# ENTOSTHODON

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*Entosthodon* Schwägr., *Sp. Musc. Frond.* Suppl. 2(1): 44 (1823); from the Greek *entos* (within) and *odon* (a tooth), in reference to the position of the peristome teeth within the capsule.

T: *E. templetonii* (Sm.) Schwägr.

Autoicous, rarely paroicous or polygamous (non-Australian species). Plants medium-sized, gregarious, yellowish, brownish or bright green. Stems reddish brown, rarely pale, usually branched once by subperigonial innovation, rarely branched by forking or repeated innovation, more than 2 mm long; in cross-section with a central strand, a parencyhmatous medulla, a cortex of 1–3 layers of thick-walled cells, and a ±well developed hyalodermis, beset with smooth rhizoids. Leaves larger and more crowded near stem apices, erect-spreading, rarely erect and imbricate, concave or plane, oblong-obovate, spathulate or ovate-lanceolate; apex acuminate, acute or obtuse, often cuspidate; costa variable; margin serrate by projecting cells or entire. Upper laminal cells thin-walled, oblong-hexagonal or oblong, longer and laxer below; a few cells often somewhat inflated at the alar angles; marginal cells differentiated or not, often projecting. Axillary filaments present.

Perigonia usually single, terminating a shoot from which the perichaetial shoot arises by innovation. Calyptra cucullate, rostrate or mitrate. Seta straight, weakly hygroscopic, smooth in Australian species. Capsules erect or inclined, usually symmetrical, obovoid, broadly pyriform to narrowly cylindrical-pyriform, rarely ovoid, reddish brown at maturity, usually wrinkled at the neck and constricted below the mouth when dry, with a neck c. 1/4–1/2 the length of the capsule; mouth 2/3 to ±equal the diam. of the capsule, rarely smaller, transverse or oblique; exothecial cells usually oblong to elongate, 2–8:1, with thick cuneate or rarely non-cuneate walls, not forming vertical bands, c. 6–12 rows oblate at the mouth; operculum plano-convex or conical; annulus absent or rudimentary; stomata immersed or rarely superficial. Peristome double, single or absent, persistent or fugacious; exostome teeth variably developed, straight or sigmoid, free at apices, not or weakly appendiculate, papillose-striolate to strongly striate; endostome segments variably developed, papillose, coherent at the base. Spores subreniform, variably ornamented.

This is a cosmopolitan genus of c. 60–70 species. The generic concept presented here includes subgenus *Plagiodus* which, according to Brotherus (1924), formed part of *Funaria*. Those species referred to subg. *Plagiodus* lack the lattice disc joining their peristome teeth apices, a revoluble annulus, and the distinctive ranks of thick- and thin-walled exothecial cells which are features of *Funaria sens. str*. In global terms, the boundary between subg. *Plagiodus* and *Entosthodon sens. str*. is obscure, but it poses few problems in an Australian context. Detailed cladistic analysis may necessitate the recognition of subg. *Plagiodus* at the generic level.

## References

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**1** Marginal leaf cells longer than adjacent laminal cells, sometimes visible only in (upper) part of leaf; leaves toothed at least in upper 1/3; capsules markedly asymmetrical, inclined to horizontal; peristome teeth sigmoid in outline; spores coarsely baculate-insulate (subg. *Plagiodus*) ..... 2

**1:** Marginal leaf cells not differentiated from adjacent laminal cells; leaves entire or toothed; capsules symmetrical or weakly asymmetrical , erect or nearly so; peristome teeth straight or weakly curved in outline, or absent; spores variously ornamented but not baculate-insulate (subg. *Entosthodon*) ..... 3

**2** Leaf apices acute and apiculate; apical cells of upper leaves 30–90 µm long; capsules obovoid, 1.5–2.0 (–2.3) mm long, with a weakly defined neck less than 1/3 the capsule length; common..... **5. E. radians**

**2:** Leaf apices acuminate; apical cells of upper leaves 125–180 µm long; capsules oblong-obovoid, (2.3–) 2.5–3.2 mm long, with a well-defined neck nearly half the capsule length; rare ..... **3. E. muehlenbergii**

**3** Leaves widest in the lower 1/3, ovate-lanceolate, erect and appressed to the stem when dry or moist; setae twisted to the left throughout; capsules less than 1.5 mm long, gymnostomous ..... **4. E. productus**

**3:** Leaves widest at or above the middle, ±oblong-obovate, erect-spreading at least when moist; setae twisted to the right, at least in the upper part; capsules more than 1.5 mm long (except in small forms of *E. subnudus* var. *gracilis)*, peristomate or gymnostomous ..... 4

**4** Rhizoids cerise; exothecial cells in cross-section with anticlinal walls not or very weakly cuneate; leaves lingulate, entire, ±plane or weakly concave, with broadly acute or obtuse apices; capsules peristomate..... **2. E. laxus**

**4:** Rhizoids reddish brown; exothecial cells in cross-section with anticlinal walls distinctly cuneate (usually apparent without sectioning); leaves ±obovate and acuminate (except some forms of *E. subnudus* var. *gracilis*), serrate or entire; capsules gymnostomous or peristomate..... 5

**5** Leaf margins bluntly serrate ..... 6

**5:** Leaf margins entire (rarely ±crenulate) ..... 7

**6** Capsules obovoid-cylindrical; exostome well developed; endostome rudimentary to greater than half the height of the exostome; exothecial cells obscure in surface view (due to strongly cuneate cell walls); cells of the upper lamina 60–75 µm long; costa less than 45 µm wide in lower 1/3 of leaf; widespread throughout Australia ..... **7. E. subnudus**

