ZYGODON

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Zygodon Hook. & Taylor, *Musc. Brit.* 70 (1818); from the Greek *zygo* (yoked) and *odontos* (a tooth), in reference to the peristome teeth that are initially paired.

Type: *Z. conoideus* (Dicks.) Hook. & Taylor

Amphidium Nees, *in* J.Sturm, *Deutschl. Fl.* 2: 17 (1819), *nom. rej. non Amphidium* Schimp.; *Zygodon* sect. *Amphidium* (Nees) Müll.Hal., *Linnaea* 18: 668 (1845). T: *Zygodon forsteri* (Brid.) Mitt.

Dioicous, autoicous or synoicous. Plants in loose tufts. Stems erect to ascending, simple or sparsely branched. Rhizoids at stem base, frequently matted, smooth. Leaves flexuose or twisted when dry, lanceolate to ovate-lanceolate, entire or denticulate near the acute (rarely obtuse) apex; margin plane or recurved below; costa almost reaching apex or excurrent; upper laminal cells isodiametric (hexagonal-rounded), papillose or smooth; basal laminal cells rectangular, smooth. Gemmae on stems or in leaf axils, small, cylindrical or fusiform.

Perichaetial leaves differentiated or not. Calyptra small, cucullate, smooth, glabrous or rarely hairy. Setae long. Capsules on main stem, long-exserted, ovoid to cylindrical or pyriform, with 8 longitudinal striae when dry; stomata superficial on capsule neck; operculum obliquely long-rostrate from a low-conical base. Peristome double, single or absent; exostome teeth 16, initially joined in pairs, lanceolate, papillose; endostome segments 8 or 16, linear, papillose to striate. Spores unicellular, isomorphic, globose.

A genus of c. 77 species as circumscribed by Malta (1926), re-estimated as c. 52 species by Vitt (*Beih. Nova Hedwigia* 71: 261–268, 1982). Distributed worldwide, but most diverse in temperate regions. The genus is represented in Australia by six non-endemic species of which two, *Z. minutus* and *Z. hookeri*, occur only in Australasia. *Zygodon* is an important element in the epiphytic and epilithic floras of south-eastern and south-western Australia. Tasmania has six species, Victoria four and Western Australia three species.

Although the genus is not host-specific, usually only one species will be found on a particular tree species at a given location; in contrast, species of *Orthotrichum* or *Ulota* often grow in mixed colonies. *Zygodon intermedius*, the most widespread taxon in Australia and New Zealand, has been recorded from 47 phorophytes.

Malta (1926) recognised four sections based on gametophyte characters: *Euzygodon* Müll.Hal. (*Zygodon* sect. *Zygodon*), *Stenomitrium* Mitt., *Bryoides* Malta and *Obtusifolia* Malta. Sect. *Zygodon* is the largest section (represented in Australia by *Z. intermedius* and *Z. hookeri*), and it includes species with leaves in five ranks, smooth laminal cells and obtuse leaves. Sect. *Obtusifolia* is represented by *Z. obtusifolius*, and sect. *Bryoides* by *Z. gracillimus*, *Z. menziesii* and *Z. minutus*. Sect. *Stenomitrium* is sometimes regarded as a separate genus (Brotherus, *Nat. Pflanzenfam.* I, 3: 464–465, 1902; Vitt, *loc. cit.*), but it is not known from Australia.

Although Lewinsky (1990) revised *Zygodon* in Australia, there has not been a worldwide revision since that of Malta (1926). In a cladistic study based on rbcL sequences that was aimed mainly at circumscribing the Orthotrichaceae and reconstructing relationships between the genera, Goffinet & Vitt (1998) found *Zygodon* to be polyphyletic. They described a new genus *Bryomaltea* for *Z. obtusifolius* in a clade with *Macromitrium* and related genera. Another clade with *Z. pungens* was resolved as sister to or in trichotomy with two other representatives of *Zygodon* in addition to *Orthotrichum* and *Ulota*. Goffinet & Vitt (1998)

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reintroduced the genus *Codonoblepharon* Schwägr. with *Z. menziesii* as type and including *Z. minutus*.

