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A REVIEW OF THE TUBIFICIDAE (ANNELIDA: OLIGOCHAETA) FROM AUSTRALIAN INLAND WATERS

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Abstract

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The Australian limnic representatives of the cosmopolitan oligochaete family Tubificidae are reviewed. The four Australian species of *Telmatodrilus* Eisen, 1879 are placed in new genera (*Breviatria* and *Biprostatus*) and these are considered to belong to Rhyacodrilinae rather than Telmatodrilinae. Four new species, *Rhyacodrilus megaprostatus, Ainudrilus nharna, Breviatria arvensis* and *Biprostatus duplex* are described and *Rhyacodrilus fultoni* Brinkhurst, 1982 is transferred to *Ainudrilus* Finogenova, 1982. *Limnodrilus claparedeianus* Ratzel, 1868 and *Aulodrilus limnobius* Bretscher, 1899 are recorded in Australia for the first time. The Australian fauna now consists of 29 described species, including 11 of the most widespread species of cosmopolitan genera (*Tubifex* Lamark, 1816, *Potamothrix* Vejdovský and Mrazek, 1902, *Limnodrilus* Claparède, 1862, *Aulodrilus* Bretscher, 1899, *Rhyacodrilus* Bretscher, 1901, *Bothrioneurum* Stolc, 1886 and *Branchiura* Beddard, 1892). *Antipodrilus* Brinkhurst, 1971, with five species, and the two new rhyacodriline genera, with six species, are essentially Australian genera, except that one species of *Antipodrilus* and possibly one of *Biprostatus* also occur in New Zealand. Seven endemic species belong to more widespread genera (*Rhizodrilus* Smith, 1900, *Rhyacodrilus* and *Ainudrilus*). The Australian tubificid fauna appears to have biogeographic affinities with northern hemisphere and marine tubificids.

Introduction

The first tubificid to be described from Australia was *Branchiura pleurotheca* Benham, 1907 from Blue Lake, Mt Kosciusko. Further tubificid records and descriptions from Australia were not published until Brinkhurst (1971a, b) reviewed the aquatic oligochaete faunas of the world and Australia. In these publications, *Branchiura pleurotheca* was synonymised with *Rhyacodrilus coccineus* (Vejdovský, 1875), several other new species and a new genus (*Antipodrilus*) were described and the presence of numerous cosmopolitan species was recorded. Subsequent records and descriptions of new species were provided by Brinkhurst and Fulton (1979) and Brinkhurst (1982, 1984).

In this paper we list previous records and add many new ones for most species, improve some descriptions, describe four new species and address problems relating to the taxonomic position of Australian species of Telmatodrilinae by moving them to two new rhyacodriline genera. This contribution is intended to provide a foundation for future work, complementing the recent review of the Australian Phreodrilidae (Pinder and Brinkhurst, 1997). Our definition of the Tubificidae is conservative, excluding the Naididae which are generally acknowledged to be part of the same taxon (Brinkhurst, 1994; Erséus, 1990b), although a formal proposal to merge the families has yet to be made.

Materials and methods. Most specimens were stored in ethanol, often after fixation in formalin. They were then whole-mounted, dissected or serial sectioned. Dissected or whole-mounted specimens were usually first stained in Grenacher's borax carmine. Sectioned specimens were cut at 6 mm and stained in Mayer's haematoxylin and eosin.

Descriptions are limited to brief diagnoses, with important distinguishing characteristics, except for new species, or where an original description can be substantially amended.

The term chaetae is used in preference to setae, following a determination at the International

Symposium on Aquatic Oligochaete Biology, Presque Isle, Maine, USA, 1997. Roman numerals refer to segment numbers and two arabic numerals separated by a slash refer to the septum (or intersegmental furrow) separating two adjacent segments. Body lengths are for preserved specimens and are indicative of the length of mature specimens only.

Where details of the holotype are not given, as is the case for some of the earliest described cosmopolitan species, this information is unknown and not listed in Reynolds and Cook (1976, 1981, 1989, 1993).

Institutions and collections are abbreviated as follows: AMS, Australian Museum, Sydney, NSW; AMP, Adrian Pinder collection; AWT, Australian Water Technologies, Sydney, NSW; BGMJ, Barrie Jamieson collection, Brisbane, Qld; CALM, Wildlife Research Centre, Department of Conservation and Land Management, Perth, WA; ERISS, Environmental Research Institute of the Supervising Scientist, Jabiru, NT; IFC, Inland Fisheries Commission, Hobart, Tas.. (all collections now in QVM); MDFRC, Murray Darling Freshwater Research Centre, Albury, NSW (J. Hawking); MNHN, Museum National d'Histoire Naturelle, Paris, France; MON, Ecology and Evolutionary Biology, Monash University, Melbourne, Vic.. (P.S. Lake); MUR, Aquatic Ecosystems Research, Environmental Science, Murdoch University, Perth, WA (J. Davis); NMV, Museum Victoria, Melbourne, Vic.; NTM, Museum and Art Gallery of the Northern Territory, Darwin, NT; QVM, Queen Victoria Museum, Launceston, Tas.; ROB, Ralph Brinkhurst collection; SAM, South Australian Museum, Adelaide, SA; TAS., Tasmanian Museum, Hobart, Tas.; UCA, University of Canberra, Canberra, ACT (R. Norris); USNM, National Museum of Natural History, Washington, USA; WAM, Western Australian Museum, Perth, WA; ZMUH, Zoological Museum, University of Hamburg, Germany.

Abbreviations used in the figures are as follows: a, atrium; c, copulatory chamber; e, ejaculatory duct; f, female funnel; g, gut; gd, gut diverticulum; gt, glandular tissue; mf, male funnel; n, nerve cord; o, ovary; p, prostate; pa, papillae; pc, penial chaetae; pe, peritoneal tissue; s, spermatheca; sc, spermathecal chaetae; sd, spermathecal duct; t, testis; v, vas deferens.

Where possible, localities are given with latitude and longitude, Australian map grid (AMG) 1:100 000 coordinates (four digit map number followed by three eastings and three northings) or Tasmap 1: 500 000 coordinates (three eastings and three northings). Australian states and territories are abbreviated as follows: Australian Capital Territory (ACT), New South Wales (NSW), Northern Territory (NT), South Australia (SA), Queensland (Qld), Victoria (Vic.), Tasmania (Tas.) and Western Australia (WA).

Tubificidae

Diagnosis. Genitalia bilaterally paired. One pair of testes and 1 pair of ovaries, usually in X and XI respectively. Spermathecae mostly in the testicular segment. Male funnels on posterior septum of testicular segment leading to vasa deferentia, atria and male pores in the ovarian segment. Female funnels leading to pores on posterior furrow of ovarian segment. Chaetae from 1 to many per bundle, hair chaetae usually restricted to dorsal bundles or absent. Reproduction normally sexual.

Tubificinae

Diagnosis. Spermathecal pores in the middle of the testes segment in most species. In all but a few genera, sperm organised as spermatozeugmata of a specific type, with non-fertile sperm encapsulating fertile sperm. Atria each with a single stalked prostate gland (prostate rarely absent). Pendant penes usually present, often with cuticle of penis sac thickened to form a penis sheath. Spermathecal chaetae, when present, usually single, enlarged, grooved distally and with large chaetal glands. Penial chaetae normally absent, but when present then usually of similar form to the spermathecal chaetae. Coelomocytes not large and abundant.

Remarks. The spermatozeugmata found in tubificines are of a distinct form, with fertile sperm cells enclosed by a cortex of bound infertile sperm cells (Braidotti and Ferraguti, 1982; Ferraguti et al., 1994; Jamieson, 1992), distinct from the looser sperm agglomerations found in the rhyacodrilinae.

Tubifex Lamarck

Type species. Lumbricus tubifex Müller, 1774.

Diagnosis. Hair chaetae usually present dorsally, accompanied by pectinate chaetae, but polymorphic forms occur. Vasa deferentia long, often of two widths. Atria comma-shaped, with vasa deferentia opening close to the apex anteriorly, each with a large stalked prostate gland. Pendant penes present, each with a thin tub-shaped sheath. Genital chaetae not modified. Spermatozeugmata present.

Tubifex tubifex (Müller)

Lumbricus tubifex Müller, 1774: 27 (in part).

Tubifex rivulorum Lamark, 1816: 225.

Tubifex tubifex.—Michaelsen, 1900: 48.—Brinkhurst, 1971a: 453, figs 8.1A–D, 8.3G–J.—Brinkhurst, 1971b: 10, fig. 2A.—Timms, 1973: 11.—Timms, 1977: 170.—Timms, 1978: 435.—Timms, 1981: 188.—Timms, 1982: 126.—Marshall and Winterbourn, 1979: 205.

Material examined. NSW: Wingecarribee Creek, Berrima, 34º29´S 150º20´E, 7 Nov 1991, 4 specimens (AWT). Tas.: stream 4.9 km above Barrow Creek, 26 Nov 1978, 1 on slide (ROB); creek E of The Needles, 13 Nov 1978, 2 on slides (ROB); Arthur R., 31 Oct 1978, 1 on slide (ROB). Vic.: Beechworth Trout Hatchery, May 1994, 1 on slide (AMP) and Sep 1994, 2 on slides (NMV F77644–F77645); Thomson R. at Thompson Valley Rd, 24 Nov 1976, 2 on slides and 3 in alcohol (NMV F77646–F77648); Phytotelmata in fig tree, South Yarra, Melbourne, several on slide (MON). WA: Soak NW of Corrigin, 32º10´38´´S 117º49´08´´E, 21 Oct 1997, several on slides and in alcohol (CALM); Paperbark Swamp, E of Corrigin, 32º24´58´´S 118º05´52´´E, 8 Oct 1997, 1 on slide (CALM); Farm dam near Corrigin, 32º19´44´´S 118º02´24´´E, 7 Oct 1997, 2 on slides (CALM).

Other Australian records. Qld: Downfall Creek (Brinkhurst, 1971b). SA: A creek near Adelaide, no date, 1 on slide (AMP). Vic.: Lakes Bong Bong, Bridgewater, Purrumbete and Elusive (Timms, 1973, 1981, 1977). WA: Lake Monger, Perth (Brinkhurst, 1971b). Tas.: Lake St Clair (Timms, 1978).

Distribution and habitat. Cosmopolitan, including New Zealand (Brinkhurst, 1971b; Marshall and Winterbourn, 1979; Timms, 1982). Although widespread in Australia, *T. tubifex* is not commonly encountered. In the northern hemisphere *T. tubifex* is commonly found in marginal sites, such as those with heavy organic pollution or intense sedimentation or in highly oligotrophic waters (Brinkhurst, 1996). In sites with heavy organic pollution this species is usually associated with *Limnodrilus hoffmeisteri* Claparède, 1862 and these are the dominant oligochaetes or even the dominant benthic invertebrates (Brinkhurst, 1996). Studies of gross organic pollution are less common in Australia (as are ecological studies in which oligochaetes are speciated) and the Australian records of *T. tubifex* span a wide variety of habitats. This species can tolerate salinities up to 10 ppt (Chapman et al., 1982) and mature worms can encyst to survive short periods of drought (Kaster and Bushnell, 1981).

Diagnosis. Length 20–200 mm. Anterior dorsal bundles with 1–6 hair chaetae and 3–5 pectinate chaetae with irregular intermediate teeth. Hair chaetae and pectinate chaetae reduced posteriorly. Ventral chaetae bifid, 6–10 per bundle anteriorly, with the upper teeth thinner than but not much longer than the lower, posteriorly with the upper teeth relatively shorter and fewer chaetae. Polymorphic forms with hairs short and bifid chaetae dorsally, or bifid chaetae both dorsally and ventrally, may be found, especially where conductivity is high. Vasa deferentia elongate, divided into thin and thick sections, entering the comma-shaped atria on the concave side, near the where the prostate glands join. Penis sheaths tub-shaped but often indistinct.

Limnodrilus Claparède

Limnodrilus Claparède, 1862: 221, pl I figs 1–3, pl. III fig. 12, pl. IV fig. 6.—Michaelsen, 1900: 42.—Stephenson, 1930: 747.—Brinkhurst, 1971a: 463.

Type species. Limnodrilus hoffmeisteri Claparède, 1862.

Diagnosis. Dorsal and ventral chaetae bifid, hairs absent. Vasa deferentia long, entering short bean-shaped atria apically. Prostates large, entering atria by short stalks. Atria connect, via long ejaculatory ducts, to pendant penes lying free within thick penis sheaths (formed by the thickened cuticle of the penis sac wall) of varying lengths, some longer than the body width. No modified genital chaetae. Spermatozeugmata present.

Remarks. Mature specimens of the three species present in Australia are readily separable by examining the penial sheaths. These are usually visible through the body wall of cleared and slide mounted specimens.

Limnodrilus hoffmeisteri Claparède

Limnodrilus hoffmeisteri Claparède, 1862: 248, pl. I, figs 1–3, pl. III, fig. 12, pl. IV, fig. 6.—Brinkhurst, 1971a: 464, figs 8.3M, O, 8.4C, H, I, 8.5E.—Brinkhurst, 1971b: 112, fig. 2B.—Brinkhurst and Fulton, 1979: 1.—Fulton, 1983a: 778.—Fulton, 1983b: 792.—Timms, 1978: 428.—Timms, 1982: 126.—Marshall and Winterbourn, 1979: 205.

Clitellio (Limnodrilus) hoffmeisteri.—Valliant, 1890: 424.

Tubifex hoffmeisteri.—Ditlevsen, 1904: 422.

Material examined. ACT: Murrumbidgee R., 1987–1988, returned to R. Norris (UCA). NSW: Georges R. at Liverpool Weir, 1995, 1 on slide (AMS W7876); Meggaritys Creek at Warradale Rd, 33º54´S 150º36´E, 9 Feb 1993, 1 on slide (AWT); Rushy Billabong, 36º02´S 146º42´E, 5 Sep 1984, 1 on slide (MDFRC); Ryans Billabong, 36º06´S 146º58´E, 30 Jun 1981, 1 on slide and 1 in alcohol (MDFRC); Orphan School Creek, Kings Park, 3 May 1996, 1 on slide (AWT). Qld: Bulimba Creek, Brisbane, 4.8 km from mouth, 4 on slides (AMS W18081). SA: Valley Lake, Mt Gambier, 37º50´S 140º46´E, 26 Feb 1978, 1 on slide (AMS W18084). Vic.: La Trobe R. at Moe—Willow Grove Bridge Rd and 100 m downstream of Moe Drain, AMG 8121–346773 and 8121–359769 respectively, Jul 1980, 2 on slides (NMV F77626–7); Mitta Mitta R., 2 km downstream of Dartmouth Dam, 31 Jan 1975 and Nov 1975, 3 on slides (NMV F77628, F77629, F77631) and 4 km N of Eskdale, 1 Feb 1975, 1 on slide (NMV F776230). WA: Munday Swamp, Perth, 22 Nov 1989, 1 on slide (WAM 41–95); Fire dam on Seven Day Rd, Warren R. catchment, 34º19´S 115º58´E, 4 in alcohol, 1 on slide (WAM 39–95 and 40–95); stream across Bussell Highway, 34º08´32´´S 115º06´41´´E, 15 Sep 1996, 1 on slide (AMP).

Other Australian records. Tas.: Arthurs Lake and Lake Sorrel (Fulton, 1983ab); Great Lake (Brinkhurst and Fulton, 1979); Lakes St Clair, Dove, Sorell, Crescent, Leake and Toombs (Timms, 1978).

Distribution and habitat. Cosmopolitan, including New Zealand (Brinkhurst, 1971b; Timms, 1982; Marshall and Winterbourn, 1979). This is the most commonly encountered *Limnodrilus* and is found in many habitat types, reaching very high abundance in organically enriched sites, often with *T. tubifex* (Brinkhurst, 1965b). It can tolerate salinities up to 10 ppt (Chapman et al., 1982).

Diagnosis. Length 20–35 mm. Anterior bundles with 3–10 chaetae with upper teeth varying in length from slightly shorter than, to longer than, the lower and usually thinner than the lower. Fewer chaetae posteriorly. Penis sheaths up to 20 times longer than broad, ental ends slightly flared, ectal ends either with elaborate hood opening at right-angles to shaft or sometimes a plate with scalloped edges.

Limnodrilus udekemianus Claparède

Limnodrilus udekemianus Claparède, 1862: 243, pl. I, figs 4–5, pl. III, figs 13, 13a, pl. VII, fig. 1.—Brinkhurst, 1971a: 467, figs 8.4A–B.—Brinkhurst, 1971b: 113, fig. 2E.—Timms, 1978: 428.—Marshall and Winterbourn, 1979: 205.

Clitellio (Limnodrilus) udekemianus.—Vaillant 1890: 425.

Tubifex udekemianus.—Ditlevsen, 1904: 422.

Material examined. NSW: Dairy drains, Taree, 1 Apr 1987 (AMS). Qld: Bulimba Creek, Brisbane, 4.8 km from mouth, 2 on slides (immature, but with characteristic chaetae) (AMS W18082). SA: Valley Lake, Mt Gambier, 37º50´S 140º46´E, 26 Feb 1978, 1 (immature, but with characteristic chaetae) on slide (AMS W18083). WA: Katanning Creek at Katanning sale yards, 33º42´S 117º34´E, 16 Sep 1997 1 on slide (CALM).

Other Australian records. Qld: Moggill Creek, Brisbane; Downfall Creek, Chermside. Tas.: Lake Pedder (all previous from Brinkhurst, 1971b), Lake St Clair and Dove Lake (Timms, 1978). WA: Lake Monger, Perth, uncertain identification (Brinkhurst, 1971b).

Distribution and habitat. Cosmopolitan, including New Zealand (Brinkhurst, 1971b; Marshall and Winterbourn, 1979). Often, though not exclusively, found in organically polluted situations.

Diagnosis. Length 20–90 mm. Anterior chaetal bundles with 3–8 bifid chaetae with the upper teeth much thicker and longer than the lower, fewer chaetae posteriorly with teeth more nearly equal. Penis sheath usually only up to 4 times as long as wide with a simple plate-like hood usually reflected back over the shaft.

Limnodrilus claparedeianus Ratzel

Limnodrilus claparedeianus Ratzel, 1868: 590, pl. XLII, fig. 24.—Michaelsen, 1900: 45.—Brinkhurst, 1971a: 468, figs 8.3Q, R.—Brinkhurst, 1971b: 113, fig. 2F.

Tubifex claparedeianus.—Ditlevsen, 1904: 422.

Material examined. Vic.: Lake Thirlemere, 8 Sep 1981, 2 on 3 slides (NMV F81432).

Distribution and habitat. Cosmopolitan (Brinkhurst, 1971b), occurring in a wide range of habitat types.

Diagnosis. Length 30–60 mm. Anterior bundles with 4–9 bifid chaetae, some with the upper teeth much longer than and as thick or somewhat thicker than the lower, fewer chaetae posteriorly. Penis sheaths up to 50 or even 80 times longer than broad with small triangular plates set at an angle to the shaft distally.

Remarks. This is the first and only record of this species from Australia. The shape of the penis sheath is normally diagnostic except in North America, where variants between this species and *Limnodrilus cervix* Brinkhurst, 1963 can be observed.

