Fig. 10.76. \textit{Diporochaeta (Vesiculodrilus) evansi}. Right spermatheca of IX. Holotype TM K382. After Jamieson (1974a).
oesophagus internally rugose in VI-XV, especially so in XIV and XV in which it is conspicuously dilated, but lacking specialized internal lamellae. Intestinal origin XVI; typhlosole absent. Nephridia simple stomate vesiculate exonephric holonephridia; first seen in III but pores apparently commencing anteriorly in II; funnels present at least as far forward as VII; the bladders at first pyriform but by IX becoming distinctly bilobed, the ectal nephridial duct joining the median lobe. Holandric; seminal funnels in X and XI; seminal vesicles racemose, in IX and XII. Penial setae needle like, not filiform; tip smooth and rounded; ornamentation absent, length = 0.71 mm. Metagynous; ovisacs very large, multiloculate, in XIV. Prostates appearing racemose, in XVII-XX, XXI but resolvable into a compressed and minutely lobulated tubular form. Spermathecae 2 pairs; diverticulum (inseminated) single, clavate, uniloculate.

REMARKS
Vesiculodrilus evansi was considered (Jamieson, 1974a) to be closest morphologically to D. lacustris. However, substantial differences from the latter were noted: the lumbricin setae, the two pairs of spermathecal pores, the presetal rather than postsetal location of the anterior genital markings and the configuration of those of the male genital field. It does not appear to placeable in the V. frenchi-group and is here tentatively placed in a separate V. evansi-group.
Diporochaeta (Vesiculodrilus) frenchi (Spencer, 1892a)
(Fig. 10.77-10.80)

*Cryptodrilus frenchi* Spencer, 1892a: 135-136, Pl.14, fig.10-12, Pl.19, fig.66.
*Megascolides frenchi*; Beddard, 1895: 493.
*Platellus frenchii*; Michaelsen, 1900: 175; Sweet, 1900: 116; Jamieson, 1971c: 87.
*Vesiculodrilus frenchi*; Jamieson, 1973: 225-227, Fig.2A.
*Perionychella (Vesiculodrilus) frenchi*; Jamieson, 1974a: 222.
*Diporochaeta frenchi*; Jamieson, 1976b: 4

**TYPE LOCALITY:** 37°25'S.149°40'E., Croajingolong (East Gippsland; coordinates as C. National Park) - Vic.

**SYNTYPES:** AM W1289 (Re-examined; also 3 slides, labelled *Plutellus frenchii*, not seen).

**OTHER RECORDS:** (Jamieson, 1973) 36°27'S.148°16'E. Mt. Kosciusko AMW 4691-4693 - NSW.

Length 75-122 mm. Width 3-6 mm. Segments 112. Form circular in cross section throughout, moderately stout; segments after the first 2 or 3 biannulate; a faint dorsal canalicula present in the forebody. Peristomium bifid ventrally. Pigmentless buff in alcohol. Prostomium epilobous 1/2 or 3/4 (Spencer) or tanylobous, dorsal tongue narrow and parallel-sided and canaliculate. First dorsal pore 3/4 (imperforate); 4/5 perforate. Setae in 8 longitudinal rows, commencing on II; all rows irregular at the caudal extremity; setae *a* and *b* replaced by penial setae in XVIII. Nephropores in *c* lines, commencing on III (Spencer) or not externally visible. Clitellum annular, XIV-XVI; intersegmental furrows and setae retained; dorsal pores absent. Male pores
Fig. 10.77. *Diporochaeta (Vesiculodrilus) frenchi*. Genital field. Syntype 1 AM W1289. (Jamieson, 2000).

Scale still to get!
equatorial in \textit{ab} of XVIII, on fairly small but strongly protuberant papillae; a penial seta projecting from each pore. Two or three pairs of oval-oblong genital markings present, a pair in each of segments IX, X-XI, presetally in \textit{ab}; each marking with narrow raised margins; these markings present only in X and XI in specimens 2 and 3 and unilateral only, on the right, in 3. Five pairs of intersegmental genital markings present: in \textit{b} lines in 16/17 and 17/18 and in \textit{a} lines in 18/19, 19/20 and 20/21. Female pores, on slight swellings, shortly anteromedian of setae \textit{a} of XIV. Spermathecal pores minute, inconspicuous, 5 pairs in 4/5-8/9, at the anterior margins of their segments in \textit{a} or \textit{ab}.

Septa 4/5 thin; 5/6 slightly thickened; 6/7 moderately; 7/8-13/14 strongly thickened; 14/15 and 15/16 slightly thickened; the remainder thin. Last septal (pharyngeal) glands in IV. Dorsal blood vessel single, continuous onto the pharynx. Dorsoventral commissural vessels in V-XII; those in V-IX slender and dorsoventral only, each giving a lateral branch to the parietes before joining the ventral vessel; sufficiently enlarged in IX to be termed hearts; those in X-XII forming 3 pairs of large latero-oesophageal hearts, each arising from the dorsal vessel and receiving a connective from the supra-oesophageal vessel but not branched ventrally. Supra-oesophageal vessel in IX-XIII; very thin in XIII but elsewhere almost as wide as the dorsal vessel; distinct from the oesophagus. Latero-oesophageal vessel on each side of the gut observable in IV to IX, becoming sub-oesophageal in IX. Subneural vessel absent. Oesophagus thin-walled and moderately wide in IV; gizzard large and strongly muscular though easily compressible, in V (VI, Spencer), widening to a rim-like anterior expansion. Oesophagus slender and intersegmentally slightly constricted in VI-VIII; wider and evidently vascularized in IX-XV; much elongated and sinuous.
Fig. 10.78. *Diporochaeta (Vesiculodrilus) frenchi.* A: Right prostate. B: Right spermatheca of IX. C: Penial seta. Syntype 1 AM W1289. (Jamieson, 2000).
Fig. 10.79. *Diporochaeta (Vesiculodrilus) frenchi*. Genital field. Mt. Kosciusko specimen 1 (17/2). After Jamieson (1973).
Fig. 10.80. *Diporochaeta (Vesiculodrilus) frenchi*. A: Right prostate. B: Right spermatheca of V. Mt. Kosciusko specimen 140/2/T36. (Jamieson, 2000).

Scale still to get!
Not yet 100% identified???
in XIV and XV; narrow, long and non-vascular in XVI; intestine commencing and about twice as wide as oesophagus in XVII; typhlosole absent. Nephridia stomate, vesiculate holonephridia throughout, postseptal bodies commencing in II; bladder, elongate-ovoid narrowing ectally to a slender stalk (terminal duct) which enters the parietes presetally in c lines; the bladder receiving the slender nephridial tubule slightly subterminally. Nephridia of II and III appearing more coiled than elsewhere but not tufted and not notably enlarged. Testes, iridescent sperm funnels and sperm masses free in X and XI; seminal vesicles 2 pairs, in IX and XII (Spencer) or 3 pairs, on the posterior walls of IX and X and the anterior wall of XII, decreasing in size posteriorly; slightly lobulated; those in IX elongated dorsoventrally but sessile on the septum throughout their lengths. Prostates one pair, tubular, compact and much wound, occupying XVII, XVIII-XIX, XXI; the slender convoluted muscular duct restricted to XVIII. Penial setae slightly bowed, tapering to a fine point, the ectal region of the shaft bearing a few anteriorly directed inconspicuous spines produced by notching of the margins, widely spaced lengthwise and not forming circlets; length 1.6 mm, maximum width (near base) 15 µm. Ovaries consisting of a few chains of small oocytes in XIII; oviducal funnels not visible; ovisacs absent. Spermathecae 5 pairs, basically elongate ovoid with short, poorly demarcated duct which is joined entally by a small shortly clavate iridescent diverticulum; occasionally aberrant, with several small supernumerary pouches which are not iridescent and are apparently ampullary.
REMARKS

_Vesiculodrilus frenchi_ is here placed, because of date priority, at the head of a substantial group of species with paired intersegmental genital markings in the vicinity of the male pores. This field type resembles that in the _bakeri_-group in _Diporochaeta_ (see generic remarks for the latter genus).

Agreement of Mt. Kosciusko material with the type material is close. Differences in Spencer's (1892a) description from the Mt Kosciusko specimens are: the epilobous prostomium; spermathecal pores apparently in _ab_; restriction of anterior genital markings to X and XI; location of the posterior markings of XVIII in _ab_ and extension of markings to 21/22 (though ending in 20/21 in a re-examined syntype), and restriction of seminal vesicles to IX and XII.

_Diporochaeta (Vesiculodrilus) gippslandica_ (Spencer, 1892a)
(Fig. 10.81,10.82)

_Cryptodrilus gippslandicus_ Spencer, 1892a: 132-133, Pl.14, fig.1-3, Pl.19, fig.63; Jensz and Smith, 1969: 87.
_Megascolides gippslandicus_; Beddard, 1895: 492.
_Platellus gippslandicus_; Michaelsen, 1900: 176-177.
_Woodwardia gippslandica_; Michaelsen, 1907b: 162; Buchanan, 1909: 61-63, Pl.14, Fig.1A, Pl.17, Fig.20; Bage, 1910: 233-234, Pl.46, figs 16, 17.
_Perionychella (Vesiculodrilus) gippslandica_; Jamieson, 1974a: 222.
Diporochaeta (Vesiculodrilus) gippslandica.
Genital field. Lectotype NMV F4057. (Jamieson, 2000).

**TYPE LOCALITY:** 37°25'S, 149°40' E., Croajingolong (coordinates as National Park) - Vic.

**LECTOTYPE:** NMV F4057 (Re-examined)

**PARALECTOTYPES:** NMV F401405 (see Jamieson, 1970a).

**OTHER RECORDS:** AM W1286, Victoria, J.J. Fletcher collection, 11 1924, Identified by Spencer.

Length 92-125 mm. Width 7.2-ca 10 mm. Segments 113. Prostomium tanylobous with deep dorsal groove; peristomium ribbed. First dorsal pore 3/4 or 4/5. Setae eight per segment; in couples anteriorly; all rows irregular posteriorly; in segment XII, \( ab: bc: cd: dd = 2.0: 1.0: 2.3: 2.2: 5.5; dd: u = 0.3 \) (lectotype). Nephropores in \( c \) lines, commencing anteriorly in III. Clitellum annular, posterior XIII-anterior XVII. Male pores on papillae on XVIII in \( ab \), 3.3 mm, 0.15 body circumference, apart. Genital markings a pair of eye-like markings at each of the 6 intersegments 16/17-21/22; all shortly median of \( a \) lines excepting those of 17/18 which are lateral of \( b \) lines and therefore lateral of the male pores (lectotype); only those at 17/18, in this lateral position, illustrated by Spencer (1892a). Female pores anteromedian to setae \( a \) of XIV. Spermathecal pores 5 pairs, in \( a \) lines; the first in 4/5, 3.4 mm, 0.15 body circumference apart.

Dorsal blood vessel double intrasegmentally, uniting at each septum but single in front of VI and at the tail end. Dorsoventral commissural vessels beginning in VI; a pair of vessels from the dorsal vessel in IV running posteriorly as far as IX as a pair of lateral vessels which in X-XII receive segmental branches from the alimentary plexus and form, on each side, a suboesophageal vessel. Dorsoventral commissurals of VI-IX
Fig. 10.82. *Diporochaeta (Vesiculodrilus) gippslandica*. A: Left prostate. B: Right spermatheca of VIII. C: Right nephridial bladder of XVI. Lectotype NMV F4057. (Jamieson, 2000).
giving vessels to the body wall ventrally before joining the ventral vessel. Supra-oesophageal vessel from anterior VIII to posterior XII where it joins the dorsal vessel. Hearts three pairs, in X-XII, arising only (?) from the supra-oesophageal vessel; the latter vessel receiving circumoesophageal vessels from the suboesophageals. Gizzard large, in V; vascular swellings of the oesophagus in VIII-XIII. Calciferous glands in XIV and XV (scarcely extramural). Intestine commencing in XVII. Nephridia stomate, vesiculate holonephridia each with an extremely small preseptal funnel; bladders strongly diverticulate in the intestinal region but not anteriorly. Testes and iridescent funnels in X and XI. Seminal vesicles two pairs, on the posterior walls of IX and X. Prostates coiled, tubular, when well developed extending through XVIII and XIX. Ovaries in XIII. Spermathecae in V-IX, each consisting of a long ampulla with a single lateral diverticulum about a fourth as long as the ampulla.

REMARKS

*Diporochaeta (Vesiculodrilus) gippslandica* is a characteristic member of the *frenchi*-group, closely allied to the nominate species.

**Diporochaeta (Vesiculodrilus) (?) glandifera** Jamieson, 1974a
(Fig. 10.83-10.85)

*Perionychella (Vesiculodrilus) glandifera* Jamieson, 1974a: 237-238, Fig.1, 10A, B, 15D, 16L, M, Table 2.

TYPE LOCALITY: 41°20'S.148°15'E., St. Helens. 41°20'S.147°55'E., St. Columba.
Falls - Tas.
HOLOTYPE: TM K283.

Length 73-75 mm. Width 6.5-7.5 mm. Segments 98. Prostomium canaliculate, broadly tanylobous. Body rectangular in cross section. First dorsal pore 3/4 (imperforate?), 4/5 perforate. Setae 8 per segment in regular longitudinal rows throughout; in XII, $aa: ab: bc: cd: dd = 1.9: 1.0: 3.4: 2.4: 4.0; dd: u = 0.21$. Nephropores in $c$ lines. Clitellum annular XIII-1/4XVIII. Male pores equatorial in $a$ lines of XVIII on weakly developed papillae on the setal ridge; 2 pairs of eye-like, or at full development large sucker-like genital markings with pore-like centres in intersegments 17/18 and 18/19, the centres lateral to $b$ lines, each marking spanning the distance between the setal arcs of adjacent segments; a transverse glandular depression linking each marking with that of the other side. Female pores shortly anterior to the setal arc of XIV at 1/3 $aa$. Spermathecal pores minute, 5 pairs in 4/5-8/9 in $a$ lines.

Dorsal vessel segmentally bifid in VIII, or IX, -XVIII; last hearts in XII (latero-oesophageal). Supra-oesophageal weakly developed. Gizzard large, in V but extending well posteriorly. Oesophagus in XV expanded to form a subspherical unpaired calciferous gland with many closely packed internal radial laminae which fill the oesophageal lumen but do not unite centrally. Intestinal origin 1/2XVII or posterior XVII; typhlosole absent. Nephridia vesiculate, exonephric holonephridia
Fig. 10.83. *Diporochaeta (Vesiculodrilus) glandifera*. Genital field. Holotype TM K283. After Jamieson (1974a).

*Diporochaeta glandifera* = *Perionychella (V.) glandifera*

Diporochaeta glandifera =Perionychella (=V.) glandifera
Spermatheca (A & B)
A- Left, seg. IX
B- Right, seg. IX
C- Nephridial bladder, Right

*Diporochaeta glandifera* = *Perionychella glandifera*
discharging by large bladders throughout, commencing (always?) in II; those in II forming small tufts and lacking detectable funnels; the remaining nephridia simple and each with a preseptal funnel; bladders in the anterior segments very long, wide tortuous tubes; in VI or somewhat more posteriorly the bladder is bent near its ectal end and the bend is drawn out slightly as a diverticulum; succeeding bladders are increasingly diverticulate; full development of the diverticulum as a long lateral digitiform process is attained by segment XIX and is maintained to the caudal extremity although caudal nephridia are smaller than those in the anterior region. Holandric (funnels iridescent); cleistorchous, pericardiac testis-sacs formed by longitudinal fusion of septa 9/10, 10/11 and 11/12; seminal vesicles racemose in XI (in the testis-sac) and XII (free). Prostates depressed tubular, compactly coiled, in XVIII-XX; vas deferens joining ectal end of gland; penial setae absent. Metagynous. Ovisacs sometimes visible in XIV. Spermathecae 5 pairs; diverticulum (inseminated) single, clavate, uniloculate.

REMARKS
_Vesiculodrilus glandifera_ is unique among the known Tasmanian species of the genus in the bifid dorsal vessel (also seen in the Victorian _Diporochaeta (V.) gippslandica_ and in _Diporochaeta willsiensis_), the extramural oesophageal gland in XV, in possessing testis-sacs and in location of the seminal vesicles in XI and XII. It is a very distinct species worthy of its own species-group and is a strong candidate for separation as a distinct genus. It is here placed in a monotypic _V. glandifera_-group.
Diporochaeta (Vesiculodrilus) hellyeri Jamieson, 1974a
(Fig. 10.86, 10.87)

Perionychella (Vesiculodrilus) hellyeri Jamieson, 1974a: 238-241, Fig.1, 9B, 16N, O, Table 2.


Type Locality: 41°20'S.145°35'E., Hellyer Gorge - Tas.
HoloType: TM K284.
Other Records: (Jamieson, 1974a) 41°15'S.147°20'E., Mt. Arthur, TM K285-286.

Length 54-62 mm. Width 2.6, 3.0 mm. Segments 97-104. Prostomium indistinctly epilobous 1/2, open. First dorsal pore 4/5. Setae 8 per segment, the rows becoming irregular in the posterior 12 or so segments in which there are 20-24 setae per segment. Nephropores in c lines. Clitellum annular, 1/2XIII-XVI. Male pores on prominent rounded papillae, equatorial in XVIII, in b; the papillae transversely conjoined by a midventral boss which bears presetally two widely conjoined pore-like markings, a similar boss present with conjoined presetal markings on XVII; a pair of eye-like genital markings present in 17/18 in b lines; or presetal markings absent from XVII and the median boss in XVIII replaced with 2 small circular markings in aa joined to the male papillae by slight ridges; eye-like markings present in 17/18. Two pairs of eye-like markings presetally in b, present or absent on IX and X. Female pores paired, on XIV, anteromedian of a. Spermathecal pores 3 pairs, in 6/7-8/9, in b, on small papillae each of which is preceded by a lip-like prominence.
Fig. 10.86. *Diporochaeta (Vesiculodrilus) hellyeri.* Genital field. Holotype TM K284. After Jamieson (1974a).
Fig. 10.87. Diporochaeta (Vesiculodrilus) hellyeri. A: Right spermatheca of VIII. Holotype TM K284. B: Right spermatheca of IX. Paratype 2 BMNH 1972.8.10. After Jamieson (1974a).
Last hearts in XII (latero-oesophageal). Supra-oesophageal in VIII-XIII, well developed. Gizzard vestigial (questionably present), in V. Extramural calciferous glands absent but oesophagus enlarged and vascularized with lamellar internal rugae in XIV and XV. Intestinal origin XVII; typhlosole absent. Nephridia simple, vesiculate exonephric holonephridia; preseptal funnel demonstrated in those of III; possibly rudimentary nephridia in II; bladder large, subspherical to transversely elliptical, the lateral extremity protuberant and almost forming a diverticulum. Holandric (gymnorchous) or probably incipiently metandric; only posterior funnels iridescent and seminal vesicles large in XII but vestigial in IX; male organs of IX and X completely absent in some individuals (metandric). Metagnous; ovisacs in XIV. Prostates flattened tubular, with lobulated, compacted coils in XVIII-XX, XXI. Penial setae moderately stout, not filiform, but ectal region sigmoid; tip simple; ectally weakly ornamented with anteriorly directed \^shaped scales flush with the surface and commonly in triads; the tip of a reserve seta has a delicate, hooked extremity; length of a well-developed seta = 1.00-1.18 mm. Spermathecae 3 pairs; diverticulum (inseminated) single, clavate, uniloculate.

REMARKS
The affinities of *Vesiculodrilus hellyeri* are uncertain. It is here tentatively placed in its own, monotypic species-group.
**Diporochaeta (Vesiculodrilus) hobartensis** (Spencer, 1895)
(Fig. 0.22(97-98), 10.88-10.90)

*Cryptodrilus hobartensis* Spencer, 1895: 37-38, Pl.1, fig.10-12.
*Cryptodrilus insularis* Spencer, 1895: 41-42, Pl.2, fig.19-21.
*Perionychella (Vesiculodrilus) hobartensis*; Jamieson, 1974a: 241-245, Fig.1, 11A-F, 15A, B, 16P-R, Pl.97, 98, Table 2.

**TYPE LOCALITY:** 42°21'S.147°25'E., Parattah. 42°54'S.147°14'E., Mt. Wellington - Tas.
**LECTOTYPE:** NMV F4050.
**PARALECTOTYPES:** NMV F4049.
Fig. 10.88. *Diporochaeta (Vesiculodrilus) hobartensis*. Genital field. Lectotype NMV F4050. After Jamieson (1974a).
Length 75 mm. Width 2.7-3.0 mm. Segments 91+. Form moderately stout; approximately circular in cross section but flattened between adjacent setae. Prostomium epilobous 2/3, open but apparently with a transverse groove at about half peristomium; a middorsal groove commencing on the prostomium and continuous throughout the body. First dorsal pore 4/5. Setae readily visible, in 8 regular longitudinal rows throughout, commencing on II; ab absent, cd present, on XVIII; aa: ab: bc: cd: dd: dc: cb: ba = 1.62: 1.00: 1.85: 1.82: 3.07: 1.8: 1.84: 0.97. Nephropores in c lines at the anterior borders of their segments (clitellum and posteriorly). Clitellum annular, strongly protuberant on XIV-XVI but XVII with clitellar modification, especially dorsally over the anterior third; dorsal pores present but imperforate; setae and intersegmental furrows retained but less distinct; nephropores visible. Small indistinct (imperforate) male porophores in ab nearer b, of XVIII; paired eye-like accessory genital markings in a lines in 16/17 (almost constant), 17/18, 18/19, 19/20 and (exceptionally) 20/21, the anterior pair large and more conspicuous than the second pair, the posterior pair rudimentary. Female pores minute, shortly anteromedian of a in XIV, each with a distinctly visible white 'halo'. Spermathecal pores not always externally visible, usually 5 pairs, sometimes 4 pairs (Jamieson, 1974a); in a lines (Spencer, 1895).

Last hearts in XII (latero-oesophageal). Supra-oesophageal well developed in VIII-XII, and with a slender posterior continuation into XIII and apparently intramurally to 1/2XV. Gizzard in V, small to vestigial, sometimes very large; easily compressible; preceded in IV by a less muscular proventriculus of the same width, from which it is not separated by any appreciable constriction. Oesophagus narrow (though not much narrower than the gizzard) and not evidently vascularized in VI and VII; still narrow
but with intramural circumferential vascular striae, which form the supra-oesophageal vessel in VIII-XI; forming a segmental unpaired annular dilatation in each of segments XII, XIII and XIV, the dilatations increasing in size posteriad; the oesophagus also widened, but less so, to 1/2XV but narrow and chloragogenous looking in the posterior half of this segment; the internal walls of the dilatations with rounded longitudinal ridges too low to be considered lamellae. Intestinal origin XVII; less commonly XVI, 1/2XVI, 1/2XVII; typhlosole absent. Nephridia simple vesiculate holonephridia throughout; the first discharging at intersegment 2/3, each with a wide elongate bladder bent into a U or J shape, all bladders discharging in front of setae c; 'necks' to septa seen but no funnels demonstrated with certainty. Holandric (funnels iridescent in X and XI); seminal vesicles in IX and XII; in putatively parthenogenetic forms not recognizable and prostates represented only by thick muscular ducts each with the form of a short, straight, entally narrowing cone. Prostates long, widely tubular and tortuous, extending into XXIV (Spencer). Penial setae filiform and sinuous, tip frequently worn or damaged but when intact widely bifid, or simple and hooked; ornamentation a few faint longitudinal ridges or groups of several scarcely protuberant, approximately palmately arranged, apically directed teeth at intervals near the tip or a few very faint triangular marks and longitudinal ridges; length = 0.97-1.71 mm. A specimen lacking penial setae lacks seminal vesicles, has prostate ducts but no glands and has abnormal spermathecae; this suggests occurrence of parthenogenetic, uniparental morphs and that absence of penial setae, in a species normally possessing these, is further evidence of parthenogenesis. Ovaries (laminate with several strings of large oocytes) and stout funnels in XIII; ovisacs usually demonstrable. Spermathecae 5 pairs, the last in IX;
with ovoid ampulla sessile on the body wall and a lateral clavate diverticulum as long as or longer than the ampulla; occasionally the diverticulum very short and a further diverticulum on the median aspect of the spermatheca further entally. Length of the right spermatheca of IX = 0.75 mm; ratio total length: length diverticulum = 0.8.

REMARKS
The genital markings at 17/18 in *V. hobartensis* are median to the male pores whereas those in *mortoni* extend laterally of the pores and differ in typically being connected by a median oval papilla.

Spencer (1895), who had the advantage of seeing this species alive, states that it is almost identical with *V. mortoni* but that the two are distinct in external appearance, *hobartensis* being a whitish stout form (although the dorsal surface is also described as purple), whereas *mortoni* is darkly coloured, with conspicuous setae, and is long and narrow.

**Diporochaeta (Vesiculodrilus) mortoni** (Spencer, 1895)
(Fig. 0.37A-C, 0.22(99-102), 10.91)

_Cryptodrilus mortoni_ Spencer, 1895: 36-37, Pl.1, fig.7-9.
_Platellus mortoni_; Michaelsen, 1900: 176.
_Perionychella (Vesiculodrilus) mortoni_; Jamieson, 1974a: 247-250; Fig. 1, 12B, 15E-G, 16T; Plates 99-102. Table 2.
Type Locality: 42°17’S.146°37’E., Dee Bridge. 42°54’S.147°14’E., Mt. Wellington - Tas.
Syntype: NMV F4083.
Other Records: (Jamieson, 1974a) 41°05’S.145°55’E., Fern Glade, Emu River, Burnie. 41°15’S.147°20’E., Mt. Arthur (east), wet sclerophyll forest. 41°20’S.147°55’E., St. Columba Falls. 42°50’S.147°10’E., Collinsvale. 42°55’S.147°15’E., Mt. Wellington. 42°50’S.147°20’E., Hobart. 42°50’S.147°20’E., East Risdon, Risdon. 43°00’S.147°55’E., Eagle Hawk Neck (TM K. AM W5199-5201. BMNH 1972.8.18-30. BJ) - Tas.

Length 56-212 mm. Width 3.5-6.5 mm. Segments 113-274. Prostomium epilobous 1/2-2/3, epitanylobous or tanylobous; often canaliculate. First dorsal pore usually in 4/5, rarely in 3/4 or 5/6. Body strongly canaliculate to not canaliculate. Setae in 8 regular longitudinal rows throughout. Nephropores conspicuous, commencing anteriorly in II in c lines but shortly below c lines behind the midclitellum. Clitellum annular, XIII-XVII, strongly developed and pigmented in XIV-XVII, unpigmented and weakly developed in XIII; possibly some slight clitellar modification in XVIII. Male pores on small papillae in ab of XVIII. Genital markings: paired elliptical pads with depressed centres in ab in 17/18, 19/20, 20/21 and 21/22, those in 17/18 with centres slightly lateral of those of the other markings and truly intersegmental; the markings in 19/20-20/21, 21/22, though intersegmental actually postsetal in XIX-XXI, respectively; a median elliptical pad present in 17/18 bridging the paired markings of the intersegment (absent from most East Risdon specimens). Median markings each with the form of a depressed transverse intersegmental band with
Fig. 10.91. Diporochaeta (Vesiculodrilus) mortoni.
anterior rim in \textit{aa} in 5/6-8/9; sometimes (Fern Glade specimens) paired. Female pores anteromedian of setae a of XIV, midway between the setal arc and anterior border of the segment in a common oval field. Spermathecal pores 5 pairs on minute circular papillae immediately in front of intersegmental furrows 4/5-8/9, in \textit{a} lines.

Last hearts in XII (latero-oesophageal). Supra-oesophageal well developed, in VIII-1/2XIII. Gizzard very large and firm, in V but projecting posteriorly to the level of XI. Calciiferous glands absent. Oesophagus strongly vascularized and increasingly dilated in XIII-XVI with well-developed internal vascular rugae, especially in XV and XVI. Intestinal origin XVIII, less commonly XVII; typhlosole absent or a low dorsal ridge present. Nephridia stomate, vesiculate exonephric holonephridia commencing in II (diverticula absent from St. Columbia Falls specimens); tortuously coiled but simple, none tufted; bladders at first elongate, wide tubes, each of slightly irregular diameter; by XII bent midway at a right angle; thereafter with a lateral diverticulum extending from the bend, the portion ectal to the diverticulum being eliminated after a few segments. Holandric (funnels iridescent in X and XI); gymnorchous; seminal vesicles racemose in IX and XII. Prostates much coiled depressed tubes, in XVIII-XXI; vas deferens joining the duct shortly ectal of the gland. Penial setae short and moderately stout, the tip irregular, widened, roughly spatulate and bent a little or through a right angle, this apical modification visible under the light microscope; shaft ornamented ectally with a few groups of anteriorly directed scarcely protuberant teeth regularly spaced along it; the surface of the seta undercut beneath them; length 0.5 mm. Metagynous; ovisacs present. Spermathecae 5 pairs; diverticulum (inseminated) single, clavate, uniloculate.
REMARKS

*Vesiculodrilus mortoni* and *V. hobartensis* are the most widespread and commonly found megascolecid earthworms in Tasmania and are morphologically close. A notable difference is location of the paired genital markings at the posterior borders of their segments in *V. mortoni* whereas in *V. hobartensis* they are anterior, in both taxa appearing virtually intersegmental. The validity of separating the two taxa is questionable.

**Diporochaeta (Vesiculodrilus) purpurea** Jamieson, 1973
(Fig. 10.92, 10.93)

*Vesiculodrilus purpureus* Jamieson, 1973: 227-229, Fig. 2B, 6D, 7C, H.
*Perionychella (Vesiculodrilus) purpureus;* Jamieson, 1974a: 222.

**TYPE LOCALITY:** 36°27'S.148°16'E., Mt. Kosciusko - Vic.
**HOLOTYPE:** AM W4695.
**PARATYPES:** BJ. CSIRO.

Fig. 10.92. *Diporochaeta (Vesiculodrilus) purpurea*. Genital field. Holotype AM W4695. After Jamieson (1973).

*Diporochaeta purpureus* = *Vesiculodrilus purpureus*
throughout; \(a\) and \(b\) absent in XVIII; in XII, \(aa: ab: bc: cd: dd = 1.7: 1.0: 2.0: 1.8: 4.9; dd: u = 0.3\). Nephropores minute, faintly visible anteriorly in their segment in \(c\) lines, commencing on II. Clitellum annular, XIV-XVI, strongly tumid, intersegmental furrows fainter than elsewhere, dorsal pores suppressed at 14/15 and 15/16, setae clearly visible; faint glandularity of the posterior two thirds of XIII may be clitellar modification. A pair of combined male and prostatic pores equatorial in XVIII on low papillae which fill \(ab\) and the length of the segment. Paired eye-like accessory genital markings in 16/17 in \(ab\) nearer \(a\), 17/18 in mid \(ab\), 18/19 slightly median to \(a\) and in 19/20 further medianly, the two markings in each furrow medianly contiguous, and those in 19/20 broadly united. Additional markings may consist of midventral, postsetal elliptical protuberances with depressed centres one in each of segments VII-XI. Female pores minute, anteromedian of setae \(a\) of XIV. Spermathecal pores 5 pairs of minute depressions in 4/5-8/9, in \(a\) lines.

Septa 12/13 the strongest. Last septal glands in IV (?) but enveloping the gizzard in V. Dorsal blood vessel single, traced to the brain. Dorsoventral commissural vessels in VI-XII; those in VI-IX slender and dorsoventrual only; those in X-XII forming 3 pairs of large latero-oesophageal hearts, each receiving a connective from an indistinct supra-oesophageal vessel and from the dorsal vessel. Supra-oesophageal vessel indistinct, only distinguishable from the oesophageal vascularization in X-XII. Gizzard in V though displacing septa to approximately 1/2 VIII, strongly muscular but slender and easily compressible. Oesophagus in VI-VIII moniliform, thin-walled and not evidently vascularized; in IX-XV more swollen, moniliform and with conspicuous circumferential vascular striae; slender and appearing non-vascularized in XVI. Intestine beginning abruptly, with well developed oesophageal valve, in
Fig. 10.93. Diporochaeta (Vesiculodrilus) purpurea. A: Prostate. B: Right spermatheca of VIII. C: Nephridial bladder of XIV. Holotype AM W4695. After Jamieson (1973).
XVIII; typhlosole and muscular thickening absent. Nephridia stomate vesiculate exonephric holonephridia throughout (the single, preseptal funnels of the nephridia of III posteriorly recognizable in the segment anterior to the nephridial body; nephridia of II each with a neck to the anterior incomplete septum and funnel presumably present though not demonstrated). Anterior bladders elongate-ovoid, becoming progressively more elongate and once bent, the bend sometimes projecting medianly but no true diverticulum present; slender ectal duct of nephridium joining the apex of the bladder or very slightly subapical; bladders again shorter (elongate-ovoid) in caudal segments; tufted nephridia absent. Testes, sperm masses and very large iridescent funnels free in X and XI; seminal vesicles in IX and XII, those in IX ovoid and undivided; those in XII elongate and transversely incised. Prostates thickly tubular, winding posteriorly from XVIII to XXII; each with a long sinuous muscular duct; vas deferens joining the gland well ental of the duct. Penial setae present; very slender, almost straight, drawn out to a delicate point, ornamented ectally with three widely spaced sets of two or three coarse spines; length 1.44 mm, greatest width (near base) 10 µm. Ovaries, large, tongue-like with many large oocytes, and funnels in XIII; ovisacs absent. Spermathecae 5 pairs, discharging anteriorly in their segments, each with a slender, clavate ampulla, a shorter duct and a bulbous narrow-stalked inseminated diverticulum joining the ental of the duct; size uniform, length of the right spermatheca of VIII = 2.2 mm; ratio of total length: length duct = 4.2; ratio of total length: length diverticulum = 3.2.
REMARKS
In having midventral, unpaired accessory genital markings in anterior segments, this species resembles *V. victoriae* (Spencer, 1892), from which, however, it differs in the postsetal location of the markings and in the form of the penial setae (strongly hooked in a paralectotype of *victoriae*, Nat. Mus. Vict. G. 1410). It also closely resembles *Diporochaeta (V.) frenchi*, described above, but differs from that species in the unpaired condition of the anterior accessory genital markings and their postsetal location. With the doubtful exception of *dd*, setal ratios in samples of *D. (V.) frenchi* and *D. (V.) purpurea* from Mt Kosciusko do not appear to differ significantly but the small number of specimens precluded rigorous demonstration of this (Jamieson, 1973). *D. (V.) purpurea* is unquestionably a member of the *V. frenchi* species-group.

**Diporochaeta (Vesiculodrilus) tanjilensis** (Spencer, 1892a)
(Fig. 0.37I, 10.94-10.96)

*Cryptodrilus tanjilensis* Spencer, 1892a: 134-135, Figs. 7, 8, 9, 65; Jensz and Smith, 1969: 91.
*Megascolides tanjilensis*; Beddard, 1895: 177.
*Perionychella (Vesiculodrilus) tanjilensis*; Jamieson, 1974a: 222.

**TYPE LOCALITY:** Tanjil Track, near source of Yarra River (ca. 37°44'S. 145°44'E.?).
**LECTOTYPE** NMV F4054 (Re-examined).

B.G.M. Jamieson 11/10/00
**Paralectotypes:** NMV F4055 (Re-examined).


Length 112-138 mm. Width 1.2-1.3 mm. Segments 133. Tanylobous, with a dorsal longitudinal groove continuous along the body. Ventrally, a median groove only at the very posterior end. First dorsal pore 3/4? Setae 8 per segment, in regular longitudinal rows; in XII, \(aa:\ ab: bc: cd: dd = 1.5: 1.0: 1.88: 1.31: 4.38\); \(dd = 0.31\) \(\mu\).; setae \(a\) absent in XVIII. Nephropores presetal in \(c\) lines. Clitellum strongly developed, annular, posterior XIII, XIV-XVI, anterior XVII. Male pores on papillae on XVIII, in \(ab\). Genital markings in \(a\) lines in 17/18 and 19/20 (lapse for 18/19 shown in Fig. 7, Spencer); in the paralectotype: a pair of elliptical presetal compact protuberances in \(ab\), usually nearer \(a\), in each of segments VIII-XII, and a pair of intersegmental ellipses in each of 17/18 and 19/20, lateral of \(b\) lines. Female pores on XIV anteromedian of setae \(a\). Spermathecal 5 pairs of minute pores, in 4/5-8/9 in \(a\) lines.

Septa 12/13 and 13/14 very strongly thickened. Gizzard in V (or VI?). Vascular swellings on the oesophagus in VII, IX-XV, XVI; large in XV. No true calciferous glands. Intestine commencing in XVII (Raff, 1910) (or XVIII?). Single dorsal vessel. Hearts in VII-XII. Supra-oesophageal vessel in segments containing the hearts and extending back into XIII. Nephridia in II-V tufted, decreasing posteriorly but all nephridia with a single bladder which is larger in and before the clitellum than in the segments posterior to this. Testes and sperm filled funnels in X and XI; saccular
Fig. 10.94. *Diporochaeta (Vesiculodrilus) tanjilensis*. Genital field. Paralectotype NMV F4055.
Fig. 10.95. *Diporochaeta (Vesiculodrilus) tanjilensis.* Spermatheca. Paralectotype NMV F4055.

**Diporochaeta tanjilensis**

= Cryptodrilus tanjilensis
10x25, M7
Paralectotype G55
A - Spermatheca
B - Nephridial bladders, Right

Scale still to get!
Fig. 10.96. *Diporochaeta (Vesiculodrilus) tanjilensis*. Penial setae. Paralectotype NMV F4055.
seminal vesicles in XII. Prostates, coiled, tubular, in XVIII; in the paralectotype extending far laterally, appearing almost racemose but made up of tightly adpressed coils; duct long and muscular, coiled, widening ectally but not bursate. Penial setae present (not reported by Spencer); tip bifid but the two rami joined by a web; a few small teeth on the distal eighth. Ovaries, flattened, palmate, and funnels in XIII; ovisacs absent. Spermathecae 5 pairs, in V-IX; each a long ampulla, with a simple diverticulum, about one-quarter the length of the ampulla or, in paralectotype, the right anterior spermatheca with 1 bifid and 2 separate diverticula; the left anterior with 1 bifid and 1 simple diverticulum; the other spermathecae with a single diverticulum though this sometimes bears a sessile knob of approximately equal size.

REMARKS

*V. tanjilensis* is unequivocally a member of the *frenchi*-group.

In addition to the lapse of 17/18 and 19/20 for 17/18 and 18/19, Spencer (19892a) appears in error in illustrating the markings at 18/19 as median to those of 17/18. In the lectotype both pairs are approximately in line longitudinally and are well lateral of the male pores.

**Diporochaeta (Vesiculodrilus) tunnackensis** Jamieson, 1974a
(Fig. 10.97-10.99)

*Perionychella (Vesiculodrilus) tunnackensis* Jamieson, 1974a: 253, Fig.1, 14A, B, 16X, Table 2.

**Type locality:** 42°25'S.147°30'E., Tunnack - Tas.

**Holotype:** TM K312.

**Paratypes:** BMNH 1972.8.32.

Length 33-35 mm. Width 1.3-1.4 mm. Segments 81-82. Prostomium faintly canaliculate, epilobous 1/2. First dorsal pore 4/5. Setae 8 per segment in regular longitudinal rows throughout. Nephropores in c. Clitellum annular, XIII-XVI. Male pores in ab on small papillae on XVIII, the two papillae joined by a low median ridge, intersegmental ridges at 17/18 and 18/19 flank the male papillae and correspond in extent to the ridge between the papillae. Paired eye-like transversely conjoined genital markings in ab at 19/20 or this and 20/21; paired post-setal eye-like markings occur with centres in a in VII, VIII and IX. Female pores a pair anteromedian of a on XIV. Spermathecal pores 3 pairs in a at 6/7, 7/8 and 8/9.

Last hearts in XII (latero-oesophageal). Supra-oesophageal not distinguishable from the well-developed oesophageal plexus. Gizzard in V, moderate to small, muscular but easily compressible. Calciferous glands absent. Oesophagus with circumferential vascular striae in (VII ?), VIII-XV; in X-XV with at first few and small, posteriorly increasingly numerous and larger longitudinal rugae which in XIV and XV approach the appearance of laminae. Intestinal origin XVII; typhlosole absent. Nephridia simple stomate, vesiculate holonephridia, commencing in II (funnels traced at least from IV); bladders subspherical, tapering to the pore; large in all but a few anteriormost segments. Holandric (funnels iridescent in X and XI)
Fig. 10.97. *Diporochaeta (Vesiculodrilus) tunnackensis*. Anterior genital field. Holotype TM K312. After Jamieson (1974a).

=Perionychella tunnackensis
Anterior

*Diporochaeta tunnackensis*
Fig. 10.98. *Diporochaeta (Vesiculodrilus) tunnackensis*. Posterior genital field. Holotype TM K312. After Jamieson (1974a).
Fig. 10.99. *Diporochaeta (Vesiculodrilus) tunnackensis*. Right spermatheca of IX. Holotype TM K312. After Jamieson (1974a).
gymnorchous; seminal vesicles racemose in IX (?) and XII. Penial setae filiform; tip pointed and slightly upturned; no ornamentation; length = 0.76 mm. Metagnymous; ovisacs large, in XIV. Prostates depressed tubular with incised adpressed coils, in XVIII-XX; vas deferens joining the gland shortly ental to the muscular duct. Spermathecae 3 pairs, decreasing in size anteriorly; diverticulum (uninseminated) single, clavate uniloculate.

REMARKS
Vesiculodrilus tunnackensis shares with the poorly known V. ellisii, lumbricin setae, the presence of three pairs of spermathecal pores, and anterior genital markings. The location of the anterior and posterior genital markings differs, however, and tunnackensis differs further in lacking calciferous glands.

The appearance of the genital markings around the male pores and of the two pairs of eye-like markings in 19/20 and 20/21 differs considerably from the typical V. frenchi configuration and placement in the frenchi-group is tentative.

Diporochaeta (Vesiculodrilus) uncinatus (Stephenson, 1933)
(Fig. 10.100)

Plutellus uncinatus Stephenson, 1933: 907-910, Fig.6-8; Jamieson, 1971c: 88.
Perionychella (Vesiculodrilus) uncinatus; Jamieson, 1974a: 222.

TYPE LOCALITY: 37°50'S.146°17'E., Mt. Baw Baw - Vic.
TYPES: Not traceable.

Length 125-135 mm. Width in front of the clitellum (the anterior end rather bulbous) 11 mm., behind the clitellum maximum 10 mm. Segments (longer worm) 136. Colour light brownish-grey, no difference between dorsal and ventral surfaces; the clitellum purple. Prostomium tanylobous, the tongue as broad as the projecting lobe; a narrow median furrow along the whole length of the prostomium, and backwards as far as the clitellum, or indistinctly still further. First dorsal pore (4/5?), 5/6. Setae 8 per segment, widely paired; in the midbody \( ab = 2/3aa \) or slightly more, and usually \( \approx 1/2bc \) and \( \approx 2/3 cd \), while the interval between \( d \) and the mid-dorsal line = nearly 2\text{cd}. Towards the hinder end bc is rather smaller, about equal to aa. Behind the clitellum, in the male genital region and a little behind it, ab is somewhat contracted and \( = 1/2aa = 1/3bc \), while cd = half the distance from \( d \) to the middorsal line. In front of the clitellum \( ab = 1/2aa \) or rather more, \( \approx 2/5bc \), cd being about equal to aa, and to 3/5 of the interval between \( d \) and the middorsal line. Thus \( d \) is much above the lateral line throughout. Nephropores in setal lines \( c \); no alternation. Clitellum annular, XIV-XV, purple in colour; the intersegmental furrows and dorsal pores visible, and with indications of nephropores and setae. Male pores, on XVIII (a short segment), on small papillae between a and b, nearer a. Female pores are situated on XIV anteromedian to setae \( a \). Spermathecal pores not recognizable externally; from internal dissection 5 pairs, in 4/5-8/9 in \( a \) lines.

Septa 11/12 - 13/14 are very strongly thickened. A membrane passing back from septum 9/10 to join 10/11, and enclosing only the alimentary canal and dorsal vessel. Last hearts in XII. Gizzard, in V, large, firm, and barrel-shaped, with the anterior end
Fig. 10.100. *Diporochaeta (Vesiculodrilus) uncinatus*. A: Prostate. B: Spermatheca. C and D: Penial setae. After Stephenson (1933).
broader than the posterior; no calciferous glands. Intestine beginning in XVIII. Holonephric; bladders opening to exterior in c lines, extending upwards on the body-wall as far as setae d, and behind the region of the prostates extend downwards also for an equal distance; but in XIV and more anterior segments the dorsal extension is absent, and the terminal portion of the reservoir is very thick and muscular. Testes and funnels free in segments X and XI. Seminal vesicles in IX and XII, lobulated. Prostates tubular, but each forming a compact mass; length equal to about 4 segments; duct narrow but gradually widening ectally, with muscular sheen, and, though short, twisted and looped; one loop directed inwards, another outwards. Penial setae 1.84 mm. long (measured across the bend), 14 µm in diameter at the middle of the shaft, 9 µm near the tip, 17 µm near the base; the shaft slightly bowed, the tip hooked and cut off rather squarely at the end; a number of fine spines or pointed scales, closely adpressed to the shaft, and irregularly arranged, on the terminal 0.25 mm. One of three mounted setae with a short, sharply pointed process on the inner side of the curve of the hook, close to the tip. Spermathecae 5 pairs, each with a rounded subspherical ampulla, with a short duct, not marked off from the sac; diverticulum pear-shaped, with a length nearly equal to half that of the main pouch, and joining the duct close to its entry into the body-wall.

REMARKS
Stephenson observed that *Plutellus uncinatus* was morphologically close to *Perichaeta tanjilensis* (here synonymized in *Diporochaeta yarraensis*), also from Victoria. It is distinguished, *inter alia*, by the absence of copulatory papillae, by possessing two pairs of seminal vesicles, and by the lobulation of the latter. A further
important difference, requiring confirmation, is the constant number of 8 setae per segment. It is no longer distinguished by the possession of penial setae as these have now been observed in *yarraensis*. It is questionable that the absence of genital markings represents the mature condition. In the absence of known genital markings, placement is difficult but as a lumbricin species nevertheless allied to the perichaetin *yarraensis* of the *D. bakeri*-group it would be referable to the *V. frenchi*-group. It further indicates the artificiality of separating *Vesiculodrilus* from *Diporochaeta* on the grounds of setal numbers but retention in *Vesiculodrilus* is justified until such time as the relationship of the New Zealand type-species of *Diporochaeta* to Australian species is investigated in molecular procedures.

**Diporochaeta (Vesiculodrilus) victoriae** (Spencer, 1892a)  
(Fig. 10.101-103)

*Cryptodrilus victoriae* Spencer, 1892a: 139-140, Pl.15, fig.19-21, Pl.19, fig.69.  
*Megascolides victoriae*; Beddard, 1895: 488.  
*Perionychella (Vesiculodrilus) victoriae*; Jamieson, 1974a: 222.  