**6:** Capsules broadly pyriform, gymnostomous; exothecial cells with distinct lumina, cells of the upper lamina 30–50 µm wide; costa c. 60–65 µm wide in lower 1/3 of the leaf; NE N.S.W. and SE Qld ..... **6. E. smithurstii**

**7** Capsules (2.0–) 3.0–4.5 mm long, oblong-cylindrical; neck gradually tapered, c. half the capsule length; gymnostomous; spores usually finely verrucate and with a trilete scar .....**1. E. apophysatus**

**7:** Capsules 1.8–2.5 mm long, obovate or rarely oblong-cylindrical; neck markedly less than half the capsule length; peristomate; spores lacking a trilete scar .....8

**8** Capsules obovate; setae 9–22 mm long..... **7b. E. subnudus** var. **gracilis** (incl. "*cuspidata* form")

**8:** Capsules oblong-cylindrical; setae usually less than 7 mm long .....9

**9** Spores coarsely gemmate (under high magnification, dry); exostome teeth variably developed and irregular in outline; operculum conical.....**7c. E. subnudus** var. **phymatodeus**

**9:** Spores finely verrucate (under high mag., dry); exostome teeth well developed and regular in outline; operculum plano-convex..... **7a. E. subnudus** var. **subnudus**

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

*Gymnostomum apophysatum* Taylor, *London J. Bot.* 5: 43 (1846); *Physcomitrium apophysatum* (Taylor) Wilson, *in* J.D.Hooker, *Fl. Nov.-Zel.* 2: 91 (1854); *Funaria apophysata* (Taylor) Broth., *in* H.G.A.Engler & K.A.E.Prantl, *Nat. Pflanzenfam.* 1(3): 523 (1903). T: Swan R., W.A., 1843, *J.Drummond s.n.*; lecto: FH-Taylor, *fide* A.J.Fife & R.D.Seppelt (2001); isolecto: BM-Wilson, FH-Taylor, H-BR, NY-Mitten.

*Entosthodon clavaeformis* Müll.Hal. & Hampe, *Linnaea* 26: 490 (1855); *Amphoritheca clavaeformis* (Müll.Hal. & Hampe) Hampe, *Fragm.* 11 (Suppl.): 46 (1881); *Funaria clavaeformis* (Müll.Hal. & Hampe) Broth., *in* H.G.A.Engler & K.A.E.Prantl, *Nat. Pflanzenfam.* 1(3): 525 (1903). T: Torrens R., S.A., *F.Mueller s.n.*; lecto: BM-Hampe, *fide* A.J.Fife & R.D.Seppelt (2001); isolecto: BM-Schimper.

*Funaria aristata* Broth., *Öfvers. Förh. Finska Vetensk.-Soc.* 35: 46 (1893); *Entosthodon aristatus* (Broth.) Paris, *Index Bryol.* 422 (1896). T: Lilyvale, N.S.W., 12 Sept. 1891, *T.Whitelegge 407*; holo: H-BR.

*Funaria taylorii* Kindb., *Enum. Bryin. Exot.* 60 (1888), *nom. nud.*

Plants yellowish green. Stems reddish brown, 2–5 (–7) mm tall, branching once by subperigonial innovation, with reddish brown rhizoids. Leaves erect to erect-spreading, broadly obovate to oblong-spathulate, 1.5–3.5 mm long, 0.75–0.90 wide mm (including arista), concave, tapered in upper 1/3 to a yellowish acuminate arista; costa c. 30–50 µm wide near the base, ending a few to several cells below the base of the arista or fusing with it and appearing long-excurrent; margins entire. Upper laminal cells oblong-hexagonal, (24–) 30–60 × 17–30 µm, longer and more oblong below; marginal cells not differentiated; apical cells (150–) 180–300 (–400) µm; alar cells 2–4, moderately inflated.

Calyptra cucullate, rostrate. Setae 2–4 mm long, twisted weakly to the right, pale reddish brown, weakly hygroscopic. Capsules usually erect, rarely inclined, symmetrical, oblong-cylindrical, constricted below the mouth when dry, (2.0–) 3.0–4.5 mm long, with a well-differentiated tapered neck c. half the capsule length, reddish brown; mouth from 2/3 to equal the diameter of the capsule, transverse; exothecial cells c. 5–8:1, 50–90 µm long, with thick strongly cuneate cell walls, c. 6–8 rows, quadrate to oblate and strongly pigmented at the mouth; operculum plano-convex. Peristome absent. Spores (28–) 33–43 µm, ±smooth, with a trilete scar, often persisting in tetrads, when dry usually appearing strongly wrinkled following their collapse.

Known from all States and Territories, especially in rather dry habitats. Also in southern South America and New Zealand.

W.A.: Yallingup Natl Park, *D.H.Norris 25815*. S.A.: Alligator Gorge, Flinders Ra., *D.G.Catcheside 78.351*. N.S.W.: Cowra, *H.Streimann 4899*. Tas.: Brighton, *W.A.Weymouth 3018*.

The long, oblong-cylindrical gymnostomous capsules, short setae and markedly aristate comal leaves set this species apart from all other Australian *Entosthodon*. The leaves are similar in form to those of *E. muehlenbergii*, but the latter has toothed leaf margins and asymmetrical peristomate capsules. *Entosthodon apophysatus* differs from *E. subnudus* var. *subnudus* in leaf form and the length of the apical cell, seta and capsule length, peristome development and spore ornamentation.

*Entosthodon clavaeformis* Müll.Hal. & Hampe, *Funaria aristata* Broth. (N.S.W.) and the South American *E. clavellatus* Mitt. (Uruguay) are considered to be synonymous. Although

Sim (1926: 294) compared the South African *E. rottleri* (Schwägr.) Müll.Hal. to *E. apophysatus*, the African species differs in a number of ways, including shorter capsules with less defined necks, longer setae and clearly excurrent costae.

