

Native Earthworms (Oligochaeta) from Southeastern Australia, with the Description of Fifteen New Species

R.J. BLAKEMORE

P.O. Box 414, Kippax ACT 2615, Australia
robblakemore@bigpond.com

ABSTRACT. This paper describes 15 new and five known endemic earthworm species, and provides keys to New South Wales genera. Two new species of *Plutellus* require expansion of the generic diagnosis to allow species with short stalks to the calciferous glands (always subordinate to the plesiomorphic tubular prostates that characterise this genus and distinguish it from *Heteropordrilus*). For *Vesiculodrilus*, the nominal type species of the genus, *V. frenchi* (Spencer, 1892), is redescribed and figured on a neotype. Nephridial vesicles, essential for inclusion in *Vesiculodrilus*, are newly reported in *V. frenchi*. Two new species from Mt Kosciuszko are added to this genus.

Syntypes of *Heteropordrilus canaliculatus* (Fletcher, 1889) and *H. mediterraeus* (Fletcher, 1887b) are rediscovered, lectotypes are designated, and these species are redescribed. Six new species are added to *Heteropordrilus* requiring the generic diagnosis to be amended to accept calciferous glands that are stalked, sessile, or annular. Intermittent nephropore alternation to mid-setal lines, once thought diagnostic only of *H. shephardi* (Spencer, 1900), is reported in several other species. The close affinities amongst heteropordrilids widely distributed in New South Wales, Queensland, Victoria and South Australia is accounted for by fluvial transport along the river systems such as the Murray-Darling.

New material of *Cryptodrilus fastigatus* Fletcher, 1889 is described and a congeneric species proposed, allowing explanation of the intraspecific variation in their male fields: The pore-like “genital markings” are actually modified nephropores that function for excretion, rather than copulation. One species of *Megascolides* from Bago-Maragle State Forest is newly described; variation in forms of tubular prostates is briefly considered in remarks following this species’ description. Two new species are added to *Notoscolex*, and one new species to *Digaster*.

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Australian native earthworms belong to the Acanthodrilidae, a relatively primitive family now predominantly confined to the northerly regions (Blakemore, 1997b), and the Megascolecidae which is both more derived and more widespread. This paper considers various megascolecid genera from the southeastern states, especially New South

Wales, complementing a paper (Blakemore, 2000) that dealt only with the genus *Anisochaeta*. The methodology employed in both these studies is similar as much of the material examined was from Easton’s 1983 NSW Collection at the Australian Museum, Sydney. Many unidentified specimens in this collection were found to be new species

requiring description. The opportunity was also had to inspect type material of described taxa of earlier workers that are housed in the Australian Museum. Additional material was mainly from specimen identification requests to the author relating to ecological, agronomic or conservation studies.

There are various systems of higher level classification currently in use, those that are most widely accepted owe much to the "classical system" (as defined by Gates, 1959: 235), devised by Michaelsen (1900) as adopted by Stephenson (1930) and extended by Sims (1982) (see Lee, 1994). In the current paper the arrangement of genera largely follows Michaelsen (1907), updated for the most current

taxonomic nomenclature, in which the plesiomorphic character states are tubular prostates, holoic nephridia, and lumbricine setae. Any derivation from these basic states are considered apomorphies. Characters of the digestive system (position and development of gizzard, calciferous glands and intestine) are of secondary taxonomic importance. Australian native species characteristically have one or more oesophageal gizzards in or near segment 5.

The following key to native earthworm genera in NSW is only preliminary, pending revision of genera from other Australian states and from New Zealand (currently in preparation by the author). Information and lists of exotic species known from Australia are presented by Blakemore (1999).

Preliminary key to native earthworm genera of New South Wales

- 1 Pores from two pairs of tubular prostates on 17 and 19 (or one pair on 17) separate from male pores on 18 (or on 17):
Acanthodrilidae *Diploptrema*
- Pores from tubular to racemose prostates combined with male pores on 18: Megascolecidae 2
- 2 Prostates tubular (i.e., glandular part elongate with simple unbranched canal) 3
- Prostates tubuloracemose (i.e., elongate but with incised surface and central canal receiving canalicules) or racemose (i.e., lobular with branching or ramifying canal system) 9
- 3 Holoic (i.e., nephridia one pair per segment, excluding pharyngeal tufts) 4
- Meroic (i.e., nephridia more than one pair, at least in fore-body) *Megascolides*
- 4 Lumbricine (i.e., 8 setae per segment) 5
- Perichaetine (more than 8 setae, at least in mid- or hind-body) *Diporochaeta*
- 5 Nephridia absent from anterior until c. segment 13 (littoral) *Pontodrilus*
- Nephridia present from anterior (terrestrial or semi-aquatic) 6
- 6 Male pores (and spermathecal pores) paired 7
- Male pores and spermathecal pores unpaired *Fletcherodrilus*
- 7 Nephridia vesiculate (i.e., with ducts dilated to form terminal bladders) 8
- Nephridia avesiculate *Graliophilus* (mostly in WA?), *Simsia* (Vic.), or *Hiatidrilus/Sebastianus* (mostly in Qld)—these genera require resolution.
- 8 Nephridia exiting with regular alternation in *d* to *b* lines *Plutellus*
- Nephridia without regular alternation *Vesiculodrilus*
- 9 Holoic (i.e., nephridia one pair per segment, excluding pharyngeal tufts) 10

— Meroic (i.e., nephridia more than one pair, at least in fore-body)	13
10 Lumbricine (i.e., 8 setae per segment)	11
— Perichaetine (more than 8 setae, at least in mid- or hind-body)	12
11 Nephridia avesculate	<i>Zacharius</i> (NSW) or <i>Woodwardiella</i> (in WA, Vic.).
— Nephridia vesiculate with regular alternation in <i>d</i> to <i>b</i> lines	<i>Heteroprodilus</i>
12 Gizzard well developed (in segment 5)	<i>Perionychella</i> or <i>Terriswalkerius</i> (in Qld).
— Gizzard rudimentary	<i>Perionyx</i> (not native to Australia).
13 Lumbricine (i.e., 8 setae per segment)	14
— Perichaetine (i.e., more than 8 setae, at least in mid- or hind-body).....	18
14 Gizzard single (in, or adjacent to, segment 5)	15
— Gizzards in two or three segments (between 4–7)	16
15 Nephridia avesculate	<i>Notoscolex</i>
— Nephridia vesiculate	<i>Cryptodrilus</i>
16 Two or three gizzards, dorsal pores present	17
— Three gizzards, dorsal pores absent	<i>Perissogaster</i>
17 Spermathecal pores (two pairs) intersegmental	<i>Digaster</i>
— Spermathecal pores (three pairs) segmental	<i>Didymogaster</i>
18 Gizzard in segment 5 (or adjacent)	<i>Anisochaeta</i>
— Gizzard in segment 8	non-native pheretimoids (see Blakemore, 1999).

Methodology and abbreviations

Methods and terminology are similar to those in Blakemore (2000). Segments are counted from the anterior in Arabic numerals (female pores are on 14 and male pores on 18 in megascolecids, unless counts are reduced by suppression of anterior segments); intersegments are designated by a slash (e.g., 1/2); variations are shown by a comma and range by a dash (e.g., 3,4–5). Setae, counted from the ventral-most on each side, have lower case letters (e.g., *a b c d*); variations are shown by a comma and range by a dash (e.g., *a,b-c*); setal lines refer to longitudinal setal series. In lumbricine species, the relative position of the four setae on one side of segment 12 are figured. Dissection is by dorsal incision longitudinally, the specimen being pinned on a wax tray while immersed in ethanol. While most features and anatomical details are symmetrical, where these differ on one side to the other the description always refers

to the observers point of view (lhs—left hand side; rhs—right hand side). The clitellum is shaded and other structures of taxonomic significance are shown in the figures (these are labelled in Fig. 1). All specimens were sketched in the author's usual style using a camera lucida, and all scale bars are 1 mm.

Notes on distribution and habitat follow each species' description—these are intended (along with the morphology and gut contents) to give some indication of ecological strategy and species associations, as well as to assist fieldworkers locate further material.

Abbreviations: AM—Australian Museum, Sydney; ANIC—Australian National Insect Collection (CSIRO Entomology, Canberra); NMV and MOV—formerly National Museum of Victoria, now Museum of Victoria, Melbourne; SAM—South Australian Museum, Adelaide. H refers to holotype, N to neotype, P to paratypes and S to specimens.

Systematics results

Genus *Plutellus* Perrier

Plutellus Perrier, 1873: 250; Michaelsen, 1900: 163, 1907: 159; Stephenson, 1930: 833; Jamieson & Nash, 1976: 45; Dyne, 1981: 96; Blakemore, 1994b: 35.

Diagnosis. Setae lumbricine (i.e., eight per segment). Male pores on 18 combined with pores of tubular prostates. Gizzard well developed in 5; four pairs of extramural calciferous glands present in 10–13 on long, or (*P. buckerfieldi*) short, stalks. Nephridia vesiculate holoic (i.e., one pair per segment with terminal dilations of the ducts forming large bladders); nephropores in anterior in setal *d* or *c* lines then, after segments 5–7, alternating regularly from *d* to *b* lines. Spermathecae five or fewer pairs with single, uniloculate diverticulum.

Type species. *Plutellus heteroporus* Perrier, 1873, from Port Macquarie and Barrington Tops, central NSW. (Types in the Muséum national d’Histoire naturelle, Paris).

Included species

Plutellus barringtoni n.sp. from Barrington Tops, NSW.
Plutellus buckerfieldi n.sp. from Namoi Rv., Gunnedah, NSW.

Plutellus heteroporus Perrier, 1873, from Port Macquarie and Barrington Tops, central NSW.

Plutellus hutchingsae Jamieson, 1977 from Lord Howe Island.

Plutellus manifestus (Fletcher, 1889: 1538) from Waterfall, Royal National Park, and Bulli, in southern coastal NSW. (Syntypes, AM W1371).

Species inquirendum

Plutellus rubens (Fletcher, 1887a: 381) from Mt Wilson, Blue Mountains, NSW.

Distribution. Central and southern coastal New South Wales, (Lord Howe Island). Perrier supposed his type series was from Pennsylvania, but the locality is now known to be Australian in coastal New South Wales, in the vicinity of Port Macquarie (Gates, 1972: 38; Blakemore, 1994b: 35–37; see also Distribution and habitat under *P. barringtoni* below).

North American species of *Plutellus* were transferred to *Argilophilus* (as mooted by Gates, 1972: 38) and to other genera by Fender & McKey-Fender (1990).

Remarks. The most recent revision of this genus is by Blakemore (1994b); see also remarks after *Heteroporodrilus* below.

Key to the known species of *Plutellus*

- 1 Spermathecae five pairs 2
- Spermathecae four pairs 3
- 2 Spermathecae five pairs in setal *b* lines *Plutellus heteroporus*
- Spermathecae five pairs in setal *a* lines *Plutellus hutchingsae*
- 3 Last hearts in 13; penial setae present; calciferous glands on short stalks *P. buckerfieldi* n.sp.
- Last hearts in 12; penial setae absent; calciferous glands on long stalks 4
- 4 Spermathecal pores mid-ventral *P. manifestus*
- Spermathecal pores lateral of setal *a* lines *P. barringtoni* n.sp.

***Plutellus barringtoni* n.sp.**

Figs. 1, 20

Material examined. HOLOTYPE: AM W24409 (H), Barrington Tops, c. 31°59'S 151°30'E, Ed Easton, 16.iii.1983; labelled, “Jar 12 Sp 55”, “AM No 12 *Diporochoeta* gp., ♂ [spermathecae symbol] ×3 or 4, Barrington Tops Trail. Colourless”, (complete mature,

figured and dissected). PARATYPES: ANIC RB.98.2.4, (P1), same details as H, (acelitellate mature, damaged in mid-body, dissected); AM W24411, (P2), same details as H, (subadult, dissected); ANIC RB.98.2.5, (P3), same details as H, (subadult).

External features. Body almost triangular in section posteriorly with *b-b* flat, dorsum not canaliculate. Lengths mm: 80 (H), 60–74 (Ps). Width: c. 2–3 mm. Segments: 158

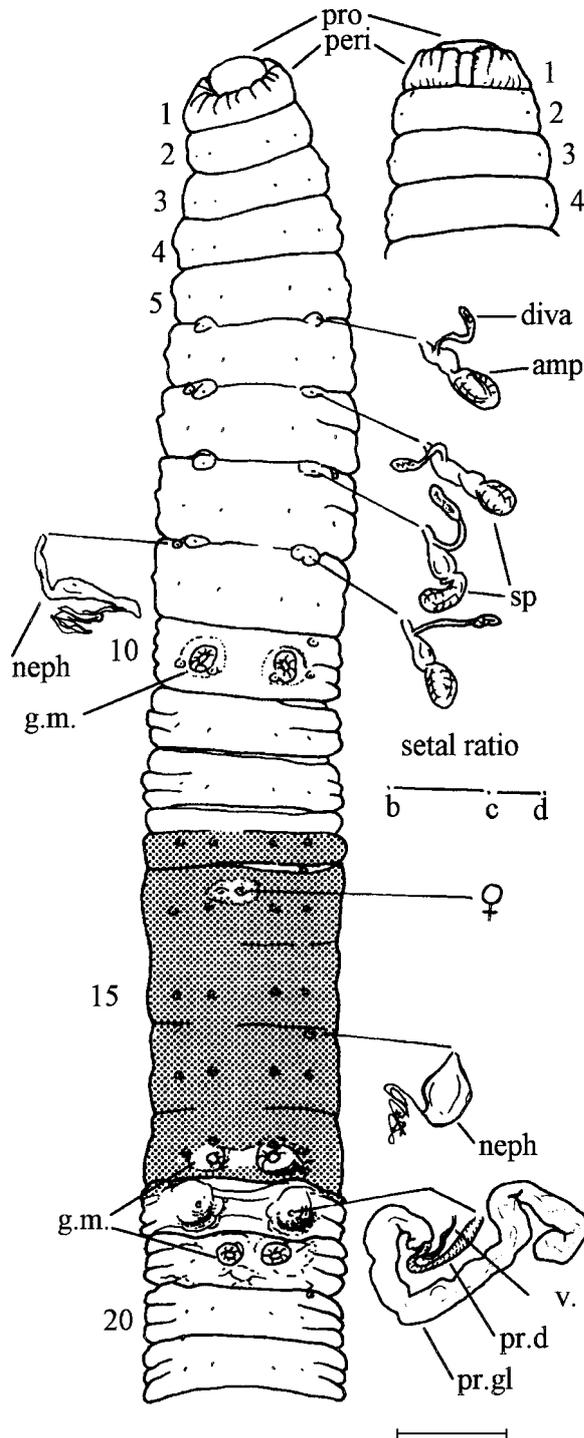


Figure 1. *Plutellus barringtoni* n.sp., ventral view of holotype with dorsal view of prostomium; spermathecae *in situ*; nephridial bladders in segments 9 lhs, 16 rhs; tubular prostates and vasa deferentia in 18 (penial setae are absent). Abbreviations: amp—spermathecal ampulla; diva—spermathecal diverticulum; g.m.—genital marking; neph—nephridium (to nephropore); peri—peristomium; pro—prostomium; sp—spermatheca (opens to spermathecal pore); pr. d.—prostatic duct (opens to male pore); pr. g.—prostatic gland; v.—vasa deferentia. Scale 1 mm.

(H), range 147–196 (Ps). Colour: unpigmented, mid-body almost translucent, clitellum russet. Prostomium: narrowly tanylobous. Clitellum: $\frac{1}{2}13$ – $\frac{1}{2}18$ (pale ventrally in $\frac{1}{2}17$ – $\frac{1}{2}18$). Dorsal pores: possibly in 10/11 but not definite till 13/14, as white dots on clitellum and small afterwards (H); from 7/8 (P1–3). Setae: small 8 per segment in regular rows. Nephropores: at anterior margin of segment in *d* lines in 2, 7 (rhs) then with regular alternation; in *c* lines in 3–6; in *b* lines 7 (lhs) then with regular alternation (H). Spermathecal pores: on small papillae in 5/6/7/8/9 in *ab* lines but closer to setal *a* lines. Female pores: paired on 14. Male pores: paired on wide mounds in *ab* lines on 18. Genital markings: paired, presetal sucker-like discs in *ab* lines on 10 (H) or 10 and 11 (P1–3); more ventrally paired in 17 and 19 but postsetal and presetal, respectively; (plus in P1 only) smaller paired postsetal discs median of *aa* in 19 and 20.

Internal anatomy. Septa: 5/6–10/12 slightly thickened. Gizzard: large muscular barrel in 5. Oesophagus: paired reniform calciferous glands ventrolateral on long stalks in 10–13 (i.e., four pairs); valval in 14. Nephridia: vesiculate holoic, bladders elongate in anterior, more sub-spherical in posterior, position alternating with nephropores. Vascularization: large dorsal blood vessel single onto gizzard; hearts paired in 10–12; weak supra-oesophageal vessel seen in 11–13 only. Spermathecae: four pairs in 6–9, bulb-like ampulla on equally long thick duct, narrow long-stalked ectal diverticulum with dilated terminal bulb (inseminated). Male organs: holandric, iridescent testes and funnels in 10 and 11; seminal vesicles small paired in 9 and 12. Ovaries: compact in 13; small ovisacs in 14. Prostates: tubular in 18–19, duct slight (H) to strongly dilated (P1), vasa deferentia join at junction of gland and duct; penial setae not found. Intestine: origin 15; no typhlosole; gut contains fine yellow soil.

Remarks. Although there is slight variation in position of dorsal pores and genital markings in the paratypes, all specimens are regarded as conspecific as the dissected specimens agree internally. *Plutellus barringtoni* has four pairs of spermathecae in segments 6–9 as have *P. manifestus* and *P. buckerfieldi*. In *P. manifestus* however, the spermathecal pores are mid-ventral and remarkably close together; *b* setae converge on either side of the male pores and the distribution of genital markings differs. Differences from *P. buckerfieldi* are given in the description of this species below. The major differences from *P. heteroporus* are four, rather than five, pairs of spermathecal pores that are closer to setal *a* lines, rather than setal *b* lines, and longer spermathecal diverticula.

Etymology. Named after the type locality.

Distribution and habitat. Barrington Tops National Park is an elevated, forested plateau north of the Hunter River and c. 150 km inland from the Port Macquarie type-locality of *Plutellus heteroporus*. In the current study, specimens of *P. heteroporus* (viz. AMW24416–24417, ANIC RB.98.2.9–10) were found sympatrically with *P. barringtoni* in material collected by Ed Easton from Junction Holes, Barrington Tops. Also found in the Easton collection from the vicinity

of Barrington Tops were an unidentifiable, damaged plutelloid (W24418); *Anisochaeta erica* and *A. palustris*, both described by Blakemore (2000); several other *Anisochaeta* spp. that are currently undescribed; plus a specimen (W20775) labelled "Moniligastridae" that is actually a tubificid (pers. obs.).

***Plutellus buckerfieldi* n.sp.**

Figs. 2, 20

Material examined. HOLOTYPE: ANIC RB.97.3.3 (H), from clay riverbanks of Namoi River, near Gunnedah, central NSW, specimen donated by J.C. Buckerfield, labelled "Coll: Brian Dawson ('Active Earthworms'), Grovers Lane, Glen Innes, NSW 2370, 22.iv.1994", (complete mature, figured and dissected). PARATYPES: none.

External features. Body faintly dorsally canaliculate throughout. Length: 170 mm. Width: c. 6 mm. Segments: 203. Colour: body grey, dorsum to *c* lines darker slate; clitellum puce. Prostomium: tanylobous, dorsally furrowed. Clitellum: weak 1/3–17. Dorsal pores: vestigial in 6/7, open from 7/8. Setae: 8 in regular series. Nephropores: at anterior margin of segments in *d* lines in 2–4; ventral of *c* lines in 5 and 6 (rhs); in *b* lines with regular alternation from 6 (lhs) or 7 (rhs) and in *d* lines from 7 (lhs) or 8 (rhs); but by final third of body alternations become symmetrically aligned in each segment. Spermathecal pores: small in 5/6/7/8/9 in setal *a* lines. Female pores: paired just anteromedian to setae *a* on 14. Male pores: aligned with setal *a* lines on small papillae on 18. Genital markings: paired, presetal in line with spermathecal pores in 9–12; paired, postsetal in *ab* lines in 17 and paired presetal in *ab* lines in 19; both sets of posterior markings converge towards the male pores.

Internal anatomy. Septa: 9/10–12/13 slightly thickened. Gizzard: in 5 muscular tapering barrel. Oesophagus: paired reniform calciferous glands ventrolateral on short ducts, almost sessile in 10–13 (i.e., four pairs); valvular in 14–1/215. Nephridia: vesiculate holoic with bladders elongate in anterior and ocarina-shaped in posterior, alternating in position with nephropores. Vascularization: dorsal blood vessel single; hearts paired in 10–13; supra-oesophageal vessel seen in 10–13 with connectives to hearts and calciferous glands. Spermathecae: four pairs in 6–9, tapering ampulla on almost equally thick duct with long stalked ectal diverticulum having dilated terminal bulb (iridescent). Male organs: holandric, iridescent testes and funnels in 10 and 11 invested in mucus; seminal vesicles paired, racemose in 9 and 12, latter pair with many small nodules. Ovaries: fan-shaped composed of numerous minute egg-strings in 13; no ovisacs found in 14. Prostates: tubular in 18–19, vasa deferentia attach at junction of gland and thickened duct; long and fine penial setae overlies duct. Intestine: from 1/215, especially dilated to 17; no typhlosole; gut contains gritty organic soil and plant remains.

Remarks. *Plutellus buckerfieldi* differs from other known members of the genus in the reduced stalks to the extramural calciferous glands (requiring the introduction of this

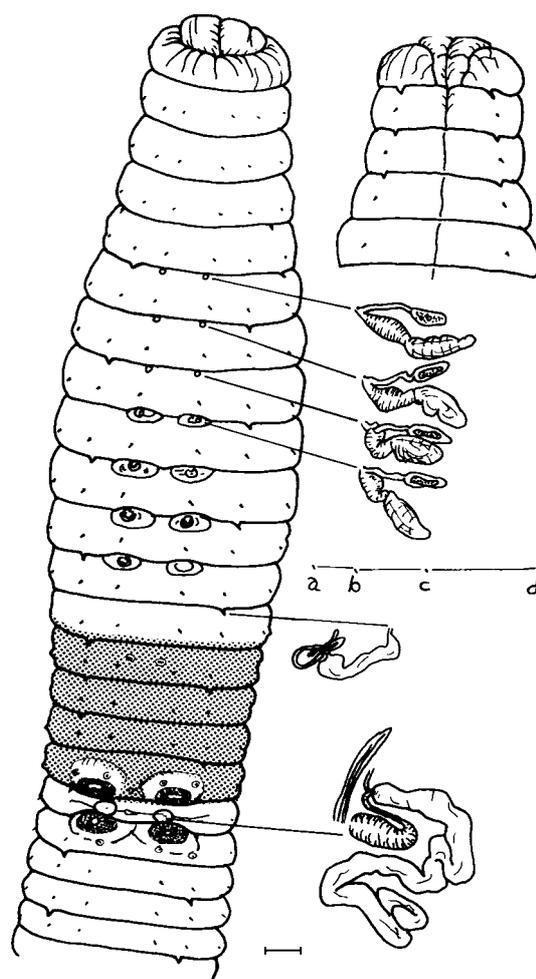


Figure 2. *Plutellus buckerfieldi* n.sp., ventral view of holotype with dorsal view of canaliculate prostomium; spermathecae; nephridial bladder in 13 rhs; tubular prostate and penial setae in 18. Scale 1 mm.

characterization, always subsidiary to tubular prostates, in the generic diagnosis above). *Plutellus buckerfieldi* has four pairs of spermathecae and four pairs of calciferous glands, as have *P. manifestus* and *P. barringtoni*. However, in these latter two species the last hearts are in 12, they lack penial setae and dorsal canaliculation, and the genital markings differ. There is a gradation in position of spermathecal pores: midventral in *P. manifestus*, in setal *a* lines in *P. buckerfieldi*, lateral of *a* lines in *P. barringtoni*, and (with an extra pair in 4/5) in *b* lines in *P. heteroporos*. The male pores of these species diverge correspondingly.

