FISSIDENTACEAE

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Fissidentaceae Schimp., *Coroll. Bryol. Eur.* 20 (1856).

Type: *Fissidens* Hedw.

Dioicous or monoicous. Plants usually minute to medium-sized, occasionally large. Stems simple or branched, growing from a 2-sided apical cell except at the earliest stage. Leaves distichous, complanate, with an equitant basal sheath, composed of 2 vaginant laminae inserted ±horizontally and joined above, and a dorsal and an apical blade arranged vertically (like an *Iris* leaf), costate, rarely ecostate. Vaginant laminae equal and sutured above from the costa to the margin (closed), or unequal, either with the minor lamina joining by a shorter suture extending part way to the margin (part open), or lacking a suture and free to the costa (open). Apical (adaxial) lamina small or large; dorsal (abaxial) lamina reaching the leaf base, ceasing above or rarely decurrent. Laminal cells usually small, isodiametric, smooth or papillose, occasionally longer (especially basally), often differentiated at the margins.

Sporophyte terminal or lateral, mostly exserted. Calyptra smooth or rough, cucullate or mitrate. Capsules erect or inclined, symmetrical or asymmetrical. Operculum conical and apiculate to rostrate. Peristome haplolepidous, of 16 teeth, usually forked (rarely entire to rimose), the arms filamentous.

The family has been divided into four, five or more genera, but it is now usual to treat all species in a single genus, *Fissidens*, divided into subgenera and sections. More than 450 species are currently accepted, together having an almost world-wide distribution, except for high Arctic and Antarctic regions, and with the greatest diversity in the tropics.

Seventy-two species and infra-specific taxa of *Fissidens* are reported here from the mainland States and Territories of Australia, ** are apparently endemic, and many are restricted to coastal Queensland. Plants can be erect or ±prostrate, scattered or gregarious, occasionally forming dense turfs or cushions, terrestrial, rupestral, epiphytic or occasionally aquatic. Some species are important colonisers of bare soil, particularly roadside banks.

Fissidentaceae is characterised by the peculiar leaf structure which is essentially isobilateral (not dorsiventral as in most other mosses) and for which there have been several explanations that were fully discussed by Salmon (1899) and, more recently, by Robinson (1970). The most widely accepted interpretation (supported by Salmon) dates back to Robert Brown (1819) who proposed that the vaginant laminae represent the true leaf, with the addition of apical and dorsal appendicular outgrowths. Another theory, initiated by Spruce (1881), suggests that the whole *Fissidens* leaf constitutes the true leaf, the apical and dorsal laminae being the middle lobe of a trilobed leaf turned on its axis. Robinson (1970) elaborated on this by suggesting that a mutation caused a change in the mitotic spindle of the leaf primordium resulting in reorientation of the upper part of the leaf.

Peristome characters were studied by Fleischer (1902) who recognised two types in which the filaments (forks) were, respectively, spirally thickened or papillose. Following SEM observations, Allen (1980) recognised seven distinct types that were only partly correlated with the sections of *Fissidens* subg. *Fissidens*. Bruggeman-Nannenga & Berendsen (1990) investigated many species, including 28 identified as Australian (some by SEM, but most by LM) and distinguished five basic types, as separated in the key below. They also recognised several other types of peristome found in very few species and not characteristic of any section. The *scariosus*-type is correlated with (28–) 32 (–40) exothecial cells around the capsule periphery above mid-capsule; other peristome types usually have more than 40 exothecial cells.

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Key to main peristome types

[adapted from Bruggeman-Nannenga & Berendsen (1990)]

1 Trabeculae distinct throughout the filament; teeth broad and flat; lamellae of the abaxial (outer) side of filaments with rather high oblique riblets ..... ***taxifolius*-type**

1: Trabeculae not distinct in the distal part of the filament; teeth various 2

2 Trabeculae of abaxial side in undivided basal part of tooth higher than lamellae 3

2: Trabeculae and lamellae of abaxial side in undivided part of tooth approximately equal in height 4

3 Trabeculae of abaxial side at bifurcation coarsely papillose, double at the margins, not forked; distal part of filament appearing spirally thickened (actually oblique riblets on abaxial and adaxial surfaces) ..... ***bryoides*-type**

3: Trabeculae of abaxial side at bifurcation smooth and double with forked ends; distal part of filament with irregular squamae or spikes ..... ***zippelianus*-type**

4 Distal part of filament appearing spirally ornamented (actually oblique riblets on abaxial and adaxial surfaces); abaxial surface at the bifurcation with trabeculae, and marginal vertical walls forming a continuous smooth ridge with rounded corners ..... ***scariosus*-type**

