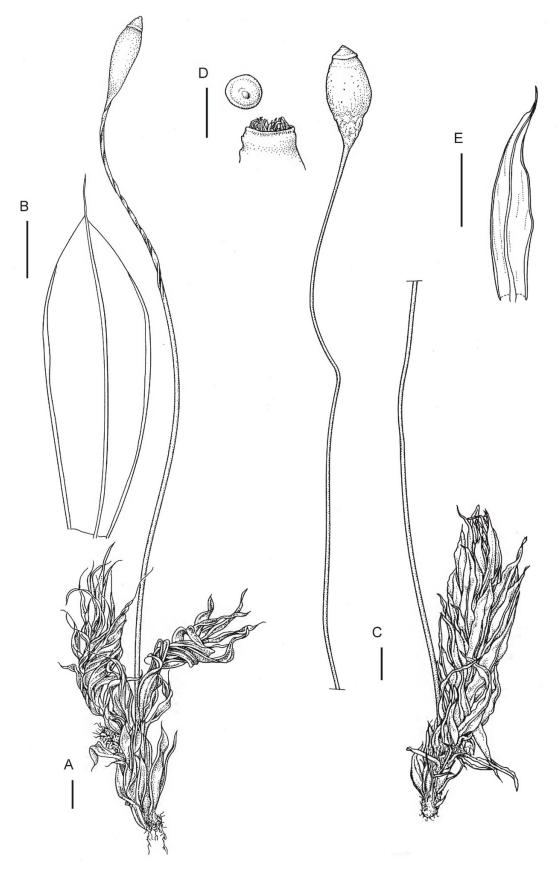


Fig. 3. A-B: *Brachymenium nepalense* A: habit with sporophyte. B: leaf (*I.G. Stone* 15718 MEL); C-E: *Brachymenium lanceolatum* C: habit with sporophyte. D: capsule and operculum. E: leaf (redrawn from *H. Ochi 1970* fig 1). Scale bars 1.0 mm habit and enlarged capsule apex; 0.5 mm leaves.

Keys and Brief Descriptions of species

Each genus is described with keys and brief descriptions to each species. For more detailed data on species and lists with selected specimen citations refer to Spence and Ramsay (2006, 2012).

1. Anomobryum Schimp.

Plants small, stems <30 mm, julaceous; leaves <1.5 mm, ovate; costa weak, not reaching apex, limbidium lacking, distal laminal cells elongate-vermicular, proximal cells quadrate; asexual gemmae absent; dioicous; capsule cylindrical, inclined to nodding, peristome well developed; spores <15 μ m.

A. auratum (Mitt.) A.Jaeger (*Bryum auratum* Mitt.): a small yellowish-green plant that is strongly julaceous, has a weak costa, and rounded leaf apex. Capsules have not been reported from the region. Known only from Queensland; a widespread paleotropical species (Fig. 2 A-B).

2. Brachymenium Schwägr.

Plants small to medium sized, stems 10--30 mm, \pm rosulate; leaves to 3.5 mm, ovate-lanceolate to obovate; costa strong, excurrent in short to long awn, limbidium present, distal laminal cells rhomboidal, proximal cells rectangular; asexual gemmae absent; autoicous; capsule ovate to orbicular, erect, peristome reduced, cilia absent, endostome often fused to exostome, spores >25 μ m.

A tropical-subtropical epiphytic genus related to *Rosulabryum* with two species having tropical affinities with the type section of *Brachymenium*. Five species traditionally included in the genus, *B. acuminatum*, *B. coarctatum*, *B. exile*, *B. indicum*, *B. priessianum*, have been transferred to *Gemmabryum* (Spence and Ramsay 2005).

Key to Brachymenium species

1.	Leaves obovate, often spirally twisted around stem when dry, red-green; tropical QLD
1:	Leaves oblong-lanceolate, irregularly contorted when dry, yellow-brown; TAS only
	chymenium lanceolatum Hook.f. & Wilson: this species is only known from the type collection in northeast
Tas	mania and has not been found since. Spence and Ramsay (2006) discuss the possibility that it is a mislabeled

specimen originally collected in India, where the species is common (Fig. 3 C-E). *Brachymenium nepalense* Hook. *in* Schwägr.: a rare tropical epiphyte which is paleotropical in distribution, found generally at high elevations in Queensland. The gametophyte is very similar to *Rosulabyum* species,

especially R. capillare and R. torquescens, but these species are never epiphytic on rain forest trees (Fig. 3 A-B).

3. Bryum Hedw.

Plants small, stems 10–20 mm, gemmiform to julaceous; leaves <1.5 mm, ovate-lanceolate to ovate; costa variable not reaching apex to excurrent in awn, apiculus sometimes present, limbidium absent, distal laminal cells rhomboidal to hexagonal, proximal cells quadrate; asexual gemmae of leafy bulbils in leaf axils; dioicous; capsule ovate, nodding, peristome well-developed, spores $<25 \,\mu m$.

These species were previously included in *Anomobryum* (Spence and Ramsay 2002) but have been returned to *Bryum* (Spence and Ramsay 2005).

Key to Bryum species

Bryum argenteum Hedw. (Synonyms: Anomobryum argenteum (Hedw.) J.R.Spence & H.P.Ramsay; B. subrotundifolium A.Jaeger; Anomobryum subrotundifolium (A.Jaeger) J.R.Spence & H.P.Ramsay): a widespread silver-green species found in virtually all habitats away from the tropics, also abundant in cities. Bulbils are fairly common in sterile material. Some material lacks the apiculus and has been traditionally referred to B. argenteum var. muticum Brid. Australian material is genetically distinct from Antarctic collections, which often differ in being yellow-green, and has been referred to B. subrotundifolium in the past. Hills et al. (2010) show that Australian material of the two varieties are often genetically related. The name B. subrotundifolium has also been applied to the muticous Australian material, but Hills et al. (2010) recovered that species nested within B. argenteum and it is similar to B. a. var. muticum, so the species is not recognized here (Fig. 2 C-D).

B. harriottii R.Br. bis (=Anomobryum harriottii (R.Br. bis) J.R.Spence & H.P.Ramsay): a small bright green julaceous species with short rhomboidal distal laminal cells and obtuse leaf apices, found on damp soil in montane areas of New Zealand and Tasmania. It occurs on subantarctic Macquarie Island (Seppelt 2004) and should be looked for in montane areas of southeast Australia (Fig. 2 G-H).

Bryum lanatum (P.Beauv.) Brid. (=Anomobryum lanatum (P.Beauv.) J.R.Spence & H.P.Ramsay): a hoary white species with costa strong, excurrent into a recurved awn, usually found in drier habitats than B. argenteum, primarily distributed in Australia but found throughout much of the drier regions of the world. The type of B. lanatum from Europe may simply be a dry-site form of B. argenteum and growth studies suggests that the strong excurrent costa is lost in greenhouse populations (Longton 1981). However, the species in the Australasian region seems quite distinct so it has been retained until molecular studies are done (see also Spence 2014) (Fig. 2 E-F).

4. Gemmabryum J.R.Spence & H.P.Ramsay:

Plants small, stems 10-30 mm, gemmiform to evenly foliate; leaves <2.5 mm, ovate-lanceolate to ovate; costa percurrent to excurrent in short to long awn, limbidium absent or weak, distal laminal cells elongate rhomboidal to hexagonal, proximal cells quadrate to short-rectangular; asexual gemmae include leafy bulbils in leaf axils, stem tubers and rhizoidal tubers at stem base or in substrate on sterile material; dioicous; capsule ovate, often with inflated neck, to pyriform, nodding, peristome well-developed, spores <25 μm.

The first five species included in Gemmabryum in Spence and Ramsay (2006) keys have been moved to the more recently described Imbribryum (Spence and Ramsay 2013). These are G. australe, G. cheelii, G. clavatum, G. crassum and G. laevigatum.

Key to Gemmabryum species

1.	Laminal areolation homogeneous, similarly shaped elongate hexagonal to rectangular cells throughout leaf except at leaf base near insertion and in alar region where cells shorter, some median cells >80 µm long
1:	Laminal areolation heterogeneous, cells in distal 1/3 of leaf distinctly different in shape, length and/or width from proximal cells in lower 1/3 of leaf, longest cells typically <70 µm
2.	Plants pale green, yellow-white to yellow-green, older leaves sometimes becoming hyaline; rhizoidal tubers absent
2:	Plants bright green, red-green, pink-green or red, leaves not hyaline with age; rhizoidal tubers present
3.	Plants yellow-green; capsules tapering to narrow mouth; peristome well developed; primarily southern species
3:	Plants green or yellow-white to silver; capsules widest at the mouth; peristome reduced, segments absent or rudimentary, cilia absent; primarily tropical, QLD-WA
4.	Leaves ovate to obovate, green-red, contorted when dry; tubers red-brown, flattened with undulate margins
4:	Leaves broadly lanceolate to narrowly ovate or ovate-lanceolate, imbricate to somewhat contorted when dry, green, pink-green or red; tubers pyriform to spherical, not flattened
5.	Plants red or red-green; leaves ovate-lanceolate, acuminate, limbidium distinct, costa excurrent in fairly long denticulate red awn; tubers red to orange, pyriform, 40–60 µm long, 1–3 cells across face, leaf axil bulbils not produced; autoicous or divisous