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

*Gymnostomum (Physcomitrium) laxum* Hook.f. & Wilson, *Fl. Antarct.* 2: 399 (1847); *Physcomitrium laxum* (Hook.f. & Wilson) Müll.Hal., *Syn. Musc. Frond.* 2: 546 (1851); *Funaria laxa* (Hook.f. & Wilson) Broth., *in* Drygalski, *Deutsch Südpolar Exped.* 8: 88 (1906). T: Kerguelen: *J.D.Hooker 744*, Antarctic Expedition 1839–43 ("*Wilson no. 257*"); lecto: BM-Hooker; isolecto: BM-Hooker, NY-Mitten.

*Funaria (Entosthodon) subattenuata* Broth., *Öfvers. Förh. Finska Vetensk.-Soc.* 40: 173 (1898). T: "swamp at top of Arthur's Pass, Canterbury", New Zealand, Jan. 1888, *T.W.N. Beckett 93*; holo: H-BR; iso: CHR-Beckett, CHR-Allison .

*Tayloria maidenii* Broth., *Proc. Linn. Soc. New South Wales* 41: 583 (1916). T: Merritt's Camp, Mt Kosciuszko, N.S.W., Jan. 1899, *W.Forsyth 184*; holo: H-BR; iso: N.S.W.

Plants yellowish or bright green, gregarious. Stems pale brown to reddish brown, to 15 mm high, branching once by subperigonial innovations, or forking beneath the soil surface and producing subperigonial innovations above with cerise rhizoids. Leaves erect-spreading, lingulate, 1.5–3.0 (–4.0) × 0.6–1.0 mm, plane to weakly concave, tapered in upper to an acute (often broadly so) apex; costa rather thin and weak, c. 30–40 (–50) µm wide near base, failing c. 5–10 cells (rarely more) below leaf apex; margin entire or weakly crenulate above; cells of upper lamina oblong-hexagonal, c. 70–100 (–130) × 24–30 (–45) µm, longer below and more oblong but not thinner-walled; marginal cells not differentiated (rarely weakly differentiated above); apical cell 25–55 (–100) µm long; alar cells not differentiated or slightly more pigmented than adjacent cells. Axillary filaments present

Calyptra mitrate, or splitting on one side to become cucullate, rostrate. Setae (5–) 10–20 (–23) mm long, twisted to the right above, pale brown, weakly hygroscopic. Capsules erect, symmetrical, oblong-obovoid or oblong-pyriform, scarcely constricted below the mouth when dry, 1.5–2.5 (–3.0) mm long, with a well-differentiated neck 1/3–1/2 the capsule length, reddish brown at maturity; mouth c. 3/4 the diameter of the capsule; exothecial cells with distinct lumina, c. 2–3:1, mostly 30–40 µm long, in cross section with anticlinal walls not or very weakly cuneate, c. 6–8 rows isodiametric to oblate and darker at capsule mouth; operculum mammillate or strongly convex. Peristome double; exostome teeth straight, bright red, to 300 × 50–75 µm, acute or rounded at apices, baculate-papillose, not or weakly striate, weakly nodulose, scarcely trabeculate, often fugacious; endostome rudimentary and fugacious, segments irregular and hyaline, to 120 µm, gemmate to low-insulate. Spores 25–35 µm, gemmate to low-insulate.

Known from subalpine and alpine N.S.W., Vic. and Tas. Occurs on waterlogged, shaded humic soil (usually with sand or gravel fragments) at the margins of streams; also on wet outcrops or in seepages; grows over various bedrocks, but rare in calcareous areas. Also in Macquarie Island, New Zealand, Kerguelen Island, Marion Island, the Crozet Islands, and in Andean Chile, Bolivia, Peru, Ecuador and Venezuela.

N.S.W.: Crackenback, Thredbo, *I.G.Stone 9738*. Vic.: Australian Alps, *F.Mueller 132*. Tas.: Cummings Head, Western Mtns, *Archer 28*.

The broadly acute or obtuse lingulate leaves of *E. laxus*, the mammillate, conical or strongly convex opercula and oblong-obovoid capsules facilitate identification, as does its subalpine to alpine distribution. Microscopically, the short exothecial cells with distinct lumina and non-cuneate anticlinal cell walls are very distinctive. The unusual sporophytic features cited above isolate *E. laxus* within subg. *Entosthodon*.

Although there is potential for confusion with *E. subnudus* var. *gracilis*, the latter is a much smaller lowland plant with plano-convex opercula. A review of the ecology, world distribution and synonymy of *E. laxus* was provided by Fife (1986).

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

*Funaria muehlenbergii* Turner, *Ann. Bot. (London)* 2: 198 (1805). T: Copgrove, Yorkshire, Great Britain, *Rev. J.Dalton*; BM-Turner.

*Funaria glabra* Taylor, *London J. Bot.* 5: 57. (1846), *nom. illeg., non* Sainsbury. T: Swan R., W.A., 1843, *J.Drummond s.n.* holo: FH-Taylor; iso: H-Lindberg.

*Funaria tasmanica* Müll.Hal. & Hampe, *Linnaea* 26: 490 (1855). T: Tas., *F.Mueller 6*; BM-Hampe.