Potamothrix Vejdovský and Mrazek

Potamothrix Vejdovský and Mrazek, 1902: 24.—Brinkhurst, 1971a: 486.—Holmquist, 1985: 311.—Finogenova and Poddubnaja, 1990: 55.

Euilyodrilus Brinkhurst, 1962: 329.

Type species. Potamothrix moldaviensis Vejdovský and Mrazek, 1902.

Diagnosis. Hair chaetae present in dorsal bundles of most species. Vasa deferentia short, joining elongate tubular atria apically, prostate glands rudimentary or absent. Pendant penes small, without cuticular sheaths. Large grooved genital chaetae associated with spermathecal pores. Spermatozeugmata present.

Remarks. While the genus is largely holarctic, and mostly palearctic, some of the many Ponto-Caspian species appear to have been introduced to North America, Africa and South America (Peru) and others are spreading through Europe (G. Milbrink, pers. comm.). The single species occurring in Australia, *Potamothrix bavaricus* (Öschmann, 1913), is a cosmopolitan species, although it may have been introduced to some parts of its current range, e.g., South America (Brinkhurst and Marchese, 1989).

Potamothrix bavaricus (Öschmann)

Tubifex (Ilyodrilus) bavaricus Öschmann, 1913: 559, figs 1–5.

Ilyodrilus bavaricus.—Stephenson, 1930: 746.

Euilyodrilus bavaricus.—Brinkhurst, 1962: 321.

Potamothrix bavaricus.—Brinkhurst, 1971a: 492, figs 8.12H,I.—Brinkhurst, 1971b: 113, fig. 2G.—Timms, 1981: 188.—Marshall and Winterbourn, 1979: 205.

Holotype. Type locality unknown (ZMUH 7704).

Material examined. NSW: Gowrie Creek, 54 km downstream of sewage treatment plant, 27º20´S 151º27´E, 28 Sep 1995, few in alcohol (AWT). Tas.: Big Waterhouse Lake, 40º53´20´´S 147º36´50´´E, 1 Mar 1997, 2 on slide (AMP). Vic.: Curdies R., 38º20´S 143º08´E, 7 and 29 Feb 1992, 2 on slides (NMV F77641–2). WA: Malaga Wetlands, Perth, 2 Nov 1989, 2 on slides (WAM 76–95, 77–95); Herdsman Lake, Perth, 2 and 13 Nov 1989, 13 on slides, 8 in alcohol (slides WAM 55–95, 67–95, alcohol 54–95, 78–95); Lakes Nowergup, 31º38´16´´S 115º44´42´´E, Yonderup, 31º34´S 115º41´E, and Carabooda, 31º37´S 115º43´E, 8 on slides (WAM 68–95 to 75–95); Coogee Springs, Perth, 9–14 Nov 1989, several on slides (MUR); Shark Lake, N of Esperance, 33º46´S 121º51´E, 5 Sep 1996, many specimens in alcohol (AMP); Congelin Dam, 32º49´07´´S 116º53´05´´E, 26 Oct 1997, 3 on slides (CALM).

Other Australian records. Vic.: Lake Purrumbete, Camperdown (AMS W4275) (Timms, 1981). WA: Corio Pool, Rottnest Island (Brinkhurst, 1971b).

Distribution and habitat. Eurasia, North, Central and South America, Australia and New Zealand (Brinkhurst, 1971a; Brinkhurst and Marchese, 1987; Coates and Stacey, 1994; Marshall and Winterbourn, 1979). *Potamothrix bavaricus* is quite widespread in southern Australia, occurring in both lentic and lotic sites and often very abundant when present.

Diagnosis. Length 15–35 mm. Dorsal anterior bundles with 1–5 hair chaetae and 2–5 pectinate chaetae. Ventral chaetae with teeth equally long but the upper thinner than the lower. Spermathecal chaetae relatively stout, about equal in length to the somatic ventral chaetae, with triangular blade-like ectal half. Vasa deferentia short joining tubular atria apically. Prostate glands absent. Penis sheaths absent.

Antipodrilus Brinkhurst

Antipodrilus Brinkhurst, 1971a: 523.—Brinkhurst and Wetzel, 1984: 50.

Type species. Tubifex davidis Benham, 1907.

Diagnosis. Dorsal chaetal bundles with or without hairs. Vasa deferentia long and narrow, joining atria apically or subapically. Atria globular, narrowing to form ejaculatory ducts that terminate in pendant penes (or protrusible pseudopenes?). Apparent penis sheaths (formed by thickened cuticular lining of the ectal part of the male duct) present in some species. Single stalked prostate gland attached apically each atria. Spermathecae with elongate spermatozeugmata. Spermathecal chaetae thin with grooved elongate tips.

Remarks. Antipodrilus is known only from Australia (all five species) and New Zealand (one species, *A. davidis*). In a cladistic analysis of the subfamily by Brinkhurst (1991), *Antipodrilus* appeared to group with two genera that are widely distributed in the northern hemisphere: *Psammoryctides* Hrabe, 1964 and *Haber* Holmquist, 1978. These northern genera have protrusible pseudopenes, with a crumpled cuticular lining to the inverted ectal part of the male duct, which then forms a penis sheath when the penis is everted. *Antipodrilus magelensis* Brinkhurst, 1984 and possibly *Antipodrilus timmsi* Brinkhurst, 1971, appear to have similar crumpled sheaths within the ectal part of the male duct and so the genus was coded as having protrusible pseudopenes in Brinkhurst (1991). Unfortunately further *Antipodrilus* specimens were not available for this study. *Antipodrilus davidis* (Benham, 1907) does appear to have pendant penes (though these may be protruded pseudopenes) and the nature of the penes is not clear for the other two species (*Antipodrilus multiseta* Brinkhurst and Fulton, 1979 and *Antipodrilus plectilus* Brinkhurst and Fulton, 1979). Further anatomical study is required to confirm the presence of pseudopenes and to generally improve descriptions of *Antipodrilus* species.

Antipodrilus davidis (Benham)

Tubifex davidis Benham, 1907: 252, figs 1–6.—Hrabe, 1962: 307.—Hrabe, 1966: 74.

Euilyodrilus heuscheri (Bretscher).—Brinkhurst, 1963: 49 (in part).

Antipodrilus davidis.—Brinkhurst, 1971a: 523.—Brinkhurst, 1971b: 112, fig. 2b.—Brinkhurst, 1982: 1.—Timms, 1979: 121.—Timms, 1982: 126.—Marshall and Winterbourn, 1979: 205.

Holotype. Blue Lake, Mt Kosciusko, NSW, 1906, sectioned on 4 slides (AMS G5610–11).

Material examined. NSW: Holotype, as above. SA: The Bubbler Spring, near Lake Eyre, 3 Dec 1974, 2 on slides, 1 in alcohol (SAM E2823–E2825); Coopers Creek, southwest branch, 27 Mar 1987, 1 on slide (SAM E2817); Freeling Springs, 1987 (AMS W198716); Davenport Spring Bore, near Hermit Hill, Lake Eyre South, 21 Sep 1989, 5 on slides (SAM E2818–E2821). WA: Spectacles Lake (North Eye), Brownmans Swamp, Lake Mariginiup and Thomson Lake, Perth, 30 Oct and 3–9 Nov 1989, 11 on slides, 8 in alcohol (WAM 42–95 to 47–95, 49–95 to 53–95 and 81–95).

Other records. NSW: Mt Kosciusko lakes (Timms, 1979). Following records all from Brinkhurst (1971b). SA: Lakes Edward and Leake, Glencoe. Vic.: Lakes Surprise and Mumblin, western Victoria. Tas.: Cambridge, 30 Aug 1966 (TAS. K221). Also recorded from New Zealand (Brinkhurst, 1971b; Marshall and Winterbourn, 1979; Timms, 1982).

Distribution and habitat. Southern Australia and New Zealand (Brinkhurst, 1971b; Marshall and Winterbourn, 1979; Timms, 1982). Favours lentic habitats.

Diagnosis. Length 25–40 mm. Anterior dorsal bundles with 2–5 non-hispid hair chaetae and 2–4 pectinate chaetae with teeth approximately equal. Ventral chaetal bundles with 3–5 bifid chaetae with the upper teeth longer and thinner than the lower anteriorly and teeth equal or the upper shorter posteriorly. Spermathecal chaetae single, grooved or with short lower tooth (probably when partially developed), about equal in length to somatic ventral chaetae, rarely absent. Vasa deferentia long, atria small, narrowing abruptly to form long ejaculatory ducts leading to (pendant?) penes.

Antipodrilus timmsi Brinkhurst

Antipodrilus timmsi Brinkhurst, 1971b: 112, fig. 12c.—Brinkhurst and Wetzel, 1984: 50.—Timms, 1981: 187.—Timms, 1983: 168.

Holotype. Lake Bullenmeri, Vic., 13 Aug 1969, 5 on slides (AMS W4276–W4278, typus amissus).

Material examined. NSW: Lake Jillamatong, near Cooma, 3 Apr 1986, many in alcohol (NMV F77614). Vic.: Type locality and date, 5 on slides (ROB); Lake Colangulac, 2 on slides (NMV 77612–F77613).

Other Australian records. Vic.: several lakes in western Victoria (Timms, 1981, 1983).

Distribution and habitat. Lakes in southeastern mainland Australia. Has been collected in sites with up to 25 ppt salinity, in both sandy and muddy sediments and at depths of up to 65 m (Timms, 1981, 1983).

Diagnosis. Length at least 14.5 mm (length of largest fragment). Anterior dorsal bundles with 2–5 serrate hairs and 3–5 pectinate chaetae with the upper teeth slightly longer than the lower, fewer posteriorly with upper teeth becoming longer and pectinations less apparent or absent. Ventral bundles with 3–5 chaetae anteriorly with the upper teeth markedly longer and somewhat thinner than the lower, fewer chaetae posteriorly with upper teeth less markedly longer than the lower. Spermathecal chaetae single, grooved and narrowly blade-shaped distally, slightly longer than somatic ventral chaetae. Vasa deferentia long, atria small and almost spherical, narrowing abruptly to form ejaculatory ducts. Penes present, possibly with thickened inner cuticle.

Remarks. The crumpled cuticle within the penes is indicative of a protrusible penis, but the structure of this requires closer examination from fresh specimens.

Antipodrilus magelensis Brinkhurst

Antipodrilus magelensis Brinkhurst, 1984: 142, figs 1–2.

Holotype. Mudginberri Billabong, Magela Creek, NT, 4 May 1981, 1 on slide (USNM 80692).

Material examined. NT: Holotype, as above, and paratypes from type locality as well as Georgetown and Bowerbird Billabongs, Magela Creek, 11 on slides, 19 in alcohol (USNM 80693–80697, 80700) and several on slides (ROB); Nankeen Billabong, Magela Creek, 1 immature on slide (ROB); South Alligator R., Oct 1988 and Dec 1989, 1 on slide (NMV F77611) and 2 on slides (ERISS). SA: Charles Angus Bore, 15 km N of Alberri Creek railway siding, Lake Eyre South, 2 Dec 1974, 1 on slide (SAM E2815); Coopers Creek, northwest branch, 27 Mar 1987, 1 on slide (SAM E2816).

Distribution and habitat. Northern Territory (coastal riverine sites) and South Australia (few arid inland sites). The new South Australian specimens are the first to be recorded outside of the Northern Territory.

Diagnosis. Length up to 9 mm. Anterior bundles with 4–6 bifid chaetae with teeth equal in length and breadth, diminishing in number posteriad to 2 per bundle with upper teeth becoming shorter and thinner than the lower. Spermathecal chaetae single with grooved tips, about equal in size to somatic ventral chaetae. Vasa deferentia moderately long, joining atria subapically. Short atria terminate in coiled ejaculatory ducts, which lead to (protrusible?) penes with crumpled cuticular lining forming apparent penis sheaths.

Antipodrilus multiseta Brinkhurst and Fulton

Antipodrilus multiseta Brinkhurst and Fulton, 1979: 2, figs 6–8.—Brinkhurst and Wetzel, 1984: 50.—Fulton, 1983a: 778.—Fulton, 1983b: 792.

Holotype. Great Lake, Tas., 1975 (QVM:14:316).

Material examined. Tas.: Holotype and paratypes from type locality and date, four on slides (QVM:14:316–319); Lake Sorell, 3 on slides, uncertain identification (ROB).

Other Australian Records. Tas.: Great Lake, Arthurs Lake and Lake Sorell (Fulton, 1983ab).

Distribution and habitat. Known only from large lakes of Tasmania's central plateau. Collected at depths of up to 17.5 m and in both silt/sand and clay sediments (Fulton, 1983b).

Diagnosis. Length up to 50 mm. Chaetae 12–15 per bundle in II, gradually diminishing in number to 3 or 4 posteriorly. Anterior chaetae with blunt teeth of equal thickness, the upper slightly longer, posterior chaetae with upper teeth shorter than the lower. Spermathecal chaetae single, thin with grooved-tips, about equal in size to somatic ventral chaetae. Vasa deferentia moderately long, atria and prostate glands small, ejaculatory ducts long and thin, leading to small penes. Posterior end of body tapering to a coiled tail. Living within tubes of fine sand grains (at least in the type locality).

Antipodrilus plectilus Brinkhurst and Fulton

Antipodrilus plectilus Brinkhurst and Fulton, 1979: 2, figs 1–5. —Brinkhurst and Wetzel, 1984: 50.—Fulton, 1983a: 778.—Fulton, 1983b: 792.

Holotype. Great Lake, Tas., 1975 (QVM:14:309).

Material examined. Tas.: Holotype and paratypes from type locality and date (QVM:14:309–315); Lake Sorell, 2 Feb 1981, 7 on slides (ROB).

Other Australian records. Tas.: Great Lake and Arthurs Lake (Fulton, 1983a, b).

Distribution and habitat. Known only from large lakes of Tasmania's central plateau. Collected at depths of up to 17.5 m and in both silt/sand and clay sediments (Fulton, 1983b).

Diagnosis. Length at least 20 mm. Thin, red worms that may be found in clusters of up to 50 specimens. Dorsal and ventral bundles with 7–9 chaetae anteriorly, reduced in number posteriorly to 3 or fewer per bundle. Chaetae of II with upper teeth shorter and thinner than the lower, chaetae of other preclitellar bundles with teeth equally long and with teeth equal in width or the upper teeth thinner than the lower. Posterior chaetae with upper teeth shorter and thinner than the lower. Spermathecal chaetae single, thin and groove tipped, twice as long as somatic ventral chaetae. Vasa deferentia moderately long, atria elongate, distended where vasa deferentia and prostates attached. Ejaculatory ducts moderately long.

Remarks. The type specimens have all chaetae bifid, but those from Lake Sorell have pectinate chaetae posteriorly. Further investigation may be required to substantiate the unity of this taxon, although chaetal polymorphism is known for other oligochaetes (Chapman and Brinkhurst, 1986, 1987).

Aulodrilus Bretscher

Aulodrilus Bretscher, 1899: 388.—Michaelsen, 1900: 55.—Stephenson, 1930: 752.

Type species. Aulodrilus limnobius Bretscher, 1899.

Diagnosis. Dorsal bundles with or without hair chaetae. Often with gonads replicated and/or genital apparatus shifted forwards due to asexual reproduction. Vasa deferentia short, atria globular, bean-shaped or cylindrical with solid prostate glands. Penes pendant without cuticular sheaths. Penial chaetae (but not spermathecal chaetae) may be modified. Sperm stored as loose bundles, spermatozeugmata absent.

Remarks. Asexual reproduction is common in *Aulodrilus* (Brinkhurst, 1984) and most Australian records are of immature worms. However, the three species found in Australia have distinctive chaetae that permit identification of immature specimens. Finogenova and Arkhipova (1994) provide scanning electron micrographs of the distinctive chaetae of the following species.

Aulodrilus limnobius Bretscher

Aulodrilus limnobius Bretscher, 1899: 388, figs 8.23G–H.—Brinkhurst, 1971a: 524, figs 8.24G, H. —Finogenova and Arkhipova, 1994: 8, figs 1–2, 4–5, 19.

Material examined. NSW: Murray R. at Heyward's Gauge, 36º06´S 147º01´E, 6 Jan 1988, 1 on slide (MDFRC). Vic.: Wentworth R., 17.7 km upstream of

Tabberabbera, 37º31´S 147º23´E, 2 Oct 1975, 1 in alcohol (NMV F77618); Mitta Mitta R., 2 km downstream of Dartmouth Dam wall, 5 Nov 1976, 1 in alcohol (NMV F77615); Branjee Creek, Goulburn Valley, 36º42´S 148º20´E, 23 Apr 1992, 1 on slide, 3 in alcohol (NMV F77616, F77617).

Distribution and habitat. Recorded from Africa, Europe, Asia and North and South America (Brinkhurst, 1971a) and now southeastern Australia.

Diagnosis. Length 12–15 mm. Anterior dorsal and ventral chaetae similar with up to 10 bifid chaetae with upper teeth shorter and thinner than lower, the chaetae of first bundles often shorter and thicker than the rest. Chaetae of mid and posterior segments with lateral wings which appear as narrow oar-shaped blades when viewed frontally, with the upper teeth visible as a small projection beyond the blade. The wings can be discerned as a ridge on the lateral aspect of the chaetae. Vasa deferentia long, entering long cylindrical atria apically. Pendant penes large. Genitalia may be shifted forwards.

Remarks. These are the first Australian records of this otherwise widespread species.

Aulodrilus pluriseta (Piguet)

Naidium pluriseta Piguet, 1906: 218.

Aulodrilus pluriseta.—Piguet and Bretscher, 1913: 118, figs 1–2.—Brinkhurst, 1971a: 524, figs 8.23J–N.—Brinkhurst, 1971b: 114, fig. 2I.—Brinkhurst, 1984: 147.—Timms, 1982: 126.—Marshall and Winterbourn, 1979: 205. —Finogenova and Arkhipova, 1994: 11, figs 11–13, 20–22.

Aulodrilus japonicus Yamaguchi, 1953: 298, fig. 12, pl. VII, figs 5–7.—Finogenova and Arkhipova, 1994: 8, figs 3, 6, 9, 10.

Material examined. No new specimens examined.

Other Australian records. NT: Georgetown and Mudginberri Billabongs, Magela Creek, Kakadu National Park (Brinkhurst, 1984). Qld: Yule Creek, Yanda Yarra (Brinkhurst, 1971b).

Distribution and habitat. Cosmopolitan (Brinkhurst, 1971b) but in Australia only known from the north so far.

Diagnosis. Length 10–25 mm. Anterior dorsal bundles with up to 8 short hair chaetae and up to 10 bifid chaetae with the upper tooth shorter and thinner than the lower and frequently replicated. Anterior ventral chaetae up to 16 per bundle with very thin, short upper teeth. Vasa deferentia long, entering ovoid atria apically. Atria with large lobate prostate gland, terminating in pendant penes. Genitalia may be shifted forwards.