**TYPE LOCALITY:** 37°45'S.145°42'E., Warburton, Yarra Valley (typical form). Thompson Valley, Tanjil Track ("var. a"). Locality(?), Victoria ("var. b").  
**LECTOTYPE:** NMV F4036 (Re-examined, aclitellate but mature).
Length 100 mm. Width 9 mm (typical form); 70 mm by 6 mm (Thompson Valley form); 75 mm by 6 mm ("var. b"); colour unspecified but "var. b" more robust and lighter in colour than Thompson Valley form. Tanylobous. A very distinct median, dorsal and ventral groove running the whole length of the body. First dorsal pore (2/3?), 3/4. Setae prominent, and in four couples regularly arranged, except at the posterior end of the body, where the last few segments are distinct from and smaller than the others; in XII, \[aa : ab : bc : cd : dd = 1.64 : 1.00 : 1.64 : 2.22 : 3.79\]. Setae in Thompson Valley form irregular and extending slightly higher along the body; the irregularity extends further forwards along the body in "var. b". Nephropores in \(c\) lines. Clitellum annular, XIV-XVI. Male pores on papillae on XVIII, each slightly dorsal to \(a\) lines; setae \(a\) and \(b\) absent. Genital markings a median, ventral, glandular patch on the anterior halves of IX and X, (in X only but very prominent in re-examined type, G36) together with faintly marked intersegmental patches, or (G36) eyelike markings, immediately in front of and behind the male pores, in 17/18 and 18/19, shortly lateral of \(a\), each traversed by a groove coinciding with the intersegmental furrow. Thompson Valley form differs in the presence of a curious elongate white smooth surface, extending vertically from XVII-XXIII, as does "var. b" which in addition has a similar surface on IX-IX. First dorsal pore 2/3(?), 3/4. Nephridiopores in \(c\) lines, commencing in II. Female pores on XIV, anteromedian of \(a\). Spermathecal pores, 5 pairs, in 4/5-8/9, in \(a\) lines, or in Thompson Valley form slightly dorsal of \(a\) lines.
Fig. 10.101. *Diporochaeta (Vesiculodrilus) victoriae*. Genital field. Redrawn from Spencer (1892a).
Fig. 10.102. *Diporochaeta (Vesiculodrilus) victoriae*. Genital field. Lectotype NMV F4036. (Jamieson, 2000).
Fig. 10.103. *Diporochaeta (Vesiculodrilus) victoriae*. A: Prostate. B: Right spermatheca of VIII. Lectotype NMV F4036. (Jamieson, 2000).
Septa 10/11 and 11/12 strongly thickened. Last septal glands anterior in V. Dorsal blood vessel single; dorsoventral commissurals in VII (and further anteriorly?) to XII; those in X-XII forming 3 pairs of large latero-oesophageal hearts; commissurals in IX and anteriorly each giving off a lateral branch near its junction with the ventral vessel, this branch absent in X-XII. Supra-oesophageal vessel in VI-XII; receiving circumoesophageal intramural vessels. Subneural vessel absent. Gizzard large and firmly muscular, in V, but extending posteriorly and backwardly deflecting septa, to intersegment 8/9. Oesophagus almost suppressed in VI and VII; vascular and dilated in IX-XIV (-XV, Spencer); especially large and vascular in XIII and XIV but extramural calciferous glands absent. Intestine commencing abruptly in XVII; typhlosole and muscular thickening absent. Nephridia: a pair of tufts in II, each with about 40 loops and a composite duct, of 7 tubules, joining the bladder; those in III and IV also tufted but each apparently consisting of only 2 or 3 much-coiled loops, the duct to the bladder with only 2 tubules. Succeeding nephridia simple, with subspherical bladders which develop a small posteriorly directed diverticulum in the intestinal region; preseptal funnels observed in V, posteriorly; hind nephridia smaller and thicker walled (Horan, 1971). Much divided testes and funnels in X and XI; tubular, terminally swollen and racemose seminal vesicles in IX and XII. Prostates tortuous, tubular, extending posteriorly into XXVI; ducts muscular and sinuous. Penial setae almost straight but with the ectal end hooked "dorsoventrally" flattened, and at its extremity slightly widened, terminally embayed and concavo-convex in cross section with concavity ventral; a series of slender, ectally directed spines giving the ectal sixth of the seta a notched appearance, the spines numbering 15 on the "ventral" and 9 on the "dorsal" side in profile; other spines sparsely scattered along
the ornamented region; length of a well developed seta 1.6 mm, maximum width (at base) 28 µm, width of ental region of ornamentation 10 µm. Ovaries, with large oocytes in several chains which are mostly united to form a lamina, in XIII. Ovisacs absent. Spermathecae each with ovoid-fusiform ampulla and ductlike portion consisting of a wide ental half and narrow, muscular ectal half (the duct proper); a terminally strongly swollen, clavate diverticulum joining the ectal end of the muscular duct; size approximately uniform; length of right spermatheca of VIII = 1.5 mm; ratio total length: length duct = 4.2; ratio total length: length diverticulum = 3.5. Diverticulum in Thompson Valley form longer and knob-like (Spencer) but similar to typical form in "var. b".

**REMARKS**

The lectotype agrees sufficiently well with Spencer’s description to leave no doubt that it was correctly designated by Jensz and Smith (1969). *D. victoriae* is morphologically close to *D. tanjilensis*, differing notably in having unpaired anterior genital markings. It conforms closely to the *frenchi*-group.

**Diporochaeta (Vesiculodrilus) volvens** (Spencer, 1900)

*(Fig. 10.104, 10.105)*


Perionychella (Vesiculodrilus) volvens; Jamieson, 1974a: 222.

TYPE LOCALITIES: Gullies amongst the ranges near the source of the River Yarra (ca. 37°44'S.145°44'E.? - Vic.
SYNTYPES: NMV F40590 (desiccated; Jensz and Smith, 1969). A further specimen, AM W1292, in good condition, has collecting data indicating it is part of the type series (Jamieson, 1974a) (examined).

Length 75-100 mm. Width (midclitellar) 3-3.5 mm. Segments 129. Pigmentless buff in alcohol. Form moderately stout; somewhat dorsoventrally depressed and posteriorly flattened below adjacent setal rows. Prostomium broadly tanylobous it and the entire body canaliculate; 2 transverse furrows present on the dorsal tongue. First dorsal pore 4/5, perforate. Setae prominent, in 8 longitudinal rows throughout commencing in II; d lines a little irregular in the last few segments, the other rows entirely regular; ab absent, cd present in XVIII; in XII, aa: ab: bc: cd dd = 1.5: 1.0: 1.95: 2.1: 3.0; dd: u = 0.21 (W1292). Nephropores rather inconspicuous, though clearly visible on the clitellum, in c lines; not recognizable in anterior segments. Clitellum annular, forming a slight constriction, embracing XIV-XVI; intersegmental furrows, setae and nephropores clearly developed; dorsal pores present only at its limits. Male genital field: combined male and prostatic porophores a pair of low, not certainly perforate mounds in ab connected by a tumid intervening area which, with the porophores, forms a whitish transversely elongate-elliptical tubercle invisible to the naked eye. Paired eye-like, elliptical accessory genital markings weakly developed, in 17/18 in b lines; in 18/19, in a lines; and, though apparently absent on
Fig. 10.104. *Diporochaeta (Vesiculodrilus) volvens*. Genital field. Syntype AM W1292. (Jamieson, 2000).
Fig. 10.105. *Diporochaeta (Vesiculodrilus) volvens*. A: Prostate and accompanying nephridial bladders. B: Right spermatheca of VII. Syntype AM W1292. (Jamieson, 2000).
the left side, slightly median of $a$ in 19/20. Female pores a pair of inconspicuous orifices in XIV, anteromedian of $a$, in a faintly developed common field. Spermathecal pores 5 pairs, all inconspicuous, in 4/5-8/9, very slightly lateral of $a$ lines.

Septal thickening: 5/6 delicate; 6/7 slightly, 7/8 and 8/9 moderately thickened; 9/10-13/14 strongly thickened, 12/13 the strongest; the remainder thin. Last septal (pharyngeal) glands anterior in IV. Dorsal blood vessel single, continuous anteriorly at least to the brain, which lies in III. Dorsoventral commissural vessels in V-XII; those in V-IX slender and dorsoventral only; those in X-XII wider and forming 4 pairs of latero-oesophageal hearts each of which originates from the slender supra-oesophageal vessel and receives only a very slender connective from the dorsal vessel. Supra-oesophageal recognizable in X-XII. Subneural vessel absent. Gizzard large, firmly muscular and anteriorly widening in V; oesophagus wide posteriorly in IV, fairly muscular but flaccid. Oesophagus moniliform but not especially vascularized, in VIII-XIV; wider and more vascular in XIII and XIV than elsewhere; elongate, narrow and chloragogenous looking in XV and XVI. Intestine beginning with marked expansion, in XVIII; muscular thickening and typhlosole absent. Nephridia in II and III forming large tufts with many spiral loops, each tuft sending several ducts towards the pharynx; a terminal bladder present in III and apparently also in II. Succeeding nephridia less tufted until in approximately VI they are hardly more complex than normal holonephridia; bladder clearly visible in IV and posteriorly; very large, ovoid, and joined by the nephridial duct ectally and terminally in IX; from X duct connecting subterminally; by XVIII the basal part of the bladder begins to project as a discrete lateral diverticulum; preseptal funnels were observed in
immediately preclitellar region. Testes, iridescent sperm funnels and very large sperm masses free in X and XI; seminal vesicles large elongate, lobulated sacs in IX and XII. Prostates tubular, dorsoventrally somewhat depressed, meandering from XVIII to XXIV, the coiled depressed and slightly flattened in contact; the muscular S-shaped ducts restricted to XVIII. Penial setae approximately straight but with the ectal end hooked, "dorsoventrally" flattened and at its extremity slightly indented, concavo-convex in cross section with concavity ventral; a series of slender ectally directed spines giving the ectal fifth of the seta a mottled appearance, the spines numbering about 15 in the "ventral" to somewhat less on the "dorsal" side of the profile; other spines sparsely scattered along the ornamented region. Length of a well developed seta = 1.5 mm, width at base = 10 µm. Width in ectal region of ornamentation = 8 µm. Ovaries (large rounded masses with many rows of large oocytes) and funnels in XIV; ovisacs absent. Spermathecae discharging anteriorly in their segments; each with a somewhat irregular, depressed ovoid ampulla and shorter duct consisting of a wide ental half which is neither texturally nor structurally clearly demarcated from the ampulla and a muscular glossy narrow ectal half; a single sperm-filled clavate lateral; diverticulum with slender duct joining the middle of the duct; size uniform; length of the right spermatheca of VII = 2.2 mm; ratio of total length: length duct = 4.3; ratio of total length: length diverticulum = 3.8.

REMARKS
Diporochaeta (Vesiculodrilus) volvens is morphologically very close to the prior D. (V.) gippslandica. Further investigation is needed to ascertain whether the longer series of genital markings in the latter is a constant difference. There are patent errors
in Spencer’s (Fig. 25) illustration of the genital field in his, albeit invaluable, text. It is
clearly referable to the *frenchi* group.

**Diporochaeta (Vesiculodrilus) warragulensis** (Spencer, 1900)
(Fig. 10.106)


**TYPE LOCALITY:** c. 38°10’S.145°56’E., S. Warragul - Vic.
**TYPES:** NMV (Lost, Jensz and Smith, 1969).

Length (in ethanol) 113-138 mm. Width 2.5 mm. Prostomium slightly epilobous, wedge-shaped; peristomium with a distinct middorsal groove. First dorsal pore 5/6. Setae 8 per segment, regularly arranged, except at the very posterior end (about 16 segments). Elsewhere the setae of each pair close together, *cd* being placed about half way up the side of the body. Clitellum well developed, posterior XIII-XVIII, annular but ventrally the posterior part of XVII and XVIII not included. A glandular ridge present ventrally at 18/19. Male pores on papillae in *ab*, on XVIII. Female pores on XIV. Spermathecal pores 2 pairs, in *a* lines, in 7/8 and 8/9.

Dorsal vessel single; last hearts in XII. Gizzard in V; no vascular swellings or calciferous glands; intestine commencing in XIX. Holonephric. Testes and funnels, 2
Fig. 10.106. *Diporochaeta (Vesiculodrilus) warragulensis.* Genital field. Redrawn from Spencer (1900).
pairs, in X and XI. Racemose seminal vesicles attached to the anterior wall of XII. Prostates coiled, tubular; in XVIII; a large mass of glandular tissue midventral between the two glands. Spermathecae, 2 pairs, each consisting of a sac with a very small mammillated diverticulum close to the body wall.

REMARKS

*Vesiculodrilus warragulensis* is poorly characterized and its generic affinities are uncertain. Pending discovery of new material, it is here provisionally placed in its own monotypic species-group within *Vesiculodrilus* on the basis of its lumbricin condition, though nephridial bladders have yet to be demonstrated.
11. Eastoniella Jamieson, 1977b


DIAGNOSIS
Setae 8 per segment. Combined male and prostatic pores a pair on XVIII. Spermathecal pores pretesticular and intersegmental. Gizzard in VIII or IX. Calciferous glands absent. Intestine simple. Meronephric; pharyngeal nephridia or tufts absent; oesophageal and anterior intestinal nephridia astomate; caudally the median ventral nephridium on each side with a preseptal funnel which is at first multilipped but further posteriorly is simple; those nephridia with simple funnels enlarged as megameronephridia; enteronephry absent (?). (Holandric; metagynous). Prostates tubular.

DESCRIPTION
Terrestrial. Body circular in cross section. Prostomium epilobous (to tanylobous?). Dorsal pores absent. Setae 8 per segment, commencing on II; widely paired; cd very slightly smaller than bc; dd 0.3-0.4 circumference. A pair of combined male and prostatic pores on XVIII. Clitellum annular (extending behind the male pores?). Intersegmental unpaired accessory genital markings present. Female pores inconspicuous, paired, anteromedian of setae a of XIV. Spermathecal pores 2 pairs, in 7/8 and 8/9.
Some oesophageal septa strongly thickened; none aborted. Dorsal blood vessel single, continuous onto the pharynx. Last hearts in XIII; those in X, XI-XIII latero-oesophageal, with connectives from the dorsal vessel and the oesophageal plexus- supra-oesophageal vessel weakly developed or unrecognizable; subneural vessel absent. Gizzard vestigial or strongly developed in VIII or IX; extramural calciferous glands absent. Intestinal origin XVI; typhlosole, caeca and muscular thickening absent. Meronephric; anteriorly with numerous astomate, exonephric, parietal micromeronephridia on each side. Pharyngeal or anterior tufted nephridia absent. Caudally with astomate micromeronephridia and a median ventral meronephridium, on each side, with preseptal funnel which is at first multilipped, but further posteriorly is simple; those nephridia with simple funnels are enlarged as megameronephridia; enteronephry absent? Testes and funnels in X and XI; testis-sacs absent; seminal vesicles in IX and XII (or XI only?). Ovaries and funnels in XIII; ovisacs (always?) absent. Prostates tubular though minutely lobulated. Penial setae absent. Spermathecae 2 pairs, each with a simple diverticulum.

**DISTRIBUTION**

Lord Howe Island.

**TYPE-SPECIES:** *Eastoniella howeana* Jamieson, 1977b.

**REMARKS**

The presence in caudal segments of a stomate nephridium with preseptal funnel, median to astomate meronephridia placed *Eastoniella* in a *Digaster*-group of the
formerly recognized tribe Dichogastrini (i.e. non-acanthodrine species) in which location of the gizzard in VIII or IX rendered it unique. Elsewhere in the Megascolecidae the most posterior known location of the oesophageal gizzard is VIII, in Phoretima and Pleionogaster, genera which show no close relationship to Eastoniella. The multilipped funnels of some of the stomate nephridia are a further peculiarity. They somewhat resemble those of some Glossoscolecidae. Intestinal gizzards in the Tasmanian genera Hickmaniella and Nexogaster occur more posteriorly but are distinct from and additional to the oesophageal gizzard.

CHECKLIST OF SPECIES OF EASTONIELLA
1. E. howeana Jamieson, 1977b
2. E. modesta Jamieson, 1977b

KEY TO THE SPECIES OF EASTONIELLA

a. A strongly protuberant oblong ovoid tubercle with its length transverse to the body axis, filling XVII and XVIII longitudinally  E. howeana
b. A slight midventral tumescence or transverse segmental papilla filling the posterior two thirds of XVIII and impinging very slightly on XIX. A further transversely elliptical midventral pad present intersegmentally in 17/18  E. modesta

Eastoniella howeana Jamieson, 1977b  
(Fig. 11.1, 11.2)

Eastoniella howeana Jamieson, 1977b: 281-282, Fig.1, 3B, 6D, 7D, L, Table 1.
TYPE LOCALITY: 31°35'03"S.159°04'56"E., Mt. Gower Ridge-Lord Howe Island.
HOLOTYPE: AM W6591.

Length 80 mm. Width (midclitellar) 9 mm. Segments 140. Form circular in cross section- first four segments simple; the remainder triannulate with, frequently, further subdivision of the annuli; triannulation especially clear in the forebody; postclitellar segments only about half as long. Prostomium epilobous, almost 1/2, almost square though slightly rounded anteriorly; demarcated posteriorly by a transverse furrow which continues on the peristomium on each side of it. Dorsal pores absent. Setae minute; not clearly discernible in the forebody; commencing on II, in 8 regular longitudinal rows throughout; in XXV, \( aa: ab: bc: cd: dd: dc: cb: ba: u = 8.5: 5.0: 10.6: 10.4: 38.7: 9.7: 11.1: 5.8: 29.50 \). Nephropores not externally visible. Clitellum imperfectly developed and damaged but appearing at the dorsal incision to occupy the posterior 1/3 XIII - anterior 2/3 XIX; intersegmental furrows and setae retained. Male genital field: an exceedingly protuberant oblong ovoid tubercle with its length transverse to the body axis, filling XVII and XVIII longitudinally and including the anterior third of XIX, extending laterally almost to b lines, the tubercle traversed by a deep transverse furrow which divides it into an anterior larger portion, occupying the whole of XVII, and the anterior 1/3 of XVIII, though this portion appears to originate from the posterior and anterior annuli (thirds) of XVII and XVIII respectively and a posterior, smaller portion which appears to originate from the posterior two annuli (two thirds) of XVIII and the anterior annulus (third) of XIX. Male pores represented by inconspicuous mounds slightly lateral of a lines on the genital marking and in a position corresponding with the equatorial annulus of XVIII; the pores 2.8 mm, 0.13
Fig. 11.1. *Eastoniella howeana*. Genital field. Holotype AM W6591. After Jamieson (1977b).
body circumference, apart. Female pores a pair, very inconspicuous, shortly median to a lines, midway between the setal arc and the anterior margin of XIV. Spermathecal pores 2 pairs of inconspicuous orifices in 7/8 and 8/9 in a lines; the last pores 2.4 mm, 0.11 body circumference, apart.

Septa 4/5-7/8 strongly thickened; 8/9 very strongly thickened; 9/10 and 10/11 immensely thick; 11/12-13/14 moderately thick; the succeeding septa thin. Vascular system indeterminable (macerated and damaged). Oesophagus in VI-VII, and XI, elongate, vascular and tortuous, the anterior half in VIII forming a rudimentary but elongate and conspicuous gizzard; the vascularized region internally simple, noteworthy rugosity or recognizable calciferous development absent; intestinal origin indeterminable; typhlostome, muscular thickening and caeca absent. Astomate, avesiculate exonephric integumentary micromeronephridia approximately 10-15 on each side in each segment commencing in II; approximately 75 segments from the caudal extremity the median or sometimes next lateral nephridium on each side has a preseptal composite nephrostome. The nephrostomes are largest anteriorly, where they are at least as large as a nephridium. Each has two rami; on the anterior face of each ramus, arranged in single file, are approximately 16 juxtaposed ciliated lobes each in the form of a simple nephridial funnel. Posteriorly on each ramus, there is a single such ciliated lobe on each side of the neck. At approximately 15 segments from the posterior end, the biramous funnels are replaced by simple funnels and the median nephridium is greatly enlarged to form a conspicuous megameronephridium. Pharyngeal nephridia absent and no intestinal or other enteronephry demonstrable. Sperm funnels (and testes?) free in X and XI, only the funnels in X iridescent; seminal vesicles moderately large, racemose, in XI only, dependent from the anterior septum.
Fig. 11.2. *Eastoniella howeana*. Genital field. A: Right prostate. B: Right spermatheca of IX. Holotype AM W6591. After Jamieson (1977b).
Ovaries, a few attenuated strings of small oocytes, and funnels in XIII; oviducts paired. Ovisacs absent. Prostates tubular, minutely lobulated, with very narrow sinuous ducts entering a glandular mass which corresponds with the external genital marking, in XVIII; the glandular part extending anteriorly of the ducts for one to three segments, its free end attenuated as a slender tail; vas deferens joining the gland at its junction with the duct. Penial setae absent. Spermathecae 2 pairs opening anteriorly in VIII and IX; each with a broad sacciform ampulla and a wide, well demarcated, ectally tapering duct which receives the short duct of a subspherical diverticulum at its ectal third; size approximately uniform; length of right spermatheca of IX = 2.1 mm; ratio total length: length duct = 2.0; ratio total length: length diverticulum = 3.0.

REMARKS

*Eastoniella howeana* is diagnosed within the genus by location of the gizzard in VIII and incipient proandry, with seminal vesicles in XI only. Its affinities are further discussed under *E. modesta*.

**Eastoniella modesta** Jamieson, 1977b
(Fig. 11.3, 11.4)

*Eastoniella modesta* Jamieson, 1977b: 282-284, Fig.1, 3C-E, 6G, Table 1.

**TYPE LOCALITY:** 31°31’.159°04’, Lord Howe Island.

**HOLOTYPE:** AM W6592 (ex W4567).

**PARATYPE:** AM W4564.
Eastoniella modesta

Length 90-100 mm. Width (midclitellar) 5-10 mm. Segments 119-144. Circular in cross section. Pigmentless in alcohol. Prostomium tanylobous?, extending to the posterior border of the first annulation or broadly epilobous. Canalicula and dorsal pores absent. Setae 8 per segment, in regular longitudinal rows excepting posteriorly where d line is very slightly irregular. Seta a or a and b absent in XVIII. Nephropores not externally recognizable; in XX-XXV, aa: ab: bc: cd: dd: dc: cb: ba: u = 12.4: 5.9: 10.3: 9.3: 39.3: 7.5: 9.4: 6.0: 20.35. Clitellum questionably embracing XIII-XXI. Male pores on XVIII, shortly lateral (and posterior?) to the sites of setae a; 2.2, 2.9 mm, 0.15, 0.10 body circumference, apart, each pore on a small, low, domed protuberance which is clearly delineated laterally (shortly median of b) but medially is continuous with a slight midventral tumescence or with a transverse segmental papilla which fills the posterior two thirds of XVIII and impinges very slightly on XIX. A further transversely elliptical midventral pad present intersegmentally in 17/18, extending longitudinally from the setal arc of XVII to that of XVIII and laterally to a or into ab; segment XVII (in holotype) slightly tumid from the pad to intersegmental furrow 16/17. Female pores distinct minute pits shortly anteromedian of setae a of XIV. Spermathecal pores not externally visible; from internal examination 2 pairs, in 7/8 and 8/9, in a lines; the pores 1.8, 1.9 mm, 0.13, 0.09 body circumference apart.

Septa 9/10-12/13 very strongly thickened; 10/11 and 11/12 the thickest. Dorsal blood vessel single, continuous onto the pharynx. Supra-oesophageal present, as judged from union of supra-oesophageal connectives to the hearts, but not visibly differentiated (because of maceration?) as a vessel from the roof of the oesophagus but visible in XIII, though weakly developed and not certainly continuous in XI and
Fig. 11.4. *Eastoniella modesta*. A: Right prostate. B: Gizzard in segment IX. Holotype AM W6592. After Jamieson (1977b).
XII. Dorsoventral commissurals in VI-XIII; those in X, XI-XIII each receiving a slender connective from the dorsal vessel and from the middorsal line of the oesophagus or from the distinguishable supra-oesophageal vessel; slender commissurals in IX anteriorly dorsoventral only; subneural not demonstrable. Gizzard barrel-shaped, very large, and strongly muscular or thinner walled and slenderly fusiform, in IX; its location in this segment clearly indicated by the intervention of a section of narrow oesophagus which is short or half the length of the segment between its anterior limit and the thick septum 8/9 (the difference in size of the gizzard and length of preceding oesophagus presumably due to different contraction); septum 9/10 only slightly displaced posteriorly by the gizzard. Oesophagus in VI-VIII unusually long and capacious, so that it is contorted in each segment, its walls vascular but simple; shorter but similar in appearance in V; pharynx and buccal cavity in I-IV tubular, narrower than the oesophagus, and invested in III and anteriorly in a small glandular mass in which (apparently in III) the brain is embedded. Oesophagus behind the gizzard virtually suppressed in X and XI but wide and vascular in XII-XIV in which it has numerous fine low internal circumferential ridges narrow in XV; morphologically differentiated calciferous glands absent; intestine commencing, with abrupt dilatation, in XVI; typhlosole, caeca and muscular thickening absent. Nephridia as for E. howeana with multilipped funnels. Holandric; large sperm funnels, with spermatozoal iridescence, in X and XI; testis-sacs absent; multiloculate seminal vesicles paired in IX and XII that in XII extending through septum 12/13 into XIII. Metagynous (from disposition of pores in XIV); ovaries, oviducal funnels and ovisacs not demonstrable or funnels only seen. Prostates a pair of narrow distinctly flattened straplike structures; almost straight, extending from XVIII to XXVIII, the
surface minutely lobulated and occasionally slightly incised but with the appearance of tubular rather than racemose prostates; each with a short contorted, moderately muscular duct which is thinly ensheathed in parietal connective tissue; the ducts entering an internal glandular mass corresponding with the external genital marking in XVIII; slender vas deferens joining the duct shortly ental of the midlength of the latter. Penial setae absent. Spermathecae 2 pairs, in VIII and IX, each with an ovoid to spherical ampulla and an initially wide ectally tapering duct; an inseminated clavate diverticulum joining the duct medially where the duct reaches the preceding septum and commences to run ventrally in the septum; ectal half of the spermathecal duct concealed in this septum; length of right spermatheca of IX = 2.1, 2.2 mm, ratio total length of spermatheca: length duct = 2.8, 2.9; ratio length spermatheca: length diverticulum = 3.2, 3.1.

REMARKS
Location of the oesophageal gizzard in segment IX in *Eastoniella modesta* appears to be the sole known case in the Megascolecidae. Its occurrence in two of the three known specimens of *Eastoniella* suggests that it is not an abnormality. This location of the gizzard, the holandric condition, with seminal vesicles in IX and XII, and maximal thickening of septa 10/11 and 11/12 rather than 9/10 and 10/11, all distinguish it from *E. howeana*. Otherwise the general morphology, including the genital field, is very similar in the two species and it is possible that discovery of larger series of specimens will necessitate regarding *E. modesta* as a junior synonym of *E. howeana*. Such variation in location of the gizzard infraspecifically is unknown elsewhere, however, except as an abnormality, and separation of the two entities as
distinct species appears justified. The setal ratios of the two species do not at present aid distinction of the two entities but similarity of the ratios is not greater than that between different species in other genera.


**DIAGNOSIS**
Setae 8 to numerous in setigerous segments A single midventral combined male and prostatic pore (though, *menurus* only?) evaginable as a pair of pores). Calciferous glands 2 or 3 pairs, in XIII and XIV, or XIII-XV; intestinal origin in XVIII. Thickly tubular (tubuloracemose?) prostates; junction of vasa deferentia with the prostate ducts well ectal of the glands. Spermathecae unpaired, each with irregularly ovoid ampulla and two digitiform diverticula at the body wall.

**DESCRIPTION**
Medium to large terrestrial worms (85-600 mm) with <ca. 200 segments. With strong purplish to brown parietal pigmentation. Prostomium slightly epilobous to epitanylobous. Body dorsally canaliculate. First dorsal pore 4/5 or 5/6. Setae 8 to numerous in setigerous segments; if 8, setae *c* and *d* distant (*cd* wider than *bc*). Penial setae absent. Nephropores in *d* lines or, in perichaetin species, in a variable or sinuous line. Clitellum annular, occupying 4 to 6 segments, beginning in XIII or XIV. The combined opening of the male and prostatic pore externally unpaired, midventral, in XVIII, but in at least *menurus* ejaculatory ducts apparently evaginable as a pair of
pores. Accessory genital markings present (midventral plications in the vicinity of the spermathecal pores) or absent. Female pores anteromedian to setae a of XIV, inconspicuous. Three or 5 unpaired, midventral spermathecal pores, ending at 8/9.

Some preclitellar septa thickened. Dorsal blood vessel continuous onto the pharynx. Last hearts in XII; those in X-XII latero-oesophageal. Supra-oesophageal vessel in IX (and further forward?) to XII and XIII. Subneural vessel absent. Gizzard well developed, in VI or VII. Calciferous glands lateral, sessile pouches in XIII and XIV or XIII, XIV and XV, with internal laminae but not constricted off from the oesophagus. Intestine commencing in XVIII; typhlosole and caeca absent. Nephridia stomatic, vesiculate holonephridia; postseptal bodies commencing in II; bladders with or without lateral diverticula. Testes and funnels free, in X and XI; seminal vesicles 4 pairs, in IX-XII, or 2 pairs in XI and XII, with or without pseudovesicles in X or XIII. Ovaries and funnels in XIII; ovisacs absent. Prostates thickly tubular (tubuloracemose?); vasa deferentia joining the muscular prostate ducts ectal to the glands to as far as the midlength of each duct; the ducts sometimes at least discharging through a midventral bursa. Spermathecae unpaired (or with a paired rudiment), each discharging anteriorly in its segment; duct shorter than the ampulla and bearing ectally 2 digitiform diverticula.

**DISTRIBUTION**
Widespread from the Richmond River, in New South Wales, to Cape York Peninsula, in Queensland.

**TYPE-SPECIES:** *Cryptodrilus (?) unicus* Fletcher, 1889
REMARKS

Fletcherodrilus was placed by Michaelsen (1910a) in the synonymy of Plutellus because he had found an Indian species, supposedly belonging to the latter genus, in which the spermathecal pores were unpaired. The genus was re-established by Jamieson (1971c) as the type-species was clearly not congeneric with the type-species of Plutellus (P. heteroporus) or its conger P. manifestus.

Three species, F. unicus (Fletcher, 1889a); F. purpureus (Michaelsen, 1889a) and F. fasciatus (Fletcher, 1889b), were first assigned to Cryptodrilus. Michaelsen (1891) considered these to be 'varieties' of one species, F. unicus, and added a further variety, pelewensis. Later (1900) he placed purpureus in the synonymy of 'F. unicus typicus' and referred pelewensis to F. unicus fasciatus. Jamieson (1971c) agreed that purpureus was a synonym of unicus but reinstated fasciatus as a distinct species. Material from Binna Burra, examined differed from unicus in having the gizzard more posteriorly situated and no calciferous glands in XV, two differences noted also by Fletcher in the type-description of fasciatus. Michaelsen’s var. pelewensis, with gizzard in VI and calciferous glands in XIII-XV was referred to unicus.

A morphological cladistic analysis (Jamieson, 1994) showed that the Terrisswalkerius-Fletcherodrilus assemblage was a monophyletic entity. Fletcherodrilus formed a terminal, monophyletic clade, and therefore separation of Fletcherodrilus as a distinct genus rendered Terrisswalkerius paraphyletic. The Terrisswalkerius-Fletcherodrilus assemblage was found to be defined by the synapomorphy loss of accessory genital markings (and intestinal origin in XVII). Fletcherodrilus appeared to form an apomorphic, terminal clade in which the spermathecal and male pores had united midventrally, the spermathecal condition
being a homoplasy with *T. mcdonaldi*, and, less significantly, the seminal vesicles had come to occupy segments XI and XII. *F. sigillatus* and *F. menurus* were shown to have departed from the condition in the type-species, *F. unicus*, and all *Terrisswalkerius* species, in which accessory genital markings are apomorphically absent, by developing a distinctive type of pleated genital markings ventrally in the vicinity of the spermathecal pores. However, the molecular analysis (Jamieson *et al.*, in preparation; see Fig. 0.42) showed *Fletcherodrilus* to be the sister-group of all *Terrisswalkerius* species represented, with the exception of the enigmatic *T. athertonensis* which appeared basal to both groups. From the molecular evidence *T. athertonensis* would merit a separate generic (or even suprageneric) status. Leaving aside the latter species, molecular evidence thus supports recognition of *Fletcherodrilus* and *Terrisswalkerius* as separate genera, or sister-clades at whatever arbitrary Linnean rank they be given.

**CHECKLIST OF SPECIES OF FLETCHERODRILUS**

1. *Cryptodrilus (?) fasciatus* Fletcher, 1890
2. *Fletcherodrilus menurus* Jamieson, 1994
3. *Perionyx (Diporochaeta)sigillatus* Michaelsen, 1916a
4. *Cryptodrilus (?) unicus* Fletcher, 1889
   Syn. *Pluttellus affinis* Stephenson, 1933

**KEY TO THE SPECIES OF FLETCHERODRILUS**

1. a. Setae 8 per segment 2
   b. Setae > 8 per segment 3
2(1a) a. Body uniformly pigmented reddish brown though paler ventrally. Gizzard in segment VI. Calciferous glands 3 pairs, in XIII, XIV and XV
   
   b. Body with transverse pigmented greyish stripes. Gizzard in segment VII. Calciferous glands 2 pairs, in XIII and XIV
   
   *F. unicus*

3(1b) a. Spermathecal pores 3, midventrally, in 6/7, 7/8 and 8/9. Ventral surface in VII-IX tumid and with several longitudinal (glandular?) plications
   
   b. Spermathecal pores 5, midventrally in 4/5 to 8/9. An oval, superficially pleated genital marking midventrally in VIII
   
   *F. sigillatus*

   *F. menurus*  

**Fletcherodrilus fasciatus** (Fletcher, 1890)
(Figs 0.6, 12.1-12.3)

*Cryptodrilus (?) fasciatus* Fletcher, 1890: 988-989.

*Fletcherodrilus unicus var. fasciatus*; Michaelsen, 1891: 32.

*Fletcherodrilus unicus fasciatus*; Michaelsen, 1900; Boardman, 1932: 130.


**TYPE LOCALITY:** ca 28°25'-29°04'S.152°46'-153°21'E., Richmond River District - NSW.

**SYNTYPES:** Macleay Museum (Lost).


Length 128-290 mm. Width (midclitellar) 7-9 mm. Segments 90-130. Dorsally and laterally encircled by deep purple-brown segmental strips separated by unpigmented intersegmental strips. First few segments single; thereafter faintly biannulate, with presetal furrow. Ventral pale with very slight indication of the dorsal striping. Clitellum unstriped, uniform chocolate brown. Cross-section of body appreciably depressed dorsoventrally but (Fletcher) not as much as in _F. unicus_. Prostomium wide, epilobous, slightly to about 1/3. Peristomium not bisected ventrally, though with some fine longitudinal grooves. First dorsal pore 3/4 (rudimentary), 4/5 perforate. A narrow dorsal groove present throughout, well developed in the first few segments, faint further posteriorly, or groove not apparent. Setae commencing in II, in 8 regular longitudinal rows throughout; _a_ and _b_ absent in XVIII. In XII, _aa_: _ab_: _bc_: _cd_: _dd_ = 2 0: 1.0: 1.9: 2.4: 12.1. Nephropores conspicuous slits near the anterior borders of their segments, in II to the posterior end, all in _d_ lines. Clitellum annular, tumid but constricted; XIII-XVIII, 1/2XIX, interrupted in 1/2XVII-XIX (maximally in XIX) throughout _bb_ by the whitish glandular field which includes the median male porophore; dorsal pores obscured, intersegmental furrows and setae less clear than elsewhere, nephropores retained. A single pore of the pair of prostates and the vasa deferentia midventral in XVIII on a hemispheroidal strongly protuberant equatorial...
Fig. 12.1. *Fletcherodrilus fasciatus*. Dorsal dissection, semidiagrammatic. After Jamieson and Wampler, 1979.
Fig. 12.2. *Fletcherodrilus fasciatus*. A and B: Anterior and posterior genital fields. Specimen 1 QM G8795. After Jamieson and Wampler (1979).
male porophore which bears the male pore on a small truncated cone or as a transverse slit, the two conditions presumably representing eversion and retraction of the terminal ducts; the base of the porophore filling approximately $1/3aa$. A diamond-shaped midventral whitish glandular field in $1/2XVII-1/2XX$, filling $aa$ at its greatest width, in XIX, deeply insunk in XVII and anterior XVIII and interrupting the clitellum from $1/4XVII$ posteriorly. Accessory genital markings absent. Female pores small paired transverse slits, shortly anteromedian of setae $a$ of XIV; on development of the clitellum seen to lie in a common whitish tumid field. Spermathecal pores unpaired midventral, small but with considerable elliptical borders, in intersegments $4/5-8/9$.

Septa $4/5-16/17$ thickened; $4/5-8/9$ only slightly to moderately, $9/10-12/13$ increasingly strongly with $12/13$ very strong; $13/14-16/17$ less thickened but still strong; $4/5-8/9$ or-$10/11$ funnel-shaped. Dorsal blood vessel single, continuous onto the pharynx. Last hearts in XII; those in X-XII latero-oesophageal, slender in X, very large in XI and XII, each receiving a connective from the dorsal vessel and one from the supra-oesophageal vessel. Commissurals in VII-IX dorsoventral only, differing from the hearts of X-XII in giving off lateral, parietal branches. Supra-oesophageal vessel slender, traceable in IX-XII, $1/2XIII$, but probably continuous with a very slender vessel in VII, not present behind the anterior region of the first calciferous glands (XIII and XIV) but presumably confluent with their sinuses; apparently fusing with the dorsal vessel at septum 9/10. Subneural vessel absent. A pair of transverse parietal vessels present in each oesophageal segment; the vessels in XIV continuous via a longitudinal lateroparietal with those of posterior segments at least as far as XIX. A large cylindrical gizzard in VII, ensheathed in the diaphanous septum 7/8; which is
so firmly adherent to the anterior portion of the gizzard that most of the gizzard appears to lie in VIII; backwardly displaced so that its hind end in at 9/10 relative to external segmentation. Postgizzard oesophagus beginning in IX. Oesophagus in XIII and XIV forming large, lateral pouch-like swellings which are in not constricted of or separate from the central oesophageal lumen; those of the two sides separated by a deep groove or united medianly so as to form an annular (calciferous?) gland in each segment. Each gland has low lamellar internal folds which contain blood sinuses and externally longitudinal striations corresponding with these lamellae. Intestine commencing at the anterior limit of XVIII; muscular thickening, caeca and typhlosole absent. Nephridia preseptally stomate, vesiculate holonephridia, commencing in II. First 3 pairs with long club-shaped bladders which the end tube enters immediately subterminally (segment II) or distinctly subterminally (segment IV). From the 4th pair posteriorly each bladder has a well developed lateral caecum, as large as or larger than the bladder. Free. testes and iridescent sperm funnels in X and XI. Seminal vesicles small, smooth surfaced, in IX and X; large, with some deep incisions, in XI and XII; the types also with pseudovesicles (?) in XIII. Weblike ovaries with many conjoined strings of oocytes, and funnels, in XIII; ovisacs absent. Prostates restricted to XVIII in which the thickly tubular tortuous glandular portion passes laterally from the duct or is wound on itself in a single plane and greatly depressed. The duct almost straight, widening to join a median mound corresponding with the porophore. Vas deferens joining the prostate duct at approximately its midlength. Spermathecae 5, unpaired, discharging anteriorly in V-IX, each with an ovoid ampulla (on one side or the other of the nerve cord) and a well demarcated, slender, though short, muscular duct which is joined at the body wall by 2 slender almost tubular, slightly clavate, beaded,
inseminated diverticula; size of spermathecae increasing posteriorly, length of spermatheca of VII = 6.7 mm, ratio of total length: length duct = 5.3; ratio length: length diverticulum = 1.3.

REMARKS
As Fletcher observed, this species differs from both *Fletcherodrilus unicus* in having the body more robust and transversely striped. It supposedly differed further from *purpureus* (here retained in the synonymy of *unicus*), in the straight setal rows. Fletcher (1890) recognized the claims of the three taxa, then in *Cryptodrilus*, to be placed in a distinct genus.

*F. fasciatus* is very weakly luminescent (ca $10^7$ protons s$^{-1}$) requiring full dark adaptation to be seen (Jamieson and Wampler, 1979).

**Fletcherodrilus menurus** Jamieson, 1994
(Fig. 12.4-12.7)


**TYPE LOCALITY:** 18°56'S, 146°13'E., Mt. Spec National Park, North Queensland, under logs and rocks in rainforest, K.R. McDonald and R.A. Atherton, 4.i.1977.
**HOLOTYPE:** Queensland Museum G211435.
**PARATYPES:** QM G211436-211441.

B.G.M. Jamieson 11/10/00
Fig. 12.4. *Fletcherodrilus menurus*. Genital field. Paratype. After Jamieson (1994).
Length 140-199 mm. Width (midclitellar) 6 mm. Segments 204-202. Form dorsoventrally slightly depressed. Pigmented purplish brown dorsally, buff ventrally. Prostomium epilobous 1/3- >1/2, closed, but with lateral margins continuing to 1/2 or 2/3 peristomium (sometimes flanked by other longitudinal furrows); it and entire body with a narrow middorsal longitudinal groove (canalicula); prostomium also bisected ventrally. First dorsal pore 5/6. Setae 36-40 in XII; 36-41 in XX; caudally, about 12 segments from posterior end, 29-44; ventral gap not apparent in forebody, becoming recognizable on clitellum, not apparent far caudally; dorsal gap conspicuous but not large, and only slightly irregular, throughout. Setal ratios: mean \( aa : ab : bc : cd : yz : zz = 1.35 : 1.0 : 1.15 : 0.95 : 1.4 : 3.6 \). Nephropores sporadically visible; in setal lines 14 in XIV; setal lines 7 in XVIII. Clitellum annular, greyish brown; 1/2XIII-XVIII, but interrupted ventrally in XIII, sometimes weakly developed dorsally to 1/2XIX; intersegmental furrows retained but not as sharp as elsewhere; dorsal pores occluded. The male genital field shows two distinct forms which are here deduced from dissection to be stages in eversion. In the holotype, what may be termed the 'lyrate' condition obtains. Here the two minute male pores, posterior to the setal arc of XVIII and well median of setal lines \( a \), being 0.4 mm apart; each is connected by a short laterally running groove to a longitudinal groove which itself gives off short side branches. The longitudinal grooves are slightly convergent anteriorly. The male pores and the system of grooves lie in an approximately circular depressed field which extends almost to the anterior border of XVIII, where it is bordered by a semicircular rim, and extends onto the anterior region of XIX. In the other paratypes, in marked contrast, the male pore appears unpaired, midventral in the setal arc of XVIII, as a minute slit in a very small low, oval papilla. Transverse incision of the male papilla in
Fig. 12.5. *Fletcherodrilus menurus*. Detail of everted genital field. Holotype QM G211435. After Jamieson (1994).
Fig. 12.6. *Fletcherodrilus menurus*. Semidiagrammatic representation of dissection of male porophore by transverse incision, revealing internal bursa with two male pores. Paratype QM G211441 After Jamieson (1994).
paratype 6 (QM G 211441) revealed an inner cavity or bursa from the rear (dorsal) wall of which projected a pair of muscular ducts, the ectal end of the prostate ducts. It was therefore deduced that the lyrate condition is brought about by eversion of the dorsal wall of the bursa and that when this is retracted it leaves a single pore at the surface of the papilla. Accessory genital marking a large transversely oval pad midventrally in VIII, extending laterally to about setal lines 5, traversed by a deep furrow which coincides with the anterior margin of the setal annulus; longitudinal pleats arising from this furrow (not present in holotype). Female pores paired, minute, immediately anteromedian to setae a, concealed in a transverse furrow which has tumid margins. Spermathecal pores 5, unpaired, midventral, in intersegmental furrows 4/5-8/9, each on a small, low oval papillae which creates a semicircular forward indentation of the furrow.

Last hearts in XII; those in X-XII latero-oesophageal. Supra-oesophageal vessel in X-XVI. A subneural vessel present. Gizzard large, elongate, and moderately firm, in VI, deflecting the diaphanous septum 6/7 posteriorly; septum 5/6 very delicate and attached shortly anterior to middle of gizzard or near its anterior rim, giving the impression that this septum primitively passed to rear of gizzard; a wide, flaccid proventriculus present in segment IV. Oesophagus with circumferential vascular striae in IX-XVI, especially XII-XVI; in each of XIII, XIV and XV dilated on each side of dorsal vessel, and with moderately high radial laminae on its lateral walls; these dilatations not constricted off from oesophageal lumen, but to be considered true calciferous glands. Intestinal origin in XVIII but sometimes not widening until XIX; typhlosole absent. Nephridia stomate, vesiculate holonephridia; bladders very large, elongate-fusiform wide, adiverticulate tubes, joined at ental extreme by nephridial
duct, each ectally continued to pore as a long narrow duct; egress of ducts is near dorsal in II, slightly more ventral in III, and thereafter progressively more ventral until in anterior intestinal region it forms an irregular, ventrolateral or ventral line or still far dorsal, though in slightly irregular longitudinal rows. Holandric; small free funnels in X and XI; seminal vesicles on anterior septa of XI and XII, not subdivided into loculi, or also (pseudovesicles?) X, each with a few large loculi. Ovaries small masses with few large terminal oocytes in XIII; ovisacs not recognizable. Prostates tubuloracemose, externally thickly tubular and smooth walled, restricted to XVIII in which they wind laterally from their ducts; or compacted as a single large lobe with no subdivision; each muscular duct widens in its ectal half to form a bursa which is fused along most of its length to body wall; conjoined vasa deferentia of its side joining anteromedian limit of bursa. Penial setae absent. Five unpaired spermathecae present, increasing size posteriad, each with large, irregularly ovoid ampulla, tapering duct and 2 tubular, tortuous, inseminated diverticula which enter body wall on either side of duct; ampullae lying to one or other side of ventral nerve cord and contralateral diverticulum passing under the cord.

REMARKS

*Fletcherodrilus menurus* is clearly the sister-species of *F. sigillatus*. Both show a striking departure from the other species of *Fletcherodrilus*, *F. unicus* (Fletcher, 1889) and *F. fasciatus* (Fletcher, 1890), in the development of accessory genital markings and in the perichaetin condition of the setae. The genital markings consists of longitudinally pleated areas and are of a type unknown elsewhere in Australian genera. Development of these markings represents a remarkable apomorphic departure from
the absence of markings throughout the remainder of the monophyletic *Fletcherodrilus-Terrisswalkerius* clade. *F. menurus* is well defined from, and presumably plesiomorphic relative to, *F. sigillatus* in having 5 spermathecal pores in contrast with the 3 pores in the latter. Furthermore, the 'lyrate' condition of the putative seminal grooves of the male field in *F. menurus* differs from the anteroposteriorly duplicated, mirror image, array of grooves in *F. sigillatus*.

Dissection of the male porophore of a specimen with a single male pore, revealing two internal prostate pores was considered (Jamieson, 1994) to indicate that such specimens were conspecific with the externally lyrate holotype with its two male orifices. In the unlikely event of this being shown not to be the case, the name *F. menurus*, would be restricted to lyrate individuals.

**Fletcherodrilus sigillatus** (Michaelsen, 1916a)
(Fig, 12.8, 12.9)

*Perionyx (Diporochaeta) sigillatus* Michaelsen, 1916a: 16-19, Pl.1, fig. 3, 4.
*Diporochaeta sigillata*; Jamieson, 1971c: 83.
*Fletcherodrilus ? sigillatus*; Jamieson, 1974a: 221.

**TYPE LOCALITY:** 17°21'S.145°36'E., Malanda, in Cairns District - Qld.

Length 101-170 mm. Width (midclitellar) 4.5 mm. Segments 148-(180?). Form dorsoventrally slightly depressed. Pigmented purplish brown to dark flesh coloured dorsally, pale, greyish ventrally. Prostomium epitanylobous, it and entire body with a narrow middorsal longitudinal groove (canalicula). First dorsal pore 5/6 but an imperforate rudiment at 4/5. Setae 34/XII; 32/XX; caudally 38 (33/IX, 34/XII, XXII, 36/XXVI, Michaelsen); rows slightly more widely spaced ventrally than dorsally; ventral gap (aa) recognizable only behind clitellum, maximally (posteriorly) 2 ab; dorsal gap (zz) visible throughout, anteriorly ca = 2zy; posteriorly ca = 4 zy but narrowing posteriorly as setae are more closely spaced caudally. Nephropores: a pair in each segment, commencing anteriorly in II, but forming an irregular sinuous line on each side, varying in position from near middorsum (in II) to dorsolateral, lateral, or ventrolateral and only occasionally symmetrically disposed in a segment. Clitellum annular, XIII, 1/2XIII-1/2XVII, XVII. Male pore unpaired, midventral equatorially in XVIII at bottom of a deep pit of specialized epithelium which extends anteriorly and posteriorly almost to setal arcs of XVII and XIX and laterally to setal lines 4-6, margin of pit slightly thickened and a little indented at setal arc of XVIII; bottom of
pit in vicinity of male pore differentiated as an elliptical field, around pore, traversed by a conspicuous equatorial furrow in which male pore lies, this central field pleated by several, mostly transverse ridges; walls of pit with similar plications extending radially from central field. Discrete accessory genital markings absent but ventral surface in VII-IX tumid and with several longitudinal (glandular?) plications. Female pores paired, close together, shortly anteromedian of (or, Michaelsen, in front of) setae a of XIV. Spermathecal pores 3, unpaired, midventral, in 6/7, 7/8 and 8/9, each an eye-shaped aperture with tumid, almost papillate margins.