5:	Plants green to pink-green; leaves narrowly ovate or lingulate, acute, limbidium absent or very indistinct, costa percurrent or short-excurrent, smooth, brown or green; tubers a mix of spherical and pyriform, red-brown, $40-100 \mu m \log 2-4 \text{ cells across face}$; leaf axil bulbils with leafy tips sometimes present; dioicous
6.	Specialized asexual gemmae present as leaf axil bulbils or rhizoidal tubers (many species can only be identified if diagnostic asexual gemmae are present and cannot usually be identified without them)
6:	Specialized asexual gemmae lacking (species that are not known to produce asexual gemmae, or species that rarely produce gemmae and they are not diagnostic for those species)22
7.	Bulbils present in upper stem leaf axils of sterile shoots, rhizoidal tubers rarely present
7:	Bulbils absent, rhizoidal tubers present, often common
8.	Plants synoicous; leaves ovate-lanceolate, costa excurrent into a medium to long denticulate awn, bulbils single with leafy tips; capsules erect, peristome reduced; tropical northern Australia ——————————————————————————————————
8:	Plants dioicous; leaves ovate or ovate-lanceolate, costa variable, short to long-excurrent, smooth to denticulate, bulbils single to $4(-5)$ in leaf axils, generally common in sterile material, primordia well-developed and leafy to short and peg-like or absent; capsules nodding, peristome mostly well developed, rarely capsule erect with reduced peristome ($G.\ exile$); distributions various but often temperate
9.	Bulbils green to brown, 1(–2) per leaf axil, with leafy primordia
9:	Bulbils green, brown, red or orange, often 2–5 per axil, primordia present or lacking or with short peglike projections at the apex
10.	Leaves ovate, concave, glossy green or yellow-green, costa weak, percurrent to short-excurrent, distal laminal cells long, often $60-70~\mu m$ or sometimes longer; wet sites
10:	Leaves ovate, ovate-lanceolate or triangular, colours various, usually not glossy, flat to weakly concave, costa percurrent to excurrent in short to long awn, distal laminal cells shorter, typically $<60 \mu m \log;$ seasonally wet to dry sites
11.	Leaves ovate, often folded lengthwise along costa, margins plane; capsule erect, peristome reduced (cilia lacking, endostome segments short)
11:	Leaves ovate, ovate-lanceolate to triangular, margins recurved proximally to near tip; capsule nodding, peristome well-developed
12.	Leaves ovate-lanceolate or triangular, margins strongly recurved to near apex; capsules with distinctly thick and rugose neck; tropical
12:	Leaves ovate or ovate-lanceolate, recurved only at base; capsule with smooth neck, somewhat tapered to seta; temperate
13.	Bulbils (2–)3–5 or more per leaf axil; costa strong, long excurrent in somewhat denticulate awn
13:	Bulbils 1(-2); costa short excurrent in smooth awn Gemmabryum dichotomum
14.	Bulbils lacking apical groove and primordia, smooth; awn typically coloured, yellow, golden-brown to red, smooth
14:	Bulbils with two short peg-like primordia at apex, often irregularly grooved between primordia; awn typically hyaline above, often denticulate
15.	Tuber size variable, but largest tubers present small, $<100 (-125) \mu m$ in largest dimension
15:	Tuber size variable, but largest tubers >150 μm in largest dimension, often >250 μm
16.	Tubers spherical, red, cell walls protuberant, 2–3 across face
16:	Tubers pyriform, brown, cell walls not protuberant, 3 or more across face
17.	Plants golden-green, costa long-excurrent in golden-yellow awn, laminal cells somewhat incrassate; tubers large, at least some ≥500 μm, up to 1 mm, cell walls protuberant, tubers arising mostly in leaf axils (axillary)

17:	Plant colour various, awn short to medium-length, coloured but rarely golden-yellow, laminal cells mostly thin walled; tubers smaller, mostly $<300(-350)~\mu m$, cell walls not protuberant, tubers arising at stem base on long rhizoids in soil
18.	Leaves ovate, often folded longitudinally along costa when dry, margins plane; tubers brown to redbrown, $100-200~\mu m$
18:	Leaves ovate or ovate-lanceolate, not folded longitudinally when dry, margins recurved proximally; tubers brown, red or golden-yellow, $100-300~\mu m$
19.	Tubers golden or yellow, 100–200 µm, cells with red walls, rhizoids pale yellow or brown
19:	Tubers brown or red, $100-300(-350)~\mu m$, cell walls same colour as tuber, rhizoids brown or red 20
20.	Plants in dense compact turfs, dull green or green-yellow; costa long-excurrent; tubers 100–200 μm, red-brown; synoicous; tropical
20:	Plants in loose open turfs or gregarious, green to green-red; costa short to long excurrent, tubers $100-300(-350)~\mu m$, red or red-brown; dioicous; widespread, often temperate, rarely tropical21
21.	Costa short-excurrent in short slender awn, distal laminal cells mostly short-rectangular mixed with quadrate cells; tubers (100–)150–300(–350) μ m; acidic substratesGemmabryum subapiculatum
21:	Costa long-excurrent in long awn, distal laminal cells mostly quadrate; tubers 100–200(–250) µm; calcareous substrates
22.	Costa percurrent or excurrent in short awn23
22:	Costa distinctly excurrent in medium to long awn
23.	Costa mostly percurrent, many distal laminal cells elongate, $>60-80~\mu m$ long, leaves glossy green or green-yellow; wet sites in riparian zones and at springs or seeps
23:	Costa mostly short-excurrent, distal laminal cells <60 µm long, leaves lacking glossy sheen; dry sites
24.	Leaves folded lengthwise along costa when dry; capsule erect, peristome reduced, cilia absent Gemmabryum exile
24:	Leaves more or less imbricate, not folded or contorted; capsule nodding or erect, peristome various
25.	Leaves strongly imbricate, ovate, margins strongly revolute; capsule nodding, peristome well developed; operculum apiculate
25:	Leaves loosely imbricate, ovate-lanceolate to triangular, margins plane; capsule erect, peristome reduced, cilia absent; operculum rostellate
26.	Leaves ovate, folded lengthwise along costa when dry, margins plane, costa excurrent in long denticulate hyaline awn; capsule erect, peristome reduced, cilia absent
26:	Leaves ovate to ovate-lanceolate, imbricate to contorted when dry but not folded lengthwise along costa, margins recurved proximally, costa excurrent in smooth coloured or sometimes hyaline awn; capsule erect or nodding, peristome various
27.	Leaves lacking a limbidium, flat or weakly concave, awn green or yellow coloured, rhizoidal tubers and bulbils sometimes present; synoicous; capsule erect, peristome reduced, cilia absent
25	
27:	Leaves with a narrow limbidium, weakly to strongly concave, awn coloured or hyaline; tubers and bulbils absent; dioicous; capsule nodding or erect, peristome well developed to reduced
28.	Awn and lamina coloured green or brown, not hyaline, leaves concave, more or less imbricate when dry, group of inflated pinkish subalar cells present on leaves on fertile stems; stem tubers absent; capsule nodding, pyriform, peristome well developed (temperate)
28:	Awn and sometimes upper lamina hyaline, leaves weakly concave, somewhat twisted-contorted when dry; inflated subalar cells absent; stem tubers often present; capsule erect, peristome reduced, cilia absent (tropical)

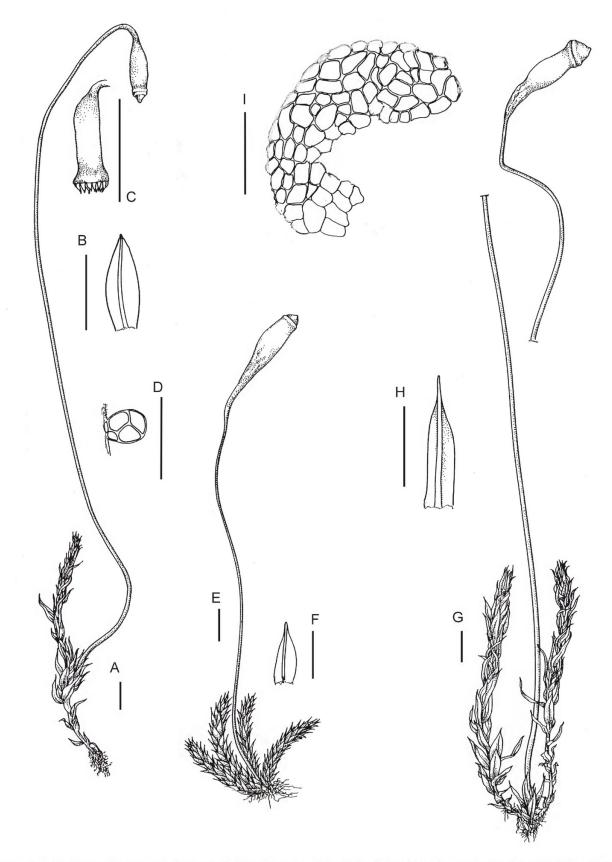


Fig. 4. A-D: *Gemmabryum apiculatum* A: habit with sporophyte. B: leaf. C: enlarged capsule. D: rhizoidal tuber (*C.B. Kaye s.n.* MEL 1516914); E-F: *Gemmabryum inaequale* E: habit with sporophyte. F: leaf (*L.D. Williams* 3537 AD); G-I: *Gemmabryum chrysoneuron* G: habit with sporophyte. H: leaf. I: rhizoidal tuber (*G.K. Thomson* MEL 29852). Scale bars 1.0 mm habit; 0.5mm leaves; 100 μm gemmae.

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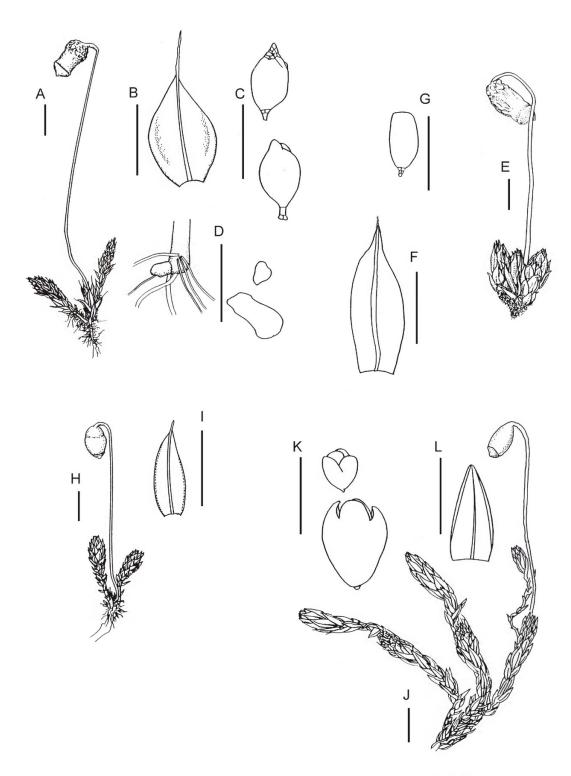


Fig. 5. A-D: *Gemmabryum eremaeum*: A: habit with sporophyte. B: leaf. C: bulbils. D: stem tubers (holotype *R.E. Grandison s.n* AD); E-G: *Gemmabryum pachythecum* E: habit with sporophyte. F: leaf. G: axillary bulbil (isolectotype *L. Preiss* 2466 MEL 30783;); H-I: *Gemmabryum austrosabulosum* H: habit with sporophyte. I: leaf holotype (*F. Mueller s.n.* MEL); J-M: *Gemmabryum sullivanii* J: habits. K: sporophyte. L: leaf, (*W.A. Weymouth 2706* AD), M: axillary bulbils (*J.R. Spence 4288* NSW). Scale bars 1.0 mm habit; 0.5mm leaves; 100 μm gemmae.