Etymology. Named after John Buckerfield of Adelaide.

Distribution and habitat. Gunnedah, on the banks of the Namoi River, is about 250km inland from the NSW central coast. Introduction of these worms, collected at Gunnedah, into paddocks on clay soils of a property in Glen Innes was made in an attempt to improve soil structure and pasture production (B. Dawson, pers. comm., 7 October 1998). It is not known whether the introduced specimens survived.

Genus *Vesiculodrilus* Jamieson

Vesiculodrilus Jamieson, 1973: 224.

Perionychella (*Vesiculodrilus*) Jamieson, 1974a: 216.

Pinguidrilus Jamieson, 1974a: 263, **new synonym**.

Diagnosis. Setae lumbricine. Male pores on 18 combined with pores of tubular prostates. Gizzard in 5; extramural calciferous glands absent (rudimentary annular glands may be present); typhlosole absent. Nephridia vesiculate holoic (i.e., one pair of tubules per segment with terminal dilations of the ducts forming large bladders); nephropores in a single row on each side near *c* lines or sinuous in *c* lines and above. Spermathecae five or fewer pairs each with single, uniloculate diverticulum. Penial setae present or absent.

Type species. *Cryptodrilus frenchi* Spencer, 1892 from Croajingolong, Victoria. (NEOTYPE, newly designated: AM W1289).

There is some confusion with the type species of this genus. Jamieson (1973) considered the NSW specimens, on which he based the genus, to agree with *C. frenchi* Spencer. However, comparison of these NSW specimens with the neotype of *C. frenchi* as described below demonstrates that they are not conspecific. Nevertheless, the neotype of *C. frenchi* happens to agree with the genus as defined, in particular by having vesiculate nephridia (previously unmentioned by Spencer). The type species is herein fixed (under Article 70.3 of the Code, ICZN, 1999) as *Cryptodrilus frenchi* Spencer, 1892 misidentified with *Vesiculodrilus nivalis* n.sp. in the original designation by Jamieson (1973).

Included species. Three NSW species, all from Mt. Kosciuszko region, are *Vesiculodrilus nivalis* n.sp., *Vesiculodrilus purpureus* Jamieson, 1973 [probably a junior synonym of *V. victoriae* (Spencer, 1892)], and *Vesiculodrilus vallis* n.sp. Of the Victorian species included in *Vesiculodrilus* by Jamieson (1973: 225), *Megascolides tisdalli* and *M. volvens*, both of Spencer, 1900, have setae reputedly increasing beyond 8 per segment (i.e., perichaetine) which would place them in *Diporochoeta* Beddard, 1890. Similarly, several perichaetine species from Tasmania, Victoria and Queensland listed under *Perionychella* (*Vesiculodrilus*) by Jamieson (1974a: 222) are excluded from *Vesiculodrilus* as defined above. Complete lists of species are currently precluded by lack of information on nephridial states from some earlier descriptions. Checking of Victorian species with five or fewer pairs of spermathecae for presence or absence of nephridial bladders is beyond the scope of the present work; however, studies by the author have identified 10 known and approximately 50 new species of *Vesiculodrilus* from Tasmania that comply with the diagnosis above (Blakemore, in prep.).

Distribution. Tasmania, Victoria, southern New South Wales.

Remarks. Retained as a subgenus of *Perionychella* Michaelsen, 1907 by Jamieson (1974a) and reassigned to *Diporochoeta* by Jamieson (1976), *Vesiculodrilus* is herein restored to its original generic rank in recognition of its morphological distinctness. The generic definition is

expanded: Firstly, to accept species with nephropores in irregular series as found in *Vesiculodrilus tasmanianus* (Fletcher, 1887b) following the present author's discovery of spermathecal diverticula in the Museum of Victoria lectotype (Blakemore, in prep.)—thereby removing justification for the monotypic genus *Pinguidrilus* Jamieson, 1974a. Secondly, to accept species with fewer than the five pairs of spermathecae diagnosed by Jamieson (1973). Several Tasmanian species have fewer than five pairs of spermathecae, but the nephridial states of such species from Victoria have yet to be determined.

Characteristics of holonephry, lumbricine setae and tubular prostates are all plesiomorphic states shared with *Graliophilus* Jamieson, 1971, its possible junior synonym *Hiatidrilus* Jamieson, 1994, and with *Sebastianus* Blakemore, 1997b, indicating the relatively primitive nature of these genera. However, the type species of these latter three genera lack nephridial vesicles whereas these structures invariably occur in *Vesiculodrilus*. Possibly this character is apomorphic in *Vesiculodrilus*, although the vesiculate state is found in the more primitive family Acanthodrilidae in some species endemic outside Australia. Related genera in the eastern subregion of mainland Australia are *Plutellus* which, unlike *Vesiculodrilus*, has regular alternation of nephropores and extramural calciferous glands, and *Fletcherodrilus* Michaelsen, 1891 that typically has unpaired male and spermathecal pores. Species with holonephridia (with or without bladders) but attaining greater than eight setae (the perichaetine condition) are assignable to *Diporochoeta* s.str. if they have tubular prostates, or to *Perionychella* s.str. if their prostates are other than tubular (i.e., tubuloracemose or racemose). (A recently proposed Queensland genus, *Terriswalkerius* Jamieson, 1994, on the justification presented, appears to subsume the characteristics of either of these two prior genera, and therefore its included species should probably be reallocated to *Diporochoeta* or *Perionychella* depending on whether they have tubular or non-tubular prostates, respectively).

Vesiculodrilus frenchi (Spencer, 1892)

Fig. 3a,b

Cryptodrilus frenchi Spencer, 1892: 135–136, figs. 10–12, 66.

Megascolides frenchi.—Beddard, 1895: 493.

Plutellus frenchi.—Michaelsen, 1900: 175.

Non *Vesiculodrilus frenchi* sensu Jamieson, 1973: 225–227, fig.

2A; non *Cryptodrilus frenchi* Spencer, 1892a sensu Jamieson,

1974a: 221–222; non *Vesiculodrilus frenchi* (Spencer) sensu

Jamieson, 1974a: 222; non *Perionychella* (*Vesiculodrilus*)

frenchi sensu Jamieson, 1974a: 221–222.

The specimens described by Jamieson (1973) do not agree sufficiently with Spencer's species to be considered conspecific (see *Vesiculodrilus nivalis* n.sp. below). In his synonymy, Jamieson (1973) has also confused *Cryptodrilus frenchi* Spencer, 1892 with *Perichaeta frenchii* Spencer, 1893.

Material examined. NEOTYPE: AM W1289 (N), part of the Fletcher Collection presented to the Australian Museum; the sample jar contained a metal tag "W1289" plus three

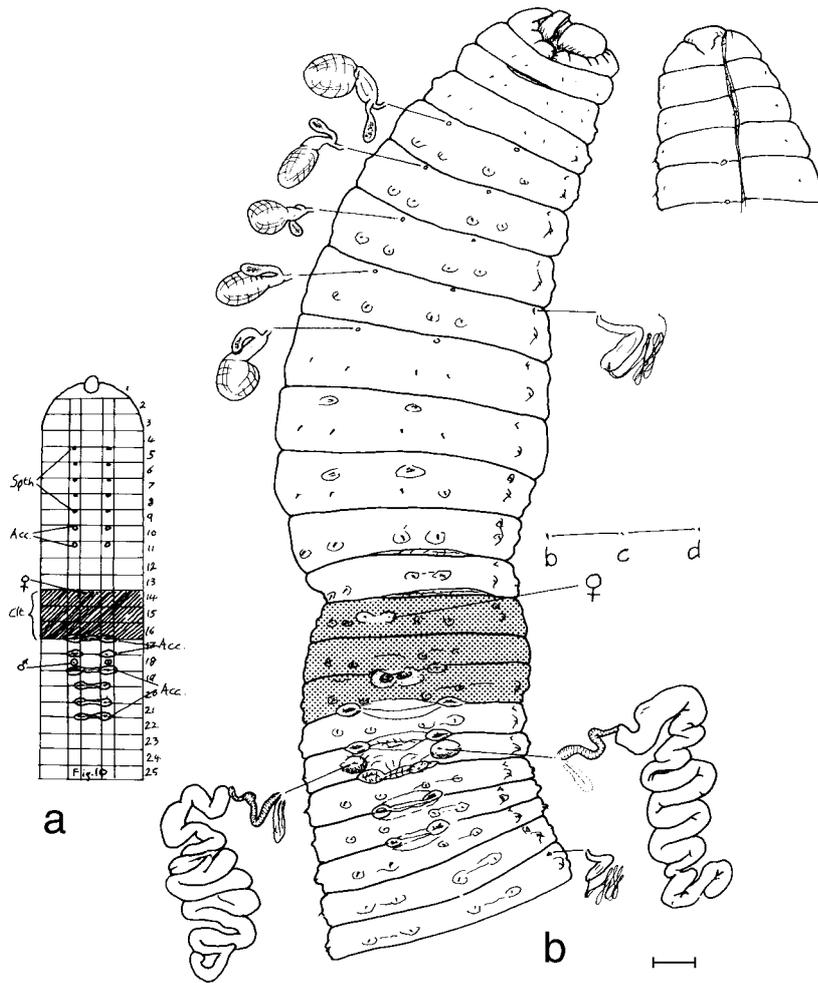


Figure 3. a, *Vesiculodrilus frenchi* (Spencer, 1892), after Spencer's original figure 10; b, *Vesiculodrilus frenchi* (Spencer, 1892) ventral view of neotype with dorsal view of sectioned prostomium, spermathecae *in situ*; nephridial bladders in 8 rhs and 23 rhs; both sets of prostates in 18–21, 22 with penial setae remaining only on lhs. Scale 1 mm.

labels: "*Plutellus frenchi* (Sp.)" [in pencil in Fletcher's hand?]; "W1289 *Plutellus frenchi* / Croajingolong, VICTORIA / Pres: J.J. Fletcher"; "AM W1289 *Diporochaeta frenchi* / Locality: Croajingolong, Vic. / Pres: J.J. Fletcher / Id: by E. Easton, '83". Two specimens were originally present, plus a middle fragment of a third specimen. The previously dissected, complete mature specimen with metal stud in tail (part of metal tag?) described and figured here is designated the neotype (N); the other specimen, AM27081 (ex W1289) a complete mature specimen, also previously dissected, is designated specimen (S1) (see Remarks below).

External features (compared with Spencer's type description). Body circular in section, fairly stout. Lengths mm: 85 (N), 80 (S1) (cf. 75 Spencer). Width: 5–6 mm (cf. c. 4 mm Spencer). Segments: 113 (N), 103 (S1). Colour: uniform light brown in alcohol, clitellum only slightly darker. Prostomium: tapering epilobous; peristomium ventrally cleft. Clitellum: 14–16. Dorsal pores: from 4/5. Setae: 8 in regular rows except final 16 (N) or 30 (S1) segments where all but setal *a* lines irregular. Nephropores:

in *c* lines. Spermathecal pores: at anterior of segments near 4/5–8/9 in *ab* just lateral to *a* lines ("just on the very anterior boundaries of segments 5–9, at the level of the interval between the inner couple of setae", Spencer). Female pores: paired on 14. Male pores: at centres of small mounds at interval of *ab* lines on 18. Genital markings: on 10 and 11 (N) (ditto Spencer), or on 11 only (S1), small paired pinched ellipses with pore-like centres at anterior of segments just lateral to setal *a* lines; in 15/16 (N only) a pair of weak markings median to setal *a* lines; in 16/17–20/21 (N), or 16/17–19/20 (S1) (cf. between 16–21,22 Spencer) paired intersegmental markings, in *ab* lines anterior to male pores, in *a* lines posterior to male pores, each conjoined by tumid furrows.

Internal anatomy. Septa: 5/6 thin to base of gizzard, 10/11/12 slightly thickened. Gizzard: compact muscular in 5 but displaced to appear in 6 (removed from S1) (cf. "small in 6", Spencer). Oesophagus: dilated in 12–14 perhaps forming rudimentary annular calciferous glands (cf. "vascular swellings in 9–15, but no true calciferous glands", Spencer). Nephridia: vesiculate holoic, bladders elongate;

pharyngeal tufting not noted. Vascularization: dorsal blood vessel (damaged by dissection, where visible) single; last hearts in 12, supra-oesophageal vessel 8–½13 (ditto Spencer). Spermathecae: five pairs in 5–9 (in both specimens, those from 9 rhs removed and missing from jar), large saccular ampulla on tapering duct with medium-sized diverticulum ectally. Male organs: holandric, iridescent testes and funnels in 10 and 11; seminal vesicles paired large posteriorly in 9, small posteriorly in 10, anteriorly in 12 (cf. in 9 and 12 Spencer). Ovaries: in 13 (only oviducts found); ovisacs not noted. Prostates: tubular 18–21, 22; penial setae present (in N, rhs removed). Intestine: damaged by dissection (both N and S1), origin perhaps near 16 (not determined by Spencer); typhlosole absent; gut contains mainly woody organic material.

Remarks. The body cavity of specimen (N) was heavily infected with *Monocystis*. The material examined above agrees with Spencer's original description. The only notable differences are slight variations in the distribution of genital markings, the gizzard in the more normal position in segment 5 rather than in 6, and the presence of small seminal vesicles in segment 10 as well as in 9 and 12 (although only the "finger-shaped" pair in 9 shown in Spencer, fig. 12). Newly recorded here are the presence of nephridial bladders and of penial setae, and the absence of a typhlosole. (In his preliminary notices, Spencer [1892: 130] purposely refrained from recording these structures).

Spencer (1892: 135) was ambiguous regarding the location of the posterior genital markings: "Patches on each side of the body at the level of the interval between the inner couple of setae from segments 16–21. Each patch is composed of a small part of two contiguous segments and the pairs are united across the mid-ventral line by glandular ridges." They may thus be interpreted as occurring between *ab* in 16/17–20/21, although Spencer (fig. 10) shows them in 16/17–21/22 narrowing posteriorly. (Similar ambiguity occurs in the description and figure of his preceding species, *Vesiculodrilus tanjilensis* [Spencer, 1892]).

Jensz & Smith (1969: 87) were unable to locate type specimens in the Spencer Collection at the Museum of Victoria. Documentation is lacking (e.g., no inventory nor labels in Spencer's hand), but the material examined above is probably part of this missing type-series because, apart from their close morphological agreement, the labelling shows they are identified from the type-locality. Moreover, some other missing material has been located during the present study in Spencer's associate Fletcher's donation to the Australian Museum (e.g., *Megascolides diaphanus* Spencer, 1900, see under this genus' Remarks below; see also *Heteropodrilus shephardi* below). However, as it is not possible to prove indisputably that they are part of the lost type series (i.e., syntypes), and in absence of any other known material, one specimen is here designated the neotype (under Article 75 of the ICZN Code).

Distribution and habitat. Croajingolong National Park is a large coastal reserve in East Gippsland, Victoria, bordering NSW at its northern end. Species described by Spencer (1892, 1893) from the same locality along with *Cryptodrilus frenchi*, were *C.* (= *Vesiculodrilus*?) *gippslandicus*,

Megascolides (= *Notoscolex*) *cameroni*, *Perichaeta* (= *Anisochaeta*) *frosti*, *P. goonmurk* and, probably, *Cryptodrilus dubius*. For this last species, Jensz & Smith (1969: 87) reiterate Spencer's statement "This probably comes from Croajingolong" but the distinct locality other than Victoria is not noted; they also report that the types of the other species were collected at Croajingolong in January 1889, during an expedition of the Field Naturalists' Club of Victoria.

Vesiculodrilus nivalis n.sp.

Vesiculodrilus frenchi (Spencer, 1892); Jamieson, 1973: 225–227, fig. 2A (misidentification).

Material examined. HOLOTYPE: AM W4693, labelled "*Cryptodrilus frenchi*, Mt Kosciuszko, NSW 36°59'S 148°59'E, 17(140/2), Alpine herffield... Coll: T.G. Wood, 10 Nov. 1967. Det. B. Jamieson"; and "*Cryptodrilus Frenchi* Spencer, 1892 No. 89 one specimen" [in Wood's hand], tagged "T36" (complete mature, previously dissected, and agreeing externally with Jamieson's fig. 2A [of his Specimen 1?] and mostly agreeing internally with Jamieson's description [of his Specimen 4?], especially in the multi-diverticulate form of one spermatheca). There is some confusion with Jamieson's "Specimen" numbers, descriptions, and registrations. It is deduced that Jamieson's "Specimen 1" and "Specimen 4" are variously the same as the previously dissected specimen, "Specimen 3", herein designated the holotype (H). PARATYPES: AM W4692, from same sample, labelled "*Cryptodrilus Frenchi* Spencer, 1892 No. 87 one specimen" [in Wood's hand], tagged "T34" (complete mature, length = 140 mm, undissected but cuticle removed and cut in mid-body)—probably Jamieson's "Specimen 2", here designated paratype (P1). AM W4691, from same sample, labelled "*Cryptodrilus Frenchi* Spencer, 1892 No. 88 one specimen" [in Wood's hand], tagged "T35" (mature posterior amputee; previously undissected now desiccated and, despite re-immersion in ethanol, of little use)—possibly Jamieson's "Specimen 1", here designated paratype (P2). Additional material—Jamieson's "Specimen 4" from the same site, lodged at CSIRO Department of Soils (= Division of Land and Water), Glen Osmond, Adelaide, not located.

External features from Jamieson (1973) and reinspection of type-series. Body faintly canaliculate dorsally in forebody. Lengths (mm): 120 (H), 140 (P1). Width: c. 5 mm. Segments: 112 (H). Colour: pale; clitellum buff. Prostomium: tanylobous; peristomium ventrally cleft. Clitellum: 14–16. Dorsal pores: minute in 3/4, open from 4/5. Setae: 8 in regular rows except on tail. Nephropores: *c* lines? Spermathecal pores: minute at anterior of segments near 4/5–8/9 in setal *a* lines. Female pores: on 14 near *a* lines. Male pores: equatorial on small mounds in *ab* lines on 18. Genital markings: on 9–11 (H) or 10–11 (P1) small sucker-like discs presetal in *ab* lines; markings in 16/17–20/21 (i.e., five pairs), in *b* lines in 16/17/18 and in *a* lines in 18/19/20/21.

Internal anatomy. Septa: 7/8–13/14 thickened. Gizzard: large muscular in 5. Oesophagus: slightly dilated and vascularized in 9–15. Nephridia: vesiculate holoic, bladders elongate exiting in *c* lines; pharyngeal tufting absent. Vascularization: dorsal blood vessel single; hearts in 9, 10–12 with connectives to supra-oesophageal vessel in 9–13. Spermathecae: five pairs in 5–9, elongate ovoid ampulla

on short duct with small inseminated diverticulum ectally; (Jamieson states that 7 rhs spermatheca in "Specimen 4" has several supernumerary pouches; I found this only in 6 rhs spermatheca of H, although some other rhs spermathecae had been removed and were missing from jar). Male organs: holandric, testes and funnels iridescent in 10 and 11; seminal vesicles paired, elongate and sessile on posterior septa of 9 and lobulated posteriorly in 10, and anteriorly in 12. Ovaries: as few chains of egg-strings in 13; ovisacs absent. Prostates: tubular, compact and much wound, occupying 17–19; penial setae present. Intestine: origin in 17; typhlosole absent.

Remarks. The designation of *Vesiculodrilus nivalis* is based on those specimens from Mt Kosciuszko that Jamieson (1973: 225–227, fig. 2A) described and partly figured which, despite differences from Spencer's account, he identified with *Cryptodrilus frenchi*, and one of which he used as exemplar when erecting his genus. Major differences in Jamieson's account of these Mt Kosciuszko specimens from Spencer's *Vesiculodrilus frenchi* (as augmented above) are: larger size (120–140 mm cf. 85 mm); canaliculate tanylobous prostomium (rather than epilobous); five pairs of spermathecal pores in setal *a* lines in 4/5–8/9 (erroneously stated by Jamieson, 1973: 226 to be "in 4/5–7/8") rather than just lateral of setal *a* lines; a large gizzard, rather than small or compact gizzard, in 5; and some other differences in genital markings. These gross morphological deviations from Spencer's species are confirmed by examination of those of Jamieson's specimens available for study (i.e., AM W4691–4693, Jamieson's Specimens 1–3). In view of the redescription of *V. frenchi* above, and of the differences of *Vesiculodrilus nivalis* from this, it is therefore concluded that these two species are not conspecific.

Other mainland species with five pairs of spermathecae are *Vesiculodrilus uncinatus* (Stephenson, 1933) that lacks genital markings; *V. purpureus* Jamieson, 1973 (stated to have setal ratios not differing significantly from his other Mt Kosciuszko specimens [of *V. nivalis*], although Jamieson's description of *V. purpureus* is confused: with H and P1 apparently being interchangeable with an anterior amputee specimen, now in a private collection and unavailable for study) and the closely similar *V. victoriae* (Spencer, 1892), and its varieties, all of which have median, unpaired markings; as well as *V. vallis* n.sp. that is described and differentiated below.

Etymology. The name *nivalis* (Latin) means "snowy" or "of the snow" and refers to the Snowy Mountains and Snowy River localities.

Distribution and habitat. Mt Kosciuszko, known from a single site: Alpine herbfield of *Poa caespitosa*, *Celmisia longifolia*, near the Snowy River at 6,200ft (1,900m). Found with earthworm species: *Graliophilus woodi* Jamieson, 1973, *Cryptodrilus fastigatus* Fletcher, 1889, *Notoscolex montiskosciuskoi* Jamieson, 1973, and *Anisochaeta celmisiae* (Jamieson, 1973). The ecology of this community is reported by Wood (1974). Specimens of three of these species have recently been identified by the current author: *Cryptodrilus fastigatus* is described below; specimens

(ANIC RB.95.30.1) of *Notoscolex montiskosciuskoi* from Sawpit at the Park entrance were sent for identification by Liz Wren of National Parks and Wildlife Service (Blakemore, 1995)—these worms were being dug up and used as bait by anglers; and *Anisochaeta celmisiae* as reported by Sims & Gerard (1985: 136)—one of the species surviving introduction in the 1970's into the Highlands of Scotland in an attempt to reduce peat turf mats (see Blakemore, 1999: 184; 2000: 3).

Vesiculodrilus vallis n.sp.

Fig. 4

Material examined. HOLOTYPE: ANIC RB.97.3.5, Perisher Valley, Mt Kosciuszko, NSW, collected by Keith Vallard, "just above Perisher, in mountains". Live specimen donated by Gerard Gillespie of Queanbeyan, 5.iii.1997, (mature, complete, dissected and figured). PARATYPES: none.

External features. Body faintly canaliculate dorsally after clitellum. Length: 220 mm. Width: 15 mm. Segments: 132. Colour: (in life) dorsum dark gunmetal grey to flanks, brown from *c* to *b* lines, light brown ventrally, setal aurioles and markings pale; clitellum buff. Prostomium: closed epilobous; peristomium ventrally cleft. Clitellum: ½13–½18. Dorsal pores: minute in 3/4, open from 4/5. Setae: 8 in regular rows only in the anterior, after segment 21, *d* lines first become sinuous then other setal lines vary so that by tail all setae are very irregular but still lumbricine. Nephropores: just lateral of *c* lines in anterior from 2. Spermathecal pores: minute at anterior of segments near 4/5–8/9 in setal *a* lines. Female pores: widely paired on 14. Male pores: at centres of small mounds at interval just lateral of setal *a* lines on 18. Genital markings: on 10 and 11 large paired hollowed sucker-like discs presetal just median of *b* lines within tumid rims that extend from *a* lines to just lateral of *b* lines; in 15/16–22/23 (i.e., eight sets) paired and midventral discs median to *a-a* within slightly swollen common field.