Last hearts in XII; those in X-XII latero-oesophageal. Supra-oesophageal vessel in IX-XIII; moderately developed. Gizzard large and moderately firm, in VI; septum 5/6 very delicate and attached near anterior limit of gizzard, giving the impression that this septum primitively passed to rear of gizzard; a wide, flaccid proventriculus present in the segment preceding gizzard. Oesophagus with circumferential vascular striae in IX-XVI; in each of XIII, XIV and XV dilated on each side of dorsal vessel, and with moderately high vertical laminae on its lateral walls; these dilatations not constricted off from oesophageal lumen, but probably to be considered true calciferous glands. Intestinal origin XVIII; typhlosole absent. Nephridia stomate, vesiculate holonephridia (funnels demonstrated for those discharging in II); bladders very large, elongate-fusiform wide, adverticulate tubes, joined at ental extreme by nephridial duct, each ectally continued to pore as a long narrow duct which equals bladder in length only when pore is far dorsally. Holandric; funnels slightly iridescent in X and XI; gymnorchous; seminal vesicles racemose in XI and XII. Ovaries (webs of many oocytes) in XIII; rudimentary ovisacs in XIV. Prostates tubuloracemose, externally thickly tubular (ca. 18 mm long and 0.7 mm wide, Michaelsen) and smooth
walled, winding from XVIII to XXVII, each with a central lumen occupying a small fraction of total diameter (one eighth in middle of organ and with many lateral canals, Michaelsen); short but considerable muscular duct joined near glandular portion by vasa deferentia which then run distally in duct wall; transverse muscles present on body wall in vicinity of duct. Penial setae absent. Three unpaired spermathecae present, each with large, flattened irregularly ovoid ampulla, well demarcated though stout duct and 2 tubular, tortuous diverticula which enter body wall on either side of duct; length spermathecae = 4 mm; ratio length: length duct = 2.7; ratio length: length diverticulum = 1.8.

REMARKS
All that remains of the single type-specimen in the Hamburg Museum, V8475, is an isolated gizzard. Michaelsen reported that the type was strongly macerated and that he was unable to determine with certainty whether the anterior rudimentary seminal vesicles were in X or XI. He concluded that they were in XI but on this basis the gizzard appeared to be in VII, at which he expressed doubt. Calciferous glands were reported for XIV and XV, with a rudimentary pair, hardly to be considered glands, in XVI, and last hearts were stated to be in XIII. This sequence is one segment behind that of the material, from Wallacha Falls and 40 Mile Scrub, described by Jamieson (1994), and Michaelsen's fear that it might be incorrect by one segment clearly was warranted.

Despite its perichaetin setal arrangement, Jamieson (1974a: 221) considered sigillatus to be related to Fletcherodrilus rather than to Perionychella (i.e. Diporochaeta). Among its similarities with the three species already placed in
Fletcherodrilus was the unpaired male and prostatic pores (a condition unknown in Perionychella but now known in Terrisswalkerius mcdonaldi), presence of calciferous glands in XIII-XV; intestinal origin in XVIII; the thickly tubular prostates; junction of the vasa deferentia with the prostate ducts well ectal of the glands; and the form of the spermathecae with their irregularly ovoid ampullae and digitiform diverticula at the body wall. The presence of diverticula on the nephridial bladders in the other species of Fletcherodrilus and their lumbricin setae cannot be considered significant obstacles to inclusion of F. sigillatus as these variations occur within Diporochaeta. The perichaetin condition is foreshadowed in F. unicus in which the posterior setal lines are sometimes irregular and there are occasionally supernumerary setae and a strongly perichaetin condition is now known for F. menurus.

**Fletcherodrilus unicus** (Fletcher, 1889)
(Fig. 12.10-12.14)

_Cryptodrilus (?) unicus_ Fletcher, 1889: 1540-1541; Fletcher, 1890: 991-992; Raff, 1910: 251-252, Pl.48, fig. 2; Pl. 51, fig. 14.
_Cryptodrilus purpureus_ Michaelsen, 1889a: 3-5, Fig.1.; Fletcher, 1890: 990-991.
_Fletcherodrilus unicus typicus_; Michaelsen, 1891: 32; Michaelsen, 1900: 178.
_Fletcherodrilus unicus var. purpureus_; Michaelsen, 1891: 32 (AM missing).
_?Fletcherodrilus unicus var. pelewensis_ Michaelsen, 1891:32.
Fletcherodrilus unicus var. major Spencer, 1900: 44; Bage, 1910: 236-237, Pl. 47, figs 22-26.
Plutellus affinis Stephenson, 1933: 904-907, Fig. 4, 5.
Fletcherodrilus affinis; Jamieson, 1971c: 85.

TYPE LOCALITY: 30°20'S.149°47'E., Narrabri. 31°16'S.149°17'E., Coonabarabran - NSW.
TYPES: ?.
OTHER RECORDS: (Fletcher, 1890) banks of Lake Cudgellico, a few miles from the Lachlan River - NSW. (Michaelsen, 1889a, and Spencer, 1900) 25°37'S.151°37'E., Gayndah. 22°56'S.148°05'E., (Michaelsen, 1889a) 22°56'S.148°05'E., Peak Down Station (HM, missing). (Fletcher, 1890) 24°20'S.151°34'E., Miriam Vale. 21°42'S.150°20'E., Percy Island - (Macleay Museum, missing). (Michaelsen, 1916a) 26°34'S.152°52'E., Christmas Creek, Blackall Range. 24°24'S.151°37'E., Colosseum. Glen Lamington (HM?). (Michaelsen, 1891) Pelew Islands location shown (Michaelsen, 1900) to be erroneous (HM?). (Jamieson and Wampler, 1979) 28°19'S.153°05'E., Lamington National Park, QM G8795, 8796; 26°23'S.153°07'E., Noosa, QM G8833; BMNH 1979.1.2, BJ 1978.5.1, 2; 26°51'S.151°34'E., Bunya Mountains National Park, BMNH 1979.1.1, QM G8847; 28°08'S.153°14'E., Numinbah Valley (BJ 1975.4.2) - Qld.

Length 33-163 mm. Width (midclitellar) 3.6-7.0 mm. Segments 100-161. Pigmented uniform deep purplish or reddish brown dorsally, paler ventrally; no paler intersegmental strips. Body noticeably depressed. First few segments single; thereafter with a tendency to a biannulate condition, with presetal furrow. Prostomium epilobous, open 1/3, 1/2, with dorsal median groove which extends throughout the
Fig. 12.12. *Fletcherodrilus unicus*. Form of nephridial bladders on right side in segments indicated. QM G8795. After Jamieson and Wampler (1979).
body. Peristomium not bisected ventrally. First dorsal pore 4/5 (rudimentary), 5/6 well developed. Setae commencing on II, in 8 regular longitudinal rows though (details in Stephenson, 1933) c is occasionally shifted laterally in the forebody; all rows are irregular caudally; a and b absent unilaterally, or bilaterally, in XVIII. In XII \( aa: ab: bc: cd: dd = 1.8: 1.0: 1.8: 2.0: 9.6 \) (mean of 8). Nephropores conspicuous slits at the anterior border of their segments, a pair in \( d \) lines in V posteriorly; those in II, III and IV progressively further dorsal anteriorly, those of II lying about halfway between \( d \) and the middorsum. Clitellum annular, protuberant, well developed in XIV-XVII but some clitellar development apparently present from 1/2XIII, XIV-XVII, XVIII; dorsal pores obscured but intersegmental furrows and setae retained. A single pore of the pair of prostates and the vasa deferentia midventral in XVII, a small circular orifice concealed in the equatorial but presetal furrow. Accessory genital markings absent. Female pores small, shortly anteromedian (or, Fletcher, dorsomedian) of setae a of XIV. Spermathecal pores unpaired midventral, concealed in the 5 intersegments 4/5-8/9.

Septa 9/10-15/16, 16/17 strongly thickened, with 13/14 and 14/15 the thickest. Dorsal blood vessel single, continuous onto the pharynx and passing under the brain. Last hearts in XII; those in X-XII large latero-oesophageal, each receiving a broad connective from the supra-oesophageal vessel and a very slender connective from the dorsal vessel; commissurals in VII-IX slender, dorsoventral only and differing from the hearts of X-XII in giving off branches to the septa and body wall shortly before joining the ventral vessel. Supra-oesophageal vessel traceable in 1/2X, X-XII, 1/2XIII. Subneural vessel absent. A pair of large latero-oesophageal vessels arising from the suboesophageal vessel in X and passing forward to the wall of the pharynx.
Fig. 12.13. **Fletcherodrilus unicus**. Dorsal dissection, showing the calciferous glands, in segments XIII-XV, and neighbouring organs. Type of *Plutellus* affinis Stephenson (1933), BMNH 1922.5.5.1. (Jamieson, 2000).
Fig. 12.14. *Fletcherodrilus unicus*. A: Left prostate in situ. B: A spermatheca, showing the presence of two diverticula. Type of *Plutellus affinis* Stephenson (1933), BMNH 1922.5.5.1. (Jamieson, 2000).
A pair of latero-parietal vessels arising beneath the oesophagus in XIII and running posteriorly, crossing the prostate ducts. A large, strongly muscular gizzard with the form of an anteriorly widening truncated cone or almost cylindrical, in VI, preceded in IV and V by narrower or equally wide tortuous oesophagus. The oesophagus in VII and VIII narrow, non-vascular, largely suppressed by backward extension of the gizzard; in IX-XV (S2) or XVII (S1) segmentally dilated; in XIII, XIV and XV expanded to form 3 pairs of broadly sessile lateral uniform calciferous glands, largest in XIV. These glands with numerous radial lamellar villi which are not, however, high and do not unite, the lumen of the glands not separated from that of the oesophagus. Intestine commencing at the anterior limit of XVIII, wide and chloragogenous; muscular thickening, caeca and typhlosole absent. Nephridia stomate vesiculate holonephridia, commencing in II: each with a preseptal funnel; the funnels very large in the intestinal region. Nephridial bladders large, at first elongate sacs but by XI or X with knob-like rudiment of a diverticulum which by XI (S2) has become almost as large as the ental region of the bladder. By the intestinal region the bladders are transversely elongate and the diverticulum, of equal width, extending laterally from the pore is almost 1/4 the length of the portion median to the pore. Entry of the nephridial ducts into the bladders is slightly penultimate. Free testes and iridescent fairly small sperm funnels, when detectable, in X and XI; multiloculate, iridescent, racemose seminal vesicles in XI and XII, those in XII slightly the larger; (or, Fletcher, 4 pairs, in IX-XII). Weblike ovaries with many conjoined strings of large oocytes, and funnels in XIII; ovisacs absent. Prostates restricted to XVIII in which the thickly tubular glandular portion passes laterally from the duct. The duct consisting of an ental straight slender portion and ectal thick, initially once coiled, strongly muscular
portion which joins that of the other side within a muscular mound, midventral on the body wall, beneath the ventral nerve cord. Vas deferens joining the thick portion of the muscular prostate duct immediately ectal of the coil. Spermathecae (type material, Fletcher) 5 pairs of stalked pouches with single stalked diverticula, those of each pair opening to the exterior by a common aperture under the nerve cord, but one of each pair rudimentary, and then the pouch and the diverticula about the same length, usually alternately on opposite sides, at other times so consecutively for two or more segments; or (Jamieson and Wampler, 1979) spermathecae 5, unpaired, discharging anteriorly in V-IX; each with an ovoid to sacciform ampulla (on one side of the other of the nerve cord) and a well demarcated, thinner, though short, muscular duct which is joined at the body wall by 2 digitiform to slightly clavate inseminated diverticula; size approximately uniform; length of spermatheca of IX, 1.99 mm; ratio of total length: length duct, 3.1; ratio length: length diverticulum, 1.9.

REMARKS

*Fletcherodrilus unicus*, although restricted to Eastern Australia, between latitudes 20 and 35°S., is the most widely distributed native earthworm. *F. affinis* of Stephenson, 1933, is here regarded as a junior synonym as re-examination of the holotype has revealed that each spermatheca has two diverticula, not the single diverticulum described in Stephenson's account. One of the two diverticula emerges from the ventral body wall on the opposite side of the nerve cord to the ampulla. It is doubtful that this separation of the diverticulum from the spermathecal duct deserves recognition of a separate species. Nevertheless, analysis of this widespread species by
molecular sequencing would be desirable to determine the degree of genetic heterogeneity which might exist.

Fletcher (1889), describing the type specimens, appears to have observed a stage in reduction of paired spermathecae, each of the pair with a single diverticulum, and with one of the ampullae rudimentary, to the unpaired condition observed by Jamieson and Wampler (1979), and seen in all other species of the genus. He noted four pairs of seminal vesicles, in IX-XII, a questionably significant distinction from other material. Stephenson separated *affinis* from *unicus* partly on the absence of vesicles in IX and X. He also noted a third pair of vesicles, small, yet still rather too large to be called vestigial, in XIII. Presence of these is confirmed here for the holotype but their nature is uncertain.

*F. unicus* is weakly to moderately luminescent (*ca* $10^8$ photons s$^{-1}$). The luminescence system cross-reacts with that of the North American acanthurid *Diplocardia longa* (see Jamieson and Wampler, 1979).

*Gemascolex*; Jamieson, 1974b: 87.

**Diagnosis**
Perichaetin throughout the body. First dorsal pore 4/5, rarely 3/4 or 5/6. A combined pair of male and prostatic pores on XVIII. Genital markings intersegmental. Spermathecal pores always intersegmental, 2-4 pairs, the last in 8/9. Gizzard robust, in V or VI. Calciferous glands absent. Meronephric, caudally with two or more (always?) enteronephric nephridia on each side, each with a preseptal funnel. Tufted nephridia present in the pharyngeal region. Holandric. Prostates tubuloracemose. Spermathecae diverticulate.

**Description**
Terrestrial. Body circular in cross section or (*G. bursatus*) dorsoventrally depressed. Prostomium epilobous to tanylobous; peristomium bisected by a longitudinal furrow ventrally (as in *Spenceriella*), which is more conspicuous than other grooving which may be present, or (*G. mirabilis* and *G. stirlingi*) grooving present all round but not more conspicuous ventrally. First dorsal pore 4/5, rarely 3/4 or 5/6. Setae numerous (more than 8) in each segment. Nephropores not externally recognizable. A pair of combined male and prostatic pores on XVIII. Clitellum annular anterior to 18/19; its
intersegments and dorsal pores obscured at maturity but setae visible. Intersegmental genital markings always present. Female pore presetal in XIV and midventral or, as a rare individual variation (*G. lateralis*) paired. Spermathecal pores 2-4 pairs in 5/6, 8/9, 2 pairs in 6/7 and 7/8, or a pair in 5/6 only.

Dorsal blood vessel single; continuous onto pharynx. Hearts in X posteriorly latero-oesophageal, each arising from the short supraoesophageal vessel and from the dorsal vessel. Last hearts in XII or XIII, latero-oesophageal vessels (always ?) present median to the hearts. Subneural vessel absent. Gizzard large, in V or VI. Oesophagus lacking extramural calciferous glands. Intestine commencing in XVII; a ridge-like low or (*G. walkeri*) deep dorsal typhlosole present; caeca and muscular thickening absent. Excretory system meronephric. Paired tufts present in II, III-V of which at least those in IV and V are enteronephric, with ducts entering the buccal cavity and/or the pharynx. Caudally with two to numerous enteronephric meronephridia, each with a preseptal funnel, (always?) discharging into the intestine in each segment and with or without a longitudinal collecting duct (ureter) on each side. Testes and funnels in X and XI; testis-sacs absent; seminal vesicles in XI and XII or rarely in IX, XI and XII. Ovaries and funnels in XIII; ovisacs present or absent. Prostates tubuloracemose; linear, lobulated, with axial lumen throughout which receives lateral canaliculi; vas deferens joining their muscular ducts. Penial setae absent. Spermathecae with diverticula.

**DISTRIBUTION**

Eastern Subregion, Kosciuskan Division. Chiefly South Australia but also Victoria, New South Wales. Questionably Tasmania.

**REMARKS**

The closest morphological affinities of *Gemascolex* lie with three endemic Australian genera, *Spenceriella* Michaelsen, 1907b, *Anisochaeta* Beddard, 1890, and *Oreoscolex* Jamieson, 1973. The four genera possess more than one pair of stomate nephridia per segment. This feature is also seen in *Begemius* which, as a "pheretimoid" is considered by an apomorphic relative of *Spenceriella* (see Jamieson, 1977b). *Spenceriella* and *Gemascolex* are especially close to each other, as in *Gemascolex* and, though requiring confirmation, some species of *Spenceriella*, at least some of the caudal nephridia are enteronephric, opening into the intestine (as probably in *Begemius*), whereas in *Oreoscolex* caudal enteronephry has been deduced only very questionably in the type-species and *O. simulans* is unknown in other species. It is not known whether caudal enteronephry occurs in *Anisochaeta*. *Oreoscolex* further differs from *Gemascolex* and *Spenceriella* among other respects, in having only eight setae per segment and in usually having penial setae.

*Gemascolex* differs from the type-species and many other species of *Spenceriella*, and from typical *Anisochaeta*, in lacking extramural calciferous glands, but these are absent in those species of *Spenceriella* assigned to the *howeana* and *cormieri* species-groups; a further difference is the intersegmental location of the genital markings typical of *Gemascolex* in contrast with the segmental location usual in *Spenceriella*. Both *Gemascolex* and *Spenceriella* differ from the type-species of *Megascolex* in having stomate nephridia, in their enteronephry where this occurs (Bahl, 1946, 1947; personal observations) and in having spermathecal diverticula. In *Gemascolex*, as in
Anisochaeta, the nephridial funnels are preseptal whereas in Spenceriella they are (always?) intrasegmental, in the same segment as the body of the nephridium, excepting the medianmost nephridium which has a presegmental funnel. Despite considerable variation in anatomy in Spenceriella, the type-species, S. notabilis, is clearly not congeneric with that of Gemascolex. Although nephridial systems may show considerable homoplasy, parsimony demands that the different excretory anatomy in Gemascolex compared with Spenceriella, coupled with distinctive features of morphology, be accepted as indicating that Gemascolex is a monophylum. The calciferous gland arrangement in Anisochaeta is distinctive. The generic distinctness of the three genera is borne out, a posteriori, by their strong, though not complete, allopatry.

CHECKLIST OF SPECIES OF GEMASCOLEX
1. G. bursatus Jamieson, 1974b
2. Megascolex crateroides Boardman, 1943
4. Perichaeta dorsalis Fletcher, 1887b
5. G. flindersi Dyne, 2000
6. G. gelasinus Dyne, 2000
7. Perichaeta gracilis Fletcher, 1886b
8. Perichaeta lateralis Spencer, 1892b. syn. Megascolex zietzi Michaelsen, 1907b
9. G. mirabilis Jamieson, 1974b
10. G. newmani Edmonds and Jamieson, 1973
11. G. octothecatus Jamieson, 1974b
12. *G. similis* Jamieson, 1974b
14. *Megacolex terangiensis* Spencer, 1900
15. *G. walkeri* Jamieson, 1974b

**KEY TO THE SPECIES OF GEMASCOLEX**

**Spermathecal pores 1 pair**

1  
   a. Spermathecal pores 1 pair, in 5/6  
      *G. walkeri*  
   b. Spermathecal pores more than 1 pair, in 7/8 or 8/9 anteriorly  
      2

**Spermathecal pores 2 pairs**

2(1b)  
   a. Spermathecal pores 2 pairs  
      3  
   b. Spermathecal pores more than 2 pairs  
      5

3(2a)  
   a. Last spermathecal pores in or near 7/8  
      *G. mirabilis*  
   b. Last spermathecal pore in or near 8/9  
      4

4(3b)  
   a. Preclitellar genital markings present, ectal end of each prostatic duct with discrete bursa copulatrix  
      *G. bursatus*  
   b. Preclitellar genital markings absent, ectal end of each prostatic duct dilated, but lacking a bursa  
      *G. gelasinus*

5(2b)  
   a. Spermathecal pores 3 pairs  
      6  
   b. Spermathecal pores 4 pairs  
      12

6(5a)  
   a. Last hearts in XII  
      10  
   b. Last hearts in XIII  
      7
| 7(6b) | a. Genital marking(s) unpaired, mid ventral | \( G. \text{newmani} \) |
| 7(6b) | b. Genital markings paired | \( G. \text{newmani} \) |
| 8(7b) | a. Spermathecal pores dorsal to the setal rings | \( G. \text{terangiensis} \) |
| 8(7b) | b. Spermathecal pores in setal lines 4-7, about half of the body circumference apart | \( G. \text{terangiensis} \) |
| 9(8b) | a. Male pores about one third of the body circumference apart, median to \( c \). Genital markings paired subcircular, button-like, filling the presetal part of \( X \) in \( b \); in 16/17 and 17/18 in \( ab \) filling the space between the setal arcs of the adjacent segments, those in 16/17 more median than those in 17/18. Spermathecal pores in setal lines 4-6 | \( G. \text{similis} \) |
| 9(8b) | b. Male pores about one fifth of the body circumference apart, each a low porophore lying in a depression and accompanied laterally by a raised slightly larger transverse ridge; a small intersegmental tubercle or papilla (sometimes rudimentary) present in front of and behind each pore at 17/18. Paired eyelike genital markings in 16/17 and in 19/20-22/23. Paired postsetal oval genital markings with pore-like centres immediately in front of and slightly lateral of but contiguous with the spermathecal pores, in VI, VII and VIII (sometimes posterior lateral in the succeeding segment; none reported for the types). Spermathecal pores in setal lines 5-7 | \( G. \text{stirlingi} \) |
| 10(6a) | a. Paired genital markings present intersegmentally and/or on the male porophores. Midventral pores absent | \( G. \text{stirlingi} \) |
b. Genital markings 3 single midventral pores, in 16/17, 17/18 and 18/19; a small single papilla in the middle of XVIII; and a pair of small papillae also on XVIII just in front of the male porophores; only the pair anteriorly in XVIII constant, some or all of the other markings may be absent

\[ G. gracilis \]

11(10a) a. Paired intersegmental genital markings usually present in 18/19, 19/20, commonly in 20/21 and 21/22 and less frequently in 17/18 and 22/23, varying from \( a \) lines at 17/18 to slightly median of \( a \) at 22/23

\[ G. lateralis \]

b. A pair of small circular markings on the male porophores anterior or also posterior to the male pores. Paired markings present or absent intersegmentally in 10/11, 19/20-21/22

\[ G. crateroides \]

12(5b) a. Last hearts in XII, preclitellar genital markings absent

13

b. Last hearts in XIII, preclitellar genital markings present

14

13(12a) a. Spermathecal diverticulum about 2.5 times the total length of the spermatheca; genital markings absent.

\[ G. flindersi \]

b. Spermathecal diverticulum about equal to the total length of the spermatheca; paired post-clitellar genital markings present

\[ G. disparatus \]

14(12b) a. Spermathecal pores in setal lines 5-7. Genital markings including but not restricted to X and XVII

\[ G. octothecatus \]

b. Spermathecal pores in ca. setal lines 8. Genital markings, if present, restricted to X and XVII

\[ G. dorsalis \]
**Gemascolex bursatus** Jamieson, 1974b  
(Fig. 0.40B-E, 13.1, 13.2)

*Gemascolex bursatus* Jamieson, 1974b: 87-88, Fig. 3A, 10C, 11B-E., Table 4.

**TYPE LOCALITY:** 35°22'S.138°30'E., 8 km from Myponga - SA.  
**HOLOTYPE:** AM W6084.  
**PARATYPE:** BJ.

Length 52-64 mm. Width (midclitellar) 1.5-2.5 mm. Segments 81-102. Pigmented purplish-brown dorsally, pale ventrally; setae in pale circular fields. Prostomium tanylobous, narrow, acute, or epilobous, 3/4, open. Canalicula absent. Dorsal pores minute, the first in 4/5. Setae of each side more closely spaced laterally than dorsally and ventrally; *ab* and *bc* approximately equal. Numbers of setae per segment 18 in XII, 16 in XX, 20-22 fifteen segments from the caudal end; *a* and *z* lines straight throughout; anteriorly with a wide break in the setal circlet dorsally and ventrally; posteriorly with a moderate ventral and almost inappreciable dorsal break. Setae *a* and *b* but not *c* absent in XVIII. Clitellum XIII-XVI. Male pores extensive transverse slits, with puckered lips but no porophores, immediately median to setae *c* of XVIII, 1.05-1.30 mm, 0.29-0.38 circumference, apart. A circular, low dome shaped paired (sometimes unilateral) genital marking present at 17/18 and 18/19 in front of and behind the male pore. A pair circular to elliptical markings in 8/9 slightly lateral of *b* lines; a pair of elliptical eyelike markings in sometimes present in 16/17 in *ab*. 
Spermathecal pores 2 pairs, in 7/8 and 8/9, laterally situated gaping clefts, shortly lateral of setal lines 4, 1.37-2.0 mm, 0.48-0.56 circumference, apart.

Strongest septa 9/10-13/14, moderately strongly thickened. Last hearts in XII. Supra-oesophageal recognizable in VII, VIII-1/2 XIII, XIII, well developed. Gizzard in V. Intestine originating in XVII in which it resembles the vascularized regions of the oesophagus; a low tortuous dorsal typhlosole first considerably developed in XXVIII but traceable forward as a rudiment to XXIII. Nephridia: a pair of tufts in each of segments II-V, increasing from small to large posterior; those in IV and V sending composite ducts to the pharynx; those in II and III apparently exonephric; small exonephric tufts in VI accompanied laterally by micromeronephridia; numerous integumentary micromeronephridia in VII posteriorly, at first posterior in their segments; in XVI-XVII especially conspicuous and densely crowded on the body wall; thereafter moderately numerous on each side and posterior in each segment; caudally with several (as many as 8 or 9) enlarged nephridia on each side with a preseptal funnel, at least some of these nephridia on each side sending ducts to the roof of the intestine; accompanied by smaller astomate, (exonephric ?) nephridia; no ureters demonstrable. Sperm funnels in X and XI (iridescent); seminal vesicles racemose, in XI and XII. Ovaries oval laminae with several large oocytes; accompanied medianly by small sacs of unknown function; ovisacs present. Prostates tubularacemose, each with flattened leaflike glandular portion, in XXII-XXVI, XXVII, deeply incised by the septa and adherent to the intestine: the muscular duct straight in XIX-XXII but in XVIII curving medianly around the anterior face of a large subspherical bursa copulatrix. A conical penis-like structure projecting from the bursa into the male genital aperture though not visible externally; vas deferens joining
the junction of prostate duct and gland. Spermathecae 2 pairs, in VIII and IX; duct, ampulla and diverticulum tortuous; the diverticulum (inseminated) slender, tubular, uniloculate, a little larger than the ampulla.

**REMARKS**
The muscular bursae at the ectal ends of the prostate ducts in *Gemascolex bursatus* are unique in the genus.

**Gemascolex crateroides** (Boardman, 1943)
(Fig. 13.3)

*Gemascolex crateroides* Boardman, 1943: 174-176, Fig. 4, 5.
*Megascolex crateroides*; Jamieson, 1971c: 95.
*Anisocheta gracilis* (part.); Blakemore, 2000: 3.

**TYPE LOCALITY:** 31°53'S.152°11'E., Mt. George (8 km from Caves House) - NSW.
**HOLOTYPE:** AMW3320 (Re-examined).

Length 145 mm. Width at mid-body 3 mm. Colour in general a pale cream. Segments 130. Prostomium epilobous 3/5; open; sides converging backwards. First dorsal pores
Fig. 13.3. *Gemascolex crateroides*. Genital field. AM W3388. (Jamieson, 2000).
4/5. Setae in rings interrupted dorsally and ventrally, the dorsal break being slightly the larger; \( aa = 2ab \) in front of the clitellum; slightly less than \( 2ab \) immediately behind the clitellum, and in the remainder of the body = \( 2.5ab \); \( zz \) 1.5-1.75yz in front of the clitellum, 1.5-2yz behind the clitellum and as far back as the commencement of the caudal third, in which \( zz = 2-2.3yz \). In general, setal rows irregular, but \( a \) and \( b \) are paired and in regular lines; owing to the irregularity of line of setae \( c \), \( ab \) may be equal to or slightly greater or less than \( bc \); no other pairing among the setae was observed; numbers 16/V, 17(8+9)/IX, 19(10+9)/XII, 20/XIX, about 20 at midbody (commonly plus or minus 2). Clitellum weakly developed, most of XIII to XVI (= 31/n) (holotype) but annular in XII-XVII (=5) in Bowral specimen, AM W3388, where well developed; it characteristically has a narrow ‘waist’ in preserved specimens. Male pores paired on XVIII, at the summits of low conical swellings of indefinite outline which extend from slightly medial of \( a \) laterally to about \( d \) and from border to border of the segment; between them the body-wall thicker than in XVII and XIX. Male pores large, each a transverse slit with puckered lips, in \( bc \), their most medial limit lying almost in \( b \). In front of the male pores on the slope of the cone and in \( b \), medial of the centre of the male pores, there is a small circular raised glandular ring (probably the opening of a gland pore), here designated as a genital marking. Other genital markings absent in holotype but in a Bowral specimen, there is an additional pair of markings on the male porophores behind and almost occluding the male pores, and there are small but distinct circular genital markings, each with a pore-like centre, in \( ab \) nearer \( a \), in 10/11 (unilateral right), 19/20 (paired), 20/21 (unilateral left) and 21/22 (paired). Female pores paired, open, very close together presetally on XIV (holotype), appearing single, midventral in AM W3388.
Spermathecal pores 3 pairs with slightly tumid lips lying normally intersegmentally between lines of setae c and d, but nearer to d; the presence of additional setae, however, may place them apparently between d and e; as shown in Bowral specimen, almost lateral in location.

Septa 5/6-7/8 slightly thickened; 8/9-13/14 somewhat thicker, 10/11 and 11/12 thicker than the rest; 14/15 and 15/16 about the same as 7/8 and 6/7 respectively. Gizzard, in V, large, firm and muscular (moderately strong); oesophagus in front of the gizzard invaginated backwards into it. Behind the gizzard as far back as segment XV the oesophagus wide and thin-walled and with some not very marked segmental swelling, especially in XII-XIV; in XV and XVI progressively and conspicuously narrowing. Calciferous glands absent. Intestine beginning in XVII (confirmed, AM W3320). Dorsal vessel single, continuous onto the pharynx; last hearts in XII; subneural vessel absent. Meronephric; in the pharyngeal region, nephridia tufted, the tufts converging towards the anterior borders of the segments; a large tuft in V and a smaller one in IV; in VI, nephridia nearer the midventral line are larger than those more laterally placed and show a tendency to tufting. In segment XIV and in those which follow, the tubules are very small and are arranged in each segment in a narrow anterior and posterior transverse band. In XIII anteriad, the band present only along the posterior border; in the spermathecal segments there are, in addition, scattered tubules in the ventral portion of the segment with a tendency to be aggregated towards the anterior border. The tubules in front of XVII appear to be less delicate than those further back. From re-examination, several preseptal nephrostomes on each side caudally (AM W3320) Testes and funnels free in X and XI. Seminal vesicles in XI and XII; the pair in XII, of moderate size but four or five times as large as the more
anterior pair; both pairs finely granular and close in texture and elongated dorsoventrally lateral of the oesophagus but not meeting above or below it. Prostates in XVII and XIX; flattened, irregular in outline, their borders much but shallowly lobed. The left prostate in XIX has its lateral border produced outwards as a conspicuous lobe; the same feature is present in the right prostate, but in XVIII; duct leaving the gland on the left side near its anterior end, but near the posterior end of that on the right; S-shaped, the long axis of the S being approximately parallel with the long axis of the body; vasa deferentia joining prostate duct near but not at its ental end; distal to this point the duct is thin-walled and soft, but proximally it is thicker, shiny and muscular, and widens slightly as it proceeds to the body-wall. Penial setae absent. Ovaries and funnels in segment XIII; ovisacs in XIV. Spermathecae 3 pairs; ampulla ovoid with a series of more or less irregular latitudinal grooves; clearly demarcated from the duct. Duct half or somewhat less of the length of the ampulla and two-fifths of its greatest diameter; proximally, on the side opposite where it is joined by the diverticulum the duct presents a conspicuous swelling which, in a cleared preparation, is seen to be a sessile sac communicating with the duct by a small orifice. Diverticulum tubular, rounded distally, and narrowing for a short distance proximally before joining the duct below the level of the body-wall; at its wide part about three-fifths of the width of the duct and extending outwards to almost half-way along the ampulla. In one spermatheca the diverticulum was very narrow with a spherical swelling at its distal end.
REMARKS

The above account is from the holotype and is chiefly taken from the account of Boardman (1943) but the genital field is illustrated from a Bowral specimen. Boardman considered *Gemascolex* (then *Megascolex*) *crateroides* to be related through its setae and spermathecae to *M. austrinus* and *M. wilsonianus*, both of which are here placed in *Spenceriella*. In a brief examination of the holotype of *crateroides*, which confirms the account of Boardman, the author has demonstrated several preseptal funnels on each side caudally, the *Gemascolex* condition. Combined with the intersegmental position of the genital markings, this militates against placement in *Spenceriella*. In the number of spermathecae and the configuration of the genital markings *G. crateroides* is here considered to be closest to *G. gracilis*. The two species have contiguous distributions considerably to the north of the main *Gemascolex* domain.

**Gemascolex disparatus** Dyne, 2000

(Figs. 13.4, 13.5)

*TYPE LOCALITY:* 35°15'S.138°37'E., Kyeema National Park, closed *Eucalyptus* and *Banksia* woodland, under dense litter cover; Coll. G. Dyne, 11 July 1978 (Holotype; paratypes 1-5); 35°19'S.138°41'E., Mt. Magnificent National Park, in peaty sand podsols under heath vegetation, including *Eucalyptus cosmophylla*, *Banksia ornata*, and *Hakea* spp.; G. Dyne and J. Crosby, 11 July 1978 - SA.

*HOLOTYPE:* ANIC. GD.99.4.1.
Paratypes: ANIC.GD.99.4.2-16.
Other records: 35°20'S, 138°45'E., Cox's Scrub Wilderness Reserve, low heath on sand podsols, G. Dyne, 11 July 1978, specimens not designated as types, ANIC.GD.99.4.17.

Length ?70 (posterior regenerate), 56 mm. Width 3.9, 5.2 mm. Segments 99-120. Form uniformly circular in cross-section. Pigmentless buff in alcohol, pale greyish coloration in life, lacking dorsal pigmentation. Prostomium epilobous 1/3, peristomium not deeply furrowed. First dorsal pore 4/5. Setae 10 on each side in XII, XX, in somewhat irregular rows throughout. Intersetal distances variable, ab being the most consistent; aa = zz (approximately). bc is, on average, the widest intersetal interval on each side, the distance between adjacent setae diminishing dorsally. Nephropores not externally recognizable. Clitellum well-developed, annular, over XIII-XVI. Dorsal pores sporadically visible, setae projecting, but intersegmental furrows mostly obscured. Male pores a pair of slits atop projecting, annulated pseudopenes, in bc of XVIII. Female pore a single median orifice, in XIV, virtually in the setal line; it is situated in a slightly discoloured elliptical patch on the clitellum. Spermathecal pores 4 pairs in 5/6-8/9, appearing as small slits on conspicuously projecting lips, lateral in c-lines. Accessory markings: 2 pairs of elliptical tumescences with sunken central areas, and well-demarcated margins, present in 17/18 and 18/19, ventral of the pseudopenes, in ab.

Septa: no noticeable septal muscularization anteriorly, but some very slight thickening apparent in 10/11 and 11/12. Dorsal blood vessel single, continuous onto the pharynx, sending 3 obvious commissurals ventrally around the gizzard. Last hearts in XII, those in X-XII large with minute connectives from the dorsal vessel and
Fig. 13.4. *Gemascolex disparatus* Dyne, 2000. Genital field. Holotype ANIC. GD.99.4.1.
receiving substantial connectives from the roof of the oesophagus. Supra-oesophageal vessel present in XIII, not recognizable in XI, XII, where the major connectives (which join by a short bridging vessel in those segments) meet a latero-oesophageal afferent, running ventrally around the oesophagus. Supra-oesophageal vessel again discrete in X, IX. Remaining commissurals are dorsoventral only. Gizzard globose, firm and muscular, in VI, with compressible anterior rim. Oesophagus well vascularized, moniliform, in VII-XV, lacking pouching or calciferous glands, though somewhat dilated in X-XIII. Intestine commences with abrupt expansion in XVI. Typhlosole well developed. Meronephric; pharyngeal tufts present in III-V, the latter tufts particularly well developed, with a composite sheaf of ducts which join the pharynx. Composite ducts from the more anterior tufts are also present, and were traced anteriad, presumably entering the buccal cavity. In the intestinal region, there are a large number of small, astomate, presumably exonephric nephridial bodies in each segment, just posterior to the forward septum. In addition to these, there are (commencing in early intestinal segments), 2 conspicuously enlarged (?megameronephridia) on each side, both with preseptal funnels and enteronephric ducts; the far dorsal nephridium sends its duct ventrally, directly to the roof of the intestine, the ventralmost megameronephridium with duct directed dorsolaterally, across the septum. The ventral duct appears to directly enter the intestinal wall, whilst the other joins a pair of longitudinal collecting ducts (ureters) which run the length of the intestine on either side of the dorsal blood vessel; whether these ureters have segmental connectives to the lumen of the gut was not established with certainty, but appears likely. This nephridial arrangement persists caudally, with a slight discernible increase in size of the various nephridial bodies as a whole. Holandric; 2 pairs faintly
Fig. 13.5. *Gemascolex disparatus* Dyne, 2000. Right spermatheca of IX. Holotype ANIC. GD.99.4.1.
iridescent, highly convoluted sperm funnels and dense, flocculent sperm masses are present in X and XI; 2 pairs smoothly rounded seminal vesicles on the anterior septa of XI, XII. Vasa deferentia traceable as a pair of translucent, fairly straight tubes on each side of the nerve-cord, joining the prostatic duct some distance from the gland. Prostataes a pair of simple leaf-like glands restricted to XVIII or large, bilobed, racemose structures extending into XIX, in either case, with a medium-length, strongly muscular duct with ectal dilation, which enters the body wall in XVIII. Ovaries, present as sheaves of numerous oocytes, and large, simple funnels, present in XIII, the oviducts passing posteriorly through septum 13/14 and entering the parietes as quite distinct tubes, presumably fusing within the body wall. Small, paired loculated structures, found both on the posterior faces of both septa 12/13 and 13/14 may be ovisacs. Spermathecae 4 pairs, in VI-IX, subequal in size, and each consisting of a small bulb-like ampulla, long muscular duct (tapering ectally) and elongate-digitiform diverticulum joining the latter near its entry to the body wall. Length right spermatheca of IX = 1.7 mm; ratio length spermatheca: length duct = 1.65; ratio length spermatheca: length diverticulum = 1.19.

REMARKS
In overall morphology, particularly with respect to the development of pseudopenes, and the mutual possession of 4 pairs of spermathecae, *Gemascolex disparatus* resembles *G. octothecatus* (and the Victorian species, *G. dorsalis*). The two South Australian forms are readily separable by consistent differences in the configuration of genital markings: *G. octothecatus* having anterior markings in X, 16/17, and 19/20, which are invariably absent (in all specimens examined) from *G. disparatus*. Further
distinctions include position of the last hearts (XII in *G. disparatus*, XIII in *G. octothecatus*), form of the spermathecae, proportion of stomate megameronephridia present caudally (numerous in *G. octothecatus*, 2 only in the new species), and the more dorsal position of the spermathecal pores in *G. octothecatus*.

*G. disparatus* and *G. octothecatus*, together with *G. similis*, and the Victorian *G. dorsalis*, are members of a distinct species-group, probably resultant from comparatively recent radiation from a common ancestral line. *G. disparatus*, *G. octothecatus* and *G. dorsalis* also form an interesting series exhibiting progressive dorsalwards shifting of the spermathecal pores, suggestive of a departure from the insemination procedure presumed for the majority of Australian megadriles. The coincident retention of pseudopenes in all species of the group may have some relevance to the latter proposal, though a tendency towards parthenogenesis has been noted in at least one species (*G. octothecatus*) by Jamieson, 1974b and in the present study. Isolation of spermatozoa from the spermathecal diverticula of *G. disparatus*, however, is indicative of normal amphimictic reproduction.

**Gemascolex dorsalis** (Fletcher, 1887b)
(Fig. 13.6-13.8)

*Perichaeta dorsalis* Fletcher, 1887b: 618-620.
*Perichaeta dorsalis*; Spencer, 1892b: 26, Pl. 3, figs. 22-24, Pl. 7, 75.
Megascolex dorsalis; Beddard, 1895: 376-377; Sweet, 1900: 118, 119; Michaelsen, 1907a: 15, 1916a: 52; Buchanan, 1909: 72, 73, Pl. 15, fig. 12; Bage, 1910: 225-227, Pl. 44, figs 1-4; Raff, 1910: 249-250, Pl. 50, figs 9, 10; Jamieson, 1971c: 95.
Gemascolex dorsalis; Jamieson, 1974b: 87.

**TYPE LOCALITY:** 38°10’S.145°56’E., Warragul - Vic.

**SYNTYPES:** Lost?

**OTHER RECORDS:** (Spencer, 1892b) Warragul; 35°52’S.145°17’E., Fern Tree Gully; 37°56’S.145°37’E., Gembrook; 37°58’S.145°18’E., Narre Warren; 37°58’S.145°11’E., Dandenong; 37°24’S.143°53’E., Creswick; 37°04’S.144°13’E., Castlemaine; 37°36’S.144°20’E., Myriong; 37°01’S.142°29’E., Grampians; 38°26’S.143°43’E., Gerangamete; and 37°56’S.146°26’E., Walhalla - Vic. (Michaelsen, 1907a) 37°39’S.145°32’E., 37°39’S.145°30’E., The Glen by Healesville, HM V6881 - Vic. 37°53’S.145°18’E., Fern Tree Gully; a paralectotype supposedly of Diporochaeta davallia, NMV F40. 1412, removed by Jensz and Smith (1969) from G121, is in fact a specimen of Gemascolex dorsalis.


Length 56-95 mm. Width 5-7 mm. Segments ca. 130. Colour darker above, especially anteriorly, reddish brown, lighter ventrally. Prostomium epilobous > 1/2. First dorsal pore 4/5. Setae for the first few segments 16, then 20; 24 in front of the clitellum; caudally about 30 per segment; aa well marked, about 2 ab or a little less preclitellar; zz well marked, somewhat narrower than aa, about 2zy. Clitellum annular, XIV-
Fig. 13.6. *Gemascolex dorsalis*. Genital field. (Supposed paralectotype of *Diporochaeta davallia*). NMV F401412. (Jamieson, 2000).
Male pores on conspicuous papillae just ventral of setae c. Genital markings: on the anterior margins of X and XVII, a pair of circular depressions with raised and swollen margins in setal lines \textit{ab} or \textit{bc}; female pores a pair [?] on XIV; or genital markings absent and female pore unpaired midventral in 5 clitellate Eltham specimens (W1401). Female pore also unpaired in \textit{davallia} material. Spermathecal pores 4 pairs, in 5/6-8/9, in approximately setal lines 8-10, the setal rows being not quite straight so that there may be 1 to 3 setae dorsal of the pores; the pores visible from the dorsal aspect.

Six septa, commencing with 8/9, thickened. Last hearts in XIII. Gizzard very large followed by very thin septa (Fletcher); in VI; oesophagus simple in VII and XVI, dilated into vascular swellings in VIII-XIV (Raff),-XV (Fletcher); extramural calciferous glands absent; internally ciliated in XVI (Raff); intestine commencing in XVII (Fletcher; Raff). Nephridia: astomate micromeronephridia, with a pair of stomate exonephric (?), megameronephridia ventrally in all segments behind XX; a pair of dorsal stomate megameronephridia also present in caudal segments, from 50 to the posterior end (Bage). Testes and funnels in X and XI; seminal vesicles 3 pairs, in IX, XI and XII. Ovaries and ducts as usual. Prostates in XVIII and XIX; longer than wide with a central canal throughout which has side-branches (Michaelsen, 1916a); ducts rather long, S-shaped, emerging just behind the anterior extremities of the glands; vasa deferentia joining the duct close to the gland. Spermathecaeae 4 pairs, dorsally situated, in VI-IX; long, slightly tapering pouches, each with an equally long or longer diverticulum.
Fig. 13.7. *Gemascolex dorsalis*. Spermapheca. (Supposed paralectotype of *Diporochaeta davallia*). NMV F401412. (Jamieson, 2000).

Scale still to get!

Gemascolex dorsalis
spermatheca

Diporochaeta davallia?????? Megascolex dorsalis
spermathecae
REMARKS
The above account paraphrases published accounts with some additions from five
clitellate Eltham specimens (W1401). Spencer (1892b) found Gemascolex
(=Perichaeta) dorsalis to be present in a much greater proportion than any other
single species, and he obtained it from very many parts of Victoria. He did not,
however, secure it in Croajingolong, and it did not appear to extend into the east and
north-east parts of Victoria. This distribution accords with the largely South
Australian range of the genus.

Gemascolex flindersi Dyne, 2000
(Figs. 13.9, 13.10)

TYPE LOCALITY: 138°36'E., 31°32'S, on the banks of Wilpena Creek, on the road from the
chalet to sliding rock, in black compacted soil containing much organic matter (subject to
periodic inundations, G. Dyne, 15 July 1978 - SA.
HOLOTYPE: ANIC.GD.95.113.2.
Length 42 mm. Width 2.96 mm. Segments 102. Circular in cross-section; pigmentless
buff in alcohol, whitish-grey in life. Prostomium epilobous 2/3, open. Position of first
dorsal pore 4/5. Setae variable in number, in XII 9 on each side; some ventral setae in
the vicinity of the male pores are conspicuously enlarged, on microscopical
examination seen to possess obscure toothing and notching on the distal extremity.
The latter ornamentation could not be demonstrated for the regular sigmoid setae
elsewhere on the body. The enlarged setae are present in b-lines immediately in front
Fig. 13.9. Gemascolex flindersi Dyne, 2000. Genital field. Holotype ANIC.GD.95.113.2.
of and posterior to the male pores, in XVII and XIX on the right side of the body, whereas on the left side, it is the a setae that are modified. This irregularity may indicate that the acquisition of modified setae in the male genital region is not yet stabilized. Nephropores not visible externally. Clitellum well developed, annular, over XIV-XVII, not protuberant, with intersegmental furrows and setae obvious. Male pores atop small papillae, contoured with wrinkle-marks, in bc, in XVIII. Female pore an inconspicuously centrally located orifice on XIV, presetally in aa. Spermathecal openings 4 pairs, opening far laterally, near f-lines. Accessory markings absent.

Septa: no septa strongly thickened, though 9/10-11/12 appear slightly muscularized. Dorsal blood vessel single, continuous onto the pharynx. Last hearts in XII, only the commissurals in segments X-XII large and heart-like, receiving connectives from both the dorsal vessel and a supra-oesophageal vessel, the latter traceable only in the above segments. Remaining commissurals small, and dorso-ventral only. Gizzard large, muscular, and barrel-shaped, though somewhat compressible, located in VI, with a distinct, readily collapsible rim anteriorly. Oesophagus narrow, internally rugose, and moderately vascular, in VI-XVI, undergoing a pre-intestinal dilatation in XIV-XVI, the intestine proper commences in XVII, typhlosole strongly developed after XX. Meronephric; tufted nephridial bodies present in III-V, increasing in size posteriad, all sending composite ducts anteriorly; these were not traced, but are presumably enteronephric to the pharynx and/or the buccal cavity. In the intestinal region, there are 2 conspicuously enlarged megameronephridia on each side: one near the mid-dorsal line, the other laterally disposed. Both pairs possess obvious preseptal nephrostomes, and independently enteronephric ducts to the intestine in the vicinity of the dorsal blood vessel (the
Fig. 13.10. *Gemascolex flindersi* Dyne, 2000. Right spermatheca of IX. Holotype ANIC.GD.95.113.2.
excretory ducts travelling across the septa). In addition, there are a number of small nephridial bodies with attachment to the junction of septum and parietes in each segment. No discernible change in the above system noted caudally. Holandric; 2 pairs of thin, convolute, but non-iridescent spermatic funnels present in X, XI, associated with a whitish ?spermatozoal coagulum. Two pairs of subequal, compact seminal vesicles apparently undivided into component loculi, in XI and XII. Vasa deferentia visible as translucent, non-iridescent, ducts travelling in fairly straight lines on the body wall, quite separated until XVII, and joining the prostatic duct at its point of exit from the gland. Prostate glands large, indented, leaf-like organs extending into XXI, the duct obviously shiny and muscular, entering the body wall in XVIII, after a single loop. Small clusters of oocytes, and small funnels present in XIII; obscure whitish structures adherent to the posterior faces of septa 12/13 and 13/14 may be ovisacs. Spermathecae 4 subequal pairs, laterally situated, discharging anteriorly in their segments, in VI-IX. Each consists of an urn-like ampulla, short duct, and long, slender -digitiform diverticulum joining the duct at its entry to the body wall. The ental portion of the diverticulum is slightly swollen and, as the remainder of the spermatheca, translucent. No spermatozoal iridescence was demonstrable in any of the diverticula, which, though by no means conclusive evidence, militates against biparental reproduction. Length right spermatheca of IX = 0.87 mm; ratio length spermatheca: length diverticulum = 0.44.

