The genus *Trematodon* (Bruchiaceae) in Australia.

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Abstract

A detailed revision of the genus *Trematodon* Michx. is given together with a key to species, illustrations and distribution maps for the five species of *Trematodon* now recognised in Australia. Of the nine species previously recorded for Australia, one species, *T. amoenus* (Müll.Hal.) I.G.Stone & G.A.M.Scott is endemic while *T. flexipes* Mitt., *T. mackayi* (R.Br.bis.) Broth. and *T. suberectus* Mitt., occur in Australia and New Zealand. Three species previously considered Australian endemics, *T. baileyi* Broth., *T. brachyphyllus* Müll.Hal. and *T. longescens* Müll. Hal., are now considered conspecific with the widespread *T. longicollis* Michaux, the type species for the genus.

Introduction

Based on molecular studies by La Farge et al. (2002), the morphologically heterogeneous family Dicranaceae was found to be polyphyletic and several subfamilies, including Trematodontoideae, were excluded. The now segregated family Bruchiaceae (Buck 1979; Buck and Goffinet 2000; Goffinet et al. 2004, 2009, 2012), contains five genera: *Bruchia* Schwägr., *Cladophascum* Dixon, *Eobruchia* W.R.Buck, *Pringleella* Cardot and *Trematodon* Michx, of which only *Bruchia* and *Trematodon* occur in Australia. The family Bruchiaceae includes small mosses that commonly occur as colonists on soil, and are often overlooked. In the absence of mature sporophytes, they are difficult to identify with any certainty.

Worldwide, the genus *Bruchia* includes about 58 names of which 20 are currently recognised, with 25 requiring verification, while 13 are considered illegitimate (TROPICOS accessed 2017). Rushing (1986) recognised 15 species and excluded ten. Stone and Scott (1973) transferred *Bruchia whiteleggei* Müll.Hal. to synonymy with *Eccremidium whiteleggei* Broth., *Bruchia minuta* Mitt. to synonymy with *Eccremidium minutum* (Mitt.) I.G.Stone & G.A.M.Scott, and transferred *Bruchia amoena* Müll.Hal. to synonymy with *Trematodon amoenus* (Müll.Hal.) I.G.Stone & G.A.M.Scott.

In Australia, *Bruchia* is currently represented by *B. brevipes* Harv. ex. Hook. and *B. queenslandica* I.G.Stone (syn. *B. foveolata* Magill.) both of which occur in southern Africa (Magill and Schelpe 1979), while *B. queenslandica* is recorded from California and north-western Mexico (Crum 1994). In addition, a putative new taxon is recorded from Queensland. A revision of *Bruchia* in Australia will be published separately.
Although the genus *Trematodon* includes 160 names worldwide, only 25 species are currently recognised [TROPICOS accessed September 2017]. Nine species are listed for Australia (Streimann and Klazenga 2002), of which *T. flexipes* Mitt., *T. mackayi* (R.Br. bis) Broth., and *T. suberectus* Mitt., are also found in New Zealand (Fife 2016).

In the current treatment, type specimens have been examined and illustrated where possible. A number of *Trematodon* species previously considered endemic to Australia (e.g., *T. baileyi* Broth., *T. longescens* Müll.Hal. and *T. brachyphyllus* Müll.Hal.) were transferred to synonymy with *T. longicollis* (Ramsay et al. 2018).

**Family Bruchiaceae** Schimp. *Corollarium Bryologiae Europaeae* 6. 1856.

Type: *Bruchia* Schwägr., *Sp. Musc. Frond.*, *Suppl.* 2: 91. 1824.

Dioicous or autoicous. *Plants* minute to small, yellowish-green, gregarious to densely tufted, on soil. *Stems* erect, simple or branched; central strand present. *Rhizoids* smooth, short, restricted to stem base. *Leaves* small below, becoming larger above, mostly lanceolate-subulate, straight or ± flexuose, erect-scapose when moist; upper leaves with a broader, oblong or oblong-ovate base, alar cells not differentiated, margin of subula partially to fully bistratose, apex often denticate with projecting cell ends; *laminal cells* subquadrate to rectangular or oblong linear, lower laminal cells longer and broader, becoming narrower towards the margins, those of basal angles not differentiated or forming a marginal border, distal cells short- to long-rectangular, firm-walled; *costa* single, well-developed, sub-percurrent to shortly excurrent, section poorly differentiated or with 1 row of guide cells and 2 bands of sub-stereids, the adaxial band much reduced.

*Perigonia* gemmiform at base of stem. *Perichaetia* terminal, perichaetial leaves either similar and not much differentiated from stem leaves or much larger with a long wide base and a long erect to flexuose subula. *Seta* short to long. *Calytra* mitrate (*Bruchia*, rarely in *Trematodon*) or cucullate (*Trematodon*); *operculum*, not present (*Bruchia*), or conic to obliquely long-rostrate (*Trematodon*). *Capsule* immersed to exserted, cylindric or obovate with a distinct inflated-tapering to long neck slightly shorter than, equal to or much longer than the urn, erect to curved; cleistocarpous, gymnostomous or peristomate; *annulus*, where present, usually of 2–3 rows of larger cells, usually revolute; *peristome* absent in *Bruchia*, in *Trematodon* occasionally absent or of 16 well developed simple, forked or perforate teeth, vertically barbed, and papillose. *Spores* small to large, finely to coarsely papillose, baculate, spiculate, reticulate or pitted.

*Chromosome numbers in Bruchia* include n=14, 15, 16, 28 and 30 while those reported for *Trematodon* are n=14, 15 and 28 and 30. Almost all data are from North America and include 1–2 m-chromosomes in a number of species as well as polyploidy in both genera (Fritsch 1991).

**Key to the Australian genera of Bruchiaceae**

1. Capsules cleistocarpous, immersed to short-exserted, neck conic to ovate .......................................... *Bruchia*

   1. Capsules peristomate, or rarely cleistocarpous or gymnostomous, exserted on a long seta, neck conic to long-cylindric ................................................................. *Trematodon*

**Trematodon** Michx. *Fl. Bor.-Amer.* 2: 289 (1803).

Type: *Trematodon longicollis* Fl. *Bor.-Amer.* 2: 289 (1803).