Internal anatomy. Septa: 9/10–13/14 thickened. Gizzard: large muscular cone in 5. Oesophagus: slightly dilated and vascularized in 9–16 but not forming calciferous glands. Nephridia: vesiculate holoic, bladders elongate exiting in *c* lines; pharyngeal tufting absent. Vascularization: dorsal blood vessel single onto pharyngeal mass in 4 but forming segmentally doubled loops in segments 6 and 12 (at least); hearts in 10–12 with connectives to supra-oesophageal vessel in 7–12. Spermathecae: five pairs in 5–9, large saccular ampulla on small duct with small inseminated diverticulum ectally. Male organs: holandric, testes and funnels iridescent in mucus in 10 and 11; seminal vesicles paired racemose, elongate and sessile on posterior septum in 9, small posteriorly in 10, and small anterior rosettes in 12. Ovaries: as several egg-strings in 13; ovisacs not found. Prostates: tightly coiled tubular confined within membrane in 18; penial setae present. Intestine: origin in ½17; typhlosole absent; gut contains soil and organic matter.

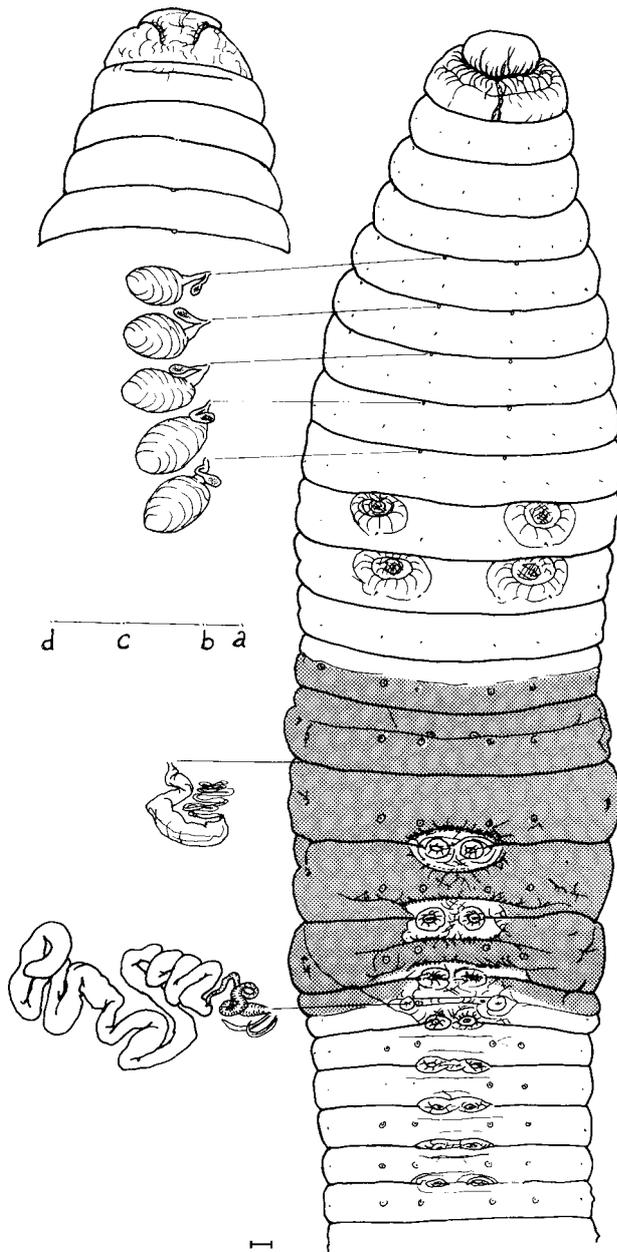


Figure 4. *Vesiculodrilus vallis* n.sp., ventral view of holotype with dorsal view of prostomium, spermathecae *in situ*; nephridial bladder in 15 lhs; and lhs prostate and penial setae in 18. Scale 1 mm.

Remarks. *Vesiculodrilus vallis* differs from the type species, *V. frenchi*, in its larger size (220 mm vs. 75–85 mm); spermathecal pores in setal *a* lines rather than just lateral of this; larger and more lateral anterior markings and narrower posterior markings (at least those in 15/16–17/18, 18/19); intermittently doubled dorsal blood vessel; and by having the prostate glands coiled and confined to segment 18. Although *V. vallis* is somewhat morphologically similar to *V. nivalis* from nearby Mt Kosciuszko, it differs: in its larger size; by having epilobous, rather than tanylobous, prostomium; clitellum extending over ½13–½18, rather than

14–16; differences in the distribution of genital markings (eight posterior pairs, rather than five pairs); its doubled dorsal blood vessel; and an intestinal origin in ½17, rather than 17.

More extensive doubling of the dorsal blood vessel is described by Spencer (1892) in his Victorian species *Cryptodrilus* (= *Vesiculodrilus*?) *gippslandicus* and *Diporochaeta willsiensis*, but both of these species differ, not least, in their arrangements of genital markings. Having coiled, tubular prostates confined to segment 18 is found in *Vesiculodrilus tanjilensis* (Spencer, 1892), that also has distinctly different genital markings.

Etymology. Named after the locality (Latin, *vallis* = of the valley).

Distribution and habitat. Perisher Valley, en route to the summit of Mt Kosciuszko, has winter temperatures as low as -22°C. Because large specimens, such as *V. vallis*, often maintain deep burrows, it is possible that this species overwinters at depth. The live specimen was supplied in a container with humic sandy soil and grass in the roots of which were several tubificid microdriles (indicative of waterlogged conditions).

Genus *Megascolides* M'Coy

Megascolides M'Coy, 1878: 21; Michaelsen, 1900: 182; 1907: 160–161; Stephenson, 1930: 835; Lee, 1959: 284–285; Blakemore, 1997a: 1689–1690.
Austrohoplochaetella Jamieson, 1971: 490.
Pseudocryptodrilus Jamieson, 1972: 172.

Diagnosis. Setae 8 per segment. Clitellum typically developed over at least four segments. Male pores from tubular prostates paired on 18. An oesophageal gizzard in 5 or 6 (or 7?). Nephridia merioic, at least in the fore-body, avesciculate or vesiculate, sometimes tufted anteriorly. Spermathecae one or more pairs, each with a clavate diverticulum. Typhlosole and calciferous glands present or absent; intestinal caeca absent. Penial setae present or absent.

Type species. *Megascolides australis* M'Coy, 1878, (synonyms: *Notoscolex gippslandicus* Fletcher, 1887b; *Lumbricus australis* Vaillant, 1889) from Gippsland, Victoria. (Syntypes AM W1253–1262).

Included species

Megascolides acanthodriloides (Jamieson, 1974a) from Tasmania;
Megascolides australis M'Coy, 1878 from Victoria
Megascolides bagomaraglensis n.sp. from NSW;
Megascolides diaphanus Spencer, 1900 from Victoria;
Megascolides kendricki (Jamieson, 1971) from WA;
Megascolides maestus Blakemore, 1997a, from Tasmania;
Megascolides nokanenaensis Michaelsen, 1907 from WA;
Megascolides tenuis (Fletcher, 1889) from NSW.

Twelve additional species from Tasmania are currently in the process of formal description (Blakemore, in prep.).

Species incertae sedis

Megascolides orthostichon (Schmarda, 1861) from Mt Wellington, there is some debate as to whether this is Mt Wellington in New Zealand, or in Tasmania.

Distribution. Victoria, New South Wales, Tasmania, Western Australia, New Zealand (confined to the north of North Island). Lee (1959) describes twenty-two known *Megascolides* species from New Zealand, but it appears that several (especially those previously attributed to the genus *Tokea*) have tubuloracemose prostates and therefore belong in *Notoscolex*. Indian species of *Megascolides* were transferred to *Scolioscolides*, *Barogaster* and *Travoscolides* by Gates (1940). North American species of *Megascolides* were transferred to *Driloleirus* by Fender & McKey-Fender (1990).

Remarks. The most recent discussion of this genus is found in Blakemore (1997a) where the above synonymies are discussed. A further genus, "*Dinephrus*" was proposed, but not formally described by Spencer (1900: 33) for species, like his *Megascolides diaphanus*, that have only a few nephridia per side. It is pertinent to the current study that Australian Museum specimens of *Megascolides diaphanus* Spencer, 1900 from Dimboola, Victoria (AM W1274) were unequivocally claimed by Jamieson (1972: 174) to be "type-series", indeed he designated one specimen the lectotype and others paralectotypes, whereas Jenz & Smith (1969: 99–100) list Museum of Victoria syntypes as NMV G179 and state only that Spencer's label was "Missing from the jar" (see also Remarks under *Heteroporodrilus shephardi* below).

Megascolides bagomaraglensis n.sp.

Fig. 5

Material examined. HOLOTYPE: ANIC RB.97.5.1, Maragle State Forest, NSW, Bago-Maragle, Environmentally Sustainable Management Project sample BM165, Sheet No. 8526 DGPS Long. 6030795 AMG zone 55, Lat. 617215 AMG zone 55, off Warnipers Rd., Dr P. Ryan, 10.iii.1997, (mature, dissected and figured). PARATYPES: ANIC RB.95.29.1 (P1–P3), Bago State Forest, south of Batlow, NSW (35°34'S 148°10'E), Phil Ryan, 13–17 February 1995 (three mature specimens, P1 acitellate, dissected; P2, clitellate, dissected; P3 acitellate, in poor condition but agreeing superficially).

External features. Body stout. Lengths (mm): 140 (H), 150 (P1, P2). Width: c. 4.5 mm. Segments: 174 (H). Colour: unpigmented in alcohol; clitellum yellow or buff. Prostomium: weakly tanylobous (H) or open epilobous (P1), faintly furrowed dorsally. Clitellum: (H, P2) 13, ½13–17, ½18. Dorsal pores: from 5/6. Setae: small, 8 in regular rows *c-d* widely spaced, almost equidistant with *d-d*. Nephropores: small pores sometimes seen just lateral of *b*, *c* and *d* lines on anterior margin of segments in anterior. Spermathecal pores: small at anterior of segments near 7/8/9 in setal *a* lines. Female pores: widely paired anteromedian to setae *a* on 14. Male pores: at centres of eye-like papillae

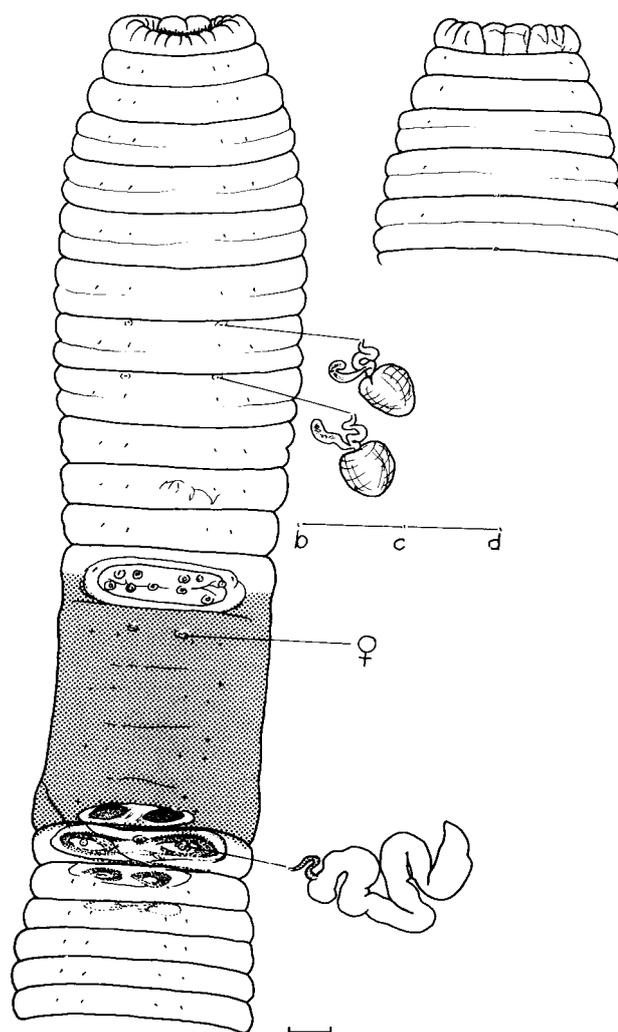


Figure 5. *Megascolides bagomaraglensis* n.sp., ventral view of holotype with dorsal view of prostomium; spermathecae; and rhs tubular prostate in 18. Scale 1 mm.

in *ab* lines within medianly conjoined elliptical darker rims on 18; small central boss often seen median to the pores. Genital markings: on 13 several small papillae laterally arranged within large sunken pad surrounded by rim that encompasses setae *b-b* and extends to 13/14 (present but less developed in P1, P2); paired dark elliptical pads postsetal in *bb* on 17; similar pads pre-setal on 19 and weakly repeated on 20 and (P1 only) on 21.

Internal anatomy. Septa: 5/6 thin to middle of gizzard but can be traced to base; 7/8–11/12 increasingly thickened. Gizzard: large muscular tapering cone in 5 displaced to occupy position of 6–8. Oesophagus: dilated and vascularized in 13, 14–16, 17 but not forming definite calciferous glands; valval in ½18. Nephridia: vesiculate merioic as lateral bands of inter-coiled tubules, two, three or more per side, ducts seen exiting in *b* and *c* lines or *c* and *d* lines, pre-septal funnels not found; pharyngeal tufts in 2–3. Vascularization: dorsal blood vessel single onto pharyngeal mass in 4; hearts in 10–13 with connectives to

supra-oesophageal vessel in 8–13. Spermathecae: two pairs in 8–9, large heart-shaped ampulla on thin spiralling duct with ectally directed clavate diverticulum at junction of ampulla and duct (duct and diverticulum often enclosed in membrane). Male organs: holandric, testes and funnels iridescent in mucus in 10 and 11; seminal vesicles paired digitiform, elongate on posterior septum in 9 and anterior septum of 12. Ovaries: as several egg-strings in 13; vestigial ovisacs on anterior septum of 14. Prostates: tightly coiled thickly tubular gland on short duct (no central canal detectable in section, but branching side ducts not found either); penial setae absent. Intestine: origin in ½18; typhlosole T-shaped from 20, becoming large and c. 1 mm deep; gut contains fine soil with few grits and charcoal grains.

Remarks. Characters separating *Megascolides bago-maraglensis* from other known members of the genus, are the arrangement of genital markings (especially those in segment 13) and the distinctive shape of the spermathecae.

The prostates are construed as tubular, albeit thickly tubular with only a small central lumen, as there are no ramifying side ducts or canalicules characteristic of tubuloracemose and racemose glands. Species such as *M. bago-maraglensis*, that attain their large size by surviving for several seasons, possibly attain particularly thick glands as the columnar gland-cells regenerate from the periphery. This conclusion is extrapolated from the detailed description of tubular prostate glands by Spencer (1888: 29–30, fig. 29), Sweet (1900), and, especially, Stephenson (1930: 364–372, figs. 152–153).

In general, when regarding tubular prostates, the question to ask is whether they resemble the form of those found in the indisputably more primitive families (e.g., Acanthodrilidae), and in the primitive genera of Megascolocidae (e.g., *Pontodrilus*, *Plutellus*, *Sebastianus*). Gradations in non-tubular glands may occur: they are either obviously racemose, especially where the duct branches externally, or tubuloracemose, where internal canalicules may be found by sectioning.

Etymology. Named after the locality.

Distribution and habitat. Bago-Maragle State Forests are adjacent to and west of Kosciuszko National Park. These specimens were collected as part of a multi-disciplinary sustainability survey of forest soil ecosystems conducted by CSIRO, the Australian National University, and various state Forestry Departments. All fauna collecting was by Phil Ryan and Neil McKenzie (CSIRO Forestry, Canberra), and David Jacquier and Peter Leppert (CSIRO Land and Water). The BM165 type locality site is described as “a shallow rocky soil on metasediments in Maragle SF”, the exact collection locality of the paratypes is not available, but they were obtained from “rich chocolate brown forest soil”. Further site and soil survey details can be obtained from Dr Phil Ryan. *Anisochaeta rava* and *A. rubeospina* have recently been described from this locality by Blakemore (2000).

Genus *Heteropodrilus* Jamieson

Heteropodrilus Jamieson, 1970: 106–109; Blakemore, 1994b: 20–23.

Diagnosis. Setae lumbricine. Male pores on 18 combined with pores of racemose or tubuloracemose prostates. Gizzard well developed in 5; three to five sets of calciferous glands: paired extramural and ventrolateral, sessile or on short stalks, the last pair in 13, or (*H. bitenax*) annular in 10–13. Last hearts in 12 or 13. Nephridia vesiculate holoic; nephropores in anterior in *d*, *c*, or mid-*bc* lines, then, from 9 or 10 posteriorly, alternating regularly from one segment to the next in *d* and *b* lines. Spermathecae five or fewer pairs with single, or multiple diverticula.

Type species. *Cryptodrilus tryoni* Fletcher, 1890, (synonym *Woodwardiella youngi* Boardman, 1932), from Milton, Sherwood, Oxford Park, Brookfield, Toowong, all are suburbs in Brisbane; Somerset Dam, Binna Burra; Mt Glorious; Mt Mee and Nambour, all in Qld. (Type material untraceable).

Included species. Six new species are described in the current account, bringing the generic total to twenty-five species, as given in the key below. Blakemore (1994a,b) listed and described 18 known species, plus one sub-species (*Heteropodrilus shephardi* (Spencer, 1900) *armatus* Jamieson, 1974b), and one dubious species (*Cryptodrilus fletcheri* Beddard, 1887). A subsequently described Queensland species was cursorily differentiated by Jamieson (1995: 580) thus: “*Heteropodrilus montiserratae* is distinguished from other species of the genus in possessing four pairs of calciferous glands and three pairs of spermathecae.” However, as previously shown (Blakemore, 1994a,b) this combination of characters is also found in *H. incommodus* (Jamieson & Nash, 1976) and *H. raveni* (Jamieson & Nash, 1976) as well as in *H. canaliculatus* (Fletcher, 1889), *H. mediterreus* (Fletcher, 1887b) and *H. shephardi* (Spencer, 1900). This latter species, redescribed below, was divided into sub-species by Jamieson (1974b: 87) who stated: “*H. shephardi* belongs to a group of species with four pairs of calciferous glands [and three pairs of spermathecae]”.

Distribution. Widespread, especially in proximity to rivers (Fletcher, 1887b: 602). In catchments of the Murray-Darling in New South Wales through to Victoria and South Australia; Wimmera River in Victoria; Tweed River in northern NSW; and various tributaries in southeastern Queensland (Blakemore, 1994b). One species, *H. oxleyensis* (Fletcher, 1889), as redescribed by Blakemore (1994b: 29–32) from southeast Qld, has a particularly wide range having recently been found at Broulee in central coastal NSW (Blakemore, 1997b: 1838); other samples of this taxon from the Sydney region are in the Australian Museum collection (e.g., W3064, pers. obs.).

Remarks. The most recent revision is by Blakemore (1994b). Related genera are *Zacharius* Blakemore, 1997b

from northern NSW and *Woodwardiella* Stephenson, 1925 that is predominantly found in WA (although monotypic *Pseudoperichaeta* Jamieson, 1970 from Victoria is a probable junior synonym of this latter genus). These other genera lack the nephridial vesicles and calciferous glands of *Heteroporodrilus*. Furthermore, *Woodwardiella* is differentiated from *Zacharius* by having prostates that

are racemose (rather than tubuloracemose), penial setae, intestine commencing from 17–19, and nephridia supposedly becoming tufted.

The above generic diagnosis is expanded slightly to permit annular calciferous glands and to note the occurrence, more commonly than previously believed, of nephropores in mid-*bc* in some anterior segments.

Key to the known species of *Heteroporodrilus*

- 1 Calciferous glands five pairs; spermathecae three pairs each with three diverticula (size up to 580 mm) *Heteroporodrilus tryoni*
- Calciferous glands four pairs; nephropores occasionally in 4–9 in mid-*bc* 2
- Calciferous glands three pairs; nephropores not in mid-*bc* lines 16
- 2 Spermathecae three pairs 3
- Spermathecae two pairs 11
- 3 Spermathecal diverticula paired 4
- Spermathecal diverticula single (infrequently doubled) 5
- 4 Prostomium prolobous, dorsum canaliculate, first dorsal pore 10/11, last hearts in segment 12; small penial setae present *H. canaliculatus* (Fletcher, 1889)
- Prostomium epi-tanylobous, dorsum not canaliculate, dorsal pores from 6/7/8; last hearts in 13; penial setae absent *H. kaputar* n.sp.
- 5 Size < 100 mm; (penial setae absent or not recorded); (Qld) 6.
- Size > 100; penial setae present; (NSW, Qld, Vic., SA) 7.
- 6 Dorsal pores 6/7; genital markings 7–8 *H. raveni*
- Dorsal pores 5/6; genital markings 10–11 *H. montiserratae*
- 7 Seminal vesicles in 11 & 12; few genital markings in 11–12 and 18–19; (NSW) *H. mediterreus* (Fletcher, 1887b)
- Seminal vesicles in 9 & 12; markings more numerous (Qld, NSW, Vic., SA) 8.
- 8 Size < 135 mm; nephropores not in mid-*bc* in anterior; prostates with short ectal duct; penial setae absent; (Qld) *H. incommodus* (Jamieson & Nash, 1976)
- Size > 160 mm; nephropores intermittently in mid-*bc* in anterior; prostates with large duct to centre of (bilobed) gland; penial setae present (NSW, Vic., SA) 9
- 9 Size < 160 mm; prostates bilobed, duct branches externally; (Vic., SA) *H. shephardi* (Spencer, 1900)
- Size > 160 mm; prostates not so clearly divided; (NSW) 10

- 10 Dorsal pores from 5/6/7; spermathecal diverticula near exit of duct *H. namoi* n.sp.
- Dorsal pores from 10/11/12; spermathecal diverticula midlength on duct *H. narrabri* n.sp.
- 11 Spermathecal diverticula single; prostates bilobed; penial setae; (Vic.) *H. hirthi* n.sp.
- Spermathecal diverticula paired; prostates not bilobed; penial setae absent; (Qld, NSW) 12
- 12 Spermathecal diverticula paired multiloculate 13
- Spermathecal diverticula paired clavate 14
- 13 Size > 200 mm; epilobous; dorsal pores from 10/11; female pores paired; prostates racemose; (Qld) *H. thompsoni* Blakemore, 1994b
- Size < 100 mm; tanylobous; dorsal pores from 5/6; female pore single; prostates tubuloracemose; (NSW) *H. editus* n.sp.
- 14 Size > 200 mm; epi-tanylobous; dorsal pores from 10/11; (Queensland) *H. bongeen* Blakemore, 1994b
- Size < 100 mm; tanylobous; dorsal pores from 4/5/6/7; (NSW, Queensland) 15
- 15 Dorsal pores from 4/5/6; spermathecae intersegmental; markings in 7 (& 10); female pores paired; prostates tubuloracemose; (NSW) *H. bitenax* n.sp.
- Dorsal pores from 6/7; spermathecae segmental; markings in 10 (or 11); female pore single; prostates racemose; (Qld) *H. notatus* (Dyne, 1981)
- 16 Spermathecae five pairs *H. jamiesoni* Blakemore, 1994b
- Spermathecae fewer than five pairs 17
- 17 Spermathecae four pairs; (Qld, NSW) *H. oxleyensis* (Fletcher, 1889)
- Spermathecae fewer than four pairs 18
- 18 Spermathecae three pairs 19
- Spermathecae two pairs 20
- 19 Spermathecal diverticula paired; (NSW) *H. sloanei* (Fletcher, 1889)
- Spermathecal diverticula single; (prostates often aborted); (Queensland) *H. dioecius* (Stephenson, 1933)
- 20 Spermathecal diverticula paired 21
- Spermathecal diverticula single (rarely paired) 22
- 21 Prostomium epilobous; markings 7–9; prostates tubuloracemose; (NSW) *H. doubei* Blakemore, 1994b
- Prostomium tanylobous; markings 10–11; prostates racemose; (Queensland) *H. lamingtonensis* (Jamieson, 1970)

- 22 Size 400 mm; epilobous; female pores paired..... *H. minyoni* (Dyne, 1981)
- Size < 100 mm; tanylobous; female pore single 23
- 23 Prostates tubuloracemose; female pore single (NSW) *H. clarkei* (Dyne, 1981)
- Prostates racemose (bilobed); female pores paired (Qld) *H. cooraniensis* (Spencer, 1900)

***Heteropodrilus bitenax* n.sp.**

Figs. 6, 20

Material examined. HOLOTYPE: AM W24421 (H), 6km west of Grafton, NSW, c. 29°44'S 152°52'E, Ed Easton, 18.iii.1983, "Jar 20", (mature, dissected and figured). PARATYPES: ANIC RB.98.2.12, same details as H, (P1), (aclitellate subadult, dissected); W24422, (P2), same details as H, (aclitellate subadult, inspected).