REMARKS
Dyne notes that possession of four pairs of laterally disposed spermathecae and pseudopenis-like papillae qualify *Gemascolex flindersi* for inclusion in the *G.*
octothecatus species assemblage, though the characteristic arrangement of genital markings is lacking. Consideration of additional morphological details (e.g. position of last hearts, number of stomate megameronephridia, presence of ovisac-like structures), suggest close alliance to G. disparatus. Further phyletic speculations are reserved, however, pending a larger series of this species, since the above description is based on a single specimen, the holotype.

Of considerable interest is the presence of apparently modified and enlarged setae in segments in the vicinity of the male pores, a condition which is rare in Australian perichaetins (though of not uncommon occurrence amongst Indian and Burmese forms). These are not identifiable with penial setae which are present in Oreoscolex leai (Michaelsen, 1910b), O. longus Jamieson, 1974a, O. peculiaris Jamieson, 1974a; O. sexthecatus Jamieson, 1974a; O. simulans (Fletcher, 1890); O. wellingtonensis (Spencer, 1895); Trichaeta fielderi (Spencer, 1892b); and Spenceriella (?) macquariensis (Fletcher, 1890). Any correlation between the absence of genital markings in G. flindersi, and the presence of such setae requires confirmation from a large series of specimens.

Gemascolex flindersi appears to be rare in occurrence: extensive careful excavation of a large area immediately adjacent to the site from which the holotype was recovered produced large numbers of the known species, G. stirlingi, but no further specimens of G. flindersi. The former species, for which the locality in question represents a new northernmost record of distribution, bears very little resemblance to G. flindersi, though sympatric with it.
**Gemascolex gelasinus** Dyne, 2000
(Fig. 13.11, 13.12)

**TYPE LOCALITY:** 39°59'S.138°43'E., Mount Lofty, near summit, in Eucalyptus woodland, under dense leaf litter, G. Dyne and H. Clarke, 7 July 1978 - SA.
**HOLOTYPE:** ANIC.GD.99.5.1, ex GD.95.104.1.

Length 88 mm. Width 4.4 mm (midclitellar). Segments 103. Circular in cross-section; buff coloured, with pale dorsal pigmentation in alcohol. First dorsal pore 4/5. Prostomium epilobous 2/3, sides strongly canaliculate, peristomium otherwise smooth. Setae numerous, 19 in XII and XX, in rather irregular longitudinal rows throughout. Setae absent between the male pores. Nephropores externally unrecognizable. Clitellum annular, well developed, though not especially protuberant, in XIV-XVI, dorsal pores partially obscured, setae and intersegmental furrows still pronounced. Male pores a pair of transverse slits with puckered surrounds, each in a slightly raised lateral field in bc (closer to c) in XVIII. Accessory markings consist of small, elliptical, pit-like dimples with glandular surrounds, a pair on each side immediately anterior and posterior of the male pores (roughly aligned with these); a series of 3 median intersegmental markings (the lateral ones in line with a), in 17/18, 18/19 (the latter group missing the left marking), and 19/20, with a single unpaired dimple in line with right setal line a, in 20/21. Preclitellar markings absent. Female pore a single median orifice slightly presetal in XIV. Spermathecal pores 2 pairs not visible without intersegmental teasing: present as unelaborated pits in 7/8, 8/9.
Fig. 13.11. *Gemascolex gelasinus* Dyne, 2000. Genital field. Holotype ANIC.GD.95.104.1.
Septa 5/6 diaphanous, 6/7-8/9 thin, 9/10-11/12 Slightly muscularized, 12/13 moderately so; 13/14-15/16 with slight thickening. Dorsal blood vessel single, continuous onto the pharynx. Supra-oesophageal vessel present 1/2IX-1/2XIII. Last hearts in XII, commissurals in X-XII the only ones of sufficient size to be considered hearts, and are latero-oesophageal; the remainder are diminutive and dorso-ventral only. Gizzard large, shiny, and obviously muscular, in V, lacking a distinct anterior rim. Gizzard connected to the pharyngeal mass by a short length of oesophagus; remaining oesophagus present in VI-XVI; for the most part narrow and internally rugose, though somewhat dilated and more vascularized in XIV-XV, narrowing again in XVI. Intestine commences with abrupt expansion in XVII, a low, rudimentary dorsal typhlosole present. Meronephric; large, convoluted tufts present in IV and V, the latter agglomeration the larger, both sending composite ducts anteriad. Smaller tufts are also found in II and III, the former sending its duct to the extreme anterior region of the buccal cavity (at the mouth), the other to the central buccal cavity region. Oesophageal and intestinal nephridia consist of numerous bilobed, astomate loops (presumed to be exonephric) concentrated in roughly uniform rows at the bases of the anterior and posterior septa of each segment, usually with a greater preponderance of tubules at the posterior septum. Caudally, there are approximately 5 large, coiled megameronephridial bodies on each side, all with prominent preseptal funnels, associated with a number of considerably enlarged, though astomate, nephridia situated more posteriorly in the same segment. Each of the stomate bodies has a duct individually enteronephric to the walls of the intestine; longitudinal ureters are lacking, the dorsal-most excretory ductule entering the gut wall well below the dorsal vessel. Holandric; 2 pairs medium-sized, convoluted and iridescent sperm
Fig. 13.12. *Gemascolex gelasinus* Dyne, 2000. Right spermatheca of IX. Holotype ANIC.GD.95.104.1.
funnels in X and XI, in each segment associated with a dense coagulum of spermatozoa. Pectinate structures adherent to the posterior walls of septa 9/10 and 10/11 may be testes. Seminal vesicles 2 conspicuous subequal pairs in XI and XII. Vasa deferentia traceable as tortuously winding iridescent paired ducts on the body wall, posteriad of XI; these are seen to join the prostatic duct as separate tubes, close to duct/gland junction. Prostatic glands tubulo-racemose; appearing as long, flattened, much indented structures running posteriad to XXIV; the shiny, muscular duct has a single hair-pin loop, and pronounced ectal dilation prior to entering the body wall (though not bulbous and bursa-like). Ovaries, comprising densely packed conjoined oocytic strands and large funnels found in XIII; paired structures adherent to the posterior face of 12/13 may be ovisacs; these ‘organs’ absent from XIV. Spermathecae 2 pairs in VIII and IX, each consisting of an ectally widening conico-sacciform ampulla, long, fairly narrow duct, and greatly elongate, profusely coiled diverticulum, which appears to be inseminated; the latter with a slightly swollen ental tip, and very compactly coiled in situ. The diverticulum joins the duct close to the insertion of the duct into the body wall. Length right spermatheca of IX = (base of ampulla to pore) 2.83 mm; ratio length spermatheca length duct = 2.8.

REMARKS
A number of similarities, including lack of male porophores, position of last hearts and gizzard, number and general form of the spermathecae, indicate fairly close affinities of Gemascolex gelasinus with G. bursatus, a view supported by their geographical proximity. The most striking resemblance is in the mutual possession of much elongate prostate glands, and ectal elaboration of the associated duct (though to
a greater extent in *G. bursatus*). The puckered insinking of the male pores in the new species is also strongly reminiscent of *G. bursatus*. The unique genital field and extreme prolongation of the spermathecal diverticulum (as sometimes seen in *G. lateralis*), however, leaves the integrity of *G. gelasinus* in no doubt.

**Gemascolex gracilis** (Fletcher, 1886b)

(Fig. 13.13, 13.14)

*Perichaeta gracilis* Fletcher, 1886b: 958-960.


*Anisochaeta gracilis* (part.); Blakemore, 2000: 3.

**Type Locality:** 32°09’S.147°44’E., Auburn near Parramatta - NSW.

**Types:** Lost?.

**Further Records:** Newington and 33°52’S.151°04’E., Homebush, AM W1395. 33°57’S.151°04’E., Penshurst, AM W1405. 33°51’S.151°01’E., Auburn (Type locality but not type material), AM W1411. 33°30’S.150°21’E., Mount Wilson, AM W1419. ca 33°40’S.150°40’E., Richmond to Penrith Rd, AM W1433. 33°35’S.150°49’E., Grose Vale, near Richmond, AM W1442. 34°35’S.150°30’E., Burrawa(a)ng, AM W1469. 33°32’S.150°39’E., Kurrajong Heights, AM W1481. W 197552. 33°46’S.151°02’E., Carlingford, AM W1529. 35°43’S.149°09’E., Michelago, AM W2379. Duckmolo Crossing, between Hampton & Oberon, AM W3414. 33°25’S.149°34’E., Bathurst, AM W197548. Wellington Caves, AM W197549, valley off road from Bell - Little Hartley Vale, W 197551. 33°48’S.151°06’E., Ryde, AM W197553. Old Newington, AM W197554. valley off Mt York
Rd towards Hartley Vale, AM W197555. 35°41’S.150°12’E., Kanimbla Valley. AM W197550, W. 197556, both examined) - NSW. 41°11’S.147°15’E.?, Denison Gorge, AM W20797 - Tas?.

Length reaching 110 mm. Width 4 mm. Segments 155. Colour in life a rich dark almost port-wine red above; lighter (yellowish-white) below. Prostomium pear-shaped, epilobous 1/2, 2/3 or more. Peristomium completely bisected by a midventral longitudinal groove (Fletcher only). First dorsal pore about 5/6 or (Kanimbla specimens, AM W197550) in 4/5. Setae from 20 to 24, the number on the anterior segments being slightly greater than that elsewhere (one specimen having 24 per segment in front of, and 20 per segment behind the clitellum); not in perfectly straight longitudinal rows. Setae a retained between the male pores. Clitellum annular, 1/nXIII, XIII-XVI. Male pores slit-like, on papillae, the pores well separated on the lateral margins of the ventral surface in or behind the setal arc in bc; one seta visible on each side on the ventral surface between the pores (confirmed in AM W1433, 197556); a small penis like conical structure protruding from the male pores in AM W1433. Genital markings in types, single midventral 'pores', in 16/17, 17/18 and 18/19; apparently a small single papilla in the middle of XVIII; and a pair of small papillae also on XVIII just in front of the male porophores; only the pair anteriorly in XVIII constant, some or all of the other markings may be absent. There may be additional midventral markings at 19/20 and 20/21, those in 19/20 accompanied by a pair in ab (AM W1433). Female pore single midventral and presetal in XIV (confirmed in AM W197556, 1433). Spermathecal pores 3 pairs, in 6/7, 7/8 and 8/9,
rather lateral in position, from setal lines 4 to 5; the right pore at 6/7 transversely duplicated in (AM W197556).

Dorsal blood vessel single, continuous onto the pharynx. Very large hearts in X, XI and XII. Gizzard in VI, large and moderately compressible (AM W1433); oesophagus in XII to XV very vascular and segmentally dilated but calciferous glands absent. Intestine commencing in XVII, with no lateral caeca. Nephridia meronephric; in AM W1433 tufts in V send ducts to the anterior pharynx and caudal nephridia have preseptal funnels and are enteronephric. Seminal funnels in X and XI, embedded in free sperm masses. Seminal vesicles (incorrectly termed "testes") paired in XI and XII (confirmed in AM W1433). Ovaries elongate, flattened, stalked structures in XIII; oviducts said by Fletcher to open separately on the ventral surface of XIV, but see single pore, above). Prostates a pair of long laterally incised bodies (tubuloracemose) commencing, in XVIII and extending back to XXII (AM W1433) or about XXIV (Fletcher); duct U-shaped, the long leg of the U being anterior, and the concavity of the bend turned towards the prostates; or the duct irregularly S-shaped; vasa deferentia join the prostatic ducts close to the gland. Spermathecae 3 pairs, in segments VII, VIII, and IX, opening anteriorly; each spermatheca consists of a large pear-shaped or rounded ampulla with a narrow but distinct stalk from which, at the level that it enters the body-wall, gives off a long filiform diverticulum, much crimped otherwise it would be longer than the stalked pouch (confirmed, AM W1433).
Fig. 13.14. *Gemascolex gracilis*. Showing dorsal and spermathecal pores. AM W197550. (Jamieson, 2000).
REMARKS
The above account is drawn from Fletcher (1886b), augmented from a Kanimbla Valley specimen (AM W197556) and a specimen from the Richmond to Penrith Road (AM W1433). This species is close in morphology and distribution to *Gemascolex crateroides*. It is apparently unique in having setae (the a setae) between the male pores, as in *Propherentima* but differs from the latter in having multiple preseptal nephrostomes.

It is questionable that the Denison Gorge locality is correct, or at least that it is the Tasmanian locality of that name. The coordinates were not given and have been entered from a gazetteer.

**Gemascolex lateralis** (Spencer, 1892b)
(Fig. 0.40 F, 13.15-13.17)

*Perichaeta lateralis* Spencer, 1892b: 11-12, Pl. 4, fig. 55-57, Pl. 7, fig. 78.
*Megascolex zietzi* Michaelsen, 1907a: 17-19, Fig. C, Pl. 12; Jamieson, 1971c: 95.
*Gemascolex lateralis*: Jamieson, 1974b: 88-92, Fig.4A, B, 10D-F, 11F, Table 5.

**TYPE LOCALITY**: (Spencer, 1892b). 37°04'S.144°13'E., Castlemaine; Talarook, Goulbourn Valley.
**LECTOTYPE**: NMV F40214.
**PARALECTOTYPES**: NMV F401424.
Length 45-80 mm. Width (midclitellar) 3-4 mm. Segments 87-109. Circular in cross section. Pigmented purplish brown dorsally with the setae in pale fields. Prostomium epilobous 1/2, 2/3, or appearing tanylobous; not or faintly canaliculate, closed or open. First dorsal pore 4/5. Setae more closely spaced ventrolaterally than dorsally and ventrally on each side; \(ab\) significantly, but not greatly larger than \(bc\) in most segments; numbers of setae per segment 21-31 in XII, 17-24 in XX, 20-38 fifteen segments from the caudal end; a distinct though only moderately wide ventral break present throughout; a dorsal break present in the forebody but behind the clitellum only initially recognizable, or present but narrow throughout. Setae \(a\), \(b\) and \(c\) absent in XVIII or \(a\) and \(b\), only absent. Clitellum XIII, XIV-XVI, 1/3XVII (= 3-4 1/3 segments). Male pores on prominent rounded porophores in \(c\) lines of XVIII, distance apart = 2.04-4.92 mm; ratio of this to circumference = 2.6-0.33. Genital markings: a
Fig. 13.15. *Gemascolex lateralis*. Genital field. SAM 15. After Jamieson (1974b).
pair of eyelike markings in each of intersegments 9/10 and 10/11 in \( ab \); sometimes present in 10/11 only and rarely in 8/9 only; there are rarely 3 pairs, in 8/9, 9/10 and 10/11. These anterior genital markings are commonly absent in specimens with well developed markings in the vicinity of the male genital field. A pair of markings is invariably present in XVIII in front of the male pores and a further pair is usually present behind the pores. In no specimens are the posterior marking, present in the absence of the anterior pair. Paired intersegmental genital markings in the vicinity of the male pores may be absent but they are usually present in 18/19, 19/20, commonly in 20/21 and 21/22 and less frequently in 17/18 and 22/23, varying from \( a \) lines at 17/18 to slightly median of \( a \) at 22/23. Female pore median, unpaired; very rarely paired. Spermathecal pores 3 pairs. clearly visible sunken orifices or inconspicuous in 6/7-8/9, between setal lines 4 and 5: distance between pores = 2.04-5.62 mm; ratio of this distance to circumference = 0.24-0.42.

Several pre-intestinal septa thickened but none strongly. Last hearts in XII. Supraoesophageal vessel in 1/2VIII-1/2XIII. Gizzard in V. Intestinal origin XVII: a very low, rudimentary, dorsal typhlosole first definitely recognizable in XXVII. Nephridia: small paired tufts in II and III with anterolaterally directed composite ducts which in some specimens appear to be exonephric but in the lectotype join the buccal cavity at its anterior limit. Large tufts in IV and V enteronephric, their composite ducts running anteromedially to join the pharynx. Numerous exonephric astomate micromeronephridia present in one or more bands in V posteriorly or visible from II in some specimens, associated with the anterior and posterior septa in XV or XVII posteriorly. Caudally with approximately 8 enlarged nephridia, each with a preseptal funnel on each side: one or two nephridial ducts traced to the roof of the intestine but
Fig. 13.16. *Gemascolex lateralis*. Genital field. SAM 271. After Jamieson (1974b).
probably all enteronephric; no longitudinal collecting ducts demonstrable. Holandric (sperm funnels iridescent in X and XI); seminal vesicles slightly racemose, almost sacciform, 2 or 3 pairs, in IX (some specimens), XI and XII (all specimens). Ovaries, flattened webs or lobes with several conjoined strings of large oocytes, and funnels; a crescentic sac of unknown function sometimes seen on the anterior septum of XIII median to the ovaries; sacs on the anterior septum of XIV questionably ovisacs. Prostates tubuloracemose, with a very narrow central lumen; the broad glandular portion linear, in XVIII-XXII, XXIII deeply incised by the septa; the muscular duct forming a loop at least the ectal limb of which widens strongly but a copulatory bursa absent; the vas deferens joining the duct near its junction with the gland. No glandular masses distinguishable internally at the sites of the external genital markings. Spermathecae 3 pairs, diverticulum (inseminated) single, tubular, very long and much coiled.

REMARKS
The possibility that an infraspecific morph, subspecies (exemplified by AM W6806) or, less likely, a sibling species should be recognized for at least some populations which have genital markings on XVIII both behind and in front of the male pores deserves investigation. In such specimens the male and spermathecal pores, although in the same setal lines as the typical morph, (exemplified by the lectotype) are usually closer together transversely. The spermathecal diverticula are, so far as investigated, shorter and less convoluted. Furthermore, paired intersegmental genital markings in the vicinity of the male pores may be absent though frequently present. The occurrence sympatrically on Mt. Lofty of specimens with or without markings behind
the male pores, in addition to those in front, at present militates against recognition of subspecies. However, it is hoped that a statistical examination of morphology in populations of *G. lateralis* and of their biology, together with molecular studies, will be undertaken with a view to determining the status of the variants mentioned.

Baker (1996a) gives a valuable report on the activity of *Gemascolex lateralis* in eucalypt woodland in South Australia. It is described as one of the most common native earthworm species in South Australia (see also Rainfall, in Introduction).

**Gemascolex mirabilis** Jamieson, 1974b
(Fig. 13.18, 13.19)

*Gemascolex mirabilis* Jamieson, 1974b: 92-94, Fig. 5, 10G, Table 6.

**TYPE LOCALITY:** 32°48'S.138°10'E., Mt. Remarkable. 32°46'S.138°03'E., Alligator Gorge National Park.

**HOLOTYPE:** AM W6087.

**PARATYPES:** AM W6088-6091. P1-6 BMNH 1978.21-7-8. SAM E1568-1569.

Length 60-83 mm. Width (midclitellar) 5.5-6.9 mm. Segments 120-128. Circular in cross section. Pigmentless with the exception of the brownish clitellum. Prostomium epitanylobous, closed at 1/3 peristomium and lateral borders to 0/1 not certainly distinguishable from longitudinal furrows on the peristomium but bisected by a deep canalicula to 0/1. Peristomium longitudinally grooved all round but not bisected ven-
trally. First dorsal pore 3/4, (imperforate ?), 4/5. Setae subequally spaced, though bc is slightly wider than ab throughout. Numbers of setae per segment 20-21 in XII, 21-22 in XX, 20-21 fifteen segments from the caudal end; a lines straight throughout; z lines straight anterior to, irregular posterior to the clitellum; a ventral and a dorsal break present throughout. Setae a and b but not c, absent in XVIII. Clitellum XIII, 1/3XIII-XVII, 1/3XVIII (= 4 2/3-5 1/3 segments). Male pores minute longitudinal slits in ab near the median borders of a pair of large porophores; the pores 1.40-1.79 mm, 0.09-0.10 circumference apart. The male porophores in some specimens are surrounded by a common, medially narrowing field raised at its edges as a rim-like tumescence which is closely adjacent to the lateral borders of the porophores. Genital markings paired, occasionally unilateral, transversely elliptical tumescences, with slit like centres, extending from lateral of c to median of b in 19/20 and 20/21, often also in 16/17, less commonly in 15/16, 21/22 or 22/23. Spermathecal pores 2 pairs of small pores concealed in 6/7 and 7/8, in ab nearer a, with a faintly demarcated lip in front of each on the preceding segment; the pores 1.371.72 mm, 0.09-0.11 circumference apart.

Strongest septa 9/10-12/13, moderately strongly thickened. Last septal glands in IV, not involving the gizzard. Last hearts in XIII, connectives in X-XIII from supra-oesophageal larger than the dorsal connectives and each joined before it reaches the latter vessel by a vessel from the corresponding side of the oesophageal wall. Supra-oesophageal in XXIII, weakly developed despite the large size of the connectives to the hearts. Gizzard in V. Oesophagus almost suppressed to VIII and short in IX owing to backwards projection of the gizzard; vascularized (though not conspicuously) and dilated in X-XIII, with high internal villi almost occluding the lumen but not uniting
Gemascolex mirabilis

Spermatheca

Right, IX, Holotype

Fig. 13.19. *Gemascolex mirabilis.* Right spermatheca of IX. Holotype AM W6087. After Jamieson (1974b).
axially. Intestinal origin XVII; a well developed, though low, tortuous dorsal
tryplosole commencing in XXV or XXVI. Nephridia: a large pair of tufted nephridia,
with innumerable spiral loops, in VI sending several composite ducts anterolaterally
and anteromedially to the body wall anteriorly in this segment; an extremely large
pair of tufts in V sending composite ducts to the pharynx and additional long
composite ducts running far forward to the vicinity of intersegment 1/2. Pharyngeal
tufts commencing, very small, in III or in IV. Lateral bands of astomate, exonephric
micromeronephridia posterior in their segments in VII-XII or XIII then becoming
progressively more anterior until in XV or XVI they are attached to the anterior
septum, the bands especially dense in XIII-XVII; in the anterior intestinal region with
approximately 13 compact astomate micromeronephridia on each side dependent
from the anterior septum but exonephric. Caudally with approximately 8 enlarged
nephridia on each side, closely adjacent to and encircling the intestine from almost the
middorsal line laterally; each with a large, long-stalked preseptal funnel; these
nephridia sending separate ducts medially to unite as a common duct which passes
diagonally, posteromedially, beneath the dorsal blood vessel on each side, to enter the
body wall posteriorly in the segment; the diagonal duct on each side communicating
by a narrower duct with that of the next adjacent segments. Numerous astomate
apparently exonephric, septal micromeronephridia present at the parietes, surrounding
and concentric with the enlarged, enteronephric nephridia. Holandric (sperm funnels
weakly iridescent in X and XI); seminal vesicles racemose, in XI and XII. Ovaries
composed of several partly united strings of large oocytes. Flattened saclike structures
in XIV may be ovisacs. Prostates tongue-shaped, restricted to and passing laterally in
XVIII, incised once to twice so as to suggest a modified, depressed tubular form; with
a narrow central lumen throughout which has epithelium-lined side branches; the muscular duct widening significantly towards the pore and joined near its ental end by the vasa deferentia, these male ducts running separately from each other in the thick muscular wall of the prostate duct near the lumen of the latter, but not penetrating the lining epithelium to join the lumen until the male pore is almost reached; copulatory bursa absent. Spermathecae 2 pairs, in VII and VIII, the single diverticulum subspherical, sessile, with several internal inseminated loculi: the duct inflated, spindle shaped.

REMARKS
Location of the two pairs of spermathecal pores in 6/7 and 7/8 distinguishes *G. mirabilis* from all published *Gemascolex* species.

**Gemascolex newmani** Edmonds and Jamieson, 1973
(Fig. 13.20, 13.21)

*Gemascolex newmani* Edmonds and Jamieson, 1973: 24-27, Fig.1; Jamieson, 1974b: Fig. 7B.

**TYPE LOCALITY:** 34°50'S.138°49'E., Cudlee Creek. 35°02'S.138°48'E., Hahndorf - SA.

**HOLOTYPE:** AM W6103.


**OTHER RECORDS:** (Jamieson, 1974b) 32°11'S.138°00'E., Warren Gorge - SA.
Length 180-270 mm. Width (midclitellar) 7-11 mm. Segments 155-198. Colour in life: dorsal surface brownish purple, ventral surface pale grey; a dark purplish colour more noticeable at the extremities; some iridescence. Cross section approximately circular. Prostomium epilobous 1/3, bisected by a longitudinal furrow, appearing epitanylobous, owing to longitudinal grooves continuing its lateral limits to the first intersegmental furrow, but numerous equally developed parallel grooves present around the peristomium. Peristomium not bisected ventrally though in some specimens a mid-ventral groove is more conspicuous than others. First dorsal pore 4/5. Perichaetin, setae of each side more closely spaced laterally than dorsally and ventrally; bc slightly wider than ab. Numbers of setae per segment 32-33 (in XII, 26-30 in XX, 31-32 fifteen segments from the caudal end; a lines straight, z lines irregular; a ventral and a dorsal break in the setal circlet appreciable throughout. Setae a and b but not c, absent in XVIII. Nephropores not externally recognizable. Clitellum annular, 1/nXIII, XIV-XVII, 1/n XVIII; intersegments and setae retained but only a and b conspicuous; dorsal pores 13/14-17/18 occluded. Male pores a pair in XVIII, transverse slits in ab or b and almost as wide as ab, each on a low transversely oval papilla, the two papillae outlined by a common medianly narrowing field; the pores 2.8-3.2 mm, 0.08-0.09 circumference apart. Genital markings unpaired, midventral, transverse, elevated pads, with lateral limits in ab in one or, most commonly, all of 15/16, 16/17 and 19/20, each pad traversed by a glandular trench corresponding with the intersegmental furrow but not reaching to the ends of the pad; the markings sometimes absent even in clitellate specimens. Female pore unpaired, midventral, in a deep transverse groove at the anterior border of the setal annulus of XIV.
Fig. 13.20. *Gemascolex newmani*. A and B: Anterior and posterior genital field. Holotype AM W6103. After Edmonds and Jamieson (1973).
Spermathecal pores 3 pairs of sunken orifices, concealed in intersegments 6/7, 7/8 and 8/9, very shortly lateral of setal lines a, 2.8-2.9 mm, 0.09 circumference apart.

Septa 10/11-12/13 very strong. Dorsal blood vessel single, continuous onto the pharynx. Supra-oesophageal vessel occupying VII-XIV, ramifying on the oesophagus at each end. Dorsoventral commissural vessels in V-XIII; those in X-XIII forming large latero-oesophageal hearts, each originating from the supra-oesophageal vessel but also receiving, at its junction with the latter, a slender short connective from the dorsal blood vessel; these hearts otherwise unbranched. Commissurals in V-IX dorso-ventral only, lacking supra-oesophageal connectives, but giving branches to the posterior septum, gut and lateral parietes; all commissurals, including the hearts, valvular. A pair of large vessels originating on the parietes in IV passes posteriorly as a pair of ventrolateral trunks (latero-oesophageal vessels), median to the dorsoventral commissurals, into IX at the posterior septum of which they give branches to the ventral wall of the oesophagus and to the septum. Similar paired trunks (suboesophageal vessels) present in XI-XVI, closely adherent to the ventral surface of the oesophagus and lying under its peritoneum; no continuity demonstrable between the latero-oesophageal vessels in IX anteriorly and the suboesophageal vessels in XI posteriorly; both pairs of vessels give a pair of vessels to the oesophageal plexus in each segment. Subneural vessel absent. Gizzard moderately large, fusiform, and firmly muscular in VI; septum 5/6 adherent to its anterior end; its posterior end projecting a little behind intersegment 7/8; the oesophagus much narrower in V, short and narrow in VII; dilated and vascularized with low internal rugae, but no calciferous glands, in VIII-XV, narrow and short in XVI. Intestinal origin XVII or, more usually, XVIII; a low ridgelike dorsal typhlosole commencing in XXIII; caeca and muscular

B.G.M. Jamieson 11/10/00
thickening absent. Nephridia: meronephric; large paired tufts, with very many spiral loops, in II, III, IV and V increasing in size posteriad and very large in V. Those in V and IV sending anteromedianly thick sheaves of numerous ducts, which loosely aggregate as a composite duct common to both pairs of tufts, the ducts passing forward to join the lateral wall of the buccal cavity in front of the brain. Those in III and II sending slender composite ducts to the lateral walls of the buccal cavity immediately behind the mouth. Nephridia in succeeding segments astomate, exonephric, micromeronephridia: very dense transverse bands of spiral tubules, which laterally may be considered to form tufts, anterior in VI, their numerous discrete or partly aggregated ducts discharging exonephrically at the anterior limit of the segment; some exonephric nephridia present posteriorly in the segment; VII-X each with an anterior and a posterior parietal band of numerous nephridia; XI, XII and XIII with similar but rather sparse bands; XIV with sparse anterior and dense posterior bands; XV with denser anterior and sparse posterior bands; XVI (the last oesophageal segment) and succeeding intestinal segments with only anterior bands; bands dense in XIV-XVII. Caudally, commencing at segment 120 (about 70 segments from the posterior end), with numerous enlarged nephridia (almost megameronephridia) in each segment on the anterior wall of the segment near to and encircling the intestine, the nephridia about five deep and each with a long-stalked conspicuous preseptal funnel, the nephridial ducts in each segment running medially as a common duct on each side to enter the wall of the intestine anteriorly in the segment on each side of the dorsal blood vessel, though some individual nephridial ducts reach the wall of the intestine independently in the vicinity of their nephridial bodies. Concentric with and external to the enlarged, enteronephric nephridia are parietal astomate, apparently
exonephric, micromeronephridia in dense transverse bands. The number of enlarged nephridia decreases, and that of the micromeronephridia greatly increases, in the last twenty or so segments. Holandric; sperm funnels iridescent in X and XI; testis-sacs absent; seminal vesicles large lobulated sacs in XI and XII; similar, smaller, structures on the anterior septum of X are of unknown function but cannot positionally be seminal vesicles and do not show spermatogenesis. Ovaries (webs of large oocytes) and funnels in XIII; ovisacs absent. Prostates limited to XVIII, always flattened, lobulated S-shaped glands with short, slightly tortuous, muscular ducts joined near their ental ends by the vasa deferentia. Penial setae absent. Spermathecae 3 pairs, in VII, VIII and IX, diverticulum (inseminated) single, subspherical, internally multiloculate, with a short stalk.

REMARKS

_Gemascolex newmani_ is distinguished from the equally large _Gemascolex stirlingi_, so far as it is described by Fletcher (1887a) in (a) location of the spermathecal and male pores in _ab_ lines whereas in _G. stirlingi_ they are markedly more lateral, in setal lines 6 and between setal lines 3 and 4 respectively; (b) the unpaired instead of paired genital markings and their forward extension to intersegment 15/16; (c) the S-shaped, not straight, prostates and in other respects.

_Gemascolex octothecatus_ Jamieson, 1974b
(Fig. 13.22-13.24)
**Gemascolex octothecatus** Jamieson, 1974b: 94-97, 6A, B, 10H, I, Table 7.

**TYPE LOCALITY:** ca 37°28’S.140°49’E., 11 km S. of Penola. 38°01’S.140°55’E., 27 km from Mt. Gambier- SA.

**HOLOTYPE:** AM W6092.

**PARATYPES:** AM W6093. BMNH 1978.21.9. SAM E1570.

Length 45-64 mm. Width (midclitellar) 4.7-5.4 mm. Segments 71-84 (posterior regenerates ?). Generally circular in cross section but the ventral surface somewhat flattened at and anterior to the male genital field. Pigmented purplish brown dorsally, colourless ventrally, in alcohol; each seta in the pigmented areas surrounded by a colourless circular field. Prostomium not canaliculate or with weak dorsal canalicula, epilobous 1/3-1/2, closed by a deep transverse furrow but continuing posterior as an acute or parallel-sided tongue which almost reaches the first intersegment. First dorsal pore 4/5. Setae of each side more closely spaced laterally than dorsally and ventrally; ab significantly larger than bc; the setae of the ventral couple more conspicuous than others. Numbers of setae per segment: 20 in XII; 18-19 in XX; 26-28 fifteen segments from the caudal end; a lines straight, z lines irregular; a wide ventral and dorsal break in the setal circllet present throughout. Setae a, b and c absent in XVIII. Clitellum XIII, XIV-1/2XVII dorsally (= 3 1/2-4 1/2 segments) annular but ventrally weakly developed in XIII and apparently not developed in XVII; setae a and b clearly visible. Male pores minute, on stump-like, annulated pseudopenes, in cd of XVIII, which are strongly protuberant from gaping slit-like surrounding basal areas which may represent the male pores before eversion of the pseudopenes, the basal slits each borne
on a large annulated porophore; the bases of the pseudopenes 6.4 mm, 0.35 circumference apart. Genital markings paired with pore-like centres, invariably present: presetally in X in b; in 16/17 centred in or slightly median of b; in 17/18 and 18/19 slightly lateral of b; and in 19/20; sometimes present in 12/13, 15/16, and 20/21 slightly median of b. In the high proportion of specimens lacking male pores the genital markings in 17/18-18/19 are slightly more median, lying in ab nearer b, rather than in b lines. Spermathecal pores 4 pairs of distinctly visible small whitish oval papillae, in 5/6-8/9; in a straight line on each side but between setal lines 5 and 6 in 5/6, and between 6 and 7 in 8/9; the last pair 7.7-9.9 mm, 0.57-0.58 circumference apart, i.e. slightly dorsal.

Strongest septa 11/12-13/14, moderately strong. Last hearts in XIII. Supraoesophageal vessel in VII, 1/2VIII-1/2XIII, well developed. Hearts in V, VII-IX dorsoventral only, though still valvular; giving branches to septa and body wall, unlike the more posterior hearts. Gizzard in VI. Intestinal origin XVII; a very low, fairly broad dorsal typhlosole commencing in XIX. Nephridia: a pair of large tufts with many spiral loops in each of segments II-V, increasing in size posteriad, to very large in V; the tufts in II and III sending composite ducts forward in common to join the body wall near the buccal cavity and into the peristomium where they possibly enter the buccal cavity; those in IV and V discharging into the pharynx. Meronephridia parietal and apparently exonephric in transverse bands in VI posteriorly; caudally, from approximately the 50th segment with 8 or more long-necked preseptal funnels on each side and with the median 2 of these stamate nephridia enlarged as megameronephridia the 4 of which lie on the dorsal surface of the intestine and send their ducts to the intestinal wall; the two ducts uniting on each
side of the dorsal vessel, and in continuity with those of neighbouring segments; the longitudinal duct apparently but not certainly opening into the intestine posteriorly in each segment. Laterally the nephridia become progressively smaller, though each retains a preseptal funnel; they are dependent from the anterior septum and some at least send ducts to the roof of the intestine and are apparently also enteronephric. Elongate lobed testes and large complexly folded, pearly but not iridescent sperm funnels in X and XI; 2 or 3 pairs of moderately large saeciform seminal vesicles in XI and XII, or IX also. Prostates large, broad lobed structures in XVIII-XXI, XXII, each deeply incised laterally and less so medianly by the septa; the looped, muscular duct entally narrow, widening strongly and uniformly ectalwards but lacking a terminal bursa; vas deferens joining it near its junction with the gland. Large, paired, low internal glandular masses in XVI-XXI corresponding with external genital markings. Prostates and ectal vasa deferentia absent from individuals which lack male porophores; genital markings retained. Ovaries, when well developed bushy with many large oocytes, and funnels in XIII, accompanied medianly by sacs of unknown function; sacs on the anterior septum of XIV may be ovisacs. Spermathecae 4 pairs, diverticulum single, elongate clavate, uniloculate, shorter or longer than the spermatheca, sometimes coiled.

REMARKS

*G. octothecatus* resembles *G. disparatus, G. dorsalis, and G. flindersi* in possessing four pairs of spermathecae but resembles only *G. dorsalis* in the dorsal location of the spermathecal pores. A further similarity between *G. octothecatus* and *G. dorsalis* is the pair of genital markings at the anterior margins of X and XVII. *G. dorsalis* differs,
however, in restriction of genital markings to these locations in all localities from which it has been reported and in the more dorsal location of the spermathecal pores. *G. similis* also has somewhat dorsal spermathecal pores but differs from *G. octothecatus* in the smaller number of pores, restriction of genital markings to X, 16/17 and 18/19, and the greater development of these markings. These differences of *G. octothecatus* from *G. dorsalis* and *G. similis* are minor compared with those between other species of the genus but union of the three entities in *G. dorsalis* nevertheless does not appear justified.

The prevalence of individuals lacking male terminalia suggests that *G. octothecatus* is commonly parthenogenetic.

Baker (1996a) mapped the occurrence of *Gemascolex octothecatus* at 163 sites near Mortlake, Victoria (see Rainfall, in Introduction).

**Gemascolex similis** Jamieson, 1974b
(Fig. 13.25, 13.26)

*Gemascolex similis* Jamieson, 1974b: 97-98, Fig. 3B, 10J, K, Table 8.

**TYPE LOCALITY:** 37°41'S.140°32'E., 17 km SE of Millicent along road to Mt. Gambier- SA.

**HOLOTYPE:** AM W6094.

Length 40+ mm. Width (midclitellar) 4.5 mm. Segments? Pigmented, purplish brown, dorsally. Circular in cross section. Prostomium epilobous 1/3, closed. Preclitellar

*Gemascolex similis*
setae large, postclitellar indistinct, setae of a side more widely spaced dorsally and ventrally than between, decreasing in size dorsally; \(ab\) slightly wider than \(bc\) throughout. Numbers of setae per segment 18 in XII and XX, 20? (indistinct) in XXXV; \(a\) lines straight, \(z\) lines irregular throughout; a wide ventral break evident throughout; dorsal break wider and clearly visible anterior to the clitellum, poorly defined behind it owing to minuteness and irregularity of the setae; \(a\) and \(b\) absent in XVIII, \(c\) and \(d\) faintly visible on the lateral face of the porophore. Clitellum, apparently occupying XIV-1/2XVII. Male pores minute, on stump-like, annulated pseudopenes, median to \(c\) of XVIII; a basal circumferential groove around each pseudopenis may represent the margins of male pore before eversion of the pseudopenis, this basal groove is itself borne on a large annulated porophore; the centres of the bases of the pseudopenes 4.8 mm, 0.33 circumference, apart. Genital markings paired subcircular, button-like, sharply demarcated tumescences, each differentiated into a peripheral rim and flat or depressed central area, filling the presetal part of X in \(b\); in 16/17 and 17/18 in \(ab\) filling the space between the setal arcs of the adjacent segments, those in 16/17 more median than those in 17/18. Female pore unpaired, midventral in XIV, presetal in an elliptical field. Spermathecal pores 3 pairs, in 6/7, 7/8 and 8/9, inconspicuous whitish ellipses, in setal lines 5-6, 4-5 and 5-6 respectively; 9 mm, 0.54 circumference apart, i.e. slightly dorsal.

Strongest septa 10/11 and 11/12, very strong; 8/9, 9/10, 12/13 and 13/14 also strong. Last hearts in XIII. Supra-oesophageal vessel in IX-1/2XIII; moderately developed. Gizzard in VI. Intestinal origin XVII, a very low ridgelike dorsal typhlosole commencing in approximately XVIII. Nephridia: paired tufts in II-V, increasing posteriads from small to large; those in II and III discharging exonephrically
Fig. 13.26. *Gemascolex similis*. A and B: Left spermatheca of IX and VIII, respectively. Holotype AM W6094. After Jamieson (1974b).
anteriorly in their respective segments; those in IV apparently, but not certainly, discharging into the pharynx; those in V each with a wide composite (multiple) duct running anteromedially to the pharynx wall in III. Numerous exonephric micromeronephridia mostly in posterior bands in their segments in VI-XII; mostly presetal in XIII; anterior and posterior bands of micromeronephridia in XIV-XXI; thereafter mostly anterior in each segment; no nephrostomes present but posterior end missing behind the 40th segment. Holandric: sperm funnels iridescent in X and XI; seminal vesicles saccular, in XI and XII; a pair of small sacs on the anterior wall of X resemble seminal vesicles but in this location presumably do not have a seminal function. Ovaries with several chains of large oocytes, small flattened sacs on each side of them; ovisacs absent. Prostates large flattened lobes, with irregular, lobed, moderately deeply incised margins, restricted to but greatly enlarging XVIII; the tortuous muscular duct gradually but considerably widening through its length to the pore. Large intracoelomic glandular masses are associated with the genital markings. Spermathecae 3 pairs, approximately uniform in size; diverticulum (inseminated) single, digitiform, but that of the left spermatheca of IX with a triloculate terminal dilatation.

REMARKS
G. similis, known only from a single specimen, belongs to a G. dorsalis complex including also G. octothecatus. It differs from both the latter species in having only 3 pairs of spermathecae. Its genital markings have the same distribution as in G. dorsalis though better developed, but it differs from this species in the unpaired female pore and absence of seminal vesicles from IX, in addition to the smaller
number of spermathecae and their more ventral location relative to setal lines. Differences between the three species are minor relative to those between most other species of the genus but union of the three entities under *G. dorsalis* at present appears unjustified.

**Gemascolex stirlingi** (Fletcher, 1887a)
(Fig. 0.40G, 13.27-13.29)

*Perichaeta stirlingi* Fletcher, 1887a: 395-398; 1890: 1017-1019.
*Megascolex stirlingi*; Jamieson, 1974b: 98-100, Fig. 8A, B, 10L, 11G, Table 9.

**TYPE LOCALITY:** (Fletcher, 1887a) 34°58'S. 138°42'E., Lofty Ranges, near Adelaide.
**SYNTYPES:** AM W1351.
**OTHER RECORDS:** (Shannon, 1920) 34°21'S. 138°55'E., 10 miles E. of Kapunda.
SAM E1590. 32°48'S. 138°10'E., Mt. Remarkable, AM. 33°05'S. 138°18'E., 21 km from Gladstone, BJ. 35°00'S. 138°42'E., Crafers, BJ - SA.
**FURTHER SPECIMENS:** "topotypes" of *M. fletcheri* from Kapunda, AM W3432; Burton Station, 64 km from Broken Hill, AM W3032; Torrens, AM W1496.
Fig. 13.27. *Gemascolex stirlingi*. Genital field. AM W6095. After Jamieson (1974b).
Length 100-300 mm. Width (midclitellar) 8-12 mm. Segments 130-258. Pigmented dark olive-brown dorsally. Circular in cross section. Prostomium deeply bisected by a dorsal canalicula, epilobous 1/2, closed, but peristomium with numerous longitudinal furrows all round so that prostomium might be considered epitanylobous; transverse furrows render peristomium and prostomium mammillate. First dorsal pore 4/5 with, in specimen 1, an imperforate rudiment at 3/4. Setae well developed ventrally to midlaterally, rudimentary further dorsally; \( aa \ ca = ab \) but setae progressively more closely spaced dorsally. Numbers of setae per segment not or only approximately countable, 22 in XII, 20 fifteen segments from the caudal end in one specimen; said to number 30-40 per segment in the types; \( a \) lines straight, \( z \) lines irregular, a wide ventral and wider dorsal break in the setal circlet present throughout. Setae \( a \ b \) and \( c \) absent in XVIII. Few intersetal distances measurable. Clitellum 1/2XIII, XIV-XVII; annular except in XIII where it is dorsal only. Male pores transverse slits with low but tumid lips, shortly median of setal lines \( c \) of XVIII (said to be between \( c \) and \( d \) in types), the pores 6.43-6.71 mm, 0.20-0.21 circumference apart; each low porophore lying in a depression and accompanied laterally by a raised slightly larger transverse ridge; a small intersegmental tubercle or papilla (sometimes rudimentary) present in front of and behind each pore at 17/18. Paired eyeliike genital markings in 16/17, centred in \( ab \) nearer \( b \) and in 19/20-22/23, those in 19/20 centred slightly median of \( c \), those in 22/23 slightly lateral of \( c \) or those in 19/20-22/23 all in \( bc \); the markings with raised whitish central area. Paired postsetal oval genital markings with pore-like centres immediately in front of and slightly lateral of but contiguous with the spermathecal pores, in VI, VII and VIII (sometimes posterior lateral in the succeeding segment; none reported for the types). Spermathecal pores 3 pairs, in 6/7, 7/8 and 8/9,
large pores with wide lips forming an ellipse, in the 5th to 7th setal line; the pores, at 8/9, 13.57-14.43 mm, 0.44-0.45 circumference apart.

Strongest septa 9/10-12/13, very thick. Last hearts in XIII. Supra-oesophageal 1/2VIII-XIII, well developed. Gizzard in VI (V according to Fletcher). Intestinal origin XVII (XVIII, Fletcher); typhlosole rudimentary, a slight thickening of the roof of the intestine middorsally first discernible in XXVI. Nephridia: paired tufts with composite (multiple) ducts in II, III, IV and V, all large but increasing in size posteriorly, those in V very large; the tufts in IV and V open into the pharynx; the ducts of those in III apparently join the buccal cavity though some ducts open at intersegment 1/2; whereas those in II appear all to be exonephric in the vicinity of 1/2. Dense lateral bands of numerous (exonephric ?) micromeronephridia lie in VI-XI on the parietes at the posterior septum; in XII-XIX nephridia are anterior as well as posterior in the segment, being especially dense in XIII-XVI; in XX posteriorly they are anterior only in the segment. Caudally with numerous large meronephridia on each side, adherent to the posterior faces of the septa on the intestine and body wall, each with a large single preseptal funnel which has a long inflated neck, the nephridial ducts difficult to trace but apparently (all ?) opening into the intestine. Holandric: sperm funnels iridescent in X and XI. Seminal vesicles racemose, in XI and XII; a further pair of similar but smaller sacs on the anterior septum of XIII median to the ovaries or separate ovaries not developed. Ovaries consisting of many attenuated chains of large oocytes. Large sacs on the anterior septum of XIV may be ovisacs but show no loculi. Prostates tongue-shaped, lobulated and incised, restricted to XVIII, the glandular part passing directly laterally, with slit-like central lumen the greatest width of which is only about one tenth the width of the gland, i.e. gland
Fig. 13.29. *Gemascolex stirlingi*. Left spermatheca of IX. BMNH 1978.21.10. After Jamieson (1974b).
tubuloracemose; the muscular duct S-shaped, with an abrupt bursa-like terminal dilatation. White paired glandular masses in each of segments XVII, XIX-XXIII, corresponding with the external genital markings, large with the exception of those in XIX which correspond with the rudimentary markings in 18/19. Similar paired masses on the body wall in VI, VII and VIII in line with the spermathecal ducts; and corresponding with the external genital markings. Spermathecae 3 pairs, in VII, VIII and IX, increasing in size posteriorly; diverticulum (inseminated) single, clavate, uniloculate.

REMARKS
Location of the genital markings in 16/17 median to the male pores, while those in 17/18-22/23 are approximately in line with these pores, permits ready identification of *G. stirlingi*.

**Gemascolex terangiensis** (Spencer, 1900)

*Megascolex terangiensis* Spencer, 1900: 51-52  

**TYPE LOCALITY:** 38°14'S.142°55'E., Terang - Vic.  
**TYPES:** Lost (Jensz and Smith, 1969).

Prostomium epilobous ca. 1/2. Setae 14-16 per segment in front of the clitellum. Clitellum XIV-XVI. Genital markings a pair of glandular patches in *ab* of XVII, and a
small patch just in front of the male pore on each side. Male pores on prominent papillae on XVIII in bc. Female pores on XIV. Spermathecal pores close to the middorsal line (dorsal of all the setae), 3 pairs, in intersegments 6/7, 7/8 and 8/9.

Alimentary canal, circulatory system, excretory system, and reproductive system similar to those of G. dorsalis, except that the prostate glands extend over more segments.