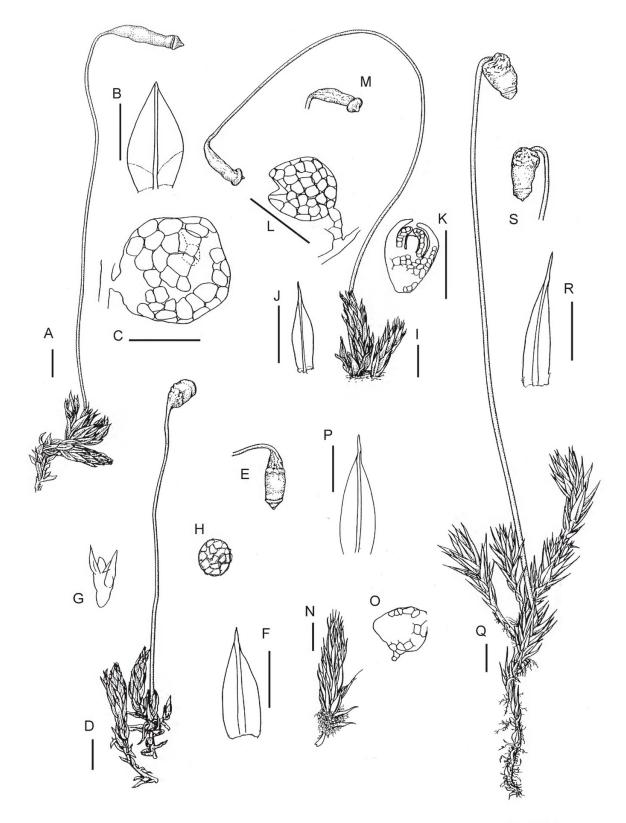


Fig. 6. A-C: *Gemmabryum subapiculatum* A: habit with sporophyte, B: leaf. C: rhizoidal tuber (*W.B. Schofield* 982632 NSW); D-H: *Gemmabryum dichotomum*: D: habit with sporophyte. E: capsule, F: leaf, G: axillary bulbil, H: rhizoidal gemma (*H.P. Ramsay* 22/73 NSW); I-M: *Gemmabryum tenuisetum* I: habit with sporophyte, J: leaf, K: axillary bulbil, L: rhizoidal tuber, M: capsule (*I.G. Stone* 1719 MEL); N-P: *Gemmabryum radiculosum* N: habit sterile, O: rhizoidal tuber P: leaf (*H. Streimann* 38988 CANB); Q-S: *Gemmabryum coronatum* Q: habit with sporophyte, R: Leaf, S: capsule (*H.P. Ramsay R174* NSW). Scale bars 1.0 mm habit; 0.5mm leaves; 100 μm gemmae.

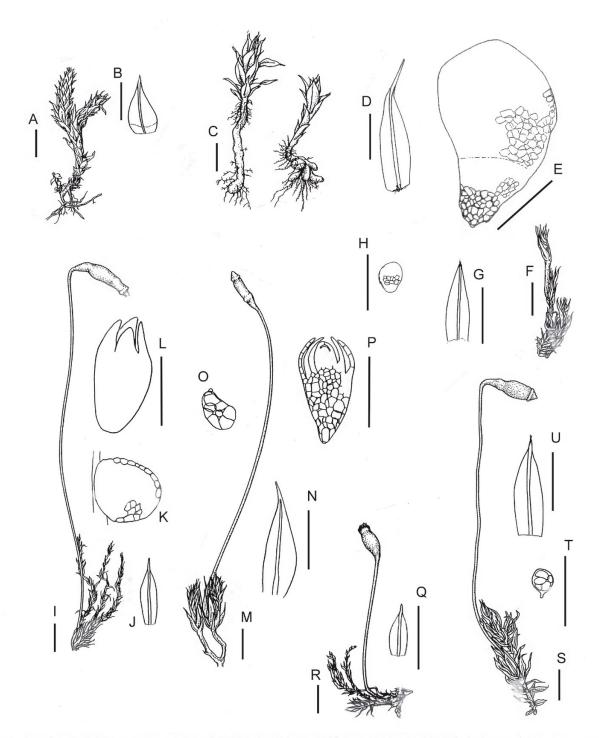


Fig. 7. A-B. Gemmabryum acuminatum A: habit sterile. B: leaf (J.R. Spence 5136 NSW); C-E: Gemmabryum coarctatum C: habits showing stem tubers. D: leaf. E: stem tuber (I.G. Stone 21742 MEL); F-H: Gemmabryum klingraeffii F: habit sterile. G: leaf. H: rhizoidal tuber (J.B. Cleland s.n. AD); I-L: Gemmabryum indicum I: habit with sporophyte. J: leaf. K: rhizoidal tuber. L: leafy bulbil (J.R. Spence 5116 NSW); M-P: Gemmabryum exile M: habit with sporophyte. N: leaf. O: rhizoidal gemma. P: leafy bulbil (H. Streimann 10681 CANB); Q-R: Gemmabryum preissianum Q: habit with sporophyte. R: leaf (L.D. Williams s.n. AD); S-U: Gemmabryum sauteri S: habit with sporophyte. T: rhizoidal tuber. U: leaf (W.W. Watts 1633 NSW). Scale bars 1.0 mm habit; 0.5 mm leaves; 100 μm gemmae.

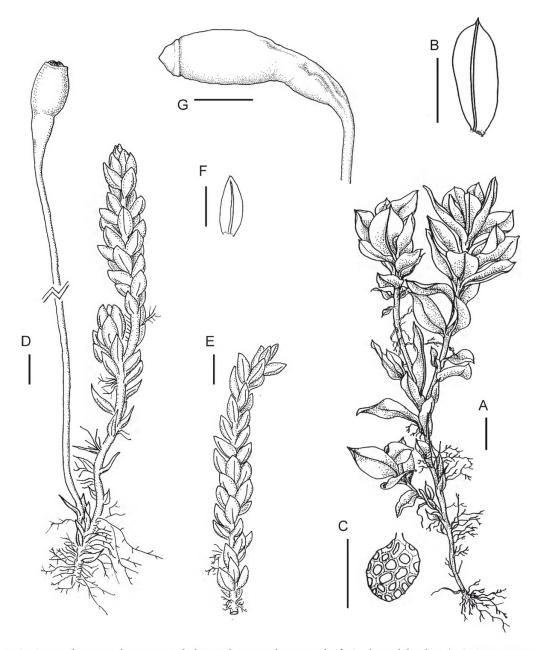


Fig. 8. A-C: *Gemmabryum tuberosum* A: habit with sporophytes. B: leaf. C: rhizoidal tuber (*I.G. Stone 16751* MEL); D-G: *Plagiobryoides cellularis* D: habit with sporophyte. E: habit sterile. F: leaf. G: enlarged capsule (as *Plagiobryum* in 2006; *C.J. Wild s.n.* NSW). Scale bars 1.0 mm habit; 0.5mm leaves; 100 μm gemmae.

Gemmabryum acuminatum (Harv. ex Hook.) J.R.Spence & H.P.Ramsay (=Brachymenium acuminatum Harv. ex Hook.): a silvery-yellow pantropical species related to *G. apiculatum* and *G. inaequale*, characterized by slender stems, a capsule with a broad mouth, and a reduced peristome. It is found on dry soil in tropical to arid regions of Queensland and Western Australia (Fig. 7 A-B).

Gemmabryum apiculatum (Schwägr.) J.R.Spence & H.P.Ramsay (=Bryum apiculatum Schwägr.): a widespread pantropical small pinkish-green species associated with wet soil and rock in the subtropical and tropical north, characterized by elongate laminal cells and small brown pyriform tubers. This species probably represents a species complex, as some collections elsewhere in the world also produce bulbils (Fig. 4 A-D).

Gemmabryum austrosabulosum (Catches. ex J.R.Spence & H.P.Ramsay) J.R.Spence & H.P.Ramsay (synonyms: Bryum austrosabulosum Catches. ex J.R.Spence & H.P.Ramsay; Bryum sabulosum Catches. ex J.R.Spence & H.P.Ramsay nom. illeg.): a tiny species with imbricate to julaceous stems found in southern Australia, often associated with rock outcrops and soil-filled crevices. The species is very similar to G. exile, but differs in the leaves remaining imbricate when dry, the margins recurved, the nodding capsule with a well-developed peristome, and lack of bulbils or tubers (Fig. 5 H-I).

Gemmabryum caespiticium (Hedw.) J.R.Spence (=*Bryum caespiticium* Hedw.): a worldwide species, characterized by its strongly caespitose-comose habit, long awn, weak limbidium, and elongate distal laminal cells. Small rhizoidal tubers have been reported from northern hemisphere material (Fig. 11 E-F).

Gemmabryum chrysoneuron (Müll. Hal) J.R.Spence & H.P.Ramsay (=Bryum chrysoneuron Müll. Hal.): a widespread often coastal yellowish-green species with glossy leaves, a long golden-yellow awn and large red rhizoidal tubers that have a dimpled look, like miniature golf balls, resulting from protuberant cell walls. This species is more reminiscent of a small *Imbribryum* such as *I. australe*. In New Zealand this species has (in part) been known under the name *Bryum duriusculum* Hook. f. & Wilson (Fig. 4 G-I).

Gemmabryum coarctatum (Müll. Hal.) J.R.Spence & H.P.Ramsay (=*Brachymenium coarctatum* (Müll. Hal.) Bosch. & Sande Lac.): a paleotropical species found in northern Australia on seasonally wet soils, characterized by a hyaline awn and sometimes hyaline upper lamina with a limbidium, a more or less comose habit, and erect capsules with reduced peristomes. Some material produces stem tubers (see Spence & Ramsay 1996) (Fig. 7 C-E).

Gemmabryum coronatum (Schwägr.) J.R.Spence & H.P.Ramsay (=*Bryum coronatum* Schwägr.): a pantropical species related to *G. dichotomum* but with a distinctly swollen and rugose apophysis, strongly recurved leaf margins, and often triangular-shaped leaves (Fig. 6 K, Q-S).

Gemmabryum dichotomum (Hedw.) J.R.Spence & H.P.Ramsay (=Bryum dichotomum Hedw.): a widespread boreal-temperate and subantarctic-southern temperate species that typically avoids drier regions, characterized by its single leafy bulbils, plane to weakly recurved leaf margins, and thick capsule with a smooth and non-inflated apophysis (Fig. 6 D-H).

Gemmabryum eremaeum (Catches. ex J.R.Spence & H.P.Ramsay) J.R.Spence & H.P.Ramsay (=Bryum eremaeum Catches. ex J.R.Spence & H.P.Ramsay): a distinctive southern Australian endemic related to *G. pachythecum*, characterized by its more or less hyaline awn, bulbils with short projections at the tip with a groove in between, and occasional production of stem tubers (see Spence and Ramsay 1996). It prefers more arid regions than *G. pachythecum*. The species has been recently found as an introduced exotic in botanic gardens in California (Fig. 5 A-D).

Gemmabryum erythropilum (M.Fleisch.) J.R.Spence & H.P.Ramsay (=Bryum erythropilum M.Fleisch.): a recently documented species from Queensland (Spence and Ramsay 2013) related to *G. apiculatum*, with red leaves, long awns, and small pyriform orange-red tubers. The species is found elsewhere in tropical regions of Asia, Malesia and New Guinea (Spence and Ramsay 2013). It is reported to be autoicous but our material is sterile. This species may be the same taxon as *Bryum thomsonii* Mitt. of south-east Asia (no available illustrations).

Gemmabryum exile (Dozy & Molk.) J.R.Spence & H.P.Ramsay (=Brachymenium exile (Dozy & Molk.) Bosch. & Sande Lac.): a small evenly foliate plant on soil and rock with small ovate leaves that fold in half along the costa when dry, giving the shoots a string-like appearance, erect capsules, and a reduced peristome. This species is widespread in the world's semi-arid subtropics, including warmer regions of Australia and New Zealand, and is one of the only Gemmabryum species that produces both leaf axil bulbils and rhizoidal tubers. It can sometimes be found on concrete. Some arid-land material exhibits long somewhat hyaline awns (Fig. 7 M-P).