External features. Lengths, mm: 80 (H), 72 (P1), 55 (P2). Width: c. 3 mm. Segments: 180 (H), 175 (P1). Colour: unpigmented almost transparent in alcohol, clitellum cream. Prostomium: widely tanylobous. Clitellum: ½13–17. Dorsal pores: 4/5 minute, open from 5/6. Setae: 8 per segment in regular series. Nephropores: at anterior margin of segments, in *d* lines on 2–4, 5 rhs, 6 lhs, then regular alternation; in mid-*bc* lines on 5 lhs, 6 rhs, 7 lhs, 8 rhs, 9 lhs; in *b* lines on 10 rhs, 11 lhs then with regular alternation (H). Spermathecal pores: in 7/8/9 in *b* setal lines. Female pores: widely paired just anterior to setae *a* on 14. Male pores: at centres of low papillae in *b* lines on 18. Genital markings: large paired sucker-like discs occupying most of *ab* lines in 7 (H, P1, P2) and 10 (H, P2); paired postsetal discs approximately in *ab* lines in 16, 17, 19 (rhs only in P1), and 20 (H, lhs only P2); smaller secondary pair of discs median to those in 16 also present.

Internal anatomy. Septa: 5/6–9/10 increasingly thickened. Gizzard: large muscular flask-shaped in 5. Oesophagus: dilated and with deep internal lamellae in 10–13 (i.e., four sets of annular calciferous glands, in H and P1), tapering to valve in 14. Nephridia: vesiculate holoic with small sub-spherical or elongate bladders exiting at nephropores. Vascularization: dorsal blood vessel single; hearts paired in 10–12. Spermathecae: two pairs in 8 and 9, conical ampulla on narrow duct with opposed, clavate diverticula ectally. Male organs: holandric, testes and iridescent funnels in 10 and 11; seminal vesicles racemose in 9 and 12. Ovaries: palmate with several egg-strings in 13; ovisacs not found. Prostates: flattened, tubuloracemose in 18 on thin duct; penial setae absent. Intestine: origin in 15 widening in 16; typhlosole absent; gut contains coarse soil with grits and mucus.

Remarks. *Heteropodrilus bitenax* is unique in the genus for having annular, rather than extramural, calciferous glands, requiring the inclusion of this character state in the generic diagnosis. Other distinctive characters are the two pairs of bi-diverticulate spermathecae with ingresses in *b* lines; and the arrangement of genital markings, having these anterior to the spermathecal pores is a rare occurrence in megascolecid earthworms.

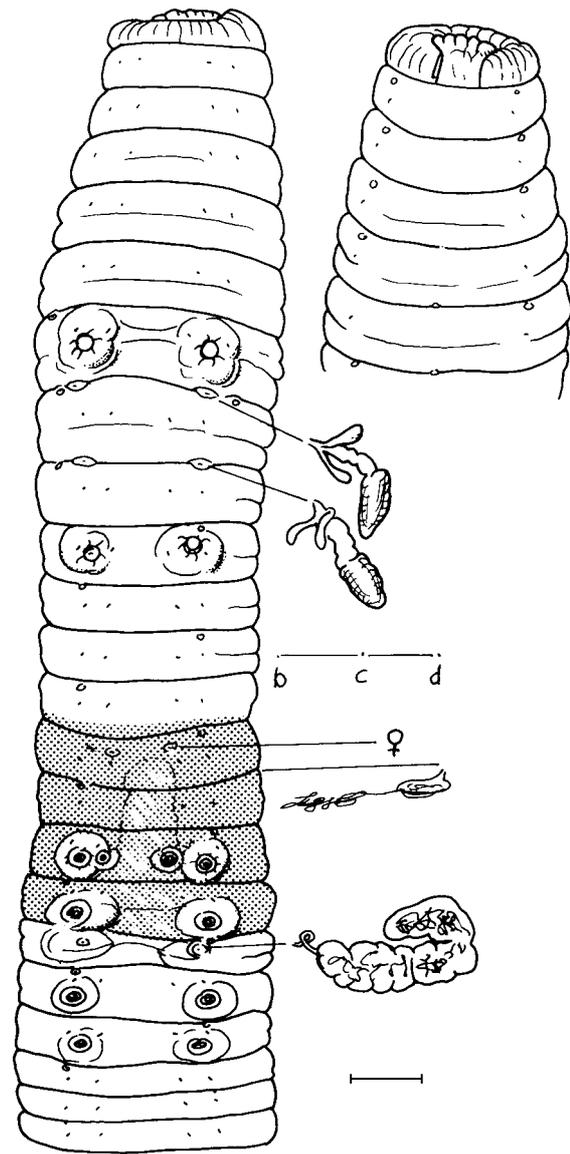


Figure 6. *Heteropodrilus bitenax* n.sp., ventral view of holotype with dorsal view of tanylobous prostomium; spermathecae *in situ*; nephridial bladder in 15 rhs; and prostate in 18 rhs. Scale 1 mm.

Etymology. The word *bitenax* means double-gripping in Latin and refers to the sucker-like markings found on either side of the spermathecal pores.

Distribution and habitat. Grafton lies on the Clarence River in northern coastal NSW. Collection notes state from a "stand of Eucalypt".

Heteropordrilus canaliculatus (Fletcher, 1889)

Figs. 7, 20

Cryptodrilus canaliculatus Fletcher, 1889: 1534–1536; 1890: 995–996.*Plutellus canaliculatus*.—Michaelsen, 1900: 171–172.*Woodwardia canaliculatus*.—Michaelsen, 1907: 162.*Heteropordrilus canaliculatus*.—Jamieson, 1970: 111–112; Blakemore, 1994b: 21–22.

Material examined. LECTOTYPE: AM W1373, two labels in jar: “*C. canaliculatus* / Forbes (H.F.) NB. Ap 24/88” [in pencil in Fletcher’s hand]; “W1373 *Heteropordrilus canaliculata* Forbes, NSW types id. E. Easton ’83”. (Mature specimen, amputated after segment 32, here designated the lectotype—under ICZN Article 74, as it complies with the original type description, being previously dissected and having spermathecae agreeing unequivocally with those described by Fletcher in one of his specimens). This specimen is unsuitable for external illustration due to previous dissection and handling although the spermathecae, prostates and nephridial bladders are figured herein. PARALECTOTYPES: AM W24582 (ex W1373) (14 specimens: 5 complete matures, 2 matures missing tips of tails, 1 mature posterior amputee previously dissected, 1 mature in two halves, 4 acitellate subadults, 1 acitellate subadult missing tail, plus two tail portions;—a complete mature, representative of the series with length 230 mm, here described and externally figured). Additional material unknown. Fletcher (1889: 1534) based his description on “twelve spirit specimens” collected by his relative Mr H.J. Fletcher (identified as “H.F.” on the label), that he stated were “not well preserved and much extended”. Nevertheless, most specimens remain in reasonable condition, apart from slight damage and dissection, and all agree superficially with each other and with the lectotype.

External features (compared with Fletcher’s description). Body robust, marked by faint but distinct dorsal canal (indeterminate in lectotype where dissected). Lengths, mm: complete matures 210–290, subadults 130–160 (cf. 125–250 mm, Fletcher). Widths: 5–7 mm (cf. 3.5–5 mm, Fletcher). Segments: figured paralectotype 230 (cf. about 250–265, Fletcher). Colour: bleached yellow in alcohol, clitellum buff. Prostomium: prolobous in paralectotypes (peristomium “bi-annulate superiorly, not divided by the prostomium, though being ribbed all round it sometimes appears as if it were completely or half divided by the prostomium”, Fletcher). Clitellum: $\frac{1}{2}$ 13,14–17. Dorsal pores: small in 7/8, larger in 8/9 (from 8/9, Fletcher), retained on clitellum. Setae: 8 per segment in regular series. Nephropores: (in lectotype) at anterior margin of segments in *d* lines in 2, 3, 4, 7, then with regular alternation; in *c* lines in 5, 6, 8 rhs, 10, 12, 14 lhs; in mid-*bc* in 8 lhs (confirmed by internal inspection); in *b* lines in 14 rhs, 16, then regular alternation. (Paralectotypes sometimes have nephropores in mid-*bc* in several segments between 8–13). Spermathecal pores: small in 6/7/8/9 in setal *b* lines. Female pores: widely paired just anteromedian to setae *a* on 14. Male pores: paired just lateral of *b* lines on small papillae on 18. Genital markings: small indistinct paired papillae in tumid yellow pad weakly marked in 11 in middle annulus between *a-a* (seen in lectotype and paralectotype, but not described by Fletcher); broad paired papillae in *ab* in 18 on anterior and posterior annuli (latter pair absent in lectotype),

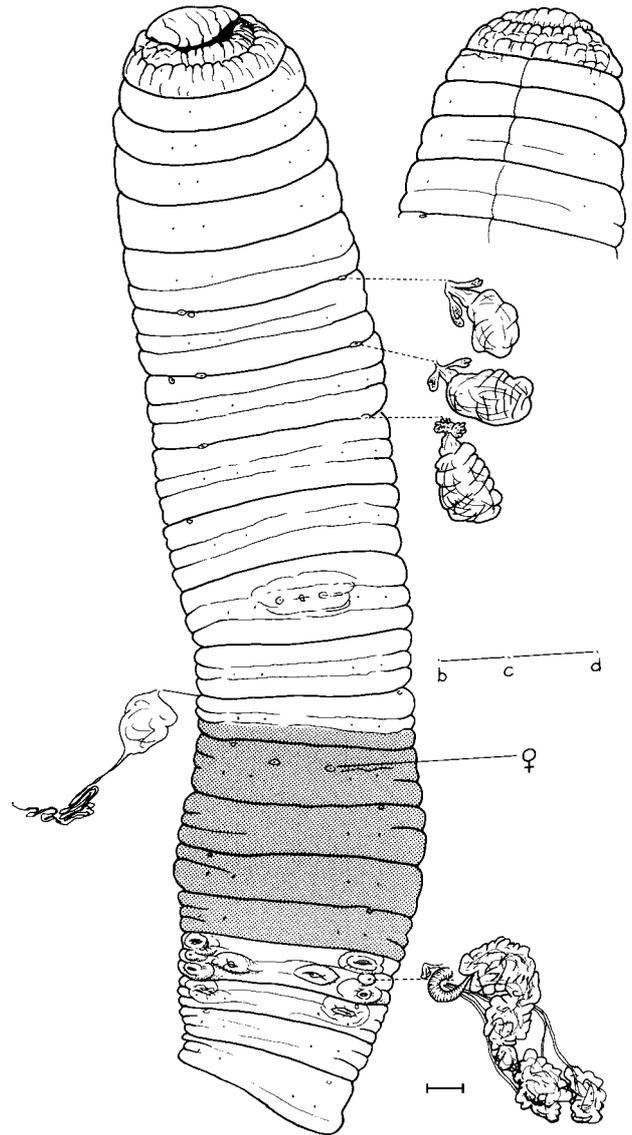


Figure 7. *Heteropordrilus canaliculatus* (Fletcher, 1889), ventral view of a paralectotype and dorsal view of prostomium and canaliculus; nephridial bladder in 13 lhs; the spermathecae and prostate with penial setae in 18 are of the lectotype. Scale 1 mm.

and on anterior annulus of 19, plus secondary pair sometimes seen median to male pores (not in lectotype).

Internal anatomy. Septa: 5/6–12/13 thickened. Gizzard: compact, muscular in 5. Oesophagus: ventrolaterally sessile calciferous glands paired in 10–13 (i.e., four pairs); narrows in 14. Nephridia: vesiculate holoic with large spherical bladders in position of nephropores. Vascularization: dorsal blood vessel single; hearts paired in 10–12. Spermathecae: three pairs in 7–9 “each with usually two short caeca [diverticula], one on each side and in front of the duct near its exit (nearer than in [*H.*] *mediterraeus*), but either of these may be slightly bifid or even trifid just at the tip, or completely sub-divided into two or three, or in one case there was but a single broad flat caecum 5– or 6–lobed just

at the tip" (from Fletcher). Male organs: holandric, iridescent testes and funnels in 10 and 11 in mucus; seminal vesicles paired, racemose in 9 and 12. Ovaries: in 13; small paired ovisacs in 14. Prostates: flattened, elongate tubuloracemose in 18–19, 20 on short muscular duct but with tendons from median of duct extending back to terminal lobes in 19 and 20; vasa deferentia join gland near duct; very small ensheathed penial setae seen just ventral of duct (as noted by Fletcher, 1890: 996). Intestine: origin in 15 (lectotype, cf. 16 Fletcher); typhlosole absent; gut contains remnants of brown soil.

Remarks. As these specimens correspond with Fletcher's description, despite being three more than the "twelve" specimens stated by him, there is little doubt that they are the missing type series (especially the description of the lectotype's spermathecae correspond). Slight differences from Fletcher are the weak genital markings on 11, and the intestinal origin in 15 rather than 16. Recorded for the first time are nephropores in mid-*bc* in some anterior segments, hearts in 10–12, tendons on the prostates, and lack of a typhlosole.

Fletcher distinguished *H. canaliculatus* from *H. mediterraeus* as the latter species had a less robust body with fewer segments, lacked the dorsal canal, had seminal vesicles in 11 and 12 (rather than 9 and 12 as here) and because the spermathecae were noticeably different (each having only a single diverticulum). To this list may now be added last hearts in 13 (rather than 12 as here).

Distribution and habitat. Fletcher: "Forbes, NSW; from the banks of the Lachlan River". Five specimens, AM W1375 labelled, possibly in Fletcher's hand: "*Cryptocanaliculatus* (?) Warren. Recd. 25/6/[18]90" are not considered conspecific as they are not canaliculate and have variations in the genital markings, amongst other differences. There is a Warren (near Dubbo) in NSW (see Other material under *H. narrabri* below).

Heteroporodrilus editus n.sp.

Figs. 8, 20

Material examined. HOLOTYPE: AM W24505 (H), Lyrebird Lookout, Mt. Warning National Park, c. 28°23'S 153°17'E, Ed Easton, 21.iii.1983, "Jar 30 Sp 4", (mature, dissected and figured). PARATYPES: none.

External features. Length: 95 mm. Width: c. 2.5 mm. Segments: c. 158. Colour: unpigmented grey in alcohol, tumid ventral region of ½6–9 yellow. Prostomium: tanylobous with faint furrowing. Clitellum: not pronounced. Dorsal pores: from 5/6. Setae: 8 per segment in regular series. Nephropores: at anterior margin of segments, in *d* lines on 2–3, 4 rhs, 8 rhs, 9 lhs then regular alternation; in mid-*bc* lines on 4 lhs, 5 lhs, in *c* lines on 5 rhs, 6, 7, 9 rhs, 10 lhs; in *b* lines on 11 rhs, 12 lhs then with regular alternation; (after male pores alternations become even). Spermathecal pores: at anterior of segments 8 and 9 in setal *b* lines. Female pore: single mid-ventral just anterior to *aa* on 14. Male pores: paired on raised mounds in *ab* lines within yellow tumid areas that spread from setal *a* lines almost to

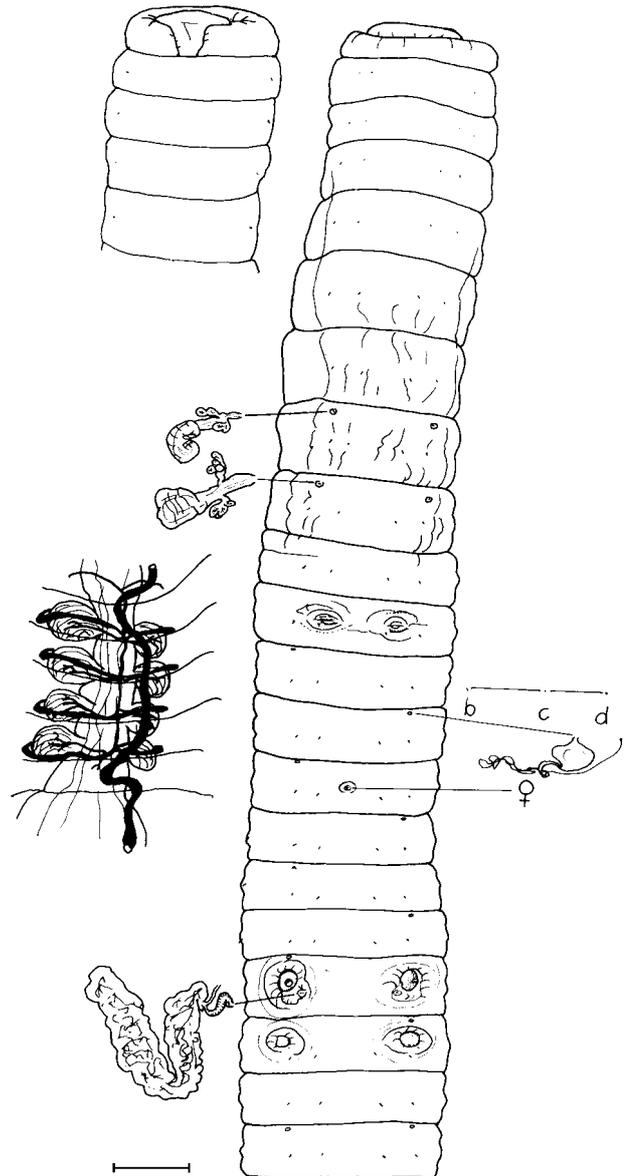


Figure 8. *Heteroporodrilus editus* n.sp., ventral view of holotype with dorsal view of prostomium; and four pairs of calciferous glands in 10–13; spermathecae *in situ*; nephridial bladder of 13 rhs; and tubuloracemose prostate in 18. Scale 1 mm.

c lines on both sides on 18. Genital markings: weakly defined paired pads in and just anterior to *ab* on 11; large sucker-like paired discs corresponding to markings around male pores centred in *b* lines presetally on 19.

Internal anatomy. Septa: 6/7–9/10 increasingly thickened. Gizzard: large muscular barrel in 5. Oesophagus: with large laterally sessile calciferous glands paired in 10–13 (i.e., four pairs). Nephridia: vesiculate holoic with small sub-spherical bladders, becoming ocarina-shaped in intestinal segments. Vascularization: dorsal blood vessel single; small hearts paired in 10–13 with connection to supra-oesophageal vessel which also projects vessels to calciferous glands. Spermathecae: two pairs in 8 and 9, saccular ampulla on

thin duct with opposed, multiloculate diverticula mid-length. Male organs: holandric, testes and iridescent funnels in 10 and 11; seminal vesicles elongate in 9 and 12. Ovaries: as numerous fine egg-strings in 13 anterior to oviducts; small ovisacs in 14. Prostates: flattened, tubuloracemose in 18–17 on short duct; penial setae absent. Intestine: origin in 15; typhlosole absent; gut contains soil with grits.

Remarks. With two pairs of bidiverticulate spermathecae, four pairs of calciferous glands, and a single female pore, *Heteroprodrius editus* is comparable to *H. notatus*. It differs from *H. notatus* in the distribution of genital markings, lack of stalks to the calciferous glands, intestinal origin in 15 rather than 21 or 16, and prostates that are elongate rather than square.

Etymology. The word *editus* in Latin means “from on high”.

Distribution and habitat. Other species found at the Mt Warning locality are listed in the account of *Digaster eastoni* below.

***Heteroprodrius hirthi* n.sp.**

Figs. 9, 20

Material examined. HOLOTYPE: ANIC RB.97.9.1 (H), from near Black Dog Creek on David Terrill’s property near Rutherglen, Vic., c. 36°07'38"S 146°29'04"E, Jeff Hirth, 8.ix.1995, “collected from an old fence line” (mature, posterior amputee, dissected and figured). PARATYPES: MOV: F86778 (P1), same details as H, (mature, posterior amputee, dissected); ANIC RB.97.3.2 (P2), same details as H, (mature, posterior amputee, dissected).

External features. Lengths, mm: 150+ (H), 130+ (P1), 80++ (P2). Width: c. 6 mm. Segments: 100+ (H). Colour: unpigmented light grey in alcohol. Prostomium: epitylobous with faint furrowing. Clitellum: 14–½17. Dorsal pores: minute from 8/9 (H) or from 7/8 (P1, P2). Setae: 8 per segment in regular series. Nephropores: at anterior margin of segments (H) in *d* lines on 2–4, 6 rhs, 7, 9 then regular alternation; in mid-*bc* lines on 5, 6 lhs, and 8; in *b* lines on 10, 12, then with regular alternation; (P1 and P2 basically agree except the pores are asymmetrical in P1). Spermathecal pores: 7/8/9 in setal *b* lines. Female pores: paired just anteromedian to setae *a* on 14. Male pores: paired just lateral of *b* lines on prominent papillae on 18. Genital markings: large but flat paired pads in *ab* presetally in 11 and 12 (all specimens, except on rhs only on 11 in P2); small paired discs postsetal in *aa* on 17 near 17/18 (H) or with two pairs of discs posteromedian to setae *a* and setae *b* on 17 (P1) or absent from 17 (P2); larger sucker-like pads near intersegmental furrow median of *ab* anteriorly in 18 and 19 each with smaller pair of discs posteriorly and also posterolaterally, the latter pair just anterior to male pores on 18 (H) and with additional pair posterior to the male pores (P1).