*Plants* 1.0–7.0 mm long, loosely tufted to gregarious, light-green or yellowish; stems branched or unbranched, with rhizoids at base. *Leaves* short and scale-like at stem base, becoming rapidly longer above with a broad sheathing oblong-ovate base narrowing gradually or abruptly to an acuminate subula, subula erect or +/- contorted or crispate when dry; margins entire or with a few teeth near apex, unistratose in base but in subula partially or fully bifascate in some species. *Costa* subpercurrent to excurrent. Distal *laminal cells* short rectangular, longer and broader in sheathing base.

*Perichaetal leaves* distinctly larger than stem leaves, subulate from a sheathing base. *Setae* elongate, straight or flexuose 5–40 mm long. *Calytra* usually cucullate in most species except *T. mackayi*. *Capsules* erect or curved, short to long-exserted, cylindric with a strongly differentiated conic to long-cylindric neck (apophysis) often strumose at base; *peristome* single or lacking, when present of 16 simple, forked or perforate teeth, vertically striolate on outer surface. *Operculum* obliquely long-rostrate. *Spores* (15–)20–30(–70) μm in diameter, finely to coarsely papillose or verrucose.

**Distribution and Ecology:** *Trematodon* occurs worldwide, mainly in temperate regions but extending poleward at least into the subantarctic region. The genus is a terrestrial coloniser of soil, earth banks or soil over rock, similar in habit and foliation to *Dicranella*, with which it may be found intermixed.
Recognition: *Trematodon* differs from *Dicranella* in sexuality, being mostly autoicous rather than dioicous, and has a distinctly different sporophyte. The apophysis or neck of the capsule is elongate and frequently strumose at the base. The neck varies in length relative to the urn both within and between species, is photosynthetic and appears to elongate prior to urn development and spore production.

**Notes:** Chromosome numbers have so far been reported for 6 species of *Trematodon* from North America and India with *T. longicollis*, the Type and most widespread and variable species, having a range of chromosome numbers with n=14, n=15(14+m), and including polyploids, n=28 and n=28+2m (Fritsch 1991). Chromosome numbers for additional species from Australia in Ramsay (2009, 2011) are: n=14 for *T. flexipes* and n=14 for *T. suberectus* from New Zealand and Australia. Counts reported for the species *T. baileyi* (n=14) and *T. longiscens* (n=15 (14+m), both now considered synonymous with *T. longicollis*, are thus referable to it (Ramsay et al. 2018).

A worldwide revision is needed to clarify the taxonomy of the genus *Trematodon*, but is beyond the scope of this treatment. While treatments exist for specific regions e.g. North America (Crum and Anderson 1981, Zander 2007), South Africa (Magill 1981), Japan (Noguchi 1987, Iwatsuki and Suzuki 2006), Malaysia (Eddy 1988), Papua New Guinea (Norris and Koponen 1990), New Caledonia (Tixier 1986, Thouvenot and Bardat 2010, 2013), China (Cao and Gao 1988) and India (Gangulee 1987, Schwartz 2014), this is the first treatment of the genus for Australia.

The gametophytes of many *Trematodon* species are similar and there are few apparent features to separate species in the absence of sporophytes. Cao and Gao (1988) indicate that reliable gametophyte characters for differentiating species are the relative width of the costa in the subula and the cell structure in the margins of the base and subula in both stem and perichaetial leaves. In addition, Ramsay et al. (2018) showed that leaf and costal anatomy are significant characters.

The early Australian collections of *Trematodon* held at the National Herbarium of New South Wales (NSW) were mostly identified by Brotherus. His key (Brotherus 1924-176) emphasised sporophytic features such as peristome, spore size, length of capsule relative to the urn, and whether or not the capsule was strumose. In this work species were assembled into groups. Within these groups almost identical species from distant geographical localities are included under different species names. For example, along with other taxa, he synonymised *T. brachyphyllus* Müll.Hal., *T. cheesemani* Müll.Hal. and *T. integrifolius* Müll.Hal., distinguishing them from *T. suberectus* Mitt., based on the length of the capsule versus the urn. Brotherus (1924) distinguished *T. longiscens* Müll.Hal., together with *T. pallidens* Müll.Hal., *T. drepanellus* Besch., *T. megagophysatus* Müll.Hal. and *T. hookeri* Müll.Hal., from the group of taxa which included *T. longicollis* Michx. and *T. baileyi* Broth. (as *T. braileyi* sic.) based on presence or absence of a struma. However, such groupings have limited use and are not followed here due to considerable variation in seta, neck and urn length and presence or absence of a struma.

Taxonomic identification relies primarily on sporophyte characters, particularly features of the capsule urn and neck and their relative lengths, and the size and structure of the peristome teeth where present and range of spore size (Brotherus 1924, Cao and Gao 1988, Iwatsuki and Suzuki 2006). The characteristic *Trematodon* capsule has an urn with neck (apophysis) which is variable in length, from short to very long, in different species. There is also considerable variation within a taxon and considerable between-taxon overlap in dimension of the ratio of neck to urn, rather than capsule to urn as used by Brotherus (1891). Development of a struma at the base of the neck varies within and between species and is unreliable as a taxonomic character. Most species are annulate, have a long-rostrate operculum, and when present the peristome consists of 16 flat, deeply divided and often asymmetrically bifid, mostly perforate teeth. Peristome teeth are absent in *T. amoenus* (Broth.) I.G.Stone & G.A.M.Scott, reduced or absent in *T. mackayi* (R.Br.bis) Broth. and variable in *T. flexipes* Mitt. Spores differ between species from small to large, usually with baculate-verrucose ornamentation. Identification of species is difficult, but capsule and spore dimensions and cross-sectional anatomy of the leaf, in both the base and subula, may yield the most reliable features. Ornamentation of spores is a significant character in the genus *Bruchia* but less so in *Trematodon*.

**Key to *Trematodon* species in Australia**

1. Peristome reduced to a short membrane or gymnostomous ..........................2

1: Peristome well developed ..................................................................................3

2. Plants minute, <1.0 mm; seta very short; capsule often cleistocarpous; spores small, 25–38 μm diam., finely ornamented .........................................................1... *Trematodon amoenus*
1. **Trematodon amoenus** (Müll.Hal.) I.G.Stone & G.A.M.Scott, *J. Bryol.* 7: 603 (1973).