Remarks. All Australian specimens observed so far have had replicate upper teeth on the dorsal chaetae. Specimens with replicate teeth were originally described as a separate species, *Aulodrilus japonicus* Yamaguchi, 1953, but this species was synonymised with *A. pluriseta* by Brinkhurst (1971a). Some Russian specimens, identified as *A. japonicus* by Finogenova and Arkhipova (1994), had replicate upper teeth, male pores in X and there were other minor differences in the form of the male ducts. Replicate teeth on these specimens were shown to be lateral, occurring either side of the main teeth. These may be a separate species, but forward shifting of the reproductive organs is commonly associated with asexual reproduction and other *A. pluriseta* (including other specimens described by Finogenova and Arkhipova (1994) have testes as far anterior as V (Brinkhurst, 1971a). Furthermore, the replicate teeth are essentially a form of pectination which has been shown to vary in other tubificids, including as a response to environmental conditions (Chapman and Brinkhurst, 1986, 1987).

Aulodrilus pigueti Kowalewski

Aulodrilus pigueti Kowalewski, 1914: 625, fig. 12.—Brinkhurst, 1971a: 526, fig. 8.23I.—Brinkhurst, 1971b: 114, fig. 2J.—Brinkhurst, 1984: 147. —Finogenova and Arkhipova, 1994: 13, figs 14–17.

Material examined. NSW: Ryans Billabong (station 61), 36º06´S 147º58´E, 30 Aug 1978, 1 on slide (MDFRC); Manning R. at Wingham Bridge, 31º52´S 152º23´E, 29 May 1996, 1 immature (AWT). NT: Main stream in Compartment L of CSIRO Kapalga Research Station, 20 Aug 1992, 10 in alcohol (NMV F77619). Vic.: La Trobe R. below Moe Drain, AMG 8121 359769, 3 Jul 1979 and Jul 1980, 7 immature in alcohol (NMV F77621–F77624); Steavenson R., 19 Feb 1991, 1 immature in alcohol (NMV F77625); Branjee Creek, Goulburn Valley, 23 Apr 1992, 1 immature in alcohol (NMV F77620). WA: Geegully Creek, Kimberley region, 18º13´34´´S 123º44´36´´E, 5 May 1995, few immature in alcohol (CALM); Meda R. near Lennard R. Gorge, 17º20´58´´S 124º30´27´´E, 20 May 1996, 2 mature in alcohol (CALM).

Other Australian records. NT: Georgetown, Mudginberri and Nankeen Billabongs, Magela Creek, Kakadu National Park (Brinkhurst, 1984). WA: Pine Hill Rock, near Balladonia, locality uncertain (Brinkhurst, 1971b). Qld: Pond near Tully (Brinkhurst, 1971b).

Distribution and habitat. Cosmopolitan (Brinkhurst, 1971b) and widespread in Australia, occurring in a variety of habitats.

Diagnosis. Length 2–28 mm. Dorsal anterior bundles with 2–5 hairs and 4–5 (rarely to 10) other chaetae which are either simple-pointed or bifid with the upper teeth shorter and thinner than the lower. Beyond VII the bifid dorsal chaetae become oar-shaped when viewed laterally (i.e. in the same plane as the teeth), often with rudimentary teeth visible on the end of the oar blade. Dorsal chaetae or just hair chaetae may be absent from some or all of II–VII. Ventral bundles with 3–6 bifid chaetae, with upper teeth shorter and thinner than the lower, not becoming oar-shaped. Large spoon-shaped penial chaetae beside each male pore on XI in mature specimens. Vasa deferentia short, atria bean-shaped. Pendant penes open via a median inversion of the body wall.

Remarks. The chaetae of *A. limnobius* are also oar-shaped, but more narrowly so than in *A. pigueti* and the blade-like wings of the former are in a plane perpendicular to the orientation of the teeth rather than in the same plane.

Rhyacodrilinae Hrabe

Diagnosis. Spermathecal pores close to anterior border of their segment (usually the testes bearing segment, normally X). Spermathecal ampullae containing loose or loosely bundled sperm. Atria with prostate glands diffuse or formed into distinct glands, rarely absent. Pendant penes generally absent; protrusible or eversible pseudopenes often present. Penial chaetae often modified, often numerous and typically arranged fanwise or in a row, with the blunt or bifid ectal ends close together. Spermathecal chaetae usually not modified. Coelomocytes usually large and abundant, rarely absent.

Remarks. Without doubt, the most problematic Australian freshwater tubificids are the four species placed in the Telmatodrilinae by Brinkhurst (1971a) and Brinkhurst and Fulton (1979) and two similar new species to be described below. The Telmatodrilinae is diagnosed by the presence of multiple prostate glands, each attached to the atria by short stalks. *Telmatodrilus multiprostatus* Brinkhurst, 1971 and *Telmatodrilus pectinatus* Brinkhurst, 1971 were placed within the Telmatodrilinae because the prostate cells are grouped into several glands, each of which appear to have a discrete connection to the atrial lumen. Later, two other Australian species, *Telmatodrilus (Alexandrovia) papillatus* Brinkhurst and Fulton, 1979 and *Telmatodrilus? (Telmatodrilus?) bifidus* Brinkhurst and Fulton, 1979, were tentatively placed here for the same reasons, although *T. bifidus* has only two prostates per atrium and these are not stalked. Of the two new species described below, one has prostate tissue similar to that of *T. multiprostatus* and the other has a pair of unstalked prostate glands, like that of *T. bifidus*.

Prior to the description of the Australian forms, the subfamily Telmatodrilinae consisted of three or four northern hemisphere species in two genera (or subgenera): *Telmatodrilus* Eisen, 1879 from western USA and Canada, and *Alexandrovia* Hrabe, 1962 from Alaska and Russia. This subfamily is generally considered to be closely related to the Tubificinae, based on cladistic analyses using the few characters available (Erséus, 1990b; Brinkhurst, 1994).

The Australian species differ from the holarctic forms in many respects. Their atria are ovoid to pear-shaped with apical prostates, rather than tubular with prostates along their length. In two of the Australian species the prostates lack stalks, instead being attached rather broadly to the anterior and posterior walls of the atria (Figs 9E, 11A, B). The Australian species have simple male pores, usually on the inner aspects of ventrolateral folds of the body wall, whereas the northern forms have pendant penes. Grooved spermathecal chaetae are found in two of the northern species and most of the Australian species, but all except one of the Australian forms also have modified penial chaetae which are absent in the northern forms. Coelomocytes are present in the two new species but have not been observed in the other Australian forms and appear to be absent in the holarctic species.

Before discussing the subfamilial relationships of these Australian species we should indicate that we intend to assign them to two new genera, described below. *Breviatria* gen. nov. will include *B. multiprostatus, B. pectinatus, B. papillatus and B. arvensis* sp. nov. and *Biprostatus* gen. nov. will include *B. bifidus* and *B. duplex* sp. nov. These names are mentioned here to facilitate the following discussion.

Erséus (1990b), in a cladistic analysis of the Naididae and subfamilies of Tubificidae, showed the two subfamilies Tubificinae and Telmatodrilinae (based on the northern species) as sharing plesiomorphic character states for modified spermathecal chaetae, absence of penial chaetae, unmodified oesophagus, absence of multiple large granular coelomocytes, lack of atrial ciliation, and absence of posterior prostates. Tubificinae and Telmatodrilinae share the apomorphic states for penes and spermatozeugmata present. While these subfamilies share the presence of stalked prostates, the former has one per atrium, the latter many, and the analysis suggested that the stalked prostates of these two groups had 'evolved independently from the diffuse prostate condition in the tubificid ancestor'. These subfamilies are also separated in that analysis by the apomorphic state of the spermathecal pore position in midsegment in Tubificinae (anterior in the Telmatodrilinae). Erséus (1990b) found that the telmatodrilines and tubificines formed a sister clade to another containing the phallodrilines, marine and freshwater rhyacodrilines and the Naididae, which share the presence of numerous coelomocytes and penial chaetae. The codings in Erséus' analysis depend on the coding of the outgroup (Phreodrilidae) adopted and are not necessarily accepted here.

We reran the analysis with the Australian forms as a separate group (AUS) using PAUP 3.1 and the original options. AUS was coded as lacking spermatozeugmata, atrial cilia and penes, but possessing coelomocytes, penial chaetae and multiple prostates (the coding was thus 10100 01101 000). Three equally parsimonious trees of 24 steps (CI 0.708) were obtained (unpublished data). In all of these, the Australian species appear within a clade which also included Phallodrilinae and marine and freshwater Rhyacodrilinae, separate from a Tubificinae-Telmatodrilinae-Limnodriloidinae clade. This was predictable because of coding for the presence of coelomocytes and penial chaetae, and implies that the multiple prostates of AUS are a convergent development to those of the (northern) Telmatodrilinae. Within this group, AUS was associated with the Phallodrilinae and marine Rhyacodrilinae, rather than the freshwater Rhyacodrilinae and associated Naididae, because of the lack of hair chaetae and the apical vasa deferentia.

Brinkhurst's (1994) cladistic analysis had the broader aim of investigating the evolutionary relationships within the whole of the Clitellata and the characters and choice of states used reflected this. Again, Telmatodrilinae was coded based on the northern species, on the assumption that these were plesiomorphic within the subfamily. A clade including Tubificinae, Telmatodrilinae and Limnodriloidinae, recognised by possession of spermathecal chaetae (not unique) and stalked prostates, loss of penial chaetae (presence of which was considered plesiomorphic for the family), and organised bundles of sperm in the spermathecae, separated from a clade containing the Rhyacodrilinae and Naididae. As discussed below, the Phallodrilinae was associated with the tubificine clade rather than that including Rhyacodrilinae.

This analysis was also rerun using PAUP 3.1 and the original options and weightings and with all characters unordered. AUS was coded as lacking spermatozeugmata but having coelomocytes, penial chaetae and stalked prostates (the coding was thus 10110 11111 50010 01000 012). Twelve trees of equal length (88, CI 0.568) were produced (unpublished data). In this rerun, AUS appeared within a clade with the Tubificinae, northern Telmatodrilinae, Phallodrilinae and Limnodriloidinae, which formed a sister group to the clade including Rhyacodrilinae and Naididae. The appearance of AUS and Phallodrilinae with the northern Telmatodrilinae, Tubificinae and Limnodriloidinae, rather than with the Rhyacodrilinae (as in Erséus' study), appears to result from the fact that this analysis saw penial chaetae as plesiomorphic for the whole family and that the prostates were coded differently by Erséus.

The lack of consistency in the above analyses requires that we consider some of the character states in detail.

Prostate. Traditionally, the prostate tissue of Rhyacodrilinae has been described as diffuse (e.g., Brinkhurst, 1971a), meaning that the prostate cells form a continuous layer over the atrium, with each cell communicating with the atrial lumen independently. More recently, this view (which focused on the freshwater forms) has been modified following the description of numerous marine forms with prostate tissue that is more clumped. Thus, Baker and Brinkhurst (1981) describe the Rhyacodrilinae as "having prostate glands forming a diffuse glandular covering; the cells communicating with the atrial lumen independently or in small clusters". Erséus (1984) describes the subfamily as having "Prostates diffuse or irregularly scattered in two or more clusters of cells broadly attached to the atrial surface, or absent". Some rhyacodrilines, including the marine *Heronidrilus* Erséus and Jamieson, 1981 and *Heterodrilus* Pierantoni, 1902, the freshwater monotypic *Macquaridrilus* Jamieson, 1968 and the Lake Baikal endemic *Rhyacodriloides* Chekanovskaya, 1975, have some or all of the prostate cells formed into two or more glands (Erséus, 1981; Erséus and Jamieson, 1981; Jamieson, 1968; Martin and Brinkhurst, 1998). There are therefore precedents for including *Breviatria* and *Biprostatus* in Rhyacodrilinae in respect to the form of the prostates. Although most of the rhyacodrilines mentioned above have the prostate clumps broadly attached to the atrium, rather than narrowly stalked, the same is true for the two *Biprostatus* species. Furthermore, some *Heterodrilus* (*H. inermis* (Erséus, 1981) and *H. rapidensis* Erséus, 1997) do have prostate glands that narrow into stalks like *Breviatria*. The Phallodrilinae is the only other subfamily to have more than one prostate gland per atrium and so should be mentioned here. Like *Biprostatus*, phallodrilines have a pair of prostates on each atrium, but these are almost always stalked and typically placed ental and ectal in position on the atria (Erséus, 1992), unlike the symmetrically placed prostate tissue of *Biprostatus*. A few phallodrilines (*Pacifidrilus* Erséus, 1992 and *Pirodrilus* Erséus, 1992) do have the prostates placed symmetrically on the atria but this appears to be a consequence of the small size of the atria. There is a need for more knowledge on the histology and morphogenesis of prostate tissue in various tubificids to more adequately use prostate characters in phylogenetic work, as highlighted by Gustavsson and Erséus (1997).

Coelomocytes. An abundance of coelomocytes (a rhyacodriline trait) has been found in both of the new species described below but their presence in the older Australian taxa cannot be established because of the condition of the scarce material. They have recently been observed in rhyacodrilines such as *Torodrilus* Cook, 1970 and *Rhizodrilus* Smith, 1900, in which they were previously thought to be absent (Erséus, 1994). Coelomocytes have not been observed in *Rhyacodriloides*, but that genus is nonetheless now associated with the Rhyacodrilinae (Baker and Brinkhurst, 1981; Martin and Brinkhurst, 1998). Coelomocytes have not been reported for any of the northern telmatodrilines (Holmquist, 1974) and, with few exceptions, are not abundant in the Phallodrilinae (Erséus, 1992).

Genital chaetae. Groove-tipped genital chaetae are common in the Tubificinae and Limnodriloidinae and some northern Telmatodrilinae. These are generally few in number (usually 1 or 2 per bundle) and lie in enlarged chaetal glands, usually on the spermathecal segment. A few rhyacodrilines, some *Rhizodrilus* and *Rhyacodriloides*, do have similar chaetae (Baker and Brinkhurst, 1981; Erséus, 1990a; Martin and Brinkhurst, 1998), although these are on the male pore segment in the latter. The superficially similar chaetae of the rhyacodriline *Torodrilus*, appear to be a separate apomorphic development (Erséus, 1994). More typical in the Rhyacodrilinae and Phallodrilinae is modification of the penial chaetae associated with the male pores. These have bifid or simple (often club-shaped) tips, arranged in a row or fanned out with the tips close together, always on the male pore segment. Chaetae of the male pore segment are not modified in the northern Telmatodrilinae and only rarely modified in the Tubificinae (two *Varichaetadrilus* Brinkhurst and Kathman, 1983 and the few species of *Krenedrilus* Dumnicka, 1983). *Biprostatus* and *Breviatria* are unusual within the family in possessing both grooved chaetae on the spermathecal segment (absent in two *Breviatria*) and modified penial chaetae on the male pore segment (absent in one *Breviatria*). *Krenedrilus* (Tubificinae) and some *Rhizodrilus* (Rhyacodrilinae) are the only other tubificids to have both types of genital chaetae. This means the genital chaetae may be of little help in classifying the new genera, unless grooved spermathecal chaetae are seen as plesiomorphic for the family (almost identical chaetae do occur in the Phreodrilidae) and modified penial chaetae are seen as an apomorphic development in the ancestral rhyacodriline, as tentatively suggested by Erséus (1990b). In that case, the presence of penial chaetae in the new genera might suggest their inclusion within the Rhyacodrilinae.

Somatic chaetae. Somatic chaetae are generally difficult to use in higher oligochaete taxonomy because of a lack of consistency among and within taxa. Both the northern telmatodrilines and *Breviatria* and *Biprostatus* have some unusual chaetae, but there are no chaetal features that would indicate a close relationship between the Australian and northern species. Neither do the chaetae provide evidence of a relationship to any other particular group of tubificids.

Sperm. Some *Breviatria* and *Biprostatus* appear to have sperm in the spermathecae arranged into numerous bundles with the nuclei aligned at one end, others have the sperm cells in loose masses, both arrangements typical of the Rhyacodrilinae and Phallodrilinae. The spermatozeugmata more typical of the Tubificinae, with fertile sperm encapsulated by infertile sperm (Braidotti and Ferraguti, 1982; Ferraguti et al., 1989; Ferraguti et al., 1994), are absent. Of the northern telmatodrilines, *Alexandrovia* species have some kind of sperm bundles (Holmquist, 1974), which require ultrastructural analysis to investigate homology with tubificine spermatozeugmata, and *Telmatodrilus* have loose sperm in the spermathecae. This character is thus ambiguous in terms of relationships.

Spermathecal pores. In general, tubificines have spermathecal pores near the middle of the segment (Brinkhurst, 1991) while rhyacodrilines and phallodrilines have these pores at or just behind the anterior septa (Baker and Brinkhurst, 1981; Erséus, 1992). All *Breviatria*, at least one of the two *Biprostatus*, and the northern telmatodrilines have anterior spermathecal pores but, since this may be the plesiomorphic state for the family (Erséus, 1990b; Brinkhurst, 1991), it indicates little about the relationship between these worms.

Penes. Pendant penes may constitute an apomorphy for tubificines and northern telmatodrilines (Erséus, 1990b; Brinkhurst, 1994), although they are also present in some Phreodrilidae. Absence of penes in *Biprostatus* and *Breviatria* may be a plesiomorphic state shared by rhyacodrilines and phallodrilines.

In summary, the argument that *Breviatria* and *Biprostatus* belong within the Telmatodrilinae simply because they have prostate cells formed into multiple glands is not strong, particularly considering the lack of knowledge about prostate homology and the number of rhyacodrilines that are now known to have clumped prostate tissue. *Breviatria* and *Biprostatus* have several other features, including lack of pendant penes and spermatozeugmata and presence of penial chaetae and coelomocytes (in at least some species) which indicate a closer relationship with the Rhyacodrilinae. Therefore, as anticipated by the discussion of these and other problem taxa by Martin and Brinkhurst (1998), we now propose to consider the Australian former telmatodrilines to be properly associated with Rhyacodrilinae, described below as two new genera.

While this is undoubtedly not the last word on the position of these worms, we believe that this move represents a more parsimonious classification, pending further ontogenetic and ultrastructural analyses of some characters (especially prostate glands and organised sperm) and further phylogenetic work on the rhyacodrilines. It does seem that the Rhyacodrilinae is paraphyletic (Erséus, 1990b; Brinkhurst, 1994) and we may be trying to force the Australian ex-telmatodrilines into a group that has no phylogenetic reality. A thorough study of rhyacodriline phylogenetics is yet to be undertaken but Erséus (1990b) canvasses the possibility that the Rhyacodrilinae will have to be split into a number of smaller groups to achieve monophyly, perhaps with each raised to family level. If this were to be given effect then the Australian ex-telmatodrilines may form one (or more) such groups.

Rhyacodrilus Bretscher

Rhyacodrilus Bretscher, 1901: 205.—Stephenson, 1930: 742.—Brinkhurst, 1971a: 544.

Diagnosis. Dorsal chaetal bundles with or without hair chaetae. Vasa deferentia moderately long, entering atria subapically, atria usually bulbous or rounded, usually covered with a diffuse layer of prostate cells. Protrusible pseudopenes present or absent. Penial chaetae usually modified, numerous with blunt tips held close together. Coelomocytes usually large and abundant.

Rhyacodrilus coccineus (Vejdovský)

Tubifex coccineus Vejdovský, 1875: 193.—Michaelsen, 1909: 32, figs 55–58.

Ilyodrilus coccineus.—Stolc, 1886: 656.

Rhyacodrilus coccineus.—Michaelsen, 1909: 31.—Brinkhurst, 1971a: 537, figs 8.31A–D.—Brinkhurst, 1971b: 115, fig. 2K.