Internal anatomy. Septa: 6/7–12/13 increasingly thickened. Gizzard: in 5 muscular barrel, occupying 7–8. Oesophagus: small ventrolaterally sessile calciferous glands paired in 10–13 (i.e., four pairs); valval in 14. Nephridia:

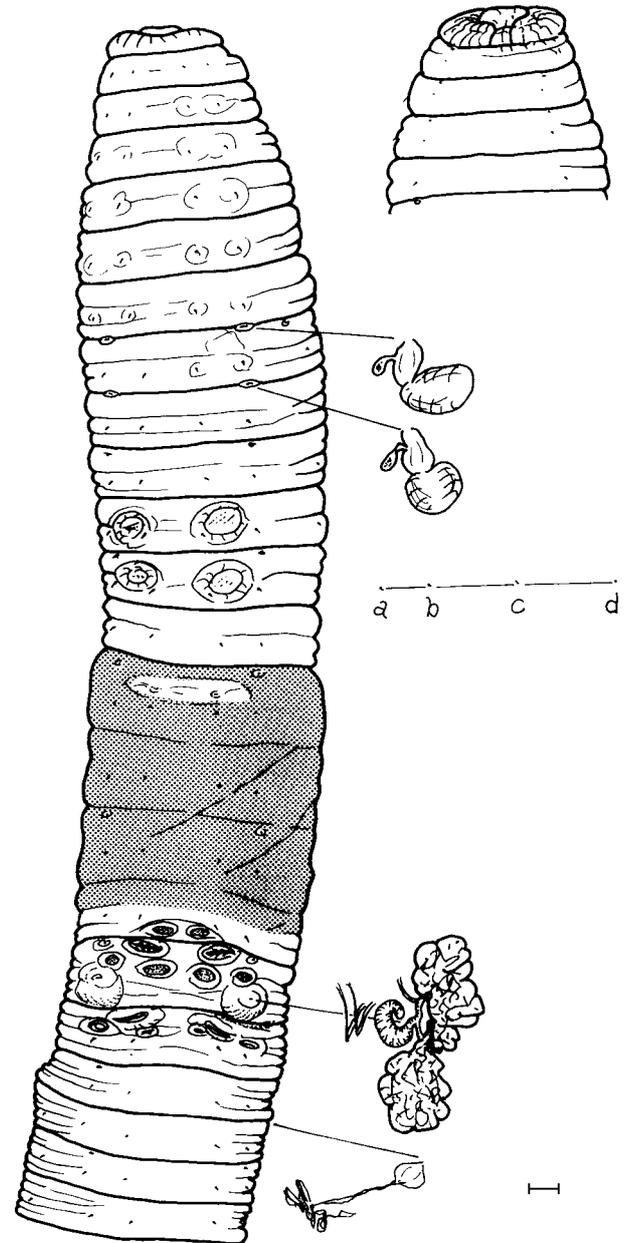


Figure 9. *Heteroprodrius hirthi* n.sp., ventral view of holotype with dorsal view of prostomium; spermathecae *in situ*; bilobed racemose prostates in 17–19 with penial setae; and nephridial bladder in 21 rhs. Scale 1 mm.

vesiculate holoic with small spherical bladders (not found in clitellar region). Vascularization: single dorsal blood vessel onto pharyngeal mass; large hearts paired in 10–13 with connection to supra-oesophageal vessel that itself connects with calciferous glands on each side. Spermathecae: two pairs in 8 and 9, as flattened heart-shaped ampulla on muscular duct with rudimentary club-shaped diverticulum approximately mid-length. Male organs: holandric, testes and iridescent funnels in 10 and 11 (obscured by mucus); paired seminal vesicles small racemose (H) or vestigial in 9 (P1 and P2), absent from 11,

and larger in 12 (all specimens). Ovaries: as long egg-strings in 13 anterior to oviducts; ovisacs absent from 14. Prostates: flattened, racemose in 17–19; large duct to middle of gland bifurcates to incompletely separated anterior and posterior lobes, the anterior fork joined by vas deferens close to junction with gland; penial setae present. Intestine: origin in 15; typhlosole absent; gut contains fine textured loamy soil with fibrous root fragments and seed cases plus a few red quartz grits and occasional large pebbles (one 3 mm diameter in H).

Remarks. *Heteroporodrilus hirthi* is morphologically close to *H. shephardi*, as redescribed herein, especially with regard to the genital markings and shape of the prostates and spermathecae. What distinguishes *H. hirthi* are two, rather than three, pairs of spermathecae; the delayed onset of dorsal pores; and the apparently reduced seminal vesicles in 9. Having two pairs of spermathecae and four pairs of calciferous glands are features shared with several other species that are differentiated in the key above.

Etymology. Named after the collector, Dr Jeff Hirth.

Distribution and habitat. Rutherglen, Vic. is near the Murray River.

***Heteroporodrilus kaputar* n.sp.**

Figs. 10, 20

Material examined. HOLOTYPE: AM W24403 (H), Mt Kaputar National Park, NSW, c. 30°10'S 150°10'E, Ed Easton, 29–30.iii.1983; four labels in jar: “Mt Kaputar N. Pk, 30 March, 1983”, “Mt Kaputar [sic] NP—Junction of Mt K + Dawson’s Spring Rd 29/3/83”, “*Diporochoeta* sp. nov.?” , “Jar 39 Sp 6 Mt Kaputar [sic]”, (mature, posterior amputee, dissected and figured). PARATYPES: ANIC RB.98.2.1, (P1), same details as H, (mature, complete but with slight anterior damage, dissected); W24405, (P2), same details as H, (acilitellate mature posterior amputee, dissected); ANIC RB.98.2.2, (P3), same details as H, (acilitellate mature); W24406, (P4), same details as H, (subadult or juvenile); ANIC RB.98.2.3, (P5), same details as H, (juvenile); W24407, (P6–P9), (in original jar with labels), same details as H, (four immature specimens that agree superficially plus four tail fragments); AM W24408, (P10–P12), same location as H, labelled “Dawson’s Spring Mt Kaputar N.Pk. 30 March, 1983”, “Ed Easton Collection”, “AM 40 *Diporochoeta* sp2 nov. (see 39) dark brown/purple dorsally alt nephs”, “Jar 40 Sp 6 Mt Kaputer [sic]”, (three acilitellate mature specimens, one dissected here).

External features. Body stout, not dorsally canaliculate, tail sometimes square in section. Lengths, mm: range of matures 150–270; 140+ (H), 270 (P1), 180 (P3), 175 (P4), 125 (P5), 90–130 (P6–P9), c. 150 (P10–P12). Width: c. 10 mm. Segments: 190 (P1), 169 (P3). Colour: dark dorsally in life (see W24408 label), uniform brown or golden in alcohol, clitellum russet. Prostomium: epi-tanylobous (i.e., can appear closed epilobous but often has furrows extending to intersegment). Clitellum: 14–17. Dorsal pores: open from 7/8. Setae: 8 per segment in regular series. Nephropores: at anterior margin of segments, in *d* lines on 2–4, 8, 10 then regular alternation; in *c* lines on 5, 6; in mid-*bc* lines on 7, 9; in *b* lines on 11, 13 then with regular alternation (in H).

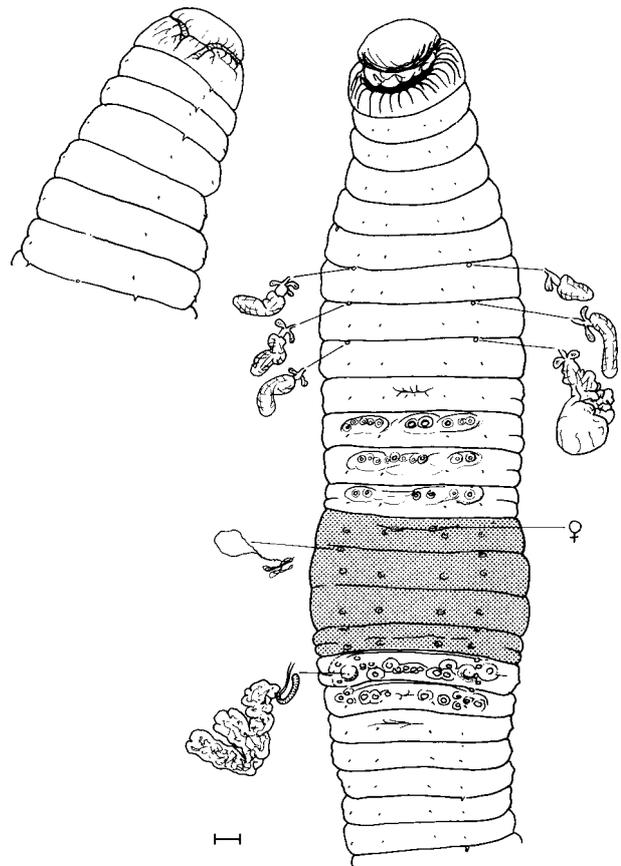


Figure 10. *Heteroporodrilus kaputar* n.sp., ventral view of holotype with dorsal view of prostomium; spermathecae showing pseudovesicle attached to 9 rhs ampulla; nephridial bladder in 15 lhs; and prostate with vasa deferentia in 18–20. Scale 1 mm.

Spermathecal pores: at anterior margin near 6/7/8/9 in setal *b* lines. Female pores: widely paired anteromedian to *a* setae on 14. Male pores: at centres of small papillae in *b* lines on 18. Genital markings: on 11 (not P1, P4, P5, P10), and/or on 12 and 13 (all matures and juveniles), presetal battery of irregularly numerous small discs between *b-b*; on 18 and 19 (all matures and juveniles) whole ventral aspect to just lateral of *b* with several irregularly arrayed small discs (sometimes reduced in number on 19).

Internal anatomy. Septa: 7/8/9–12/13/14 only slightly thickened; attached to the anterior base of septum 8/9 are large paired glands or pseudovesicles of unknown function as no connection found to oesophagus nor to male organs. Gizzard: compact muscular in 5. Oesophagus: with ventrolaterally sessile extramural calciferous glands in 10–13 (i.e., four pairs); valval in 14–½15. Nephridia: vesiculate holoic with large spherical bladders exiting at nephropores; not tufted in anterior. Vascularization: dorsal blood vessel single onto pharyngeal mass in 4; hearts paired in 10–13 from supra-oesophageal vessel in 10–13 that also supplies calciferous glands. Spermathecae: three pairs in 7–9 (in H the 9 rhs spermathecae is displaced anteriorly into segment 8 although it still exits in 8/9 and is intimately implicated with 8 rhs pseudovesicle—see Fig. 10), elongate ampullae

on short ducts with small opposed or single diverticula mid-length (i.e., diverticula paired except in H 7 lhs has small supernumerary diverticulum; in H 7 rhs has single but slightly bifid diverticulum on spermatheca, single diverticula also in P1 in 7 and 9, P2 in 7, and P10 in 7 and 9). Male organs: holandric, testes and iridescent funnels in mucus in 10 and 11; small seminal vesicles saccular in 9 and 12. Ovaries: palmate with fine egg-strings in 13; small ovisacs in 14. Prostates: flattened, tubuloracemose in 18–20 on thin duct; penial setae absent. Intestine: origin in $\frac{1}{2}$ 15 (H, P2, P10) or 16 (P1); typhlosole absent; spiralling gut contains grey soil with few grits and charcoal, and some fibrous material.

Remarks. *Heteropordrilus kaputar* has four pairs of calciferous glands and three pairs of spermathecae that often have paired diverticula (sometimes single or triple). It therefore resembles the similarly large *H. canaliculatus*, but it differs notably in the arrangement of small disc-like markings in (11), 12, 13, 18 and 19. Another distinctive feature is the large pair of pseudovesicles (of unknown function) in segment 8, that are larger than the seminal vesicles in 9 and 12. The intestinal origin appears to vary between $\frac{1}{2}$ 15 and 16.

Etymology. Named after the type locality.

Distribution and habitat. Mt Kaputar National Park is just east of Narrabri en route to Warialda, NSW; it is in the catchments of the Namoi and Gwydir Rivers, tributaries of the Murray-Darling.

***Heteropordrilus mediterrus* (Fletcher, 1887b)**

Figs. 11, 20

Cryptodrilus mediterrus Fletcher, 1887b: 602, 614–616.
Cryptodrilus mediterrus.—Fletcher, 1889: 1535–1538; 1890: 995–996.

Woodwardia mediterrus.—Michaelsen, 1907: 162.

Heteropordrilus mediterrus.—Jamieson, 1970: 117–120, figs. 4a,b,e–g,9d,10e; Blakemore, 1994b: 21–23.

Material examined. LECTOTYPE: AM W1338, part of Fletcher Collection donated to Australian Museum; sample contains two labels: “*Crypto mediterrus* H.F. R. Darling / Big specimen—Gragin T.G.S.” [in Fletcher’s hand]; “W.1338 *Heteropordrilus mediterrus* Gragin & Warialda Pres. J.J. Fletcher”. Fletcher (1887b: 616) gives locality as “The banks of the Darling River between Bourke and Brewarrina, NSW”, the latter c. 29°30’S 140°30’E, collected by Mr H.J. Fletcher (identified as H.F. on label). The original sample contains 17 specimens that were shrivelled and in less than ideal condition: 6 clitellate matures (3 previously dissected); 6 acitellate matures (one dissected, one damaged); 3 anterior portions; an immature that measures 38 mm × 2.5 mm and has 134 segments; a large clitellate mature that is darker and more square and is undissected but broken into about four pieces that combined measure about 80 mm long × 10 mm wide; plus 3 tail portions. Most of these specimens are syntypes, one of the matures that was previously dissected is redescribed, figured, and is here designated the lectotype. The remaining specimens from AM W1338 are now PARALECTOTYPES: AM W24579, (ex W1338), (14 specimens and 3 tail portions) and

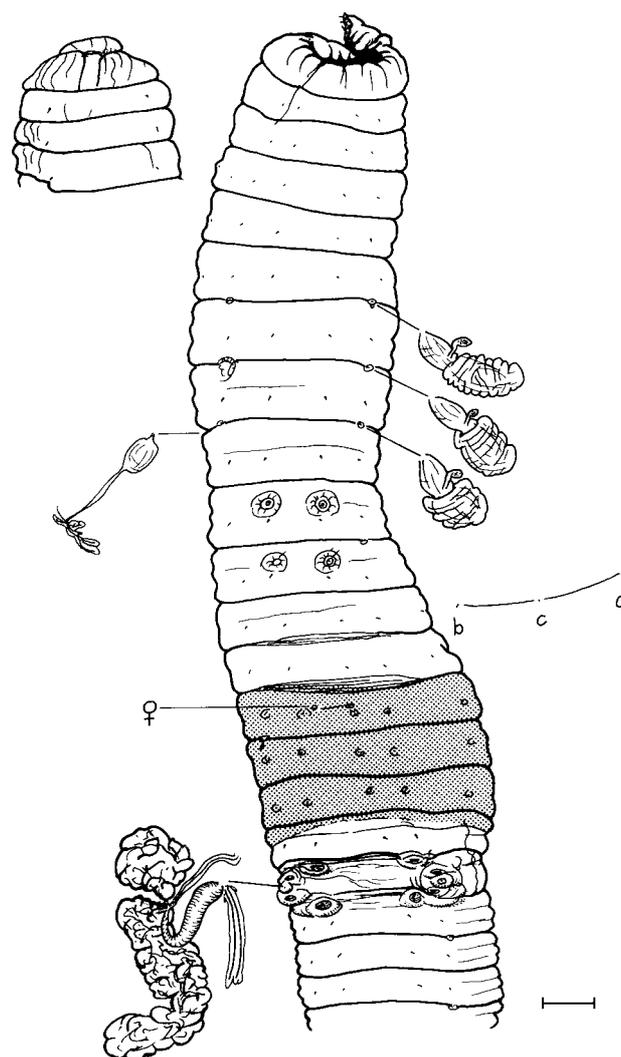


Figure 11. *Heteropordrilus mediterrus* (Fletcher, 1887), ventral view of dissected lectotype; spermathecae *in situ*; nephridial bladder in 9 lhs; and lhs bilobed prostate with vasa deferentia and long penial setae in 17–20, 21; the dorsal view of prostomium is of a paralectotype. Scale 1 mm.

W24580 (the immature specimen). (The larger specimen, W24581, from Gragin according to the label, is not a syntype as it did not form part of the original description and the label indicates it was from a different locality). Arguments for these decisions are presented in Remarks below. Jamieson (1970: 119) inspected W1338, but recorded only six specimens, did not appreciate its significance as the type series, and misinterpreted both the type localities and the original label: erroneously stating they were all from “Gragin and Warialda, Victoria”. Additional material unknown.

External features (compared to Fletcher’s description). Body fairly stout, not dorsally canaliculate. Lengths, mm: 105 (lectotype); other clitellates 80–100; acitellates 65–100 (cf. 73–110 mm, Fletcher). Width: 4–5 mm (ditto Fletcher). Segments: 144 (lectotype), (cf. 130–150, Fletcher). Colour: yellow-brown in alcohol; clitellum buff (cf. “above sooty-brown, darkest in the anterior portion of

the body, especially in front of the clitellum, lighter below, the clitellum with a tinge of red or purplish", Fletcher). Prostomium: (in paralectotypes, lectotype damaged) epitanymbous, i.e., looks tanylobous but peristomium is also deeply furrowed transversely (Fletcher concluded that the longitudinal groovings were not part of the prostomium). Clitellum: weak $\frac{1}{2}$ 13,14–16, $\frac{1}{2}$ 17. Dorsal pores: from 5/6 or 6/7 (ditto Fletcher). Setae: 8 per segment in regular series. Nephropores: (difficult to discern) at anterior margin of segments, in *d* lines in 2–4, 6 lhs?, 7 rhs, 8 lhs, 9 rhs, then alternating; in *c* lines in 5, 6 rhs?, 8 rhs?, 9 lhs; in *b* lines in 10 rhs, 11 lhs, then alternating. Spermathecal pores: 6/7/8/9 in *b* setal lines. Female pores: widely paired just anteromedian to setae *a* on 14. Male pores: paired just lateral of setal *b* lines on conspicuous papillae on 18. Genital markings: (lectotype) two pairs of papillae just anterior to setae *a* in 10 and 11; two pairs of papillae in *ab* lines at anterior margins of 18 and 19; two pairs of small papillae are on porophores just median and adjacent to male pores on 18; (mature paralectotypes agree with the lectotype, some have slight tumidity around the spermathecal pores in 6–9, as described by Fletcher, although the lectotype does not).

Internal anatomy. Septa: 5/6 to base of gizzard, 6/7–13/14 some thickening. Gizzard: muscular barrel with anterior crop in 5. Oesophagus: small ventrolaterally sessile calciferous glands paired in 10–13 (i.e., four pairs, slightly damaged in lectotype). Nephridia: vesiculate holoic with small spherical bladders in position of nephropores. Vascularization: dorsal blood vessel single; hearts paired in 10–13. Spermathecae: three pairs in 7–9, pouch-like ampulla on thick duct with rudimentary club-shaped diverticulum attaching at some distance from the exit (lectotype 8 lhs removed and missing from jar). Male organs: holandric, iridescent testes and funnels in 10 and 11 in mucus; seminal vesicles very small paired, racemose anteriorly in 11 and 12 (i.e., none recorded in 9). Ovaries: in 13 as usual; ovisacs not found. Prostates: flattened, racemose in 17–20,21; with smaller anterior and larger posterior lobes, ductules from each combine and joined with vasa deferentia at muscular duct; large paired sacs each containing delicate, curved penial setae about 2.4 mm long and minutely spinose towards tips (in lectotype, rhs prostate and setae removed and missing from jar). Intestine: origin in 15 (in paralectotype that agrees externally with lectotype, gut removed from lectotype after 14), (cf. in 18, Fletcher); typhlosole absent (lectotype and paralectotype); gut contains fine light grey soil, some sand grains and much fibrous material (root hairs?).

Remarks. Fletcher (1887b: 614–616) based his description on "Ten (spirit) specimens" and "A young specimen 4.2 cm long, and 2½ mm. wide [that] comprises 132 segments" that were "sent to me by my relative Mr H.J. Fletcher, who found one by accident, and obtained the others by digging for them." The label accompanying AMW1338 shows them to be from the Darling River locality with the named collector ("H.F."). The above specimens, although numbering a few more, agree with each other and concur with Fletcher's description on most points, except that the intestine commences in 15 rather than 18. Moreover, the dimensions of the immature specimen (W24580) are especially close, reinforcing the syntype status.

The anomalous larger specimen (W24581) is a damaged mature that has genital markings in 10 and 11 but is otherwise in too poor condition to identify with certainty. It is identified with a different locality (Gragin is near Warialda, NSW, about 350 km east of Brewarrina), and a different collector ("T.G.S." is probably Mr T.G. Sloane who Fletcher [1889: 1523, 1537, 1541] states also collected samples of earthworms from Coonabarabran and Narrabri, central NSW, both localities en route to Gragin). It is therefore not considered a syntype and may well be a different species although it is now too damaged to decide.

H. mediterreus has many characters in common with *H. shephardi* (Spencer, 1900), not least: four pairs of calciferous glands, three pairs of spermathecae each with a single, small diverticulum, and similar distributions of genital markings. What distinguishes *H. mediterreus* are the seminal vesicles in 11 and 12, rather than the more usual 9 and 12. (Other differences from *H. shephardi* and from *H. canaliculatus* are made under these species' descriptions).

Distribution and habitat. Fletcher: "The banks of the Darling River between Bourke and Brewarrina, NSW". For reasons given in Remarks above, Gragin and Warialda are no longer considered type-localities.

Dyne (1984: 266) believed that a specimen (NMV G70) listed under *Cryptodrilus queenslandicus* in Jenz & Smith (1969: 90) was referable to *H. mediterreus*. If confirmed, this specimen collected from Gayndah, Qld would greatly extend the distribution of this species although it is probable, in view of the subsequent generic changes and number of new taxa now added, that this specimen is not conspecific.

Heteroporodrilus namoi n.sp.

Figs. 12, 20

Material examined. HOLOTYPE: ANIC GD.95.114.1 (H), Walgett, NSW, c. 30°10'S 148°0'7E, collector Tom McCredie, November, 1991, "MYALL", (the original plastic container in which the specimens were provided, had to be cut open to remove them during curatorial processing by the author in 1995, they had not previously been inspected), (complete mature, dissected and figured). PARATYPE: ANIC GD.95.114.2 (P), same details as H, (mature, dissected). Specimens: ANIC RB.97.5.2 (S1–S4), Walgett, NSW, collector Y. Chan of NSW Dept. Agriculture, October, 1994 (four slightly macerated specimens, complete matures but clitella not developed, one dissected).