**Basionym**: *Bruchia amoeona* Müll.Hal. *Flora* 71:11 (1888).

**Type citation**: *Patria*. Australia, New South Wales, Mossvale: Whitelegge Nvbr. 1884. Hb. Melbourne No. 138.

**Type**: Near Fitzroy Falls, 8 Nov 1884, *T. Whitelegge* 138 (holotype: MEL 0029254A!; isotype: NSW 294667!)

**Autoicous**. **Plants** small, gregarious forming dense patches. **Stems** erect, 0.5–1.5 mm, branched or unbranched, in section with central strand of small thin-walled cells, cortical cells not differentiated. **Leaves** at stem base ovate-lanceolate with a short subula; upper leaves gradually long-subulate from an ovate base, subula 1–2 times as long as base; **costa** narrow in base, filling upper subula, subpercurrent, in cross section with a median row of guide cells and weakly differentiated to small adaxial and abaxial stereid bands, near the leaf insertion consisting of a median stereid band and differentiated adaxial and abaxial epidermal layers; **leaf margins** mostly unistratose, occasionally bistratose near apex of subula; **apex** weakly denticate. **Lamina cells** elongate and thin-walled throughout; those of subula irregularly polygonal, rhomboid or rectangular and 2–4:1, becoming broader and longer below the subula and elongate, 5–10:1 in the base.

**Perigonia** gemmiform, terminal on short basal shoots. **Perichaetial leaves** terminal. **Perichaetial leaves** with a long, ovate base gradually tapering to a long subula twice as long as base; **costa** filling upper subula. **Seta** short, 1–3 mm long. **Capsule** small, 1.0–1.5 mm, cleistocarpous, slightly exerted, orange when mature, with a short neck ±equal to urn, weakly strumose, cumulatively exerted; **annulus** variable, conspicuous, of very thick-walled cells or reduced or absent. **Spores** 25–38 μm, coarsely baculate-verrucose. Chromosome number unknown. Figure 1.

**Distribution and Ecology**: *Trematodon amoenus* is endemic to Australia: New South Wales and Victoria, Map 1. *Trematodon amoenus* is a tiny moss of silty soils, rotting logs and tree roots, in higher altitude regions, sometimes forming large patches, made conspicuous by the massed orange capsules.

**Recognition**: When fruiting, *T. amoenus* is readily distinguished by its small size, short seta, a capsule which opens irregularly, lack of a peristome, and a capsule neck that is more or less the same length as the urn. While the neck to urn ratio is about equal, this feature is also present in some other species and the ratio does not, therefore, provide an unequivocal means of separating species. The most reliable features for distinguishing the species are a combination of tiny plants each with a short seta; capsule held more or less erect on the seta and not arcuate; neck and urn more or less equal in length; absence of peristome. Other features found in Australian species include spores with a diameter of 25–32 μm, about middle for the spore diameter range of the genus; marginal cells are mostly unistratose in the leaf base and subula and the costa fills the upper subula but is narrow in the leaf base.

**Notes**: This moss was originally described as a species of *Bruchia* but was transferred to *Trematodon* by Stone and Scott (1973) because the operculum is sometimes dehiscent.

**Representative specimens examined**: NEW SOUTH WALES: Central Tablelands: Neates Glen, Blackheath, 33°37’S 150°17’E, 4 Jan 1911, W.W. Watts NSW10145 (NSW 754625); Southern Tablelands: Fitzroy Falls, 34°59’S 150°29’E, 1 Nov 1884, T. Whitelegge s.n. (NSW 754623); 34°38’S 150°28’E, 1 Nov 1886, T. Whitelegge s.n. (NSW 754628); **Southwest Slopes**: Kosciuszko National Park, near Thredbo chairlift, 36°29’S 148°17’E, 13 Jan 2002, A.J. Downing, D. Meagher and K. Clarke s.n. (NSW 606395). VICTORIA: **Snowfields**: Mt Baw Baw, 37°49’S 146°16’E, 1 Dec 1952, T. Dakin s.n. (MEL 1046861A); **East Gippsland**: Boggy Creek, Omeo, 37°04’S 147°34’E, 27 Apr 1975, I.G. Stone 10773 (MEL 2198165B); 37°04’S 147°25’E, 27 Apr 1976, I.G. Stone 11499 (MEL 2203229A).
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**Fig. 1.** *Trematodon amoenus*. A, B. Fruiting plants; C, D. Stem leaves; E, F. Perichaetial leaves; G. Cells of leaf apex; H. Cells of shoulder region of perichaetial leaf; I. Cells of shoulder region of stem leaf; J, K. Transverse sections of leaf subula; L. Transverse section of leaf shoulder region; M–O. Sections of sheathing leaf base; P. Stem section; Q. Spores. Scale bars: 1.0mm for plants and leaves; 100µm for cells, sections and spores.

Drawn from W.W. Watts 10145 (NSW 154625)
2. **Trematodon flexipes** Mitt. in Hook.f., *Flora Tasmaniae* 2: 173, 172 f.6 (1859).

*Type citation:* Australia: Tasmania, Cumming's Head, Western Mountains (no date) W. Archer s.n.

*Type:* Australia: Tasmania, Cumming's Head, *W. Archer s.n.* (holotype: NY-Mitten; isotypes: HO 73656!, HO 73657!, WELT MO 1289).

≡*Trematodon alpinus* J.H. Willis, *Victorian Naturalist* 72: 5–11. (1955) *fide* van Zanten 1971: p. 184–185, 187 Fig. 4 (1a–f).

*Type citation:* New South Wales: Mt Kosciusko, Jan 1899, *W. Forsyth 189*.

*Type:* Merritt's Camp, Mt Kosciusko, Jan 1899, *W. Forsyth 189* (holotype: MEL 32675!; isotype: NSW 299422!).

≡*Trematodon pygmaeus* Broth. *in* Willis, J.H. *Victorian Naturalist* 72: 10. Fig. G–N (1955), *nom. inval.*

*Type citation:* New South Wales: Mt Kosciusko, Jan 1899, *W. Forsyth 189*.

[Willis (1955) published *T. pygmaeus* as a separate species, but it is invalid by reason of being linked to the same type as for *T. alpinus* (MEL 32675!).]

**Illustrations:** Wilson *in* Hooker (1859:172, Fig. 60); Sainsbury (1955: plate 14, Fig. 2); Seppelt (2004: Fig. 35, p.91); van Zanten 1971 Fig. 4 (1a–f); Fife 2016, Plate 1 (G – L).