Gemmabryum inaequale (Taylor) J.R.Spence & H.P.Ramsay (=*Bryum inaequale* Taylor): a yellow-green species related to *G. acuminatum* but more widespread and mostly temperate in distribution, often associated with roadside banks on exposed soil; the capsules are narrowed to the mouth and the peristome is well developed (Fig. 4 E-F).

Gemmabryum indicum (Dozy & Molk.) J.R.Spence & H.P.Ramsay (=Brachymenium indicum (Dozy & Molk.) Bosch. & Sande Lac.): a distinctive paleotropical-Pacific species forming dull green to yellow-green turfs on rocks and soil in the tropics, related to *G. coarctatum* but lacking the hyaline upper leaf and awn. This species is synoicous, although much material is sterile, and has a slender erect capsule with a reduced peristome. Leaf axil bulbils with leafy primordia are sometimes produced in collections in other regions of its world range but are very rare in Australian material. Stem tubers have been found on material from Easter Island, although they have not yet been found in Australian material. Gemmabryum coronatum occurs in the same areas and is very similar, but has more triangular leaves with margins recurved to near the apex (vs. ovate-lanceolate leaves with margins recurved proximally), bulbils commonly present in sterile material, and a nodding capsule with swollen neck (Fig. 7 I-L).

Gemmabryum klinggraeffii (Schimp.) J.R.Spence & H.P.Ramsay (=*Bryum klinggraeffii* Schimp.): a species of disturbed soil characterized by small spherical red to scarlet tubers with distinctly protuberant cells. Probably introduced (Fig. 7 F-H).

Gemmabryum pachythecum (Müll. Hal.) J.R.Spence & H.P.Ramsay (=Bryum pachytheca Müll. Hal.): a common and widespread species throughout Australia and New Zealand, extending to southeast Asia, characterized by the strongly inflated capsule neck, coloured red-brown awn, and smooth egg-shaped bulbils without primordia (Fig. 5 E-G).

Gemmabryum preissianum (Hampe) J.R.Spence & H.P.Ramsay (Brachymenium preissianum (Hampe) A.Jaeger): a distinctive widespread Australasian species typically found on rock, often calcareous, with a more or less erect to inclined capsule with a narrow mouth, a reduced peristome and a rostellate operculum (Fig. 7 Q-R).

Gemmabryum radiculosum (Brid.) J.R.Spence & H.P.Ramsay (=*Bryum rubens* Brid.): a common and widespread species in warmer climates of the world, characterized by large red rhizoidal tubers, long awns, quadrate proximal laminal cells, and a preference for calcareous substrates (Fig. 6 N-P).

Gemmabryum sauteri (Bruch. & Schimp.) J.R.Spence & H.P.Ramsay (=Bryum sauteri Bruch & Schimp.): a common species in Australasia with yellow-green narrowly ovate leaves, a short awn, and small brown pyriform tubers. It is similar to *G. apiculatum* but has more *Bryum*-like areolation with quadrate cells across the leaf base, and shorter distal laminal cells. Much of the material named as this species in the region is distinct from typical European material, and may actually represent a new species. The species is also found on Macquarie Island in the subantarctic region (Fig. 7 S-U).

Gemmabryum subapiculatum (Hampe) J.R.Spence & H.P.Ramsay (=Bryum subapiculatum Hampe): the most common and widespread of the tuber-forming Gemmabryum species in temperate regions of the world, characterized by a relatively short to medium-length awn, large red tubers, rectangular proximal laminal cells, and a preference for acidic substrates (Fig. 6 A-C).

Gemmabryum sullivanii (Müll.Hal.) J.R.Spence & H.P.Ramsay (=Bryum sullivanii Müll. Hal.): a distinctive species associated with wet soil and rock, often along intermittent and perennial streams, with a preference for limestone. The leaves are broadly rounded-obtuse, and the costa is usually percurrent. Plants can become fairly robust, within the size range for *Imbribryum* species (Fig. 5 J-M).

Gemmabryum tenuisetum (Limpr.) J.R.Spence & H.P.Ramsay (=*Bryum tenuisetum* Limpr.): a rare scattered northern hemisphere disjunct species of disturbed soil characterized by large yellow tubers with red cell walls, and yellowish rhizoids. Probably introduced (Fig. 6 H-J, M).

Gemmabryum tuberosum (Mohammed & Damanhuri) J.R.Spence & H.P.Ramsay (=*Bryum tuberosum* Mohammed & Damanhuri): small green-red paleotropical species with ovate to obovate leaves, and strongly flattened tubers with undulate margins, found in tropical Queensland (Fig. 8 A-C).

Gemmabryum sp. (Baw Baw Plateau, *A.J. Downing s.n.*): Australia, Victoria: Baw Baw Plateau, Central Gippsland, South Face Road. Growing on sandbags, near roadside drain on damp granite derived soil in *Eucalyptus regnans* tall forest, southerly aspect. *A.J. Downing s.n.* 6.x.2003 (MQU).

A collection from Victoria at moderately high elevations consists of *G. dichotomum*-like plants with multiple small leafy bulbils per leaf axil. The costa is very strongly excurrent in a long awn, unlike typical *G. dichotomum*. This species is similar to and may be conspecific with the South African *Bryum rigidicuspis* Dix. However, long awns occasionally occur in other species in the complex, including *G. barnesii* (J.B.Wood *ex* Schimp.) J.R.Spence, which has been recently found in Tierra del Fuego and the Falkland Islands. More work is needed on those species that produce multiple leafy bulbils per leaf axil.

5. Imbribryum N.Pedersen

Plants medium sized, stems (10–)20–60 mm, gemmiform to evenly foliate; leaves 2–4 mm, ovate-lanceolate to ovate; costa percurrent to excurrent in short to long awn, limbidium absent or weak, distal laminal cells vermicular, elongate rhomboidal to hexagonal, often incrassate, proximal cells quadrate to short-rectangular; asexual gemmae of rhizoidal tubers arising from leaf axils; dioicous; capsule pyriform to cylindrical, nodding, peristome well-developed, spores $<25~\mu m$.

This genus overlaps in many characters with *Gemmabryum* section *Tuberibryum*, but molecular work to date has not resolved the relationships. Generally, small species with rhizoidal tubers especially on rhizoids in soil, should be keyed out in *Gemmabryum*. *G. chrysoneuron* is keyed out here as well as in *Gemmabryum* as it can be confused for an *Imbribryum* and is within the size range of *I. australe*.

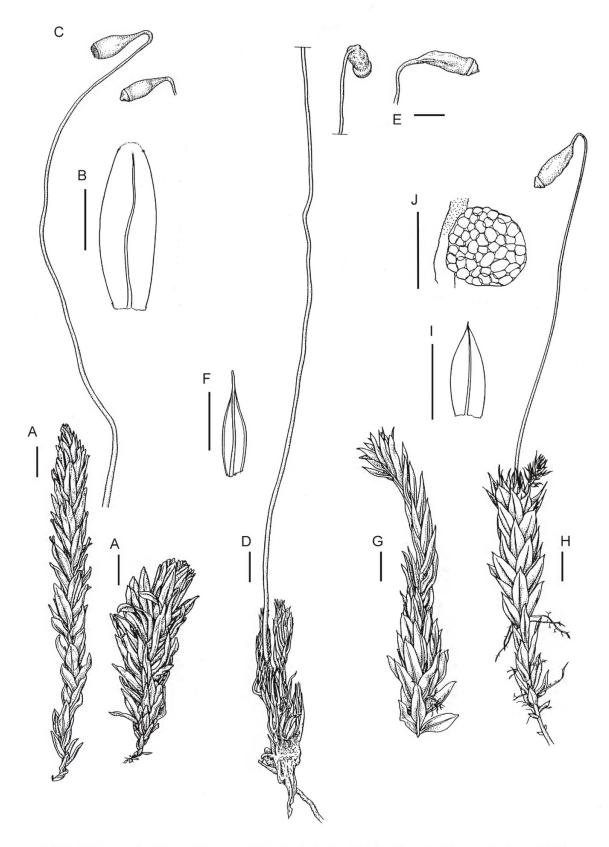


Fig. 9. A-C: *Ochiobryum blandum* A: habit sterile left (*A.E. Orchard 1931* AD), right (*M. Mueller 1795* MEL). B: leaf. C: sporophytes (from New Zealand material used for chromosome studies *H.P. Ramsay 76/84* NSW); D-F: *Imbribryum australe* D: plant with sporophyte. E: capsule. F: leaf (as *Gemmabryum* in 2006; *H.P. Ramsay 3/88* NSW); G-J: *Imbribryum cheelii* G: habit sterile. H: habit with sporophyte. I: leaf. J: rhizoidal tuber (as *Gemmabryum* in 2006; *D.G. Catcheside 73.293* AD). Scale bars 1.0 mm habit; 0.5mm leaves; 100 μm gemmae.

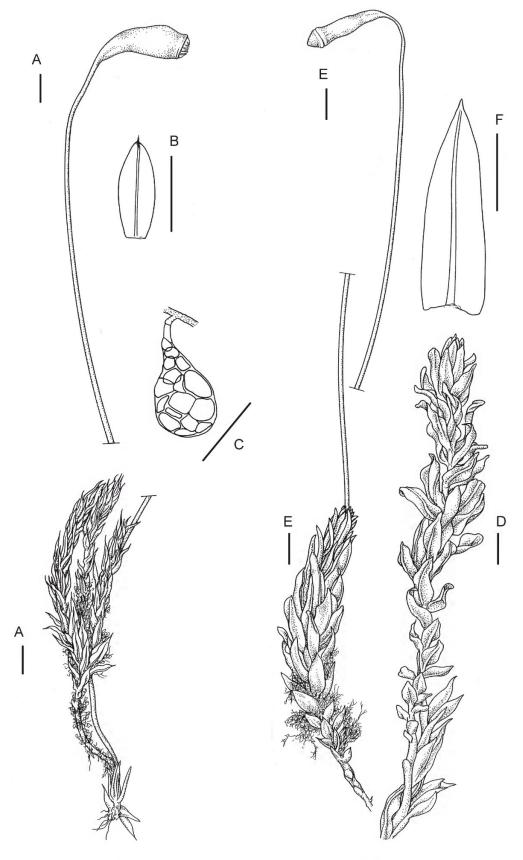


Fig. 10. A-C: *Imbribryum clavatum* A: habit with sporophyte. B: leaf. C: rhizoidal gemma (as *Gemmabryum* in 2006; *H.P. Ramsay 32/77* NSW); D-G: *Imbribryum laevigatum* D: habit sterile. E: habit with sporophyte. F: leaf. G: bulbil (as *Gemmabryum* in 2006; (*I.G. Stone 3177* MEL). Scale bars 1.0 mm habit; 0.5mm leaves; 100 μm gemmae.