External features. Body ventrally tumid 4–30, deeply serrated ventrally in 5–12; not canaliculate dorsally (H and P). Lengths, mm: 280 (H), 270 (P), c. 300 (S1–S4). Width: 6–8 mm. Segments: 194 (H), 150 (P and S1). Colour: bleached straw in alcohol. Prostomium: weakly tanylobous with faint dorsal furrow (difficult to determine as remainder of peristomium also faintly furrowed). Clitellum: $\frac{1}{2}$ 13,14– $\frac{1}{2}$ 17. Dorsal pores: small in 5/6, larger from 6/7 (H, P and S1–4). Setae: 8 per segment in regular series. Nephropores: (in H) at anterior margin of segments in *d* lines on 2–4, 6, 8, 10, then regular alternation but skips in mid-body; in mid-*bc* (or just ventral of *c* lines?) on 5, 7, 9 rhs; in *b* lines on 9 lhs, 11, 13, then

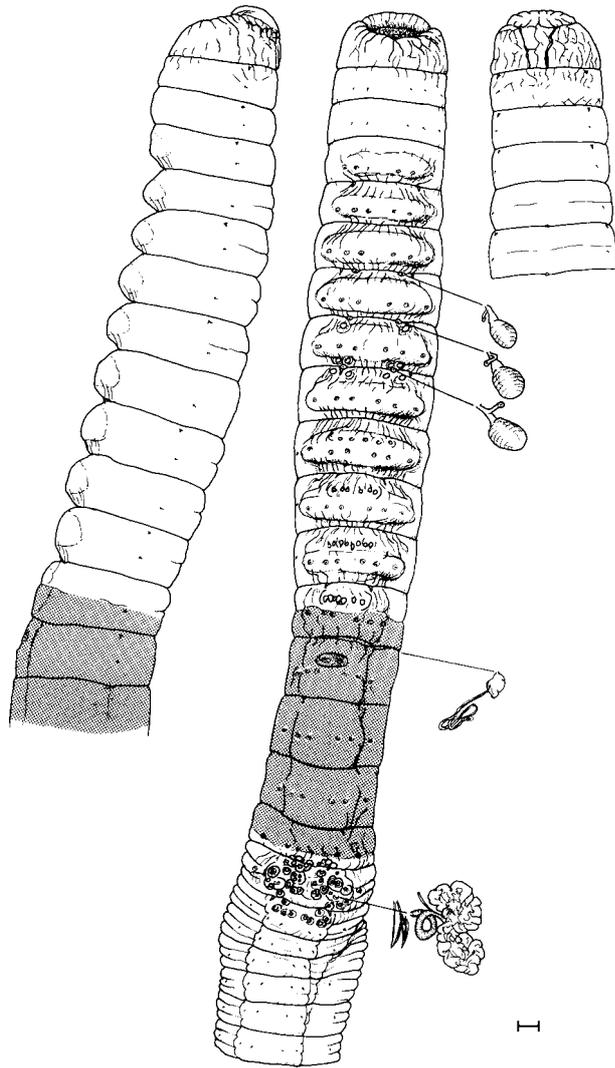


Figure 12. *Heteroporodrilus namoi* n.sp., lateral and ventral view of holotype with dorsal view of tanylobous prostomium; spermathecae *in situ*; nephridial bladder in 14 rhs; and racemose prostate with vasa deferentia and long penial setae in 18–19. Scale 1 mm.

with regular alternation but skips in mid-body; (in P) in *d* lines on 2–4, 6, 8, then regular alternation; in mid-*bc* (or *c*?) lines on 5, 7, 9; in *b* lines on 11, (13?), 15, then with regular alternation; (S1–4) have the typical arrangement of *d* lines in 2–4, then with regular alternation from 7; in *c* lines in 5, 6, and 8; and in *b* lines alternately from 10. Spermathecal pores: 6/7/8/9 in setal *b* lines. Female pores: paired just anteromedian to setae *a* on 14. Male pores: superficial, paired just lateral of *b* lines on 18; tips of penial setae protrude. Genital markings: (H and P) tumid mid-ventrally between *cc* on 4–13 with presetal row of papillae in *bb* lines in 10–13; small papillae near spermathecal pores in 8 and 9 (H) or in 6–9 (P); (in H and P) postsetal on 17 and 18, rows of small papillae in *b-b* lines; the whole of 18 with complex arrangement of numerous small papillae; on 19 presetal row of papillae in

b-b. (Markings not obvious in S1–4 although possibly some tumidity ventrally in 6–12 and in 17–19).

Internal anatomy. Septa: 5/6–13/14 increasingly thick, then thin. Gizzard: in 5 muscular onion-shaped. Oesophagus: small ventrolaterally sessile calciferous glands paired in 10–13 (i.e., four pairs); valval in 14. Nephridia: vesiculate holoic; spherical bladders in position of external nephropores, after clitellum dorsal bladders have lobe on both sides of septum. Vascularization: dorsal blood vessel single; hearts paired in 10–13 with connection to supra-oesophageal vessel in 12–13. Spermathecae: three pairs in 7–9, pouch-like ampulla on tapering duct with rudimentary club-shaped diverticulum from exit of duct, not extending as far as ampulla. Male organs: holandric, iridescent testes and funnels in 10 and 11 in mucus; seminal vesicles racemose (either irregular in outline or saccular) in 9 and elongate in 12. Ovaries: small palmate with numerous egg-strings in 13; small paired ovisacs in 14 (seen in H). Prostates: flattened, racemose in 18–19 but not divided into separate lobes; duct to middle of gland with vasa deferentia joining junction with gland; curving penial setae present. Intestine: origin $\frac{1}{2}$ 15, but difficult to determine as intestinal wall same thickness in posterior of 15 and in 16, while notable expansion occurs only in 16; typhlosole absent; gut contains soil with some organic matter and grits.

Remarks. *Heteroporodrilus namoi*, with four pairs of calciferous glands and three pairs of spermathecae, is similar to several other species in the genus (differentiated in the key above). While superficially resembling *H. mediterrus* or *H. canaliculatus*, it differs thus: from *H. mediterrus* by having seminal vesicles in 9 and 12 (rather than 11 and 12), the spermathecal diverticula are near the exit of the duct (rather than nearer the junction with the ampulla) and the prostates are not bilobed nor as extensive; from *H. canaliculatus* it differs by having spermathecal diverticula that are single rather than paired or multiple.

The arrangement of genital markings in *H. namoi* resemble those of both *H. mediterrus* and *H. shephardi*. However, they are more extensive than the “swollen ventral portion” in 6–9 described for *H. mediterrus* and not paired or single in 7–12 as in *H. shephardi*, but are smaller and much more numerous, both in the anterior and around the male field, than in either species. All three species have a tendency towards prostates that are divided into two lobes with duct near the mid-point.

Etymology. After locality—the Namoi River.

Distribution and habitat. Walgett in northern central NSW is approximately midway between Bourke and Narrabri (the known ranges of *H. mediterrus* and of *H. narrabri*, respectively) it stands at the confluence of the Namoi River and the Barwon River that flow into the Murray-Darling River system. Tom McCredie (per. comm., 9.x.1998) found the specimens on the soil surface after heavy rain in “Myall” (*Acacia snowdenii*) wattle scrub. A recent study by Friend & Chan (1995) considered the ecology of this worm under cultivated soils in the Walgett area.

Heteropordrilus narrabri n.sp.

Figs. 13, 20

Material examined. HOLOTYPE: ANIC RB.97.3.1 (H), Narrabri, NSW, under irrigated cotton that was unsprayed for 3 years, Australian Cotton Research Institute ("ACRI, B16"), January, 1996 (mature, dissected and figured). PARATYPE: ANIC RB.97.3.2 (P), same details as H, (mature, dissected). Specimens: ANIC RB.98.12.1, (S1, S2), two mature specimens (180–190 mm) from Trangie, NSW collected by Dr Yin Chan, 10.vi.1998—both agree superficially, and one dissected agreed internally except that seminal vesicles were found in 12 only. Specimens AM W1375 from Warren (near Dubbo), NSW noted under *H. canaliculatus* above also agree externally and may be conspecific with *H. narrabri* although confirmation of this requires further work.

External features. Lengths, mm: 330 (H), 265 (P), 190 (S1). Width: 6–8 mm. Segments: 200 (H). Colour: with faint grey tinge in alcohol. Prostomium: narrowly tanylobous. Clitellum: 14– $\frac{1}{2}$ 17. Dorsal pores: from 10/11 rudimentary, open from 11/12 (H, P, S). Setae: 8 per segment in regular series, small in posterior. Nephropores: at anterior margin of segments, (H) in *d* lines on 2–4, 7, 9 then regular alternation but doubles up on 21 rhs; in *c* lines on 5 lhs; in mid-*bc* lines on 5 rhs, 6, 8, 10 rhs; just lateral of *b* lines on 10 lhs, 11, then with regular alternation but doubles up on 21 lhs; (P) in *d* lines on 2–4, 6, 8, then regular alternation; in mid-*bc* lines on 7, 9; just lateral of *b* lines on 11, then with regular alternation; (in S1 in mid-*bc* in 5, 7 and 9). Spermathecal pores: 6/7/8/9 in *b* setal lines. Female pores: paired just anteromedian to setae *a* on 14. Male pores: paired just lateral of *b* lines on small papillae on 18. Genital markings: mid-ventral, presetal rows of papillae in *aa* on 9, 10–13 thus: (H) two papillae on 12 otherwise *c*. six papillae on 9–13; (P) three papillae on 10, five on 11, none on 12, eight on 13; (H and P) postsetal on 17 and 18 two pairs of papillae in approximate line with *a* and *b* setae; presetal on 18 and 19 pair of small sucker-like pads in *ab* lines each with median disc; on 18 above and between male pores, several small papillae.

Internal anatomy. Septa: 6/7–13/14 with some thickening. Gizzard: in 5 muscular barrel, preceded by crop in 4. Oesophagus: small ventrolaterally sessile calciferous glands paired in 10–13 (i.e., four pairs); valval in 14. Nephridia: vesiculate holoic with small spherical bladders in anterior, bladders not found in clitellar region; in posterior bladders bilobed either side of septum when in *d* lines and spherical when in *b* lines. Vascularization: dorsal blood vessel single; hearts paired in 10–13 with connection to supra-oesophageal vessel which also connects with calciferous glands. Spermathecae: three pairs in 7–9, as pouch-like ampulla on duct with rudimentary club-shaped diverticulum mid-length. Male organs: holandric, iridescent testes and funnels in 10 and 11 in mucus; seminal vesicles small paired, racemose in 9 and larger in 12. Ovaries: small palmate with numerous oocytes in 13; small pair of ovisacs in 14. Prostates: flattened, racemose in 18–19 (H) or 17–20 (P); duct to middle of gland with vasa deferentia joining duct near junction with gland; penial setae present. Intestine: origin in 15 (H) or $\frac{1}{2}$ 15 (P); typhlosome absent; gut contains fine (clay?) soil.

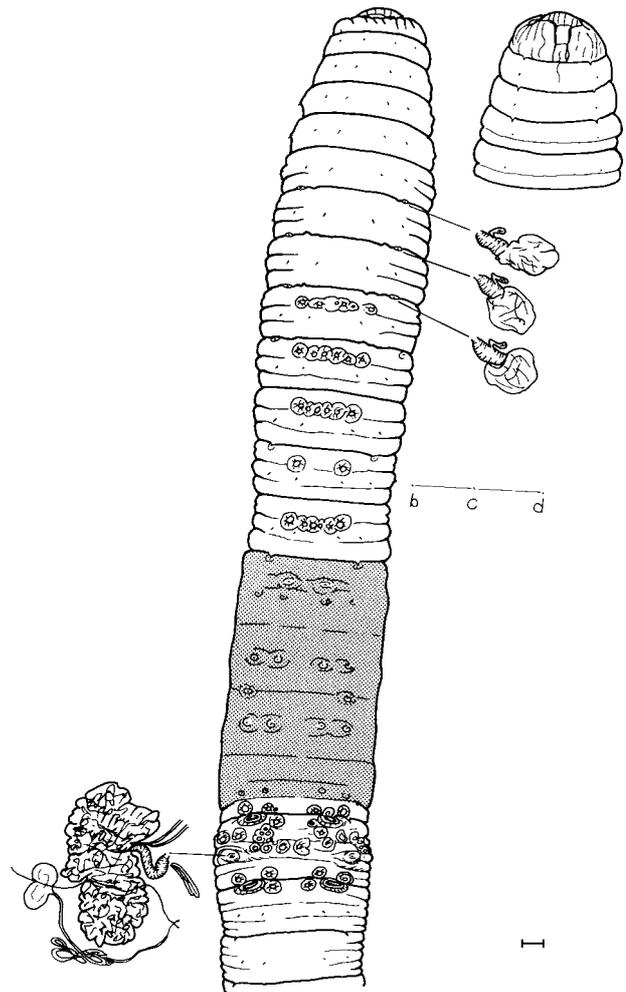


Figure 13. *Heteropordrilus narrabri* n.sp., ventral view of holotype with dorsal view of tanylobous prostomium; spermathecae *in situ*; and lhs prostate in 18–19 with vasa deferentia and long penial setae; nephridial bladder of 19 lhs is also shown on septum. Scale 1 mm.

Remarks. *Heteropordrilus narrabri*, with four pairs of calciferous glands and three pairs of spermathecae is similar to several other species in the genus. It differs from *H. mediterrans* principally by having seminal vesicles in 9 and 12 (rather than 11 and 12); from *H. canaliculatus* by having single spermathecal diverticula mid-length on the duct (rather than paired or multiple and near the exit); from *H. shephardi* by having prostate glands that are not clearly divided into two lobes; and from *H. namoi* by having diverticula near the mid-length of the spermathecal duct (rather than near the exit). From all four species, *H. narrabri* differs further by the more dorsal commencement of its dorsal pores in 11/12 (rather than in 5/6, 6/7, or 8/9) and in the complex arrangement of its genital markings.

Nevertheless, *H. narrabri* is remarkably similar to both *H. shephardi* and *H. namoi* as described herein, especially with regards the primary genital markings. These markings comprise two pairs of sucker-like pads in *ab* lines anteriorly on 18 and 19 (as in *H. shephardi*) as well as a tendency to

smaller more numerous ancillary markings (as seen in *H. namoi*). Also similar in these three species are nephropore shifts between *d* to both mid-*bc* and *c* lines in some anterior segments (it is also possible this arrangement occurs in *H. mediterraeus* as some nephropores could not be clearly determined). This alternation of nephropores from *d* to mid-*bc* was once thought (Jamieson, 1974b: 87) to be unique for *H. shephardi*—this assumption is further questioned in the remarks under the description of the latter species below.

Etymology. Named after the locality.

Distribution and habitat. Narrabri in northern central NSW, sits astride the River Namoi that, flowing approximately 200 km westwards to Walgett (the type locality of *H. namoi*), joins the Barwon River that passes through Brewarrina uniting with the Darling River near Bourke (both latter localities forming the known range of *H. mediterraeus*). Trangie and Warren, are adjacent townships on the Macquarie River that also flows to the Darling. The Murray-Darling River system leads eventually to Vic./SA where *H. hirthi* and *H. shephardi* are found.

Habitat details for these specimens (provided by the collector) are from a 2.1 ha field of raised bed rows of lucerne and cotton at the Australian Cotton Research Institute (ACRI). This field (B16) was managed without insecticides and with minimum tillage for 3 years (previously under conventional cotton i.e., sprayed and irrigated for 15–20 years), indicating that this species can recolonize or persist under such management regimes.

Heteropodrilus shephardi (Spencer, 1900)

Figs. 14, 20

Cryptodrilus shephardi Spencer, 1900: 40–41, figs. 28–30; Jenz & Smith, 1969: 91.

Woodwardia shephardi.—Michaelsen, 1907: 162.

Heteropodrilus shephardi.—Jamieson, 1970: 122–124, figs. 4c–d, 9f, 10i; Blakemore, 1994b: 21–23.

Heteropodrilus shephardi (Spencer, 1900) *armatus* Jamieson, 1974b: 85–87, figs. 2b, 10b, 11a, 13; **new synonym**.

Material examined. Spencer specimen: AM W1290, part of Fletcher Collection donated to Australian Museum. Sample contains four labels: “C. sp 1a V W Dimboola D. le Souëf” [Species code, location and collector in Spencer’s handwriting]; “*Cryptodrilus* sp 1a Nr Dimboola, Vict[oria] W.1290” [Fletcher’s writing?]; “*H. shephardi* Coll by J.J. Fletcher (Prof B. Spencer *vide* Fletcher) re-identified by Dr B Jamieson 1970”; “W.1290 *Heteropodrilus shephardi* Nr. Dimboola Vic. Id. E. Easton”. (Specimen mature clitellate, previously partially dissected in midbody—it agrees with this taxon being 140 mm long, with markings in 10–12 and 18 & 19 and has large penial setae). This specimen is clearly identified with specimen NMV G74 missing from the Museum of Victoria Spencer Collection (Jenz & Smith, 1969: 91). However, it is not part of the type-series as, in his type description, Spencer does not refer to this locality (Dimboola is approximately 35 km northwest of the Horsham type-locality) nor to this collector (here identified as Mr Dudley Le Souëf, rather than Mr J. Shephard). Specimens: (S1) ANIC RB.98.8.1, Victor Harbour, S.A., collected by C. Davoren, 23.viii.1991, “in vegy garden” (mature specimen, relaxed on preservation, dissected and figured here). (S2) SAM E3033, same details as S1, (mature specimen, contracted on preservation, dissected).

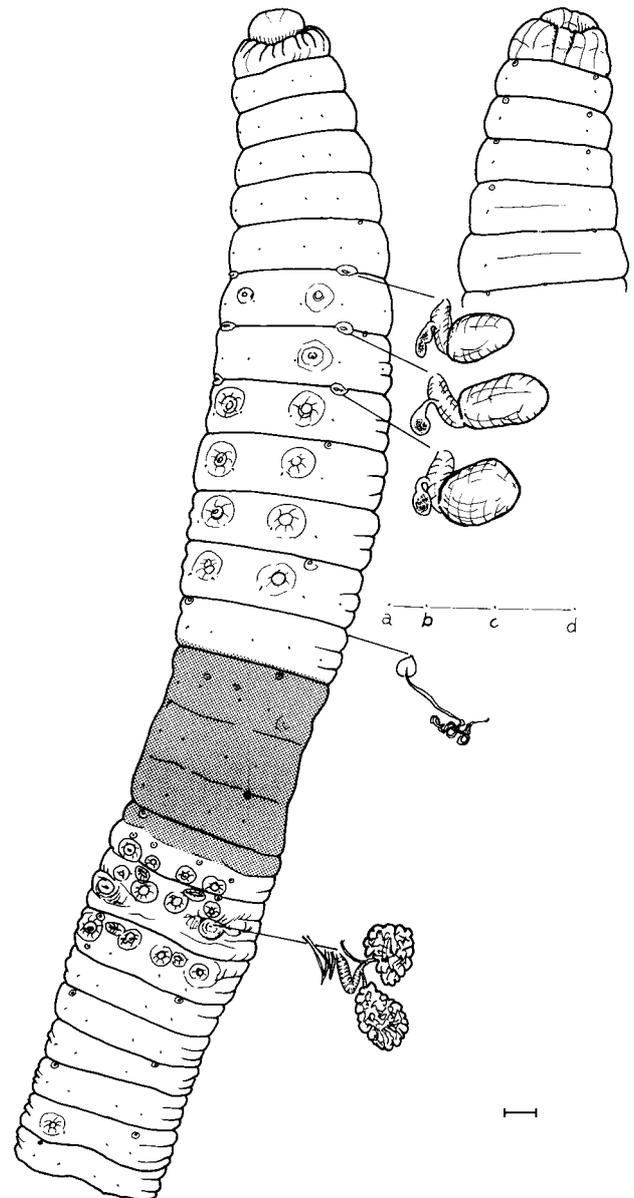


Figure 14. *Heteropodrilus shephardi* (Spencer, 1900), ventral view of Victor Harbour specimen with dorsal view of prostomium; spermathecae; nephridial bladder in 13 rhs; and bilobed prostate in 18–19 with vasa deferentia and penial setae. Scale 1 mm.

Type material not re-examined here. LECTOTYPE: NMV G34, a dissected entire specimen, in reasonable condition from Horsham, Vic., collected by Mr J. Shephard in October, 1892 (Jenz & Smith, 1969: 91). Paralectotypes: NMV G1409, two complete specimens formerly included with G34. (One of these was examined and figured by Jamieson [1970], although he makes no mention neither of the lectotype, the other paralectotype, nor the AM specimen he apparently re-identified).

External features. Body not dorsally canaliculate. Lengths, mm: 170 (S1), 90 (S2), c. 157–160 (Spencer, 1900; Jenz & Smith, 1969), 112 (Jamieson, 1970). Width: c. 5 mm (S1, S2 and Spencer) (cf. 10 mm, Jamieson, 1970—but in his figs. 4c,d the scale bars are obviously wrong). Segments:

103 (S1), 100 (S2). Colour: (new material) dorsum to *d* lines gunmetal grey, with darker spinal line, flanks between *dc* lighter grey, ventrum pale; clitellum buff. Prostomium: epi-tanylobous (possibly pro-epilobous). Clitellum: weak $\frac{1}{4}13$ – $\frac{1}{2}17$. Dorsal pores: 5/6 minute in (S1), open from 6/7 (S1, S2 and Spencer). Setae: 8 per segment in regular series. Nephropores: (in S1): at anterior margin of segment in *d* lines in 2–4, and on 5 rhs, 6 lhs, 7 rhs, 8 lhs, 9 rhs, 10 lhs, then on alternate segments; in mid-*bc* lines on 5 lhs, 6 rhs, 7 lhs, 8 rhs, 9 lhs; in *b* lines on 10 rhs, then on alternate segments; (in S2): alternations are same except on opposite sides and on 5 lhs only in *c* line; (cf. lectotype, Jamieson, 1970: in *d* lines in 2–4, 7 rhs, 8 lhs, 9 rhs; in *c* lines on 5–6 rhs; in mid-*bc* on 5–6 lhs, 7 lhs, 8 rhs, 9 lhs; then alternating in *b* and *d* lines). Spermathecal pores: 6/7/8/9 in setal *b* lines. Female pores: paired just anteromedian to setae *a* on 14. Male pores: paired near *b* lines on small papillae on 18 (S1) or on prominent mounds (S2). Genital markings: inconspicuous mostly paired discs, just anterior to *ab* in 7, 8–12, 13; in 17 two pairs of postsetal discs, just median to *b* and *a* lines (S1) or just the latter pair visible (S2); in 18 two pairs of pre-setal discs, just median to *b* and *a* lines (S1, W1290) or just the latter pair (S2), with small intervening sucker-like pad closer to intersegmental furrow on each side; in 19 two pairs of pre-setal discs, one pair just lateral to *b* lines, one pair median to *a* lines with small intervening sucker-like pad on each side; weak lhs analogue of disc in *ab* on 24 (in S1 only). Anterior markings difficult to see without adequate side-lighting; the male field in S2 in deep depression with the male pores on prominent mounds and only marking and pads (or pits) on 18 and 19 clearly visible (as Spencer).

Internal anatomy. Septa: 5/6–12/13 increasingly thickened, then thin. Gizzard: muscular barrel-shaped in 5. Oesophagus: small ventrolaterally sessile calciferous glands paired in 10–13 (i.e., four pairs). Nephridia: vesiculate holoic with small spherical bladders in position of nephropores. Vascularization: dorsal blood vessel single; hearts paired in 10–13 with connectives to supra-oesophageal vessel in 9–13. Spermathecae: three pairs in 7–9, large ampulla on moderately thick duct mid-length on which is small clavate diverticulum. Male organs: holandric, iridescent testes and funnels in 10 and 11 in mucus; seminal vesicles paired, racemose in 9 and 12. Ovaries: as sheets of numerous minute egg-strings in 13; small paired ovisacs in 14. Prostates: bilobed, racemose in 18–19 (S1) or 17–20 (S2); fine penial setae with attached muscle fibres present (S1, S2). Intestine: origin in 15 (S1 and Spencer) or $\frac{1}{2}15$ (S2); no typhlosole; gut contains dark organic soil.

Remarks. The present specimens agree with Spencer's characterization of *H. shephardi* on almost every given point. Especially similar are the prostomium (described by Spencer as "scarcely at all dovetailed into the peristomium"), the arrangement of the alimentary canal (i.e., with four pairs of calciferous glands in 10–13 and intestinal origin in 15), the position of the seminal vesicles (in 9 and 12) and the bilobed prostates. Moreover, the male field with deep depression in 17 and 18 and with paired markings anteriorly in 18 and 19 (as described and figured by Spencer) corresponds to that of the contracted specimen, S2, while more

extensive markings are visible on the less contracted S1. A questionable difference is that Spencer (1900) described the spermathecae as "consisting of a spherical sac with a long duct into the base of which [rather than into the mid-length as here] opens a short tubular diverticulum with a slightly swollen end." However, in Spencer's fig. 30, at least one spermatheca is shown with the diverticulum further from the base. While agreeing in general shape, the diverticula here open mid-length on the duct and are similar to that of a paralectotype figured by Jamieson (1970: 141, fig. 10i).

Jamieson (1970), in his redescription of one of the paralectotypes, reported more extensive genital markings than Spencer, including inconspicuous anterior markings in 8–11 and postsetal markings in 17 (as in S1 and S2 here). He was unable to detect the anterior markings in 18 and 19 (as Spencer, 1900 and also as in present account).