Diocious or rhizautoicous. *Plants* small, forming gregarious patches. *Stems* 1–4 mm tall, unbranched or occasionally branched by innovation. *Stem leaves* erect-spreading, entire; basal leaves small, 1.0 mm or less; upper leaves entire with a concave, strongly sheathing ovate base abruptly tapered to a long, +/– straight, narrow subula twice as long as base, +/– contorted when dry; *costa* narrow but well-defined below, usually filling upper part of the subula, *margins* entire, unistratose throughout or sometimes bistratose near the apex of the subula, *apex* +/– denticulate; leaf costa in section with abaxial band of smaller stereids in base and lower subula, upper subula with central row of deuters. *Lamina cells* of subula short, mostly irregularly rectangular to rhomboid or irregularly hexagonal, 1–3:1, becoming longer in sheathing base, 4–10:1.

*Male plants* clustered near base of female. *Perichaetia* terminal. *Perichaetial leaves* larger than stem leaves; subula twice as long as base; basal cells long rectangular, thin walled. *Calyptra* cucullate or occasionally mitrate, covering operculum and upper part of urn. *Setae* short, stout, 2.0–5.0 mm long, flexuose, pale. *Capsules* erect to suberect, obovoid; urn ca. 1.0 mm long; neck slender, equal to urn in length, strumose; neck:urn ratio 1:1; exothecial cells oblong polygonal; *operculum* conic, obliquely rostrate, rostrum almost as long as urn; *annulus* usually persistent, revolute, of 2–3 rows of enlarged thin-walled cells. *Peristome* variable in development, teeth 16, triangular to short lanceolate, reflexed when dry, short, 150–250 μm, mostly split or perforate halfway to base, sometimes undivided, coherent at base but free above, indistinctly striolate on upper half of outer surface, weakly papillose below; basal membrane high. *Spores* 26–38 μm, coarsely baculate-verrucose. *Chromosome number* n=14 (Ramsay 2011). Figure 2.

**Distribution and Ecology:** In Australia known from New South Wales, Victoria, Tasmania, Macquarie Island. It is also found in New Zealand and some Subantarctic Islands (Seppelt 2004) such as Marion (Zanten 1971) and Prince Edward Islands (Ochyra and Gremmen 2004; Ochyra 2008). Distribution in Australia, Map 2. In Australia, *T. flexipes* is a small, mainly alpine species found on disturbed soil.

**Recognition:** The species is well defined and distinguished from other *Trematodon* species in Australia by its habit, short seta with exerted capsule, and the more or less erect capsule with neck and urn about equal in length. The extent of division of the peristome teeth varies even within a single capsule. The leaf subula is mostly straight rather than flexuose. In both stem and perichaetial leaves the costa usually ±fills the subula and the margins are mostly unistratose throughout, although Seppelt (2004) illustrates the upper subula as sometimes bistratose in Macquarie Island specimens.

Anatomically and morphologically the taxon bears a close resemblance to *T. amoenus* but differs primarily in the size of the plants, seta length and absence of peristome. This range of variation in morphological features is present in other species such as *T. longicollis*. The relationship between *T. amoenus* and *T. flexipes* warrants further investigation and should the two taxa prove to be the same species, *T. flexipes* would take precedence.

**Notes:** After van Zanten examined the types of both *T. flexipes* and *T. alpinus* and compared them with specimens of *T. flexipes* on Marion Island, he reduced *T. alpinus* to synonymy of *T. flexipes* (van Zanten, 1971: p. 184–185, 187 Fig. 4 (1a–f). When Willis (1955) described *T. alpinus*, he wrote on the herbarium sheet "very close to *T. flexipes* and possibly only a form of it". Scott & Stone (1976: 64) also considered *T. alpinus* as a minute alpine form of *T. flexipes* with an identical range of spore size.
Fig. 2. *Trematodon flexipes*. A. Fertile plant; B–D. Stem leaves; E–G. Perichaetial leaves; H. Cells of leaf apex; I. Cells of shoulder region of stem leaf; J, K. Transverse sections of leaf subula; L. Transverse section of shoulder region of leaf; M, N. Sections of leaf base; O. Stem section; P. Peristome teeth; Q. Stomate from capsule urn; R. Stomate from capsule neck; S. Annular cells; T. Spores.

Scale bars: 1.0mm for plants and leaves; 100µm for cells, sections and spores.

Drawn from W. Archer (HO 73656).
Representative specimens examined: NEW SOUTH WALES: North Coast: Seal Rocks, 32°25’31’S 152°30’41’E, 27 Sep 2006, A.J. Downing s.n. (NSW 749532, MQU); Southern Tablelands: Mt Kosciuszko, 36°25’S 148°19’E, 2 Feb 1968, W. Weber B–29800 and D. McVean (as T. alpinus) (CANB 191568); Merritt’s Camp, Mt Kosciuszko, 36°28’S 148°18’E, Jan 1899, W. Forsyth 189 (as T. alpinus/T. pygmaeus) (NSW 299422).

AUSTRALIAN CAPITAL TERRITORY: Angle Crossing, Murrumbidgee River, 35°35’S 149°06’E, 11 Mar 1962, N.T. Burbidge 7314 (CANB 115111.1). VICTORIA: Eastern Highlands: Mt Baw Baw, 37°49’S 146°16’E, 1463.04 m., 20 Mar 1951, J.H. Willis s.n. (MEL 1031385A!); Mt Hotham, 36°58’S 147°07’E, 1828 m, 12 Feb 1966, J.H. Willis s.n. (MEL 1007573A); Snowfields: Bogong High Plains, 36°52’S 147°18’E, 2 Feb 1974, I.G. Stone 7905 (MEL 2167845A); Mt Buffalo, 36°43’S 146°46’E, 1402 m, 31 Dec 1952, R. Melville (MEL 69627A!); Bogong High Plains, Mt Cope, 36°55’S 147°16’E, 1706.88 m, 21 Jan 1952, C. Skewes s.n. (MEL 0032674A); Otway Range: Lavers Hill, Colac-Otway, 38°40’S 143°22’E, 26 Nov 1961, J.H. Willis s.n. (MEL 2056953A).