REMARKS
Because the types or other material of this species can no longer be located, the above account paraphrases the very brief description by Spencer (1900). The species is said to be closely allied to Gemascolex (=Megascolex) dorsalis but to be very clearly distinguished from this and all other species by the unique [even further dorsal] position of the spermathecal pores. It is here transferred from Megascolex to Gemascolex on the grounds of the supposed similarity to G. dorsalis.

Gemascolex walkeri Jamieson, 1974b
(Fig. 0.40H, 13.30, 13.31)

Gemascolex walkeri Jamieson, 1974b: 100-101, Fig. 7A, 10M, 11H, Table 10.

Type Locality: 35°00'S.138°38'E., Belair National Park. 34°58'S.138°42'E., Mt. Lofty.
Holotype: AM W6096.
Length 42 mm. Width (midclitellar) 3 mm. Segments 107-111. Pigmentless in alcohol. Circular in cross section. Prostomium epitanylebous, posteriorly convergent, narrow. First dorsal pore 4/5. Setae ab and bc wide throughout and approximately equal, being slightly wider than other intersetal distances of a side anterior to the clitellum; posterior to the clitellum ab and bc remain the largest intervals but spacing of other setae becomes very irregular. Numbers of setae per segment 14 in XII and XX, 18-22 fifteen segments from the caudal end; a lines straight throughout; z lines straight in the forebody, irregular in the hindbody; a moderately wide ventral break visible throughout; a dorsal break discernible in the forebody but not present in the hindbody. Setae a and b absent in XVIII. Clitellum rudimentary, some annular modification on XIV-XVI. Male pores on hemispheroidal porophores in XVIII; the pores 2.29-2.78 mm, 0.30-0.34 circumference apart. Paired (sometimes unilateral) eyelike ventrally conjoined genital markings constant in intersegments 17/18-23/24, variably also in 24/25, converging posteriorly from ab in 17/18 to a in 24/25. Spermathecal pores 1 pair, ventral in 5/6, small elliptical papillae in setal lines c, 2.43-2.64 mm, 0.34-0.38 circumference, apart.

Strongest septa 10/11 and 11/12, moderately strong. Last hearts in XIII. Supraoesophageal traced in IX-XIII. Gizzard in V. Intestinal origin XVII; a deep laminar dorsal typhlosole commencing in XXI or XXII but continuous as a rudiment forward into XVIII. Nephridia: paired meronephric tufts in II, III, IV and V with composite ducts opening into the pharynx; very large in V, decreasing in size anteriad. Transverse bands of numerous astomate, micromeronephridia exonephric on the body wall in VI-VIII; associated in IX-XV with the posterior septa, in XVI with the
Fig. 13.31. *Gemascolex walkeri*. Right spermatheca of VI. Holotype AM W6096. After Jamieson (1974b).
anterior and posterior septa, and in XVII and succeeding segments with the anterior septa; all septal nephridia lacking detectable parietal ducts (enteronephric ?). Caudally, from about segment 70, with fewer, larger nephridia, approximately 5 on each side, each with a preseptal funnel, the nephridial ducts running on the posterior face of the septum to join the ventrolateral wall of the intestine, some suggestion of a longitudinal duct joining those of adjacent segments seen on the side of the gut but requiring confirmation; postseptal nephrostomes absent; some astomate, parietal and apparently exonephric micromeronephridia present in caudal segments in addition to the stomate nephridia. Holandric: sperm funnels weakly iridescent in X and XI; seminal vesicles racemose, almost sacciform, in XI and XII. Ovaries bushy with several strings of large oocytes; small sacs in XIV may be ovisacs. Prostates flattened, leaflike, with deeply incised margins and a groove-like 'midrib'; restricted to XVIII; duct U-shaped, bent medianwards, the ental limb greatly thickened; vas deferens joining the ental limb at midlength. Spermathecae one pair, in VI, diverticulum (uninseminated) single, digitiform, uniloculate, slightly longer than the ampulla.

REMARKS
The single pair of spermathecae restricted to VI distinguishes *Gemascolex walkeri* from all other species of the genus.

Densities of up to 108 m^{-2} were recorded for *G. walkeri* in pasture soils in the Mount Lofty Ranges, south Australia. It occurred predominantly in the top 10 cm of soil for four to five months per year (autumn to spring), when soils were wettest. During other seasons, it was found lower in the soil profile. Distributions within pastures were patchy and could be explained by soil moisture. Although introduced
species of earthworms (Lumbricidae) generally predominate in pastures in southern Australia, native species such as *G. walkeri* can occasionally constitute a substantial proportion of the total earthworm population (Baker *et al*., 1993).

**14. Geofdyneia** Jamieson, 2000

**DIAGNOSIS**
Pigmented dark red in life. Dorsal pores absent. Setae 8 per segment, the dorsal couple, *cd*, further apart than the distance between the two couples. Nephropores alternating regularly between *d* and *b* from 2/3?, 3/4, throughout the body. Clitellum annular, XIV-XVI. Male pores (combined male and prostatic) on XVIII on extremely large, prominent porophores. Spermathecal pores not externally recognizable but ducts joining the body wall internally at and above *d* lines, in the intersegments.

Last hearts in XII. Gizzard absent. A weakly paired calciferous gland in XIII. Intestine commencing in XVI, muscular thickening absent; a rudimentary, short typhlosole present. Nephridia stomate vesiculate, weakly diverticulate, exonephric holonephridia throughout. Holandric; gymnorchous; seminal vesicles in XII. Prostates thickly tubular, the muscular duct narrow and coiled within the porophore. Penial setae present. Ovaries in XIII. Ovisacs absent. Spermathecae very small, adverticulate, in groups on each side in thecal segments.

**DIAGNOSIS**
As for the single species.
REMARKS
Of known extant species, *Paraplutellus insularis*, from Lord Howe Island is clearly the closest relative of *Geofdyneia rubens* and the two conform so closely, including location of the calciferous gland(s) in XIII, absence of a gizzard, broadly tubular prostates, that it would not be unreasonable to include both in *Paraplutellus*. However, the polythecal condition of *G. rubens* is unique in the native Australian Megascolecidae although it is seen in some species of the Oriental *Pheretima sensu lato* (see Sims and Easton, 1972). Furthermore the absence of dorsal pores is rare in megascolecs and where it occurs is sometimes associated with an amphibious existence, as in *Pontodrilus* and, possibly, *Diporochaeta pedderensis*, for which there is no evidence in *G. rubens*, though also seen in some, terrestrial *Cryptodrilus* species. A further difference from *Paraplutellus* is obligate alternation of nephropores between *d* and *b* lines, whereas in *Paraplutellus* some pores are in *c* lines. In view of these differences, a new genus is here erected for *Cryptodrilus rubens*.

The sister-group status of *Paraplutellus* and *Geofdyneia* suggests vicariation on rifting of the Lord Howe Rise from Eastern Australia, including Mt. Wilson.

DISTRIBUTION
The Blue Mountains region of New South Wales.

TYPE-SPECIES: *Cryptodrilus rubens* Fletcher, 1887a. (Monotypic genus).
**Geofdyneia rubens** (Fletcher, 1887a)  
(Fig. 14.1-14.4)

*Cryptodrilus rubens* Fletcher, 1887a: 381-383.  
*Megascolides rubens*; Beddard, 1895: 491.  

**Type Locality:** 33°30'S, 150°23'E., Mt. Wilson - NSW.  
**Types:** AM W24278. The three re-examined specimens, all clitellate, have not previously been recognized as types. They bear the label ‘Crypto. rubens Mt. Wilson’ in Fletcher’s handwriting. Presented J.J. Fletcher.

**Further Records:** Mount Bushell, near Gosford, J.C. Wiburd 05 08 1935, ident. E.G. Easton 1983, AM W 3390 (Re-examined). Mount Tooti, Blue Mountains, presented by J.J. Fletcher (Nov 1924) 1894 Identifier: E. Easton 1983, AM W 20794 ex W1471, registration card reads "[Diporochaeta sp. (Cryptodrilus cf rubens)]" - NSW.

The following account is drawn from re-examination of the three syntypes, with particular reference to syntype 2 (S2). It largely confirms and greatly extends the brief but careful account of Fletcher (1887a). Some points from Fletcher’s account are given in brackets indicated with his name.

Length 43 mm (S1, previously dissected syntype), 50 mm (S2), 56 mm (S3). Width (midclitellar) 3.8 mm. Segments 112. (Length 55 mm. Width 4 mm. Segments 114, Fletcher). Form moderately slender, circular in cross section throughout, lacking secondary annulation. Pigmentless buff in alcohol, with darker clitellum. (Anterior
Fig. 14.1. *Geofdyneia rubens*. Genital field. Syntype 2 AM W24278. (Jamieson, 2000).
dark red, most noticeable in front of the clitellum, posterior half of the body and ventrum much lighter, presumably in life, Fletcher). Prostomium epilobous >1/2, with moderately narrow, slightly tapering open dorsal tongue; not canaliculate. Dorsal pores absent (neither visible nor demonstrable by effusion in water). Setae in eight regular longitudinal rows, commencing on II; a present, b transformed into penial setae, in XVIII; in XII, aa: ab: bc: cd: dd = 13.8:1.0:1.3: 1.4: 3.3; dd: u = 0.27; thus the dorsal pair of setae are more widely paired than the lateral intersetal distance (bc). Nephropores difficult to discern (not seen by Fletcher) but clearly with complex alternation; in S2, on the left side, distinctly visible in the alternate intersegments 3/4, 5/6, 7/8, 9/10, 11/12, and 13/14 in b line; and in 2/3?, 4/5, 6/7?, 8/9, 10/11 and 12/13 in d lines; alternation on the right side is out of step by one segment with that on the left in S2 and S3. Nephropores are not recognizable with certainty in the hindbody but, internally, bladders alternating regularly between d and b. Thus there is alternation from d to b from 2/3?, 3/4, throughout the body.; Clitellum annular, XIV-XVI, well developed, forming a conspicuous narrow band, about half as long as wide, around the body; setae retained; intersegmental furrows almost obscured, represented by slight constrictions; nephropores partly occluded or not visible. Male pores (combined male and prostatic) on XVIII on extremely large, prominent porophores, with concentric plications, their bases extending from shortly lateral of setae a to well lateral of b lines; each male pore borne on the summit of a subspherical apical prominence; a small callous like papillae (S2) present on the porophore anterior and posterior to this prominence; the anterior of these papillae (or both, Fletcher) has a central pore which is deduced to be the penisetal follicle of its side; in S3, in a different state of protrusion of the porophore, the anterior and posterior papillae are
Fig. 14.2. *Geofdyneia rubens*. Semidiagrammatic dorsal dissection. Syntype 2 AM W24278. (Jamieson, 2000).
distinct from the larger, intermediate, one. Further accessory genital markings absent. Female pores a pair in XIV, very near the midventral line immediately in front of the setal arc. Spermathecal pores not externally recognizable but ducts joining the body wall internally at and above d lines, in the intersegments.

No septa strongly thickened but 7/8-8/9 the strongest Pharyngeal glands extending into VI. Dorsal blood vessel single, continuous onto the pharynx. Dorsoventral commissural vessels in VI-IX, dorsoventral; those in X-XII forming three pairs of large latero-oesophageal hearts each of which receives a connective from the dorsal vessel and one from the oesophageal vasculature. Subneural vessel absent. Oesophagus in V-VI enveloped by the pharyngeal glands, flaccid and in VI almost suppressed. Similar but not obscured, in VII and VIII, a gizzard being totally absent (in VI and in VII a thin-walled globular portion either or both of which may perhaps be a gizzard, Fletcher). In X to XII segmentally dilated. In XIII the oesophagus is swollen and calciferous-like and is weakly bilobed; a middorsal groove which carries the dorsal blood vessel increases the impression of a pair of reniform glands but these are continuous with each other medianly; the only internal impression of pairing is seen in the long closely set internal, free-ending septa, like gills of a mushroom, which tend to form two sets though continuous with the oesophageal lumen which they fill. Oesophagus in XIV and XV narrow. Intestine commencing with abrupt expansion and narrow oesophageal valve in XVI, muscular thickening absent; a low middorsal frill limited the first three segments may be regarded as a short typhlosole. Intestinal contents fragments of dark brown plant material, including many fern sori and portions of leaves, with soil particles, but no obvious siliceous particles, and probably derived from decaying leaf litter. Nephridia stomate vesiculate exonephric.
Fig. 14.3. *Geofdyneia rubens*. Right prostate extended. Syntype 2 AM W24278. (Jamieson, 2000).
holonephridia throughout. The ectal duct of each nephridium with a wedge-shaped expansion which enters the side of a large rounded or irregular bladder the opposite side of which, in the lateral series at least, projects sufficiently to be considered a rudimentary diverticulum; long slender necks traced to the anterior septum near the midventral line but funnels not definitely demonstrable and presumably very small (bladders and alternation not mentioned by Fletcher). Testes and large iridescent funnels, and very large sperm masses, free in X and XI; seminal vesicles racemose, in XII (confirmation). Prostates thickly tubular, restricted to XVIII in which the glands run laterally and then for an equal distance medianly before recurving shortly on itself; the duct narrow and coiled within the porophore and with a strong muscular sheen; the lumen of the gland very narrow relative to the very thick walls. Vasa deferentia not traceable (confirmation). Penial setae present in XVIII; occupying the ental portions of two long slender follicles (each containing two penial setae about 7 mm long gradually tapering to a fine point, Fletcher). Ovaries (consisting of many egg-strings) and moderate sized funnels in XIII. Ovisacs absent. Spermathecae very small, in groups of 4 or 5 on each side (the polythecal condition), discharging anteriorly in each of segments III-IX (30 spermathecae, in 7 segments, per side); each with an ovoid ampulla and a bulbous duct of equal length, but no separate diverticulum. Length of ampulla ca = 0.9 mm, ratio total length: length of duct ca = 2.1. (Spermathecae not seen by Fletcher).

REMARKS
The types of Cryptodrilus rubens were considered lost but the three specimens AM W24278 appear to be the types, for reasons indicated above. They are, at least, of
special significance as they were identified by Fletcher and are from the type locality. They would have been eligible for neotypic status if it had been doubted that they were syntypes. One of the three putative types (S1) had previously been heavily dissected, presumably by Fletcher, and some organs, including the prostates, removed.

Fletcher (1887a) noted that this small worm was the only one with eight rows of setae from Mt. Wilson. When alive it resembled in appearance the small perichaetin worms of the area.

It is noteworthy that Fletcher (1887a) stated that spermathecae are absent whereas some 30 per side are reported here. It is unlikely that Fletcher did not see the structures here identified as spermathecae as they are clearly a normal feature of the species, being present not only in the Mt. Wilson but also in the Mount Bushell specimens. He may well have dismissed them as parasitic organisms but the regularity of their arrangement in the usual spermathecal region of the worm, albeit extending further anteriorly than is usual, and their structure, which is that of adverticulate spermathecae, with ampulla and duct, together with the occurrence of the polythecal condition in some exotic earthworms in, for instance, the Megascolecidae, Lumbricidae and Almidae, leaves little doubt that they are spermathecae. Whereas polythecal spermathecae are sperm-filled in at least the Almidae (Jamieson, 1971), no spermatozoa were seen in those of G. rubens despite the very large free sperm masses in the testicular segments. It might be questioned that the large male porophores of this species could introduce sperm into such minute spermathecae but eversion of the male ducts into the external pores of the spermathecae is conceivable. It is not impossible, though, that the polythecal condition has coincided with development of
parthenogenesis in this species, a condition widespread in earthworms. Failure to detect vasa deferentia would be consistent with this. However, the reproductive biology of this interesting species requires study in new material.

The genus is named after Dr. Geoffrey Dyne in recognition of his profound knowledge of, and contribution to, the systematics and biology of Australian megascolecids.

15. Graliophilus Jamieson, 1971e


**DIAGNOSIS**
Combined male and prostatic pores a pair on XVIII. Setae 8 per segment throughout the body. Nephridia exonephric, stomate, avesiculate holonephridia forming a single series on each side discharging in c or d or above these; sometimes replaced in a varying number of anterior segments by coiled or tufted nephridia with anteriorly directed (always buccal?) ducts. Calciferous glands, present or absent. Prostates thickly tubular. Spermathecae with extramural diverticula, sometimes with sperm-chambers in the walls but never multiloculate.

**DESCRIPTION**
Dorsal pores present. Setae commencing on II, in eight longitudinal rows which are sometimes irregular posteriorly; ventral setal couples moderately closely to widely
paired \((aa = 1.5-4ab)\); setae of the dorsal couples \((cd)\) widely paired to distant \((1.3-2.4ab)\) usually smaller than, rarely equal to or slightly larger than the interval between the couples of a side \((cd = 0.5-1.3bc)\); dorsal median intersetal distance \((dd = 0.2-0.5)\) of the circumference. Penial setae present or absent. Nephropores inconspicuous, if visible; nephridia stomate, avesiculate holonephridia, the ducts of which enter the parietes preentially in \(c\) or in \(d\) or above, in a single series only on each side; present throughout the body or replaced in a varying number of anterior segments by coiled or tufted nephridia the ducts of which pass anteriorly and (always?) open into the mouth. Clitellum ending in XVII or XVIII. Pores of a pair of thickly tubular prostates and the vasa deferentia combined on XVIII. Accessory genital markings present (rarely absent?). Spermathecal pores 2 or less commonly, 3 pairs with the last in 8/9 or (asymmetricus) unpaired in 7/8 and 8/9.

Dorsal blood vessel single, continuous onto the pharynx; latero-oesophageal hearts present, the last in XII or XIII. Gizzard well developed in V (or sometimes VI?). Oesophagus simple or with vascularized dilatations or with true (internally lamellate) but sessile calciferous glands. Intestinal origin varying from XVII-XIX; typhlosole present or absent. Testes in X and XI, 1 to 3 pairs of seminal vesicles present; testis-sacs absent. Ovaries in XIII; ovisacs sometimes present. Spermathecae each with one or two extramural diverticula; the diverticulum single chambered or its wall internally complicated to form seminal chambers.

**DISTRIBUTION**

Western subregion of Australia, Eyrean division, south western faunal province. Five species from the eastern subregion and Tasmania (\(G. macedonensis\), \(G.\)
montiskosciuskoī, G. tripapillatus, G. weldboroughi and G. woodi) questionably included.

TYPE-SPECIES: *Graliophilus georgei* Jamieson, 1971e

REMARKS
The status of the predominantly Western Australian *Graliophilus* Jamieson, 1971b, relative to the *Diporochaeta* + *Vesiculodrilus* assemblage is uncertain, though it is clear that they do not belong to the *D. bakeri* + *D. alsophila* + *V. frenchi* complex. *Graliophilus* was retained by Jamieson (1974a), on the grounds that in Western Australian species the number of spermathecae was less (2 or 3 pairs) than the 5 pairs usual in *Diporochaeta* and that the avesiculate and totally lumbricin condition was constant whereas the combination of these characters was known in only one species of *Diporochaeta* from eastern Australia (Tasmania). Furthermore, some species of *Graliophilus* (though not the type-species) have a typhlosole which has not been allowed as a character of *Diporochaeta* or *Vesiculodrilus* though the eastern species *G. woodi* and *G. tripapillatus*, might be regarded as typhlosolate *Vesiculodrilus*. The low phenetic resemblance between the *Graliophilus* and *Diporochaeta* (represented by species here placed in the *Vesiculodrilus frenchi*-group) demonstrated by Wallace (1972) and the very distinct morphology of some *Graliophilus* species, mostly those of the *strelitzi*-group, suggest that *Graliophilus* should be retained at least until further Western Australian collections are examined. The defining characters recognized here, and in combination, though not individually, distinguishing the genus from *Diporochaeta* and *Vesiculodrilus*, are the lumbricin setae and holonephridia (both,
however, symplesiomorphies) combined with the apomorphic absence of nephridial bladders.

Separation from the largely sympatric *Woodwardiella* is based almost only on the presence of racemose prostates in the latter. It would be interesting to see whether molecular studies upheld this distinction.

Distinct species-groups are discernible in *Graliophilus* and some of these (particularly the *strelitzi*-group) are probably generically distinct although inadequate data on Michaelsen’s species and the refractory condition of the type material preclude formal definition of additional genera.

The following informal species-groups are recognized of which the first five were defined by Jamieson (1971e) and the other two are here defined. It should be noted, however, that some, at least, of the species-groups are sufficiently heterogeneous for their monophyly to be open to question.

(1) georgei group

\[ aa \ ca = 1.4-2.3 \ \ ab; \ cd \ ca = 0.8-1.1 \ \ bc; \ dd \ ca = 0.2-1.4 \ u. \]

Nephridia, stomate, avesiculate holonephridia, with pores in \( c \) lines; (astomate?) tufted (buccal?) nephridia sometimes present anteriorly. Gizzard well developed in V (or VI?); oesophagus simple, or dilated in 1-3 of segments XV-XVIII but not known to possess internal lamellae; intestine commencing in XVIII or XIX; typhlosole absent. Spermathecae 2 pairs, in VIII and IX, each with 1 or 2 simple diverticula, sperm chambers absent.
SPECIES
1. *Graliophilus georgei* Jamieson, 1971e
2. *Plutellus blackwoodianus* Michaelsen, 1907b
3. *Plutellus carneus* Michaelsen, 1907b
4. *Graliophilus secundus* Jamieson, 1971e
5. *Plutellus schumannii* Michaelsen, 1907b
6. *Plutellus termitophilus* Michaelsen, 1907b
7. *Plutellus varicystis* Jackson, 1931
8. *Plutellus wellingtonianus* Michaelsen, 1907b

(2) strelitzi group

\[ aa > \ 3 \ ab \ \; ; \ cd \ ca = 0.7-0.8 \ bc \ \; ; \ dd \ ca = 0.5 \ u. \]

Nephridia stomate, avesiculate holonephridia discharging in or above d lines; (astomate?) buccal nephridia present or absent anteriorly. Gizzard well developed, in V; oesophagus dilated and (always ?) internally lamellate in XVI and/or XVII; intestine commencing in XVIII or XIX; dorsal or spiral typhlosole present. Spermathecae 2 pairs, in VIII and IX, each with a single diverticulum with sperm chambers in the walls.

REMARKS
The combination of characters, nephropores in or above d lines and internally multiloculate spermathecal diverticulum distinguishes the *strelitzi*-group from other *Diporochaeta*-like genera. This apomorphic position of the nephropores is also seen in three other *Graliophilus* species, namely *G. levis*, *G. mendilai* and *G. termitophilus*.
Of these *G. levis*, with 2 spermathecal diverticula, and *G. termitophilus*, both geographically near the *strelitzi*-group, may be closely related to *strelitzi*. *G. mendilai* has a single diverticulum and is geographically distant, possibly indicating independent movement of the nephropores to *d* lines.

Inclusion of these species in *Plutellus*, in which they were originally placed, is precluded by the distinctive characters of the latter genus, including its stalked calciferous glands and alternating nephropores.

The paired eye-like genital markings in intersegments in the vicinity of the male pores may indicate relationship with the eastern Australian *frenchi* species-group of *Vesiculodrilus*, which, however, does not have nephropores in *d* lines. Apart from the questionably apomorphic similarity in genital fields, placement in *Vesiculodrilus* (*frenchi*-group) would be based on the symplesiomorphies of 8 setae per segment and holonephridia in the absence of apomorphies seen in *Plutellus* and other genera. *S. candidus*, in lacking eye–like markings in the vicinity of the male pores and in having the rare condition of a saddle-shaped clitellum is possibly not closely related to the other three species and location in it of nephropores in *d* lines may be a homoplasy. The other three species, namely *strelitzi*, *murrayensis* and *woodwardi*, form a homogeneous group and are not easily distinguished from each other.

**Species**

9. *Plutellus strelitzi* Michaelsen,1907b
10. *Plutellus candidus* Jackson,1931
11. *Plutellus murrayensis* Michaelsen, 1907b
12. *Plutellus woodwardi* Michaelsen, 1907b

(3) mendilai group

aa $ca = 1.7\ ab$; $cd\ ca = 1.3\ bc$; $dd\ ca = 0.3\ u$. Nephridia stomate, avesiculate holonephridia, with pores in $d$ lines. Gizzard in VI; oesophagus dilated in XVI, with high internal lamellae; intestine commencing in XVII; dorsal typhlosole present. Spermathecae 2 pairs, in VIII and IX, each with a single, simple diverticulum; sperm chambers absent.

**Species**

13. *Plutellus mendilai* Michaelsen, 1907b

**Remarks**

The setal ratios of *mendilai* set it apart from all other species of *Graliophilus*. It approaches the *strelitzi*-group in having calciferous glands in XVI and in possessing a dorsal typhlosole but differs in having simple spermathecal diverticula.

(4) levis group

$aa\ ca = 1.5-2\ ab$; $cd\ ca = 1-1.1\ bc$; $dd\ ca = 0.24-0.27\ u$. Nephridia stomate, avesiculate holonephridia, with pores in $d$ lines. Gizzard in V or VI; oesophagus calciferous gland like in XIV or (*whistleri*) segmentally dilated in VII-XVI; intestine (always ?) commencing in XVIII; typhlosole absent. Spermathecae 3 pairs, in VI-IX, each with a single, simple diverticulum (rudimentary in *dalgarangae*).
Species
14. *Plutellus levis* Michaelsen, 1907
15. *Plutellus dalgarangae* Jackson, 1931

Remarks
The grounds for distinguishing these three species from others of *Graliophilus* and for associating them in a single-group are the somewhat distinctive setal ratios (unknown, however, for *dalgarangae*) the 3 pairs of spermathecae, and the calciferous gland like modification of the oesophagus is XIV in *levis* and *dalgarangae*. *G. dalgarangae* is the only Western Australian holonephric megascolecid in which the spermathecal diverticulum is not strongly extramural. In the latter feature it resembles American holonephric megascolecines referable to *Argilophilus*.

(5) asymmetric group

\[ aa \ ca = 1.5 \ ab; \ cd \ ca = bc; \ dd \ ca = 0.3-0.4 \ u. \]  
Nephridia holonephridia, with pores in \( c \) lines. Gizzard in \( V(?) \) or \( VI(?) \); oesophagus segmentally dilated but lacking calciferous glands; intestinal origin?; typhlosole? Spermathecae unpaired, in VIII and IX, each with a single diverticulum with sperm chambers in the walls.

Species
17. *Plutellus asymmetricus* Michaelsen, 1907b
REMARKS
The distinctive but imperfectly known setal ratios together with the unpaired condition of the spermathecae are unique characters, within *Graliophilus*, which, in conjunction with other characters mentioned in the diagnosis, exclude *asymmetricus* from other species-groups of the genus.
The four Eastern Australian species follow.

(6) macedonensis group

*aa ca = 2-4 ab; cd ca = 0.5-1.0 bc; dd ca = 0.3-0.5 u.* Nephridia holonephridia, with pores in *c* lines. Gizzard in *V*; oesophagus segmentally dilated but lacking calciferous glands; intestinal origin XVII or XVIII; typhlosole very strong (*macedonensis, tripapillatus*), or absent? Penial setae present. Spermathecae 3 to 5 pairs, the last in *IX*, each with a single, uniloculate diverticulum.

**Species**
18. *Cryptodrilus macedonensis* Spencer, 1892a
20. *Graliophilus(?) tripapillatus* Jamieson, 1974a
21. *Perionychella (Perionychella) weldboroughi* Jamieson, 1974a

REMARKS
There is sufficient heterogeneity in this group, for instance in setal rations, number of spermathecae, origin of the intestine and presence or absence of a typhlosole, to
suggest that it may not be monophyletic. The first two species share a series of midventral genital markings. The genital field in *G. weldboroughi* is distinctive.

(7) woodi group

aa ca = 3 ab; cd ca = 0.9 bc; dd ca = 0.35 u. Spermathecal pores 2 pairs, in 7/8 and 8/9 in *a* lines. Gizzard in *V*, widening. Intestine commencing at 1/2XVIII; a low typhlosole present. Nephridia avesiculate simple holonephridia throughout, with pores in *c* lines. Penial setae absent. Genital markings corresponding internally with large, rounded sessile glandular masses. Spermathecae 2 pairs, discharging anteriorly in VIII and IX; diverticulum single, uniloculate.

**SPECIES**

22. *Graliophilus woodi* Jamieson, 1973

**REMARKS**

The unusual configuration and structure of the genital markings distinguishes this monotypic taxon from all other *Graliophilus* species and restriction to two pairs of spermathecae separates it from other eastern species of the genus. Association with *Graliophilus* is based on the symplesiomorphic lumbricin, holonephric condition and the synapomorphy (possibly, however, a homoplasy) of avesiculate nephridia. The two pairs of spermathecae is, however, a notable similarity to western species of *Graliophilus*, though not restricted to the genus.
## KEY TO THE SPECIES OF *GRALIOPHILUS*

1  
- a. Spermathecal pores in two intersegments, 7/8 and 8/9  
- b. Spermathecal pores in or near three to five intersegments

2  
- (1a) Spermathecal pores in 2 intersegmental furrows
  - a. Spermathecal pores unpaired, midventral, in 7/8 and 8/9  
    - *G. asymmetricus*  
  - b. Spermathecal pores 2 pairs, in or near 7/8 and 8/9

3  
- (2b) Spermathecal pores 2 pairs appreciably posterior to intersegmental furrows 7/8 and 8/9. Two or three diverticula per spermatheca
  - a. Spermathecal pores 2 pairs in, not posterior to, intersegmental furrows 7/8 and 8/9. One diverticulum per spermatheca; sometimes *(varicystis)* with additional tumescences

4  
- (3a) Two or three diverticula per spermatheca. Clitellum saddle-shaped. Nephropores in *d* lines
  - *G. termitophilus*
  - b. Two diverticula per spermatheca. Clitellum annular. Nephropores in *c* lines
  - *G. wellingtonianus*

5  
- (3b) Nephropores in *d* lines
  - a. Nephropores in *d* lines
  - b. Nephropores in or dorsal to *c* lines

6  
- (5a) Clitellum saddle-shaped
  - a. Clitellum saddle-shaped
  - b. Clitellum annular
7(6a) a. Genital markings four pairs of eye-like genital markings, in 11/12, 12/13, 20/21 and 21/22. Spermathecal diverticulum uniloculate
b. Genital markings a pair of elliptical tumescences at each of intersegmental furrows 7/8 and 8/9, with or without an oval midventral patch on the anterior border of each of VIII and IX; a pair of hemispheroidal markings in 16/17, (17/18), and 18/19; sometimes an unpaired elliptical tumescence, bearing 2 pore-like markings, midventrally in 19/20.

8(6b) a. A pair of very large true calciferous glands in XVII
b. Paired extramural calciferous glands absent. Oesophagus in XV and XVI or XVI and XVII swollen, with internal lamellae

9(8b) a. Oesophagus in XV and XVI swollen, with internal lamellae. Penial setae tipped by a tiny curved tooth; with the exception of this flattened region the distal end marked by two somewhat irregular, longitudinal rows of teeth

G. mendilai
G. candidus
G. strelitzi
G. murrayensis
b. Oesophagus in XVI and XVII swollen, with internal lamellae. Penial setae beset distally with thorns; the distal tip flattened at each side, forming two lateral seams at right angles to the plane of the curve, which extend in front of the point, their junction being marked by a small notch.

G. woodwardi

10(5b)  a. Genital markings include paired and midventral circular prominences, each with a pore like centre, in each of XVII, XVIII and XIX. (Eastern Australian)  
        b. Genital markings not as in 'a'

G. woodi

11(10b) a. An oval midventral glandular field, bearing a small papilla, in each of 12/13, 16/17 and 19/20. Penial setae present
        b. Genital markings not as in 'a'. Penial setae absent

G. blackwoodianus

12(11b) a. Genital markings paired oval papillae occur in furrows 10/11, 16/17, 17/18 and 18/19, in ab, each with a suggestion of a central papilla
        b. Genital markings not as in 'a'

G. carneus

13(12b) a. Large ovoid tumid pad with pore-like centre which is situated in ab paired, or unilateral, extending from midventral to shortly lateral of b line, in 9/10, 10/11, 16/17 and 17/18.
        b. Genital markings not as in 'a'

G. secundus
14(13b) a. Genital markings include a median unpaired low glandular papilla at 16/17 and 19/20, that in 19/20 flanked at least on the right side by a dark tumid circular area lateral of $b$ line, the lateral and median markings lying in a common genital field which reaches from the setal arc of XIX to the posterior border of XX. Indistinct paired genital markings with depressed centres and very wide oval rims present in each of intersegments 12/13 and 13/14; the anterior pair contiguous medianly

b. Genital markings include a pair of ventrally conjoined markings in 11/12, a triplet of conjoined eye-like markings one median, and 2 lateral in 16/17; and paired or unilateral markings in 20/21 or 21/22

c. Genital markings two pairs of large ventral-median oval areas in furrows 13/14 and 14/15; 2 or 3 pairs of papillae in the anterior regions of XIX and XX, or XIX, XX and XXI; these papillae connected in pairs by a ventro-median glandular field; sometimes with less developed marking(s) anteriorly in XVIII.

$G. \text{ georgei}$

15(1b) a. Spermathecal pores 3 pairs, in 6/7-8/9

b. Spermathecal pores 4 or 5 pairs

$Spermathecal \text{ pores 3 pairs}$

16(15a) a. Spermathecae lacking distinct diverticula; a swelling present on each side of the duct

b. Spermathecae each with one pear-shaped to clavate diverticulum; rarely (levis) with a supernumerary diverticulum below this

$G. \text{ dalgarangae}$

17(16b) a. Spermathecal pores well median of $a$ lines, almost contiguous midventrally

b. Spermathecal pores in $a$ to $b$ lines

$G. \text{ whistleri}$
18(17b) a. Genital markings midventral unpaired transverse pads in 16/17 and 19/20, sometimes in 15/16; faintly indicated glandular and slightly tumid interruptions of the intersegments, in 17/18 and 18/19
b. Accessory genital markings absent

G. tripapillatus  
G. levis

Spermathecal pores 4 pairs

19(15b) a. Spermathecal pores 4 pairs. Genital markings include unpaired, median transverse glandular tumescences with depressed, groove-like central portions in intersegments 17/18-21/22
b. Spermathecal pores 5 pairs

G. macedonensis  
20

Spermathecal pores 5 pairs

20(19b) a. Paired eye-like markings genital markings present in 17/18-21/22, confluent medianly so as to form transverse midventral tumid bands; those in XVIII lateral to the male pores; a very strongly protuberant unpaired midventral transverse pad in IX to XII
b. Male pores preceded by a pair of medianly contiguous small papillae in 17/18, with a further midventral unpaired papilla at 18/19. Weak presetal midventral unpaired markings present in IX and possibly in more anterior segments

G. montiskosciuskoi  
G. weldboroughi
**Graliophilus asymmetricus** (Michaelsen, 1907b)  
(Fig. 15.1, 15.2)

*Plutellus asymmetricus* Michaelsen, 1907b: 183-185, Fig.11, Pl.1, fig.25.  
*Graliophilus asymmetricus*; Jamieson, 1971e: 476.

**TYPE LOCALITY:** 35°00'S, 117°52'E., Albany - WA.  
**SYNTYPES:** MNHU4229. HM V7100 (Re-examined).

Length 27-35 mm. Width 2-2.8 mm. Segments 95-106. Epilobous. Setae wide apart;  
In XII, \(aa: ab: bc: cd: dd = 1.63: 1.0: 1.83: 1.0: 6.13\); \(dd = 0.40\)u. Nephropores in \(c\) lines. First dorsal pore in furrow 5/6. Clitellum complete, 1/2XIII, XIV-XVII. Male pore indistinct in XVIII, apparently unpaired ventral; 2 unpaired ventral-median spermathecal pores in furrows 7/8 and 8/9. Elongated ventral-median glandular fields, extending almost to the \(b\) line of setae on each side, occur in two or more of segments XIII, XIV, XVI, XVII, XVIII, XIX; the margins of these fields, or only the lateral margins and those distal to the male pores, are thickened and glandular and the centre of each field is marked by a minute papilla. Spermathecal pores unpaired, ventral in 7/8 and 8/9.  

Septa 9/10-11/12 moderately thickened. Gizzard in segment VI (V?); oesophagus simple and sacculated segmentally, without calciferous glands. Nephridia stomate avesiculate holonephridia with long, very slender ducts. Last hearts in XII. seminal funnels in X and XI; 3 pairs of irregular sac-like seminal vesicles, in IX, XI and XII;
Fig. 15.1. *Graliophilus asymmetricus*. Genital field. Syntype HM V7100. (Jamieson, 2000).
Graliophilus asymmetricus
Fig. 15.2. Previous page. *Graliophilus asymmetricus*. Spermatheca. From Michaelsen (1907b).
prostate glands large and tightly coiled with a very short delicate duct. Central canal very narrow, with many irregular inskinkings; gland cells not definitely grouped but appearing to open into them (Michaelsen, 1916a). Penial setae apparently lacking. Spermathecae unpaired; the ampulla sac-like, irregular, and doubled over, the distal part fairly distinct and narrower (constituting an indistinct duct?); the diverticulum contains 2 sperm chambers separated externally by a notch, and opens into the narrow region of the ampulla.

**Graliophilus blackwoodianus** (Michaelsen, 1907b)
(Fig. 15.3, 15.4)

*Plutellus blackwoodianus* Michaelsen, 1907b: 179-180, Fig.8, Pl.1, fig.21, 22; Michaelsen, 1916a: 43; Jackson, 1931: 88.
*Graliophilus blackwoodianus*; Jamieson, 1971e: 476.

**TYPE LOCALITY:** 33°58'S.116°08'E., Bridgetown-WA.
**SYNTYPES:** WAM V4427. MNHU4228. HM V7097 (Re-examined).

Length 18-28 mm. Width 1.3 mm. Segments 90-95. Colour a dirty white, the grey gut contents, nephridia and prostates visible through the skin. Epilobous. Setae wide apart: anteriorly $aa: ab: bc: cd: dd = 2.33: 1.0: 2.0: 1.5: 4.5: dd = 0.28 u$; posteriorly $aa: ab: bc: cd: dd = 1.5: 1.0: 1.17: 1.17: 2.33: dd = 0.22 u$. First dorsal pore 6/7. Clitellum annular (?) XIV-1/2XVIII. Nephropores (clitellar region) in $c$ lines. Male
Fig. 15.3. *Graliophilus blackwoodianus*. Genital field. Syntype HM V7097. (Jamieson, 2000).

Graliophilus (=Plutellus) blackwoodianus

Approximate scale
Fig. 15.4. Previous page. *Graliophilus blackwoodianus*. A: Distal end of penial seta. B: Spermatheca. From Michaelsen (1907b).
pores in XVIII, in a lines, in a transverse pad which extends to b lines. Spermathecal pores 2 pairs in 7/8 and 8/9 apparently medial to a lines. Oval, ventral median glandular fields, each bearing a small central papilla, in 12/13, 16/17, and 19/20.

Septa in the testes-region slightly less delicate than the rest. Gizzard in VI(?); oesophagus lacking calciferous glands. 2 Pairs of testes and seminal funnels in X and XI; 1 pair of seminal vesicles in XII (a second pair further forward?); Prostates long and coiled, the coils becoming tightly pressed together towards the duct, which is short and narrow. Central canal simple; 1/4 thickness of gland (Michaelsen, 1916a). Penial setae curved, gradually tapering distally; the distal end flattened and slightly wider, with an uneven outline; except for the flattened region the setae bear irregular rings of teeth. Spermathecae with a sac-like ampulla merging into a duct which narrows distally; diverticulum opening into the distal end of the ampulla.

**Graliophilus candidus** (Jackson, 1931)
(Fig. 15.5, 15.6)

*Plutellus candidus* Jackson, 1931: 90-92, Fig.6, Pl.15, fig.9, 12, 13.
*Graliophilus candidus*; Jamieson, 1971e: 486-487, Fig.3, 6d, 7e.

TYPE LOCALITY: 32°07'S.116°05'E., Roleystone - WA.
HOLTYPE?: (Jamieson, 1971e) WAM V15-61 (Re-examined).
Fig. 15.5. *Graliophilus candidus*. Genital field. Probable holotype WAMV 15-61. After Jamieson (1971e).
Length 100 mm. Width 0.5 mm. Segments 140. In life unpigmented with a pinkish tinge; in alcohol white and opaque. From VII posteriad, segments triannulate; secondary annuli faint behind the clitellum. Prolobous; peristomium with middorsal longitudinal groove bifurcating on the prostomium. Setae 8 per segment; in XII \( ab: bc: cd: dd = 3.2: 1.0: 1.8: 1.3: 13.2; dd: u = 0.53 \). Clitellum saddle-shaped, XIII-2/3 XVIII, extending to \( b \) lines ventrally. Male pores in \( b \) lines of XVIII on inconspicuous medianly conjoined porophores. Accessory genital markings consisting of elliptical tumescences with depressed centres, a pair at each of intersegmental furrows 7/8 and 8/9, asymmetrically arranged; those on the right side located behind the intersegmental furrows and median to \( a \) lines; those on the left side in front of the furrows and in \( b \) lines (re-examination) or both pairs in \( b \) lines and accompanied by an oval ventral median patch on the anterior border of each of VIII and IX (Jackson). A pair of hemispheroidal accessory genital markings present in 16/17 and weakly represented in 18/19 in \( ab \) nearer \( b \) lines (those in 18/19 tiny, almost contiguous patches in an elongate ventral median papilla, according to Jackson), a suggestion of similar markings being present in 17/18. An unpaired elliptical tumescence, bearing 2 pore-like markings, located midventrally in 19/20 (re-examination). Female pores a pair, in \( ab \) (Jackson) or shortly anteromedian of setae \( a \) (re-examination) of XIV. Spermathecal pores not identified with certainty; a minute pore, with raised circular rim, observable within each of the left accessory markings at 7/8 and 8/9 is presumably a spermathecal pore, therefore median to \( a \) or in \( b \) lines.

Septa 7/8-12/13 slightly thickened, the strongest 11/12. Dorsal blood vessel continuous onto the pharynx. Latero-oesophageal hearts in XXIII. Gizzard large and firmly muscular, in V (small according to Jackson); a muscular but easily compressed
proventriculus present in IV. True but sessile calciferous glands in XVI, a pair of indistinctly separated dorsolateral pouches with longitudinal internal lamellae convergent to the ventrally situated oesophageal lumen; the laminae from anterior and posterior walls not contiguous across the gland. Intestinal origin not certainly determinable, apparently XIX, rather than XVIII cited by Jackson; a very low dorsal typhlosole present. Nephridia stomate, avesiculate, exonephric holonephridia throughout; post-septal bodies commencing in II. Nephridia in the forebody very large and thickly tubular but always simple, their terminal ducts correspondingly wide but not forming bladders, running laterally to enter the body wall presetally in \( d \) lines, anteriorly, then progressively more laterally so that by XVI the duct enters the parietes far dorsally of \( d \) line as at the posterior end of the body. Holandric (free sperm masses in X and XI); a single pair of seminal vesicles, in XII. Prostates tubular, moderately tortuous, the glands slightly lobulated and depressed; in XVIII but projecting into XVII; with narrower, muscular moderately long duct. Penial setae evenly curved with a slight bend at the extreme distal point; the distal third with small spines in rows encircling the seta and become scantier and more scar-like proximally. Two of the three setae of a follicle project from the sac and measure 2.5 and 2.6 mm, respectively, being proximally 0.3 and distally 0.01 mm. in diameter. Spermathecae 2 pairs, discharging anteriorly in VIII and IX, each with a long clavate ampulla, a shorter sacciform diverticulum, and a short conical duct; the internal walls of the diverticulum honeycombed by numerous long seminal chambers; size uniform, length of right spermatheca of IX = 1.47 mm; ratio total length: length duct \( ca = 7 \); ratio total length: length diverticulum \( ca = 2.5 \).
Graliophilus carneus (Michaelsen, 1907b)  
(Fig. 15.7, 15.8)  

_Plutellus carneus_ Michaelsen, 1907b: 182-183, Fig.10, Pl.1, fig.23; Jackson, 1931: 89.  

**TYPE LOCALITY:** 35°00'S.117°52'E., Albany - WA.  
**HOLOTYPE:** HMV7106 (Re-examined).  

Length 90 mm. Width 3 mm. Segments 190. Colour, unpigmented, in life flesh-pink.  
Pro-epilobous. Setae wide apart: $aa = 2$ $ab = bc = 1.3cd = 0.4dd$. First dorsal pore 6/7.  
Clitellum not developed. Nephropores (clitellar region) in _c_ lines. Male pores in _ab_, nearer _a_ (in _b_ lines, Michaelsen) on oval papillae. Female pores close together anteriorly in XIV. Genital markings paired oval papillae occur in furrows 10/11, 16/17, 17/18 and 18/19, in _ab_, each with a suggestion of a central papilla. Spermathecal pores 2 pairs in 7/8 and 8/9 in _a_ lines.  
Septa 5/6-11/12 thickened. Gizzard small, in _V_; oesophagus lacking calciferous glands. Holandric: 2 pairs of seminal funnels in _X_ and _XI_; 1 pair of racemose seminal vesicles in segment 12. Prostates with an irregularly coiled glandular region about 8-10 times as long as the duct. Penial setae absent. Spermathecae with a long sac-like ampulla and a short duct which is entirely hidden in the body wall; diverticulum, simple opening into the distal end of the ampulla.
Fig. 15.7. *Graliophilus carneus*. Genital field. Holotype HM V7106. (Jamieson, 2000).
Graliophilus carneus
Fig. 15.8. Previous page. *Graliophilus carneus*. Spermatheca. From Michaelsen (1907b).
**Graliophilus dalgarangae** (Jackson, 1931)

*Plutellus dalgarangae* Jackson, 1931: 90.
*Graliophilus dalgarangae*; Jamieson, 1971e: 476.

**Type Locality:** 27°47'S.117°01'E., Dalgaranga Station, under rocks, E. of Yalgoo-WA.
**Types:** ?

Length 45 mm. Width < 2 mm. Segments 92. Creamy flesh-colour, the contents of the gut showing through the body-wall and imparting a grey tinge. Spermathecal pores 3 pairs, in 6/7, 7/8, and 8/9.

Holandric; a pair of developing seminal vesicles in XII. Gizzard moderately large in V. Wall of the oesophagus in XIV divided longitudinally into a number of lobes having a rich blood supply. Spermathecae 3 pairs, widely set; ampulla shaped, merging gradually into the duct; distinct diverticulum lacking but with a swelling on either side of the base of the ampulla, which is larger, more distinct, and rather more proximally placed on one side than on the other.

**Remarks**

*G. dalgarangae* resembles *G. levis* in the structure of the oesophagus in XIV and in having 3 pairs of spermathecae, but these spermathecae are of a different type and the gizzard apparently occurs a segment earlier.
Graliophilus georgei Jamieson, 1971e
(Fig. 15.9, 15.10)

Graliophilus georgei Jamieson, 1971e: 476-478, Fig.1a, 7a.

TYPE LOCALITY: 34°04'S.115°02'E., Mammoth Cave, S. W. Australia.
HOLOTYPE AND PARATYPES: WAM V30-70.

Length 80 mm. Width (midclitellar) 2 mm. Segments 145. Form slender approximately circular in cross section throughout; preclitellar segments at first simple to biannulate; but mostly triannulate; postclitellar segments with additional annuli. Pigmentless buff in alcohol but with the clitellum pigmented pale brown. Prostomium very slightly proepilobous. First dorsal pore 4/5. Setae 8 per segment, commencing on II; in regular longitudinal rows throughout with the exception that d becomes irregular at the posterior extremity; ab absent in XVIII. In XII, aa: ab: bc: cd: dd: dc: cb: ba = 2.14: 1.00: 2.07: 1.64: 7.31: 1.71: 2.15: 0.92. Nephropores anterior in their segments, in c lines. Clitellum annular, strongly protuberant, concave ventrally, embracing XIII-XVII with lesser extension to 1/2 XVIII; interrupted ventrally by the male field; intersegments clearly visible; setae and nephropores less clear; dorsal pores obliterated. Male pores in XVIII in ab on a pair of ill-defined but large porophores which fill the segment longitudinally but are crossed by the setal annulus on which the pores are situated. Accessory genital markings a median unpaired low glandular papilla at 16/17 and 19/20, that in 19/20 flanked at least on the right side by a dark tumid circular area lateral of b line, the lateral and median
Fig. 15.9. *Graliophilus georgei*. Genital field. Holotype WAMV 30-70. After Jamieson (1971e).
markings lying in a common genital field which reaches from the setal arc of XIX to the posterior border of XX. Indistinct paired genital markings with depressed centres and very wide oval rims present in each of intersegments 12/13 and 13/14; the anterior pair contiguous medianly. Female pores apparently a pair of medianly almost contiguous pores shortly in front of the setal arc of XIV. Spermathecal pores minute, paired in 7/8 and 8/9, median of a lines. Small papillae in 6/7, 7/8 (and 8/9 ?) are accessory genital markings. The postsetal annulus of VIII and the presetal annulus of IX slightly tumid midventrally.

