

BRYACEAE

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Bryaceae Schwägr., in C.L. von Willdenow, *Sp. Pl.* 5(2): 47 (1830).

Type: *Bryum* Hedw.

Dioicous, synoicous or, rarely, autoicous. Plants mostly tufted, usually green or yellowish, sometimes with pink or red colouration. Stems erect, sometimes arising from stoloniferous primary stems (*Rhodobryum*), simple or branched by subperichaetial innovations, sometimes radiculose below with coloured papillose rhizoids. Leaves in many rows, usually small and remote below, larger and crowded above, frequently in comal tufts or rosulate, usually erect to erect-spreading, rarely complanate, sometimes twisted or crisped when dry, lanceolate to ovate, rarely triangular, obovate or spatulate, mostly acute, sometimes long-acuminate or piliferous, frequently bordered, unistratose; border rarely bistratose; margin smooth or denticulate to serrate; costa single, well developed, often excurrent, sometimes with a stereid band in cross-section. Laminal cells smooth, prosenchymatous, typically transparent, relatively large; upper cells rhomboidal-hexagonal to rhomboidal or, less frequently, linear or vermicular, rectangular or sometimes short-rectangular or quadrate towards base. Gemmae frequently produced.

Perichaetia and perigonia mostly terminal; perichaetia rarely on short basal branches; perichaetial leaves not well differentiated. Calyptra cucullate, smooth, usually shed early in capsule development. Setae elongate, usually solitary, rarely multiple, erect or ±curved near tip. Capsules mostly inclined to pendent or nutant, occasionally curved, rarely erect, usually symmetrical, almost always smooth, ovoid, pyriform or oblong-cylindrical, rarely subglobose, with a well-developed neck tapered to the seta and wrinkled when dry; annulus usually present, large and revolute; operculum convex to short-conical, umbonate or apiculate, rarely short-rostrate; stomata numerous, restricted to neck, mostly superficial. Peristome usually present, diplolepidous, double, rarely single; exostome teeth 16, mostly lanceolate and slender-pointed, often bordered, prominently trabeculate, papillose on the outer surface; endostome segments typically 16, alternating with teeth, hyaline or yellow, keeled, arising from a generally well-developed smooth basal membrane; cilia delicate, 1–3. Spores smooth to finely papillose, 8–50 µm diam. $n = 10, 11 (10 + m), 20, 30$ for Australian species, *vide* H.P.Ramsay & J.R.Spence, *J. Hattori Bot. Lab.* 80: 151–170 (1996); see also R.Fritsch, *Bryophyt. Biblioth.* 40: 1–352 (1991).

The cosmopolitan Bryaceae includes 15 genera and up to 600 species and is found in most habitats, from running streams to dry deserts and from the polar regions to tropical latitudes. It is most common in open situations, less so in dense forest. Species usually grow on earth, rock or rotting wood, less commonly as an epiphyte. The family is represented in Australia by eight genera and 54 species.

The family traditionally consisted of four subfamilies: Orthodontoideae, Mielichhoferioideae, Pohlioideae and Bryoideae. This classification placed particular emphasis on the sporophyte, especially the position of the gametangia, capsule orientation, and reduction in the peristome. Recent and current studies are redrawing subfamily relationships more along gametophytic lines (Cox & Hedderson, 2003; Pederson *et al.*, 2003). Peristome reduction appears to have occurred independently several times, and is probably not the best indicator of phylogenetic affinities. Most problems lie in the large polyphyletic genera *Bryum* and *Brachymerium* which

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require a re-assessment of generic and subfamily limits. *Pohlia*, *Mniobryum* and *Schizymenium* apparently share a more recent ancestor with *Mnium* (Mniaceae) and related genera than with genera in the Bryaceae subfam. Bryoideae. *Leptobryum* belongs in the Meesiaceae with other genera having a well-developed, sterile capsule neck. *Orthodontium*, long enigmatic within the Bryaceae (and placed in its own subfamily by Brotherus), is positioned by molecular investigations in the resurrected family Orthodontiaceae (Buck & Goffinet, 2000). The inclusion of *Pleurophascum* in the family (Buck & Goffinet, 2002) was due to misreading the rps4 in the matrix, and it has now been excluded and returned to its own family Pleurophascaceae (Goffinet & Buck, 2004). The Bryaceae *s. str.* thus includes mostly genera with heterogenous laminal areolation and comparatively short cells and typically bordered leaves (subfam. Bryoideae *sensu* Brotherus).

Earlier studies of Australian Bryaceae (Ochi, 1970, 1972, 1973, 1984, 1988) were based entirely on herbarium specimens, while more recent investigations (Spence, 1996, 2005; Spence & Ramsay, 1996, 1999, 2005) have also benefited from extensive field studies by J.R. Spence. This treatment represents the first major revision in more than 100 years. Groups of species are described based primarily on features of the gametophyte, which appears to provide a relatively stable basis for delimitation of genera in the Bryaceae. A new genus *Rosulabryum* was described for the rosulate species (Spence, 1996). New concepts are included here for *Brachymenium*, and *Bryum* has been restricted to those species formerly placed in *Anomobryum* (Spence & Ramsay, 2002). The genus *Ptychostomum* has been resurrected for species previously placed in *Bryum* section *Cladodium* (Spence, 2005). Two new genera, *Ochiobryum* and *Gemmabryum*, have also been described (Spence & Ramsay, 2005).