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Fig. 11. A-B: Imbribryum crassum A: habit with sporophytes. B: leaf (as Gemmabryum in 2006; W.W. Watts s.n. NSW); C-D: Ptychostomum altisetum C: habit with sporophyte. D: leaf (W.B. Schofield s.n NSW); E-F: Gemmabryum caespiticium E: habit with sporophyte. F: leaf (W.W. Watts 8625 NSW 39468). Scale bars 1.0 mm habit; 0.5mm leaves; 100 μm gemmae.

Key to Imbribryum species

1.	Plants large, stems often >4 cm, dull green to olive, julaceous, costa percurrent; leaf apex broadly acute to obtuse, distal laminal cells rhomboidal (2–4:1), oblique to costa in rows, strongly incrassate
1:	Plants medium sized, stems mostly <3 cm, pale yellow, green-yellow to red, not or weakly julaceous; costa excurrent in short to long awn, distal laminal cells rhomboidal to hexagonal (3–6:1), oblique or parallel to costa
2.	Leaves lanceolate to narrowly ovate, flat, distal laminal cells incrassate, often oblique to costa, limbidium present on proximal margins; capsule elongate, to 6 mm, often somewhat curved; wet sites, often encrusted with carbonate deposits
2:	Leaves ovate, ovate-lanceolate or obovate, flat to strongly concave, distal laminal cells thin walled or incrassate, not oblique to costa, limbidium absent or very weak; capsule pyriform, <3 mm; wet to dry sites, not usually encrusted with carbonates
3.	Excurrent costa forming a long awn, many awns >1/2 lamina length
3:	Excurrent costa forming a slender to stout awn or mucro, mostly <1/10 lamina length
4.	Plants yellow-green; leaves stiff and rigid, triangular, margins strongly recurved beyond mid-leaf, lamina sometimes plicate
4:	Plants golden-green; leaves less rigid, somewhat loosely set, ovate-lanceolate to broadly lanceolate; margins recurved proximally; lamina never plicate
5.	Plants with red tints, often entirely red; stems elongate, evenly foliate; laminal cells thin to firm walled, not incrassate, distal laminal cells parallel to costa
5:	Plants pale yellow, yellow-green or straw coloured, lacking red tints; stems short, distinctly gemmiform, sometimes in 2 or more interrupted tufts along stem; laminal cells distinctly incrassate, distal cells often

Imbribryum australe (Hampe) J.R.Spence & H.P.Ramsay (=Bryum australe Hampe; Gemmabryum australe (Hampe) J.R.Spence & H.P.Ramsay): a small species with rigid imbricate triangular leaves which are often but not always plicate, a long stiff awn, and strongly revolute margins. This species is based on an atypical type that differs somewhat from other material (Fife 2015), but we follow Ochi (1970) as the type and other material is similar in most respects. Found on damp to wet soil or soil over rock, often along rivers (Fig. 9 D-F).

Imbribryum cheelii (Broth.) J.R.Spence & H.P.Ramsay (=*Bryum cheelii* Broth.; *Gemmabryum cheelii* (Broth.) J.R.Spence & H.P.Ramsay): a distinctive Australian endemic that is characterized by stiff red imbricate leaves, short-excurrent awn in a stout point, and serrulate distal leaf margins. It prefers seepage to intermittent rock and soil over rock along streams in temperate regions (Fig. 9 G-J).

Imbribryum clavatum (Schimp.) J.R.Spence & H.P. Ramsay (=*Bryum clavatum* (Schimp.) Müll. Hal.; *Gemmabryum clavatum* (Schimp.) J.R.Spence & H.P.Ramsay): a variable species found in calcareous seeps and springs and along streams in temperate to cool climates. The ovate leaves with a limbidium in the proximal margins, a short awn, incrassate distal laminal cells which are sometimes oblique to the costa, and very long curved capsules, are diagnostic (Fig. 10 A-C).

Imbribryum crassum (Hook.f. & Wilson) J.R.Spence & H.P.Ramsay (=*Bryum crassum* Hook.f. & Wilson; *Gemmabryum crassum* (Hook.f. & Wilson) J.R.Spence & H.P.Ramsay): a distinctive southern hemisphere species with green-yellow leaves in a strongly gemmate or comal tuft, often interrupted along elongate stems, incrassate laminal cells oblique to the costa, and a short excurrent costa in a stout mucro are diagnostic. This species often occurs in drier habitats than other *Imbribryum* species, and is largely temperate in distribution in southern Australia, New Zealand and southern South America (Fig. 11 A-B).

Imbribryum laevigatum (Hook.f. & Wilson) J.R.Spence & H.P.Ramsay (=*Bryum laevigatum* Hook.f. & Wilson); *Gemmabryum laevigatum* (Hook.f. & Wilson) J.R.Spence & H.P.Ramsay): a common and distinctive robust southern hemisphere species associated with rivers, streams and wetlands on wet soil, peat and rock, characterized by rounded mostly obtuse thick leaves, strongly incrassate laminal cells, and distal cells oblique to the costa. Found throughout the southern hemisphere in subantarctic and montane climates (Fig. 10 D-G).

6. Leptostomopsis (Müll. Hal. ex Broth.) J.R.Spence & H.P.Ramsay

Plants small, stems 10–20 mm, gemmiform to evenly foliate; leaves 1–2 mm, ovate-lanceolate; costa excurrent in long spinose silver awn, limbidium absent or weak, distal laminal cells elongate rhomboidal to hexagonal,

proximal cells quadrate; asexual gemmae of leafy bulbils in leaf axils; dioicous; capsule cylindrical, erect, peristome strongly reduced, cilia and endostome segments absent, spores <25 μm.

Leptostomopsis pulchra (Hook.) Ochyra & Bedn.-Ochyra: a recently reported record from near Melbourne, Victoria (Spence and Ramsay 2013). It was collected under Leptospermum and Melaleuca shrubs on wood in undisturbed vegetation. This species is very small, with concave ovate leaves, a very long silver-white awn, and small leafy bulbils in the leaf axils. The collection is sterile, but it agrees well with named material from Africa (illustrated in Magill 1987).

7. Ochiobryum J.R.Spence & H.P.Ramsay

Plants medium sized, stems 20-60 mm, evenly foliate, often somewhat complanate; leaves 1-3 mm, ovate; costa percurrent to short-excurrent, limbidium present, distal laminal cells elongate vermicular to hexagonal, proximal cells similar; asexual gemmae absent; dioicous; capsule pyriform, nodding, peristome well developed, spores <25 µm.

A small genus with stems that are often weakly complanate, red, pink, silver-green to green colouration, very long and narrow laminal cells, and a nodding pyriform capsule. Molecular work shows that it appears to be related to Imbribryum.

Ochiobryum blandum Hook.f. & Wilson) J.R.Spence & H.P.Ramsay (=Bryum blandum Hook.f. & Wilson): a beautiful species characteristic of cold-temperate, subantarctic, to subalpine-alpine habitats, forming dense turfs on rocks and soil in or near streams. The turfs are typically vary from bright to dark glossy green, but the leaves often become glossy red or pink-silver to pink-green as they dry out (Fig. 9 A-C).

8. Plagiobryoides J.R. Spence

Plants small to large, stems 10-60 mm, evenly foliate; leaves 1-4 mm, ovate; costa percurrent to short-excurrent, limbidium absent or present, distal laminal cells irregularly rhomboidal to hexagonal, proximal cells longrectangular; asexual gemmae absent (in Australia); dioicous; capsule pyriform, nodding, peristome variable, well-developed to reduced, cilia variable, short to sometime longer than exostome teeth, spores 20-35 μm.

A group of species with lax areolation (wide thinwalled cells), mostly short distal laminal cells, long proximal laminal cells, and capsules that usually have a distinct slender apophysis. Most prefer wet soil. The genus is morphologically similar to Plagiobryum and Ptychostomum. Two species of Plagiobryoides occur in Queensland and are very different from each other morphologically.

Key to Plagiobryoides species

- Plants small, pinkish to yellow-green, somewhat julaceous, upper laminal cells >3:1, capsules ovate with
- Plants large, olive green to red-green, not julaceous, upper laminal cells very short and broad, sometimes quadrate, capsules short, top-shaped with wide flaring mouth; spores >30 μmPlagiobryoides sp.

Plagiobryoides cellularis (Hook.) J.R.Spence (=Bryum cellulare Hook.; Plagiobryum cellulare (Hook.) J.R. Spence & H.P. Ramsay): a widespread pantropical species characterized by small pink-green leaves, and a reduced peristome. This species is highly variable and likely represents a species complex including, among others, the local endemic form in Queensland known as *Plagiobryum wildii* Broth. which may be specifically distinct from true *P. cellularis* (Fig. 8 D-G).

Plagiobryoides sp.: material seen (currently unavailable) from Moreton, Queensland, appears to be related to the New Guinean Bryum decurrens Brid., but differs in its capsule shape (short, flaring with wide mouth vs. elongate cylindric to clavate, narrow mouth in B. decurrens) and much larger spores (32–36 μm vs. 18–22 μm). It is a robust plant with evenly foliate stems, broadly ovate olive-green contorted leaves when dry, short wide distal laminal cells, and long proximal cells. The gametophytes of this plant are very similar to B. decurrens, which is illustrated in Eddy (1996).

9. Ptychostomum Hornsch.

Plants small to large, stems 10-60 mm, comose-tufted to evenly foliate; leaves 2-4 mm, ovate to ovatelanceolate; costa short to long-excurrent in awn, limbidium present, distal laminal cells irregularly rhomboidal to hexagonal, proximal cells rectangular; asexual gemmae rare, of short filiform gemmae on stems; dioicous, synoicous, autoicous or polyoicous; capsule ovate, cylindrical to pyriform, inclined to nodding, peristome variable, well-developed to reduced, cilia often short or absent, spores 10–30 μm.

A large, exceedingly confusing genus often defined by capsule and peristome characters, which means that many sterile collections cannot be identified. Many species are monoicous, and have reduced peristomes. Most are found on soil in boreal-temperate to arctic-alpine regions and are less common in the southern hemisphere except for subantarctic regions of southern South America where the genus is common. Several northern species are disjunctly distributed to cool climate regions of New Zealand and Australia.

Key to Ptychostomum species

1.	Plants medium to large, stems elongate, evenly foliate, often to 4 cm; leaves more or less same size distally, ovate, costa short-excurrent as stout awn, laminal cells incrassate
1:	Plants small to medium, stems comose, tufted to rosulate, not elongate and evenly foliate, 1–3 cm; leaves ovate to ovate-lanceolate or rarely obovate, costa excurrent in medium to long awn, cells mostly thin walled
2.	Leaves not or weakly decurrent, distal laminal cells incrassate, somewhat oblique to costa; synoicous
2:	Leaves strongly decurrent, distal laminal cells firm walled to somewhat incrassate, more or less parallel to costa; dioicous
3.	Leaves ovate, costa excurrent in short awn, limbidium partially bistratose, leaves green, leaf base green; synoicous, spores large, 25–28(–30) μm, peristome reduced, cilia absent; subantarctic
3:	Leafy ovate, obovate or ovate-lanceolate, limbidium variable but usually present, unistratose, leaf colour various, leaf bases usually reddish, spores small to medium-size, $10-26\mu m$; synoicous, autoicous or dioicous; temperate to montane-subantarctic
4.	Leaves ovate or obovate, concave, limbidium weak; dioicous
4:	Leaves ovate-lanceolate or sometimes lingulate, flat or weakly concave, limbidium present, distinct; synoicous or autoicous
5.	Autoicous; plants loosely comose-tufted, leaves ovate-lanceolate to lingulate
5:	Synoicous; plants comose to caespitose, leaves ovate-lanceolate (sporophytes needed beyond this couplet)
6.	Peristome well developed, spores 12–16 μm; widespread temperate-montane
6:	Peristome reduced, cilia short or absent, spores (18–)20–26 µm; montane-alpine
ъ.	