Septa: 5/6 slightly thickened; 6/7-12/13 moderately thickened; 12/13-18/19 slightly thickened. Last septal (pharyngeal) glands in IV. Dorsal blood vessel single, continuous on to the pharynx. Dorsoventral commissural vessels in VI-XIII; those in VI-IX very slender, dorsoventral only, and each giving off ventrally a lateral branch to the body wall; those in X-XIII wider, though never large, and at least in XI-XIII (and X?) each forming a latero-oesophageal heart, originating from the dorsal vessel and receiving a connective from the slender supra-oesophageal vessel. Supra-oesophageal obscured in VII-XIV. Subneural vessel absent. Gizzard large, firmly muscular and thick-walled in V; preceded in IV by a muscular, transparent proventriculus of similar width and not clearly demarcated from it. No free oesophagus in VI; in VII to XVIII the oesophagus somewhat moniliform, transparent and noticeably vascularized; in the paratype dilatation is most pronounced in XV and XVI and, to a lesser extent XVII; the intestine commences abruptly in XIX: typhlosole and muscular thickening absent. Purely holonephric; stomate, avesiculate exonephric holonephridia conspicuous in XIII posteriorly but traceable forward to III, diminishing in size anteriorly. Large testes, free sperm masses and large iridescent
Fig. 15.10. *Graliophilus georgei*. Spermatheca. Holotype WAMV 30-70. After Jamieson (1971e).
funnels in X and XI; racemose seminal vesicles in IX and XII, larger in XII. Flattened bushy ovaries and funnels in XIII; racemose ovisacs in XIV. Prostates very tortuous somewhat flattened tubes, with closely adpressed coils, in XVIII; each with a very short muscular duct; vas deferens joining the duct near the ectal end of the latter. Penial setae absent. Spermathecae 2 pairs, in VIII and IX, each with a well demarcated sacciform ampulla wider than long and a slightly shorter duct joined at its ectal extremity by a somewhat longer, iridescent, clavate diverticulum; ducts enter body wall in a lines. Size uniform; length of right spermatheca of IX = 0.82 mm; ratio of total length spermatheca: length duct = 2.24; ratio of total length: length diverticulum = 1.27.

REMARKS
Graliophilus georgei is widely different from all south-western Australian "plutelli," with the exception of G. blackwoodianus (Michaelsen, 1907b) and G. whistleri (Michaelsen, 1935), in the disposition of the accessory genital markings and in other characters. G. whistleri differs, among other respects, in its tanylobous prostomium and in having three pairs of spermathecae. The genital field in G. blackwoodianus has similarities to that of G. georgei but differs notably in presence of a marking (median and constant) on XI. It also differs from G. georgei in the ental origin of its spermathecal diverticula and in possessing penial setae.
**Graliophilus levis** (Michaelsen, 1907b)
(Fig. 15.11, 15.12)

*Plutellus levis* Michaelsen, 1907b: 173-175, Fig.5, Pl.1, fig.15, 16; Jackson, 1931: 87.
*Graliophilus levis*; Jamieson, 1971e: 476.

**TYPE LOCALITY:** 32°01'S.115°57'E., Cannington - WA.
**SYNTYPES:** WAM V4430. MNHU4225. HM V7098 (Re-examined).

Length 55 mm. Diameter 2.1mm. Segments 121. Colour, clear grey. Epilobous. Dorsal setal couples widely paired; in XII, \(aa: ab: bc: cd: dd = 2.72:1.0:2.40:2.16:6.56\); \(dd = 0.32 \mu\). First dorsal pore 4/5. Clitellum saddle-shaped, XIII-XVIII. Male pores in \(ab\) (immediately ventral to \(a\) lines, Michaelsen), on distinct oval papillae in XVIII. Spermathecal pores 3 pairs in 6/7-8/9 in \(ab\) (a lines, Michaelsen). No genital markings known though re-examined syntype is fully clitellate.

Septa 9/10-12/13 slightly thickened. Gizzard in VI; oesophagus wrinkled and with a rich blood supply in VII-XIV, and in XIV with an annular sacculcation which resembles a calciferous gland; similar but smaller sacculations in XI, XII, and XIII. Last hearts in XII. Nephridia stomate, avesiculate holonephridia, with very slender ducts discharging in \(d\) lines. 2 pairs of testes and seminal funnels in segments 10 and 11; 2 pairs of seminal vesicles in IX and XII, the foremost sac-like, the hinder racemose. Prostate glands closely coiled with a short narrow duct. Central canal with circular depressions but no definite side branches (Michaelsen, 1916a). Penial setae
Fig. 15.11. *Graliophilus levis*. Holotype HM V7098. (Jamieson, 2000).
Graliophilus levis
Fig. 15.12. Previous page. *Graliophilus levis*. Spermatheca. From Michaelsen (1907b).
irregularly bent and very delicate; the distal tip flattened and rounded and the convex curve immediately below this tip beset with tiny teeth which are extremely difficult to discern. Spermathecae irregular, sac-like and flattened, merging into a short duct; a small pear shaped diverticulum opening into the distal end of the ampulla; a second still smaller diverticulum may occur, opening immediately below the first.

**Graliophilus macedonensis** (Spencer, 1892a)
(Fig. 15.13, 15.14)

*Cryptodrilus macedonensis* Spencer, 1892a: 138-139, Pl.15, fig.16-18, Pl.19, fig.68; Jensz and Smith, 1969: 89.
*Megascolides macedonensis*; Beddard, 1895: 493.

**TYPE LOCALITY:** 37°23'S.144°35E., Mt. Macedon - Vic.
**LECTOTYPE:** NMV F4047 (Re-examined, undissected).
**PARALECTOTYPES:** NMV F401407 (Re-examined). Further (type?) specimens from Victoria, ident. W.B. Spencer, AM W1287 (Re-examined).

Length 75 mm. Width 3 mm. Segments 135 (lectotype, but apparent amputee). Pigmentless buff in alcohol; clitellum brown. Prostomium prolobous (or protanylobous ?). Canalicula absent. First dorsal pore 4/5. Setae commencing in II, in 8 regular longitudinal rows; setae ab absent in XVIII; in XII, \(aa: ab: bc: cd: dd = 3.23: 1.00: 4.84: 2.43: 17.26\); \(dd = 0.47\) µ. Nephropores not generally visible but
Fig. 15.13. *Graliophilus macedonensis*. Lectotype NMV F4047. (Jamieson, 2000).
distinguishable on the clitellum as minute white points in c lines; in a single series on each side. Clitellum annular, embracing XIV-XVII; the posterior third of XVIII also with clitellar modification; dorsal pores visible only at 13/14 and 17/18; setae present; only intersegment 17/18 visible. Combined male and prostatic papillae a pair in XVIII on a pair of small elliptical papillae (almost contiguous or, lectotype, well separated, medianly) with their centres in or very slightly median of a lines. Well developed unpaired, median transverse glandular tumescences with depressed, groove-like central portions in intersegments 17/18-21/22, extending laterally to mid bc and contiguous longitudinally (lectotype and AM W1287); tumid equatorial ridges, perhaps equivalent to the anterior portion of the former markings, present in aa of XXII (AM W1287), XXIII-XXVII (lectotype and AM W1287). A transverse glandular slightly tumid pad in 10/11 fills aa and is surrounded by an approximately oval tumid area expanding laterally beyond b lines and longitudinally from the setal arc of X to that of XI (lectotype), or 10/11 and 11/12 (AM W1287); (markings alternatively in XI and XII, Spencer). Female pores minute points, presetal in XIV, in or immediately median of a lines; they and, in a paralectotype, setae ab enclosed in a slightly tumid transverse field. Spermathecal pores 4 pairs, in 5/6-8/9, elliptical swellings with central pore slightly median to a lines.

Thickest septa 9/10-11/12 which are strongly and equally thickened. No post-pharyngeal septal glands present. Morphology of the vascular system largely indeterminable owing to previous dissection. Dorsal blood vessel single, continuous onto the pharynx. Last hearts in XII (AM W1287). Dorsoventral commissurals of IX slender each giving off a parietal branch ventrally but lacking supra-oesophageal connective; those in X wide hearts lacking the parietal branch but with supra-
oesophageal connective; supra-oesophageal vessel visible in IX and X extent indeterminable elsewhere. No suboesophageal vessel detectable. Gizzard large, cylindrical fusiform, segmental (in V, Spencer), sessile paired lateral swellings of the oesophagus in XV and XVI are probably to be regarded as rudimentary calciferous glands. Intestine commencing, with abrupt expansion, in XVIII; typhlosole very pronounced, a deep narrow middorsal lamina consisting of a single longitudinal blood sinus with thin epithelial covering, commencing shortly behind the intestinal origin. Muscular thickening of the intestine absent. Nephridia all exonephric and avesiculate; present in II posteriorly and one pair per segment; those of II-IV tufted, consisting of numerous loops without recognizable funnels and with apparently composite ducts; tufting most developed in II, those in III and IV with about half the number of loops. Those in V to the last pre-intestinal segment (XVII) each with a very small rounded preseptal funnel, a single ectal duct and three main intermediate loops; the amount of coiling decreasing posteriad. Nephridia in the intestinal region have each a slightly larger nephrostome, and single main intermediate loop, and a narrower duct than more anterior nephridia (Horan, 1971). Testes and large convoluted sperm funnels in X and XI; no testis-sacs seen; much subdivided racemose seminal vesicles in XI and XII (XII only, Spencer). Prostates very thickly tubular and with slight superficial lobulation, bent in a U-shape; restricted to XVIII, each with a short looped muscular duct. Penial setae present, each fairly stout and only slightly curved, length (1 seta) = 0.6 mm, greatest width (mid-shaft) = 18 μm; the tip forming a spout like slightly down-curved projection; the ectal fourth ornamented by transverse, minutely serrate cicatrices which correspond with approximately 13 notches on the profile of the seta, the posterior margin of each notch having the form of a minute anteriorly directed
Fig. 15.14. *Graliophilus macedonensis*. A: Right prostate. B: Right spermatheca of IX. Paralectotype NMV F401407. (Jamieson, 2000).

Diporochaeta macedonensis

G1407, Paralectotype

A - Right, prostate
B - Right, Posterior spermatheca
tooth adpressed to the setal surface. Ovaries somewhat folded large laminae composed of chains of numerous oocytes in XIII; ovisacs absent. Spermathecae four pairs in VI-IX, with ovoid ampulla not sharply demarcated from the nevertheless distinct, ectally tapering duct; the duct as long as or somewhat shorter than the ampulla; a short, inseminated clavate diverticulum situated, anterolaterally on the duct near its ectal end. Spermathacae decreasing somewhat in size anteriorly; length in IX (right side) = 2.7 mm; ratio total lengths: length duct = 1.9 ; ratio total length: length diverticulum = 5.4.

REMARKS
Relationships of *Graliophilus macedonensis* are obscure. It is here placed in *Graliophilus* on the basis of its lumbricin condition with avesiculate holonephridia. This decision is endorsed by presence of typhlosole, a structure absent in *Diporochaeta*. That is it closely related to the other, predominantly Western Australian species of *Graliophilus* is uncertain, however.

The anterior tufted nephridia, avesiculate holonephridia, and the unpaired intersegmental anterior and posterior genital markings suggest relationship with *Woodwardiella* but that genus has racemose prostates.
**Graliophilus mendilai** (Michaelsen, 1907b)
(Fig. 15.15, 15.16)

*Plutellus mendilai* Michaelsen, 1907b: 177-179, Fig.7, Pl.1, fig.19, 20; Michaelsen, 1916a: 43; Jackson, 1931: 88.

*Graliophilus mendilai*; Jamieson, 1971e: 475.

**TYPE LOCALITY:** 28°42’S,115°02’E., Eradu - WA.

**SYNTAXYPES:** WAM V4428. MNHU4227. HM V7102 (Re-examined).

Length 30-35 mm. Width 2-2.5 mm. Segments 78-98. Unpigmented, a clear or a dirty grey owing to the gut contents being visible through the body-wall. Epilobous. Setae: in XII, aa: ab: bc: cd: dd = 0.80: 0.50: 0.83: 0.88: 1.70; dd = 0.25. First dorsal pore 4/5. Clitellum saddle-shaped, XIII-XVII. Male pores in XVIII on small indistinct papillae in b lines. Female pores apparently on a glandular ridge filling aa in XIV. Spermathecal pores, 2 pairs in 7/8 and 8/9 in b lines. Genital markings 4 pairs of transversely elongated thickenings (eye-like markings in HM V7102) deeply incised by the intersegmental furrows in 11/12, 12/13 (confirmation), 13/14 (re-examination), 20/21, and 21/22 (confirmation) in ab.

Septa 6/7-l0/ll moderately thickened. Nephridia stomate avesiculate holonephridia, the slender ducts discharging presetally in d lines. Gizzard in VI; oesophagus thick, swollen, and longitudinally striped in XVI, the internal structure resembling that of a calciferous gland. Intestine beginning in XVII, broad with a distinct typhlosole. Holandric; 2 pairs of testes embedded in free seminal masses in X and XI; 2 pairs of
Fig. 15.15. *Graliophilus mendilai*. Genital field. Syntype HMV7102. (Jamieson, 2000).
Fig. 15.16. Previous page. *Graliophilus mendilai*. A: Penial seta. B: Spermatheca. From Michaelsen (1907b).
large seminal vesicles in IX and XII, the former simple, the latter multilobed. Prostate glands in XVIII, or in XVII and XVIII, with a thick coiled glandular region and a short s-shaped duct. Central canal entirely simple; 1/4 thickness of gland (Michaelsen, 1916a). Penial setae delicate and curved, the distal end flattened, slightly widened, truncate and curved at the sides so as to resemble a spatula or a scoop. Spermathecae with a large irregular sac-like ampulla about 3 times as long as the duct; a thick club-shaped diverticulum opens about half-way down the duct.

REMARKS
The alimentary canal had previously been removed from the two re-examined specimens.

**Graliophilus montiskosciuskoi** Jamieson, 1973  
(Fig. 15.17, 15.18)

*Graliophilus montiskosciuskoi* Jamieson, 1973: 219-221, Fig. 4A, 6A, C, 7A.

**TYPE LOCALITY:** 36°27'S.148°16'E., Mt. Kosciusko - Vic.  
**HOLOTYPE:** AM W4740.

Length 42 mm. Width (midclitellar) 4.5 mm. Segments 77. Form moderately stout, circular in cross section excepting the male genital region. Pigmentless in alcohol. Prostomium tanylobous with very indistinct lateral margins, acute. Dorsal canalicula
Fig. 15.17. *Graliophilus montiskosciuskoii*. Genital field. Holotype AM W4740. After Jamieson (1973).
absent throughout the body. First dorsal pore 4/5. Setae in 8 regular longitudinal rows throughout, commencing on II; in XII, \( aa: ab: bc: cd: dd = 3.8: 1.0: 5.4: 3.2: 10.6; dd: u = 0.3. \) Clitellum annular XIV-XVII, strongly tumid but narrower than the forebody; dorsal pores, intersegmental furrows and setae distinctly visible. Male pores minute on small medianly confluent papillae, each pore located median to \( a \) line and visible by virtue of an externally projecting penial seta; flanked laterally by a tumescence which extends almost to \( c \) line. Genital markings present intersegmentally in 17/18-21/22, consisting of pairs of eye-like markings in \( a \) lines with tumid anterior and posterior lips which extend longitudinally to unite with those of adjacent segments and are confluent medianly so as to form transverse midventral tumid bands; the eye-like centres clearly visible in 19/20-21/22 not detected with complete certainty in 17/18 and 18/19 although tumid lips are present adjacent to these furrows; those in XVIII forming the already mentioned tumescences lateral to the male pores. Additional accessory genital markings present in segments IX to XII, each consisting of a very strongly protuberant unpaired midventral transverse pad which laterally extends almost to setae \( b \), the anterior pad leaving the anterior third of segment IX free. Female pores inconspicuous in XIV, anteromedian to setae \( a \) at approximately \( 1/3 aa \), both in a common transverse field. Spermathecal pores 5 pairs on inconspicuous papillae well median to \( a \) lines, in 4/5-8/9.

Septa 10/11 and 11/12 fairly strongly thickened; 12/13 and 13/14 moderately but decreasingly thickened; other septa slightly thickened or thin. Last septal glands anterior in IV. Dorsal blood vessel single, continuous onto the pharynx; commissural vessels heart-like only in X-XII, in which they form 3 pairs of latero-oesophageal hearts, each of which receives a connective from the dorsal vessel and one from the
supraoesophageal vessel; the latter vessel slender, present in IX-XII. A pair of latero-
oesophageal vessels extending from the pharynx to VIII median to the commissural
vessels becomes suboesophageal by IX. Gizzard very large and firmly muscular,
almost cylindrical though widening slightly anteriorly; restricted to V but displacing
posterior septa so that its posterior end lies approximately at the level of intersegment
9/10, oesophagus suppressed by it until VIII in which it is well developed although
slender. Oesophagus moderately expanded, moniliform and with circumferential
vascular striae in IX to XIV; similar although narrower and apparently less
vascularized in XV and XVI; intestine commencing gradually in XVII. No typhlosole
detectable but maceration precludes certainty that it is absent. Nephridia stomate
holonephridia commencing in III; ducts avesiculate, penetrating the parietes in c lines;
tufted nephridia absent. Testes and iridescent seminal funnels free in X and XI;
seminal vesicles racemose in IX and XII. Ovaries not recognizable; ovisacs absent.
Prostates a single pair, thickly tubular, describing several coils laterally from the ducts
and restricted to XVIII; ducts sinuous and muscular, bulbous ectally; vasa deferentia
of each side joining the prostate gland considerably ental of the duct. Penial setae
present in XVIII; that on the right moderately stout, almost straight though slightly
bowed entally; tapering to a fine point which is terminally hollowed out and widened
in the form of a spatula; ornamentation restricted to a few anteriorly directed spines
on the curved side of the profile near the ectal end (only two spines distinguishable
with certainty). Length = 575 µm; greatest width of shaft = 10 µm. Spermathecae 5
uniform pairs, discharging anteriorly in segments V-IX, each with an elongate ovoid
to sacciform ampulla and a short, poorly muscularized duct which bears a lateral
digitiform, slightly clavate diverticulum near its junction with the ampulla; length of
the left spermatheca of IX = 1.8 mm; ratio of total length: length duct = 3.3; ratio of total length: length diverticulum = 3.6.

REMARKS
This species differed from all species currently referred to *Graliophilus*, excepting the similarly eastern Australian *G. macedonensis*, in having 5 pairs of spermathecae. The presence of a long series of median genital markings is a further resemblance. However, the paired eye-like genital markings posterior to the male pores are reminiscent of the *Vesiculodrilus frenchi* species-group and it noteworthy that *D. frenchi* occurs with this species on Mt. Kosciusko. The avesiculate condition of the nephridia differs however, from the vesiculate condition seen in all members of the *frenchi*-group.

*Graliophilus murrayensis* (Michaelsen, 1907b)
(Fig. 15.19, 15.20)

*Plutellus murrayensis* Michaelsen, 1907b: 175-177, Fig.6, Pl.1, fig.17, 18.
*Graliophilus murrayensis*; Jamieson, 1971e: 474.

TYPE LOCALITY: 32°20'S.116°07'E., Jarrahdale - WA.
SYNTYPES: WAM V4426. MNHU4226. HM V7101 (Re-examined).
Fig. 15.19. *Graliophilus murrayensis*. Genital field. Syntype HM V7101. (Jamieson, 2000).
Graliophilus murrayensis
Fig. 15.20. Previous page. *Graliophilus murrayensis*. A: Spermatheca. B: Penial seta. From Michaelsen (1907b).
Length 42-54 mm. Width 2-3 mm. Segments 109-114. Colour, a darkish yellow, or green-grey, the head region faintly brown or flesh-coloured. Epilobous. Setae faintly ornamented distally; in XII, \(aa: ab: bc: dd = 1.15: 0.33: 0.63: 4.2; \) \(dd = 0.49\) u. Nephropores clearly visible on the clitellum in \(d\) lines. First dorsal pore in 5/6. Clitellum annular, but only slightly developed ventrally, XIII-XVII. Male pores in \(ab\), on oval papillae. Genital markings indistinctly-bounded glandular pads in the ventral-median region of VIII and IX (those in IX, at least, paired) a pair of small oval papillae linked medianly by a narrow glandular field, in \(ab\), or median to \(a\) lines, posteriorly in XVII, and in 19/20 and 20/21; a suggestion of a similar transverse field but no papillae sometimes present at 18/19. Spermathecal pores, 2 pairs, in 7/8 and 8/9, in \(a\) lines.

Septa 8/9-11/12 faintly thickened. Gizzard in V. Oesophagus swollen in XV and XVI in which it does not have high internal lamellae but folds are well developed, giving annular calciferous glands, walls also wrinkled and vascular in X-XIV. Last heart in XII. Holandric; 2 pairs of testes and seminal funnels in X and XI; 1 pair of simple seminal vesicles in IX, and 1 pair, compressed and racemose, in XII. Prostates with an irregular and loosely wound glandular region and a distinct short duct. Central canal with irregular insinkings mostly minute but some groove-like (Michaelsen, 1916a). Penial setae long, delicate, and irregularly bent; the distal end flattened, with a convex; terminal margin tipped by a tiny curved tooth; with the exception of this flattened region the distal end is marked by two somewhat irregular, longitudinal rows of teeth. Spermathecae irregular and sac-like with a sharply defined duct, into which, half-way down its length, opens a sausage-shaped diverticulum containing 2 or 3 ill-defined sperm-chambers.
**Graliophilus schuemanni** (Michaelsen, 1907b)
(Fig. 15.21, 15.22)

*Plutellus Schümanni (sic)* Michaelsen, 1907b: 181-182, Fig.9, Pl.1, fig.24.
*Plutellus Schünemannii (sic)*; Michaelsen, 1916a: 46.
*Plutellus schümanni*; Jackson, 1931: 88-89.
*Graliophilus schumanni*; Jamieson, 1971e: 474.

**TYPE LOCALITY:** 35°00'S.117°52'E., Albany-WA.
**SYNTYPES:** HM V7105 (Re-examined).

Length 40 mm. Width 2-2.5 mm. Segments 120. Colour, yellowish-white, the grey gut-contents visible through the skin; in life with a reddish tint. Epilobous. Setae set very wide apart: aa = 2ab, ab = 0.6bc, bc > or =cd, dd = 2aa. Dorsal pores indistinct. Nephropores (clitellar region) in c lines. Clitellum annular but thinner ventrally, appearing saddle-shaped, 1/3XIII, XIV-XVII, XVIII. Male pores on oval papillae in XVIII, in ab. Genital markings two pairs of large ventral-median oval areas with raised margins and sunken centres in furrows 13/14 and 14/15; 2 or 3 pairs of papillae in the anterior regions of XIX and XX, or XIX, XX and XXI, the hindmost in ab lines, the others slightly more lateral; these papillae connected in pairs by a ventro-median glandular field in each segment; sometimes with less developed marking(s) anteriorly in XVIII. Spermathecal pores 2 pairs, in 7/8 and 8/9, in or slightly lateral of a lines.

Septa 6/7 13/14 thickened. Gizzard in VI; oesophagus swollen in each segment but lacking calciferous glands. Nephridia stomate, avesiculate holonephridia. Holandric; 2 pairs of irregular seminal vesicles. in IX and XII; 2 pairs of seminal funnels in X and XI. Prostates with a very thick coiled glandular region; coils somewhat flattened and
Fig. 15.21. *Graliophilus schuemanni*. Genital field. Syntype HM V7105. (Jamieson, 2000).
Gralliophilus schuemannii
Fig. 15.22. Previous page. *Graliophilus schuemanni*. Spermatheca. From Michaelsen (1907b).
adpressed, and a sharply defined short bent duct. Central canal very narrow, with many irregular insinkings; glad cells not definitely grouped but appearing to open into the insinkings (Michaelsen, 1916a). Penial setae absent. Spermathecae with a pyriform ampulla the proximal swollen end of which is bent to the side; the ampulla narrowing distally to the duct which is extremely small and entirely hidden in the body-wall; a simple diverticulum opens into the distal end of the ampulla.

_Graliophilus secundus_ Jamieson, 1971e
(Fig. 15.23, 15.24)

_Graliophilus secundus_ Jamieson, 1971e: 478-480, fig.1b, 6a, 7b.

**TYPE LOCALITY:** 34°30'S.116°02'E., near Thomson's Bridge - WA.
**HOLOTYPE:** WAM V33-70.

Length 50+mm (posterior amputee). Width 2.5 mm. Segments ? Form: circular in cross section throughout; first 5 segments simple, thereafter, in the forebody, triannulate; postclitellar segments with additional annuli. Pigmentless buff in alcohol. Prostomium epilobous 1/3, closed, acute. First dorsal pore 5/6. Setae in 8 regular longitudinal rows (as far as the caudal amputation) commencing on II; _ab_ absent on XVIII; a pigment spot present on each side in _bc_ in the forebody, varying in position from _b_ to _c_; in XII, _aa: ab: bc: cd: dc: cb: ba_ = 1.82: 1.00: 2.09: 1.64: 6.45: 1.55: 1.91: 0.91. Nephropores visible almost only on the clitellum, inconspicuous anteriorly
Fig. 15.23. *Graliophilus secundus*. Genital field. Holotype WAMV 33-70. After Jamieson (1971e).
in their segments in c lines. Clitellum only slightly protuberant, annular, XIV-XVIII; intersegmental furrows, dorsal pores and setae retained. Male pores shortly median of a lines, on a pair of medianly conjoined papillae which fill all but a small posterior portion of XVIII. Large ovoid accessory genital markings, extending from the ventral midline to shortly lateral of b line, paired in 9/10; unpaired, on the right side only, in 10/11; and paired in 16/17 and 17/18; each an ovoid tumid pad with pore-like centre which is situated in ab, nearer b. Female pores shortly anteriomedian of a on a pair of low medianly conjoined papillae. Spermathecal pores minute, concealed in intersegmental furrows 7/8 and 8/9, immediately median of a lines.

Septa: 5/6 and 6/7 moderately, 7/8-11/12 strongly, 12/13 and 13/14 slightly thickened; the remainder thin. Last septal (pharyngeal) glands in V. Dorsal blood vessel single. Dorsoventral commissural vessels in VII-XIII; those in VII-IX slender, dorsoventral only; those in X-XIII forming 4 pairs of large latero-oesophageal hearts, each receiving a connective from the dorsal vessel and from a slender supra-oesophageal vessel which runs through VIII-XIII. Gizzard small and globular, with muscular sheen but easily compressible, in V. Oesophagus well developed in VI; somewhat moniliform in VII-XVIII but with no special dilatations, though widest in XV and XVI. Intestine commencing in XIX, at first only about one and a half times the width of the preceding oesophagus; typhlosole and muscular thickening absent. Nephridia avesiculate stomate exonephric holonephridia, the postseptal portions commencing in II; the slender duct of each entering the body wall presetally in c. Testes and iridescent sperm funnels in X and XI; large racemose seminal vesicles with many large rounded loculi in IX and XII. Ovaries consisting of many chains of oocytes, and funnels in XIII; ovisacs absent. Prostates moderately wide much coiled
tubes restricted to XVIII; each with a very short narrow duct joined ectally by the vas deferens. Penial setae absent. Spermathecae 2 pairs, opening anteriorly in VIII and IX, each with an ovoid ampulla poorly demarcated from an almost equally wide, longer duct which is joined, just before it narrows to the spermathecal pore, by a clavate inseminated diverticulum. Size uniform; length of right spermatheca of VIII = 1.26 mm; ratio of total length: length duct = 1.95; ratio of total length: length diverticulum = 3.0.

REMARKS
*Graliophilus secundus* resembles *G. candidus*, in location of the last hearts in XIII. It differs from the latter species, and all other species assigned to *Graliophilus*, in the configuration of the accessory genital markings.

*Graliophilus strelitzi* (Michaelsen, 1907b)

(Fig. 15.25, 15.26)

*Plutellus strelitzi* Michaelsen, 1907b: 168-171, Fig.3, Pl.1, fig.11, 12.
*Graliophilus strelitzi* Jamieson, 1971e: 481-485, Fig.2c, d, 6c, 7f.

**TYPE LOCALITY**: Lion Mill - WA.
**SYNTYPES**: WAM V4429. MNHU4223. HM V7104.
**OTHER RECORDS**: (Jamieson, 1971e) 31°54'S.116°08'E., Mahogany Creek (WAM V40.1944).
Fig. 15.25. *Graliophilus strelitzi*. A and B: Anterior and posterior genital field. WAMV 40.1944. After Jamieson (1971e).
Length 50-95 mm. Width 6-7 mm. Segments 155-171. Form moderately stout; approximately circular in cross section throughout; the first three segments biannulate, the remainder of the forebody strongly triannulate; the postclitellar segments with barely perceptible secondary annulation. Pigmentless buff in alcohol; in life with a faintly pink head region and orange clitellum. Prostomium epitanylobous (not proepilobous); closed wedge shaped to 1/3 peristomium but continued as a very narrow strip to intersegment 1/2. First dorsal pore 3/4 (imperforate); perforate from 4/5. Setae in 8 longitudinal rows, commencing in II; d lines (and also c lines in Mahogany Creek material) irregular posteriorly; ab absent in XVIII. Setal ratios (Lion Mill) aa = 2.5 ab; ab = 0.6 bc; bc = or > cd. In Mahogany Creek specimen aa: ab: bc: cd: dd = 3.7: 1.0: 2.8: 2.3: 14.7; dd: u. Nephropores not certainly visible externally. Clitellum XIII-XVIII, annular but stronger above than below b; intersegmental furrows, setae and dorsal pores retained but fainter than elsewhere. Male pores in XVIII in ab shortly median of b lines on small papillae. Eye-like accessory genital markings with centres in or median to a lines, paired in two or more of intersegments 15/16-20/21, often indistinct or lacking. Female pores very shortly in front of and almost imperceptibly median of a, in XIV. Spermathecal pores on small distinct papillae in or slightly above a lines in 7/8 and 8/9.

Septa: 5/6 greatly attenuated by the gizzard; 6/7 slightly thickened; 7/8 moderately thickened; 8/9-13/14 strongly thickened; 14/15-16/17 slightly thickened; the remainder thin. First septal (pharyngeal) glands in III. Dorsal blood vessel single, continuous on to the pharynx. Dorsoventral commissural vessels a pair in each of segments IV-XII; those in IV-IX slender, dorso-ventral only, each giving off a lateral
branch, ventrally, to the body wall; those in X-XII forming 3 pairs of large latero-oesophageal hearts, each receiving a very slender filamentous connective from the dorsal vessel and a wide connective from the supra-oesophageal vessel which extends through IX-1/2 XIII. Subneural vessel absent. A large soft walled proventriculus in IV; gizzard very large, in V, and firmly muscular, widening slightly anteriorly where it is overlapped by folds of the proventriculus, extending posteriorly to the level of intersegment 9/10. Oesophagus suppressed in VI-VIII by backward extension of the gizzard; unmodified in IX; vascularized and slightly moniliform, sending paired vessels to the supra-oesophageal vessel, in X-XIII; narrow in XIV-XVII but in XVII bearing laterally a pair of very large true calciferous glands; globular and chloragogenous-looking in XVIII; intestine commencing, with abrupt expansion, in XIX (not XVIII recorded by Michaelsen); typhlosole and muscular thickening absent. Each calciferous gland (in XVII) kidney-shaped though slightly trilobate viewed along the body axis, opening into the lateral face of the oesophagus by a narrow orifice and therefore well cut off from the oesophagus, extending dorsally of this almost to touch the gland of the other side, and extending also for a considerable distance ventrally of its connection with the gut; the interior filled by deep thin laminae arranged radially relative to the wall of the gland and coalescing towards the oesophagus. Nephridia stomate avesiculate, exonephric holonephridia, in X posteriorly, with the preseptal funnel in a line, the postseptal body extending between a and d lines, the ectal, narrow duct longer than the nephridial body, extending far laterally to penetrate the parietes shortly below the mid dorsal line, slightly widening as it enters the body wall. First nephridium in III, it and that in IV, much coiled, thickly tubular, but not tufted, preseptal funnel present; the narrow ectal duct opening
into the mouth; those in V and VI sending ducts up around the pharynx which pass forwards to the junction of buccal cavity and body wall (whether exonephric or enteronephric not determinable); those in VII also discharging far anteriorly; those in VIII and IX, still coiled appearing to discharge presetally in b; those in X above d.

Testes and non-iridescent large, pleated funnels free in X and XI; seminal vesicles racemose with many rather large loculi in IX and XII, the posterior the larger. Prostates tubular, coiled, restricted to XVIII each with a moderately long, slender, muscular duct; central canal about 3/10 thickness of gland and lined with side branches (Michaelsen, 1916a); vas deferens joining the ectal extremity of the gland. Penial setae present; follicles very conspicuous and long, extending far laterally in XVIII. Penial setae long, curved, attenuated and flexible; each ornamented distally by a series of approximately 15-20 long, sharp anteriorly directed spines on each side; few apparent across the seta, the spines on each side sometimes opposite, sometimes out of phase with those of the other side; the seta wider and flatter near the distal extremity which forms a broad shallow gutter. Length of two right penial setae (Mahogany Creek) = 3.8 and 5.0 mm, greatest width (near base of one) = 24 µm; width of shaft behind ornamented region = 14 µm; width of distal expansion = 15 µm. One of the setae is periodically scooped out so that its profile is very irregular, a condition apparently observed also by Michaelsen. Ovaries (small thick folded laminae with few large terminal oocytes) and funnels in XIII; ovisacs absent. Spermathecae 2 pairs opening anteriorly in VIII and IX; lacking spermatozoal iridescence; each bipartite, with a short muscular duct, the larger median ramus constituting the ampulla; the other ramus, the diverticulum, (large and leaflike in Lion Mill specimens but short in the Mahogany Creek specimen) subdivided internally into
elongated oblique loculi. Size (Mahogany Creek) uniform; length of the right spermatheca of IX = 2-04 µm; ratio of total length of the spermatheca: length duct = 6.1; ratio of total length: length diverticulum = 3.1.

**Graliophilus termitophilus** (Michaelsen, 1907b)
(Fig. 15.27, 15.28)

*Plutellus termitophilus* Michaelsen, 1907b: 164-166, Fig.1, Pl.1, fig.9, 10.
*Graliophilus termitophilus*; Jamieson, 1971e: 474.

**TYPE LOCALITY:** 33°16'S.115°59'E., Fernbrook, formerly Lunenberg, in the wall of a termite nest. - WA.
**SYNTYPES:** WAM V4431. HM V7103 (Re-examined). MNHU4221.

Length 50-65 mm. Width 3-31/2 mm. Segments 130-150. Yellowish grey in the anteclitellar and hind regions, the midbody being a patchy green-grey owing to visibility of the gut-contents through the skin. Epilobous. Setae wide apart, in XII: ab: bc: cd: dd = 2.8: 1.0: 2.7: 2.4: 2.9; dd = 0.35u; the ventral pairs narrow towards the male pore; setae of the hind end irregularly arranged. First dorsal pore in furrow 6/7 though rudimentary pores occur in 5/6 or 4/5 and 5/6. Clitellum saddle-shaped and covering XIV-XVII. Male pores fine slits of which the medial end reaches b line. Female pores immediately anterior to seta a, on transverse papillae united by a median bridge. Genital markings in the form of oval transversely elongated, intersegmental areas,
Fig. 15.27. *Graliophilus termitophilus*. Genital field. Syntype HM V7103. (Jamieson, 2000).
Fig. 15.28. Previous page. *Graliophilus termitophilus*. A: Penial seta. B: Spermatheca. From Michaelsen (1907b).
each of which bears one to three minute papillae. These areas are midventral and unpaired in furrows 12/13-16/17, the first 2 bearing 3 papillae (in the re-examined specimen no marking has more than one papilla), the rest 1 papilla each; paired and bearing 1 papilla in 17/18-21/22, the distance between them widening then narrowing again; median and unpaired and bearing 1 papilla in 21/22 to 22/23, 23/24; only the markings in 12/13 and 13/14 and those in 17/18-20/21 are constant. Spermathecal pores 2 pairs, immediately behind 7/8 and 8/9, conspicuous on small papillae in or just above b lines.

Septa 6/7-14/15 thickened. Gizzard in V. Distinct calciferous glands lacking, but the dilatation in XVI has slight dorsal sacculations. Nephridia of anterior intestinal region with exceedingly slender ducts discharging in d lines. 2 pairs of testes and seminal funnels projecting freely into X and XI or embedded in free sperm masses; 2 pairs of sperm sacs in IX and XII; prostate glands coiled, with a distinct s-shaped muscular duct. Central canal very narrow, with many deep insinkings into which the gland cells appear to open (Michaelsen, 1916a). Penial setae delicate, irregularly curved, sharply pointed distally, and covered, except for the extreme end with moderately coarse scattered thorns. Spermathecae irregular and cylindrical opening directly to the exterior through a narrowing of the distal end; 2 elongated ampulla-like diverticula opening opposite each other into the narrowing distal end of the main pouch, while a third may be present, opening further up.
**Graliophilus(?) tripapillatus** Jamieson, 1974a

(Fig. 0.13-1, 15.29, 15.30)

_Graliophilus(?) tripapillatus_ Jamieson, 1974a: 261-263, Fig.4, 17, 32A, Pl.1, Table 3.

TYPE LOCALITY: 42°20'S.146°25'E., Tarraleah - Tas.
HOLOTYPE: TM K313.

Length 60 mm. Width 3.2, 3.0 mm. Segments 130-135. Epilobous 1/3, closed. Dorsal pores not visible. Setae 8 per segment, in regular longitudinal rows throughout XII, _aa_: _ab_: _bc_: _cd_: _dd_: _u_ = 2.4: 1.0: 1.5: 4.4: 7.9: 0.4. Nephropores in _c_ lines. Clitellum annular, 1/2XIII-1/2XVIII. Male pores on XVIII in _a_ on dome-shaped papillae reaching from _b_ to an approximately equal distance median to the pores. Genital markings midventral unpaired transverse pads constant in 16/17 and 19/20, sometimes in 15/16, extending laterally into _ab_ or beyond _b_ and longitudinally to or over the setal rows of adjacent segments; the pads increasing in size and prominence posteriorly; faintly indicated glandular and slightly tumid interruptions of the intersegments, in 17/18 and 18/19. Female pores paired on XIV, anterior and only slightly median to setae _a_. Spermathecal pores 3 pairs, in 6/7-8/9, on small papillae in _a_.

Last hearts in XII (latero-oesophageal); supra-oesophageal moderately developed in XIII-XIII. Gizzard large and firm in V. Calciferous glands absent; oesophagus internally rugose and with circumferential vascular striae in VIII-XVI. Intestinal origin XVIII; deep dorsal typhlosole commencing in XX. Nephridia simple stomate,
Fig. 15.29. *Graliophilus tripapillatus*. A and B: Anterior and posterior genital field. Holotype TM K313. After Jamieson (1974a).
avesiculate, exonephric holonephridia (funnels demonstrated in fore- and mid-body); ducts entering the parietes presetally in c lines, in the forebody forming wide-tubes but not sufficiently dilated to be termed bladders; slender in the midbody. Holandric (funnels iridescent in X and XI); gymnorchous; seminal vesicles racemose, in IX and XII. Metagynous; ovisacs in XIV. Prostates much coiled, depressed tubular; vas deferens joining the sinuous ectally widening duct shortly ectal of the gland. Penial setae very slender, tip bifid, chelate, the two branches terminally contiguous, a coarse tooth, almost large enough to be considered a bifurcation, on one branch; ornamentation absent; length?, general width of shaft = 3 µm. Spermathecae 3 pairs; diverticulum (inseminated) single, clavate, uniloculate.

**Graliophilus varicystis** (Jackson, 1931)  
(Fig. 15.31, 15.32)

*Plutellus varicystis* Jackson, 1931: 92-93, Fig.7, 8, Pl.15, fig.4.
*Graliophilus varicystis*; Jamieson, 1971e: 480-481, fig.4a, 6b, 7c, d.

**TYPE LOCALITY:** 34°41'S.117°54'E., Porongorups - WA.
**SYNTYPES:** WAM V18-61 (Re-examined).

Length 63 mm. Width 2.5 mm. Segments ca 120. Flesh-coloured, sometimes with a brown tinge, in alcohol. Form approximately circular in cross section; preclitellar segments weakly triannulate. Prostomium epilobous 2/3, with broad, closed dorsal
Fig. 15.31. *Graliophilus varicystis*. Genital field. Probable syntype WAMV 18-61. After Jamieson (1971e).
tongue slightly narrowing posteriorly. First dorsal pores 4/5, 5/6; absent on the clitellum. Setae large, in 8 longitudinal rows, commencing on II; ab absent, bc present on XVIII, but no penial setae; in XII, aa: ab: bc: cd: dd: dc: cb: ba = 1.43: 1.00: 1.64: 1.57: 3.93: 1.43: 1.64: 0.79. Nephropores inconspicuous white spots in c lines, most clearly developed on the clitellum; not present on several of the anteriormost segments. Clitellum annular, posterior 1/3 XIII-XVII. A pair of combined male and prostatic pores (not seen by Jackson) on XVIII in ab, nearer a, on inconspicuous, small porophores but both lying in a common, transversely elliptical slightly tumid field which fills XVIII longitudinally, extends laterally to shortly above b lines, and posteriorly reaches the setal arc of XIX. Accessory genital markings; a triplet of conjoined eye-like markings one median, and 2 lateral in ab nearer b in intersegmental furrows 16/17; a pair of ventrally conjoined markings with knoblike pore-bearing central portion and tumid border, in ab, nearer b, in intersegmental furrow 11/12; and a similar unpaired marking at mid-ab, in 21/22 or all markings similar but that in 21/22 replaced by a pair in 20/21. (The post-clitellar accessory genital markings were not reported by Jackson). Female pores clearly visible in XIV, anterior to and well median of setae a, in a common elliptical field. Spermathecal pores 2 pairs, on low mounds, in 7/8 and 8/9, with centres slightly median of a lines.

Some preclitellar septa moderately strongly thickened. Septal (pharyngeal) glands delicate, elongate lobed structures extending into V (and VI ?) on each side of the gizzard. Dorsal blood vessel single; continuous onto the pharynx. Dorsoventral commissural vessels in VI-XIII; those in VI-IX slender and dorsoventral only; those in X-XIII forming 4 pairs of thick latero-oesophageal hearts arising from the wide distinct supra-oesophageal vessel, their connections with the dorsal vessel not
verifiable. Supra-oesophageal vessel clearly developed in and limited to VII-XIII. Gizzard large cylindrical and firmly muscular in V (assuming a very delicate peritoneum-like sheath to be septum 5/6) but occupying the entire length of segment VI; preceded by and anteriorly partly enfolded in a wide thick walled proventriculus. Oesophagus with obvious vascular striae and at least in the anterior segments moniliform, in VII-XVI, elongate but less vascular in XVII; intestine commencing with abrupt expansion in XIX; typhlosole and muscular thickening absent. Nephridia in II-VII much coiled and sending coalescent ducts far forwards into segment I in which they possibly open into the mouth or, if they are exonephric, closely approach this. By IX (VIII?) the nephridia are large, simple, stomate avesiculate holonephridia and are exonephric, with the slender duct entering the parietes presetally in c line. Testes, iridescent sperm funnels and free sperm masses in X and XI; racemose seminal vesicles in IX and XII, the posterior pair very large. Ovaries, bushy with large oocytes, and funnels in XIII; ovisacs absent. Prostates thickly tubular, tortuous, with once-looped, ectally widening muscular ducts which are joined at the ectal third by the vasa deferentia. Spermathecae each with a large saccular ampulla broader than long; a wide, longer duct joined near its ectal extremity by a single iridescent (inseminated) stoutly clavate diverticulum; additional tumour-like structures on the duct of some spermathecae appear to be accessory ampullae or may account for the report by Jackson of 2 to 3 diverticula; spermathecal size uniform, total length of left spermatheca of VIII = 1.1 mm; ratio total length: length duct = 2.3; ratio total length: length diverticulum = 1.5. Spermathecal diverticulum inseminated; sperm chambers are absent but the ectal portion of the wall of the diverticulum has high laminar elevations of the lining epithelium extending far into the lumen.
**Graliophilus (?) weldboroughi** (Jamieson, 1974a)
(Fig. 15.33, 15.34)

*Perionychella (Perionychella) weldboroughi* Jamieson, 1974a: 230-232, Fig.1, 7A, 16F, Table 2.

**TYPE LOCALITY:** 41°10'S.147°55'E., 1.6 miles from the eastern end of Weldborough Pass - Tas.

**HOLOTYPE:** TM K263.

Length 48 mm. Width 1.6 mm. Segments 71. Tanylobous. First dorsal pore 4/5. Setae 8 per segment in regular longitudinal rows throughout; in XII, \(aa: ab: bc: cd: dd = 2.3: 1.0: 2.0: 2.0: 7.7; dd: u = 0.39\). Nephropores faint in \(c\) lines. Clitellum annular XIII-XVI. Male pores equatorial in XVIII, on pronounced papillae in \(ab\) with centres nearer \(b\) than \(a\); preceded by a pair of medianly contiguous small papillae in \(aa\) at 17/18, with a further midventral unpaired papilla at 18/19. Suggestions of presetal midventral unpaired markings present in VII ?, VIII ? and IX. Female pores a pair on XIV anterior to and slightly median of \(a\). Spermathecal pores 5 pairs in 4/5-8/9 in or slightly lateral of \(a\).

Last hearts in XII. Supra-oesophageal very weakly developed. Gizzard moderate, but easily compressible, in V. Calciferous glands absent but oesophagus greatly dilated in XIII-XV in which vascularization is increased and internal longitudinal
Fig. 15.33. *Graliophilus weldboroughi*. Genital field. Holotype TM K263. After Jamieson (1974a).
Fig. 15.34. *Graliophilus weldboroughi*. Right spermatheca of IX. Holotype TM K263. After Jamieson (1974a).
rugae, though low, are conspicuous. Intestinal origin XVII; typhlosole absent but intestinal wall slightly thicker middorsally. Nephridia simple stomate avesiculate holonephridia commencing in II; ectal ducts lacking bladders. Holandric (funnels in X and XI iridescent); gymnorchous; seminal vesicles very large, racemose, in IX and XII. Prostates flattened, somewhat incised, tubular, in XVIII-XX; vas deferens joining gland near the tortuous duct. Penial setae filiform and sinuous, lacking ornamentation ?; length (incomplete ?) = 0.42 mm. Metagynous; ovisacs small, in XIV. Spermathecae 5 pairs, diverticulum single, slenderly clavate, uniloculate.

REMARKS
The midventral genital marking in 18/19, associated with two closely contiguous markings at 17/18, diagnoses this species. Its generic affinities are uncertain. As it has the plesiomorphic lumbricin arrangement of setae, and no unique synapomorphies with Diporochaeta, it is not assigned to that genus. The combination of lumbricin setae and avesiculate holonephridia diagnoses Graliophilus, in which it is tentatively placed.

**Graliophilus wellingtonianus** (Michaelsen, 1907b)
(Fig. 15.35, 15.36)

*Plutellus wellingtonianus* Michaelsen, 1907b: 167-168, Fig.2, Pl.1, fig.7, 8.
*Plutellus wellingtonianus*; Michaelsen, 1916a: 45; Jackson, 1931: 85-86.
*Graliophilus wellingtonianus*; Jamieson, 1971e: 474.
Type Locality: 33°22'S, 116°09'E, Collie - WA.

Length > 25mm. Width 1.5-2mm. Segments > 68. Colour, a dirty grey. Head epilobous. Setae far apart anteriorly: \(ab = 0.5\) \(aa\), \(bc = 0.9\) \(aa\), \(cd = 1.3\) \(bc\), \(dd = 2\) \(aa = 0.3\) \(u\); posteriorly slightly closer together. First dorsal pore 5/6; male pores in XVIII on small transversely-oval papillae in \(b\) lines. Genital markings transversely-elongated intersegmental glandular fields, unpaired and ventral-median in furrow 18/19, paired and connected by ventral-median bands in 11/12, 12/13, 17/18, 19/20 and 20/21. Spermathecal pores 2 pairs, posterior to 7/8 and 8/9 in setal line \(b\).