The Bryaceae are best characterised by the capsule shape: elongate with a well-formed neck that tapers to the seta. The capsules are mostly pyriform and nodding. The perfect double peristome with alternating exostome and endostome is variously reduced in a few genera. It resembles that of the Mniaceae and Aulacomniaceae as well as hypnoid pleurocarps. Chromosome numbers are based on $x = 10$ (perhaps 5) with considerable intra- and interspecific polyploidy and aneuploidy.

In the absence of sporophytes, some members of the Bryaceae are notoriously difficult to identify to species or even genus. However, details of laminal areolation can often place a specimen in the appropriate genus or section reasonably quickly. Most species conform to one of three basic patterns of areolation in older leaves as follows:

- a. **Pohlioid:** with laminal cells elongate and linear to hexagonal and \pm uniform from near the leaf tip to the base, e.g. *Ochiobryum* and *Plagiobryum*.
- b. **Rhodobryoid:** with upper laminal cells rhomboidal to hexagonal, gradually changing to more elongate and rectangular in the lower part of the leaf, e.g. *Brachymenium*, *Ptychostomum*, *Rhodobryum* and *Rosulabryum*.
- c. **Anomobryoid:** in which the upper laminal cells are elongate and linear to hexagonal, with the lower cells abruptly quadrate to short-rectangular and often broader, e.g. *Bryum* and *Gemmabryum*.

In addition to these laminal cell patterns, vegetative propagules such as filamentous gemmae, bulbils, rhizoidal tubers and stem tubers can facilitate identification, especially of sterile collections. It is important to look at *older* leaves when using a key as the current year's growth and sterile innovations often produce atypical leaves.

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Key to Genera

- 1 Laminar areolation homogeneous; cells elongate-rhomboidal to linear (> 6: 1) throughout leaf except at insertion; sporophytes sometimes appearing lateral2
- 1: Laminar areolation heterogeneous; cells in lower third of leaf either longer and regularly rectangular, or abruptly shorter, becoming short-rectangular (2: 1) or quadrate and sometimes wider; sporophytes always appearing terminal3

- 2 Leaves often complanate on stem, with a distinct smooth border of narrow elongate thick-walled cells (1)..... **OCHIOBRYUM**
- 2: Leaves not complanate, unbordered..... **PLAGIOBRYUM**
- 3 Stems gemmiform to julaceous; upper and median laminal cells elongate-rhomboidal to vermicular; cells becoming abruptly quadrate or, rarely, short-rectangular (2: 1) and broader in lower third, with transition often abrupt; leaves never obovate or spatulate with serrulate margins (1:).....4
- 3: Stems rarely gemmiform, never julaceous; upper and median laminal cells rhomboidal, becoming gradually regularly rectangular and longer below, sometimes narrower than cells above; leaves sometimes obovate or spatulate with serrulate margins5
- 4 Plants strongly julaceous, small, less than 10 mm long; leaves < 1 mm long; costa weak, usually ending below apex or percurrent; cross-section of costa with a single layer of large thin-walled ventral cells; upper lamina and apiculus (if present) markedly hyaline; asexual reproduction by axillary leaf bulbils; dioicous (3)..... **BRYUM**
- 4: Plants small to large, with imbricate or shrunken and contorted leaves, or occasionally julaceous with imbricate leaves and often more than 10 mm long; stems bud-like; leaves mostly > 1 mm long; costa strong, in cross-section with 2 layers of large thin-walled dorsal cells; upper lamina and hairpoint coloured, rarely hyaline; asexual reproduction by rhizoidal tubers, stem tubers and axillary leaf bulbils; dioicous or synoicous **GEMMABRYUM**
- 5 Plants epiphytic; leaves reddish, obovate with serrulate margins; capsules erect, long-necked, globose to pyriform (3:)..... **BRACHYMENIUM**
- 5: Plants on decaying wood or other substrata, rarely epiphytic; leaves variously coloured, obovate, spatulate or lanceolate to ovate; margins \pm smooth to serrate; capsules inclined to nutant, cylindrical to ovate, not erect or long-necked6
- 6 Leaves ovate to ovate-lanceolate, usually < 3.5 mm long and with a group of inflated coloured cells at the insertion; margin smooth to weakly serrulate near apex; filiform gemmae absent (5:)..... **PTYCHOSTOMUM**
- 6: Leaves mostly obovate to spatulate, small to large (> 4 mm long); margin usually distinctly serrulate or serrate, rarely almost entire; inflated coloured cells absent; rhizoidal tubers often present; filamentous gemmae sometimes present in leaf axils.....7
- 7 Plants large, with underground stolons; leaves often > 5 mm long, equidistant along stem; costa in cross-section with stereid band absent or greatly reduced; asexual reproductive structures absent (6:) **RHODOBRYUM**
- 7: Plants small to large; stolons absent; leaves mostly < 4 mm long, usually forming distinct terminal rosettes; costa with a well-developed stereid band (cross-section); filiform leaf axil gemmae and rhizoidal tubers often present..... **ROSULABRYUM**