Plants yellowish green. Stems reddish brown, c. 2–4 mm tall, branching once by subperigonial innovation or unbranched. Leaves erect-spreading, oblong-obovate, 2.0–2.9 mm long, 0.7–1.0 mm wide, concave, tapered in the upper 1/3 to an acuminate apex; costa c. 45–60 µm wide near the base, failing c. 8 cells and c. 0.56–0.67 mm below the apex; margins bluntly toothed in upper 1/3 by projecting cells. Upper laminal cells oblong-hexagonal, (45–) 60–90 × c. 30 µm, longer (to c. 120 µm) and more oblong below; marginal cells scarcely differentiated; apical cell 125–180 µm long; alar cells not or weakly differentiated.

Calyptra cucullate, rostrate. Setae c. 5–7 mm long, twisted weakly to the right, pale reddish brown, weakly hygroscopic. Capsules weakly inclined, asymmetrical, oblong-obovoid and curved, (2.3–) 2.5–3.2 mm long, constricted below the mouth when dry, with a well-defined strongly wrinkled neck c. half the capsule length; mouth equal to the diameter of the capsule, oblique; exothecial cells indistinct, c. 60 µm, in cross section with strongly cuneate walls; operculum plano-convex. Peristome double; exostome teeth sigmoid, c. 300–330 × 75–90 µm, acute at the apex, vertically striate ±throughout, coarsely baculate near the apices, appendiculae weak in upper half, trabeculae well developed; endostome well developed, segments at wide as teeth, c. 3/4 the height of the teeth, striate-baculate below, baculate above. Spores 29–32 µm diam., baculate-insulate.

Occurs in W.A., Qld, N.S.W., Vic. and Tas. Also in North America, Europe, the Middle East, Africa and New Zealand.

Qld: Tarraman, *J.M.Mitchell A13*. N.S.W.: Abercrombie Caves, *H.Streimann 45096*. Vic.: 2 km SW of Omeo, *H.Streimann 39821*. Tas.: Cataract [Gorge], Launceston, 6 Sept. 1855, *Archer*.

The South American *E. laevis* (Mitt.) Fife, while closely allied, appears to be distinct by virtue of its very long, yellow leaf acumen and more finely ornamented spores (Fife, 1987).

**4. Entosthodon productus** Mitt., *in* J.D.Hooker & W.M.Wilson, *Fl. Tasman.* 2: 197 (1860)

*Funaria producta* (Mitt.) Broth., *in* H.G.A.Engler & K.A.E.Prantl, *Nat. Pflanzenfam.* 1(3): 522 (1903). T: behind Cummings Head, Western Mtns, Tas., *Archer*; holo: NY-Mitten; iso: BM-Hooker.

*Entosthodon minuticaulis* Müll.Hal. ex Geh., *Rev. Bryol.* 24: 72 (1897); *Funaria minuticaulis* (Müll.Hal. ex Geh.) Watts & Whitel., *Proc. Linn. Soc. New South Wales, Suppl.* 30: 115 (1906). T: Moyston, Vic., *D.Sullivan*; H-BR.

*Funaria perpusilla* Broth., *Proc. Linn. Soc. New South Wales* 41: 583 (1916). T: Heyington, Vic., *W.W.Watts 196*; holo: H-BR.

Plants yellowish green. Stems reddish brown, to 4 mm long, branching once by subperigonial innovation or with multiple perigonia, with reddish brown rhizoids; hyalodermis faint (usually only a thin outer wall of an otherwise thick-walled epidermal cell). Leaves erect, ovate-lanceolate, 0.7–1.7 (–2.2) mm long, 0.2–0.4 (–0.6) mm wide, concave to subtubulose, gradually or abruptly tapered to a subulate apex; costa 25–37 µm wide near the base, disappearing in the acumen; margins entire. Upper laminal cells oblong, 25–70 × 12–15 µm, somewhat longer (to c. 105 µm), laxer and more hexagonal below; marginal cells not differentiated; apical cells 30–48 µm long; alar cells not differentiated.

Perigonia single or multiple. Calyptra cucullate, long-rostrate. Setae 2.5–9.0 mm long, twisted to the left throughout, reddish brown, weakly hygroscopic. Capsules erect, symmetrical, oblong-pyriform, not or very weakly constricted below the mouth when dry, 1.0–1.3 mm long, 0.5–0.7 mm wide, with a gradually tapered irregularly wrinkled neck c. half the capsule length, reddish brown at maturity; mouth c. 3/4 the diameter of the capsule (at dehiscence), transverse, gymnostomous; exothecial cells c. 30–60 µm long, 3–6:1, with

thick cuneate anticlinal walls, 6–8 rows oblate and more pigmented at the mouth; operculum plano-convex, 325–450 µm diam. Peristome absent. Spores 30–36 µm, verrucate-bullate and usually irregularly wrinkled, usually with an obvious trilete scar.

Occurs on damp, often shaded soil in scrub or grassland in W.A., S.A., Vic. and Tas.; also in New Zealand.

W.A.: Lesmurdie, *D.G.Catcheside 73.202*. S.A.: Bellevue Heights, *D.G.Catcheside 79.134*. Vic.: Nigretta Falls, Hamilton, *D.G.Catcheside 77.143*. Tas.: Blackmans Bay, *W.A.Weymouth 247*.

*Entosthodon productus* is closely allied to *E. jamesonii* (Taylor) Mitt. of the Andes, Central America and Malesia (Fife, 1987), and it could be treated as a subspecies of the latter. However, because of its consistently smaller stature (leaf dimensions, seta length and capsule size) and geographical distribution, *E. productus* is retained here.

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

*Weissia radians* Hedw., *Sp. Musc. Frond*. 73 (1801); *Bryum radians* (Hedw.) P.Beauv., *Prodr*. 49. (1805); *Eremodon radians* (Hedw.) Brid., *Bryol. Univ*. 1: 236 (1826); *Funaria radians* (Hedw.) Müll.Hal., *Linnaea* 18: 692 (1845).