The distinction of a sub-species, proposed by Jamieson (1974b) as "*Heteroporodrilus shephardi* (Spencer, 1900) *armatus*" for four or five specimens from south of Bordertown in S.A., is here questioned. Jamieson (1974b: 87) justified his sub-species on the grounds of its having detectable penial setae and slight differences in genital markings. Yet some ambiguity remains about penial setae in *H. shephardi*, since Jamieson (1970: 123) stated that "setae *a* visible immediately median" to the male porophores then asserted "Penial setae absent" from paralectotype NMV G1409. In his "descriptive notices", Spencer (1900) rarely recorded presence or absence of penial setae, and whether they actually occur in the lectotype NMV G34 is undetermined (a task beyond the scope of the present study). Moreover, new material here agreeing with Spencer's species do have penial setae, as well as variations in genital markings that encompass those of earlier descriptions of both "sub-species" (perhaps accounted for by artefacts of preservation, to observational conditions, or to ontological state of the specimens). Jamieson's sub-species is therefore synonymised with *H. shephardi*; a questionable difference remaining is the exact position of the diverticulum on the spermathecal duct (cf. Spencer, 1900: fig. 30 and Jamieson, 1970: 141, fig. 10[i] and Jamieson, 1974b: 107, fig. 10b).

When justifying his sub-species, Jamieson (1974b: 87) stated "The new material agrees with *H. shephardi* alone in the genus (*vide* Jamieson, 1970) in alternation of nephropores between *d* and mid *bc*, rather than the usual *d* to *c*" and went on to assert "it is unquestionably, from its morphology, more closely related to the latter than to any other taxon in *Heteroporodrilus*." However, this is not supported by the evidence on viewing Jamieson (1970: 122 and 117) where his redescription of the *H. shephardi* lectotype has nephropores in 5–9 in mid-*bc* or in *c* lines, and his redescription of *H. mediterreus* has nephropores "not determinable" in 7–9. Moreover, nephropores intermittently in this location have been noted for several other species newly described here.

Distribution and habitat. Specimen W1290 was from the Mallee district in Dimboola, Victoria (Jensz & Smith, 1969: 91). Dimboola, on the Wimmera River upstream from Horsham, is the type-locality of *Anisochaeta notabilis* and *Megascolides diaphanus* (Spencer, 1900 both). For the latter

species from West Dimboola, Spencer (1900) remarked that “The Flats [close to the River Wimmera] on which the worm was found are liable to be flooded at rainy seasons but are at other times perfectly dry”. Victor Harbour, near the mouth of the River Murray, is approximately 400 km west of the Horsham, Vic. type-locality. Jamieson’s specimens were collected from a region intermediate between Horsham and Victor Harbour, near the SA/Vic. border.

Heteropordrilus shephardi appears more closely related to several *Heteropordrilus* species known from floodplains of central NSW, especially *H. mediterraeus*, *H. namoi*, and *H. narrabri*. Such wide distribution of closely related forms is unusual for most native taxa, and can be attributed to fluvial transportation and migrations along connected waterways of the Murray-Darling (see Fig. 20 for present day river system).

Genus *Cryptodrilus* Fletcher

Cryptodrilus Fletcher, 1886: 570; Jamieson, 1972: 154–155, 1974a: 266; Blakemore, 1997a: 1687–1688.

Trinephrus Beddard, 1895: 483.

Diagnosis. Setae 8 per segment. Dorsal pores present or absent. Male pores from tubuloracemose or racemose prostates paired on 18. An oesophageal gizzard in 5. Nephridia vesiculate meroic, with multiple bladders in at least some segments of body. Spermathecae two (or three) pairs, with one or more clavate diverticula. Extramural calciferous glands and typhlosole absent or present; intestinal caeca absent. Penial setae present or absent.

Type species. *Cryptodrilus rusticus* Fletcher, 1886: 570–573 from Burrawang, NSW. (Syntypes, AM W1389).

Included species

Cryptodrilus dubius Spencer, 1892: 136–137, figs. 13–15, 67, from Victoria probably Croajingolong, East Gippsland. (Lectotype NMV G35).

Cryptodrilus fastigatus Fletcher, 1889, from Burrawang, Illawarra, Bega-Bombala, and Mt Kosciuszko, NSW. (Types AM W1308).

Cryptodrilus mediocris Fletcher, 1889: 1544–1546, from Newington, near Parramatta, NSW. (Syntypes AM W1313).

Cryptodrilus naroomai n.sp. from Narooma, NSW.

Cryptodrilus polynephricus Spencer, 1895: 35–36, figs. 4–6, from Mt. Wellington and Parattah, Tasmania. (Type material NMV G1436—not found, possibly on loan).

Cryptodrilus rusticus Spencer, 1892, from Victoria.

Five additional species from Tasmania are currently in the process of description (Blakemore, in prep.). The status of several taxa previously attributed to *Cryptodrilus* is uncertain as the presence or absence of nephridial bladders has not been satisfactorily determined.

Distribution. Southern New South Wales, Victoria, Tasmania.

Remarks. The most recent discussion of this genus is by Blakemore (1997a). The generic diagnosis is changed slightly to include species with extramural calciferous glands as are found in a taxon newly described below. Only the presence of nephridial bladders now distinguishes *Cryptodrilus* from *Notoscolex* (although the multiloculate spermathecal diverticula of the type species of the latter genus are possibly significant).

Cryptodrilus fastigatus Fletcher, 1889

Fig. 15

Cryptodrilus fastigatus Fletcher, 1889: 1541–1543; Jamieson, 1972: 161–166, figs. 5AB, 6AB, 7A; 1973: 229–233, fig. 3.

Trinephrus fastigatus.—Beddard, 1895: 483; Michaelsen, 1900: 185.

Notoscolex fastigatus.—Michaelsen, 1907: 162.

Material examined. Specimens: AM W24420 (S1), Fred Piper Lookout, Bega-Bombala region, NSW, c. 36°41'S 149°51'E, Ed Easton, 1.vi.1983, “Jar 75 Sp 41”, “Octochaetine sp., dark red”, (complete mature, figured and dissected); ANIC RB.98.2.12, (S2) same details, (mature specimen, posterior amputee, dissected and figured). Type material not re-examined here. AM W1308, labelled in Fletcher’s hand “*Cryptodrilus* Bg. and Illawarra”.

Fletcher based his description on “Five spirit specimens” from “Burrawang, and Illawarra, NSW”; six clitellate specimens were re-examined by Jamieson (1972): One was designated the lectotype; four others being designated paralectotypes (total 5?); though two of the type series (total 7?), supposedly from Burrawang, were not regarded as types by Jamieson (1972: 166) as details of their male fields differed slightly from that of the Illawarra specimen—see Remarks below.

External features (compared with type description). Body widest before clitellum, tapering steadily after clitellum. Lengths, mm: 85 (S1), 50+ (S2), 63–89 (Fletcher). Width: 2–3 mm. Segments: 158 (S1), c. 100–140 (Fletcher). Colour: “dark red” in life; anterior dorsum dark grey otherwise pale in alcohol; clitellum brick red, (“above reddish or purplish tinged with brown, or iridescent purplish, lighter below”—Fletcher). Prostomium: widely tanylobous; peristomium ventrally cleft. Clitellum: 14–17 with slight canal dorsally. Dorsal pores: from 4/5, larger from 5/6 (S2 and Fletcher, in S1 the dorsal pores commence from 6/7 but it is possible that there is some anterior anomaly as some setae and nephropores are missing from the first six segments). Setae: 8 per segment in regular series. Nephropores: conspicuous at anterior margin of segments in *a*, *c* and *d* lines in all segments except some around the male field (see Remarks below). Spermathecal pores: two pairs in 7/8/9 in *a* setal lines (just anterior to nephropores). Female pores: widely paired immediately anteromedian to *a* setae on 14. Male pores: paired at centres of low mounds approximately in *ab* lines on 18. Genital markings: only as indistinct tumid areas, differing variously between specimens, e.g., ill-defined ventral tumidity in 7–9 and 17–19, 20 in S1 and S2. (Paired or single midventral pore-like “markings” around the male field are just that, nephropores—see description of Nephridia, and Remarks below).

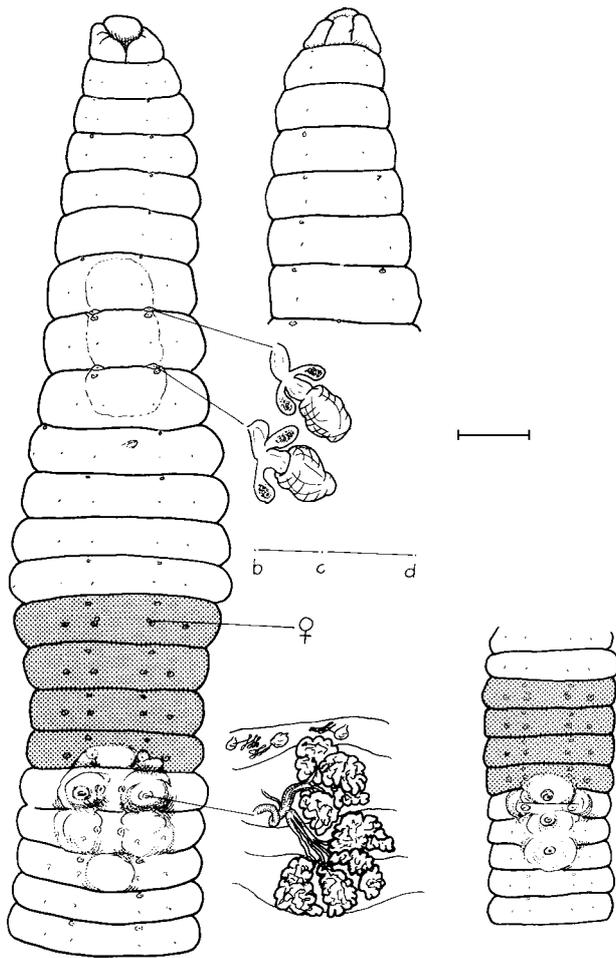


Figure 15. *Cryptodrilus fastigatus* Fletcher, 1889, ventral view of Bega specimen (S1) with dorsal view of prostomium; spermathecae; nephridial arrangement in 17 preceding the multilobed racemose rhs prostate in 18–20; also shown is male field of second specimen (S2) for comparison. Scale 1 mm.

Internal anatomy. Septa: none especially thickened except perhaps 11/12/13. Gizzard: muscular in 5, slight and barely wider than oesophagus. Oesophagus: dilated but thin walled in 12–13, then increasingly dilated and vascularized in 14–16 with internal lamellae possibly forming rudimentary annular calciferous glands; valvular in 17. Nephridia: vesiculate meroic with three sets of tubules per side, each with small spherical bladder in *a*, *c* and *d* lines; not tufted in anterior. (In S1 nephropores from setal *a* lines are displaced ventrally and posteriorly to occur median of setal *a* lines in 18 and 19; while in S2 they combine mid-ventrally as single pores in 18–20. As nephridial bladders are retained in setal *a* lines as usual in these segments, it is surmised that the ducts are extended and displaced after they enter the body wall). Vascularization: dorsal blood vessel single onto pharyngeal mass in 4–5; hearts increasingly large in 10–12 from weak supra-oesophageal vessel (Fletcher states last hearts “in 12 [in one specimen but in 13 in another].”). Spermathecae: two pairs in 8–9, pouch-like ampulla on thick duct with small pair of opposed club-shaped diverticula mid-

length. Male organs: holandric, iridescent testes and funnels in 10 and 11; seminal vesicles paired, racemose anteriorly in 11 and 12. Ovaries: large palmate with numerous oocytes in 13; small ovisacs in 14. Prostates: massive, three-dimensional highly racemose bodies with externally branching ducts in 18–20; penial setae absent. Intestine: origin in 18; typhlosole absent; gut contains organic material and gritty soil particles.

Remarks. The above specimens are darkly pigmented (as noted on Easton’s label), on this, and on all other points, they concur with each other and with Fletcher’s type description.

Jamieson (1972, 1973) went to some length describing and attempting to interpret the variations in the “genital markings” configuration around the male field in the type material, as well as in specimens from Mt Kosciuszko. Jamieson (1973: 230–233, 248) concluded that “The unparalleled diversity in the male genital field in *C. fastigatus* on Mt Kosciuszko, which exceeds variation known in any other oligochaetes, merits further investigation. Possibly polytypic variation between isolates segregated by ice flows from the former cap glacier has survived as intra-population polymorphism following introgression of the former isolates.”

However, the pore-like “genital markings” occurring variously around the male field and clitellum are here interpreted as irregularly displaced nephropores, that form tumescences for undetermined physiological reasons (such as the “nephridial packing problem” or physical dislocation due to the development of the prostate glands, oesophageal dilations and clitellum in these segments). The reasoning for this conclusion are:

- 1 Nephropores are not found in setal *a* lines in segments where these displaced pores occur (although internally the nephridial bladders retain their normal setal *a* line position and presumably these still function for excretion via pores).
- 2 Where the nephropores are in their usual position outside the male field, they sometimes develop paired or unilateral tumescences.
- 3 Although the body wall in the region of these pores is thickened, no corresponding glandular structures are found on the internal surfaces.
- 4 Actual pores associated with genital markings occur rarely in megascolecids.
- 5 Attribution of these pores to excretion, rather than to copulation, would account for their intraspecific variability and remove the need for complex explanations of compatibility. (Notwithstanding this interpretation of their nature as excretory, the secretion from these nephropores may yet have some secondary role in copulation).

In view of this conclusion, the slight differences in the “male genital fields” of the two Burrawang type specimens does not exclude them from this taxon and, as they formed part of the type description, they must be syntypes.

Spencer (1892: 137) considered his *Cryptodrilus dubius* from Victoria (probably from Croajingolong) to be closely

allied to *C. fastigatus*, except for its well developed calciferous glands in 15 and 16. Separate specific status of *Cryptodrilus dubius* is maintained on the basis of this character.

Distribution and habitat. The type-localities are Burrawang and the nearby Illawarra district of NSW; also found in the Bega-Bombala region and from Mt Kosciuszko.

Cryptodrilus naroomai n.sp.

Fig. 16

Material examined. HOLOTYPE: AM W24454 (H), Narooma/Bega Rd, NSW, c. 36°30'S 149°50'E, Ed Easton, 1.vi.1983, "Jar 74 Sp 36", "[illegible] km N of B", "Octochaetine [8 setae] colourless", (complete mature, figured and dissected). PARATYPES: all same details as (H), ANIC RB.98.2.18, (P1), (mature, dissected and figured); W24455, (P2), (clitellate mature, dissected); ANIC RB.98.2.19, (P3), (aclitellate mature, dissected); AM W24456 (P4–P17), sample in original jar (14 specimens, 9 aclitellate matures or subadults and 5 juveniles that superficially agree having various combinations of nephropore distributions around male fields).

External features. Body slender. Lengths, mm: 130 (H), 88 (P1), 70 (P2), 105 (P3). Width: c. 4 mm. Segments: 180 (H), 175 (P1). Colour: unpigmented; clitellum puce. Prostomium: widely tanylobous; peristomium ventrally cleft. Clitellum: 14–17. Dorsal pores: from 4/5 (H, P1), larger from 5/6 (P2, P3). Setae: 8 per segment in regular series. Nephropores: conspicuous at anterior margin of segments in *a*, *c* and *d* lines in all segments from 3 except some around the male field: in (H) they form tumescences in *a* lines on 16 lhs and 17 lhs and are (combined) mid-ventral on 18; in (P1) they are displaced to lateral of *b* lines at anterior of 18 within large pads. Spermathecal pores: two pairs in 7/8/9 in *a* setal lines (just anterior to nephropores). Female pores: widely paired immediately anteromedian to *a* setae on 14. Male pores: paired at centres of low mounds approximately in *a* lines on 18. Genital markings: only as indistinct tumid areas; in (H) 9 and 18 are tumid ventrally; (P1, P2, P3) have swelling around male pores.

Internal anatomy. Septa: 8/9–12/13 slightly thickened. Gizzard: large conical in 5, displaced to occupy segments 7–9. Oesophagus: with increasingly large paired lateral pouches in 14–16 (i.e., three pairs of extramural calciferous glands) supplied by capillary branches from dorsal vessel, with closely packed internal lamellae; narrows 17–½18. Nephridia: vesiculate meroic with three spherical bladder in *a*, *c* and *d* lines, some appear to have more than one set of tubules attaching to bladder; in (H) bladder in *a* line in 18 lhs goes to body wall; small tufts in 2–4. Vascularization: dorsal blood vessel single; hearts 10–12 from supra-oesophageal vessel in 10–14. Spermathecae: two pairs in 8–9, pouch-like ampulla on thick duct with small pair of opposed club-shaped diverticula mid-length. Male organs: holandric, iridescent testes and funnels in 10 and 11; seminal vesicles paired, racemose anteriorly in 11 and 12. Ovaries: large palmate with sheets of long egg-strings in 13; small

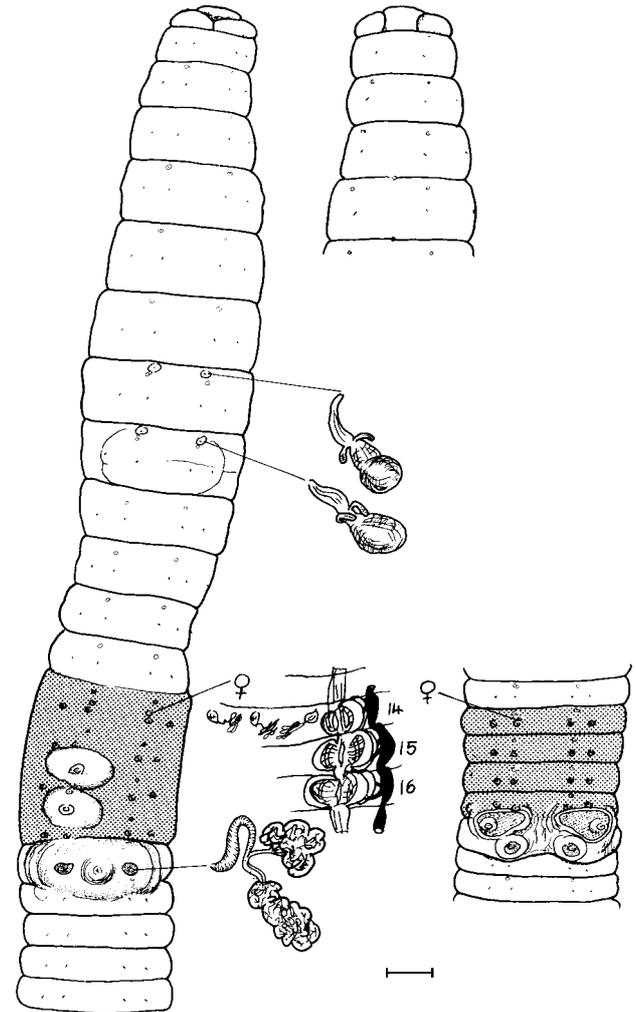


Figure 16. *Cryptodrilus naroomai* n.sp., ventral view of holotype with dorsal view of tanylobous prostomium; spermathecae; section through calciferous glands in 14–16, also showing nephridial arrangement in 14; and bilobed rhs prostate in 18–19; male field of specimen (P1) is shown for comparison. Scale 1 mm.

ovisacs in 14. Prostates: racemose, divided into two lobes with externally branching ducts in 18–19; penial setae absent. Intestine: origin ½18; typhlosome absent; spiralling gut contains loamy soil with charcoal and large sand grains.

Remarks. Morphological differences of *Cryptodrilus naroomai* from *C. fastigatus* are the larger somatic size, lack of pigmentation (see Easton's labels); a larger gizzard, and three pairs of extramural calciferous glands in 14–16. *Cryptodrilus naroomai* is also larger than *C. dubius* and has extramural calciferous glands in 14 in addition to 15 and 16. The lack of pigmentation and more developed digestive system (and the contents of the gut) suggest a different ecological strategy compared to the sympatric *C. fastigatus*. Determination of specific status depends on inferred behavioural differences conferring reproductive isolation and morphological variation.

The variations in positions of the nephropores around the male fields and their papillation on the clitella confirms the conclusions made for *C. fastigatus* above, that their primary function is excretory, rather than for mate recognition and copulation.

Etymology. Named after the type locality.

Distribution and habitat. Narooma is about 60 km north of Bega on coastal southern NSW and within the distributional range of *C. fastigatus*.

Genus *Notoscolex* Fletcher

Notoscolex Fletcher, 1886: 546; Michaelsen, 1900: 187; 1907: 160–162; Stephenson, 1930: 836; Lee, 1959: 317; Gates, 1959: 254; Jamieson, 1973: 235; Blakemore, 1997a: 1688–1689.

Tokea Benham, 1904: 240.

Pseudonotoscolex Jamieson, 1971: 496.

Oreoscolex Jamieson, 1973: 238; 1974a: 302; **new synonym.**

Diagnosis. Setae 8 per segment. Dorsal pores present or absent. Male pores from racemose or tubuloracemose prostates paired on 18. An oesophageal gizzard in 5 or 6. Nephridia meroic, at least in the fore-body, avesciculate, sometimes tufted. Spermathecae two or three pairs (or unpaired, typically with multiloculate sessile or one or more clavate diverticula. Typhlosole typically absent; extramural calciferous glands typically present; intestinal caeca absent. Penial setae typically present.

Type species. *Notoscolex camdenensis* Fletcher, 1886: 546–551, Pl. VII, figs. 1–5, from Burrawang, NSW. (Syntypes NMV G170).

Included species

About seventy species are placed in this genus, including several transferred from *Cryptodrilus*, *Oreoscolex* and *Pseudonotoscolex*. Many described *Notoscolex* species require confirmation of lack of nephridial bladders to qualify for inclusion, a task beyond the scope of the current study.

Distribution. New South Wales, Victoria, Tasmania, Western Australia, southern Queensland, New Zealand, (?South India, Sri Lanka). Gates (1972: 132) questions whether any Indian species actually belong in this genus.

Remarks. The most recent treatment of this genus is by Blakemore (1997a). As unpaired spermathecae are unlikely to be of more than specific value (see Gates, 1972: 132), *Oreoscolex* is synonymized in *Notoscolex*. Jamieson (1974: 266, 302) had expanded the definitions of *Cryptodrilus* and *Oreoscolex* so that they were not mutually exclusive and, moreover, subsumed the characters of the prior genera *Megascolides* and *Notoscolex*. The two new species added here do not require substantial change to the generic diagnosis, although it should perhaps be noted that one species has six pairs of extramural calciferous glands (in

segments 8–13), and has large tubuloracemose prostates, but lacks penial setae. The separation of *Cryptodrilus* from *Notoscolex* is thus reinforced on a single character state: vesiculate meroic in *Cryptodrilus* vs. avesciculate meroic in *Notoscolex*.

Notoscolex harenapascuus n.sp.

Fig. 17

Material examined. HOLOTYPE: AM W24423 (H), Muogamarra Nature Reserve, Berowa/Brooklyn Road, NSW, c. 33°38'S 151°12'E, Ed Easton, 6.vi.1983, "Jar 82 Sp 10", "Octochaetine colourless sp", (complete mature, figured and dissected). PARATYPES: all same details as (H), ANIC RB.98.2.13, (P1), (aclitellate mature, dissected); W24424, (P2), (aclitellate mature); ANIC RB.98.2.14, (P3), (aclitellate mature, posterior amputee); AM W24425 (P4), (subadult); AM W24426 (2 immatures that agree superficially plus a tail portion).