4: Distal part of filament with deflexed squamae; abaxial side at the bifurcation lacking marginal vertical walls; lamellae with vertical striae, often papillose ..... ***similiretis*-type**

Stone (1990) and Bruggeman-Nannenga (1990) independently studied the costal structure of *Fissidens* species in relation to classification, and the latter defined the following main types using transverse sections of the costa in the mid-region of vaginant laminae of vegetative leaves:

***Oblongifolius*-type**, with 4 or more large guide cells in a U- or V-shape with 1–5 large central cells in 1–3 rows connecting to the dorsal lamina; an adaxial and 2 lateral bands of stereids or substereids; epidermal cells differentiated or not; junction of vaginant laminae and costa formed of laminal cells (e.g. sect. *Amblyothallia*).

***Taxifolius*-type**, with 2–4 or more superficial adaxial guide cells and 1–8 central connecting cells in 1 or 2 rows or a random mass; 2 lateral stereid or substereid bands; epidermal cells with broader lumina; junction of vaginant laminae and costa formed of guide cells and stereids (e.g. sect. *Crispidium* and subg. *Serridium*).

***Bryoides*-type**, typically with 2 superficial adaxial guide cells and 1 large central connecting cell (always between the 2 guide cells) and occasionally more cells between this and the dorsal lamina; 2 lateral bands of stereids or small cells; epidermis differentiated or not; junction of vaginant laminae and costa formed of laminal cells (e.g. sect. *Aloma*, sect. *Crenularia*, sect. *Fissidens* and sect. *Areofissidens*).

Illustrations in Stone (1990) demonstrate that the arrangement of the large central cells (which are morphologically similar to guide cells) in either 1 or 2 rows (occasionally a random mass) in the simple upper part of the leaf match that of the large connecting cells in the sheathing region.

Throughout this treatment of the family, the dimensions provided are of well-soaked plants: ‘minute’ plants are up to 3 mm tall; ‘small’ plants 3–10 mm; ‘medium-sized’ plants 10–20 mm; and ‘large’ or ‘robust’ plants more than 20 mm tall. Unless stated otherwise, cell details are for those from the mid-dorsal lamina opposite the junction of the vaginant laminae in a mid-stem leaf; exothecial cell details are for those in mid-theca; costal structure refers to mid-vaginant lamina region: in ‘dorsal lamina tapered to the base’, the base refers to the leaf base; where the vaginant laminae are unequal ‘minor’ lamina refers to the smaller of the two.

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FISSIDENS

Fissidens Hedw., *Sp. Musc. Frond.* 152 (1801); from the Latin *fissio* (a split or cleft) and *dens* (a tooth), referring to the divided peristome teeth of most species.

Lecto: *F. bryoides* Hedw.

Fissidens was divided into several subgenera by Müller (1848) and, subsequently, into sections (Müller, 1900). These were adopted by Brotherus (1924) and emended by Norkett, as described by Gangulee (1971). Bruggeman-Nannenga (1978) made some refinements, and Iwatsuki & Inoue (1984) and Iwatsuki (1985) added two subgenera, including *Serridium* which occurs in Australia. *Fissidens* subg. *Serridium* was reevaluated by Bruggeman-Nannenga *et al.* (1994), and sect. *Amblyothallia* was transferred from subg. *Fissidens*. Further proposals by Pursell (1988) concerning the circumscription of subg. *Fissidens* have

also been adopted here. The subgeneric divisions are based primarily on gametophyte characters, but peristome attributes correlate reasonably well.

Five subgenera of *Fissidens* are represented in Australia, the largest (subg. *Fissidens*) having six sections.

Key to Subgenera and Sections

1 Small terrestrial plants with soft flaccid leaves; costate or ecostate; laminal cells lax and large, ±elongate-hexagonal, 20–90 µm long, if 11–25 µm long and firmer-walled then with large flaccid juxtacostal cells proximally in vaginant laminae; peristome always *scariosus*-type.....2

1: Small to large plants with firm leaves occasionally inrolled or crisped when dry; if aquatic may be lax; costate; cells of mid-dorsal lamina mostly isodiametric, usually small, less than 15 µm long, rarely more than 20 µm (if large, then firm to thick-walled); peristome various 3

2 Leaves lacking an apparent costa.....**Subg. Aneuron**

2: Leaves with a distinct costa, failing below the apex or longer ....**Subg. Fissidens sect. Areofissidens *p.p.***

3 Plants aquatic, attached to rock; leaves mostly elimbate; capsules lacking stomata.....4

3: Plants usually terricolous, corticolous or rupestral, often in moist habitats; leaves limbate or elimbate; if aquatic then with a limbidium; stomata usually present 5