This present work follows the death of Lewinsky (November 1998) on whose research this revision is based. Pending a wider revision of the genus, Lewinsky's concepts are retained here for the Australian species.

References

Goffinet, B. & Vitt, D.H. (1998), Revised generic classification of the Orthotrichaceae based on a molecular phylogeny and comparative morphology, *in* J.W.Bates, N.W.Ashton & J.G.Duckett (eds), *Bryology for the Twenty-first Century* 143–159.

Lewinsky, J. (1989), *Zygodon* Hook. & Tayl. in Australasia: a taxonomic revision including SEM-studies of peristomes, *Lindbergia* 15: 109–139.

Malta, N. (1926), Die Gattung *Zygodon* Hook. et Tayl. Eine monographische Studie, *Acta Horti Bot. Univ. Latv*. 1: 1–184.

1 Upper laminal cells smooth.....2

1: Upper laminal cells papillose.....4

2 Costa usually excurrent, rarely percurrent; stems in cross-section with uniformly thin-walled cells *(1)* ..... **5. Z. minutus**

2: Costa ending below apex; stems in cross-section with at least some of the cortical cells thick-walled 3

3 Plants yellow-green; costa strong; leaves 0.3–0.6 mm long, usually plane with flat margins *(2:)*..... .....**1. Z. gracillimus**

3: Plants olive-green to dark green-brown above, brown or brown-black below; costa less well defined; leaves 1.0–1.6 (–2.1) mm long, slightly undulate, mostly with margins recurved to revolute in central part.....**4. Z. menziesii**

4 Leaf apices obtuse; plants to 10 mm tall; leaves to 1 mm long *(1:)*.....**6. Z. obtusifolius**

4: Leaf apices acute or short-acuminate; plants to 55 mm tall; leaves to 2.4 mm long.....5

5 Dioicous; perichaetial leaves lanceolate, with an acute apex; leaves rarely denticulate near apex, with teeth formed only by part of a cell; seta 2.5–10 mm long; capsules 1.0–1.5 mm long; spores 13–20 µm diam. *(4:)*..... **3. Z. intermedius**

5: Synoicous; perichaetial leaves ovate to lanceolate, with an acuminate apex; leaves often dentate, with teeth formed by entire cells; seta 10–15 mm long; capsules 1.5–2.0 mm long; spores 20–25 µm diam..... ..... **2. Z. hookeri**

1. Zygodon gracillimus Broth. ex M.Fleisch., *Musc. Buitenzorg* 2: 392, fig. 73 (1904)

T: Handang-Badak, Indonesia; lecto: FH, *fide* J.Lewinsky, *Lindbergia* 15: 123 (1989).

Zygodon rodwayi Broth., *in* L.Rodway, *Pap. & Proc. Roy. Soc. Tasmania* 1913: 260 (1914). T: Forth R., near Sheffield, Tas., *L.Rodway 106*; holo: H; iso: NSW, WELT.

Illustrations: J.Lewinsky, *op. cit.* 15: 114, figs 21–26; 122, figs 57–76.

Dioicous. Plants in dense yellow-green tufts, very slender. Stems fastigiately branched, thin, with some thick-walled cortical cells in cross-section. Rhizoids well developed near stem base. Leaves appressed when dry, spreading to erect-spreading when moist, lanceolate, 0.3–0.6 mm long, 0.1–0.2 mm wide; apex acute; margin plane, entire or somewhat crenulate near apex; costa strong, ending below apex, 25–45 µm wide near base, pale; upper laminal cells rhomboidal, 4–12 × 3–9 µm, thick-walled, smooth, almost quadrate near margins; basal laminal cells irregular, rectangular to rhomboidal, thick-walled. Gemmae clavate, with transverse walls only, 3–7 cells, 30–110 µm long.

Perigonium terminal or pseudolateral. Perichaetial leaves somewhat longer than stem leaves. Calyptra fugacious, smooth. Setae long. Capsules long-exserted, pyriform with a long neck, deeply ribbed along entire length when dry, pale to reddish brown; mouth surrounded by 2–4 rings of quadrate thick-walled cells; exothecial cells rectangular, rarely quadrate,

differentiated into 8 bands of broader ±yellow cells; stomata few, on neck only. Peristome double; fragmentary prostome some-times present; exostome teeth 8 pairs, reflexed when dry, hyaline to pale yellow; endostome segments 8 or 16, 67–75% the height of the exostome, hyaline. Spores 12.5–14.0 µm diam., finely papillose. Chromosome number not known. Fig. 30R–Z.