TASMANIA: Ben Lomond: North Tasmanian Alpine Club, Ben Lomond National Park 41°32’S 147°30’E, Feb 1967, D. McVean 267138 (CBG 9211721.1); Macquarie Island: 2 km S of Green Gorge, 10 Jan 1980, R.D. Seppelt 20362 (MEXUBR).

3. Trematodon longicollis Michx., Flora Boreali-Americana 2: 289 (1803).

Type citation: “In arenosis Carolinae”

Type: n.v. (not located).

=Trematodon baileyi Broth., Öfvers. Förh. Finska Vetensk.-Soc. 33: 91–92 (1891).

Type citation: Patria, Queensland, Mulgrave River, ubi in terra anno 1889 legit F.M.Bailey.

Type: Mulgrave River, Mt Bellenden Ker, 1889, F.M. Bailey Hb652 (lectotype designated by Ramsay et al. (2018): H-BR 4270023! isotypotypes: BRI AQ 722014!, NSW 755030!). Residual syntype: F.M.Bailey Hb 670 (H-BR 4270021!, NSW, BRI).

=Trematodon brachyphyllus Müll.Hal., Hedwigia 37: 109 (1898).

Type citation: “Australia Tropica”, Queensland: F.M.Bailey s.n. in Hb. Brotheri.

Type: Australia Tropica F.M.Bailey, Hb233 (holotype: H-BR 4270022!)

=Trematodon longescens Müll.Hal., Hedwigia 37: 109 (1898).

Type citation: Australia, New South Wales, Sydney: Domina Kayser in Hb. Geheeb 1872; Richmond River: Capt. Stackhouse in Hb. Melbourne 1881; Brisbane, F.M.Bailey in Hb. Brotheri 1881.

Type: Queensland, Moreton, Beenleigh, Brisbane, C.J.Wild Aug 1887 (F.M.Bailey Hb. 440) (lectotype designated by Ramsay et al. (2018): H-BR 4274008!; isotypotypes: BRI AQ733989!). Epitype (designated by Ramsay et al. 2018): New South Wales, Murwillumbah, Sep 1900, T.Forsyth 656 (NSW 754640!)

Note: The epitype in Ramsay et al. (2018) was incorrectly cited as NSW 754650 in the type data, but was correctly cited later in the text.

Illustrations: Bartram (1939: plate 2, Fig. 26); Fleischer (1927, 1977): p. 296, Fig. 49 a–e as T. acutus); Crum and Anderson (1981: p.163, Fig. 67 H–L); Magill (1981: p.116, Fig. 21–29, 30); Kumar (1985: 15, plate III); Gangulee (1987: 232, Fig. 106); Eddy (1988: 106, Fig. 98 a–f)) Cao and Gao (1988: 325–326, 328, Figures 1–3); Norris and Koponen (1990: 5–9): Fig. 1 a–g; Zander (2007: 436).

Autoicous. Plants small to medium sized, in loose yellow-green tufts. Stems simple, 1–8 mm long. Leaves small and scale-like below, becoming progressively larger above, 1.0–3.0(–8.0) mm long, erect-spreading, ±flexuose when moist, from an ovate-oblong sheathing base 1.0–2.0 mm long, contracting gradually or abruptly to a broad flexuose channelled subula 2.0–6.0 mm long, subula contorted or crispate when dry; apex denticulate; margins unistratose in base, bistratose to occasionally tristratose patches in subula; lamina cells in subula and upper part of sheathing base ±irregular in outline, subquadrate, quadrate, short-rectangular to irregularly hexagonal, ±equidimensional to ca. 3 by 1, becoming more elongate and broader to ca. 5–10 by 1 in leaf base, thin-walled throughout; costa narrow throughout, occupying ca. 1/3 width of subula, subpercurrent, in section with weakly defined adaxial and abaxial bands of substereid cells.
Fig. 3. *Trematodon longicollis*. A. Fruiting plant B. detached capsule; C–D. Stem leaves; E. Perichaetial leaf; F. Cells of subula margin; G. Cells of shoulder region of leaf base; H. Cells of leaf base; I–K. Transverse sections of subula; L–M. Transverse sections of basal part of leaf from near point of attachment; N. Section of costa; O. Stem section; P. Spores.

Scales: 1.0mm for plants and leaves; 100µm for cells, sections and spores.

Drawn from Japan: Musci Japonicae Exsiccatae Ser. 21. No. 1048 (Hattori Botanical Laboratory); also see as figures 1–5 in Ramsay et al. (2018).
Perigonia terminal on short lateral branches. Perichaetia terminal. Perichaetal leaves larger than stem leaves, 5.0–8.0 mm long, subulate from an elongate ovoid sheathing base, subula 1–3 times longer than base, ±crespite when dry. Setae slender, erect to ±flexuose, 8.0–30.0 mm long. Calyptra cucullate. Capsule slender, arcuate, 5.0–7.0 mm long, urn oblong-cylindric, neck 2–2.5x length of urn, ±twisted when dry, strumose at base, stomata confined to neck; exothecal cells rectangular, 3–7 by 1, with thick curved lateral walls; annulus compound, revolute, of 2–3 layers of rectangular enlarged cells; operculum from a conic base obliquely long-rostrate, the rostrum often as long as urn; peristome single, teeth reddish, linear-lanceolate from a low basal membrane, 330–430 μm long, deeply cleft into two filaments or joined and perforate, margins pale papillose, tips of filaments often joined, pale whitish. Spores subreniform to rounded, baculate-verrucose, lacking a trilette scar, 15–25 μm in diameter. Figure 3.

Distribution and Ecology: Trematodon longicollis has been reported from Europe, North, Central and South America, Asia, Africa, India, Malesia, Papua New Guinea and Australia. Known in Australia from Western Australia, Queensland, New South Wales, Victoria. Distribution in Australia: Map 3. It is a gregarious species of damp and disturbed soils of exposed banks and soil over rock.