Ptychostomum altisetum (Müll. Hal.) J.R.Spence & H.P.Ramsay (=Bryum altisetum Müll. Hal.): an Australian species closely related to or perhaps conspecific with the northern hemisphere *P. inclinatum* Swartz ex Brid.) J.R. Spence, which has been reported from New Zealand under the name *Bryum amblyodon* Müll. Hal. (Fife 2015). The species is found primarily in cool montane-alpine climates (Fig. 11 C-D).

Ptychostomum bimum (Schreb.) J.R.Spence (=*Bryum bimum* Schreb.): a robust synoicous northern hemisphere disjunct species related to *P. pseudotriquetrum*, but with more incrassate laminal cells and weaker decurrencies. Its distribution is not fully understood as it has been considered a variety of *P. pseudotriquetum*. In Australia it is known from New South Wales, Tasmania, and Victoria (Spence and Ramsay 2013) (illustrated in Zolotov 2000).

Ptychostomum creberrimum (Taylor) J.R.Spence & H.P.Ramsay (=Bryum creberrimum Taylor): a common widespread bipolar species of soil in temperate to montane sites, common in forest clearings in the mountains and in more southern temperate climates. Ptychostomum pallescens is similar but has larger spores (16–20 μ m), and is usually autoicous (Fig. 12 E-F).

Ptychostomum cylindrothecium (R.Br. bis) J.R.Spence & H.P.Ramsay (=Bryum cylindrothecium R.Br. bis): A poorly known species on sandy soil possibly related to the Gemmabryum caespiticium complex, but larger with shorter distal laminal cells. We have retained it in Ptychostomum pending further study. Currently only known from New Zealand and South Australia (Fig. 12 A-B).

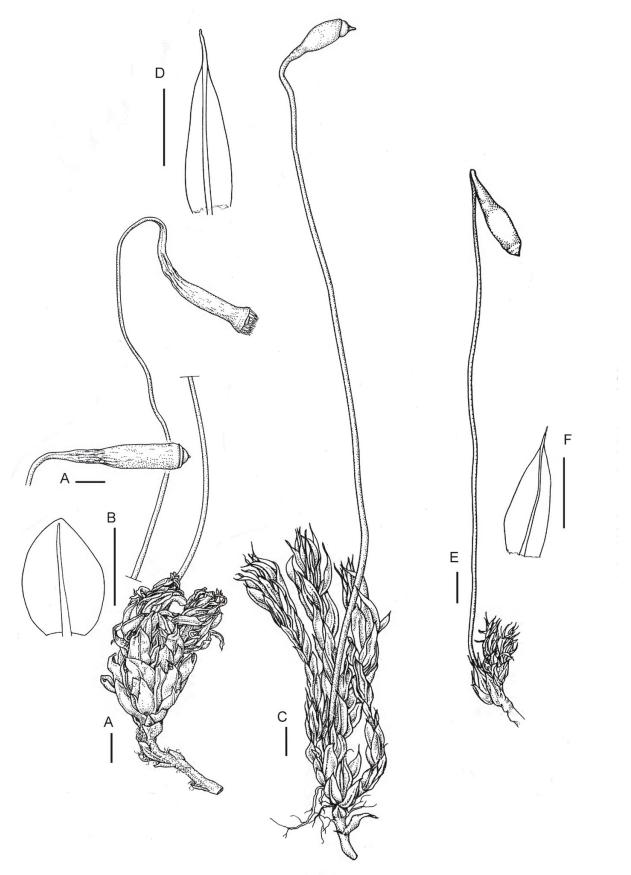


Fig. 12. A-B:. *Ptychostomum cylindrothecium* A: habit with sporophyte. B: leaf (*H.T. Clifford* MEL 1519289); C-D: *Ptychostomum pseudotriquetrum*, C: habit with sporophyte. D: habit with sporophyte (*H.B. Womersley* AD); E-F: *Ptychostomum creberrimum* E: habit with sporophyte. F: leaf (*M. Mueller* MEL 25997). Scale bars 1.0 mm habit; 0.5 mm leaves; 100 μm gemmae.

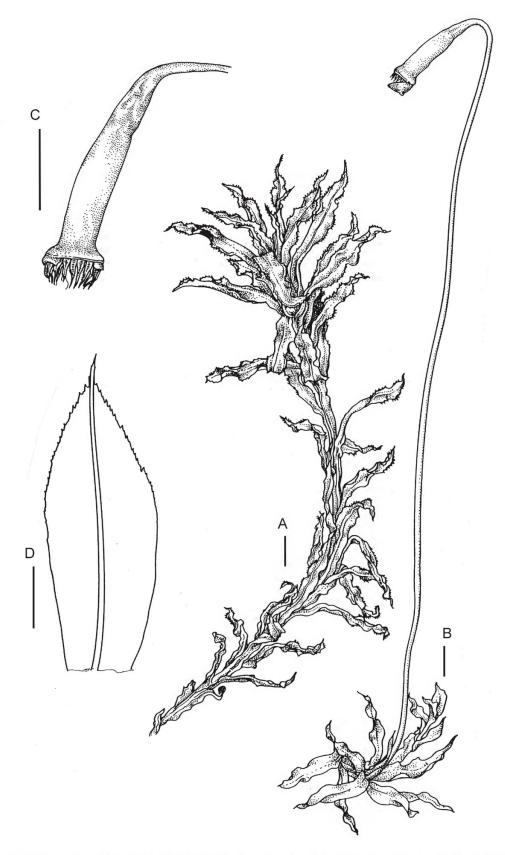


Fig. 13. A-D: *Rhodobryum graffeanum* (as *R. aubertii* in Spence & Ramsay 2006) A: habit sterile (*I.G. Stone 12347* MEL), B: apex of female with sporophyte. C: enlarged capsule showing peristome. D: leaf (*W.B. Schofield 8039* NSW). Scale bars 1.0 mm habit and enlarged capsule, 0.5mm leaves; 100 µm gemmae.

Ptychostomum mucronatum (Mitt.) Ochyra & Bedn.-Ochyra (=Bryum mucronatum Mitt.): a cool climate New Zealand-subantarctic species with leaves with a short mucronate awn and a bistratose border, large spores, more or less uniformly green to yellow-green leaves, and a reduced peristome. The species is included in the keys as it occurs on Macquarie Island (Seppelt 2004) and should be looked for in alpine regions of Tasmania; also known from other subantarctic islands, New Zealand and southern South America (illustrated in Sainsbury 1955).

Ptychostomum pallescens (Schleich. ex Schwägr.) J.R.Spence (=Bryum pallescens Schleich. ex Schwägr.): a rare disjunct from the northern hemisphere known from New Zealand and Tasmania found on wet soil, characterized by rather broadly ovate-lanceolate to lingulate leaves, and autoicy. The capsules are usually nodding, but in some collections can be suberect to nearly erect (Spence and Ramsay 2013) (illustrated in Spence 2014).

Ptychostomum pseudotriquetrum (Hedw.) J.R.Spence & H.P.Ramsay ex D.T.Holyoak & N.Pedersen (=Bryum pseudotriquetrum (Hedw.) P.Gaertn., B.Meyer & Scherb.): a highly variable robust species with a world-wide distribution in temperate, arctic-alpine and Antarctic regions. The typical form consists of evenly foliate elongate stems, ovate leaves that are strongly decurrent, and a short awn. Sometimes filiform gemmae occur, primarily on the stems. The stems are often strongly matted with rhizoids (Fig. 12 C-D).

10. Rhodobryum (Schimp.) Limpr.

Plants large, stems to 50 mm, evenly foliate, stolons present; leaves 3-10 mm, obovate to ovate; costa short excurrent in awn, limbidium present, distal laminal cells irregularly rhomboidal to hexagonal, proximal cells rectangular; asexual gemmae absent; dioicous; capsule cylindrical to pyriform, inclined to nodding, peristome well-developed, spores <20 μm.

A predominantly tropical-warm temperate genus characterized by strongly rosulate to evenly foliate stems (in Australia), stolons, and polysety. Although similar to Rosulabryum, chromosome morphology, costal anatomy and the presence of stolons separate the two genera.

Rhodobryum graeffeanum (Müll. Hal.) Paris (=Rhodobryum aubertii (Schwägr.) Thér.): a large tropicalsubtropical species with elongate evenly rosulate stems and large obovate to ovate leaves with strongly denticulate margins. In Australia the name Bryum aubertii (Schwägr.) Brid. is misapplied as that African species is a Rosulabryum producing filiform gemmae directly on the leaves (Spence unpubl. data), unique in the family (see also Magill 1987). The oldest valid name for the Australasian species is R. graeffeanum (Fig. 13 A-D).

11. Rosulabryum J.R.Spence

Plants small to large, stems 10-100 mm, rosulate to rarely evenly foliate, stolons absent; leaves 2-8 mm, obovate to ovate; costa short to long-excurrent in awn, limbidium usually present, often strong, distal laminal cells irregularly rhomboidal to hexagonal, proximal cells rectangular; asexual gemmae of filiform gemmae in leaf axils and rhizoidal tubers on rhizoids in substrate; dioicous or rarely polyoicous (R. torquescens only); capsule cylindrical to pyriform, inclined to nodding, peristome well-developed, spores <25 μm.

A large nearly worldwide genus of mostly rosulate species with obovate to ovate leaves, with serrulate to serrate distal leaf margins, occasional polysety, and cylindrical to clavate capsules with small spores. Most species produce rhizoidal tubers, and a few produce leaf axil filiform gemmae. Larger species are superficially similar to Rhodobryum, but differ in lacking stolons and having well developed costal stereid bands.