Known from Tas.; also in New Zealand, Java and Bolivia. Epiphytic on trees.

Tas.: Forth R., near Sheffield, *L.Rodway 106* (HO, NSW); Forth R., N coast, *L.Rodway 2492* (HO); Kingston-Longley, *L.Rodway s.n.* (HO); Sumac Rd, 9 Oct. 1993, *J.Jarman s.n.* (HO).

This species is characterised by its long, clavate gemmae.

Goffinet & Vitt (1998: 150) referred this species to *Codonoblepharum* Schwägr.

2. Zygodon hookeri Hampe, *Linnaea* 30: 632 (1860)

T: Grampians, [Vic.], 1854, *F.Mueller*; holo: BM.

[*Zygodon reinwardtii auct. non* Schwägr.: L.Rodway, *Pap. & Proc. Roy. Soc. Tasmania* 1913: 58 (1914)]

[*Zygodon anomalus auct. non* Dozy & Molk.: L.Rodway, *Pap. & Proc. Roy. Soc. Tasmania* 1913: 58 (1914)]

Illustrations: J.Lewinsky, *Lindbergia* 15: 116, figs 31–33; 134, figs 156–175 (1989).

Synoicous. Plants in loose tufts or mats, 10–30 mm tall, green to yellowish green above, red-brown or brown below. Stems branched. Rhizoids extending up stems. Leaves crisped, flexuose and loosely curled around stem when dry, spreading or somewhat recurved when moist, lanceolate or linear-lanceolate, 1.4–2.4 mm long, 0.5–1.2 mm wide; apex sharply acute; base slightly decurrent; margin ±undulate, often dentate, with teeth formed by whole cells; costa ending below apex or, rarely, percurrent and broadened at apex; upper laminal cells irregularly arranged, isodiametric, 6.0–12.5 × 4.5–11.0 µm, thick-walled, with 3–6 short papillae per cell. Gemmae rare, small, clavate, 3-celled, green with hyaline walls.

Perichaetial leaves ovate-lanceolate, with acuminate apices. Calyptra smooth. Setae 10–15 mm long. Capsules oblong or cylindrical, 1.5–2.0 mm long, with 8 deep ribs along entire length when dry. Peristome single; exostome absent; endostome segments 8, rarely 16, filiform, smooth, hyaline. Spores 20–25 µm diam., papillose. Chromosome number not known.

Local in southern N.S.W., southern and south-western Vic. and Tas.; also in New Zealand. Occurs at elevations of 400–1000 m, most commonly as an epiphyte (often on trunks of *Nothofagus* in wetter areas) and occasionally on rocks.

N.S.W.: Deep Ck, Batlow, *W.W.Watts 7631* (NSW). Vic.: Mt William, Grampians, *H.Streimann 3031* (CANB). Tas.: Mt Wellington, *W.A.Weymouth 3049* (HO); Forth R., *L.Rodway 2492* (HO); Great L., *D.H.Norris 33028* (HO).

This species can be separated from *Z. intermedius* by the more open habit, the more twisted and undulate leaves and longer setae, synoicous rather than dioicous reproduction, larger spores, longer capsules and differences in the perichaetial leaves. The two species also differ in their ecology and distribution; *Z. hookeri* occurs in wetter habitats and is endemic to Australasia, whereas *Z. intermedius* tolerates a wider ecological amplitude and is more widespread.

3. Zygodon intermedius Bruch & Schimp., *Bryol. Eur.* 3: 41 (1838)

T: "Dusky Bay" [Dusky Sound], New Zealand, 1791, *A.Menzies*; holo: BM.

Zygodon brownii Schwägr., *Sp. Musc. Frond.*, Suppl. 4: 317 (1842). T: Terra van Diemen [Tas.], *R.Brown*; holo: G.