*Funaria acaulis* Hampe, *Linnaea* 30: 624 (1860); *Entosthodon (Plagiodus) acaulis* (Hampe) Fife, *J. Hattori Bot. Lab*. 58: 192 (1985). T: Gippsland, Vic., 1855, *F.Mueller 119*; holo: BM-Hampe; iso: BM-Hooker, H-Lindberg.

*Funaria crispula* Hook. f. & Wilson, *Fl. Tasman.* 198 (1859). T: *s. loc.*, New Zealand, 1769–70, *J.Banks*; holo: BM; isotypes: BM-Hooker, H-Lindberg.

[*Funaria glabra auct. non* Taylor: G.O.K.Sainsbury, 1955]

Plants yellowish or brownish green. Stems reddish brown, to 25 mm high, with reddish brown rhizoids. Leaves erect-spreading, broadly obovate to spathulate, 1.5–3.5 (–4.0) mm long, 1.0–1.8 mm wide, ±concave, tapered in the upper 1/3 to a broadly acute cuspidate apex; costa pale brown or reddish brown, c. 45 µm wide near the base, ending (5–) 7–10 (or more) cells below the apex; margin weakly toothed above. Upper laminal cells oblong-hexagonal, 45–90 (–105) × 30–36 µm, longer and more oblong below; marginal cells longer and firmer-walled, forming a weak border of 1–3 rows, often yellowish; apical cell 30–90 µm long.

Calyptra cucullate, rostrate. Setae 5–12 (–14) mm long, twisted to the right throughout, pale brown or reddish brown, weakly hygroscopic. Capsules inclined to nearly horizontal, asymmetrical, obovoid, constricted below the mouth when dry, 1.5–2.0 (–2.3) mm, with a weakly defined neck c. 1/3 (–1/2) of the capsule length, reddish brown (but often dehiscent when lower portion of capsule still green), strongly wrinkled below when dry; mouth equal the diameter of the capsule, ±oblique; exothecial cells with indistinct lumina, c. 2–4:1, in cross section with strongly cuneate anticlinal walls, c. 6 rows isodiametric to oblate at mouth; operculum plano-convex. Peristome double; exostome teeth sigmoid, (225–) 250–300 (–475) × (60–) 75–90 µm, acute at the apices, vertically striate ±throughout, coarsely baculate near the apices, with appendiculae weak in upper half or lacking, trabeculae well-developed; endostome variable, segments c. 90 µm wide, acute, c. 3/4 the height of teeth, or irregular and shorter, striate-baculate below, baculate above. Spores (24–) 27–33 (–35) µm diam., insulate-baculate.

Known from all States and Territories, this species occupies a variety of seemingly dissimilar habitats. Throughout its range it is most common on steep clay and/or silt banks at low elevations. Also in New Zealand, New Caledonia and Andean Equador and Venezuela.

Qld: Ashgrove, *C.Wild*. N.S.W.: Ballina, *W.W.Watts*; Kittys Ck, Lane Cove R., *W.W.Watts*. Tas.: Myrtle Gully, Mt Wellington, 22 Nov. 1978, *A.V.Ratkowsky*.

The shorter capsule and shorter leaf apical cell preclude confusion with the much rarer *E. muehlenbergii*. Endostome development varies within populations and even within single capsules.

**6. Entosthodon smithhurstii** (Broth. & Geh.) Paris, *Ind. Bryol.* 506 (1896)

*Funaria smithhurstii* Broth. & Geh., *Öfvers. Förh. Finska Vetensk.-Soc.* 37: 164 (1895). T: Bundaberg, Qld, June or July 1885, *W.H.Smithhurst 215* ("com. sub no. 247 Whitelegge, 1885"); holo: H-BR.

*Funaria squarrifolia* Broth., *Öfvers. Förh. Finska Vetensk.-Soc.* 40: 174 (1898); *Entosthodon squarrifolia* (Broth.) Paris, *Ind. Bryol.* Suppl. 142 (1900). T: German Ck, Richmond R., N.S.W., 5 May 1896, *W.W.Watts 320*; lecto: H-BR, *fide* A.J.Fife & R.D.Seppelt (2001).

Plants yellowish green, gregarious. Stems pale brown, to 7 (–12) mm high, branching once by subperigonial innovation, with brown to reddish brown rhizoids, in cross-section with a hyalodermis and a central strand. Leaves erect-spreading (rarely widely spreading), obovate to spathulate, 2.0–3.0 (–3.5) mm long, (1.0–) 1.5–2.0 mm wide, weakly concave, tapered in the upper 1/3 to a broadly acute cuspidate apex; costa c. 60–65 µm wide near the base of perichaetial leaves, failing a few to 10 cells below the apex; margins weakly to strongly obtusely toothed in upper 1/3–1/2 by projecting cells. Upper laminal cells short-hexagonal, c. 30–50 × 22–30 µm, longer and more oblong below but not thinner walled; marginal cells not differentiated, projecting; apical cell 60–75 µm long; alar cells not differentiated. Axillary filaments present.

Calyptra cucullate, long-rostrate. Setae 2.5–4.5 (–5.0) mm long, twisted to the right throughout (when dry), pale brown, scarcely hygroscopic. Capsules erect, symmetrical, broadly pyriform, not or scarcely constricted below the mouth when dry, 1.5–2.0 (–2.5) mm long, c. 1 mm wide, with a well-differentiated gradually tapered neck 1/3–1/2 the total capsule length, pale reddish brown at maturity; mouth 3/4 to equal the diam. of the capsule; exothecial cells with distinct lumina, variable in outline, 30–60 µm long, in cross-section with anticlinal walls distinctly cuneate, c. 8 rows oblate and more pigmented at capsule mouth; operculum plano-convex. Peristome absent. Spores (27–) 33–39 (–40) µm diam., smooth or very finely papillose (visible only under oil or weakly visible under hi-dri), often with a trilete scar, thin walled and ±wrinkled.