Branchiura pleurotheca Benham, 1907: 256, pl. XLVI, figs 7–12.

Holotype: Type locality unknown (ZMUH 6948).

Material examined. NSW: Blue Lake, Mt Kosciusko, 36º24´24´´S 148º18´50´´E, Jun 1906, several on slides (2 sectioned) (AMS W5612–W5613). WA: Power Rock, Balladonia, 1 on slide, uncertain id. (ROB).

Distribution and habitat. Holarctic, Australia and South America (Brinkhurst, 1971a; Brinkhurst and Marchese, 1989). This species is not commonly collected in Australia.

Diagnosis. Length 10–35 mm. Anterior dorsal bundles with 3–5 hair chaetae and up to 5 pectinate chaetae, hairs missing in many posterior segments. Ventral chaetae 2–5 per bundle with the upper teeth thinner and not much longer than the lower (but longer in Australian specimens described as *B. pleurotheca*). Ventral chaetae of XI with 3–5 club-headed penial chaetae per bundle, equal in size to somatic ventral chaetae. Spermathecal pores ventrolateral (lateral in the *B. pleurotheca* specimens). Vasa deferentia not coiled around atria, which are globular and covered with a diffuse layer of prostate cells. Coelomocytes large and abundant.

Remarks. Benham (1907) described *Branchiura pleurotheca* from Blue Lake, Mt Kosciusko, but Brinkhurst (1971ab) considered this to be synonymous with *R. coccineus*. The long upper teeth of the anterior ventral chaetae and the lateral position of the spermathecal pores of Benham's material may prove to be diagnostic of a distinct species once intra-specific variation in *R. coccineus* is better documented. Further specimens from the type locality of *B. pleurotheca* (Blue Lake, Mt Kosciusko) are required to substantiate the synonymy. The Power Rock specimen is dissected but not stained and little can now be seen of the genital anatomy. The most recent accounts of species with hair chaetae are Ohtaka (1995) and Timm (1990). The Tasmanian specimens from Southwell R., mistaken as *R. coccineus* by Pinder and Brinkhurst (1994), are attributable to *Ainudrilus fultoni* Brinkhurst, 1982. Other worms attributed to this species by Pinder and Brinkhurst (1994) are described below as a new taxon.

Rhyacodrilus megaprostatus sp. nov.

Figure 1

Non *Rhyacodrilus coccineus* (Vejdovský, 1875).—Pinder and Brinkhurst, 1994: 94.

Material examined. Holotype: Curdies R., Vic., (38°20′S 143°08′E), 7 Feb 1992, G. Quinn (MON), 1 mature on slide (NMV F81869).

Paratypes. Vic: Grassy Creek, Otway Ranges, 38°28′S 144°00′E, 6 Jun 1989, 1 mature on slide (NMV F81868); Lake Purrumbete, 38°17′S 143°14′E, 31 Jan 1992, G. Quinn (MON), 1 mature on slide (NMV F81866); Lake Purrumbete, no date, A. Glaister (MON), 1 mature on slide (NMV F81867); Branjee Creek, Goulburn Valley, 36°42′S 148°20′E, 23 Apr 1992, A. Pinder, 1 mature on slide (NMV F81870).

Distribution and habitat. All of the above localities are in central southern Victoria. Collected from lentic and lotic sites and from a variety of

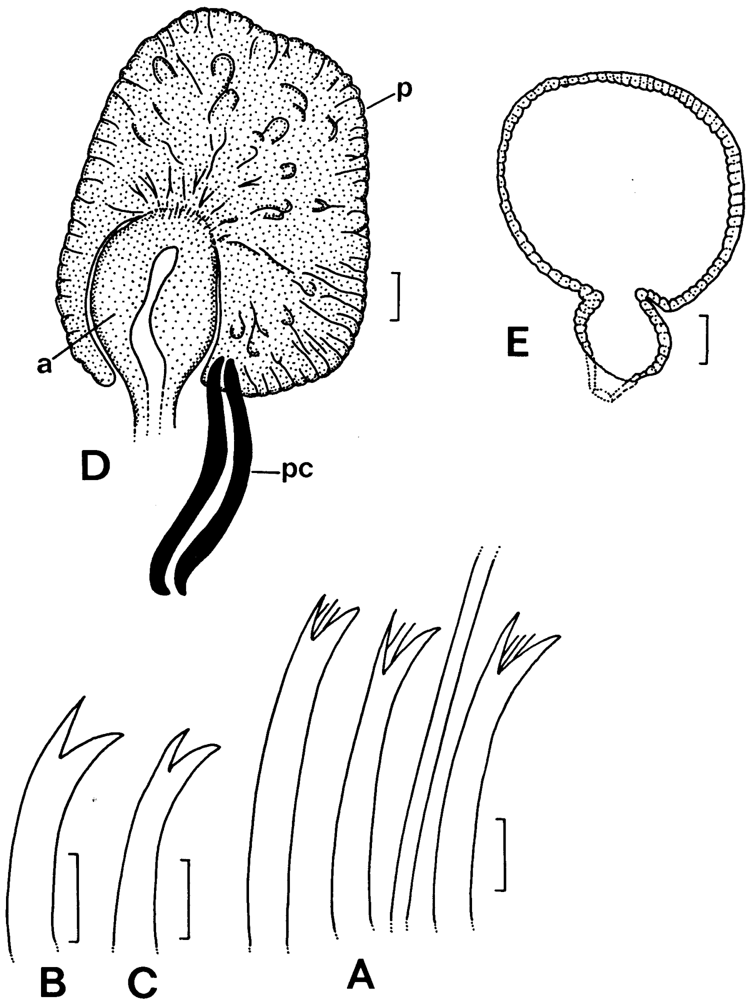

Figure 1, *Rhyacodrilus megaprostatus* sp. nov.: A, tips of anterior dorsal chaetae with section of hair; B, tip of ventral chaeta of II; C, tip of posterior ventral chaeta; D, atrium with prostate tissue and penial chaetae of holotype; E, spermatheca of NMV F81868. Scales: A–C, 0.01 mm; D, 0.04 mm; E, 0.03 mm.

habitats including sandy sediment and rocks and bricks used for colonisation studies.

Etymology: Named for the size of the prostate gland in relation to the small atrium.

Description. Length 5–9 mm, diameter when slide mounted about 0.3 mm. Number of segments 40–70. Coelomocytes abundant.

Hair chaetae in preclitellar dorsal bundles normally 3–4 per bundle (1 long and 1 short in one Lake Purrumbete specimen), 270–300 µm long. Hairs accompanied by 3–6 pectinate chaetae, 100–110 µm long, with upper teeth slightly shorter than lower and few pectinations (Fig. 1A). Fewer dorsal chaetae posteriorly. Anterior ventral bundles with 3–5 chaetae (those from Curdies R. with as many as 7), 90–140 µm long, with upper teeth thinner than lower, teeth about equal in length on II (Fig. 1B), upper teeth slightly shorter than lower posteriorly (Fig. 1C). Penial chaetae in XI bluntly simple-pointed, 90–100 µm long, 1–3 per bundle, projecting medial to the line of the somatic ventral chaetae (Fig. D).

Paired male and spermathecal pores in line with ventral chaetae.

Atria small, spherical (Fig. 1D), opening into smaller spherical chamber with a lobed pore. Atria enclosed by a voluminous prostate gland (Fig. 1A), concealing the vas deferens-atrial union. Prostate not closely applied to the sides of the atrium. Ovaries large and obscuring the vasa deferentia. Male funnels observed in some specimens, often closely associated with the spermathecae and a part of vasa deferentia folded and adhered to funnels. Spermathecae ovoid (Fig. 1E) containing sperm arranged in distinct masses.

Remarks. The apparent attachment of the prostate at the top of the atrium needs to be confirmed from sectioned material as this may indicates that the prostate is not as diffuse as is normal in *Rhyacodrilus*. Within the genus, the large volume of prostate tissue compared to the atria is unique to this new species.

According to the key to *Rhyacodrilus* in Brinkhurst (1971a) and notes in the update by Brinkhurst and Wetzel (1984), *R. megaprostatus* is closest to R. coccineus, from which it differs mainly in the volume of the prostate. Several other species with hair and pectinate chaetae have been described more recently. In *Rhyacodrilus okamikae* Giani and Rodriguez, 1988 the pectinate chaetae have short upper teeth, the ventral chaetae have long upper teeth and there is only a single median spermatheca. *Rhyacodrilus suputensis* Timm, 1990 has lyre-shaped pectinate chaetae and tubular atria. *Rhyacodrilus hiemalis* Ohtaka, 1995 has voluminous spermathecae with narrow ducts, more numerous chaetae and a less voluminous prostate gland.

Rhyacodrilus bifidus Brinkhurst

Rhyacodrilus bifidus Brinkhurst, 1982: 3, pl. 6.

Holotype: Blue Lake, Mt Kosciusko plateau, NSW (QVM:14:232).

Material examined: NSW: Holotype and paratype from type locality, 36º24´24´´S 148º18´50´´E, 7 Feb 1977, 5 on slides (QVM:14:232–233) and 7 on slides (ROB); Lake Cootapatamba, Mt Kosciusko plateau, 37º27´58´´S 148º15´48´´E, 7 Feb 1977, 1 on slide (ROB). Vic.: Thomson R. at Thomson Portal Rd, 3 on slides (NMV F81671–81873); Wentworth R., 17.7 km upstream of Tabberabbera, 37º31´S 147º23´E, 2 Oct 1975, 1 on slide, tentative identification (NMV F81874). New Zealand: Lake Matheson, Canterbury Highlands, 2 Nov 1978, 2 on slides (ROB); Lake Gault, Canterbury Highlands, 5 Nov 1978, 2 on slides (ROB).

Distribution and habitat. Known only from the above lakes and rivers of the far southeast of mainland Australia and the lakes on the South Island of New Zealand (Brinkhurst, 1982), although the identification of the latter could not be confirmed as the genitalia are no longer visible in the specimens examined. Australian specimens have been collected from coarse sediments in rivers: sand and gravel, often between cobbles and pebbles (Ahern and Blyth, 1979; Malipatil and Blyth, 1982) but possibly in finer sediments from the Mt Kosciusko sites (Timms, 1979).

Diagnosis. Length up to 7 mm. Ventral and dorsal bundles with 3–8 chaetae anteriorly, bifid with upper teeth 2–3 times as long as, but thinner than, the lower. Penial chaetae 6–10 bifid per bundle in XI, about 2 times longer than somatic chaetae and slightly curved ectally. Vasa deferentia as long as atria. Atria 4 times longer than broad, ending in wide bulbs with narrow pores on the anterior face of penis sacs which open to the exterior via narrow pores. Abundant prostate tissue attached to atria subapically. Coelomocytes not abundant.

Remarks. The reproductive structures of the Wentworth R. specimen are not visible and so the identification cannot be confirmed. There are only three penial chaetae per bundle in XI, but these are large and bifid and the somatic chaetae are mostly four or five per bundle with the upper teeth much longer than the lower. Similarly, the identification of the whole-mounted New Zealand specimens could not be confirmed.

Ainudrilus Finogenova

Ainudrilus Finogenova, 1982: 1255.—Erséus, 1990a.
Vadicola Baker, 1982: 3232.

Type species. Ainudrilus oceanicus Finogenova, 1982.

Diagnosis. Hair chaetae present or absent. Chaetae of penial segment modified, chaetae of spermathecal segment slightly modified in one species. Vasa deferentia usually wide and at least partially granulated, entering atria subapically. Atria variably shaped but more or less erect or directed posteriad, usually consisting of an ampullae, often with spacious lumen containing sperm, usually leading to thick, and often equally large and well developed, ejaculatory ducts, often giving the appearance of a bi-partite atria. Prostate absent. Penes absent. Spermathecae with distinct, and often complex ducts. Sperm loose in ampullae. Coelomocytes large and abundant.

Remarks. The lack of prostate on the atria distinguishes *Ainudrilus* from almost all other rhyacodrilines, bar some other highly unusual forms such as *Jolydrilus* Marcus, 1965 and *Epirodrilus* Hrabe, 1930 (see Brinkhurst, 1971a; Baker and Brinkhurst, 1981), and one freshwater *Rhyacodrilus*. The latter, *Rhyacodrilus simplex* (Benham, 1903), lacks prostate tissue but also differs from other *Rhyacodrilus* in having vasa deferentia that coil around the atria and which join the atria apically. Further study of this species may lead to it being moved back to a resurrected *Taupodrilus*, which was established by Benham (1903) for its reception.

Ainudrilus billabongus (Brinkhurst, 1984), *Ainudrilus stagnalis* (Erséus, 1997) and the following new species and new combination are the only freshwater representatives described so far. There are eight marine species, from Hong Kong, Northern Australia, the Pacific Ocean and the Caribbean (Erséus, 1990ab, 1997; Finogenova, 1982).

Ainudrilus billabongus (Brinkhurst)

Rhyacodrilus billabongus Brinkhurst, 1984: 144, fig. 3.
Ainudrilus billabongus.—Erséus, 1990a: 265.

Holotype. Bowerbird Billabong, Magela Creek, NT (USNM 80698).

Material examined: NT: Paratype, from type locality, 1 on slide, 21 Aug 1981 (ROB); Magela Creek, 24 Feb 1988, 1 on slide (ERISS).

Distribution and habitat. Recorded only from lentic and lotic sites of the Magela Creek system, Northern Territory.

Diagnosis. Length at least 7.5 mm, all specimens incomplete. Coelomocytes large and abundant. Anterior chaetae bifid with teeth of equal length, 4–6 per bundle anteriorly, reduced in number posteriorly. Up to 6 simple-pointed penial chaetae in each ventral bundle of XI, strongly recurved at the tip and about 2 times longer than somatic chaetae. Vasa deferentia wide and glandular, about twice the length of the muscular upright atria, entering the atria basally. Atria leading directly to small circular pores. Spermathecal ducts long and narrow, sharply set of from the globular ampullae.

Remarks. The original description of *A. billabongus* made mention of a bundle of sperm lying outside of the atrium. Most fully mature *Ainudrilus* seem to maintain sperm in the atrium or expanded ejaculatory ducts so the sperm bundle of the holotype illustrated in Brinkhurst (1982) was most likely extruded from the atrium during dissection.

Ainudrilus stagnalis Erséus, 1997

Ainudrilus stagnalis Erséus, 1997: 9, figs 2E–F.

Holotype. Billabong associated with Stephens Creek, Port Darwin West Arm, NT (NTM W00020).

Material examined. No new specimens examined.

Distribution and habitat. Known only from the freshwater type locality, in fine sand (Erséus, 1997).

Diagnosis. Length at least 3.2 mm (only specimen incomplete). Coelomocytes abundant. Hair chaetae absent. Anterior chaetae bifid with upper tooth much longer than lower, 4–6 per bundle anteriorly, 3–4 posteriorly. A single bifid chaeta, not larger than other ventral chaetae, near each male pore. Vasa deferentia not described. Atria with non-muscular ampullae and thick muscular ejaculatory ducts terminating in simple pores medial to the ventral chaetal line. Spermathecae absent in the only known specimen.

Remarks. Erséus (1997) suggested that the chaeta near each male pore is not a modified genital chaeta, but that such might be developed at a later stage.

Ainudrilus fultoni (Brinkhurst) comb. nov.

Figure 2

Rhyacodrilus fultoni Brinkhurst, 1982: 2, pl. 1–5.

Holotype. Lake Sorell, Tas. (QVM:14:230).

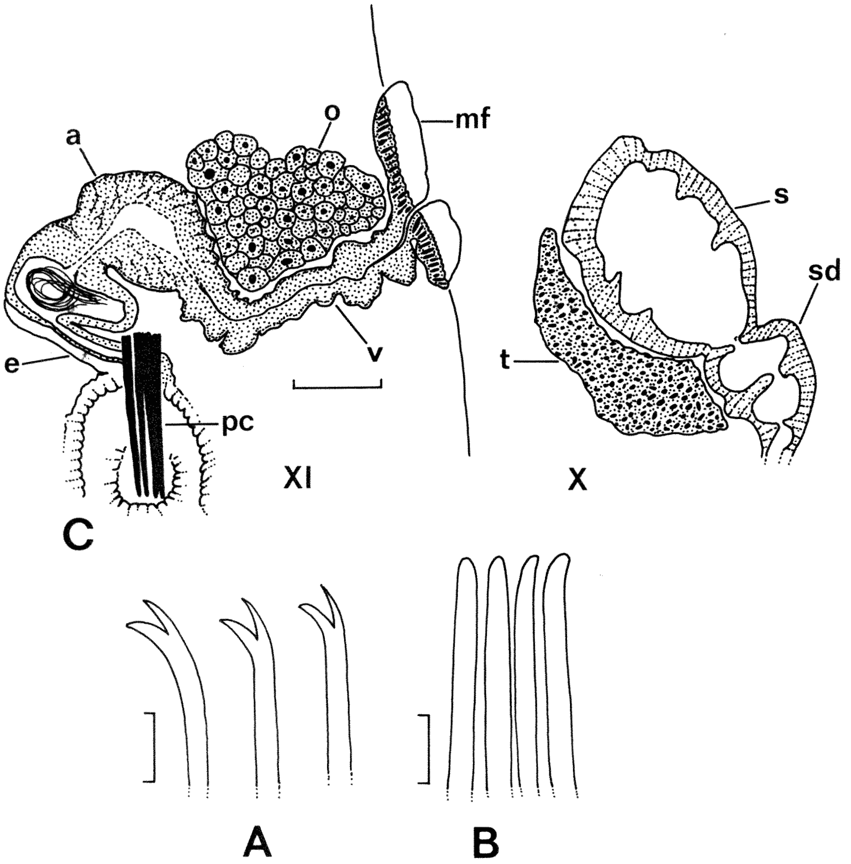

Figure 2, *Ainudrilus fultoni* (Brinkhurst) from Lake Sorell: A, somatic chaetae; B, penial chaetae; C, genitalia of QVM:14:4202. Scales: A–B, 0.01 mm; C, 0.05 mm.

Material examined. Tas.: Holotype and paratypes, type locality, several sectioned specimens and others in alcohol, 2 Feb 1981 (QVM:14:230–231 and ROB); Southwell R., 41°34′50′′S 145°44′04′′E, 20 Dec 1988, 2 on slides (QVM:14:4201–4202); Ouse R. at Marlborough Highway, 41°59′22′′S 146°38′43′′E, 16 Mar 1997, 1 on slide (AMP); Lake Perry, 43°13′10′′S 146°45′17′′E, 11 Mar 1997, 2 on slides, 3 in alcohol (AMP).

Distribution and habitat. Known only from lakes and rivers in Tasmania. The Ouse R. and Lake Perry specimens were collected from sand between cobbles in shallow water.

Diagnosis. Length up to 15 mm. Coelomocytes large and fairly abundant. Chaetae all bifid with teeth equally long, 10–13 per bundle anteriorly, fewer posteriorly (Fig. 2A). Ventral bundles of XI with 7–9 straight penial chaetae with blunt, slightly curved tips, about equal in length to somatic ventral chaetae (Fig. 2B). Short vasa deferentia enter atria subapically (Fig. 2C). Atria consisting of a thick walled ental portion with a narrow lumen, which leads into a thinner walled ectal portion with a wide lumen which usually contains sperm in mature specimens (Fig. 2C). Spermathecae with ampullae full of loose masses of sperm, ducts short and broad opening through large pores (Fig. 2C).