Recognition: The species, as presently circumscribed, is morphologically plastic (Bartram 1939; Gangulee 1987; Noguchi 1987; Eddy 1988; Cao and Gao 1988; Iwatsuki and Suzuki 2006; Zander 2007) with some 36 taxa included as synonyms (TROPICOS) and additional synonyms recently proposed by Ramsay et al. (2018). Only limited detail is given in the protologue of T. longicollis. However, the species has been illustrated for eastern North America, the type region, by Crum and Anderson (1981) and Zander (2007). Illustrations by Cao and Gao (1988) reveal the wide range of variation found in capsules, seta length and leaves in Chinese collections. They concluded that seta length, leaf size and shape and whether or not the leaf subula arose abruptly or gradually from the sheathing base, were all unreliable identification features. The most reliable identifiers were found to be the ratio of capsule neck to urn length and the costa not occupying the full subula width. More recent coloured illustrations from India (Schwartz 2014: plate 1 p3; Fig. 1–10 p. 8) demonstrate the major important features while new details in leaf cell structure, not discussed elsewhere, are presented by Ramsay et al. (2018: Figures 1 and 7).

Notes: Over 100 unnamed Trematodon collections, mostly made by Ilma Stone, were examined from Australian herbaria (NSW, MEL, BRI, HO), together with all specimens previously named as T. baileyi, T. brachyphyllus or T. longescens. These three Australian taxa, previously considered as endemic (Streimann and Klazenga 2002), are morphologically very similar to T. longicollis but had not been critically appraised since their original description until the type specimens were examined and illustrated for the first time. As a result, these have been transferred to synonymy with T. longicollis (Ramsay et al. 2018).

Representative Australian specimens examined: WESTERN AUSTRALIA: Fitzgerald: Halls Creek, Samim mining camp, 19 km E of Osmond Valley Palms Yard, 17°14′25″S 128°26′E, 15 May 1984, E.A. Chesterfield 237 with J.H. Willis and S.I. Forsyth (MEL 1047743A, PERTH) (sterile as T. acutus). QUEENSLAND: North Kennedy: Mt Bellenden Ker, 17°16′S 145°30′E, 1 Aug 1979, I.G. Stone 15625 (MEL 2226248A); Mullgrave River, Mt Bellenden Ker, 17°30′S 145°30′E, 1889, F.M. Bailey Hb652 [as T. baileyi] (BRI AQ0722014); Kennedy Highway 32 km NE of Mareeba 5 km SW of Kuranda, 16°50′S 145°35′E, 26 Apr 1984, S.P. Churchill 12519 (CBG 9211738.1); Rainforest Lodge, Kuranda, 16°49′S 145°38′E, 6 Jul 1994, R.G. Covery 16763 (NSW 775075); Cook: Cape Tribulation, 16°04′S 145°28′E, 28 May 1984, I.G. Stone 21950, (MEL 2262570A); Crystal Cascades, Cairns, 16°55′S 145°46′E, 31 Aug 1980, I.G. Stone 16757 (MEL 2237987A); Moreton: Mt Coot-tha, 27°28′S 152°57′E, 3 Aug 1983, I.G. Stone 20943 (MEL 2258208A!). NEW SOUTH WALES: North Coast: Murwillumbah, 28°19′S 153°23′E, Sep 1900, T. Forsyth 656 [epitype of T. longescens] (NSW 754640); Myocum, Brunswick River, 28°36′S 153°31′E, Sep 1897, W.W. Watts s.n. (MEL 29261A) (as T. adequans renamed as T. baileyi by I.G. Stone in 1976); Central Tablelands: Grose Vale, Berringa Lodge 6 km SSW of Kurrajong, 33°35′47″S 150°38′45″E, 25 Sep 2001, V. Stajic and N. Klazenga VS 2863 (MEL 2138621) (as T. longescens); Grose Vale, 33°35′55″S 150°38′45″E, 25 Sep 2001, R.G. Covery 18931 (NSW 795414!). VICTORIA: Eastern Highlands: Austraflora Nursery, Montrose, 37°48′2″S, 145°20′38″E, 15 Sep 1977, I.G. Stone 14411 (MEL 2219455A).

4. Trematodon mackayi (R.Br.bis) Broth., Die Natürlichen Pflanzenfamilien 1(3): 292 (1901).

Basionym: Stirtonia mackayi R.Br. bis. Trans. N.Z. Institute 32: 149 (1900).

Type citation: New Zealand, Stewart Island, Jun 1889 or Jan 1892, R. Brown s.n. holotype: CHR 330901.

Type: Stewart Island, Jan 1892, R. Brown s.n., (lectotype (designated by Fife 2016): CHR 330901, subtype or isotype: WELT MO 212581).
The genus *Trematodon* (Bruchiaceae) in Australia

**Fig. 4.** *Trematodon mackayi*. A. Fertile plant; B. Capsule with operculum; C–F stem leaves; G–I. Perichaetial leaves; J. Marginal cells of leaf subula; K. Cells of leaf shoulder region; L–N. Transverse sections of leaf subula; O–Q. Transverse sections of leaf base; R. Stem section; S. Capsule mouth showing reduced peristome and upper exothecial cells; T. Stomate at base of capsule urn; U. Annular cells; V. Spores. Scales bars: 1.0mm for plants and leaves; 100µm for cells, sections and spores.

Drawn from: *W. Forsyth* 14, ii.1902 (NSW 755021) (Figs A–S, U,V); *T.B. Moore* iii.1900, in Hb. W.A. Weymouth (HO 73687) (Fig. T).
Type citation: Tasman: West Coast, near Moore’s Lookout, T.B. Moore s.n. Mar 1900, in Hb W.A. Weymouth 2868b.

Type: near Moore’s Lookout, Mar 1900, T.B. Moore s.n. (holotype: HO 73687!, isotypes: WELT, MO 412871, MO 41286).

Illustrations: Sainsbury (1955: plate 14, Fig. 1). Fife (2016) Plate 1 (A–F).

Dioicus. Plants 2–6 mm tall, yellow-green. Stems mostly unbranched; stem leaves erect spreading, upper leaves 2.0–4.0 mm long, distant and erect-spread, from a broad oblong, concave sheathing base abruptly contracted to a narrow flexuose subula 2–3 times as long as base, contorted when dry, margins entire or denticulate at the apex; costa narrow in lower leaf base but broadening above to ±filling subula, sometimes slightly excurrent; in cross section with a median row of guide cells and adaxial and abaxial bands of smaller firm-walled stereid cells. Lamina cells at base thin-walled, 70–110 x 12–20 μm, rectangular or irregularly 4–6 sided, cells at margin of subula very short, narrowly oblong, marginal cells unistratose throughout.