Endemic to eastern Qld and north-eastern N.S.W.

Qld: Indooroopilly, *F.Whitteron 145*; Cania Gorge, near Monto, *I.G.Stone 20995*. N.S.W.: Alstonville, near Ballina, *W.W.Watts 5050*; Dungog, *I.G.Stone 11892*.

*Entosthodon smithhurstii* is characterised by the distinctly pyriform capsule virtually identical to that of *Physcomitrium pyriforme*. The exothecial cells are rather short for the genus, but sectioning reveals strongly cuneate anticlinal walls (sometimes this is apparent without sectioning). There is no peristome development, and the spores are thin-walled and nearly smooth, not persisting in tetrads but often retaining tetrad scars. The wrinkled appearance of the spores seems to be a constant feature of herbarium material.

Gametophytically, *E. smithhurstii* is distinctive by having obovate to spathulate leaves with cells in the upper lamina that are unusually short and compact. The margins lack any suggestion of a border (thus providing a means of separating it from *Physcomitrium*), and it is bluntly and finely serrate due to projecting cells. The leaf apex is shortly cuspidate, and the costa ends several to few cells below.

*Entosthodon smithhurstii* is most likely to be confused with *Physcomitrium pyriforme*, and it is under that name that additional material is most likely to be filed in herbaria. It may be differentiated from the latter by its planar operculum, cucullate calyptra, cuneate exothecial cell walls, spore ornamentation, and the unbordered, bluntly serrate upper leaf margins.

Of the three syntypes of *Funaria squarrifolia* cited by Brotherus in his protologue, *Watts 320* is the most suitable lectotype as it includes the largest number of fully mature capsules as well as being ample and including sporophytes at several stages of maturity. All three syntypes are from the vicinity of Ballina, N.S.W., and all are unquestionably referable to *E. smithhurstii*. The statement in *Index Muscorum* that *F. squarrifolia* (cited as *Entosthodon squarrifolius* (Broth.) Paris) is synonymous with *F. subattenuata* Broth. is incorrect.

The Paraguayan *E. balansae* Besch. [*Mém. Soc. Nat. Sci. Nat. Cherbourg* 21: 263, 1877. syn: Paraguay: *Balansa* 1227-1226, NY-Mitten] appears to be very similar to *E. smithhurstii*. We have been unable to satisfactorily distinguish *E. balansae* from *E. smithhurstii* and conclude

that they are probably referable to a single species. Although *E. balansae* Besch. is the earlier name, we have refrained from making this synonymy pending further study of both taxa.

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

*Funaria subnuda* Taylor, *London J. Bot*. 5: 57 (1846). T: Swan R., W.A., 1843, *J.Drummond s.n.*; holo: FH-Taylor; iso: BM-Wilson.

Plants yellowish or brownish green. Stems reddish brown, 2–5 mm high, branching once by subperigonial innovation, with reddish brown rhizoids. Leaves erect-spreading, obovate to oblong-obovate, occasionally widest below the middle and ±oblong-ovate, 1.5–2.5 mm long, 0.6–0.8 mm wide, variably concave, tapered in the upper 1/3 to a broadly acute, acuminate or rarely obtuse apex, sometimes cuspidate or aristate; costa ending below the apex, percurrent or short- to long-excurrent, often variable within a population or even within a single plant, (30–) 36–45 (–60) µm wide near the base; margins entire (rarely bluntly dentate in the upper half). Upper laminal cells oblong-hexagonal, (24–) 30–69 × 15–18 (–25) µm, larger, more oblong and laxer below; marginal cells not differentiated; apical cell (45–) 60–165 (–285) µm long; alar cells few and moderately inflated, or not or weakly differentiated. Axillary filaments present.

Calyptra cucullate, rostrate. Setae 4–16 (–30) mm long, twisted weakly to the right throughout, pale reddish brown, weakly hygroscopic. Capsules erect, symmetrical or rarely slightly asymmetrical, obovoid-cylindrical, obovoid, or occasionally pyriform, 1.5–2.5 mm long, with a neck c. 1/3 (–1/2) the capsule length, usually strongly constricted below the mouth when dry; mouth 3/4 to equal the diameter of the capsule, transverse (very rarely oblique); exothecial cells 45–55 (–75) µm long, often with an obscure lumen, in cross-section with the anticlinal walls cuneate, c. 6–8 rows oblate at mouth; operculum plano-convex or umbonate. Peristome double, rarely single; exostome teeth usually well developed, straight or rarely weakly sigmoid, reddish brown, (150–) 180–225 × 45–60 µm (c. 45–135 × 36–45 µm in var. *phymatodeus*), tapered to a slender and often ±perforate or bi-lobed apex, striate, weakly trabeculate, and not appendiculate; endostome variable, rudimentary to well-developed, rarely seeming absent and with fragments adhering to the upper adaxial surface of teeth. Spores (27–) 31–39 (–41) µm diam., finely verrucate, lirate-murate or coarsely insulate, lacking a trilete scar.

*Entosthodon subnudus* is the most variable species of the genus in Australia. Gametophytically, the form of the leaf apex and the length of the costa are quite variable, as are seta and capsule length and the degree of endostome development.