Remarks. Specimens from Southwell R. were attributed to *R. coccineus* by Pinder and Brinkhurst (1994) but conform to the description of *A. fultoni*. As these specimens are dissected, rather than sectioned like the type material, the reproductive structures are illustrated here to give a different perspective (Fig. 2C). The atrium consists of a thick-walled portion in which the lumen can be seen in only one dissected specimen and a thinner walled ectal chamber (essentially an ejaculatory duct), with a sperm bundle within the latter in examined specimens.

It seems preferable to transfer *R. fultoni* from *Rhyacodrilus* to the expanding *Ainudrilus*, which includes most species without prostate glands, whereas all *Rhyacodrilus* (except *R. simplex*, discussed above) have diffuse prostate tissue. *Ainudrilus fultoni* can be distinguished from its freshwater congeners by the more numerous somatic and penial chaetae.

Ainudrilus nharna sp. nov.

Figure 3

Material examined. Holotype: From Frankland R. at Roe Rd ford, Western Australia, 34º41´02´´S 116º51´13´´E, 9 Sep 1996, A. Pinder and R. Brinkhurst, serially sectioned specimen on three slides (WAM 1–99).

Paratypes: Collection details as for holotype, 2 specimens serially sectioned on slides and others in alcohol (WAM 2–99 to 4–99).

Other material: WA: Collection details as for types, 7 on slides, including 1 serially sectioned (AMP); Lake Wilson at track off Scott Rd, 34º25´23´´S 115º07´52´´E, 14 Sep 1996, 2 on slides (AMP); Thomas Spring, Augusta, 34º21´00´´S 115º09´35´´E, 17 Sep 1996, A. Pinder and R. Brinkhurst, 5 on slides (AMP); stream crossing Thomson Rd, approximately 5 km N of Granite Peak, 34º40´48´´S 116º42´13´´E, 12 Sep 1996, A. Pinder and R. Brinkhurst, 1 on slide (AMP); northern tributary of Collier Creek on Cemetary Rd, 34º58´30´´S 116º45´12´´E, 11 Sep 1996, A. Pinder and R. Brinkhurst, 1 on slide (AMP); Boyndiminup Rd, Lake Muir wetland system, WA, 34º30´S 116º35´E, Jul and Oct 1993, P. Horwitz (ECU), 3 on slides and others in alcohol (WAM 90–97, 91–97,

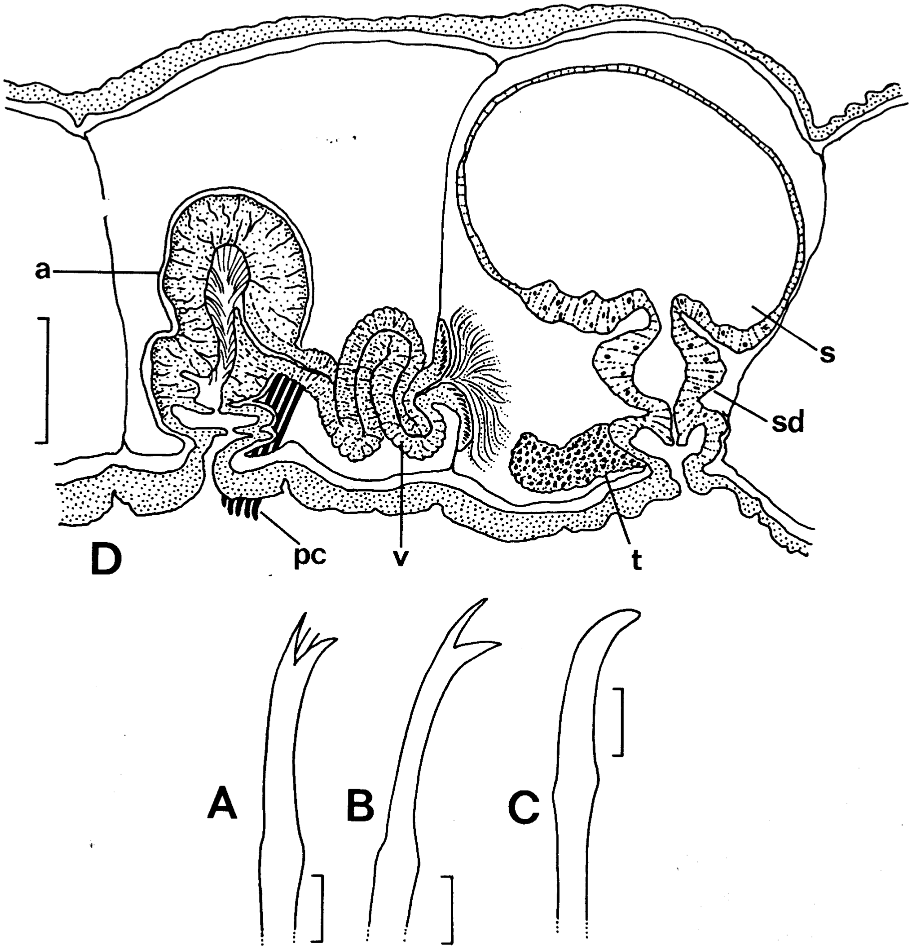

Figure 3, *Ainudrilus nharna* sp. nov.: A, tip of dorsal chaeta; B, tip of ventral chaeta; C, tip of penial chaeta; D, genitalia, based mostly on holotype. Scales: A–C, 0.01 mm; D, 0.1 mm.

92–97, 98–97 and 99–97); Peaty seepage in logging coup, Johnsons Rd, upper tributary of Deep R., 34º41´S 116º36´E, Jan 1993, P. Horwitz (ECU), 4 on slides (WAM 95–97 to 97–97, 93–97); creek in sandy shrub land at Bevan Rd, Kent R. catchment, 34º39´S 116º58´E, P. Horwitz (ECU), Oct 1993, 1 on slide (WAM 94–97); Beedelup Brook South, 34º22´39´´S 115º56´E, Sep 1993, K. Trayler (MUR), 1 on slide (WAM 36–98); Beedelup Brook South, 34º22´50´´S 115º55´E, Oct 1994, K. Trayler (MUR), 1 on slide (WAM 37–98); Carey Brook at Pile Rd, 34º21´29´´S 115º54´29´´E, 16 Sep 1996, A. Pinder and R. Brinkhurst, 1 on slide and 3 in alcohol (AMP); Lake Walbyring, 32º50´19´´S 117º35´27´´E, 18 Dec 1996, M. Smith (CALM), 1 on slide (WAM 38–98) and 2 on slides (AMP).

Distribution and habitat. Ainudrilus nharna appears to be widespread in the southwest of WA, occurring in springs, lakes, and both flowing and still reaches of streams and rivers. Sediments at collecting sites ranged from peat to mud to coarse sand. Specimens from Lake Walbyring, a brackish to saline lake, were collected in Dec 1996 when salinity in the lake was 2.8 ppt, but not in Oct 1997 when salinity was 20 ppt (unpublished data).

Etymology: From *nharna*, worm in Nhungar aboriginal language.

Description. Length about 9 mm. Number of segments 75–90. Width at clitellum (slide-mounted worms) 0.3–0.5 mm. Coelomocytes present.

Clitellum inconspicuous, half-X–half-XII. Gonopores in line with the ventral chaetae, spermathecal pores anterior on X. Male pores open into a transverse groove, lateral to the penial chaetae in the anterior half of XI.

Anterior dorsal bundles with up to 4 hair chaetae (up to 420 µm long) and up to 5 pectinate chaetae (up to 130 µm long), latter with upper teeth thinner than and equal in length to lower, with indistinct pectinations (Fig. 3A). Ventral bundles with bifid chaetae of similar size and form to the dorsals (but without pectinations), 3–5 per bundle anteriorly, fewer posteriorly (Fig. 3B). Penial chaetae 4–7 per bundle in XI, up to 120 µm long and slightly curved ectally (Fig. 3C). Penial chaetae protrude close to the mid-line, on either side of the ventral nerve cord medial to the male pores.

Testes anteroventral in X (Fig. 3D). Atria in XI, bulbous with thick lining tissue and ciliated lumen, leading to folded protrusible pseudopenes, which are protruded on one of the paratypes. Prostate tissue absent. Vasa deferentia thickened, appearing glandular and often twisted or folded once or twice between male funnel and atria, attaching anteromedially to the atria (Fig 3D). Spermathecal ampullae large and ovoid with sperm formed into loose masses, clearly separated from the ducts. Spermathecal ducts constricted at one or more points, leading to pores which are often on a protrusion within small vestibulae, located anteriorly on X (Fig 3D). Ovaries lying near the vasa deferentia in XI, female pores not observed.

Remarks. The absence of prostate tissue and the thickened vasa deferentia suggest that this new species belongs in the genus *Ainudrilus*. *Ainudrilus taitamensis* Erséus, 1990a, of Hong Kong, which was only tentatively included in the genus, is the only other species to have ciliated atria. The atria and pseudopenes resembles what was called a two-part atria in *A. fultoni* and the ectal part of the male duct is formed into pseudopenes or elaborate ejaculatory ducts in some other species (Erséus, 1990a). The thick vasa deferentia are difficult to follow in both sectioned and dissected worms as they are tightly folded with an indistinct lumen and are obscured by the ovaries. *Ainudrilus taitamensis* and *Ainudrilus brendae* Erséus, 1997, both marine/brackish, are the only other *Ainudrilus* to have hair chaetae. These differ from the new species in that the former has long tubular atria and the latter has only two small straight penial chaetae per bundle and ventral chaetae with upper teeth much longer than the lower.

Rhizodrilus Smith

Rhizodrilus Smith, 1900: 44.—Baker and Brinkhurst, 1981: 952.

Monopylephorus Levinson (in part).—Brinkhurst, 1963: 62.—Brinkhurst, 1965a: 148.—Brinkhurst, 1971a: 555.

Type species. Rhizodrilus lacteus Smith, 1900.

Diagnosis. Chaetae all bifid, hairs absent. Vasa deferentia moderately long, entering atria subapically. Atria normally tubular with diffuse prostate tissue, terminating in ejaculatory ducts which exit either on the inner aspect of large ventrolateral folds in the body wall or into a median invagination of the ventral body wall (copulatory bursa), sometimes via protrusible pseudopenes. Spermathecal chaetae and/or penial chaetae modified in mature specimens, the former associated with large glands. Some or all of the spermathecal genitalia in IX. Sperm in spermathecae in loose masses or in oriented bundles. Coelomocytes abundant.

Remarks. Rhizodrilus consists of a few marine and freshwater species with apparently disparate distributions (Baker and Brinkhurst, 1981; Erséus, 1990a). These are united by the presence in IX of at least some of the spermathecal genitalia. The following species was tentatively included in *Rhizodrilus* by Baker and Brinkhurst (1981).

Rhizodrilus arthingtonae (Jamieson)

Rhyacodrilus arthingtonae Jamieson, 1978.

Rhizodrilus arthingtonae.—Baker and Brinkhurst, 1981: 956.

Holotype. Brown Lake, North Stradbroke Island, Qld (QM G8881).

Material examined: Qld: Holotype and paratype, locality as above, 31 Jul 1975, dissected on slides (QM G8881–2).

Distribution and habitat. Known only from the type locality, a perched acidic lake. Specimens collected in organic material in sandy sediment (Jamieson, 1978).

Diagnosis. Length 66 mm (paratype). Coelomocytes numerous. Anterior chaetal bundles with 3–5 bifid chaetae with the upper teeth slightly longer than the lower, posteriorly teeth about equal. Hair chaetae absent. The chaetae are smaller anteriorly and posteriorly, largest in the clitellar region. Several clearly bifid penial chaetae per bundle in XI, 1.5–2 times longer than somatic chaetae and slightly curved towards the tip. Vasa deferentia narrow, coiled anteriorly, passing through the prostate before entering atria subapically. Atria fusiform to slenderly bulbous, prostate tissue compact but lobulated, enclosing the atrium and communicating with the lumen at numerous points. Slender ejaculatory ducts lead to male pores on the inner wall of a ventrolateral fold in the body wall. Accessory genital markings present, consisting of a pair of conspicuous elliptical papillae posteromedian to ventral bundles of IX, each with a short diagonal groove passing posterolaterally from its centre to 9/10. Spermathecae in X, with indistinct ventrolateral pores at 9/10. Worm squarish in cross-section.

Remarks. Erséus (1994) rightly questions whether *R. arthingtonae* belongs within this genus, preferring to include only those species with large tubular atria and a clear involvement of spermathecal genitalia in IX, rather than X as is normal in the family. *R arthingtonae* has only minor involvement of spermathecal genitalia in IX (just papillae on IX with grooves leading back to the spermathecal pores on 9/10). However, *Rhizodrilus lacteus* Smith, 1900, which has just the spermathecal chaetae and associated glands in IX but retains the spermathecae themselves in X is intermediate between *R. arthingtonae* and other *Rhizodrilus* in this respect and so *R. arthingtonae* may represent one extreme of a continuum. Arguing against this proposition is the fact that the atria are more upright and less tubular than those of other *Rhizodrilus* and Ferraguti et al. (1994) note the more plesiomorphic spermatozoal ultrastructure of *R. arthingtonae* compared to *Rhizodrilus russus* Erséus, 1990a and the related *Monopylephorus* Levinson, 1884. If *R. arthingtonae* is excluded from *Rhizodrilus*, then, short of creating a new genus, it is difficult to see a more suitable place for it. Erséus (1994) summarises the possible relationships between *Rhizodrilus* and other relevant rhyacodriline genera and, since we suggest no change to the status quo, these need not be repeated here. A more satisfactory placement of *R. arthingtonae* may have to await further phylogenetic studies of this and related rhyacodrilines.

Breviatria gen. nov.

Type species. Telmatodrilus multiprostatus Brinkhurst, 1971a, as the first of two species described in the original account.

Diagnosis. Atria ovoid to erect pear-shaped, with unciliated lumen, bearing numerous glands of prostate tissue apically, communicating independently with atrial lumen. Male pores simple on XI, on inner aspect of protruding ventrolateral folds of the body wall surrounding a broad median copulatory chamber. Spermathecal chaetae large and grooved, penial chaetae numerous with blunt or bifid tips. Spermathecae normally with ventrolateral to dorso-lateral pores, located anteriorly on X. Sperm in spermathecae in organised bundles (not spermatozeugmata) or loose. Coelomocytes abundant for at least one species, unknown in the others.

Etymology. Breviatria referring to the short atria, in contrast to the tubular atria of other genera with prostate formed into multiple clumps.

Remarks. Of the four species assigned to this new rhyacodriline genus, three were previously placed within the Telmatodrilinae and one is new. The reasons for re-assigning the earlier species were discussed above (in the Rhyacodrilinae remarks section). *Breviatria* is distinguished from other Rhyacodrilinae by the ovoid to pear-shaped atria with prostate tissue formed into discrete glands with separate (usually stalked) connections to the ectal part of the atria. Other rhyacodriline genera with clumped prostate tissue, mostly marine forms such as *Heronidrilus* Erséus and Jamieson, 1981 and *Heterodrilus* Pierantoni, 1902, usually have the clumps more broadly attached along the length of elongate tubular atria, although prostates are more restricted in position in a few species. The other new genus, *Biprostatus*, described below, also has small atria but these have only two large prostate glands which are broadly attached to the anterior and posterior sides of the atria. Other rhyacodrilines with short atria either have evenly distributed diffuse prostate tissue (such as most *Rhyacodrilus*) or lack prostate tissue (*Ainudrilus* and *Rhyacodrilus simplex*). *Rhizodrilus arthingtonae* (discussed above) also has ovoid atria but the lobes of prostate tissue are tightly packed over the surface of the atria and broadly attached rather than stalked. The new species described below has numerous coelomocytes but this feature needs to be re-examined when fresh material of the other species becomes available.

Breviatria multiprostatus (Brinkhurst) comb. nov.

Figures 4, 5

Telmatodrilus multiprostatus Brinkhurst, 1971a: 535, figs 8.27A–F.—Brinkhurst, 1971b: 117, fig. 3C.—Brinkhurst and Fulton, 1979: 3.—Brinkhurst, 1982: 3, pl. 7.—Holmquist, 1974: 256, figs 10–11.—Bayly, 1973: 305.—Timms, 1978: 430.—Marshall, 1975: 22, fig. 3.—Marshall and Winterbourn, 1979: 205. The species description was duplicated in Brinkhurst (1971b) but the 1971a publication should be used as the original description.

Holotype. Lake Pedder, Tas. (AMS W4178).

Material examined. Tas.: Holotype and paratypes, locality as above, 2–4 Mar 1966 (AMS W4178–W4182) and 1 on slide (ROB); Cuvier R., 10 Oct 1978, 1 on slides (ROB); Collingwood R., 4 Nov 1978, 1 on slides (ROB); trickle under the Needles, 11 Nov 1978, 1 on slides (ROB); creek in Frodshams Pass, 12 Nov 1978, 1 on slides (ROB); Lake Sorell, 2 Feb 1981, 1 sectioned (ROB); Crossing R., south of Lake Pedder, southwest Tasmania, 10 Feb 1987, 1 on slide (QVM:14:3002) and 3 in alcohol (AMP): Lake Surprise, AMG 8112 441869, 13 Nov 1976, 1 on slide (QVM:14:3001) and 1 in alcohol (AMP). Tentatively identified immature specimens from various sites in Tasmania listed by Brinkhurst (1982).

Other records. Tas.: Lake Pedder (Bayly, 1973); South Esk R. (Brinkhurst and Fulton, 1979); Lakes Sorell and Crescent (Timms, 1978). New Zealand: Leeston Drain, near Killinchy, 56 km S of Christchurch (Marshall, 1975; Marshall and Winterbourn, 1979); Freshwater R., Stewart Island (Cowie et al., 1978).

Distribution and habitat. Recorded from lakes, streams and rivers in Tasmania and possibly from New Zealand. The Lake Crescent specimens were collected from a variety of sediment types, including sand, detritus and mud (Timms, 1978). Specimens from Great Lake were collected at depths of up to 16.5 m (Fulton, 1983b).

Description. Length up to 16 mm. Pharyngeal glands present on either side of septa 2/3 to 4/5, gut expanded in VII to form a diverticulum which completely encircles the gut in VII and protrudes forward into VI (Fig. 4A).

Somatic chaetae all simple-pointed (Fig. 5A), up to 8 per bundle anteriorly, fewer posteriorly. Ventral chaetae missing on penial segment of mature specimens, or if present then not modified. Spermathecal chaetae (Fig. 5B) larger than somatic chaetae, with extensive musculature, projecting into an enlarged chaetal sac posteriorly on X, into which also empties a separate elongate gland (Fig. 4C). In one paratype, the spermathecal chaetal sac opens anteriorly in X, with the chaetal shaft protruding well anteriad into IX (Fig. 4B).

Testes anteroventral in X, with sperm funnels on 10/11 feeding broad vasa deferentia which wind upwards to enter atria apically (Figs 4B, C). Atria elongate pear-shaped, may be folded over dorsally, with unciliated lumen and thick lining tissue. Atria narrow basally, opening on inner aspect of folds in the body wall lateral to a median ventral copulatory chamber. Prostate cells grouped into numerous glands which narrow basally and connect to apical third of atria (Figs 4B, C, Fig. 5C). Spermathecae large in X with short ducts that lead to ventral pores just behind septa 9/10 (or medially in X in the Lake Sorell specimen). Sperm loose in ampulla. Ovaries attached to anterior septa of XI near sperm funnel. Female funnels large, leading to pores at intersegmental furrow 11/12 (Figs 4B, C).