Key to Rosulabryum species

1.	Slender filiform gemmae in leaf axils or stems of sterile shoots
1:	Filiform gemmae lacking (plants lacking gemmae key here)
2.	Epiphytic on orchids in forest canopy, rarely on rock; leaves equidistant, rounded ovate, margins smooth to finely serrulate
2:	On soil, rocks or tree bases and fallen logs, never epiphytic; leaves rosulate to comose, obovate to spathulate, margins sharply serrate
3.	Leaves flat, not keeled, obovate, distal laminal margins serrate, costa excurrent; gemmae coarsely papillose
3:	Leaves strongly keeled, ovate to spathulate, laminal margins sharply serrate to denticulate, often to midleaf, costa mostly percurrent; gemmae smooth to finely papillose

4.	Stems short, $<1(-2)$ cm, more or less rosulate, leaves ≤ 3 mm
4:	Stems larger, 2–10 cm, rosulate to elongate evenly foliate, leaves (3–)4–10 mm
5.	Leaves 2–3 mm, imbricate, broadly ovate or obovate, strongly concave, not much altered when dry, laminal cells incrassate; tubers lacking
5:	Leaves mostly $<2(-2.5)$ mm, ovate, obovate or spathulate, flat or weakly concave, twisted to contorted when dry, laminal cells mostly thin walled; tubers often present
6.	Plants golden-green or green-brown, costa excurrent in long straight awn; temperate-arid
6:	Plants reddish-green, costa excurrent in short often recurved awn; montane
7.	Leaves narrowly ovate, acuminate, margins more or less smooth to finely serrulate, distal laminal cells elongate, sublinear, 4–6:1
7:	Leaves ovate, obovate to spathulate, acute or obtuse, margins rarely smooth, mostly serrulate to serrate, distal cells rhomboidal 2–4:1
8.	Plants very small, <1 cm long, costa percurrent to short-excurrent, leaf margins plane, entire to finely serrulate distally, limbidium lacking; on damp soil banks in NT, QLD
8.	Plants small to large, often >1 cm, costa short to long excurrent in distinct awn, leaf margins recurved at least proximally, serrulate to serrate, limbidium present, usually distinct; habitats and distributions various
9.	Leaves obovate, spirally twisted around stem when dry, costa excurrent in long awn, tubers red-brown Rosulabryum capillare
9:	Leaves obovate, ovate or spathulate, irregularly contorted when dry, costa excurrent in short to medium-length awn, tubers red-brown, orange, red or scarlet
10.	Leaves narrowly ovate-spathulate, strongly keeled, stems evenly foliate to weakly rosulate, leaf margins sharply serrate to midleaf
10:	Leaves obovate or broadly spathulate, flat or weakly keeled, stems distinctly rosulate, leaf margins serrulate to serrate in the distal 20–30%
11.	Plants polyoicous to synoicous, limbidium strong, leaves usually lacking red tints except at base; rhizoidal tubers red, scarlet to sometimes orange
11:	Plants dioicous, limbidium variable but sometimes indistinct, leaves green to red; rhizoidal tuber colour variable but not scarlet, if red then cell walls protuberant
12.	Leaves obovate, green except at leaf base; limbidum distinct, distal margins serrate; tubers red-brown to sometimes orange, cell walls smooth (search for filiform leaf axil gemmae on sterile plants)
12:	Leaves ovate, often red throughout; limbidium indistinct, distal margins serrulate; tubers red, cell walls distinctly protuberant (filiform gemmae lacking)
13.	Stems elongate, evenly foliate
13:	Stems short, distinctly rosulate
14.	Leaves strongly keeled, limbidium 2 or 3 rows wide, becoming yellowish with age on older leaves, leaves narrowly obovate or spathulate; tubers 180–500 µm
14:	Leaves flat, not keeled, limbidium narrow or wide, 1–6 rows, green, clear or whitish-hyaline with age, leaves broadly obovate, spathulate or ovate; tubers if present 200–1000 µm
15.	Leaves broadly ovate, margins serrulate, limbidium narrow above, 1–2(–3) rows, not whitish-hyaline; gametangia conspicuously enlarged; often polysetose, seta not hooked below capsule, capsule mouth oblique; tubers lacking
15:	Leaves obovate or spathulate, distal margins sharply serrate, limbidium extremely wide, 4–6 rows, often whitish; gametangia not enlarged; rarely polysetose, seta usually hooked below capsule, capsule mouth straight; tubers present

- 17: Limbidium wide, cells in (3–)4–6 rows, often whitish-hyaline, seta usually hooked (>80%) below seta

 Rosulabryum subtomentosum

Rosulabryum albolimbatum (Hampe) J.R.Spence (=Bryum albolimbatum Hampe): a widespread Australian endemic related to the South American *R. andicola* (Hook.) Ochyra, characterized by small to medium-sized plants, leaves that are contorted and twisted but not spirally twisted when dry, serrate distal leaf margins, and filiform leaf axil gemmae (Fig. 19 A-D).

Rosulabryum billardierei (Schwägr.) J.R.Spence (=Bryum billardierei Schwägr.): the common large rosulate Rosulabryum throughout most of temperate Australia except in arid regions. This species is generally easily characterized by its strongly rosulate habit, somewhat contorted/twisted leaves when dry, strong leaf limbidium, and short awn bent sideways. This is a southern temperate-subantarctic species found also in South American and South Africa (Fig. 18 D-G).

Rosulabryum campylothecium (Taylor) J.R.Spence (=Bryum campylothecium Taylor): a distinctive species of drier woodlands in sandy sites, characterized by the strongly rosulate stems with a long awn, ovate concave imbricate leaves, and plants that are pale green-yellow or straw coloured. This species is temperate in distribution in southern portions of Australia, New Zealand and South America (Fig. 19 E-G).

Rosulabryum. capillare (Hedw.) J.R.Spence (=Bryum capillare Hedw.): a subcosmopolitan species of moist shaded sites characterized by leaves spirally twisted around the stem when dry, a long awn, and obovate leaves with a fairly strong limbidium and serrulate distal leaf margins (Fig. 15 F-I).

Rosulabryum epiphyticum J.R.Spence & H.P.Ramsay: a very small rare species typically found associated with epiphytic orchids in northern New South Wales and Queensland in subtropical-tropical forests, although it has also been found on rocks. The small evenly foliate stems, rounded leaves and filiform leaf axil gemmae are diagnostic (Fig. 14 A-D).

Rosulabryum lamingtonicum J.R.Spence & H.P.Ramsay: a species of primarily the subtropics of eastern Queensland and northeastern New South Wales, often at higher elevations, on soil or soil over rock, sometimes on logs. The species is very common in beech forests in Lamington National Park. It is similar to but much smaller than *R. subfasciculatum*, and has a strongly keeled leaf and leaf margin serrations often reaching more than halfway towards the base. Leaf axil filiform gemmae are sometimes present (Fig. 14 H-K).

Rosulabryum leptothrix (Müll. Hal.) J.R.Spence (=Bryum leptothrix Müll. Hal.): a small species of semi-arid woodlands on soil and soil over rock in Queensland, New South Wales and Victoria, with narrow ovate leaves, very long distal laminal cells and spirally twisted leaves lacking a limbidium (Fig. 15 C-E).

Rosulabryum microrhodon (Müll. Hal.) J.R.Spence (=Bryum microrhodon Müll. Hal.): a distinctive species of Tasmania and the South Island of New Zealand, where it occurs at high elevations in subalpine meadows and clearings on boulders. The short recurved awn, imbricate red-green leaves and habitat are diagnostic. Material from northwest Nelson District, South Island, New Zealand is present in CHR (as *R. billardierii*) (Fig. 15 A-B).

Rosulabryum perlimbatum (Card.) J.R.Spence =(Bryum perlimbatum Card.): a robust rosulate species similar to *R. billardierei* but with an extremely wide limbidium (4-8 rows), imparting a whitish colour to the leaf margins. This species is largely subantarctic in distribution, reaching north into southern New Zealand and southern South America. Not yet reported for Australia, it should be looked for in extreme southwestern Tasmania and Macquarie Island along and behind ocean beaches and is thus included in the key (illustrated in Magill 1987).

Rosulabryum queenslandicum J.R.Spence & H.P.Ramsay: a very small species reminiscent of a *Gemmabryum*, but with ovate to obovate leaves, serrulate distal leaf margins and a cylindrical capsule, associated with damp seepage banks, on soil in tropical regions of Queensland and the Northern Territory (Fig. 14 E-G).

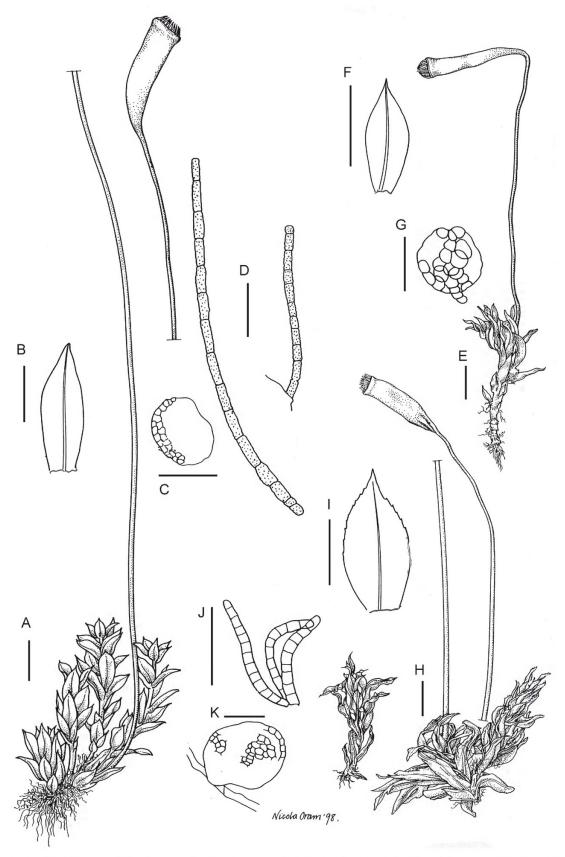


Fig. 14. A-D: *Rosulabryum epiphyticum* A: habit with sporophyte (moist). B: leaf. C: rhizoidal gemma. D: filamentous gemmae (holotype *A.J. Downing* BRI); E-G: *Rosulabryum queenslandicum* E: habit with sporophyte. F: leaf. G: rhizoidal tuber (holotype *J.R. Spence 5167* BRI); H-K: *Rosulabryum lamingtonicum* H: habit with sporophyte. I: leaf, J: filamentous gemmae. K: rhizoidal tuber (*J.R. Spence 5192* NSW). Scale bars 1.0 mm habit; 0.5mm leaves; 100 μm gemmae.