Material which Sainsbury (1955) treated as *Funaria gracilis* and *F. cuspidata*, in addition to material not known to Sainsbury, are included here within a broadly circumscribed *E. subnudus*. The pattern of variability of *E. gracilis* and *E. cuspidatus* is such that the material treated by Sainsbury (1955: 244) as two species is here assigned to the widespread and comparatively common *E. subnudus* var. *gracilis*.

Too many intermediate specimens occur between the typical variety and var. *gracilis* to permit their recognition as species. The features noted in the key to varieties (see above) should allow placement for all but a small fraction of intermediate and/or aberrant specimens.

#### 7a. **Entosthodon subnudus** var. **subnudus**

*Funaria (Entosthodon) helmsii* Broth. & Geh., *Öfvers. Förh. Finska Vetensk.-Soc.* 40: 172 (1898). T: Cardilkinna Rock Hole, Camp 10 of Elder Expedition, Musgrave Ra., S.A., June 1891, *R.Helms 815*; lecto: H-BR, *fide* A.J.Fife & R.D.Seppelt (2001).

Leaves oblong-obovate, concave to subtubulose above, cuspidate; costa c. 45–60 µm wide near the base, ending below base of cusp; margins usually entire, rarely blunty serrate. Upper laminal cells shortly oblong-hexagonal, c. 30–60 × 25–36 µm, becoming longer and more oblong below; apical cell (40–) 66–120 (–210) µm long.

Setae 4–6 mm long. Capsules narrowly pyriform to obovoid-cylindrical, 1.8–2.5 mm long, with a long gradually tapered neck c. half the total capsule length; mouth transverse; operculum plano-convex. Peristome double; exostome teeth straight or weakly sigmoid, variably developed, 150–210 × 45–60 µm, short and apically obtuse and/or bi-lobed or longer and apically acute, coarsely striate and baculate ±throughout, sometimes with a median gap in the abaxial layer near the apex; endostome segments slightly wider than teeth, irregular or bi-lobed, 1/4–1/3 the height of the teeth, papillose. Spores 39–45 µm diam., finely lirate-murate.

Occurs in W.A., N.T., S.A. and Vic., where it usually grows in crevices of granitic or calcareous rock ledges; also in New Zealand.

W.A.: Mileura Stn, Upper Murchison, *N.T.Burbidge & A.Kanis 8102*. S.A.: 75 km E of Leigh Ck, Gammon Ra., *H.J.Eichler 12922*; N of Renmark, *D.Symon 11578.O*. Vic.: Wycheproof, *W.W.Watts 544*.

Some Australian populations (including the type) have more acuminate leaf apices with longer terminal cells (to c. 210 µm) than the New Zealand material.

The longer capsules, shorter setae, and more strongly developed endostome facilitate separation from var. *gracilis*. Shorter capsules with a double peristome, cuspidate leaf apicies with relatively short apical cells, and finely lirate-murate ornamentation on spores which lack trilete scars, all differentiate *E. subnudus* var. *subnudus* from *E. apophysatus*.

*Funaria helmsii* is best regarded as fitting within the range of variability of *E. subnudus* var. *subnudus* and is characterised by the bluntly toothed upper leaf margins. The capsule in the type specimen is rather long (3.5 mm) for var. *subnudus*, but other specimens examined have shorter capsules. In Central Australia, specimens of var. *subnudus* with slightly to markedly toothed leaf margins are not unusual, and there is no clear boundary between material with toothed and entire margins.

**7b. Entosthodon subnudus** var. **gracilis** (Hook.f. & Wilson) Fife, *J. Hattori Bot. Lab.* 58: 192 (1985)

*Entosthodon gracilis* Hook.f. & Wilson, *in* J.D.Hooker, *Fl. Nov.-Zel.* 2: 91, pl. 86, fig. 7 (1855); *Funaria gracilis* (Hook.f. & Wilson) Broth., *in* H.G.A.Engler & K.A.E.Prantl, *Nat. Pflanzenfam.* 1(3): 524. (1903). T: Bay of Islands, New Zealand, *J.D.Hooker s.n.* (designated "W. 348b" by Wilson); lecto: BM-Wilson, *fide* A.J.Fife & R.D.Seppelt (2001); isolecto: BM-Wilson, BM-Hooker, BM-Besch.

*Funaria cuspidata* Hook.f. & Wilson, *in* J.D.Hooker, *Fl. Nov.-Zel.* 2: 91, pl. 86, fig. 3 (1855). T: Bay of Islands, New Zealand, *J.D.Hooker s.n.* (designated "W.348" or "W.348a" by Wilson); lecto: BM-Wilson, *fide* A.J.Fife & R.D.Seppelt (2001); isolecto: BM-Wilson, H-Solander.

*Funaria bullata* Broth., *Proc. Linn. Soc. New South Wales* 41: 584 (1916). T: Heyington, Vic., *W.W.Watts 208*; holo: H–BR.

*Entosthodon varius* Mitt., *Trans. & Proc. Roy. Soc. Victoria* 19: 67 (1882); *Funaria varia* (Mitt.) Broth., *in* A.Engler & K.Prantl, *Nat. Pflanzenfam.* 1(3): 523 (1903). T: *sine loc.*, Vic., *F.M.Adamson s.n.*; holo: NY-Mitten.

*Entosthodon sullivanii* Müll.Hal. ex Kindb., *Enum. Bryin. Exot.* 90 (1889), *nom. inval.* (in synon.)