Septa slightly thickened in the region of the testes. Gizzard in VI; oesophagus lacking calciferous glands. Last hearts in XII. Ducts of holonephridia entering the parietes in \(c\) lines. Two pairs of seminal funnels free in X and XI; a pair of slender multi-lobed seminal vesicles in XII. Prostate glands much twisted with a moderately short muscular duct as thick as the glandular region. Central canal about 2/7 the thickness of gland; with circular depressions but no definite side branches (Michaelsen, 1916a). Penial setae with a. double bend at the distal end, irregularly beset with thorns, apically bifurcating into two widely divergent tips. Spermathecae long, sac-like, and irregularly bent, with a short sharply-defined duct; 2 small tubular diverticula open opposite each other into the distal end of the ampulla.
Fig. 15.35. *Graliophilus wellingtonianus*. Genital field. Syntype HM V7079. (Jamieson, 2000).
Fig. 15.36. Previous page. *Graliophilus wellingtonianus*. A: Spermatheca. B: Distal end of penial seta. From Michaelsen (1907b).
REMARKS

G. wellingtonianus resembles G. termitophilus in the unusual location of the spermathecal pores posterior to intersegmental furrows 7/8 and 8/9 and on small papillae.

**Graliophilus whistleri** (Michaelsen, 1935)
(Fig. 15.37)

*Plutellus whistleri* Michaelsen, 1935: 39-43, Fig.1.
*Graliophilus whistleri*; Jamieson, 1971e: 476.

**TYPE LOCALITY:** 33°53'S.116°33'E., Brancaster, near Dinninup - WA.
**TYPES:** Missing (Reynolds and Cook, 1976) but (type?) specimens HM V12145 (Re-examined).

Greatest length 65mm. Width 3-4 mm. Segments ca 150. Preserved specimens dirty yellowish grey. Prostomium tanylobous, with middorsal groove; broad and short; dorsal tongue broad, divided by a transverse furrow at mid-length. First dorsal pore 5/6. Ectal end of setae bearing a few small irregularly placed punctures more or less filled by a minute blunt thorn; ornamentation distinct only on the large posterior caudal setae. Setae small in midbody, 0.16 mm long, nodulus 16 µm thick. Caudally (ca last 20 segments) setae d enlarged to 0.26 mm long, with node 32 µm thick; setae a to c only slightly enlarged. Setal rows generally straight but setae d in last 17 segments displaced to a rather large extent, ventrally, or dorsally, but in a quite
Fig. 15.37. *Graliophilus whistleri*. Genital field. Syntype? HM V12145. (Jamieson, 2000).
irregular manner, regular alternation occurring in only very short tracts. In XII, \( aa: ab: bc: cd: dd: dc: cb: ba = 0.28: 1.00: 2.85: 3.00: 5.57: 3.00: 3.29: 1.14; \)
\( dd = 0.25 \) (re-examination), thus the dorsal setae, \( c \) and \( d \), very far apart. Nephropores (anterior intestinal region) in \( d \) lines. Clitellum whitish, somewhat prominent, indistinctly annular, ventrally at least less developed, XIV to XVII inclusive; intersegmental furrows distinct. Male pores minute, in the setal zone of segment XVIII about 0.2 mm from the midventral line, on a common ventral median porophore which has the shape of a transversely oval, rather high cushion laterally reaching setal line \( a \), and occupying the whole length of XVIII. Accessory genital markings single median-ventral intersegmental tranversely oval papillae. At least four of them constant at 16/17, 19/20, 20/21 and 21/22 (confirmation), in one case a fifth at 15/16, and in another (confirmation) an indistinct fifth one at 9/10. A pair of small glandular swellings without sharp borders on segment XVIII just lateral of the male porophore, with which they merge (not seen in re-examined specimen). Female pores also minute, close median (and, re-examination, slightly anterior) of setae \( a \) of segment XIV. Spermathecal pores, also minute, 3 pairs at the intersegmental furrows 6/7, 7/8 and 8/9, near the ventral median line (confirmation). The distance between the pores of one pair diminishes posteriad, the pores of 8/9 only 0,07 mm, those of 6/7 0.15mm apart (Michaelson).

(Internal anatomy from Michaelson). Septa 6/7 very little thickened, 7/8-11/12 moderately thick, 12/13 slightly thickened, the following delicate. Gizzard large, in segment VI. Oesophagus moniliform in VII-XVI, widely swollen in the segments, strongly narrowed intersegmentally; its wall in this region with the structure of ‘chyle-organs’, densely crowded shrivelled longitudinal folds, projecting into the lumen.
Intestine seeming to begin in XVIII; typhlosole absent but lumen irregularly narrowed, partly in an irregular spiral manner. Holandric; Two pairs of free testes and funnels in X and XI, one pair of rather small, simple seminal vesicles in XII. Prostates with a thick, cylindrical glandular part, irregularly bent, about 6 mm. long, and 0.4 mm. thick, uneven at the surface, the ental tops of the glandular cells projecting in the shape of warts. The axial channel simple and very narrow. The prostate-duct sharply set off from the glandular part, shorter and much thinner, entering body wall in setal line b, and then bending medianwards, within the layer of the longitudinal muscles running towards the male pore, in the meanwhile becoming more and more attenuated. Penial setae absent. One pair of tuft-like ovaries, and posterior oviducal funnels in XIII; oviduct, in XIV, running in a nearly straight line towards the female pore. Spermathecal ampulla more or less slender, pear-shaped, lacking distinctly marked duct. Into the thin ectal end of the ampulla enters a simple club-shaped or slender pear-shaped diverticulum much shorter and thinner than the ampulla and lacking a distinct stalk though ectally slender.

REMARKS
The affinities of G. whistleri are uncertain. Michaelsen (1935), who placed it in Plutellus sensu lato, considered it to belong to the small group of Western Australia ‘Plutellus’ (here Graliophilus) species, which are devoid of penial setae and are restricted to the extreme southern part of Western Australia, namely schuemanni, carneus, and asymmetricus, all from Albany. He considered whistleri to be most closely allied to asymmetricus, in which the pairs of male pores and of spermathecal pores are replaced by single midventral pores, whereas they approach this line in
Whistleri. Michaelsen also considered whistleri to be near blackwoodianus from Bridgetown, not very far from Brancaster, agreeing with this species in the character (not in the arrangement) of the accessory genital markings. In the situation of the spermathecal pores (and of the male pores?) whistleri was considered intermediate between asymmetricus and blackwoodians in which these pores seemed to lie just ventral to setal lines a. However, it was noted that blackwoodianus differed from whistleri in having only two pairs of spermathecae, and in possessing penial setae. Alternatively, whistleri was associated with levis and dalgarangae, the three species comprising a Graliophilus levis species-group, by Jamieson 1971e. It is here agreed that the resemblance of the genital markings (and male porophore) to those of blackwoodianus is striking.

**Graliophilus woodi** Jamieson, 1973
(Fig. 15.38-15.40)

*Graliophilus woodi* Jamieson, 1973: 221-224, Fig.1A, B, 6B, 7B.

**Type Locality:** 36°27'S.148°16'E., Mt. Kosciusko - Vic.
**Holotype:** AM W4701.
**Paratypes:** AM W4696-4700. BMNH 1973.3.7-8. BJ. CSIRO SA.

Length 60-85 mm (mean of 5 = 77 mm). Width 4-4.5 mm (mean of 5 = 4.2 mm). Segments 147-151 (mean of 4 = 149). Form circular in cross section, blunt and very slightly clubbed at anterior and posterior ends, segments of the forebody at first
Fig. 15.38. *Graliophilus woodi*. Genital field. Holotype AM W4701. After Jamieson (1973).
simple, then biannulate but mostly triannulate; postclitellar segments weakly triannulate. Pigmentless in alcohol excepting the pale brown pigmented clitellum. Prostomium broadly tanylobous, parallel sided, bisected longitudinally by a moderately developed dorsal furrow which is not continuous onto the body. First dorsal pore 5/6, but probably not perforate until 6/7 or even 7/8. Setae in 8 regular longitudinal rows throughout, commencing on II; setae a and b absent in XVIII; in XII, aa: ab: bc: cd: dd = 3.1: 1.0: 3.0: 2.6: 8.7, dd: u = 0.35. Nephropores faintly visible in c lines near the anterior margins of their segments. Clitellum annular, well developed although not strongly protuberant, weaker on XIII than elsewhere; intersegmental furrows, setae and nephropores retained; dorsal pores obscured. Male pores minute on XVIII, in ab. Circular pore-like accessory genital markings with tumid borders have a variable configuration, but the following arrangement constant (illustrated): a pair anterior to, and a pair posterolateral to setae b of XVII; presetal and postsetal in ab of XVIII; presetal in ab of XIX; four midventral, unpaired markings present: postsetal in XVII, pre- and post-setal in XVIII and presetal in XIX. At greatest development of the field in addition to the constant arrangement this has a postsetal triplet in XVI and in XX; a presetal midventral marking in XVII, a unilateral (left) presetal marking in XVI and 2 additional, equatorial markings on each side in XVIII, one median to, the other lateral to, the male pores; in addition, the left-presetal and postsetal paired marking in XVII is replicated. Exceptionally lacking the paired presetal markings in XVII which are normally constant. Female pore(s?); precise location indeterminable, situated in a transverse groove spanning aa; apparently single and midventral in paratype 1. Spermathecal pores minute, on 2 pairs of inconspicuous low papillae in 7/8 and 8/9 in a lines.
Fig. 15.40. *Graliophilus woodi*. A: Prostate. B: Right spermatheca of IX. Holotype AM W4701. After Jamieson (1973).
Septa 5/6 very delicate, attenuated by backward extension of the gizzard; 6/7 thin; 7/8 moderately thickened, 8/9-12/13 fairly strongly; 13/14-16/17 decreasing from moderately to slightly thickened; the remainder thin. Last septal glands filling III; perhaps extending slightly into IV. Dorsal blood vessel single, continuous onto the pharynx. Dorsoventral commissural vessels in VII (or further anteriorly?) -XII; those in IX forming slender dorsoventral hearts; those in X-XII forming 3 pairs of moderately wide latero-oesophageal hearts, each arising from the dorsal vessel and receiving a slender connective from the supra-oesophageal vessel. Supra-oesophageal vessel occupying VII-XII. Subneural vessel absent. Gizzard large and strongly muscular, in V, widening anteriorly to a rim-like expansion which is continuous with a thin walled crop-like proventriculus in IV. Oesophagus suppressed in VI by backward extension of the gizzard; evidently vascularized and slightly moniliform in VIII-XVI; widest in XV and, especially, XVI but never conspicuously modified or enlarged; narrow in XVII and XVIII. Vascularized part with internal rugae which are thinner and more laminar in XV and XVI. Intestine commencing at 1/2XVIII, not greatly enlarged until XIX. A rather low narrow (laminar) convoluted dorsal typhlosole visible from XIX or XXI. Nephridia avesiculate simple holonephridia throughout; the post-septal bodies commencing in III; preseptal funnels demonstrated from XIV but presumably present further anteriorly; ducts entering the parietes in c lines throughout, with the exception that the ducts of those in III pass forwards to enter the parietes anteriorly in II above d lines. Testes large iridescent sperm funnels and sperm masses free in X and XI. Seminal vesicles small, elongate-ovoid on the posterior wall of IX; elongate sacs curving dorsally around the gut on the anterior wall of XII; slightly lobulated. Ovaries (extensive laminae with many conjoined chains of
large oocytes) and funnels in XIII; ovisacs present, separate from the oviducal funnel, or not developed. Prostates compactly coiled, dorsoventrally depressed, tubular, restricted to XVIII; duct narrow, muscular and tortuous; each joined entally by the two vasa deferentia of its side. Penial setae absent. Genital markings corresponding internally with large, rounded sessile glandular masses. Spermathecae 2 pairs, discharging anteriorly in VIII and IX; each with an elongate-ovoid ampulla and slightly longer, poorly demarcated narrow duct which is joined entally by a clavate anteriorly directed diverticulum. Size uniform; length = 3.7 mm; ratio total length: length duct = 1.8; ratio total length; length diverticulum = 5.1.

REMARKS
Although this species is placeable in the genus *Graliophilus*, it does not conform precisely with the definitions of other species-groups which have been recognized in the genus.

**Graliophilus woodwardi** (Michaelsen, 1907b)  
(Fig. 15.41, 15.42)

*Plutellus woodwardi* Michaelsen, 1907b: 171-173, Fig.4, Pl.1, fig.13, 14.  
*Graliophilus woodwardi*; Jamieson, 1971e: 474.

**TYPE LOCALITY:** 33°22’S.116°09’E., Collie - WA.
Length 90-100 mm. Width 4.5-6 mm. Segments 160-166. Colour, yellowish, or brownish-grey; in life whitish, the head end faintly red. Pro-epilobous (?); peristomium with a longitudinal middorsal furrow. Setae: in XII, \(aa: ab: bc: cd: dd = 1.5: 0.4: 1.2: 1.0: 5.2\) mm; setal line \(d\) irregular posteriorly. Nephridia simple, stomate, avesiculate holonephridia throughout, from ca. II; ducts slender, entering parietes anteriorly in their segments in \(d\) lines. First dorsal pore 4/5. Clitellum annular, XIV-XVII. Male pores in XVIII on small oval papillae in \(b\) lines. Genital markings in the form of paired indistinct glandular patches in \(ab\) in 15/16, 16/17, sometimes 18/19, and 19/20, the last two pairs sometimes with ventral-median connections. Spermathecal pores 2 pairs, in 7/8 and 8/9 in \(a\) lines.

Septa 6/7-13/14 thickened. Gizzard large, in V; oesophagus conspicuously swollen in XVI and XVII, with high internal lamellae, here considered annular calciferous glands. Intestine commencing in XVIII, with a very small typhlosole. Last heart in XII. Nephridia simple, stomate, avesiculate holonephridia throughout, from ca. II; ducts slender, entering parietes anteriorly in their segments in \(d\) lines. Holandric; one pair of racemose seminal vesicles in XII, and a small simple pair in IX; two pairs of seminal funnels projecting freely into X and XI. Prostate glands limited to XVIII, glandular part thickly tubular, irregularly bent and adpressed, surface uneven; wall thick with narrow lumen which (Michaelsen, 1916a) is about 1/3 the thickness of the gland; duct short and thin, muscular, sharply demarcated from the gland; vasa deferentia joining the ental end of the duct. Penial setae 4 mm long, proximally 2 \(\mu\)m.
Fig. 15.41. *Graliophilus woodwardi*. Genital field. Syntype HM V7096. (Original).
Fig. 15.42. Previous page. *Graliophilus woodwardi*. A: Distal end of penial seta. B: Spermatheca. From Michaelsen (1907b).
in the middle about 1.5 mm and distally 1.3 µm thick; irregularly curved, and beset distally with thorns; the distal tip flattened at each side, forming two lateral seams at right angles to the plane of the curve, which extend in front of the point, their junction being marked by a small notch. The main pouch of each spermatheca stout, tubular, and irregularly bent, and filled with a granulated mass and several darker irregular bodies; merging into a short duct, the lumen of which is somewhat twisted; the diverticulum, which opens distally into the duct, thick and tubular, the proximal end swollen and somewhat lobed owing to the presence of 2 or 3 sperm chambers.

REMARKS
Graliophilus woodwardi closely resembles G. strelitzi, even to details of the genital field and setal ratios.

**Diagnosis**
Setae numerous, developed on the ventrum only. Body strongly dorsoventrally compressed, the ventrum flat or slightly concave, the dorsum convex. A single pair of combined male and prostatic pores in XVIII. Spermathecal pores 1 pair, in 8/9. Gizzard lacking. Calciferous glands not developed. Holonephric; nephridia simple, without vesicles. Holandric. Prostates tubuloracemose. Spermathecae diverticulate.

**Description**
As for the single species.

**Type-Species:** *Haereodrilus reichelti*. (Monotypic genus).

**Distribution**
Eastern Subregion, Kosciuskan Division: Conondale Ranges, southeast Queensland, epizoic on *Digaster grandis*.

*Haereodrilus reichelti* Dyne, 2000
(Fig. 16.1, 16.2)

**Type Locality:** 26°39'S.152°40'E., Near Booloumba Creek, close to gold-mine, Conondale Ranges (southeast Queensland, in dense mesophyll vine-forest, living ectocommensally on...
individuals of *Digaster grandis* (q.v.), at a depth of ca. 30 cm. Coll. G. Dyne, R. Reichelt, W. Nash and J. Bennett, 7 Jan. 1976.

**SYNTYPES:** numerous mature specimens. ANIC.GD.99:9:1.

Length 18.3, 17.5 mm. Width (segment XIV) 3.2, 2.8 mm. Segments 55, 56 (H, P1). Body fusiform in overall shape, tapering somewhat anteriorly and posteriorly; semi-circular in cross-section, the ventral surface flattened or slightly concave, the dorsum arched; pigmentless buff in alcohol. Prostomium prolobous, peristomium with a ventral indentation below the mouth. Dorsal pores not demonstrable. Setae numerous across the ventrum, with a conspicuous mid-ventral gap; 12 setae present on each side in XII and XX, in fairly regular rows throughout; setae absent from the dorsum, except for a single line lying immediately dorsal of the lateral edge of the body (a further setal line runs along the latter); the ventralmost seta in all segments up to approximately segment 37 (a) conspicuously enlarged and modified, directed towards the mid-ventral line. Nephropores not externally recognizable. Clitellum not definitely demonstrable in any specimens examined, despite obvious sexual maturity in most; a slight ?glandular discoloration is present on the dorsum in segments usually occupied by the clitellum in Megascolecidae in some specimens. Male pores valvular in appearance, atop pronounced conical papillae, in *ab*, on XVIII (setae *a* and *b* absent in that segment). The male papillae lie close to each other in a shallow depression, and this, together with a narrow, circumscribing furrow, adds to their distinct relief. Accessory genital markings absent. Female pore a single, unelaborated orifice, prese tally on a small ?glandular patch, in XIV. Spermathecal pores a single pair of
conspicuous openings in line with b setae, in 8/9, the slit-like orifices with puckered and wrinkled rims.

No muscular thickening of the preclitellar septa; strong dorso-ventral musculature near the lateral margins of the worm inhibits ready access to the body cavity. Dorsal blood vessel single; last hearts in XII; recognizable commissurals also seen in X and XI, their connections not traceable; no commissurals detected further anteriorly. Subneural vessel absent. Buccal cavity/pharyngeal mass extends to VI, a gizzard not developed, even in a rudimentary state; oesophagus rather wide, internally rugose, over VII-XV, calciferous glands or other elaborations absent; oesophageal valve present at 15/16, marking the point of commencement of the intestine. A definite typhlosole present, in sections appearing as a bipartite dorsal ridge, with an additional small projection seen arising from the floor of the intestine. Intestinal walls produced into pouch-like proliferations in segments XIX-XXVII, all with connections to the central lumen (? = true caeca). Ingesta mostly mucus, unidentifiable organic material, and a small number of soil particles. Holonephric; elaborate tufting absent from the pharyngeal region; stomate, avesiculate holonephridia present throughout, each a concentrated cluster of tubules at the lateral margins of the body; ducts not seen; nephridial bodies in the pre-clitellar region larger, more complex. Follicles associated with a-setae considerably enlarged, projecting conspicuously into the body cavity, and associated with muscular bands that have a broad insertion point in the body wall and which meet at a point behind the base of the seta; a single reserve seta usually present. The setae are ornamented over the ectal 1/3 with scattered shallow scallop-marks with toothed edges, giving a distinctly crenulate appearance. Holandric; 2 pairs of spermatic funnels and compact, iridescent seminal vesicle/sperm masses all discretely
encapsulated in X and XI in testis-sacs; no other seminal vesicles seen. Vas deferens spasmodically visible on the body wall, in cross-section clearly seen as single tubes on each side of the nerve-cord, joining the prostatic duct near its exit from the gland. Prostates a pair of simple, thickened lobes (tubuloracemose), their muscular ducts disappearing into a glandular manifestation of the body wall associated with the male field. Ovaries, with large, compound oocytes, and oviducal funnels in XIII, ovisacs not seen. Spermathecae a single pair, each organ consisting of a spheroidal ampulla, a rather long, bent duct, and a small, clavate diverticulum joining the latter approximately 2/3 along its length towards the pore. Length left spermatheca of IX = 1.1 mm; ratio length spermatheca: length of duct = 1.7; ratio length spermatheca: length of diverticulum = 2.06.

REMARKS
As noted by Dyne, this remarkable epizoic species is unlike any other oligochaete, not only in its obligate commensalism, but in the gross anatomical modifications it has undergone for such an existence. The slightly concave ventrum is well adapted for close adhesion to the host; setae are well-developed on this surface (for traction), whereas the dorsal setae have disappeared completely. The ventral most setae (a) are much enlarged, and since their follicles are endowed with complex musculature, are presumed to play a major role in locomotion; efficient co-ordination between successive setal rows may be responsible for the peculiar gliding movements of the worm observed in life on the surface of the host. Elucidation of the actual mechanism involved is beyond the scope of this work, and will be the subject of future investigation; certainly, the development of a robust dorso-ventral musculature is a
further feature of this species, a modification doubtless necessitated by the acquisition of a mode of locomotion quite different to that employed by most other terricolous Oligochaetes.

Other notable commensal associations within the Oligochaeta include the unusual enchytraeids *Aspidodrilus* *vide* Baylis, 1914) living on the body of a large ?Eudrilid, and *Fridericia*, sporadically observed (Cernosvitov, 1928) on *Allolobophora robusta*. *Haereodrilus* is unique, however, in being the only known opisthoporous Oligochaete ectocommensally associated with another. The diet of the above-mentioned enchytraeid epizoites appears to be restricted to surface mucus and exuded coelomocytes from the host species, whereas in *Haereodrilus*, though mucus is present in the ingesta, a major component of the diet appears to be organic debris of a vegetable origin. Other peculiarities include the lack of a gizzard, and, perhaps in compensation for the brevity of the alimentary tract, the development of both dorsal and ventral typhlosoles, and production of the intestinal walls into caeca-like outpouchings.

*Haereodrilus* appears to represent a much modified development of the basic *Diporochaeta* facies, though agreeing with the latter genus having a perichaetin setal arrangement, holonephry, a single, uniloculate spermathecal diverticulum, and a similar appearance of the male porophores to certain *Diporochaeta* species. Jamieson (1976b) drew attention to the distinct distributional hiatus of *Diporochaeta* (*sensu lato*, including what is now *Terrisswalkerius*), which extends from approximately 19°S, in mid-Northern Queensland, to Victoria. *Diporochaeta* (now *Hiatidrilus*) *bunya* (from the Bunya Mountains) at approximately 27°S and four other, neighbouring *Hiatidrilus* species interrupt this discontinuity and it is bridged by
Fletcherodrilus unicus, a species closely allied to Terrisswalkerius. Haereodrilus may be regarded as a profoundly modified Diporochaeta that has survived in its restricted range only through its association with the deep-burrowing Digaster grandis. The virtual restriction of Terrisswalkerius to rain forest habitats in Queensland would indicate that its members are sensitive to water-loss and/or high temperatures, preferring a cool, moist environment. This may explain, Dyne reasonably considers, their absence in the drier rain forests of south-eastern Queensland and Northern New South Wales, and the monsoon forests of north Queensland. Although Diporochaeta, of which Australian species are chiefly Victorian, is not a rainforest genus, it also may have been excluded from northern New South Wales and areas further north by climatic factors. Haereodrilus, in linking its life-history inextricably to that of the larger host-species, may derive benefit from the deep-penetrating abilities of that species, the burrows of which are known to extend to the water-table.

Differences between Haereodrilus and Diporochaeta include: the absence of a gizzard, presence of typhlosole (paralleling Graliophilus?) and five autapomorphic features: presence of intestinal caeca, the dorsoventrally flattened, fusiform body shape, modified a-setae, and development of dorsoventral musculature in the former genus, although not all of these are independent characters.
17. Healesvillea Jamiesn, 2000

DIAGNOSIS
First dorsal pore 5/6. Setae 8 per segment; ventrally widely paired, dorsal separate. Nephropores generally in c lines, at the anterior end partly in b and (less commonly?) d lines. Clitellum annular, XIV-XVII. Combined male and prostatic pores a pair on XVIII, on a pair of genital pads; other genital markings absent. Spermathecal pores 2 pairs, in intersegmental furrows 7/8 and 8/9.

A large gizzard in VI(?). In each of XIV-XVI, a pair of lateral calciferous glands sharply demarcated from the oesophagus, with longitudinal lamellae; those of XIV very small, simple, transversely oval; those in XV and XVI much larger, transversely elongate bean-shaped. Intestine commencing in XVIII. Holonephric. Holandric; 2 pair of racemose seminal vesicles, in XI and XII. Prostates racemose, bipartite. Penial setae apparently absent. Spermathecae 2 pairs, each with two, multiloculate diverticula.

DESCRIPTION
As for the single species.

DISTRIBUTION
Healesville, Victoria

TYPE-SPECIES: Woodwardia healesi Michaelsen, 1924b. (Monotypic genus).
REMARKS

Woodwardia healesi was considered by Michaelsen to approach W. sloanei and W. canaliculata, (now in Heteroporodrilus), both from New South Wales in having spermathecae with two diverticula, a rather rare occurrence in the Megascolecidae but now known from additional species of Heteroporodrilus. It agreed further with W. canaliculata in that these diverticula are at least partly multiloculate. However, it differs significantly from these two species and all other species of Heteroporodrilus in the position the calciferous glands which in Heteroporodrilus are in segments X or XI to XIII. More important, alternation of nephropores, so typical of Heteroporodrilus, appears to be absent in most segments in healesi.

The wide setal interval cd in healesi is nevertheless reminiscent of Heteroporodrilus. Furthermore, despite lack of evidence for regular alternation of nephropores of the type seen in Heteroporodrilus, Plutellus, Geofdyenia and Paraplutellus, some nephropores of healesi do occupy the setal rows b, c and d occupied in these ‘heteropores’ and the occurrence of racemose prostates is shared with Heteroporodrilus.

Presence of three pairs of calciferous glands in XIV-XVI is, however, unique in holonephric Australian megascolecids and, with the apparently limited variation in nephropore position, indicates a distinct phylogenetic position for this species, though within the heteropore assemblage, and warrants recognition of a new genus. It is unfortunate that no specimens of this species are available for further evaluation.

Diporochaeta (Vesiculodrilus) gippslandica (placed by Michaelsen in Woodwardia) also has two pairs of calciferous glands in XIV and XV, where they are large and
bean-shaped as in *healesi*, but the nephropore variation and bipartite, racemose prostates preclude placement of *healesi* in *Diporochaeta*.

**Healesvillea healesi** (Michaelsen, 1924)
(Fig. 17.1)

*Woodwardia healesi* Michaelsen, 1924b: 227-229, Fig. 5.

**Type Locality:** 37°39'S.145°32'E., Healesville - Vic.
**Holotype:** HM V9423 (lost).

Length approx. 150 mm. Width 7-8 mm. Segments about 142. Colour greyish brown. First dorsal pore 5/6. Setae 8 per segment, in the forebody ventrally rather distantly paired, dorsal separate; \(\text{aa: ab: bc: cd: dd} \approx 6: 3: 6: 10: 10\). Nephropores generally in *c* lines, at the anterior end partly in *b* and (less commonly?) *d* lines. Clitellum annular, XIV-XVII. A pair of broad, rounded transverse straight-sided, somewhat raised genital fields in XVIII, extending laterally to *b* lines and midventrally adpressed but sharply divided from each other. In each rounded lateral end, between setal lines *a* and *b*, lies a male pore in a circular, crater-like depression. Medial to these the genital fields are thickened to form a transversely oval genital pad. Spermathecal pores 2 pairs, in intersegmental furrows 7/8 and 8/9, in setal lines *a*. 
Woodwardiella healesi
Redrawn from Michaelsen, 1924b

Fig. 17.1. *Healesvillea healesi*. Spermatheca. Holotype. After Michaelsen (1924b).
Septa 7/8 and 8/9 delicate, 9/10-16/17 somewhat thickened, especially those of the testis-segments, but these still rather thin. A large gizzard in VI(?). In each of XIV-XVI, a pair of lateral calciferous glands sharply demarcated from the oesophagus, with longitudinal lamellae. Those of XIV very small, simple, transversely oval; those in XV and XVI much larger, transversely elongate bean-shaped. Intestine commencing, with abrupt expansion, anteriorly in XVIII. Holonephric. Holandric; 2 pairs of racemose seminal vesicles, in XI and XII. Prostates bipartite. A slender, somewhat bent, distally hardly widening duct forks proximally into two only slightly thinner, diverging branches, each of which bears a thickish, massive gland with a reticulate surface and several deeper incisions. Penial setae apparently absent. Spermathecae with oblong oval ampulla; sharply demarcated, spindle-shaped duct which at midlength is approximately one third as thick as the ampulla; somewhat narrower at the proximal and especially the distal end. The duct approximately as long as the ampulla, mostly meandering; proximally receiving, close to its junction with the ampulla, 2 superior diverticula. The diverticula with 2 or 3 seminal chambers adpressed like a fan but apically separate and ectally almost simple. The uppermost chamber is larger than the others.

**REMARKS**

The generic attribution of Michaelsen’s *Woodwardia healesi* is discussed in the remarks on *Healesvillea*, above.


**Diagnosis**
Prostomium pro-epilobous to tanylobous. Setae 8 per segment. Dorsal pore from 5/6 or posteriorly. Combined male and prostatic pores a pair on XVIII. Racemose to tubuloracemose prostates. Spermathecal pores 2-5 pairs, in or shortly behind the intersegments. Nephropores conspicuous at the anterior border of their segments with a complex alternation from d to b lines.

Gizzard in V. Calciferous glands, 3-5 ventro-lateral pairs sessile or on short-stalks (i.e. about as long as broad) on the oesophagus, the last pair always in XIII. Holonephric with (adiverticulate but sometimes bilobed) terminal bladders. Holandric, testis and funnels free or in unpaired (pericardiac) testis sacs. Prostates tubuloracemose to racemose. Spermathecae with one or more, uniloculate or, rarely, complex diverticula.

**Description**
Moderate to large size terrestrial worms (52-580 mm long) generally with less than 200 segments (range 90-387). Sometimes dorsum canaliculate and with or without brown-grey pigmentation. Prostomium variable from pro-epilobous to tanylobous, often grooved. Setae 8 per segment (only occasionally a and/or b retained on XVIII). Dorsal pore from 5/6 or beyond. Male pores and pores of one pair of racemose to
tubuloracemose prostates in XVIII. Spermathecal pores 2-5 pairs, the last in 8/9 (H. notatus and H. clarkei near mid-IX). Nephropores conspicuous at the anterior border of their segments in d lines in II-IV or V; in c lines, or alternating between setal lines d and c (or mid-bc) for a few segments; then from X where alternation between b and d lines commences for the remainder of the body (may be asymmetrical).

Gizzard in V. Calciferous glands, 3-5 ventro-lateral pairs sessile or on short-stalks (i.e. about as long as broad) on the oesophagus, the last pair always in XIII. Holonephric with (adiverticulate but sometimes bilobed) terminal bladders. Holandric, testis and funnels free or in unpaired (pericardiac) testis sacs. Spermathecae with one or more, discrete or composite, diverticula.

DISTRIBUTION
Western Sub region, Darling Basin Province: Murray-Darling River basins in New South Wales and South Australia. Eastern Subregion, the Wimmera River, Victoria; Tweed River basins in northern New South Wales, river catchments in south-east Queensland.

TYPE-SPECIES: Cryptodrilus tryoni Fletcher, 1890.

The generic definition was augmented by Blakemore (1994b) to accommodate, not only new species, but also several species that were previously placed in Plutellus (sensu Jamieson and Nash, 1976; Dyne, 1981).
CHECKLIST OF THE SPECIES AND SUBSPECIES OF *HETEROPORODRILUS*

1. *H. bongeen* Blakemore, 1994b
2. *Cryptodrilus canaliculatus* Fletcher, 1889
4. *Cryptodrilus cooraniensis* Spencer, 1900
5. *Woodwardiella dioecia* Stephenson, 1933
6. *H. doubei* Blakemore, 1994b
7. *Cryptodrilus fletcheri* Beddard, 1887a
9. *H. jamiesoni* Blakemore, 1994b
10. *H. lamingtonensis* Jamieson, 1970a
11. *Cryptodrilus mediterreus* Fletcher, 1887b
15. *Cryptodrilus oxleyensis* Fletcher, 1889
17. *Cryptodrilus shephardi shephardi* Spencer, 1900
   *H. shephardi armatus* Jamieson, 1974b
18. *Cryptodrilus sloanei* Fletcher, 1889
19. *H. thompsoni* Blakemore, 1994b
20. *Cryptodrilus tryoni* Fletcher, 1890
The following revised key to known species of *Heteroporodrilus* is partly based on Blakemore (1994b), modified for later species.

REVISED KEY TO THE SPECIES OF *HETEROPORODRILUS*

<table>
<thead>
<tr>
<th>Key</th>
<th>Description</th>
<th>Species</th>
</tr>
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<tbody>
<tr>
<td>1</td>
<td>a. Five pairs of calciferous glands; three pairs of spermathecae</td>
<td><em>H. tryoni</em></td>
</tr>
<tr>
<td></td>
<td>b. Four pairs of calciferous glands</td>
<td>2</td>
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<tr>
<td></td>
<td>c. Three pairs of calciferous glands</td>
<td>11</td>
</tr>
<tr>
<td>2</td>
<td>a. Three pairs of spermathecae</td>
<td>3</td>
</tr>
<tr>
<td></td>
<td>b. Two pairs of spermathecae</td>
<td>9</td>
</tr>
<tr>
<td>3</td>
<td>a. Nephropores in c line and d lines in anterior segments</td>
<td>4</td>
</tr>
<tr>
<td></td>
<td>b. Nephropores alternate between d line and mid-bc in anterior segments</td>
<td>8</td>
</tr>
<tr>
<td>4</td>
<td>a. Prostates confined to XVIII, penial setae absent; genital markings may include XX</td>
<td>5</td>
</tr>
<tr>
<td></td>
<td>b. Prostates XVII-XIX or XVI-XXII, penial setae present; no genital markings in XX</td>
<td>7</td>
</tr>
<tr>
<td>5</td>
<td>a. Genital markings include a series of transverse papillae median to male pores on XVIII</td>
<td><em>H. montiserratae</em></td>
</tr>
<tr>
<td></td>
<td>b. Genital markings not as in 'a'</td>
<td>6</td>
</tr>
<tr>
<td>6</td>
<td>a. Prostates with straight duct; spermathecal diverticula variable, single or paired</td>
<td><em>H. incommodus</em></td>
</tr>
<tr>
<td></td>
<td>b. Prostate ducts long and sinuous; spermathecae each with a single, simple diverticulum</td>
<td><em>H. raveni</em></td>
</tr>
</tbody>
</table>
7(4b) a. Dorsum with a middorsal groove; spermathecae each with two diverticula, occasionally single, but always compound; seminal vesicles in IX and XII
   H. canaliculatus
b. Body lacking dorsal groove; spermathecae each with a single, simple (even rudimentary) diverticulum; seminal vesicles in XI and XII
   H. mediterreus

8(3b) a. Genital markings include eye-like pits in 17/18 and 18/19; penial setae present in XVIII
   H. shephardi armatus
b. Genital markings segmental in some or all of XVII, XVIII and XIX; penial setae absent
   H. shephardi shephardi

9(2b) a. Spermathecae paired, diverticula bifid or trifid or variously multi-lobed or numerous
b. Spermathecae with simple (paired) diverticula
   H. bongeen

10(9a) a. Size >210 mm; prostomium epilobous furrowed to 2/3; spermathecae: ampullae large and annulated, diverticula compound, opening intersegmentally
   H. thompsoni
b. Size <105 mm; prostomium tanylobous; spermathecae with simple or bifid diverticula opening to midsegment
   H. notatus

11(1c) a. Spermathecae, three or more pairs
b. Spermathecae, two pairs

12(11a) a. Genital markings ventral, transverse, wider at lateral extremities, in XVII-XXI
   H. fletcheri sp. dubium
b. Genital markings not including XXI
| 13(12b) | a. Genital markings in some of XVII-XX and may include some of IX-XI  
|         | b. Genital markings weak or absent (immature?) |
| 14(13a) | a. Spermathecae five (or four) pairs. Genital markings widely paired in XVII-XX, presetal  
|         | b. Spermathecae four (or three) pairs. Genital markings not as ‘a’ |
| 15(14b) | Spermathecal pores three pairs. Genital markings a pair of transversely oval tumescences in X and XIX, each bearing a minute pore-like point, presetally in (X) or slightly lateral (XIX) of a; paired tumescences may also be present in XVII; alternatively, tumid pads in aa in X and/or XI and possibly small unpaired genital markings on XVIII; all genital markings frequently absent  
|         | b. Spermathecae four (or three) pairs. Genital markings transverse or closely paired including XVII-XX |
| 16(13b) | a. Spermathecal diverticula paired  
|         | b. Spermathecae (occasionally one of the six absent) each with a single diverticulum; prostates absent or present |
| 17(11b) | a. Spermathecal pores presetal near mid-VIII and mid-IX  
|         | b. Spermathecal pores in or near 7/8 and 8/9 |
| 18(17b) | a. Size >300; prostomium epilobous; preclitellar genital marking a series of papillae within a tumid lateral pad ventrally in XII  
|         | b. Size <180; prostomium epi- or tanylobous; preclitellar genital markings absent or not on XII |
| 19(18b) | a. Spermathecal diverticula paired |
b. Spermathecal diverticula single

20(19a)  
 a. Genital markings numerous on VII-IX. Inconspicuous, if present, on XVIII  
 b. Genital markings on X and XI and numerous on XVIII-XXI

**Heteroporodrilus bongeen** Blakemore, 1994b  
(Fig. 18.1, 18.2)

**Heteroporodrilus bongeen** Blakemore, 1994b: 23-25, Fig. 1.

**TYPE LOCALITY:** 27°34’S.151°27’E., Bongeen on the Condamine River plain west of Toowoomba - Qld.  
**HOLOTYPE:** QMG210136  
**PARATYPE P1, QMG210137.**  
**OTHER MATERIAL:** (same data), QMG210138.

Length 250+ mm, body circular in section without dorsal groove although one specimen had the posterior 6 segments furrowed. Width 5.5-7.5 mm, widest point about VIII. Mass 3-4 g per adult. Segments 193-200; first ten segments smooth followed by moderate secondary annulation in succeeding segments. Colour dark slate grey pigmented anterior (with paler ventral tumescences on X, XI and possibly XII), dorsum and caudal segments with faint red/yellow iridescence; mid-body moderate pigmentation (soil visible in gut). Clitellum variously darker or lighter brown colour. Prostomium open epilobous or closed by fine groove but appearing
tanylobous due to longitudinal dorsal groove extensions which may almost reach as far as 1/2. First dorsal pore 10/11? (difficult to determine due to deep furrows). Setae small, 8 per segment from II, a and b obscure (modified?) on XVIII, lateral setal couples cd widely spaced; in XII aa: ab: bc: cd: dd: u: = 1.7: 1.0: 1.4: 2: 4: 0.28 (mean of 2). Nephropores: in d line 1/2-3/4, 6/7, 8/9, 10/11 or 11/12 then alternating; in b line 5/6, 11/12 or 12/13 then alternating, possibly in c line in 4/5-7/8. There is slight variation between specimens, but for most of the body length there is clear alternation between b and d lines. Clitellum 1/3XIII-XVII annular, setae and nephropores retained. Male pores minute in XVIII on small raised porophores in b line. Female pores paired in XIV in line of anterior annulus within a common darker patch anteromedian to a setae. Spermathecal pores 7/8 and 8/9 in b line concealed in deep intersegmental furrows. Genital Markings (X-XII ventrally tumid?), in XVII almost central between a setae, three small discs in raised tumid area; in XVIII, especially in anterior annulus, four or five pairs of discs (one pair ventral in setal arc) in furrowed, generally tumid area that fills the ventral aspect; in XIX similar markings, but discs tend to be smaller and more numerous.

Septa 4/5-11/12 getting progressively thicker, from 12/13 becoming weaker (10/11-12/13 thickest); pharyngeal ligatures (tendons) extend beyond VIII. Dorsal blood vessel single continues on pharynx. Vascularization: VI-IX commissurals, X-XIII larger hearts. Gizzard compact, spherical and muscular in V. Calciferous glands four pairs, compact and ventral on oesophagus in X, XI, XII, and XIII. Those in X smaller, almost rudimentary. Oesophagus narrows in XIV (valve?) then widens in XV as intestine proper; typhlosole not found. Gut contents: full of very fine grey clay soil and a few round grits coated in mucus (i.e. geophagous). Nephridia holonephric: a
pair in each segment, from at least V, with large deflate and flattened, spherical terminal bladders. Nephridia closely associated with anterior septa (pre-septal funnels). Holandric: iridescent funnels of testes in X and XI; racemose seminal vesicles in IX and XII. Ovaries in XIII, ventrally paired sheets of mesentery may be ovaries but individual oocytes not seen, the egg funnels were seen on the posterior septum. Five or six smallish, white spheres were noted in one specimen loosely attached to the septum, possibly parasitic *Monocystis* sp? Prostates a pair of large tongue-like racemose glands extending from XVIII-XIX and overlying a small, flaccid duct that soon enters the body wall. Spermathecae 2 pairs in VIII and IX: spherical but waisted ampullae clearly demarcated from shorter ducts, each bearing a pair of opposed digitiform, iridescent diverticula. One specimen had a single diverticulum on only one of its spermathecae.

**REMARKS**

*H. bongeen* is perhaps closest to *H. canaliculatus* (Fletcher, 1889) recorded from the Lachlan River at Forbes, NSW. It differs from *H. canaliculatus* in several features but especially in lacking dorsal canaliculation, in having one fewer pair of spermathecae and in the numbers and position of the genital markings. On these variations, together with its geographic location, it is separated from other species (Blakemore, 1994b).
**Heteroporodrilus canaliculatus** (Fletcher, 1889)

*Cryptodrilus canaliculatus* Fletcher, 1889: 1534-1536; Fletcher, 1890: 996.  
*Platellus canaliculatus*; Michaelsen, 1900: 171-172.  

**TYPE LOCALITY:** 33°23'S.148°01'E., Forbes, Lachlan River - NSW.  
**SYNTAXYPES:** AM W1373 (16 specimens).  
**NEW RECORDS** (2000): Woolwich, Lane Cove River, 3 specimens, presented by J.S.P. Ramsay (May 1928) 03 04 1928, AM W2558, Identifier E. Easton 1983. 33°49'S.151°14'E., Mosman, 1 specimen, presented J.C. Wiburd (June 1933) 22 06 1933 Identifier E. Easton 1983, AM W3067. 28°51'S.153°33'E., Ballina District, 3 specimens, E.M. Embury 29 01 1930 Identifier E. Easton 1983, AM W3415. 29°42'S.152°56'E., Grafton, 1 specimen, Fletcher 1923 Identifier B. Jamieson AM W18691 - NSW.

Length 125-250 mm. Width 3.5-5 mm. Segments 250-265. Prolobous but appearing epilobous to tanylobous owing to longitudinal ribbing of the peristomium. First dorsal pore 7/8. Body canaliculate throughout. Setae *bc* widely separated. The first three or four pairs of nephropores in *d* lines; in the next two or three segments in *c* lines; then alternating between *d* and *c* for some distance and thereafter alternating between *d* and *b*; not always at the same level on both sides. Clitellum annular, XIV-XVII; clitellum-like modification of the posterior annulus of XIII and the anterior annulus of XVIII may be present. Male genital field: on the anterior, middle and posterior annuli of XVIII, and on the anterior annulus of XIX, a pair of papillae in *ab*; the second pair of these apparently carrying the male pores; a small papilla sometimes present ventral to
each papilla of the second pair. Female and spermathecal pores as in *mediterreus* but the former in a groove-like depression. No modification of the ventral surface of VI-IX.

Gizzard in V; four pairs of ventrolateral calciferous glands, in X-XIII. Intestinal origin in XVI. Nephridial postseptal in II posteriorly; ectal vesicles seen in the dorsal series. Testes and funnels in X and XI; seminal vesicles two pairs, in IX and XII. Prostates in XVIII-XIX. Penial setae present. Ovaries and oviducts normal. Spermathecae three pairs, in VII-IX, each with usually two short diverticula, one on each side and in front of the duct ectally (further ectally than in *mediterreus*) either diverticulum may be slightly bifid or even trifid at the tip, or completely subdivided into two or three; in one case there being a single broad flat diverticulum five or six lobed at the tip.

**Heteroporodrilus clarkei** (Dyne, 1981)
(Figs 18.1, 18.2)

*Plutellus clarkei* Dyne, 1981: 97-100, Figs. 1A, 2C,E.

**TYPE LOCALITY:** 28°37'S, 153°24'E., Minyon Falls, Whian Whian State Forest, approx. 12 km SW of Mullumbimby - NSW.
**HOLOTYPE:** AM W6645.
**PARATYPES:** P AM W6646. P, QM G8913.
Fig. 18.1. *Heteroporodrilus clarkei*. Genital field. Holotype AM W6645. After Dyne (1981).
Length 81-96 mm. Width (midclitellar) 3.4-3.8 mm. Segments 150-154. Uniformly circular in cross-section throughout, pigmentless buff in alcohol. Prostomium tanylobous, peristomium much furrowed. First dorsal pore 5/6 or 6/7. Setae a and b absent from XVIII; in XII, 12.9: 5.7: 11.2: 11.7: 29.5. Nephropores distinctly visible; in II-IV in d lines, V-VII in c, VIII in d, IX in d, XI in c, XII in d, XIII in b, thereafter alternating regularly between d and b throughout; in paratype I a similar sequence, but with regular alternation commencing with first b line pore in XI. In P2 there is an asymmetric sequence as follows: right side: II-XI (d,d,d,c,c,d,c,d,b,d, etc.); left side: II-XIV (d,d,d,c,c,c,d,c,d,d,d,b,d, etc.); this asymmetry continues throughout. Clitellum annular, faintly developed over XIV-XVII; intersegmental furrows, dorsal pores or setae not obscured. Male genital field with series of 4 broad, tumid pads extending longitudinally across the segment, and laterally to slightly beyond b lines present in XVII-XX; each bears a varying number of small, glandular, dimple-like markings. Male pores are visible as minute orifices in b lines, each pore with a dimple-like marking immediately anterior to it. A pair of broad mid-ventral pads similar to those in XVII-XX is present in X and XI; these also bear rows of dimples. Female pore faint, unpaired median, slightly presetally in XIV. Spermathecal pores on small papillae, presetally in VIII and IX, slightly lateral to b lines.

Septa: 5/6 diaphanous, 6/7 thin, 7/8 with slight thickening, 8/9-10/11 moderately-strongly muscularized, 11/12 slightly thickened, remainder thin. Dorsal blood vessel single, continuous onto the pharynx, bifurcating under the brain. Last hearts in XIII; only commissurals XI-XIII are distinctively heart-like, though the remainder are still quite large, decreasing in size anteriorly. Commissurals X-XIII may be considered latero-oesophageal, receiving a short, thick, connective from a prominent latero-
calciferous trunk on each side, and a much thinner connective from the dorsal vessel. The calciferous vessels fuse in the mid-dorsal line to form a prominent supra-oesophageal vessel. Beginning in mid-XIII, this vessel runs forwards to XII, to join the point of fusion of the latero-calciferous trunks in that segment; with continuity of the supra-oesophageal forward to 11/12. Thereafter, the vessel continues anteriad through XI to X, where it terminates at or near 9/10. A paired sub-oesophageal vessel supplying the calciferous glands is present. Gizzard large, cylindrical, and well vascularized, in V; though obviously muscular, it is somewhat compressible, with a conspicuous anterior rim. Oesophagus of moderate width, well vascularized, over VI-XIV; 3 pairs of flattened-discoid (almost reniform) calciferous glands present ventrally in XI-XIII, or the middle pair, in XII greatly reduced, appearing like simple oesophageal pouches. Each highly vascular, lamellate gland is attached dorso-laterally to the oesophagus by a long, though broad, stalk. Intestine commences abruptly in XV, typhlosole absent. Nephridial bladders crinkled, somewhat lobulated, those overlying the dorsal-most nephropores (i.e. in d lines) more pronounced than the other series. Holandric; 2 pairs small-medium sized sperm funnels, and flocculent sperm masses in X and XI; 2 pairs of racemose seminal vesicles in IX and XII. Septa 9/10, 10/11 and 11/12 are joined dorsally by a thin, but definite, pericardial testis-sac. Vas deferens not traceable, excepting in XVII-XVIII; prostates simple tongue-shaped lobes restricted to XVIII, or simple S-shaped, extending into XIX, with a short, but much coiled duct entering the parietes in that segment. The unpaired vas deferens enters the glandular portion of the prostate ventrally, a little distance from the point of visible origin of the duct. Ovaries a discrete sheaf of small oocytes, and large funnels, in XIII; ovisacs absent. Spermathecae 2 subequally sized pairs in VIII and IX,
Fig. 18.2. *Heteroporodrilus clarkei*. A: Left prostate in situ. B: Right spermatheca of IX. Holotype AM W6645. After Dyne (1981).
discharging anteriorly in their segments. Each comprises a tubular ampulla, with long bent duct (of ill-defined origin), and a single, uniloculate, inseminated, digitiform diverticulum, arising approximately midway along the length of the duct. Length right spermatheca of IX = 1.78 mm; length spermatheca: length of duct = 4.5; length of spermatheca: length of diverticulum = 3.00. Considerable variation exists as to the number and nature of the spermathecal diverticula; the left IX spermatheca diverticulum may be flattened, and appear biloculate; in right VIII, there are may be 2 discrete diverticula; or all but left IX spermathecae have 2 diverticula.