External features. Body circular in section. Lengths, mm: 95 (H), 100 (P1), 80–85 (P2, P4). Width: c. 5 mm. Segments: 183 (H), 199 (P1). Colour: beige in alcohol; clitellum orange. Prostomium: short closed epilobous. Clitellum: ½13–17. Dorsal pores: from 9/10. Setae: 8 per segment *ab* deleted on 18, *d* lines sinuous in posterior. Nephropores: not found. Spermathecal pores: two pairs in 7/8/9 just lateral of setal *a* lines. Female pores: widely paired on 14. Male pores: paired on summits of large mounds in *b* on 18. Genital markings: large mid-ventral pads in *aa* lines in 13/14/15/16 (H) or 13/14–16/17 (P1–P3) and 21/22 (H) or 22/23 (P1), with pore-like dimples that are variously single, paired, triad or tetrad; ventral aspect of 18 occupied by waisted pad between male porophores that also has tetrad dimples (H-P4).

Internal anatomy. Septa: 5/6 thin to base of gizzard, 6/7–10/11 increasingly thick. Gizzard: large thick walled and muscular in 5. Oesophagus: large laterally paired reniform calciferous glands in 8–13 (i.e., six pairs), attach to gut by short ducts, with numerous internal lamellae and white granules, well supplied by blood vessels; narrowing in 14–15. Nephridia: avesciculate meroic with several tubules (c. 8 per side) equatorial but attaching to anterior septa; tufted in (4)–5. Vascularization: dorsal blood vessel single; hearts 10–13; weak supra-oesophageal vessel present supplying calciferous glands. Spermathecae: two pairs in 8–9, flattened saccular ampulla on tapering duct with curt or sessile, multiloculate diverticulum towards junction. Male organs: holandric, iridescent testes and funnels in 10 and 11; seminal vesicles paired, racemose anteriorly in 11 and 12. Ovaries: (not located); small ovisacs in 14. Prostates: large deeply-lobulated tubuloracemose glands in 18–27 on short coiling ducts; penial setae not found. Intestine: origin in 16; typhlosole absent; gizzard and intestine full of quartz grits and grey colloidal soil.

Remarks. The intersegmental genital markings and male field are distinctive in *Notoscolex harenapascuus*. Multiloculate, sessile diverticula on the spermathecae, and

Notoscolex meekae n.sp.

Fig. 18

Material examined. HOLOTYPE: ANIC RB.98.6.1 (H), Big Jack Mountain Rd., Rocky Hall, Wyndham, southeastern NSW, 36°52'30"S 149°30'E, Heather Meek, 5.i.1998, (complete mature, figured and dissected). PARATYPES: none.

External features. Body stout. Length, mm: 360 (extends up to 500 mm in life). Width: c. 5 mm. Segments: 225. Colour: in life pale olive; in alcohol uniform grey with darker mid-dorsal line and clitellum. Prostomium: short proepilobous. Clitellum: 14-½19 (14-17 ventrally). Dorsal pores: from 3/4, occluded on clitellum. Setae: 8 per segment, *ab* absent from 18, *d* lines slightly sinuous in posterior. Nephropores: not found. Spermathecal pores: four pairs at posterior border of segments 5-8 (i.e., almost in 5/6-8/9) just lateral of setal *a* lines. Female pores: widely paired on 14. Male pores: superficial in *ab* lines at lateral points of diamond-shaped pad within paired parentheses occupying

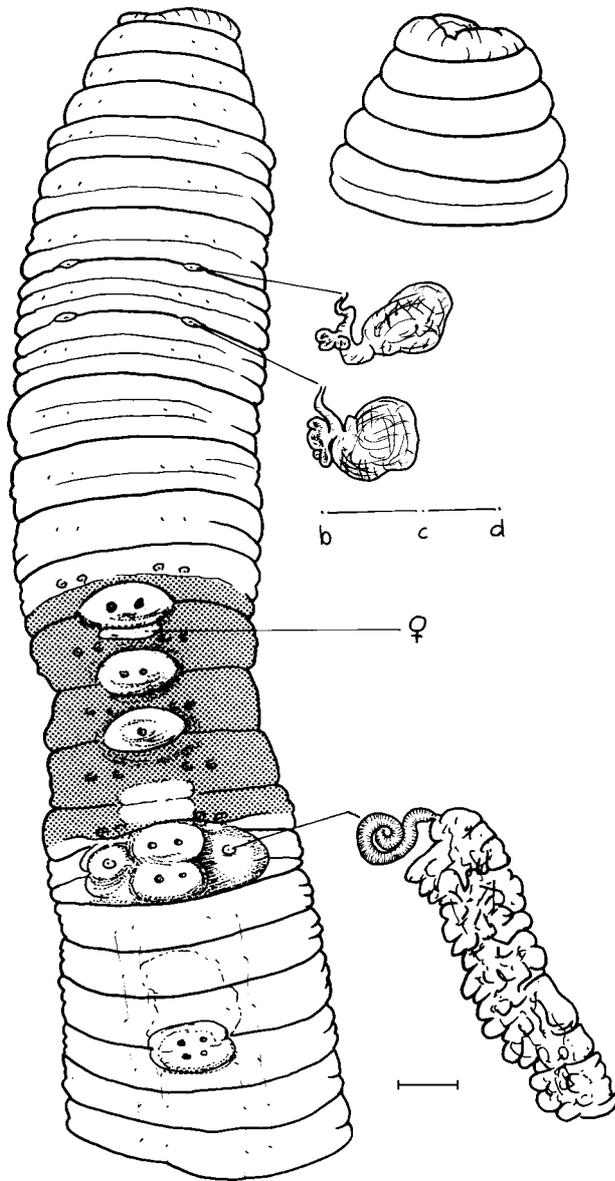


Figure 17. *Notoscolex harenapascuus* n.sp., ventral view of holotype with dorsal view of prostomium; spermathecae; and rhs tubuloracemose prostate in 18-27. Scale 1 mm.

well developed, extramural calciferous glands are additional features that are shared with the type species, *N. camdenensis* which, however, has only three pairs of these glands in 14-16 (rather than six pairs in 8-13) and prostates that are racemose (rather than elongate tubuloracemose as here). Other characteristics of *N. harenapascuus* are seminal vesicles in 11 and 12, and the last hearts in 13.

Etymology. The word combination *harena-pascuus* (Latin) means grit-grazing and refers to the gut contents.

Distribution and habitat. Berowa north of Sydney, NSW.

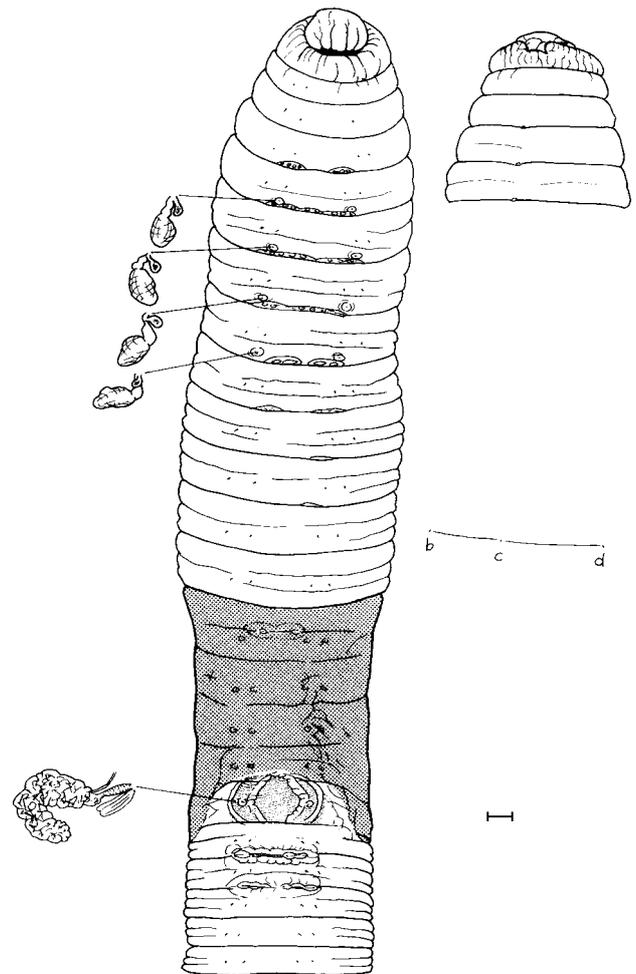


Figure 18. *Notoscolex meekae* n.sp., ventral view of holotype with dorsal view of epilobous prostomium; spermathecae; and lhs prostate with vasa deferentia and penial setae in 18. Scale 1 mm.

whole ventral aspect of 18 as wide as *b* lines. Genital markings: barely perceptible paired elongate markings seen ventrally in intersegments 4/5–9/10/11/12; more defined elongate tumid pads in *bb* in 19/20 and 20/21.

Internal anatomy. Septa: 7/8–12/13 increasingly thick. Gizzard: muscular barrel in 5. Oesophagus: not especially dilated; valval in 16. Nephridia: avesculate meroic, large forests of tubules in 3–4, smaller in 5 from whence they spread equatorially in wide band with c. 50 tubules per side; no preseptal funnels found. Vascularization: dorsal blood vessel segmentally doubled (recombining at septa) from 5; hearts 10–13 from supra-oesophageal vessel in 9–13, 14. Spermathecae: four pairs in 6–9, saccular ampulla on shorter duct with small clavate diverticulum ectally. Male organs: metandric, iridescent testes and funnels in 11 only; seminal vesicles paired, racemose anteriorly in 12 only. Ovaries: compact egg-strings in 13; small ovisacs in 14. Prostates: tubuloracemose glands in 18 on short ducts; penial setae as long as duct. Intestine: origin in 17; typhlosole absent; gut contains fine organic soil.

Remarks. Distinctive features of *Notoscolex meekae* are its large size, the four pairs of spermathecal pores at the posterior borders of segments 5–8, the doubled dorsal blood vessel, metandric male organs, and the distribution of the genital markings.

Etymology. Named after the collector.

Distribution and habitat. Rocky Hall is situated amidst the NSW Southeast State Forests. This specimens was collected from bushland next to a garden in lyre bird disturbed litter under *Eucalyptus maidenii* and *E. globoidea* plus remnant rainforest and ferns beside creek. The soil is fine loam over clay on granite (Heather Meek, pers. comm., 22.vi.1999).

Genus *Digaster* Perrier

Digaster Perrier, 1872: 94–96; Beddard, 1895: 484; Michaelsen, 1900: 196, 1907: 162; Stephenson, 1930: 839; Jamieson, 1975: 267–269, Blakemore, 1997b: 1815–1816.

Diagnosis. Setae lumbricine. Male pores and pores of racemose prostates combined on 18 (or its homeotic equivalent). Penial setae absent or present. Two gizzards (sometimes three) in some (or all) of 5–7; extramural calciferous glands absent; typhlosole absent or present. Spermathecae two pairs with one or more discrete or sessile diverticula. Meronephric, avesculate.

Some species have suppression of the first segment (*D. anomala* Jamieson, 1970, *D. lumbricoides* and the newly described *D. eastoni*) thus reducing these segmental counts by one.

Type species. *Digaster lumbricoides* Perrier, 1872, from Port Macquarie, NSW. (Types in the Muséum national d'Histoire naturelle, Paris).

Included species. Approximately 23 species are presently known as are variously listed in the references given in the generic synonymies above.

Distribution. Central coastal NSW to southeastern Qld.

Remarks. The most recent treatments of this genus are by Blakemore, (1994a, 1997b).

Digaster eastoni n.sp.

Fig. 19

Material examined. HOLOTYPE: AM W24503 (H), Mt Warning, northeastern NSW, c. 28°23'S 153°17'E, Ed Easton, 21.iii.1983, "Jar 31 Sp 21", (mature, posterior amputee, figured and dissected). PARATYPES: all same details as H, ANIC RB.98.2.46, (P1), (aclitellate juvenile, dissected); AM W24504, (P2–P4), (three specimens, one juvenile, and two immatures that agree superficially, plus three tail fragments).

External features (note: anterior segment suppressed, so all counts in following description should be increased by one to give normal segmentation). Body stout, first segment suppressed (but setae retained in P1). Lengths, mm: 70+ (H), 70–75 (P1–P2). Width: c. 3.5 mm. Segments: 280 (P1). Colour: unpigmented in alcohol; clitellum brick red. Prostomium: short pro-epilobous. Clitellum: ½12–½18. Dorsal pores: open from 4/5 (minute in 3/4 in P1), occluded on clitellum. Setae: 8 per segment, in regular series. Nephropores: small pores seen only on clitellum at anterior of segments equatorially. Spermathecal pores: two pairs in 6/7/8 in setal *a* lines. Female pore: single mid-ventral on 13. Male pores: on small mounds in *ab* lines on 17 conjoined within tumid pad that extends beyond *b* lines and encompassed marking in 16/17. Genital markings: large flat pad in position of 16/17 but distending and obscuring this furrow ventrally (H, P1, P2).

Internal anatomy. Septa: 6/7–10/11 increasingly thick. Gizzards: muscular in 5 and 6. Oesophagus: not especially dilated but thick walled with internal rugae in ½12–½17. Nephridia: avesculate meroic, scattered tubules on body wall, reducing in number after clitellum to give about 10 per side; not tufted in anterior. Vascularization: dorsal blood vessel single; hearts 9–11 from weak supra-oesophageal vessel. Spermathecae: two pairs in 6 and 7, spherical ampulla on short duct with medium-sized clavate diverticulum ectally. Male organs: holandric, iridescent testes and funnels in 9 and 10; seminal vesicles paired, racemose flat posteriorly in 8 and elongate anteriorly in 11. Ovaries: extensive egg-strings and oviducts in 12; no ovisacs found in 13. Prostates: bi-lobed racemose glands in 17; penial setae absent but many tendons surround duct. Intestine: origin in ½17; typhlosole absent; contains grey soil with quartz and obsidian grits.

Remarks. *Digaster eastoni*, like *Digaster lumbricoides*, has suppression of the anterior segment; however, in *D. lumbricoides* the prostates are not bilobed and the seminal vesicles are in 10 and 11, rather than 8 and 11 as here. Other distinctive features of *Digaster eastoni* are the single female pore on 13, the large genital pad in 16/17, and the bilobed prostates.

Etymology. Named after the collector.

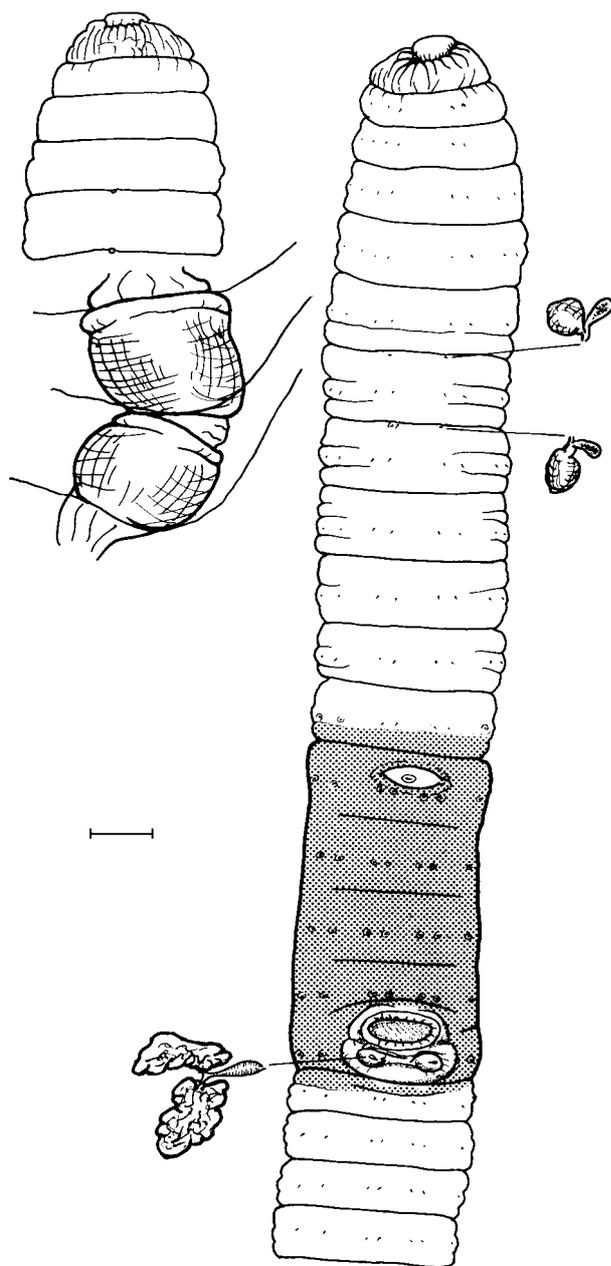


Figure 19. *Digaster eastoni* n.sp., ventral view of holotype with dorsal view of prostomium (first segment suppressed); gizzards in segments 5 and 6; spermathecae; and bilobed lhs prostate in 17. Scale 1 mm.

Distribution and habitat. In addition to *Digaster eastoni*, species from Mt Warning identified during the current study include *Heteroporodrilus editus*; *Fletcherodrilus fasciatus* (Fletcher, 1890) (specimen AM W24494 ex “Jar 31, Sp 22 Ed Easton 21 March 1983”); *Digaster lamingtonensis* Michaelsen, 1916 (specimens AM W24496 ex “Jar 31, Sp 19 1100 ft 21 March 1983” and AM W24463 “Jar 33 sp 5 Ed Easton 26 March 1983”); *Anisochaeta monsmontionis* (Blakemore, 2000) and various other undescribed *Anisochaeta* spp. (AM W21717 ex “Jar 31 Sp 31”; W24501 and W24502 ex “Jar 30, Sp 31 21 March 1983, Lyrebird Lookout”).

Discussion

The number of new species described in this paper, and the continuing need to resolve ambiguities for several known species, are indicative of the current state of knowledge of the fauna, supporting the conclusion by Abbott (1994: 117) that “Australia’s indigenous species of earthworms are poorly known”. Reasons for this deficit are not immediately obvious as earthworms are:

- 1 ubiquitous in soils capable of supporting plants;
- 2 they are vitally important, both ecologically and economically, for their role in recycling organic matter and in maintaining fertile soils;
- 3 native species are perfectly adapted to Australian soils and climates,
- 4 their process of identification is less complicated than for some other soil invertebrates (e.g., microscopic nematodes, collembolans or mites);
- 5 they have popular appeal; and,
- 6 from as early as 1861 they were initially subject to enthusiastic study.

Perhaps one reason that sustained research is frustrated, again taken from Abbott (1984), is due to “uncertainties about synonymy and higher level taxonomy, particularly at the generic level”. Several conflicting taxonomic schemes are currently in use and confusion will persist unless these are resolved. Until such a time, perhaps the most pragmatic and convenient solution is to revert to the systems devised by Michaelsen (1900, 1907), which, despite some detraction, are for the most part still phylogenetically valid and form the basis of most subsequent schemes (Lee, 1994).

Few natives have been studied in any detail, the only notable exception being *Megascolides australis*, the Gippsland Giant Earthworm (Spencer, 1888; Smith & Peterson, 1982; VanPraagh, 1995). Our knowledge of the distribution, diversity and biology of native earthworms in general is severely limited, and ecological studies are especially scarce (cf. Wood, 1974; Abbott *et al.*, 1985). It is hoped that the formal description of species as here will facilitate and encourage the overdue ecological study of native species in both natural and managed environments.

Species of *Heteroporodrilus* appear especially promising candidates for agro-ecological study (see Blakemore, 1994b; 1997c; Friend & Chan, 1995) as they are widely dispersed on the eastern seaboard and in fertile clay soil floodplains and catchments of the Murray-Darling basin through to the mallee region of Victoria and South Australia. For *Heteroporodrilus mediterreus*, Fletcher (1887b: 602) remarked that “No species has hitherto been recorded from so far inland as this; and its occurrence is of interest as showing that the dry interior, at any rate in proximity to rivers, is not destitute of earthworms, though remote from them, as far as I can learn at present, worms seem to be very scarce or are entirely wanting”. Abbott (1994) plotted the known distributions of native species, supporting Fletcher’s observation, but stressed the importance of moisture retaining refugia for harbouring earthworms. Knowledge of the distribution of *Heteroporodrilus* in the southeastern states has now been extended, the genus has



Figure 20. Known distribution of *Heteroporodrilus* and *Plutellus* species in relation to the Murray-Darling Basin. (Background map courtesy of the Murray-Darling Basin Commission). Abbreviations: H.bi—*Heteroporodrilus bitenax*; H.bo—*H. bongeen*; H.ca—*H. canaliculatus*; H.di—*H. dioecius*; H.do—*H. doubei* (note: *H. clarkei* and *H. minyoni* occur nearby); H.ed—*H. editus*; H.hi—*H. hirthi*; H.ka—*H. kaputar*; H.me—*H. mediterreus*; H.nam—*H. namoi*; H.nar—*H. narrabri*; H.ox—*H. oxleyensis*; H.sh—*H. shephardi*; H.sl—*H. sloanei*; P.bar—*Plutellus barringtoni*; H.tr—*H. tryoni*; P.buc—*Plutellus buckerfieldi*; P.het—*P. heteroporos*; P.man—*P. manifestus*. (Details of distribution of Queensland species are given in Blakemore, 1994b).

previously been found to be particularly diverse in southern Queensland where three or four species can often be obtained in the same sample from certain sites (Blakemore, 1994b).

Considering biodiversity “hotspots”, the current study appears to show that the Mt Warning locality, with more than six natives, has most variety. However, meaningful conclusions on regional biodiversity remain elusive given the present patchiness of survey—perceived diversity still

relates largely to collection effort (which has tended to centre around populous areas), and to taxonomic treatment rather than to the actual situation. This deficit is graphically illustrated in the huge unsampled voids that isolate the known distribution points of *Heteroporodrilus* in the massive Murray-Darling basin (Fig. 20). For this reason the keys to species given above can only be considered provisional: numerous additional species undoubtedly await

discovery and description. A remedy to this would require more strategic survey from unrepresented regions and habitats at those times when earthworms are most active, as indeed had been assiduously undertaken by Ed Easton in 1983. The delay in formal description of this collection exemplifies the need for concurrent taxonomic work.

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	page		page
<i>bagomaraglensis</i> n.sp., <i>Megascolides</i>	198	<i>kaputar</i> n.sp., <i>Heteroporodrilus</i>	206
<i>barringtoni</i> n.sp., <i>Plutellus</i>	190	<i>mediterraeus</i> , <i>Heteroporodrilus</i>	207
<i>bitenax</i> n.sp., <i>Heteroporodrilus</i>	202	<i>meekae</i> n.sp., <i>Notoscolex</i>	217
<i>buckerfieldi</i> n.sp., <i>Plutellus</i>	192	<i>Megascolides</i> , Genus	197
<i>canaliculatus</i> , <i>Heteroporodrilus</i>	203	<i>namoi</i> n.sp., <i>Heteroporodrilus</i>	208
<i>Cryptodrilus</i> , Genus	213	<i>naroomai</i> n.sp., <i>Cryptodrilus</i>	215
<i>Digaster</i> , Genus	218	<i>narrabri</i> n.sp., <i>Heteroporodrilus</i>	210
<i>eastoni</i> n.sp., <i>Digaster</i>	218	<i>nivalis</i> n.sp., <i>Vesiculodrilus</i>	195
<i>editus</i> n.sp., <i>Heteroporodrilus</i>	204	<i>Notoscolex</i> , Genus	216
<i>fastigatus</i> , <i>Cryptodrilus</i>	213	<i>Plutellus</i> , Genus	190
<i>frenchi</i> , <i>Vesiculodrilus</i>	193	<i>Plutellus</i> , key to known spp	190
<i>harenapascuus</i> n.sp., <i>Notoscolex</i>	216	<i>shephardi</i> , <i>Heteroporodrilus</i>	211
<i>Heteroporodrilus</i> , Genus	199	<i>vallis</i> n.sp., <i>Vesiculodrilus</i>	196
<i>Heteroporodrilus</i> , key to known spp	200	<i>Vesiculodrilus</i> , Genus	193
<i>hirthi</i> n.sp., <i>Heteroporodrilus</i>	205		