Zygodon brachyodus Müll.Hal. & Hampe, *in* G.Hampe, *Linnaea* 28: 210 (1856). T: Sealers Cove, Vic., *F.Mueller*; holo: BM; iso: H.

Zygodon confertus Müll.Hal., *Hedwigia* 37: 134 (1898). T: Vic., *F.M.Campbell*; lecto: H, *fide* J.Lewinsky, *Lindbergia* 15: 132 (1989).

Zygodon hymenodontoides Müll.Hal., *Hedwigia* 37: 135 (1898), *nom. illeg.* T: Moe R., Gippsland, Vic., *J.G.W.Luehmann*; lecto: H, *fide* J.Lewinsky, *Lindbergia* 15: 132 (1989).

Illustrations: J.Lewinsky, *Lindbergia* 15: 116, figs 27–30; 131, figs 131–153 (1990); R.D.Seppelt, *The Moss Flora of Macquarie Island* 212, fig. 84 (2004).

Dioicous. Plants in ±dense tufts or mats, 5–25 (–55) mm tall, green to yellowish green above, red-brown to brown below. Stems frequently branched. Rhizoids at stem bases. Leaves loosely twisted around stem or erect-appressed when dry, erect, open or spreading when moist, lanceolate or linear-lanceolate, 0.6–1.8 mm long, 0.2–0.3 mm wide; apex acute; base somewhat decurrent; margin plane or somewhat undulate, entire or rarely denticulate near apex, with teeth formed by part of cell; costa ending below apex; upper laminal cells ±isodiametric, 4–10 (–15) µm wide, thin- or thick-walled, with 5–8 short papillae per cell; basal laminal cells rounded-rectangular, 9–50 µm long. Gemmae occasional, small, clavate, 3-celled, with hyaline walls.

Perigonium terminal or sublateral. Perichaetial leaves lanceolate, with acute apices. Calyptra smooth. Setae 2.5–10.0 mm long. Capsules exserted, pyriform, oblong or cylindrical, 1.0–1.5 mm long, with 8 deep ribs along entire length when dry. Peristome double; exostome teeth 8, short, sometimes reduced or absent; endostome segments 8, ±reduced, hyaline. Spores 13–17 (–20) µm diam., papillose. *n* = 11 (10 + *m*), *fide* H.P.Ramsay, *J. Hattori Bot. Lab*. 74: 189 (1993).

Occurs in south-western W.A., S.A., northern and south-eastern Qld, N.S.W., A.C.T., Vic. and Tas.; also a widespread species in New Zealand, South America, Africa and Asia. Most common from sea level to 1500 m, usually epiphytic, but also found on rock. Grows on a wide range of trees and shrubs and tolerates great differences in humidity, although it is absent from the driest habitats.

W.A.: Beedelup Falls, NW of Pemberton, *W.A.Weber B33.579* (AD). S.A.: Mt Lofty, *D.G.Catcheside 55.28* (AD). Qld: Killarney, *I.G.Stone 14610* (MEL). N.S.W.: Reservoir Gully, Yarrangobilly Caves, *W.W.Watts 8670* (NSW). A.C.T.: Bendora Rd, Brindabella Ra., *W.B.Schofield 90839 & 90603* [*with H.Streimann, H.P.Ramsay & M.I.Schofield*] (NSW). Vic.: Mt William, Grampians, *H.Streimann 3047* (CANB). Tas.: Mt Dobson Rd, *H.P.Ramsay R1862* (NSW).

The small, 3-celled gemmae are especially distinctive.

4. **Zygodon menziesii** (Schwägr.) Arn., *Disp. Méth. Mousses* 15 (1826)

Codonoblepharum menziesii Schwägr., *Sp. Musc. Frond.*, Suppl. 2, 1: 142 (1824). T: "Dusky Bay" [Dusky Sound], New Zealand, 1791, *A.Menzies s.n.*; holo: G.

Zygodon drummondii Taylor, *London J. Bot*. 5: 46 (1846). T: Swan R., [W.A.], 1843, *J.Drummond s.n.*; lecto: BM, *fide* J.Lewinsky, *Lindbergia* 15: 126 (1989); isolecto: H, L.