Perigonia terminal, gemmiform. Perichaetial leaves much larger than stem leaves, 7.0–8.5 mm, suberect with long rigid subula from a large ovate-oblong sheathing base; subula 2–3 times length of leaf base. Calyptra cucullate to mitriform and 2–4 lobed at base, covering operculum and urn. Setae slender, straight to slightly flexuose, 8–15(–25) mm long, pale yellow; capsules narrow, oblong, straight or slightly arcuate, erect or suberect, (1.5–)2–3.8(–5.0) mm long, neck slender, variably strumose at base; annulus of 2–3 rows of enlarged thin-walled cells, persistent to revolute; operculum with slender, slanting rostrum from 1.0 mm to as long as the urn, dehiscent; peristome reduced to a short, hyaline basal membrane or gymnostomous. Spores large, (48–)50–66(–75) μm, coarsely baculate. Chromosome number not known. Figure 4.

Distribution and Ecology Trematodon mackayi is a distinct and relatively widespread species in temperate Australia and New Zealand. In Australia known from New South Wales, Victoria, Tasmania. Distribution in Australia, Map 4. In Australia, T. mackayi occurs on peaty soils, often in upland areas. In New Zealand the species usually occurs on peat or pakihi where it is often found following fire (Fife 2016).

Recognition: T. mackayi can be distinguished readily by the structurally different costa that completely fills the leaf subula; the large calyptra covering the operculum and urn; the highly reduced peristome lacking all but the basal membrane; and the largest spores of any species in the genus.

Notes: In Fife (2016), the following information regarding T. weymouthii is included. “Although the protologue indicates that T. B. Moore was the collector of the type, the duplicates in WELT are labelled as collected by L. Rodway.”

Representative specimens examined: NEW SOUTH WALES: Southeast Slopes: Tumut, Between Mount Gingera and Blackfellows Saddle, 35°34'S 148°46'E, May 1959, N.T. Burbridge 6919 (MEL 69631A); Southern Tablelands: Captains Flat, 35°35'S 149°27'E, 600 m, 9 Oct 1979, H. Streimann 9496 (CANB 8000275.1); Central Tablelands: Neates Glen, Blackheath, 33°39'S 150°18'E, Feb 1902, W. Forsyth s.n. (NSW 755021); Central Coast: Wyong, 33°16'S 151°26'E, (no date given) W.W. Watts NSW10913 (NSW 755028). VICTORIA: East Gippsland: Cicada Trail, 37°44'S 149°24'E, 22 Nov 1969, A.C. Beauglehole 31964 (MEL 69630A); Otway Range: Chapple Vale Flora and Fauna Reserve, Crinoline Creek, 38°37'S 143°21'E, 122 m, 27 Dec 1973, A.C. Beauglehole 74297 (MEL 2046887A). TASMANIA: West Coast: near Moore's Lookout, 42°49'S 145°30'E, Mar 1900, T.B. Moore s.n. (HO 73687).

5. Trematodon suberectus Mitt. in Hook.f. Handbook of the New Zealand Flora: 415 (1867).

Type citation: Northern and Middle Islands, on clay banks, Bay of Islands, J.D.H.; Wellington, Lyall.

Type: Bay of Islands on clay banks J.D. Hooker 341 (NY–Mitten).

=Trematodon adaequans Geh. ex Roth., Hedwigia 53: 97. 2 f 3 (1913).

Type citation: Von Whitelegge in Neu-Süd-Wales, an der Boll's (=Balls) Head Bay, entdeckt und auch von Rev. W. W. Watts am Richmond River daselbst häufig gesammelt.

Type: Bolls (=Balls) Head Bay, Sydney, 18 Oct 1885, T. Whitelege 226 (lectotype designated here: NSW 299415!; residual syntype: Tenen, Richmond River, 2 Sep 1896, W.W. Watts NSW1937 NSW 75472?)

=Trematodon cheesemanii Müll.Hal. Hedwigia 37: 110 (1898).

Type citation: New Zealand: Kermadec Group, Sunday (Raoul) Island, T.F. Cheeseman
Type: Kermadec Islands, Sunday (Raoul) Island *T.F. Cheeseman s.n.* (AK 121129; AK 121130) *fide* A. Fife 2016.

= *Trematodon abruptus* Watts et Whitelegge Proc. Linn. Soc. New South Wales Suppl. 27: 31 (1902) *nom. inval.*

Type citation: New South Wales: Bellingen and Macleay Rivers.

= *Trematodon whiteleggei* Broth. in Watts and Whitelegge Proc. Linn. Soc. New South Wales Suppl. 27: 32 (1902) *nom. inval.*

Type citation: Australia: New South Wales: clay banks opposite railway line, Clifton, Aug 1891.

*Type:* *T. Whitelegge* (NSW 299424! NSW 755017! NSW 754771!)

Illustrations: Sainsbury (1955) Plate 14, Fig. 3; Fife (2016) Plate 2.

Plants variable in size, bright or yellow–green. Stems 2–7 mm, sparingly branched by innovation. Leaves erect-spreading with a sheathing base tapering to a long subula; basal leaves small; upper stem leaves larger, base ovate-oblong ± gradually tapering to an elongate subula 1.5–2.0 times as long as base; subula narrowly laminate below; costa only 1/6 width of leaf base but ± filling upper subula and ± reaching apex; apex denticulate; margin smooth and unistratose in leaf base to lower part of subula, bistratose in upper subula. Laminal cells of leaf base and lower subula elongate rectangular, thin-walled, smooth; upper cells above shoulder small, quadrate to rhomboid; costa in section with both abaxial and adaxial stereid bands.

Autoicous or rhizautoicous. Perigonia terminal on shoots. Perichaetia terminal on shoots. Perichaetal leaves about twice the size of the stem leaves with base oblong and subula 1–2 times length of base, gradually subulate; subula straight to ± flexuose with elongate rectangular thin-walled cells in base 60–105 times ca.15–21 μm. Seta erect, slender, straight or weakly flexuose, yellow, (5–)13–15–39 mm. Capsule suberect or slightly curved, urn cylindrical, neck longer than but less than twice as long as urn; weakly to strongly strumose at base; exothecial cells elongate; annulus revoluble; operculum conic, rostrate, rostrum up to length of urn; annulate; Peristome of 16 well-developed teeth, narrowly lanceolate, usually split to base into two often unequal segments fused apically, perforations scattered; basal membrane well developed. Spores 20–25(–33) μm, coarsely baculate-insulate. Chromosome number n=14 (Ramsay 2009; 2011). Figs 5, 6, 7.