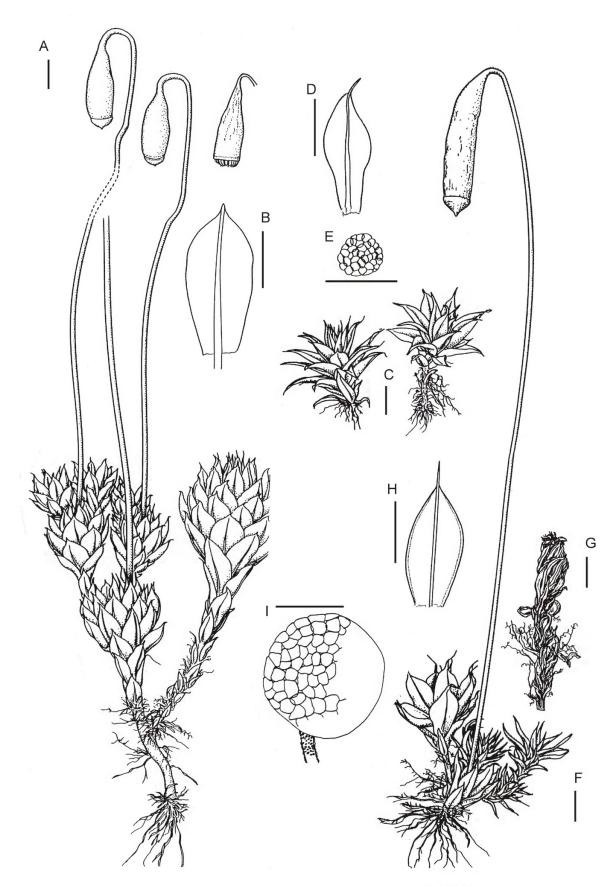


Fig. 15. A-B: *Rosulabryum microrhodon* A: habit. B: leaf (*J.R. Spence 4585* NSW); C-E: *Rosulabryum leptothrix* C: habit. D: leaf E rhizoidal tuber (*I.G. S.one 22764* MEL); F-I: *Rosulabryum capillare* F: habit with sporophyte. G: habit sterile dry. H: leaf. I: rhizoidal tuber (*J.R. Spence 4364* NSW). Scale bars 1.0 mm habit; 0.5mm leaves; 100 μm gemmae.

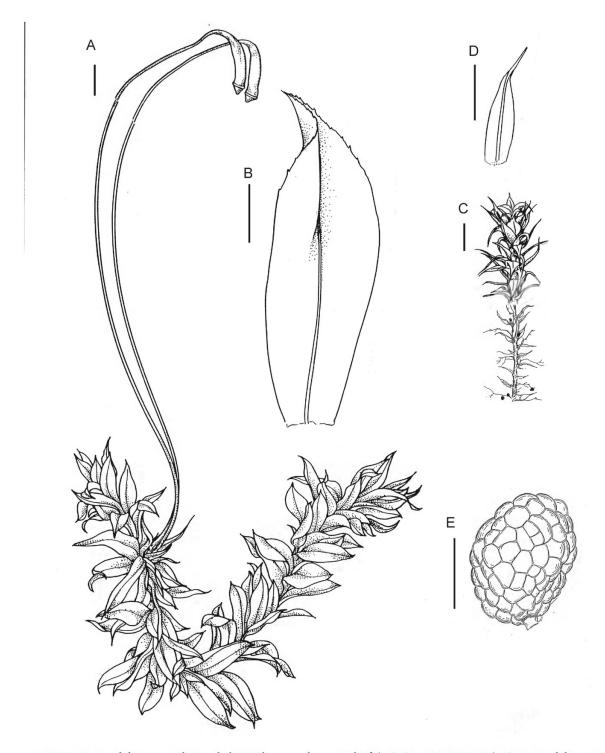


Fig. 16. A-B: *Rosulabryum wightii* A: habit with sporophytes. B: leaf (*I.G. Stone 24277* MEL); C-E: *Rosulabryum rubens* C: habit sterile, D: leaf, E: rhizoidal tuber (*H.P. Ramsay R34a* NSW). Scale bars 1.0 mm habit; 0.5 mm leaves; 100 μm gemmae.

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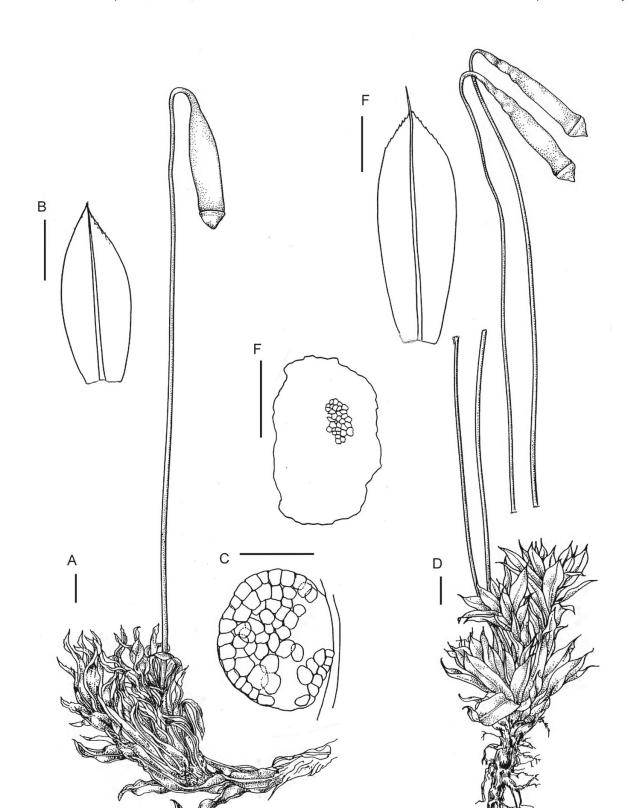


Fig. 17. A-C: Rosulabryum *subfasciculatum* A: habit with sporophyte, B: leaf. C: rhizoidal tuber (*H.P. Ramsay 26/79* NSW); D-F: *Rosulabryum subtomentosum* D: habit with sporophytes. E: leaf. F: rhizoidal tuber (*H.P. Ramsay 25/77* NSW). Scale bars 1.0 mm habit; 0.5 mm leaves; 100 μm gemmae.

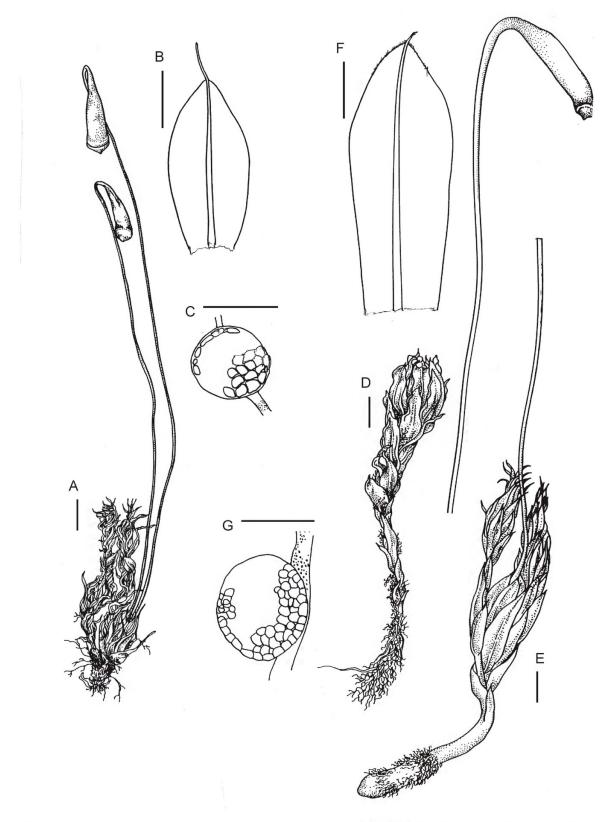


Fig. 18. A-C: Rosulabryum torquescens A: habit with sporophytes. B: leaf. C: rhizoidal tuber (*H.P. Ramsay 45/84* NSW); D-G: Rosulabryum billardierii D: habit male plant (*D.G. Catcheside* 69.266 AD). E: habit with sporophyte. F: leaf. G: rhizoidal tuber (*L.D. Williams 3874* AD). Scale bars 1.0 mm habit; 0.5mm leaves; 100 μm gemmae.

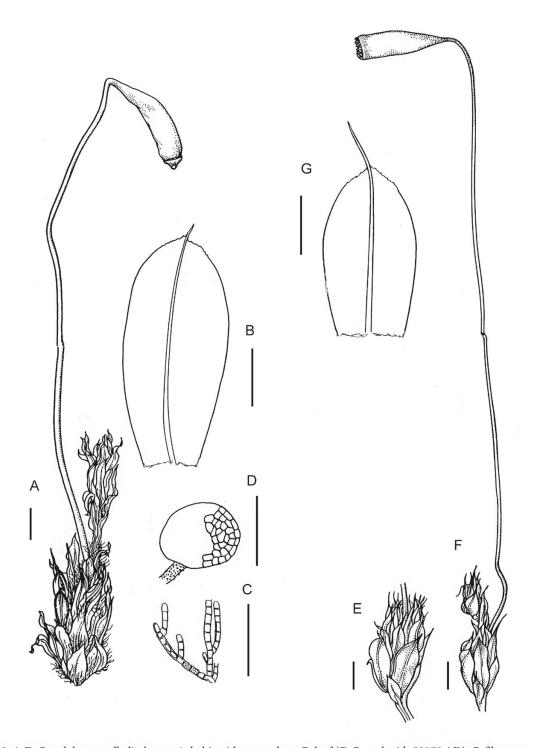


Fig. 19. A-D: *Rosulabryum albolimbatum* A: habit with sporophyte. B: leaf (*D.G.catcheside* 53079 AD). C: filamentous gemma (*W.W. Watts 3463* NSW). D: rhizoidal tuber (*P.S. & D.E.A. Catcheside J17* AD); E-G: *Rosulabryum campylothecium* E: male plant. F: plant with sporophyte. G: leaf (*W.A. Weymouth* NSW). Scale bars 1.0 mm habit; 0.5mm leaves; 100 μm gemmae.

Rosulabryum rubens (Hedw.) J.R.Spence (=Bryum rubens Hedw.): this species is local in Australasia, on disturbed soil and rock, often concrete, and is probably introduced. It has broadly ovate leaves, a weak limbidium, serrulate distal leaf margins, and large red tubers with strongly protuberant cell walls (Fig. 15 C-E).

Rosulabryum subfasciculatum (Hampe) J.R.Spence (=Bryum subfasciculatum Hampe): a distinct fairly large tropical-subtropical species found in rainforests of eastern Australia as well as in New Caledonia. The elongate stems, twisted and strongly keeled leaves with strongly serrate margins are diagnostic. Records from southwestern Australia, Tasmania and South Australia are probably misidentified material of *R. subtomentosum* (Fig. 17 A-C).

Rosulabryum subtomentosum (Hampe) J.R.Spence (=Bryum subtomentosum Hampe): a robust species closely related to *R. billardierei*, but with a much stronger limbidium, often elongate stems, and a seta that is hooked below the capsule. Found mostly across more temperate regions of southern Australia and in New Zealand (Fig. 17 D-F).

Rosulabryum torquescens (Bruch. ex De Not.) J.R.Spence (=Bryum torquescens Bruch. ex De Not.): a distinctive common and widespread species of warm climates in many parts of the world, characterized by irregularly contorted but not spirally twisted leaves, strongly serrate distal leaf margins, a strong limbidium, polyocious sexual condition, and bright red to scarlet rhizoidal tubers. The capsules are also often red at maturity (Fig. 18 A-C).

Rosulabryum wightii (Mitt.) J.R.Spence (=Bryum wightii Mitt.): a robust tropical-subtropical montane species distributed along the Great Dividing Ranges south to northern Victoria. This species is the largest member of the family in Australia, exceeding *Rhodobryum graeffeanum* in size, but it lacks the stolons, has a well-developed stereid band in the costa, and has enlarged gametangial leaves. This species is also found in southern India (Fig. 16 A-B).

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