Illustrations: J.Lewinsky, *Lindbergia* 15: 113, figs 15–20; 127, figs 100–111; 128, figs 112–128 (1990); R.D.Seppelt, *The Moss Flora of Macquarie Island* 213, fig. 85 (2004).

Dioicous. Plants densely tufted, to 10 mm tall, olive-green to dark green-brown above, brown below. Stems branched, with some thick-walled cortical cells in cross-section. Rhizoids extending up stem. Leaves firmly twisted around stem or loosely twisted with a twisted apex when dry, usually erect-open when moist, lanceolate to ovate-lanceolate, slightly undulate, often keeled above, 1.0–1.6 (–2.1) mm long, 0.3–0.5 (–0.7) mm wide, not decurrent; apex acute or rounded-acute; margin entire, recurved to revolute in lower 33–67%; costa not strong, ending below apex; upper laminal cells often in oblique rows, quadrate or rhomboidal, 9–12 × 6–12 µm, walls ±thick; basal cells rectangular, 20–45 (–60) × 12–20 µm, thin-walled near costa, thick-walled near margin, smooth. Gemmae filiform to clavate, 4–8-celled, 45–150 µm long, the walls transverse, green or brownish.

Perigonium pseudolateral. Perichaetial leaves similar to vegetative leaves. Calyptra smooth. Setae 2.5–6.0 mm long. Capsules ovoid to pyriform or cylindrical, 1.5–2.0 mm long, deeply ribbed along entire length when dry, with a wide or, rarely, narrow mouth. Peristome double, well developed; exostome teeth 8 pairs, reflexed when dry, white to yellowish; endostome segments 8 or 16, half the height of the exostome, hyaline. Spores 15–18 µm diam., finely papillose. *n* = 11 (10 + *m*), *fide* H.P.Ramsay, *J. Hattori Bot. Lab*. 74: 189 (1993).

Occurs in south-western W.A., south-eastern S.A., eastern N.S.W., southern Vic. and Tas.; also in New Zealand, Stewart, Campbell, Auckland and Macquarie Islands and Chile. This is

the only species found commonly on rock (basic and acidic), and it is also epiphytic on *Eucalyptus* spp. and introduced trees. It is known from sea level to 1500 m, and is tolerant of salt spray, being found on jetties and in mangrove swamps.

W.A.: headwaters of Joshua Brook, 16 km E of Donnybrook, *D.H.Norris 25754* (NSW). S.A.: Tantaroola, *D.G.Catcheside 72.71* (AD). N.S.W.: Fitzroy Falls, *W.W.Watts 9802* (NSW). Vic.: Mt Buck, *Harrison 20* (NSW). Tas.: L. St. Clair, *D.A.Ratkowsky H775* (HO).

The gametophytes and sporophytes are rather variable; the most common form has brown or dark green leaves firmly twisted around the stems. In wetter areas, leaves can be loosely twisted around the stems and individually twisted at their apices. Gemmae are uniseriate and filiform to clavate. Specimens having gemmae with both transverse and longitudinal walls are referred to var. *angustifolium* Malta which is known only from New Zealand.

This species was treated as *Codonoblepharum menziesii* by Goffinet & Vitt (1998: 150).

5. Zygodon minutus Müll.Hal. & Hampe, *in* G.Hampe, *Linnaea* 28: 209 (1856)

T: Sealers Cove, Wilsons Promontory, Vic., *F.Mueller*; holo: BM, iso: NSW.

Illustrations: J.Lewinsky, *op. cit.* 112, figs 8–14; 124, figs 79–97 (1989).

Dioicous. Plants in dense tufts, olive-green to green above, red-brown below; female plants 1–3 mm tall; male plants smaller. Stems simple or branched, with thin-walled cortical cells in cross-section. Rhizoids well developed at stem base. Leaves flexuose when dry, erect-spreading when moist, lanceolate to ovate-lanceolate, 0.8–1.4 (–1.7) mm long, 0.2–0.4 mm wide; apex apiculate; base non-decurrent; margin plane or slightly reflexed near base, entire; costa usually excurrent, rarely percurrent or subpercurrent, 30–50 µm wide near base, yellowish or red-brown; upper laminal cells quadrate or rhomboidal, 6.0–12.5 × 7.5–15.0 µm, thick-walled, smooth; basal cells rectangular, 15–50 × 10–20 µm, thin-walled, smooth. Gemmae abundant, in clusters in leaf axils, clavate, 4–8-celled, 50–120 µm long, the walls hyaline.