Distribution and Ecology: The species has affinities with Malesian, Japanese and South American species. Known in Australia from Queensland, New South Wales including Lord Howe Island (Brotherus and Watts 1915) and Victoria. Distribution in Australia: Map 5. *Trematodon suberectus* occurs as a coloniser of bare soil in disturbed habitats in Australia and in New Zealand where it is common and occurs on both the North and South Islands, and Stewart Island (Sainsbury 1955; Beever et al. 1992). It is also reported from the Kermadec Islands (Beever et al. 1996) where it grows on pumice and is quite tolerant of geothermal activity and heavy metal concentrations (Sainsbury 1930).

Recognition: Fife (1996) examined two collections from the Kermadec Islands collected by Cheeseman on Sunday (Raoul) Island (AK 181732, WELT MO 31623) and named by Brotherus (1891) which he believes “may be part of the original material from which a portion was sent to Mueller for description of *Trematodon cheesemani*ii” (Mueller 1890). Fife (1995) records *T. cheesemani*ii as a synonym of *T. suberectus* following Sainsbury (1930, 1955). The most recent list of mosses from the Kermadec Islands (Raoul [Sunday] Is.) lists the single species *T. suberectus* (de Lange and Beever 2015). The record of *T. suberectus* from Lord Howe Island is new here, although the genus *Trematodon* was recorded by Brotherus and Watts (1915). During re-examination of the two collections at NSW made by W.W. Watts, some capsules were located which, together with leaf structure, identified them as *T. suberectus*.

Notes: During our studies we have noted a strong similarity between *T. suberectus* and *T. longicollis*. One of the characters separating them is the ratio of capsule neckcurn — up to but not exceeding 2:1 in *T. suberectus* but more than 2:1 in *T. longicollis*. Other features such as the costa filling the upper subula, and costal anatomy in the subula also differ in the two species.

Seta length is variable. The capsule has a neck that exceeds the urn length but is rarely twice as long. The peristome teeth often have unequally bifid arms, but this also varies. A distinguishing feature of this species is the costa filling or almost filling the upper leaf subula (best seen in leaf sections — refer to Figs 5, 6) and a mostly unistratose margin, being bistratose only in the upper subula. This row of cells is absent in the costa of the upper leaf base in *T. longicollis* and the distinct lower epidermal-like cells present in *T. longicollis* are absent in *T. suberectus*. A comparison of leaf sections of *T. longicollis* (Ramsay et al. 2018 Fig. 7) and *T. suberectus* (Fig. 6 here) suggests their retention as separate species. We have therefore retained it as a separate species differing from *T. longicollis*, pending further revisionary studies.
Fig. 5. *Trematodon suberectus*. A. Fruiting plant; B–C stem leaves; D. Perichaetial leaf; E. Cells of leaf apex; F. Cells of leaf shoulder region; G. Cells of basal part of leaf; H–J. Transverse sections of leaf subula; K. Transverse sections of leaf shoulder region; L–M. Transverse sections of basal part of leaf; N. Stem section.

Scale bars: 1.0 mm for plants and leaves; 100μm for cells, sections and spores.

Drawn from *A.C. Beauglehole 73130 (HO 538855 ex MEL 1044922)*
**Fig. 6.** *Trematodon suberectus*. A. Fruiting plant; 2. B–C. capsules; D–E. Stem leaves; F–G. Perichaetial leaves; H. Cells of leaf apex; I. Cells of leaf shoulder region; J. Cells of leaf base; K–M. Transverse section of leaf subula; N–O. Transverse sections of leaf base; P. Stem section; Q. Peristome teeth; R. Spore.

Scale Bars: 1.0 mm for plants and leaves; 100μm for cells sections and spores.

Drawn from *John Child* 6462 (H0 52759 ex CHR 432666)
Fig. 7. Maps showing distribution of *Trematodon* species in Australia
1. *T. amoenus*; 2. *T. flexipes*; 3. *T. mackayi*; 4. *T. longicollis*; 5. *T. suberectus*
The genus *Trematodon* (Bruchiaceae) in Australia *Telopea* 23: 1–19, 2020 17

The only DNA record for *T. suberectus* in GenBank is for the cpDNA gene: ATP synthase beta subunit (atpB) (Fiz-Palacios *et al*. 2011), but unfortunately there are no data for *T. longicollis* for comparison (Ramsay *et al*. 2018). Until a world revision of *Trematodon* is carried out, including molecular analyses, we prefer to retain *T. suberectus* as a separate species.

**Representative specimens:** QUEENSLAND: **North Kennedy:** Wild River, Herberton, N. of Ravenshoe, 17°23’S 145°23’E, 24 Dec 1938, H. Flecker 5500 (CANB 362264, BRI AQ0733991); Kennedy Highway, 7 miles N of Ravenshoe, 17°30’S 145°30’E, 7 May 1974, D.H. Norris 41270 (BRI AQ0733990, CBG 9211740.1); Birthday Creek, Mt Spec 18°59’S 146°10’E, 29 Oct 1995, H. Streimann 58032 (CBG 9607537.1!). NEW SOUTH WALES: **North Coast:** Ballina, off Tintenbar Road, 25°50’54”S 153°33’04”E, 14 Sep 1899, W.W. Watts NSW3645 (NSW 754764); Alstonville 28°49’S 153°26’E, May 1896, W.W. Watts NSW433 (NSW 754736) (as *T. adaequans*); Coopers Creek near Federal 28°40’5’S 153°25’E, Oct 1901, W.W. Watts NSW5163a (as *T. adaequans*) (NSW 754767); **Central Coast:** Wyong 33°16’S 151°25’E, 11 Sep 1908, W.W. Watts NSW9590 (NSW 755023); **Lord Howe Island:** South of Kings 31°34’S 159°05’E, 15 Jul 1911, W.W. Watts LHI214 (NSW 755018); Nov 1981, D.H. Vitt 28749 (ALTA).

**VICTORIA:** **East Gippsland:** Errinundra, 37°24’S 148°54’E, 30 Sep 1970, A.C. Beauglehole 73130 (CANB 672109.1, MEL 1044922, HO 73817); **Snowfields:** Mt Buffalo 36°46’’S 146°46’’E, 1402 m, 31 Dec 1952, R. Melville 2653 (MEL 1031481A).

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