4 Plants small to medium-sized, rather rigid; lamina 2 or more cells thick near the costa, unistratose towards the margin, elimbate ..... **Subg. Pachyfissidens**

4: Plants very elongate, floating, rather flaccid; lamina unistratose; leaves elimbate or very weakly semilimbate at the base of vaginant laminae .....**Subg. Octodiceras**

5 Leaves with a limbidium (a border of elongate usually prosenchymatous cells, occasionally inconspicuous) on all laminae, or at least on the vaginant laminae of perichaetial leaves, rarely entirely lacking; peristome either *bryoides*- or *scariosus*-type 6

5: Leaves lacking a limbidium (except rarely intramarginal towards the base of vaginant laminae); marginal cells occasionally otherwise differentiated; peristome various 8

6 Laminal cells smooth; peristome *bryoides*-type; more than 40 exothecial cells in the capsule periphery; shoots sometimes dimorphic and peristome a deviation of *bryoides*-type (*F. taylori* group) .....**Subg. Fissidens sect. Fissidens**

6: Laminal cells uni- or pluripapillose, rarely smooth; peristome *scariosus*-type; 28–40 exothecial cells in the capsule periphery 7

7 Leaves with a limbidium throughout, although sometimes failing near the leaf apex and base; proximal cells of vaginant laminae very large and flaccid; laminal cells unipapillose (*F. biformis*), if smooth *F. zollingeri* ..... **Subg. Fissidens sect. Areofissidens *p.p.***

7: Leaves with a limbidium confined to the vaginant laminae of all leaves or only perichaetial leaves, either complete or partial, if entirely lacking then vaginant laminae often with a marginal strip of oblate cells, and proximal cells not large and flaccid; cells papillose except in *F. autoicus* .... **Subg. Fissidens sect. Semilimbidium *p.p.***

8 Plants robust; hyaline nodules lacking; leaves with a marginal strip of more thick-walled and pellucid laminal cells; margin near apex coarsely dentate; costa with 2 stereid bands; peristome *taxifolius*-type; rare, Tas. ..... **Subg. Serridium sect. Serridium**

8: Plants small or medium-sized; hyaline nodules occasionally present; leaves with marginal cells occasionally differentiated; costa with 2 or 3 stereid bands; peristome various (if *taxifolius*-type then with 3 stereid bands in costa) 9

9 Plants small, either with the vaginant laminae lacking a broad marginal strip of oblate cells and laminal cells multipapillose, *or* with the vaginant lamina having a broad marginal strip of oblate cells and laminal cells uni- or pluripapillose; peristome *scariosus*-type .... **Subg. Fissidens sect. Semilimbidium *p.p.***

9: Plants small to medium-sized, rarely large; vaginant laminae lacking a marginal strip of oblate cells; laminal cells smooth, mammillose or unipapillose; peristome various 10

10 Plants mostly small; leaves not strongly crisped when dry; costa with 2 stereid bands; exothecial cells 28–40 in capsule periphery; peristome *scariosus*-type 11

10: Plants usually medium-sized, occasionally small or large; leaves often strongly enrolled or crisped when dry; costa with 2 or 3 stereid bands; exothecial cells exceeding 40 in capsule periphery; peristome not *scariosus*-type 13

11 Laminal cells smooth, lax, collapsing when dry, very unequal; vaginant laminae in proximal part with very large juxtacostal cells and narrow elongate intramarginal cells (*F. inaequiretis*) ..... **Subg. Fissidens sect. Areofissidens *p.p.***

11: Laminal cells smooth, mammillose or unipapillose, firm to very thick-walled; vaginant laminae in proximal part usually lacking large flaccid cells; elongate intramarginal cells occasionally present..... 12

12 Leaf margin entire or weakly crenulate (occasionally intermittently semi-bistratose); cells smooth, plane or slightly convex, occasionally with an internal hyaline spot; axillary nodules not prominent ... . **Subg. Fissidens sect. Aloma**

12: Leaf margin distinctly serrate or denticulate, usually with toothing larger in vaginant laminae; cells unipapillose or highly mammillose, occasionally smooth, lacking a hyaline spot; axillary nodules sometimes differentiated ..... **Subg. Fissidens sect. Crenularia**

13 Prominent glandular hyaline nodules present in leaf axils [dissect off leaves or clear plant well to observe]; costa with 2 stereid bands; peristome *zippelianus*-type ..... **Subg. Fissidens sect. Crispidium**

13: Prominent hyaline nodules lacking, but green axillary buds sometimes present; costa with 3 stereid bands; peristome *similiretis*-, *fasciculatus*- or partly *taxifolius*-type ..... **Subg. Serridium sect. Amblyothallia**