Perigonium terminal or pseudolateral. Perichaetial leaves undifferentiated. Calyptra smooth. Setae 1.5–3.0 mm long. Capsules exserted, broadly ovoid or pyriform, 1.0–1.5 mm long, ribbed when dry. Peristome double; prostome absent; exostome teeth in 8 pairs, reflexed when dry; endostome segments 8, sometimes with 8 rudimentary segments between, 50–67% the height of the exostome, hyaline. Spores 15–18 (–20) µm diam., finely papillose. n = 16 (New Zealand), *fide* H.P.Ramsay, *J. Hattori Bot. Lab.* 74: 189–190 (1993).

Occurs in south-western W.A., south-eastern S.A., south-eastern Qld, coastal Vic. and northern Tas. (including Flinders Is.); also in New Zealand. Epiphytic on living or dead trees or old posts, and often growing in bark fissures of *Banksia integrifolia* or *Eucalyptus* spp. It has also been collected from rock, rock crevices, concrete paths and shaded limestone.

W.A.: Beedelup Falls, *D.H.Norris 25997* (PERTH). S.A.: Waterfall Gully, near Adelaide, *D.G.Catcheside 52.358* (AD). Qld: Bunya Mountains Natl Park, *D.H.Norris 35561* (BRI, HSC). Vic.: Sealers Cove, Jan. 1913, *W.W.Watts s.n.* (HO). Tas.: between Ulverstone and Devonport, *W.A.Weber & D.McVean s.n.* (CANB).

This species is characterised by narrow, elongate gemmae. Goffinet & Vitt (1998: 150) referred it to *Codonoblepharum.*

While this lowland moss is usually restricted to coastal areas (from sea level to an elevation of 70 m), it has been collected at 1000 m in open *Eucalyptus* forest in the Bunya Mtns, south-eastern Qld.

6. Zygodon obtusifolius Hook., *Musci Exot.* 2: 159 (1819)

T: Nepal, *Gardner*; lecto: BM, *fide* J.Lewinsky, *Lindbergia* 15: 21 (1989).

Illustrations: J.Lewinsky, *op. cit.* 111, figs 1–7; 120, figs 35–54.

Autoicous. Plants ±densely tufted, 5–10 mm tall, olive-green or brownish green above, brown to black below. Stems branched. Rhizoids extending up stem. Leaves appressed and erect when dry, erect-spreading when moist, ligulate or ovate-lanceolate, somewhat keeled, 0.7–1.0 mm long, 0.2–0.3 mm wide; apex obtuse; margin recurved to revolute in lower

50–67% of leaf, crenulate from protruding papillae; costa ending well below apex; base non-decurrent; laminal cells uniform, isodiametric, rounded to irregular, papillose, sometimes a few large linear or rectangular smooth cells near base. Gemmae uniseriate, elongate-clavate, 4–7-celled, 60–120 µm long, 15–25 µm wide, green.

Perichaetial leaves undifferentiated. Calyptra often papillose near apex from protruding cell ends. Setae 2–3 mm long. Capsules cylindrical to ovoid, c. 1 mm long, with 8 deep ribs along entire length when dry, red-brown. Peristome double; fragmentary prostome sometimes present; exostome teeth in 8 pairs, reflexed when dry; endostome segments 8 or 16, two-thirds the height of the exostome, lanceolate, white. Spores 12–15 µm diam., finely papillose. Chromosome number not known for Australia.

Known from only one locality in Tas.; also in New Zealand, Central and South America, Africa and Asia. This species is usually an epiphyte, but it also occurs on rocks.

Tas.: Sophia Pt, Macquarie Harbour, *T.B.Moore 26* (HO).

Goffinet & Vitt (1998: 151) treated this species as *Bryomaltea obtusifolia* (Hook.) Goffinet.