Remarks. This is the only Australian tubificid to have all chaetae simple-pointed. However, many aquatic Enchytraeidae also have multiple simple-pointed chaetae in all bundles and immature forms could be confused with *B. multiprostatus*. Of the Tasmanian records, the only identifications that can be confirmed by re-examination of specimens are those from Lake Pedder and Lake Sorell. Specimens from the other sites listed above are either immature (and so are tentatively

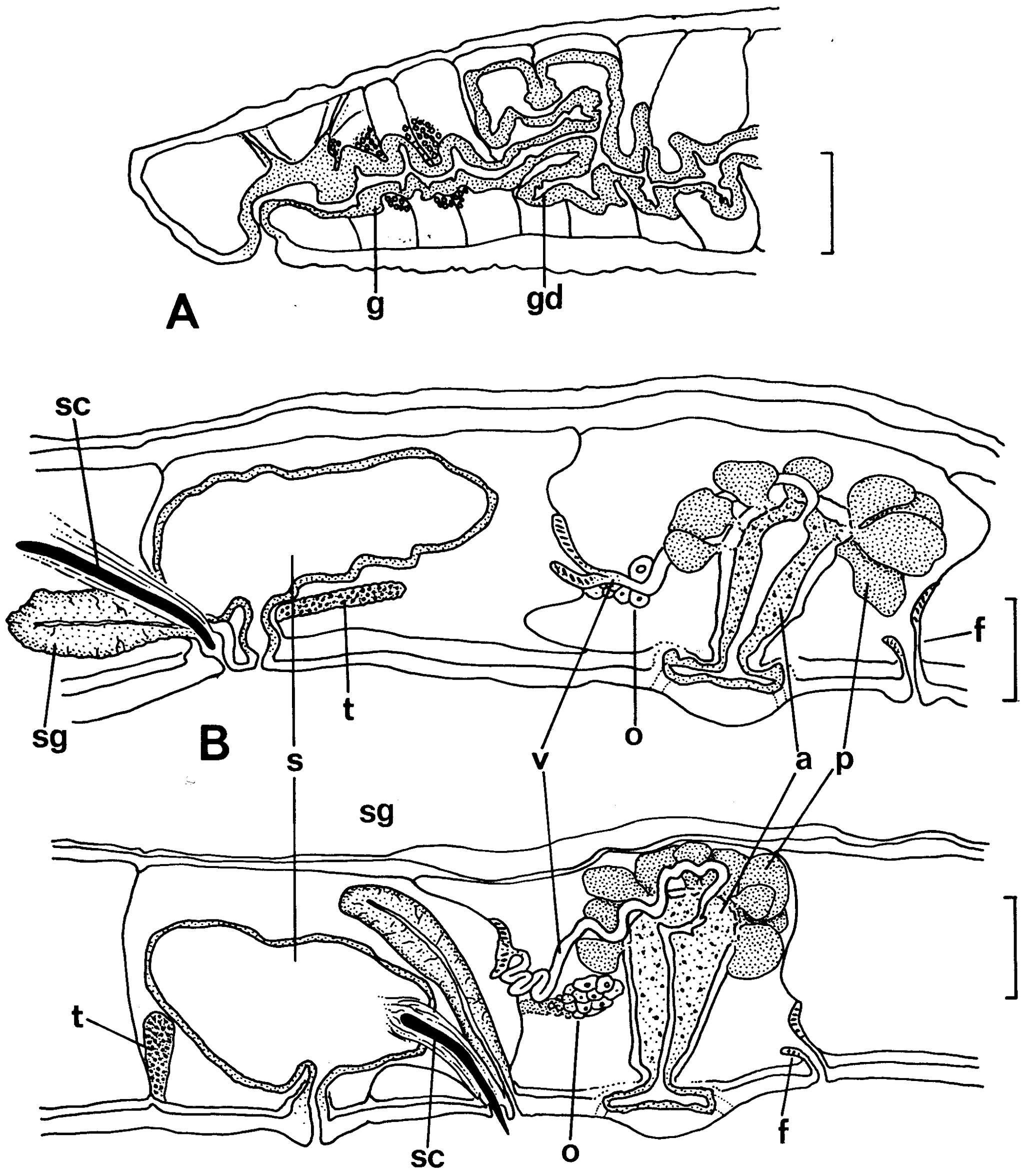

Figure 4, *Breviatria multiprostatus* (Brinkhurst): A, anterior of specimen from Lake Sorell; B, genitalia of paratype AMS W4182; C, genitalia of Lake Sorell specimen. Scales: A–C, 0.15 mm.

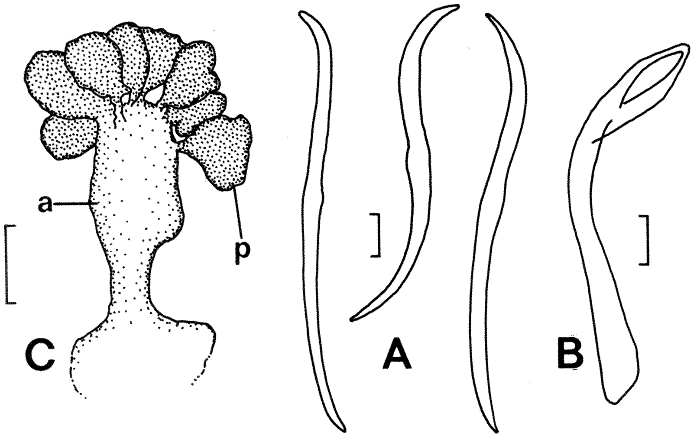

Figure 5, *Breviatria multiprostatus* (Brinkhurst): A, typical somatic chaetae; B, bent spermathecal chaeta of holotype; C, atria dissected from holotype. Scales: A, 0.02 mm; B, 0.05 mm; C, 0.2 mm.

identified from the chaetae only) or their identification can no longer be verified because of their poor condition. It is not known whether identifications of specimens from New Zealand were based on the genitalia of mature specimens or just the chaetae of immature worms so the identification must be considered tentative. One of the New Zealand records (Leeston Drain) is unusual in that the site was enriched with septic tank leachate and dairy effluent (Marshall and Winterbourn, 1979) whereas the Australian records are all from non-enriched sites, including minimally disturbed alpine streams.

The position of the spermathecal pores and spermathecal chaetae appears to vary. Paratypes W4180 and W4182 (Fig. 4B) both have spermathecal pores anterior in X, but spermathecal chaetae posterior and anterior (projecting forward into IX) in X respectively. The Lake Sorell specimen has spermathecal chaetae posterior in X but the spermathecal pore medial on X (Fig. 4C). All other features of these worms seem similar and we consider the variation in spermathecal characters to be intraspecific for now. The holotype is dissected rather than sectioned and the original position of the spermathecae is unclear.

Breviatria pectinatus (Brinkhurst) comb. nov.

Figure 6

Telmatodrilus pectinatus Brinkhurst, 1971a: 535, figs 8.25D–H.—Brinkhurst, 1971b: 117, fig. 3D.—Bayly, 1973: 305.—Holmquist, 1974: 257, fig. 12.—Timms, 1974: 276.—Timms, 1978: 435. The species description was duplicated in Brinkhurst (1971b) but the 1971a publication should be used as the original description.

Holotype. Lake Pedder, Tas. (AMS W4176).

Material examined. Tas.: Holotype and paratypes, Lake Pedder, 2 Mar 1966, 2 on slides (AMS W4176–7) and 5 on slides (ROB).

Other Australian records. Tas.: Lake Pedder (Bayly, 1973); Lake St Clair (Timms, 1978). Vic.: Lake Tali Karng (Timms, 1974).

Distribution and habitat. Recorded only from the above lakes in Victoria and Tasmania. Bayly (1973) collected this species from Lake Pedder (in 1972) in sandy sediment but the Lake Tali Karng specimens were recovered from mud at a depth of 12 m.

Description. Length unknown, but greater than 10 mm.

Anterior bundles with 9–14 chaetae, upper teeth longer than the lower and slightly hooked. Posterior bundles with 5–8 pectinate chaetae with upper teeth not so long (Fig. 6A). Spermathecal chaetae single, thin with grooved tips (Fig. 6B), up to twice as long as somatic ventral chaetae. Penial chaetae (Fig. 6C) modified with rough, blunt to bifid tips (absent on paratype W4176), about 1.5 times longer than somatic ventral chaetae.

Vasa deferentia broad, coiled once or twice before entering atria apically (Fig. 6D). Atria pear-shaped with numerous prostates with short stalks distributed around the upper half. Stalks enveloped by the atrial muscle tissue. Individual peritoneal cells form diffuse cover over basal half of atria and some present apically (Fig. 6D). Atria narrowing to pores on the inner aspect of lateral folds in the body wall around a shallow median ventral copulatory chamber. Details of the spermathecae difficult to decipher but possibly quite folded, with lateral or dorsolateral pores and containing loose sperm.

Remarks. Pectinate chaetae are more common in the Tubificinae than the Rhyacodrilinae and the former usually has pectinations more developed anteriorly, rather than posteriorly as in *B. pectinatus*.

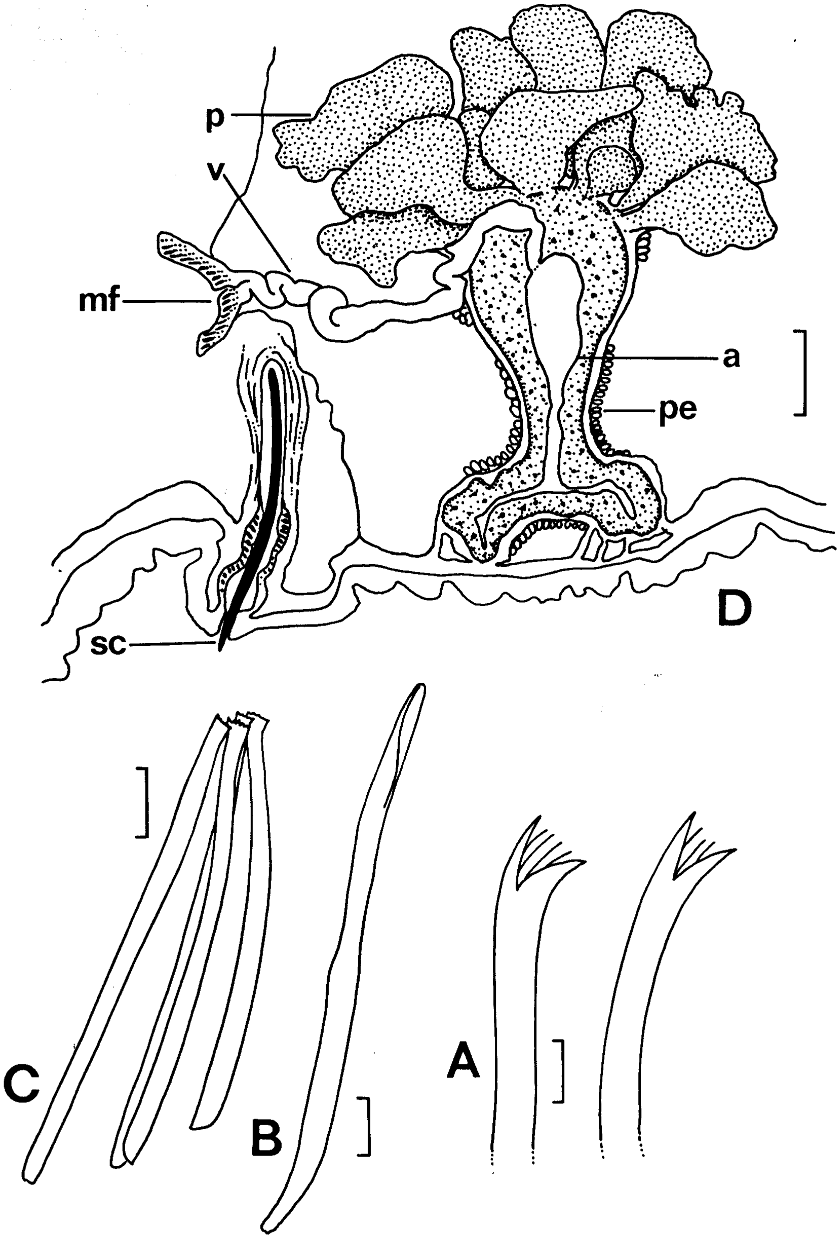

Figure 6, *Breviatria pectinatus* (Brinkhurst): A, tips of pectinate dorsal chaetae of holotype; B, spermathecal chaeta of holotype; C, penial chaetae of holotype; D, male ducts and spermathecal chaetae of paratype AMS W4177. Scales: A, 0.01 mm; B–C, 0.015 mm; D, 0.05 mm.

Breviatria papillatus (Brinkhurst and Fulton) comb. nov.

Figure 7

Telmatodrilus (Alexandrovia) papillatus Brinkhurst and Fulton, 1979: 2, figs 9–14.—Fulton, 1983a: 778.—Fulton, 1983b: 792.

Holotype. Great Lake, Tasmania (QVM:14:320 and 321).

Material examined. Tas.: Holotype and paratypes, type locality, 26 Sep 1975, 3 on slides (QVM:14:320, 321, 326 and 327) and 1 on slide (ROB); Arthurs Lake, 4 Jul 1977, 8 on slide, 2 mature and several immature in alcohol (NMV F88870, F88871 and ROB); Lake Sorrel, no date, 4 on slides (QVM:14:322–325).

Distribution and habitat. Recorded only from the above lakes of the central plateau of Tasmania. Collected in both sandy and clayey sediments, at depths up to 17.5m (Fulton, 1983b).

Description. Length 10–20 mm. Coelomocytes not observed. Worms encrusted with fine foreign material, body wall papillate with several rings of papillae per segment (Fig. 7A). Prostomium and segment I (and sometimes II) may be retracted into the body. Posterior segments narrow and

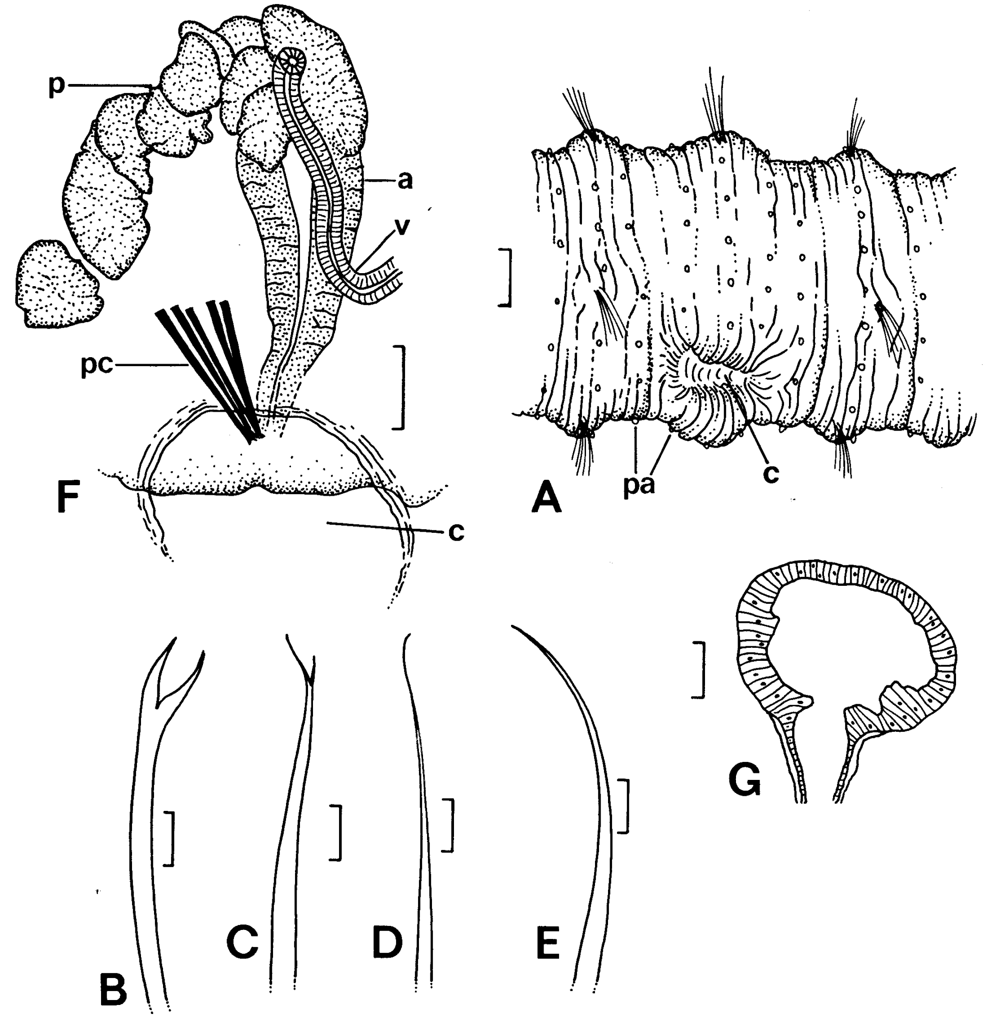

Figure 7, *Breviatria papillatus* (Brinkhurst and Fulton): A, view of body showing copulatory bursa on XI; B, tip of anterior chaeta; C–D, tips of transitional chaetae; E, tip of posterior hair chaeta; F, male ducts of NMV F88870; G, spermatheca of NMV F88870. Scales: A, 0.2 mm; B–E, 0.01 mm; F, 0.05 mm; G, 0.025 mm.

appearing highly contracted in the preserved specimens.

Anterior chaetae bifid, 5–7 per bundle, with each tooth broad and flattened (Fig. 7B). Chaetae changing to a hair-like form, some with vestiges of teeth (Figs. 7C, D) between VII and X so that postclitellar bundles have 5–9 curved hair chaetae (Fig. 7E). Penial chaetae slightly shorter than preclitellar somatic chaetae, 3–5 per bundle with bifid tips (Fig. 7F). Spermathecal chaetae not modified.

Long vasa deferentia connect to short pear-shaped atria subapically (Fig. 7F). Atria narrow gradually to enter small median copulatory chamber (which is everted in some preserved worms) near the penial chaetae which project from the protruding lateral walls of the chamber. Three or more lobes of prostate tissue on atria apically (Fig. 7F). Spermathecae small and globular (Fig. 7G) with short ducts leading to lateral pores anteriorly on X. Sperm not observed in ampullae.

Remarks. While the chaetae and papillae of *B. papillatus* are unusual, the genitalia suggest that this species is simply an apomorphic member of *Breviatria* and to exclude it would leave *Breviatria* paraphyletic. Specimens from Arthurs Lake, some of which were dissected and illustrated for this study (Fig. 7), clearly have spermathecae with lateral pores whereas spermathecae were not seen in the type specimens from Great Lake. The spermathecae of these specimens are very small (100–150 µm) and do not contain sperm, so may not be fully developed. Unfortunately, the type specimens have become too cleared for this feature to be checked. The holotype (the only type in which the genitalia can be seen) has ‘at least 2 or 3 prostate glands’ (Brinkhurst and Fulton, 1979), but the size of these and their attachment to the atria is uncertain due to clearing and distortion during slide mounting. The prostate on one atrium of the holotype appears to be formed into two or three large, stalked lobes but on the other atrium the prostate appears to be a more cohesive mass with a number of short connections. The prostate tissue of the Arthur R. specimens is clearly formed into numerous small glands but connections to the atria are obscured. Fresh specimens from the type locality are required to determine the unity of this taxon.