*Funaria sullivanii* Watts & Whitel., *Proc. Linn. Soc. New South Wales*, Suppl. 30: 115 (1906), *nom. nud.*

Leaves oblong-obovate, (1.3–) 1.5–2.1 mm long, 0.6–0.8 mm wide, concave, tapered in upper 1/3 to an acute obtuse, or acuminate apex; costa c. 36–45 µm wide near the base, variable in length, ending below the apex, percurrent, or short- or long-excurrent; margins entire. Upper laminal cells (24–) 33–69 × 15–18 µm; apical cell 60–110 (–165) µm long.

Setae 9–22 mm. Capsules obovoid-cylindrical or obovoid, 1.5–1.8 (–2.0) mm long, strongly constricted below the mouth with dry; mouth equal to the diameter of the capsule; operculum plano-convex. Peristome double; exostome teeth variably developed and usually ±irregular in outline (with sinuous margins), tapered to an acute or irregular apex; endostome rudimentary, to c. 1/3 the height of the teeth. Spores 32–39 (–45) µm diam., finely murate-lirate.

Occurs in W.A., N.T., S.A., N.S.W., Vic. and Tas.; also in New Zealand and New Caledonia. This moss grows on fine (clay or silt) soil in relatively open vegetation; often associated with *Leptospermum/Kunzea* scrub, and sometimes occuring in areas with impeded drainage.

W.A.: Caron Rock Hole, SE of Mingenew, *R.Ericson*; Araluen, Darling Ra., *D.G.Catcheside 74.381*. N.T: Chewing Ra., *P.K.Latz 6633d*. S.A.: Springs Gully, Clare, *D.G.Catcheside 78.294*. N.S.W.: Bedoura, *D.G.Catcheside 67.60*. Vic.: Mackeys Lookout, Mt Buffalo, *D.G.Catcheside 69.255*. Tas.: Cataract Hill, Launceston, *W.A.Weymouth 3012*.

Intermediates between the typical "*gracilis* form" and the "*cuspidata* form" are not uncommon, but are they very difficult to identify. The frequency with which such intermediate forms occur precludes their taxonomic recognition and designation. The Hooker collection from the Bay of Islands which Wilson designated (*in herb.)* 348 and from which he segregated the types of both *Entosthodon gracilis* and *Funaria cuspidata*, is a particularly good example of the variability of the var. *gracilis*. Similarily variable populations occur in Tas., in the Grampians Ranges in Vic., and in northern New Zealand.

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

**7c. Entosthodon subnudus** var. **phymatodeus** (Catches.) Fife & Seppelt, *Hikobia* 13: 483 (2001)

*Phyocomitrium phymatodeum* Catches., *Mosses of South Australia* 233, fig. 131a–h (1980); *Funaria phymatodea* (Catches.) Catches., *Bryologist* 96: 93 (1993), *nom. inval.* (basionym not cited). T: Spear Ck, N of Horrocks Pass, Flinders Ra., S.A., 27 Aug. 1953, *D.G.Catcheside 53.246*; holo: AD; iso: MICH.

Autoicous. Plants yellowish green. Stems reddish brown, branching by subperigonial innovation (many plants with 2 perigonia), to c. 2 mm long, in cross-section with a central strand, c. 2 layers of thick-walled reddish brown cortical cells, and a faint hyalodermis, beset below with reddish brown rhizoids. Leaves erect-spreading, obovate, 1.9–2.5 mm long, (0.6–) 0.9–1.2 mm wide, concave, abruptly tapered in the upper half to a slender yellow arista usually 250–425 µm long; costa yellowish, c. 30–45 µm wide proximally, ending c. 4 cells below the base of the arista; margin entire or weakly crenulate. Upper laminal cells oblong-hexagonal, (45–) 50–70 (–90) × 21–30 µm, becoming more oblong but scarcely larger below; marginal cells not differentiated; apical cell 195–285 µm long; alar cells not or weakly differentiated.

Perigonia single or double. Calyptra cucullate, long-rostrate. Setae reddish brown, twisted weakly to the right throughout, smooth, straight when wet 3.5–5.0 mm long. Capsules erect, symmetrical, narrowly pyriform-cylindrical, very slightly constricted below the mouth when dry, 1.9–2.3 mm long, c. 0.6–0.7 mm wide, with a gradually tapered neck c. half the capsule length, smooth when moist, irregularily wrinkled below when dry, pale reddish brown at maturity; mouth c. 3/4 the diameter of the capsule when moist, transverse; exothecial cells with indistinct lumina, 45–78 µm long, c. 4–6:1, in cross-section with thick cuneate anticlinal walls, c. 5 rows oblate and slightly more pigmented at the capsule mouth; operculum umbonate (seen only on immature capsules), c. 460 µm diam., composed of spirally arranged firm-walled cells. Peristome double; exostome teeth straight, variably developed, irregular in outline, lacking appendiculae, weakly trabeculate and papillose-baculate on the adaxial surface, longitudinally or concentrically striate on the abaxial surface, c. 45–135 × 36–45 µm, with rounded apices. Endostome rudimentary (isolated 'segments' entending to 60 µm above the rim), strongly baculate. Spores 27–36 µm diam., coarsely insulate (c. 6–8 insulae across face), lacking trilete scars; insulae 2–6 µm diam.

Endemic to southern Australia (W.A., S.A., N.S.W. and Vic.); grows on mineral soil.

W.A.: Wittenoom Gorge, *I.G.Stone 23499*. N.S.W.: Mootwingee Natl Park, *I.G.Stone 9580*. Vic.: Port Campbell, *I.G.Stone 11144*.

The presence of a peristome, cuneate anticlinal walls in the exothecium and non-physcomitrioid spores clearly necessitated the removal of this taxon from *Physcomitrium*.

Within the variable *E. subnudus*, this variety is characterised by a slender yellow arista, weakly developed peristome, an umbonate operculum and coarsely insulate spores.