Breviatria arvensis sp. nov.

Figure 8

Material examined. Holotype: Arve R. at Arve Rd, 43°11′20′′S 146°46′05′′E, Tasmania, 12 Mar 1997, R. Marchant (NMV) and A. Pinder, dissected on slide (QVM:14:3878).

Paratypes: Collection details as for holotype, 1 mature and 1 immature sagitally halved on slide, with posterior portion of 1 of these in alcohol, and 1 immature whole-mounted on a slide (QVM:14:3879–3881).

Distribution and habitat. Known only from the type locality, collected from sand/silt under cobble at a depth of 10–20 cm.

Etymology: Named *arvensis* for the type locality.

Description. Length at least 20 mm (none complete), width of slide mounted worms 0.25–0.3 mm. Prostomium squarish in preserved type material. Coelomocytes abundant but without consistent shape, entirely filling coelom in most of body, including the prostomium, making the worms appear quite solid when handled.

All chaetae bifid, 55–85 µm long, with upper teeth longer than lower and nodulus slightly ectal (Fig. 8A). Up to 8 chaetae per bundle anteriorly, reduced in number posteriorly. Chaetae of spermathecal segment (X) present but not modified, penial chaetae of XI 4 per bundle, straight, with bifid ectal ends and no nodulus (Fig. 8B), 150–165 µm long, projecting somewhat diagonally towards the midline to open into median copulatory chamber (Fig. 8C).

Testes anteroventral in X. Sperm funnels large, vasa deferentia wide and slightly coiled near funnel. Point of union of atria and vasa deferentia not established. Atria ovoid, thin walled, with short ejaculatory ducts leading to pores on inner aspect of folds in body wall lateral to a median ventral copulatory chamber (Fig. 8C). Prostate tissue present as numerous discreet glands, which presumably connect with atria individually, although this could not be confirmed. Spermathecae bulbous with short ducts leading to dorso–lateral pores anteriorly on X. Sperm in ampullae formed into numerous bundles. Ovaries anteroventral in XI, female pores not observed.

Remarks. Although the connections between the atria and prostate tissue are obscured in the available specimens, the numerous separate glands are similar to those of other *Breviatria*. The long straight penial chaetae with bifid tips also resemble those of other *Breviatria*. The bifid chaetae of *B. arvensis*, with their long upper teeth, differ from those of all other *Breviatria* but resemble those of *Biprostatus duplex*, described below.

Biprostatus gen. nov.

Diagnosis. Atria small and spherical, bearing broadly attached prostate tissue formed into

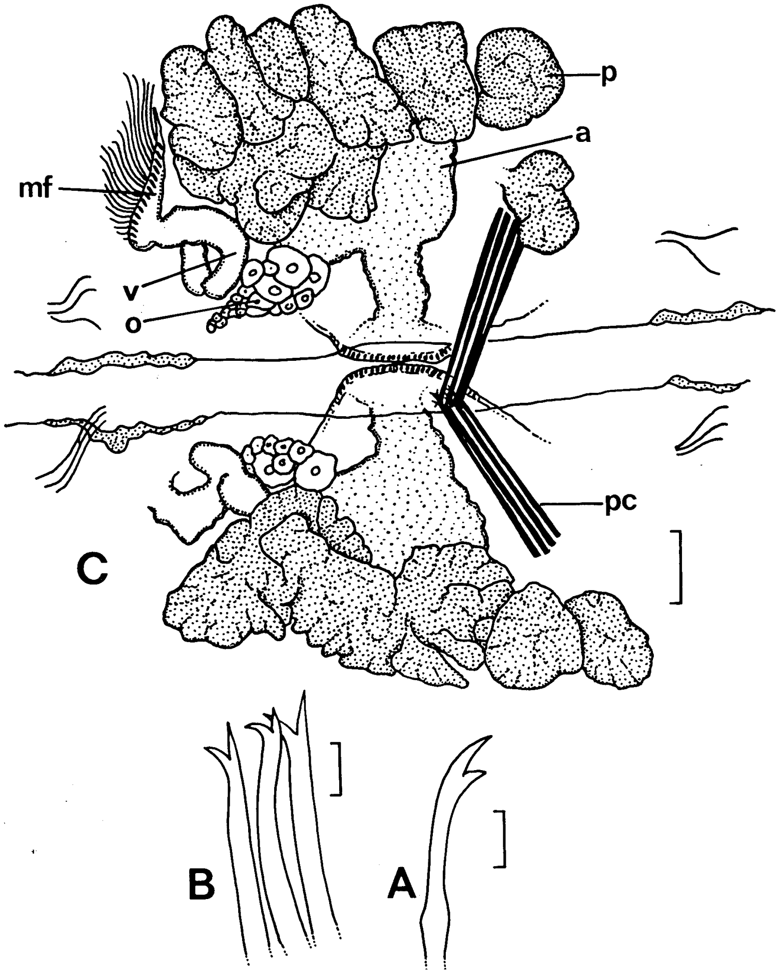

Figure 8, *Breviatria arvensis* sp. nov.: A, tip of ventral chaeta; B, tips of penial chaetae; C, male genitalia of holotype. Scales: A–B, 0.01 mm; C, 0.06 mm.

two large glands, one anterior and one posterior. Atria leading to simple pores on inner aspects of folds in body wall, lateral to a median ventral copulatory chamber. Spermathecal chaetae large and grooved, penial chaetae multiple and bluntly bifid. Spermathecal pores lateral, sperm in ampullae in loose bundles. Coelomocytes abundant in anterior segments in at least one species, to be confirmed for the rest.

Type species: Telmatodrilus bifidus Brinkhurst and Fulton, 1979.

Remarks. The type species of *Biprostatus* was originally placed within the telmatodriline genus *Telmatodrilus*, but is transferred to this new rhyacodriline genus for reasons already discussed above (see remarks for Rhyacodrilinae). This genus is separable from most others in the Rhyacodrilinae by virtue of the small atria with large bilobate prostate glands. Although some *Heterodrilus*, such as *H. inermis* and *H. rapidensis*, also have short atria with large paired prostate glands, these glands appear to be stalked and the chaetae of *Heterodrilus* (1 or 2 per bundle, at least some of which are trifid) are diagnostic (Erséus, 1981).

Biprostatus bifidus (Brinkhurst and Fulton) comb. nov.

Figure 9

Telmatodrilus ? (*Telmatodrilus* ?) *bifidus* Brinkhurst and Fulton, 1979: 3, figs 15–19.

Holotype. Great Lake, Tas. (QVM:14:328).

Material examined. Tas.: Holotype and paratypes, Great Lake, 1975, 10 on slides (QVM:14:328–339); Arthurs Lake, 4 Apr and 22 May 1977, 4 on slides (ROB).

Distribution and habitat. Recorded only from the above lakes of the central plateau of Tasmania. Collected in both sandy and clayey sediments, at depths up to 17.5m (Fulton, 1983b).

Diagnosis. Length up to 25 mm. Anterior bundles with up to 13 bifid chaetae with upper teeth longer than the broad lower. (Fig. 9A) Number of chaetae diminishing from VIII–X with upper teeth becoming shorter than the lower after the clitellar region (Fig. 9B). Chaetae of some species have groove-like markings (ornamentations) ectally. Spermathecal chaetae straight, single, with grooved tips (Fig. 9C), varying in width and length, from shorter than to 3 times longer than somatic chaetae. Penial chaetae bifid (Fig. 9D), up to 7 per bundle, twice as long and thick as somatic ventral chaetae. Atria small, elongate ovoid with short ejaculatory ducts (Fig. 9E). Each atrium with a pair of broadly attached prostate glands, one anterior, which envelops the vas deferens, the other posterior, occupying much of the coelom (Fig. 9E). Male pores and penial chaetae on the lateral walls of a large median copulatory chamber. Spermathecae ovoid, with short duct-like extension entally and lateral pores. Sperm in ampullae formed into loose bundles. Coelomocytes not recorded.

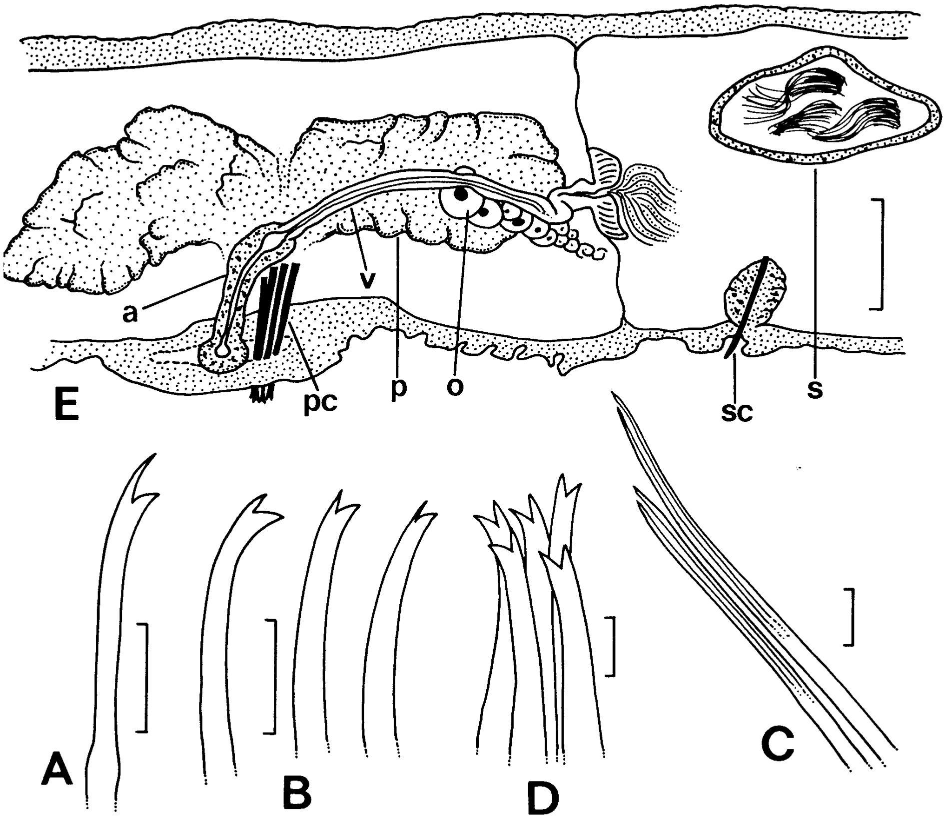

Figure 9, *Biprostatus bifidus* (Brinkhurst and Fulton): A, tip of anterior chaeta; B, tips of posterior chaetae; C, tips of spermathecal chaetae of Arthurs Lake specimen; D, tips of penial chaetae of holotype; E, genitalia of QVM:14:338. Scales: A–B, 0.015 mm; C, 0.015 mm; D, 0.01 mm; E, 0.12 mm.

Biprostatus duplex sp. nov.

Figures 10, 11

Telmatodrilus sp. 2.—Pinder and Brinkhurst, 1994.

Material examined. Holotype: Que R., just below Que R. Mine dam, Tasmania, AMG 8014 914956, 27 Apr 1987, Wayne Fulton and Brett Mawbey (IFC), transverse serially sectioned specimen (with the posterior whole-mounted) on 15 slides (QVM:14:4207).

Paratypes: Collection details as for holotype, 5 serially sectioned and 3 mounted whole or dissected on slides, (QVM:14:4208, 4210–4215, 4218); Que R. at Murchison Highway, Tasmania (AMG 8014 901963), 27 Apr 1987, W. Fulton and B. Mawbey (IFC), 2 serially sectioned and 2 whole-mounted on slides (QVM:14:4209, 4216, 4217, 4223).

Other material. Tas: Southwell R., above Hellyer mine, AMG 8014 945960, 20 Dec 1988, S. Chilcott (IFC), 1 on slide, 5 in alcohol (AMP); Douglas Creek, AMG 8114 206692, 16–17 Feb 1990, S. Chilcott and L. Mellefont (IFC), 1 on slide (AMP); Creek at Charlies Hill, AMG 8111 297938, 19 Feb 1990, B. Mawbey (IFC), 2 in alcohol (AMP).

Distribution and habitat. The above sites are all rivers in western Tasmania.

Etymology: Named *duplex* for the double prostate gland.

Description. Length up to 20 mm. Prostomium short, bluntly conical. Coelomocytes large, abundant in a few preclitellar segments.

Anterior chaetae 3–7 per bundle (Figs 10A, C), fewer posteriorly, nodulus slightly distal, upper teeth much longer than lower. Posterior chaetae 2–4 per bundle, nodulus clearly distal, upper teeth also much longer than lower. Chaetae shortest in II (75 µm) and posteriorly, otherwise about 110 µm. Spermathecal chaetae single in X and/or IX, 140–160 µm long and grooved ectally (Figs 10D, E), associated with large glands (Fig. 10G), protruding from the body wall in line with somatic ventral chaetae. Penial chaetae 4–7 per bundle, straight with notched ectal ends (Fig. 10F), no nodulus, 120–160 µm long. Penial chaetae lie medial to atria and project somewhat diagonally toward midline to open into median depression of the body wall.

Sperm funnels large, vasa deferentia thin, slightly coiled at first, then running posteriad to enter the small globular atria subapically. Atria with prostate tissue formed into large anterior and posterior lobes (Fig. 11B). Short ejaculatory ducts lead to pores on inner aspect of folds in body wall lateral to a median copulatory chamber (Figs 11A, B). Thick glandular tissue present ventrally on either side of 10/11, more so in X (Figs 10G, 11B). Spermathecae oval (Fig. 10G), with short thick-walled ducts and pores antero-laterally in X. Sperm in ampullae formed into bundles.

Remarks. This species is similar to *B. bifidus* in many respects. The genitalia, bifid or notched penial chaetae and anterior somatic chaetae are similar in the two species, although the latter are less numerous in *B. duplex*. They differ in that the upper teeth of the posterior somatic chaetae of *B. duplex* are longer than the lower (like *Breviatria arvensis*) whereas the upper teeth are shorter than the lower on the posterior chaetae of *B. bifidus*. The tips of the spermathecal chaetae also appears to differ.

Bothrioneurum Stolc

Bothrioneurum Stolc, 1886: 647.—Michaelsen, 1900: 54.—Stephenson, 1930: 752.—Brinkhurst, 1971a: 539.

Type species. Bothrioneurum vejdovskyanum Stolc, 1886.

Diagnosis. All chaetae bifid, hair chaetae absent. Prostomium with a middorsal sensory pit. Vasa deferentia short to long. Atria tubular and covered with diffuse prostate gland cells except for ectal portion, leading to protrusible pseudopenes bearing diverticula (paratria) with accessory glands. Sperm stored within external spermatophores, attached to body wall. Spermathecae absent. Penial chaetae may be modified. Coelomocytes large and abundant.

Bothrioneurum vejdovskyanum Stolc

Bothrioneurum vejdovskyanum Stolc, 1886: 647.—Michaelsen, 1900: 54.—Brinkhurst, 1971a: 540, figs 8.29A–D.—Brinkhurst, 1982: 1.

Material examined. NSW: North Katoomba sewage treatment plant constructed wetlands, 10 Aug 1994, tentative identification of immature worms (AWT).

Other Australian records. NSW: Barrington R., Gloucester (Brinkhurst, 1982). Tas.: Arve R. (Brinkhurst, 1982).

Distribution and habitat. Cosmopolitan (Brinkhurst, 1971a) but uncommon in Australia.

Diagnosis. Length 28–35 mm. Anterior bundles with 4–6 bifid chaetae with upper teeth longer than lower, posteriorly fewer with teeth equally long. Ventral bundles of XI with 4 slightly hooked, club-headed penial chaetae arranged in a fan. Vasa deferentia long, joining tubular atria apically. Atria covered with prostate gland, except for terminal portion, and leading to protrusible pseudopenes which bear paratria with accessory glands. Spermathecae absent. Body

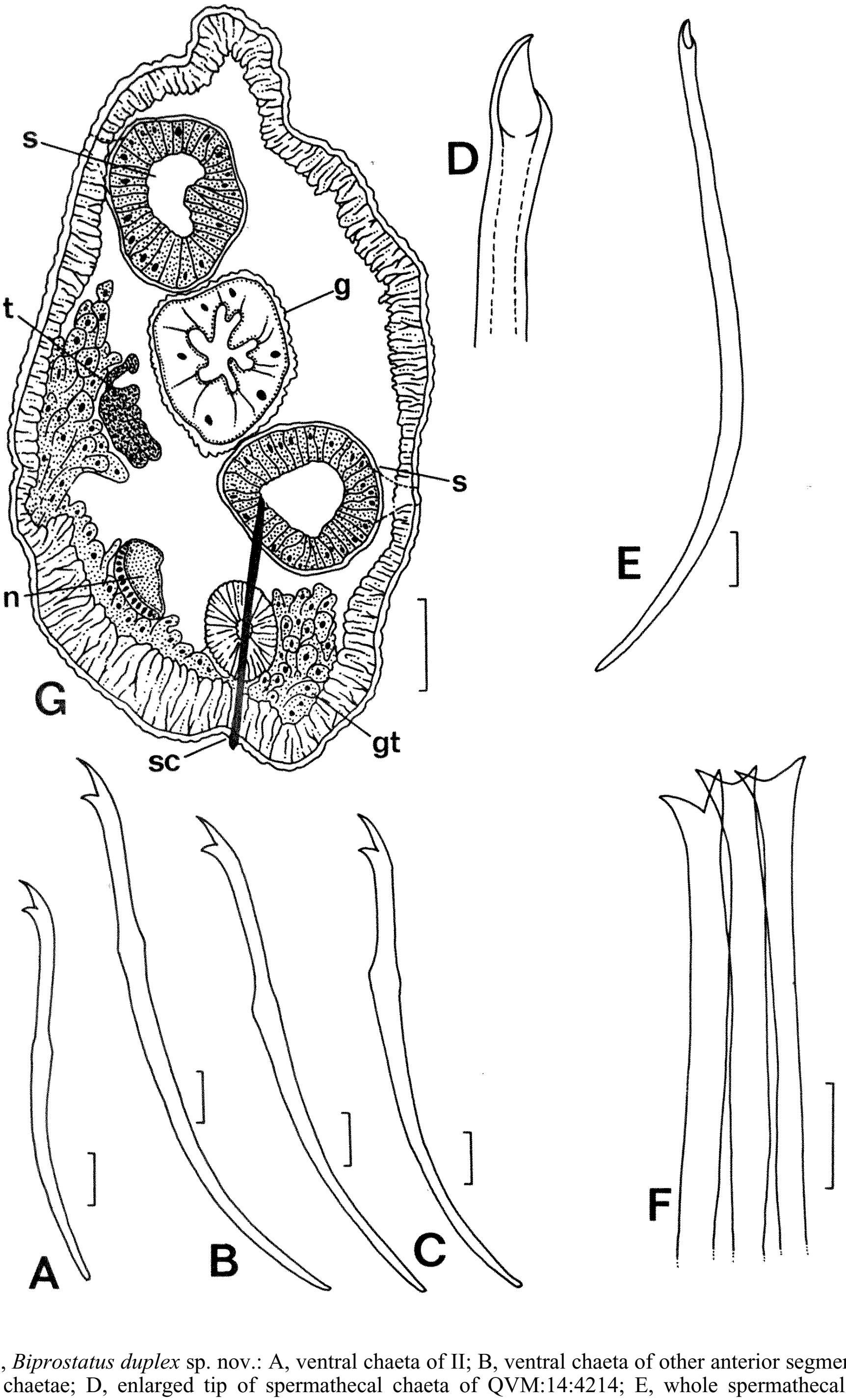

Figure 10, *Biprostatus duplex* sp. nov.: A, ventral chaeta of II; B, ventral chaeta of other anterior segments; C, two posterior chaetae; D, enlarged tip of spermathecal chaeta of QVM:14:4214; E, whole spermathecal chaeta of QVM:14:4214; F, tips of penial chaetae of QVM:14:4214; G, transverse section through segment X, composite from several sections of holotype. Scales: A–C, E and F, 0.01 mm; G, 0.05 mm.

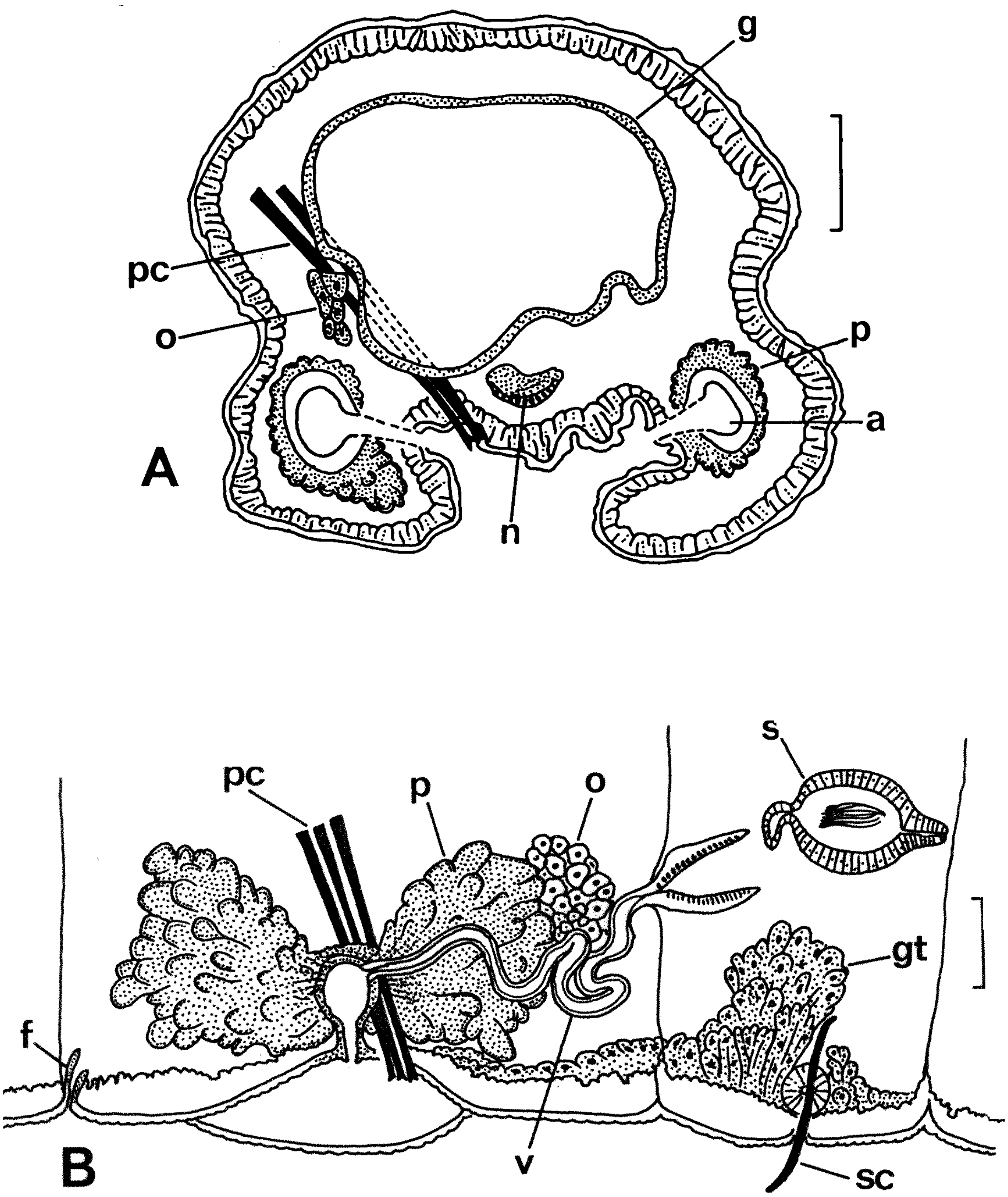

Figure 11, *Biprostatus duplex* sp. nov.: A, transverse section through segment XI, composite from several sections of paratype QVM:14:4223; B, reconstruction of genitalia from several specimens. Scales: A–B, 0.05 mm.

wall may appear spotted or papillate, but smooth. Prostomium with dorsal sensory pit, often difficult to detect but visible as a small indentation when a slide mounted specimen viewed laterally.

Remarks. The only mature specimens examined are from Barrington R. and these matched the description of the species, except that the prostomial pit was not observed. All other identifications are of immature specimens based on the presence of the prostomial pit and the form of the somatic chaetae. An electron micrograph of the prostomial pit is provided by Brinkhurst and Gelder (1991).

Branchiura Beddard

Branchiura Beddard, 1892.—Michaelsen, 1900: 40.—Stephenson, 1930: 749.—Brinkhurst, 1971a: 562.

Type species. Branchiura sowerbyi Beddard, 1892.

Diagnosis. Hair chaetae present. Vasa deferentia short, joining atria medially. Atria cylindrical, covered in prostate cells. A glandular diverticula (paratria) attached to atria where the latter join large eversible pseudopenes. Coelomocytes not conspicuous. Dorsal and ventral gill filaments present posteriorly.

Branchiura sowerbyi Beddard

Branchiura sowerbyi Beddard, 1892: 325, pl. XIX, figs 1–15.—Michaelsen, 1900: 40.—Stephenson, 1930: 750.—Brinkhurst, 1971a: 563, figs 8.36D–F.—Brinkhurst, 1971b: 114, fig. 2H.—Brinkhurst, 1982: 1.—Hogg and Norris, 1991:515.—Timms, 1981: 188.

Kawamuria japonica Stephenson, 1917: 89, figs 1–5.

Holotype. Royal Botanical Gardens, London (Typus amissus).

Material examined. NSW: Parramatta R., 17 Oct 1981 (AMS W197365); Wingecarribee R. at Greenstead, 14 Nov 1991, 2 in alcohol (AWT); Murray R. at Dora Dora, 24 Mar 1994 (MDFRC); Megarritys Creek, Fernsworth Avenue, 3 Feb 1993, 1 in alcohol (AWT); Rushy Billabong, 16 Jun 1981, 1 on slide (MDFRC); Ryans Billabong, 27 Jul and 6 Dec 1982, 1 on slide, 1 in alcohol (MDFRC). Qld: Leichhardt R., Coolullah H.S., 115 km NW Cloncurry, 25 Apr 1988, 1 on slide (SAM E2814). Vic.: junction of Thomson and MacAlister R.s, 31 Jun 1979, 1 in alcohol (NMV F77640); Mitta Mitta R., 1 Feb 1975, 2 Dec 1980 and 3 Mar 1982, 5 on slides, 3 in alcohol (NMV F77633–8). WA: Herdsman Lake, 2 Nov 1989, 1 on slide (MUR); Wungong Brook, Jan 1998, 1 two-tailed worm in alcohol (AMP).

Other Australian records. ACT: Murrumbidgee R. (Hogg and Norris, 1991). Qld: Brookfield, Goldcreek (Brinkhurst, 1971a). Vic.: Thomson R. (Brinkhurst, 1982); Lake Purrumbete (Timms, 1981). WA: Lake Claremont and Lake Monger, Perth (Brinkhurst, 1971b).

Distribution and habitat. Cosmopolitan (Brinkhurst, 1971a), widespread in Australia, occurring in a wide range of environments.

Diagnosis. Length 30–185 mm. Dorsal anterior chaetal bundles with 1–4 (or more) short hair chaetae and 5–12 (or more) chaetae that vary from simple-pointed to bifid with short upper teeth (which may be replicated). Posteriorly hairs fewer and shorter and non-hair chaetae with less replication of upper teeth. Ventral bundles with 6–11 bifid chaetae with upper teeth shorter than lower, even simple-pointed anteriorly. Gills and genital anatomy as for genus.

Other tubificid taxa

Timms (1978) records the tubificine *Peloscolex* sp. (and *'Peloscoiex'*, undoubtedly a misprint) from Lake St Clair, based on identifications by K. V. Naidu. These refer to some form of papillate tubificid, though presumably differing in chaetal morphology from *Breviatria papillatus*. These should not be considered definitive generic identifications since body wall papillae are characteristic of, but not diagnostic for, *Peloscolex* Leidy, 1850, now revised as *Spirosperma* Eisen, 1879, and other genera (Brinkhurst, 1979; Holmquist, 1978, 1979). We have seen several papillate immature worms from Victoria (including specimens from the Plenty, Glenelg, Curdies and La Trobe Rivers) and New South Wales (Georges R.) that have chaetae very similar to some *Spirosperma*, but mature specimens are required for identification.

The species coded *Telmatodrilus* sp. 1 in Pinder and Brinkhurst (1994) cannot yet be described from the few poorly preserved specimens. This species, which may be a *Biprostatus*, has anterior chaetae bifid (like those of *B. duplex*), posterior chaetae simple pointed, and has modified penial and spermathecal chaetae. Specimens have been collected from Que and Southwell Rivers in northwest Tasmania.

Numerous other undescribed tubificids, mostly from Tasmania and Western Australia, have been accumulated by the senior author since the preparation of this manuscript and no doubt others await discovery.

Zoogeography

Discussion of tubificid biogeography in the region is limited by the low number of specimens that have been examined from Australia, New Zealand and Asia. No area of Australia has been thoroughly surveyed, although projects are underway to improve coverage of particular areas such as the southwest of Western Australia, Tasmania and South Australia. Nonetheless, some patterns can be discerned.

Twenty-nine species of Tubificidae, in 12 tubificine and rhyacodriline genera, have been recorded from Australian inland waters so far (Table 1). Of these, 16 species are restricted to Australia and two more are known only from Australia and New Zealand.

The nonendemic component consists of 11 common species within widespread genera (i.e. the tubificine genera *Tubifex, Limnodrilus, Aulodrilus* and *Potamothrix* and the rhyacodrilines *Rhyacodrilus, Branchiura and Bothrioneurum*). Several of these species also occur in New Zealand (Brinkhurst and Fulton, 1979, 1982; Marshall, 1975; Timms, 1982). Of the cosmopolitan species, only *Aulodrilus pigueti, Aulodrilus pluriseta* and *Branchiura sowerbyi* have been recorded from northern Australia (the Queensland records of *Limnodrilus* and *Tubifex* are from the southeast of the state), but this may reflect the low number of worms examined from this region. So far, records of *Aulodrilus pigueti* have been restricted to northern Australia, but other cosmopolitan species are widespread in southern Australia and seem to occur in a wide range of habitats. The endemic species appear to have more restricted distributions.

One of the three endemic genera, *Antipodrilus*, is widespread, although most of the species are not. *Antipodrilus davidis*, with the new range extensions into Western Australia and South Australia, is the most widely distributed and is now known from across southern Australia and New Zealand. By contrast, *A. magelensis* appears to be

Table 1. Species list of Tubificidae known from Australia. * = known only from Australia, # = known only from Australia and New Zealand, #? = New Zealand identification dubious, others cosmopolitan. NSW includes Australian Capital Territory, n = north, sw = southwest.

Subfamily	Genus	Species	Australian state							
			NT	Qld	WA(n)	WA (sw)	SA	NSW	Vic.	Tas.
Tubificinae	*Tubifex*	*tubifex*		●		●	●	●	●	●
	Limnodrilus	*hoffmeisteri*		●		●	●	●	●	●
	Limnodrilus	*udekemianus*		●		●	●	●		●
	Limnodrilus	*clapareianus*							●	
	Potamothrix	*bavaricus*				●		●	●	●
	Antipodrilus	*magelensis**	●				●			
	Antipodrilus	*davidis#*				●	●	●	●	●
	Antipodrilus	*timmsi**						●	●	
	Antipodrilus	*multiseta**								●
	Antipodrilus	*plectilus**								●
	Aulodrilus	*pluriseta*	●	●						
	Aulodrilus	*pigueti*	●	●	●			●	●	
	Aulodrilus	*limnobius*						●	●	
Rhyacodrilinae	*Rhyacodrilus*	*coccineus*				●?		●		
	Rhyacodrilus	*megaprostatus**							●	
	Rhyacodrilus	*bifidus#*						●	●	
	Ainudrilus	*billabongus**	●							
	Ainudrilus	*stagnalis**	●							
	Ainudrilus	*nharnus**				●				
	Ainudrilus	*fultoni**								●
	Rhizodrilus	*arthingtonae**		●						
	Breviatrius	*multiprostatus#?*								●
	Breviatrius	*pectinatus**							●	●
	Breviatrius	*papillatus**								●
	Breviatrius	*arvensis**								●
	Biprostatus	*bifidus**								●
	Biprostatus	*duplex**								●
	Bothrioneurum	*vejdovskyanum*						●		●
	Branchiura	*sowerbyi*		●		●		●	●	

a species of the north and interior, *A. timmsi* is known only from the south-east mainland while *A. plectilus* and *A. multiseta* have not been recorded outside a few sites in Tasmania. All species show a preference for lentic habitats.

Both species of the new genus *Biprostatus* are known only from Tasmania. The other new genus, *Breviatria*, has four species, three of which are apparently restricted to Tasmania. One of these, *Breviatria multiprostatus*, may also occur in New Zealand (Cowie et al. 1978; Marshall and Winterbourn, 1979) but the identifications are uncertain. The fourth, *Breviatria pectinatus*, is known from a few lakes in Tasmania and Victoria.

Other endemic rhyacodrilines belong to genera with disjunct global distributions. *Rhizodrilus* mostly consists of marine species with restricted distributions, often limited to single records from the type localities (Baker and Brinkhurst, 1981; Erséus, 1990a). The only Australian species, *Rhizodrilus arthingtonae*, is known only from one lake on North Stradbroke Island, Queensland (Jamieson, 1978). *Ainudrilus* mostly consists of coastal Pacific or Caribbean marine species (Erséus, 1990ab; 1997), except for the four freshwater Australian species. Of these, *A. stagnalis* and *A. billabongus* have been recorded only from the Northern Territory, *A. nharna* only from southwest Western Australia and *A. fultoni* only from Tasmania.

Of the 18 species restricted to Australia and New Zealand, ten occur in Tasmania and eight are known only from that state (including most species of the new rhyacodriline genera). Similarly, about half of the 26 species of Australian Phreodrilidae are restricted to Tasmania (Pinder and Brinkhurst, 1997). By contrast, only three tubificids (*Rhyacodrilus megaprostatus*, *Rhyacodrilus bifidus* and *Antipodrilus timmsi*) and one phreodrilid (*Phreodriloides notabilis* Benham, 1907) are known only from southeast mainland Australia. This is despite the examination of worms from twice as many localities (and locality-dates) from Victoria and New South-Wales as from Tasmania.

Of the tubificids known only from Tasmania, three (*A. plectilus, A. multiseta* and *B. bifidus*) are known only from Great Lake and Arthurs Lake on the eastern edge of the central plateau, and one (*B. papillatus*) is known only from these lakes and nearby Lake Sorell. While not wishing to place too much emphasis on this, because oligochaete records from other lakes are limited, it is interesting to note that two phreodrilids are also known only from these lakes (Pinder and Brinkhurst, 1997). In addition, numerous other invertebrates and fish are apparently restricted to these lakes, though mostly to Great Lake (Frankenberg, 1974; Fulton, 1983ab; Invertebrate Advisory Committee, 1994; Timms, 1985; Williams, 1974). These lakes pre-date the late pleistocene glaciations that led to the creation of most other lakes in Tasmania and lie outside earlier glacial influence (Davies, 1974). Sutherland et al. (1973) and Sutherland (1980) suggest that lacustrine environments may have existed in the Great Lake basin since the late Oligocene when basalt flows blocked the upper Ouse R.. The age of Great Lake has been seen as a factor contributing to local endemicity in its fauna (Timms, 1985). Other ancient lakes, such as Lake Baikal (Russia), Lake Ohrid (Europe) and Lake Tanganyikae (Africa) also have numerous endemic oligochaetes, whereas this is rare in more recent lakes (Martin, 1996). The few Tasmanian lakes of recent (Pleistocene/Holocene) origin from which oligochaetes have been identified appear to have only species that are widespread in the state. These include pre- and post-impoundment Lake Pedder as reported by Lake (1998), a few glacial lakes (Dobson, Dove and St. Clair) surveyed by Timms (1978) and a dune barrage lake in the north-east (Blackman's Lagoon, sampled by the first author). However, records from many other Tasmanian lakes are required to confirm the apparent endemism of the oligochaeta fauna of Great Lake, Arthurs Lake and Lake Sorell.

Insufficient localities have been examined from other parts of Australia to generalise about regional diversity. The Phreodrilidae appear to be quite diverse in the southwest of Western Australia (Pinder and Brinkhurst, 1997 and unpublished data) but only one endemic tubificid is known from there so far. Three tubificids (*Ainudrilus stagnalis, Ainudrilus billabongus* and *Antipodrilus magelensis*) are known only from inland and northern Australia so far, but so few localities have been examined in these regions that it is difficult to speculate what further work will reveal.

The Australian Tubificidae seem to have a different biogeographic history to the apparently Gondwanan Phreodrilidae (Pinder and Brinkhurst, 1997). *Antipodrilus* appears most similar to genera that are widespread in the northern hemisphere but absent in Africa and South America (Brinkhurst, 1991). The new rhyacodriline genera, *Breviatria* and *Biprostatus*, are of uncertain affinity as the phylogenetic relationships are unclear in this possibly paraphyletic subfamily. Other endemic rhyacodrilines are members of a cosmopolitan freshwater genus (*Rhyacodrilus* spp.) or appear to be allied to marine forms (*Ainudrilus* spp.) or are only tentatively assigned to a widespread genus whose monophyly is uncertain (*Rhizodrilus arthingtonae*). As almost nothing is known of the oligochaete fauna of southeast Asia and New Zealand, little comment can be made about affinities within the Australasian region.

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Note in proof:

Recent survey work by Paul McEvoy (Australian Water Quality Centre) has revealed the presence of the cosmopolitan tubificids *Potamothrix bavaricus*, *Aulodrilus limnobius*, *Aulodrilus pigueti* and *Branchiura sowerbyi* in South Australia.