REMARKS
H. clarkei is very similar to its sympatric congener, H. minyoni. The comparatively close conformity in, amongst other characters, the general appearance of the genital fields and setal ratios, suggests that reproductive isolation between the two populations has been a relatively recent event. In this instance, as in the case for the vast majority of earthworm species where breeding data are unavailable, specific integrity is assumed if (a) consistent morphological differences indicate a lack of gene flow between any two populations; (b) consistent major discrepancies exist either in size and/or the configuration of the genital fields as to preclude the operation of a specific mate recognition system (sensu Patterson, 1978) (Dyne, 1981).

The long stalks of the calciferous glands approach the Putellus condition, but the racemose (or, at least, non-tubular) prostates support placement in Heteroporodrilus.
**Heteroporodrilus cooraniensis** (Spencer, 1900)
(Fig. 18.3)

*Cryptodrilus cooraniensis* Spencer, 1900: 42-43, Pl. 6, figs 34-36; Sweet, 1900: 114; Jensz and Smith, 1969: 86.

*Woodwardia cooraniensis*; Michaelsen, 1907b: 162; Bage, 1910: 234-236, Pl. 46, fig. 18-19, Pl. 47, fig. 20-21.


**TYPE LOCALITY:** 26°20'S.152°50'E., Cooran, under logs in palm scrub - Qld.

**SYNTYPES:** NMV F4044-45 (Jensz and Smith, 1969; identity here considered indeterminable owing to poor condition). F4043, said by Jensz and Smith, 1969, to be a syntype is a perichaetine worm, as the Spencer label 'Peri sp. 8?' suggests. It appears to be *Spenceriella minor*, see that species.

Length 68-75 mm. Width 3 mm. Segments about 142. Tanylobous. First dorsal pore 5/6. Clitellum well marked, XIV-XVI. Genital markings in the form of glandular patches ventrally XVII and XVIII; one pair in *ab* on XVII, and three median patches on XVII, XVIII and XIX. Setal lines regular throughout: *ab* near to the ventral midline and close together; *ab* = *bc*; setae *d* half-way between *c* and the middorsal line. Nephropores clearly marked; the first on the anterior margin of II in *d* lines as are those of II and IV; those on V, VI and VII in *c* lines; in VIII in *d* lines, in IX in *b* lines and so on alternately down the length of the body. Male pores on XVIII on papillae in *ab*. Female pores on XIV on an oval glandular patch. Spermathecal pores, 2 pairs, in 7/8 and 8/9 in *a*. 
Fig. 18.3. *Heteroporodrilus cooraniensis*. Genital field. Redrawn from Spencer (1900).
Gizzard in V; calciferous glands in segments XI, XII and XIII. Intestine, commencing in XV. Dorsal vessel single; hearts in VII-XIII. Holonephric. Testes and funnels in XI and XI, in testis-sacs which wrap around the gut and fill each segment. Seminal vesicles lobulate, in IX and XII (Spencer's Fig. 36). Ovaries in XIII. Prostates flattened, bilobed or sometimes not, in XVII. Spermathecae, 2 pairs, in VIII and IX; each with a spherical ampulla and tubular diverticulum.

REMARKS
Presence of testis-sacs is highly unusual for holonephric megascolecines. It has not been possible to re-examine this feature in the types owing to their poor condition.

Heteroporodrilus dioecius (Stephenson, 1933)
(Fig. 18.4, 18.5)

Woodwardiella dioecia Stephenson, 1933: 910-912, fig. 9, 10.
Heteroporodrilus dioecius; Jamieson, 1970a: 113-114, Fig. 5d-f, 9b, 10b, c; Blakemore, 1994b: 21,25-26, Fig. 2.

TYPE LOCALITY: 27°34'S.151°57'E., Toowoomba - Qld.
HOLOTYPE: BMNH 1932.5.5.3.
OTHER RECORDS: (Jamieson, 1970a) 27°16'S.152°59'E., Camp Warrawee, near Petrie, QMG5445. (Blakemore, 1994b) 27°30'S.152°55'E., Brookfield, Brisbane, QMG210139; 27°22'S.152°53'E., CSIRO, Samford - Qld.
Length 33-103 mm Width 2.5-3 mm. Segments 90-103. Colour anterior dorsum pigmented light to dark brown, clitellum yellow-orange with faint iridescence, ventrum pale; colourless in ethanol. Prostomium epilobous 1/2; dorsal tongue triangular continued by a middorsal groove to 1/2, sometimes appearing tanylobous. First dorsal pore 5/6, 6/7; either obvious and continuous over clitellum or not. Setae 8 per segment from II, rather indistinct; all widely paired; in XII, \(aa: ab: bc: cd: dd = 1.5-2.0: 1.0: 1.1-1.6: 2.8-3.0\); on XVIII setae \(a\) may be modified. Nephropores, commencing at the anterior border of II; in \(d\) line at 1/2-3/4, in \(c\) lines from 4/5 for 3 or more segments, to 6/7 or 8/9; briefly alternating between \(c\) and \(d\); then alternating between \(b\) and \(d\) from 10/11; alternation sometimes asymmetrical. Clitellum annular, XIV-XVI, with varying extension dorsally onto XIII and XVIII; furrows, setae and nephropores retained. Male pores minute, at or immediately lateral of the sites of setae \(b\), on indistinct papillae. Accessory genital markings a pair of transversely oval tumescences in X and XIX, each bearing a minute pore-like point, presetally in (X) or slightly lateral (XIX) of \(a\); paired tumescences may also be present in XVII; alternatively, in two Samford specimens, tumid pads seen in \(aa\) in X and/or XI and possibly small unpaired genital markings on XVIII; all genital markings frequently absent. Female pores in XIV anteromedian to setae \(a\). Spermathecal pores 3 pairs, in 6/7, 7/8 and 8/9 small and usually concealed in furrows, in \(b\) lines.

Septa 4/5-9/10 moderately thick, 8/9/10 the thickest, 10/11-14/15 weaker. Dorsal blood vessel: single continues on pharynx. Last hearts XIII. Gizzard moderate in size, wider than long, muscular but compressible, in V. Calciferous glands 3 pairs, ventral on oesophagus in XI, XII and XIII. Intestine commencing in XV, no typhlosole.
Nephridia holonephridia with large sacciform bladders seen from at least VI. Holandric; sperm funnels, which may be weakly iridescent, in X and XI; seminal vesicles racemose, in IX and XII. Ovaries paired tufts of egg strings in XIII or in XII (this anomalous position seen in Samford and Brookfield, even where female pores are in XIV). Prostates absent or flattened and incised lobes with muscular duct one sixth to nearly half the length of the gland. Spermathecae three pairs in VII-IX (or one spermatheca sometimes absent), with stoutly fusiform to subspherical ampulla tapering to short duct with a digitiform diverticulum (iridescent in several cases) a little more than half the length of the ampulla.

REMARKS

*Heteroporodrilus (= Woodwardiella) dioecius* was erected for worms from Toowoomba (Stephenson, 1933) which, like those described by Blakemore (1994b) from Samford and Brookfield, lacked prostate glands. However, Jamieson (1970a) collected specimens with racemose prostates and male pores at Petrie near Brisbane. The author has observed prostates and male pores in new Brookfield material, thus showing that Blakemore was correct, because spermathecal diverticula were inseminated, in suggesting that similarly male-fertile specimens might be present in the populations from which aprostatic specimens were collected as in his study.

**Heteroporodrilus doubei** Blakemore, 1994b

*Heteroporodrilus doubei* Blakemore, 1994b: 26-28, Fig. 3.
TYPE LOCALITY: 28°48'S.153°17'E., 10 Km NW of Lismore - NSW.
HOLOTYPE: QM G211897.
PARATYPES: QM G21198, 21199.

Length 95-120 mm. Width 3.5-4.0 mm. Segments 91. Body circular in cross section. Colour unpigmented, transparent in alcohol. Prostomium closed epilobous. First dorsal pore 5/6, not clear on clitellum. Setae 8 per segment from II, ab absent from XVIII, whole length of setae can be seen through body wall after clitellum; aa: ab: bc: cd: dd: u = 2.13: 1.0: 1.63: 1.75: 6.0: 0.36. Nephropores in D in 1/2-3/4? and 6/7 on left hand side, in C 5/6-8/9 in B in 9/10 on right hand side and 10/11 on left hand side then alternating between D and B for remainder of body. Clitellum 1/2XIII-XVII pale coloured but slightly tumid. Male pores small in site of missing b setae on slightly raised mound. Female pores paired (sometimes unilateral?) on XIV. Spermathecal pores concealed in furrows 7/8 and 8/9 in b lines. Genital markings (sometimes indistinct) single, ventrally offset disc on VII; two closely paired in anterior of VIII with more lateral sets in longitudinal series in line with spermathecal pores; similar discs to VIII on IX except the median discs are in the setal arc; possibly the raised mounds on XVIII are genital markings.

Septa 5/6 weak and finely attached to sides and base of gizzard; 6/7-10/11 moderately thickened; 11/12 on thin. Dorsal blood vessel single onto pharyngeal mass in IV. Hearts commissurals in VI-IX; hearts in X-XIII the last three pairs larger. Ventral vessel bifurcated under gizzard. Fine, supra-oesophageal vessel seen in XII and XIII with lateral branches. Gizzard large, muscular in V but displaced almost to 6/7. Calciiferous glands small, white, ventrally sessile pairs of glands in XI-XIII.
Intestine widens suddenly in XV (acaecate, atyphlosolate). Nephridia holonephric from anterior with large, flimsy vesicles obvious in the clitellar region, alternating in position. Iridescent sperm funnels seen in X and XI but fragmented during dissection; large pair of racemose seminal vesicles posteriorly in IX and anteriorly in XII. Ovaries not located. Prostates tubuloracemose, confined to XVIII but folded over flaccid duct. Spermathecae two pairs in VIII and IX, bulbous ampullae narrow to shorter ducts, each bearing a pair of opposed clavate, iridescent diverticula. Gut contents fine soil and Acarina (litter mites) suggesting geophagous/detritivores diet.

**REMARK**

*Heteroporodrilus doubei* has 3 pairs of calciferous glands and two pairs of bidiverticulate spermathecae. Similarities in distribution of calciferous glands and spermathecae are with *Heteroporodrilus minyoni* which, however, is much larger (400 mm long), and also with the bi-diverticulate *H. lamingtonensis* in which the genital markings are in X and XI and XVI-XXI rather than in VII-IX.

*Heteroporodrilus doubei* vindicates Blakemore's separation of *Heteroporodrilus* from *Platellus sensu stricto*, as it has sessile calciferous glands and tubuloracemose prostates that would have bridged the previous generic definitions.

**Heteroporodrilus fletcheri** (Beddard, 1887a)

(Fig. 18.6)

*Cryptodrilus fletcheri* Beddard, 1887a: 544-548, Fig.
Plutellus fletcheri (part.) Michaelsen, 1900: 79 (excluding C. oxleyensis Fletcher).

Type locality: Queensland.
Types: Lost.

Setae $ab$ fairly closely paired; setae $cd$ wide apart. Nephropores of segments II-IV in $d$ lines; in V-VII in $c$ lines; (in VIII?); in IX in $d$ or, on the other side, in $c$ lines; asymmetrically situated in some succeeding segments. In a second specimen (illustrated): in VI and VII in $c$ lines; in VIII and IX in $c$ (left) or $d$ (right); in X in $d$ (left) and not indicated on the right; in XI in $d$ (left) and $b$ (right), in XII reversing these positions. Clitellum in XIII-XVII (= 5 segments), annular but interrupted ventrally in XVII by an area including the ventral setae; this space occupied by an elongated genital papilla which is wider at the two extremities than centrally; similar papillae in segments XVIII-XXI. Male pores on XVIII within the area of the genital papillae, close to setae $ab$. Female pores on XIV in a single slit-like orifice with tumid lips. Spermathecal pores anterior in VI-IX in $b$ lines.

Gizzard in VI and VII (?). Paired calciferous glands located below the oesophagus, almost contiguous, but separated midventrally by the suboesophageal vessel; only two pairs described, in XI and XII, but more posterior segments not examined; (shown in segments XI-XIII in the illustration). Nephridia with a saclike muscular duct furnished at its extremity with a short diverticulum of identical structure. Testes and funnels in X and XI apparently free; seminal vesicles in IX and XII, racemose. Prostates large, racemose. Ovaries and funnels in XIII. Spermathecae four pairs, in
Fig. 18.6. *Heteroporodrilus fletcheri*. Dorsal dissection. Relabelled from Beddard (1887a).
VIIX; pyriform with a rapidly narrowing duct which bears medianly a digitiform diverticulum which is slightly shorter than the ampulla.

REMARKS

Despite contradictions and inadequacies in Beddard's account there is little doubt that Cryptodrilus fletcheri is a species of Heteroporodrilus. This is indicated by the arrangement of the nephropores and, from Beddard's illustration, occurrence of ventral, unstalked calciferous glands in XI-XIII. Location of the gizzard in VI and VII and occurrence of diverticula of the nephridial vesicles, if confirmed, would however necessitate exclusion from Heteroporodrilus. Michaelsen (1907a) did not include C. fletcheri among the species of his new genus Woodwardia, though he included C. oxleyensis Fletcher, which previously (Michaelsen, 1900) he had regarded as a junior synonym of fletcheri (within the genus Plutellus.) Leaving aside possible generic differences from oxleyensis, fletcheri is distinct in having a genital marking in segment XXI and apparently in retaining setae ab of XVIII. As no type-locality within Queensland was specified it is doubtful that it will be possible to positively identify any new material with Beddard's description and C. fletcheri must be considered nomen et species dubium.

**Heteroporodrilus incommodus** (Jamieson and Nash, 1976)
(Fig. 18.7-18.9)

*Plutellus incommodus* Jamieson and Nash, 1976: 47-50, Fig. 1A, B, 2A-G, Table 1.

**TYPE LOCALITY:** 26°42'S.153°00'E., Eudlo Creek; 27°08'S.152°57'E., near Forest Glen - Qld.

**HOLOTYPE:** QM G8376.

**PARATYPES:** BMNH 1976.1.3-4., QM G8377-8381.

Length 67-135 mm. Width (XV) 3.6-4.3 mm. Segments 144-311. Unpigmented, pale almost white in life. Anterior segments simple, becoming biannulate and then, in VII or VIII posteriorly triannulate. Prostomium tanylobous. First dorsal pore 6/7. Setae *ab* absent, *cd* present, in XVIII; in XII, *aa: ab: bc: cd: dd* = 11.9: 7.9: 11.2: 10.7: 28.0. Nephropores in *d* lines in II-IV; in *c* lines in V and VI; in *c* and/or *d* lines in VII-IX (usually alternating between *c* and *d*); alternating between *b* and *d* (or *vice versa*) in X posteriorly. In X, and occasionally a more posterior segment, the pores may lie in *c* bi- or uni-laterally and the *b* or *d* location may rarely be duplicated in two successive segments in an otherwise regularly alternating sequence. Clitellum annular, XIV-2/3XVII, XVII; if developed in the posterior third of XVII always much weaker than further anteriorly. Male pores equatorial in XVIII very slightly median of *b* lines relative to adjacent segments, on a pair of inconspicuous circular porophores which lie on longitudinal ridges which are chiefly apparent by virtue of flattening of the ventral body surface between them, the flattened region being depressed relative to the male pores so that the median ventral aspect of each ridge is clearly demarcated whereas laterally it is not demarcated from the general body surface. Each pore skirted laterally by a comma-shaped marking which occupies the summit of the low
Fig. 18.7. *Heteroporodrilus incommodus*. A and B: Anterior and posterior genital field. Holotype QM G8376. After Jamieson and Nash (1976).
male porophore; the pores 2.2, 2.4 mm, 0.25, 0.24 body circumference apart. Continuations of the male ridges and intervening flattening apparent posteriorly in XV and throughout XIX and XX. Paired or unilateral presetal and/or postsetal circular genital markings are present in some specimens in V, VII, VIII and IX from \( ab \) to approximately mid \( bc \); the presetal markings in IX being the most common. The arrangement of genital markings in segments XVII to XX, though subject to some variation in detail, shows great constancy. Thus, dark glandular, paired markings lacking evident secretory 'pores' are present in all examined specimens, in \( ab \), posteriorly in XVII; anteriorly and posteriorly in XVIII (in which they are usually conjoined longitudinally); and anteriorly in XIX. All specimens have the transverse series of presetal markings in XX but whereas in the Eudlo Creek specimens these do not exceed 8 (4 on each side), in the Forest Glen specimens they range from a transverse series of 6 to 11. Usually all but the most lateral or next median pair of these lacks a central 'pore' while the others have a discrete pore-like central region. The transverse series in XX may or may not lie on a transverse paired or unpaired pad-like tumescence of the ventral surface. In addition, postsetal markings (a pair or one, unilateral) are present in \( b \) lines of XIX in some specimens. Female pores shortly presetal in XIV well median of \( a \) lines, almost contiguous medianly in a common elliptical field or a slit. Spermathecal pores 3 pairs, very slightly median of \( b \) lines at the anterior margins of segments VII to IX on small papillae; the pores 2.9, 2.8 mm, 0.29 body circumference apart.

Thickest septa 7/8-9/10, 10/11, strongly thickened. Dorsal blood vessel closely adherent to the intestine; free on the oesophagus. Latero-oesophageal hearts in X-XIII; each arising from and lying behind the corresponding calciferous vessel and
Fig. 18.11. *Heteroporodrilus incommodus*. A: Right prostate. B-D: Right spermatheca of VII, VIII and IX, respectively. E: Right nephridial bladder of XV. Holotype QM G8376. After Jamieson and Nash (1976).

*Calciferous gland*
Right, Dorsal, Holotype

= *Plutellus incommodus*
receiving a slender connective from the dorsal vessel. The two large calciferous vessels of each segment branch at the oesophageal end of the duct to give several vessels running longitudinally in the wall of the duct and further dividing in the lamellae of the gland. Medianly the two calciferous vessels are continuous across the roof of the oesophagus and a midventral supraoesophageal vessel joins the points of fusion in XI-XIII. Oesophagus moderately thick-walled in IV; forming a medium to moderately-large, firm, muscular gizzard in V; thin-walled and tubular in VI-XIV. In segments X-XIII the oesophagus bears four pairs of long-stalked reniform calciferous glands, the stalks of which join the oesophagus dorso-laterally. Intestine beginning with abrupt expansion at the anterior septum of XV or sometimes in XVI. Nephridial bladders thin-walled, subspherical to bilobed; preseptal funnel demonstrable in I and succeeding segments. Testes, and firm flocculent sperm masses attached to iridescent sperm funnels, in X and XI; racemose seminal vesicles in IX and XII, posterior pair reduced in some specimens. Vasa deferentia single on each side, small and poorly visible, only slightly coiled, free in the coelom on the ventral body wall. One pair of subrectangular deeply incised prostate glands, restricted to XVIII, with narrow, straight poorly muscularized short ectal duct. The gland with more than one extremely narrow lumen in cross section (racemose?). Ovaries bushy. Small sacs on the anterior septum of XIV may be ovisacs. Spermaphalaeae three pairs, discharging anteriorly in their segments increasing slightly in size posteriad each with a subspherical ampulla and a stout, slightly tapering, well demarcated duct. Diverticula (inseminated) clavate, single or bifid or a pair or all simple clavate; length of right spermaphalea of VIII = 1.2 mm; ratio total length: length duct = 1.6-2.7; ratio length: length diverticulum = 1.9-2.4.
REMARKS

*H. incommodus* is close to *H. raveni*. The prostate duct is short and straight in *H. incommodus* but long and sinuous in *H. raveni* and the setal ratios differ significantly in the two species. Such small differences between the two species (in genital markings and setal ratios), in part requiring statistical demonstration, bring the two species within the criteria for sibling species.

**Heteroporodrilus jamiesoni** Blakemore, 1994b

Fig. 0.33D, 8.13-8.15

*Heteroporodrilus jamiesoni* Blakemore, 1994b: 28-29, Fig. 4.

*Heteroporodrilus ashworthi* (part., Mt. Glorious); Jamieson, 1970a: 109-111, Fig. 2, 3a, 9a, 10A.

**TYPE LOCALITY:** 27°20'S. 152°46'E., Mt. Glorious - Qld.

**HOLOTYPE:** QM G211900.

**OTHER RECORDS:** (Jamieson, 1970a, as *H. ashworthi*) 27°20'E. 152°46'E., Mt. Glorious, QM G 5444 - Qld.

Length 203 mm. Width 6 mm. Segments 230. Body spherical without dorsal canaliculation, peristomium wrinkled, preclitellar ventrum somewhat corrugated, secondary annulation slight. Colour unpigmented buff in alcohol, clitellum darker. Prostomium closed epilobous 1/3 bisected by a median longitudinal furrow. First dorsal pore 6/7, pores continuous on clitellum. Setae 8 per segment obvious from III, a and b setae absent from XVIII; lateral setal couples widely spaced; in XII aa: ab:
Fig. 18.13. *Heteroporodrilus jamiesoni*. Genital region. Mt. Glorious specimen QM G5444 (As *H. ashworthi*). After Jamieson (1971e).
Fig. 18.15. *Heteroporodrilus jamiesoni*. Semidiagrammatic dorsal dissection Mt. Glorious specimen QM G5444 (As *H. ashworthi*). After Jamieson (1971e).
Nephropores at anterior margin of segments: II/D, III/D, IV/D or C, V/C, VI/C, VII/C or D, VIII/C or D, IX/C or D, X/D, XI/B; from VIII or X alternating between \( d \) and \( b \) lines symmetrically or asymmetrically on the two sides. Clitellum annular 1/2, 1/3XIII-1/2XVII, XVII, but weak in XIII and the posterior half of XVII; interrupted ventrally in XVII. Furrows, setae and nephropores retained. Male pores on elliptical porophores on XVIII in or slightly median to \( b \) lines; setae \( b \) absent in this segment, a retained.

Genital markings in IX, X, XVII-XX (Jamieson) or only XVII-XX (Blakemore) widely spaced by the width between the \( a \) setae, wholly presetal, laterally flattened pads which just impinge on the ventral setal couples, each a transversely elliptical pad with wide rim enclosing a glandular-looking somewhat depressed centre; the midventral surface including setal lines \( b \) of segments IV to XX protuberant as ventral pads, those in XIV-XVI not readily distinguishable from the clitellum (Jamieson).

Female pores paired on XIV anteromedian to \( a \) setae. Spermathecal pores four, or typically five pairs 5/6-8/9 in \( b \) lines.

Septa 6/7-12/13 moderately to strongly thickened. Dorsal blood vessel bifurcating under the brain to join the terminal branches of the ventral vessel. Large latero-oesophageal hearts in X-XIII; those in X arising from the dorsal vessel and from a circuemoesophageal vessel on each side; those in XI-XIII each arising from the dorsal vessel and from a circuemoesophageal calciferous vessel from the corresponding calciferous gland; commissurals in VI-IX slender but valvular; each, unlike the hearts, branching before joining the ventral vessel; giving off a ventral and a lateral branch to the body wall (the lateral vessel running transversely on the parietes to the dorsum);
and also a branch to the corresponding fat-body-like appendage; valves situated immediately dorsal to the branches and, at least in IX, large valves shortly below the dorsal fourth of each commissural. The commissurals of IX, but not those of anterior segments, apparently possess connectives to an almost inappreciable supra-oesophageal vessel which is better developed in X-XIII; in XI- XIII it arises from the transverse vessels (one on each side of each segment) from the calciferous glands. In XIII the connective from the dorsal vessel to the heart very slender and distinct from the heart which has a larger, direct connection to the calciferous vessel; in X, the supra-oesophageal connective more slender than that to the dorsal vessel. An anterior supra-pharyngeal passes anteriorly over the brain in front of which it connects with the ends of a pair of suboesophageal vessels; posteriorly, this supra-pharyngeal bifurcates as a pair of large vessels which encircle the posterior end of the pharynx and join the suboesophageal vessels; follicular, multilocular bodies resembling the fat-body-like appendages of Eudrilids on the posterior walls of segments VI-IX and in V, in front of the gizzard, each apparently connected ventrally with the oesophagus and supplied by a branch from the corresponding commissural vessel. (Jamieson). Gizzard muscular in V displacing septum 5/6 and 6/7, with wide rim anteriorly then tapering to appear cone shaped or broadly barrel-shaped. On the oesophagus or posterior septum of VI-IX, small opalescent glands or sacs were also observed. Calciferous glands three pairs of spherical, almost reniform calciferous glands ventrolateral to oesophagus in XI, XII, and XIII with numerous lamellae seen externally. To each gland a short stalk extends laterally from the oesophagus, and is directed downwards to the dorsal centre of each gland i.e. on short-stalks. Intestinal origin XV; widening to reach its full width in XVI; its walls considerably thicker than
those of the preceding oesophagus; typhlosole not found. Nephridia holonephric throughout with large convoluted tubes and flattened, round terminal bladders in the position of nephropores. Small, lobed testes and large convoluted iridescent male funnels free in X and XI (Jamieson); especially in X, but in XI also, fairly thickened pericardial (testis) sacs extend between the septa and encompass the blood vessels, oesophagus and the large iridescent sperm funnels; these testis sacs not seen in the other specimen. Seminal vesicles paired and racemose in IX and XII. Ovaries small, compact, in the anterior ventrum of XIII but individual ova not visible; ovisacs absent. Prostates compact, tongue-like, racemose glands confined to XVIII each with a short, flaccid duct forming a single loop and receiving the vasa deferentia at its junction with the gland. Spermathecae four or five pairs in V-IX; each with a conical, annulated ampulla, an abruptly demarcated duct a little more than half as long and a medially directed simple clavate diverticulum, approximately as long as the ampulla, which joins the duct ectally; length of a spermatheca 1.5 mm. The right side posterior diverticulum in holotype bifid with a smaller, blunt branch. Gut contents almost entirely consisting of woody organic matter well mixed with some soil.

REMARKS
Jamieson (1970a) placed his Mt. Glorious material in *Heteroporodrilus ashworthi* but listed a number of differences which Blakemore (1994b) reasonably used to place it in a separate species, *Heteroporodrilus jamiesoni*. Jamieson also stated that *H. ashworthi* was closely similar to *H. oxleyensis* and that the possibility of synonymy should be examined when further material became available. Both authors have now formally recognized that synonymy. Differences of the holotype of *H. jamiesoni* from
Jamieson's Mt. Glorious material are that only four, rather than five spermathecae were found, and testis were free rather than in testis-sacs. Distributions of genital markings concur except for the absence of an obvious pair of presetal elliptical pads in IX and X. The two accounts of the Mt. Glorious material are combined above. A major distinctive feature relative to *H. oxleyensis* is the presetal rather than postsetal position of the genital markings on XVII.

*Heteroporodrilus jamiesoni* can be separated from *H. oxleyensis* on the basis of the genital markings, but not on testis sacs, which have been recorded as present or absent for both species. The spermathecae of *H. oxleyensis* and *H. jamiesoni* are similar in appearance and are recorded as 4 or 3 pairs and 5 or 4 pairs, respectively. Of interest is that the short stalks on the calciferous glands in this specimen are similar to those for *H. oxleyensis* (Mt Cotton specimen) as well as those illustrated for *Heteroporodrilus minyoni* (Blakemore, 1994b).

**Heteroporodrilus lamingtonensis** Jamieson, 1970a
(Fig. 18.16, 18.17)

*Heteroporodrilus lamingtonensis* Jamieson, 1970a: 115-117, Fig. 5a, 9c, 10d.

**TYPE LOCALITY:** 28°14'S.153°08'E., Lamington National Park - Qld.
**HOLOTYPE:** QM G 5446.
Fig. 18.16. *Heteroporodrilus lamingtonensis*. Genital field. Holotype QM G5446. After Jamieson (1970a).
Length 75 mm. Width 4 mm. Segments 161. Colourless with the exception of the brownish-pink clitellum. Form moderately stout, circular in cross-section throughout; not canaliculate. Prostomium tanylobous, broad and as wide posteriorly as anteriorly though narrowed between. First dorsal pore in 5/6 (imperforate ?), 6/7 perforate. In segment XII, \( aa : ab : bc : cd : dd = 1.8 : 1.0 : 1.5 : 1.9 : 3.8 \); \( dd : u = 0.26 \). Setae \( a \) and apparently setae \( b \) absent from segment XVIII. Nephropsores in II-III in \( d \) lines; in IV in \( c \) (left) or \( d \) (right); in V and VI in \( c \); in VII in \( d \) (left) or \( c \) (right); in VIII in \( c \) (left) or \( d \) (right); in IX in \( d \) (left) and \( c \) (right); in X in \( b \) (left) and \( d \) (right); in XI reversing this arrangement; thereafter alternating asymmetrically between \( d \) and \( b \). Clitellum annular, XIII-XVII but less well developed in XIII; pigmented in XIV-XVI only; strongly tumid but not protuberant; dorsal pores and intersegmental furrows obscured excepting at 13/14 where they are weakly developed; setae retained. Male genital field: in XVIII there are three low whitish, knob-like prominences on each side, two of these are median to \( b \) lines and are located in the same longitudinal line; the posterior being in the setal arc; the third "knob" is presetal and median to the sites of the absent setae \( a \); the lateral longitudinal couple lies in a single glandular field which fills the segment longitudinally and extends shortly lateral of \( b \) lines while the median knob lies in a transversely oval glandular field. A small pit seen on the left side only shortly posterolateral from the anterior knob, is presumably one of the paired combined male and prostatic pores, a similar site being determined by transfixing the body wall at the ectal limit of the right prostatic duct. Accessory genital markings: similar whitish knobs, a pair on each side, shortly anterior to the setal arc, one median to \( b \) the other median to \( a \)-line, each in an oval glandular field, in XIX-XXI; the glandular fields extending posterior of the setal arcs. Further accessory markings
consisting of a conspicuous prominence on each side in each of segments X and XI in ab; each filling its segment longitudinally and bearing a single hemispheroidal protuberance, which lies in and behind the setal arc, or with a further presetal knob. Female pores a pair of small but conspicuous pits antero-median from setae a, at about 1/3 aa, on XIV. Spermathecal pores two pairs of inconspicuous white swellings at the anterior borders of VIII and IX, in b lines.

Septa 5/6 delicate; 6/7 and 7/8 moderately thickened; 8/9-10/11 progressively more strongly thickened but none very thick; 11/12 less strongly than the latter; 12/13 moderately, 13/14-15/16 slightly and successively less thickened; the remainder thin. Pharyngeal glands in peripherally scalloped tiers, apparently on the posterior walls of their segments; the last in III but bulging into IV. Gizzard very large, firm and glossy in V; oesophagus in VI almost obliterated by posterior extension of the gizzard. Calciferous glands three pairs of large, sessile ventrolateral pouches in XI-XIII, the two members of a pair almost contiguous midventrally and slightly lobed in outline. Intestine commencing with abrupt expansion in XV; typhlosole absent. Dorsal blood vessel continuous under the brain; very slender in V anteriorly. A pair of vessels from the gizzard to the dorsal vessel in V is not commissural. Dorsoventral commissural vessels in VI-XIII, increasing in size posteriad but only those of X-XIII forming large moniliform hearts; those in X small relative to the other hearts. Commissurals of VI-IX dorsoventral only; those in X-XIII latero-oesophageal, arising from the dorsal vessel by long, very slender filamentous vessels and also from a pair of calciferous vessels in each of segments XI-XIII and from the wall of the oesophagus (vascularization not discernible) in X. Commissurals of VI-IX each ventrally sending a branch to the vicinity of the oesophagus and a lateral branch to the body wall; the
Fig. 18.17. *Heteroporodrilus lamingtonensis*. A: Prostate. B: Right spermatheca of IX. Holotype QM G5446. After Jamieson (1970a).
more posterior commissurals unbranched below their two roots. Supraoesophageal vessel paired, connecting the calciferous vessels of segments XI-XIII which join medially in XIII; not discernible in X but presumably, from the origin of the hearts of X, present in that segment and receiving homologues of the calciferous vessels; absent from IX anteriorly and behind XIII. Large lateroparietals giving off median and lateral segmental vessels to the parietes arise anteriorly in XIV as continuations of the suboesophageal vessel of XIII and extend backwards to XVIII where branches apparently supply the prostates; not apparent behind these glands. Suboesophageal vessel single between the calciferous glands, paired from 1/2 XI anteriorly and traceable beneath the pharynx. Nephridia with very large subspherical ectal bladders; in the lateral series there is a tendency for the narrow duct to join the median aspect of the bladder and for the lateral portion of the bladder to be somewhat elongate and suggestive of a diverticulum. Delicate lobed testes and large, iridescent simple, only slightly convoluted funnels lying in sperm masses in X and XI; a diaphanous pericardiac testis-sac in each of these segments. Seminal vesicles in IX and XII; those in IX small and slightly racemose those in XII elongate on the septum concentrically with the gut and ventrally swollen. Prostates with indistinctly lobulated occasionally deeply incised tongue-like glandular portions restricted to XVIII and about 3 mm long; the narrow muscular duct about one fifth as long; vas deferens (not certainly identified) apparently joining the duct entally. Ovaries large delicate tongues with many large oocytes; funnels large, stout and rather simple in XIII. Ovisacs absent. Spermathecae each with an ovoid to saclike ampulla and an abruptly demarcated duct, about half as long, which bears, shortly ectal of its middle, a lateral and a median club-shaped diverticulum; each diverticulum somewhat shorter than the duct. Sperma-
thecae of uniform size; length of the posterior right spermatheca 1-6 mm, length diverticulum 0-5 mm.

**Heteroporodrilus mediterreus** (Fletcher, 1887b)
(Fig. 0.12A-C, 18.18, 18.19)

*Cryptodrilus mediterreus* Fletcher, 1887b: 614-616.
*Platellus mediterreus*; Michaelsen, 1900: 172.
*Heteroporodrilus mediterreus*; Jamieson, 1970a: 117-120, Fig. 4a, b, e-g, 9d, 10e.

**TYPE LOCALITY:** 30°02'S.146°24'E., between Bourke and Brewarrina, banks of Darling River - NSW.
**TYPES:** Lost.
**OTHER RECORDS:** (Jamieson, 1970a) 29°32'S.150°45'E., Gragin. 29°32'S.150°35'E., Warialda AM W1338 - NSW.

Length 73-150 mm. Width 4 mm. Segments 130-150. Sooty brown, lighter below, with a reddish or purplish tinge to the clitellum; pigmentless in alcohol. Prostomium proepilobous with indistinct dorsal tongue to intersegment 1/2, i.e. tanylobous. First dorsal pore 5/6 or 6/7. Anterior end of the body only slightly tapered, mouth broad. Nephropores (from internal examination) in *d* lines in II-IV, in *c* lines in V and VI, not determinable in VII-IX, but in *b* lines by X and in XIV and XVI. In the types (Fletcher): Nephropores began at the anterior margin of II and were observed to alternate at first between *d* and *c* lines (the first two or three pairs in *d*, the pores
Fig. 18.18. *Heteroporodrilus mediterreus*. A and B: Genital field in two specimens. AM W1338. After Jamieson (1970a).
sometimes continuing at one level for several consecutive segments); behind the clitellum only the inner series was observed, in b lines on alternate segments. Clitellum annular, strongly tumid although only slightly widened relative to other segments, occupying posterior XIII, XIV-XVI or 1/3XVII also; setae and intersegmental furrows present though the latter are weaker dorsally. A pair of transversely oval, almost circular porophores in XVIII with median limits in ab, anterior margins immediately behind 17/18 and posterior margins slightly overhanging XIX; not clearly demarcated laterally from the lateral regions of the segment; the ventral portion of the segment between them tumid and clitellum-like; the pronounced setal annulus of XVIII incising the porophore laterally and faintly traceable across it. Each porophore bearing a small hemispheroideal papilla at the site of seta b which is replaced by penial setae the extreme tips of which are just discernible at the centres of the papillae. Accessory genital markings: two pairs of circular dimples in X and XI in front of setae b, each with a dark centre, a narrow white border and a "halo" of radiating cuticular striae; elliptical depressions with tumid borders anteriorly in XVIII in b lines and in XIX in ab, or an additional pair of markings present median to the male porophores or two pairs, one pair anteromedial the other posteromedial to the porophores. The ventral portions of VI-IX were swollen as additional "accessory copulatory structures" in the types. Females pores indistinct, shortly anteromedial to setae a of XIV. Spermathecal pores three pairs of inconspicuous ellipses in 6/7-8/9, in b lines.

Septa 5/6-13/14 well developed and funnel shaped; 4/5 delicate and obscured by diagonal tendons; 5/6 slightly thickened; 6/7 and 7/8 progressively and moderately thickened; 8/9-10/11 strong; 11/12 slightly less strong; 12/13 and 13/14 moderately
thickened. Last septal (pharyngeal) glands in IV. Gizzard large, firm and cylindrical, as wide as long, in V. Ventrolateral paired sessile calciferous glands, almost contiguous in the midline, four pairs, in X-XIII. Intestinal origin XVIII? Nephridia with very large transparent thin-walled vesicles which are traceable as far posteriorly as X behind which the nephridia are severely macerated. Dorsal vessel continuous onto the pharynx; hearts large in X-XIII in which they arise by slender roots from the dorsal vessel and by thicker connectives from paired calciferous vessels, which encircle the calciferous glands, at a considerable distance from the junction of these vessels with the supra-oesophageal vessel. Commissurals in VI-IX arising from the dorsal vessel only, decreasing in diameter anteriorly, those in IX slenderly heartlike. Small folded, slightly iridescent sperm funnels in X and XI; seminal vesicles small, racemose, in XI and XII, those in XII larger. Ovaries simple lamellae composed of chains of ova, in XIII. Prostate glands very large, racemose, the glandular portions occupying XVI-XXII, each with the form of a flattened, lobulated irregular tube from the mid-region of which arises the muscular duct. The duct bent into a U, convexity posterior; vasa deferentia joining the gland at its junction with the duct. Penial setae present, two functional and one reserve in the follicle of each side; 2.44-2.6 mm long and maximally 81 mm wide, at the base; each gently or ectally, strongly curved and bearing over the ectal fourth, numerous irregular circlets of fine spines which are adpressed to the surface; a short region behind the simple tip devoid of spines. Spermathecae discharging anteriorly in their segments, each with a large broad ampulla and a distinctly demarcated somewhat longer muscular duct; which bears a very small stalked curved and bluntly fusiform diverticulum medianly near its
juncture with the ampulla; lengths of the right spermathecae of VIII and IX, 1.8 and 2.3 mm.

REMARKS
The material examined by Jamieson (1970a) was identified by Fletcher and originated from sites, Cragin and Wrialda, not far distant from the type locality.

**Heteroporodrilus minyoni** (Dyne, 1981)
(Fig. 18.20, 18.21)

*Plutellus minyoni* Dyne, 1981: 100-102, Figs. 1B, 2A, B, D. Table 1.

**TYPE LOCALITY:** 28°37'S.153°24'E., Minyon Falls, Whian Whian State Forest, approx. 12 km S.W of Mullumbimby - NSW.
**HOLOTYPE:** AM W6647.
**OTHER MATERIAL:** several anterior amputees not designated as types.

Length 410 mm. Width (midclitellar) 3.3 mm. Segments 387. Form long, relatively thin, whitish in life, pigmentless buff in alcohol. Prostomium epilobous 1/3-1/2, closed, peristomium furrowed. First dorsal pore 6/7. Setae *a* and *b* absent from XVIII;
Fig. 18.20. *Heteroporodrilus minyoni*. Genital field. Holotype AM W6647. After Dyne (1981).
in XII, 13.0: 6.4: 7.1: 13.6: 32.6. Nephropore configuration II-IV in d (R and L); V-VI
in c (R and L); VII in d (R) or c (L); VIII-IX in c (R and L); X in b (R) or d (L); XI in
d (R) or b (L), thereafter alternating regularly between b and d lines, though
asymmetrically on each side of the body. Clitellum annular, strongly protuberant, in
XIV-XVII; dorsal pores and intersegmental furrows obscured, nephropores and setae
visible. Male genital field a series of conjoined or paired tumid pads in XVII-XXI,
extending across the segment to slightly beyond b lines on each side. Each
tumescence contains a series of low, roughly circular nodules appearing as small
glandular blisters. In XVII, the tumescences are paired, extending post-setally, with 2
pairs of nodules in the setal lines; in XVIII, the tumid pad fills the segment, with a
line of 6 blister-like processes across the mid-segment. At the extremities of this
series are the male pores, on very slight papillae, in b; immediately anterior to each
pore is a further nodule. In XIX, the pads are paired; in XX, the pad is median,
unpaired, with a set of 6 pre-setal nodules; similarly for XXI, with a pair of nodules
(R) and set of 3 (1 faint) on the left. The tumid pads may be furrowed to a greater or
lesser extent, or depressed at their centres. Additional markings: a single, unpaired
median tumescence extending across bb in XII, filling the segment; the centre
somewhat depressed, and containing a series of 5 more or less conjoined circular
nodules or blisters across the midsegment; immediately ventral of the lateral rims of
the tumescence are 2 larger glandular patches. Female pore a minute, unpaired median

B.G.M. Jamieson 23/11/00
slit, barely pre-setal, in XIV. Spermathecal pores 2 conspicuous pairs in VIII and IX, slightly posterior to intersegments 7/8 and 8/9, on glandular papillae.

Septa 5/6 thin, 6/7 slightly thickened, 7/8-10/11 highly muscularized and thickened; 11/12 moderately thickened, remainder thin. Dorsal blood vessel single, continuous onto the pharynx; supra-oesophageal vessel present, paired, in XI-XIII (though very faint in XI). Last hearts in XIII, commissurals in XI-XIII large and heart-like, arising from a strong pair of connectives from the lateral calciferous vessels in XI-XII, and from long, much more tenuous connectives from the dorsal vessel (Fig. 18.21B). The paired supra-oesophageal trunks connect the lateral calciferous vessels in XI-XIII, but the former are not discernible in X. Definite suboesophageal vessel apparently absent. Commissurals VI-X dorso-ventral only. Paired collecting vessels from the calciferous glands are present ventrally, and pass forwards through the septa, also sending branches to the body wall. Gizzard firm, muscular and barrel-shaped in V, with a comprehensive blood supply and distinct anterior rim. Oesophagus narrow, VI-XIV, becoming more dilated in the region of the calciferous glands. Three pairs of discrete, rounded-discoid calciferous glands ventro-laterally disposed in XI-XIII, each with a definite, broad, dorso-lateral stalk connecting the gland to the oesophagus; the diameter of the stalk lumen as it communicates with the oesophagus is quite narrow, but broadens at the gland. The latero-calciferous trunks are adherent to, and begin to bifurcate, on the stalk. Intestine commences with abrupt expansion in XV, typhlosole absent. Stomate holonephridia throughout, each with collapsed semi-spherical
bladders at the ectal extremes of their excretory ducts; these often appearing crinkled and/or bilobed. The ducts conspicuously alternate asymmetrically on each side of the body in the position of exit to the exterior. Holandric; testis tissue (7), 2 medium-sized pairs of slightly plicate, iridescent sperm funnels, and some free sperm masses in X and XI; both these segments appear to be at least partially sealed dorsally by thin, pericardial testis-sacs. Two pairs of small seminal vesicle masses in IX and XII, the latter pair the larger, comprising small dorsally situated loculi grading into much larger, globose, ventral component loculi. Seminal vesicles in IX simple glandular sacs on the anterior wall of 9/10. Prostates somewhat sinuous S-shaped glands, tubular in appearance, extending into segment XXII (L). The duct is short and narrow, with a single loop. The fused vasa deferentia join the gland on the ventral surface some distance from the entry of the duct (Fig. 18.21B). Small ovaries and small-medium funnels in XIII. Spermathecae 2 subequal pairs in VIII and IX, discharging anteriorly in their segments (Fig. 18.21C). The larger of the two inseminated diverticula may be bilobed (as R IX) or uniloculate (remainder). Length right spermatheca of IX = 3.28 mm; ratio length spermatheca: length of duct = 2.08.

REMARKS
The combinative possession of 3 pairs of calciferous glands, 2 pairs of spermathecae, and paired supra-oesophageal blood vessel is unique to this species. The affinities of *H. minyoni* with *H. clarkei* have been discussed under the relevant section for the
latter species. Of considerable interest is the striking similarity between *H. minyoni* and a species of *Heteroporodrilus* from the Lamington Plateau, S.E. Queensland, *H. lamingtonensis*. In addition to the close resemblance in the configuration and nature of the genital field markings, there is close conformation in a number of important internal characters, including the mutual possession of 3 pairs of calciferous glands, testis-sacs, and 2 pairs of spermathecae. Apart from the size discrepancy, nature of the calciferous glands (stalked or not), and some details of the vascular system, there is little to separate the two species (Dyne, 1981). Although the specific status of either is not in doubt, their gross overall similarities serve to support transfer of *minyoni* from *Platellus* to *Heteroporodrilus* by Blakemore (1994b).

**Heteroporodrilus montiserratae** Jamieson, 1995
(Fig. 18.22-18.24)


**TYPE LOCALITY:** 27°57'S. 152°21'E., Mistake Mtns, N. of Cunningham's Gap, under rocks in complex notophyll vine forest, collector R. Raven, 6 Oct 1976.

**HOLOTYPE:** QM G211443 (Ex G10311).

**PARATYPE:** QM G211444 (Ex G10311).

Length 76 mm. Width 5.0-6.4 mm. Segments 217. Pigmentless in ethanol. Prostomium tanylobous, with a transverse furrow at midlength; neither it nor the body canaliculate; peristomium short. First dorsal pore 5/6. Setae *aa: ab: bc: cd: dd* = 2.4: 1:2.0: 1.7: 4.6: 14.5: 6.1: 12: 10.6: 27.9%; in regular longitudinal rows throughout. Nephropores visible as mostly conspicuous local dimpling of the intersegments, in *d*
lines in II-IV; in c lines in V and VI, in c lines (left) and d lines (right) in VII, in VIII-X alternating from d to c (left) or the reverse (right), in XI and posteriorly, alternation is regular between d and b., though out of phase on the two sides Clitellum annular, embracing the posterior 2/3 of XIII-XVII, and dorsally the anterior 1/4 of XVIII; strongly tumid in XIV-XVII. Combined male and prostatic pores each a small dark point at the site of the absent setae b of XVIII, on indistinct round papillae which fill most of the posterior two thirds of the segment. Anterior genital markings in X and XI; consisting of a low, midventral mostly presetal papilla with pore-like centre in X, and a transverse midventral pad in the setal arc of XI, bearing a pair of pore-like markings near its lateral borders and three minute indistinct 'pores' near its posterior border; or a pair of transversely elliptical papillae in ab of X and XI but less far apart in XI, each pair almost filling its segment longitudinally and with a pore-like centre or (left posterior papilla) with two smaller pore-like markings. Posterior genital markings a narrow, slightly tumid transverse band in the setal arc median to each male papillae, each band with a row of four elliptical pore-like markings, in XVIII; in XIX a tumid area on each side which includes the seta b of its side but does not reach the anterior and posterior borders of the segment. Female pores a pair of minute apertures in a transverse furrow midway between the setal arc and the anterior border of XIV, almost 1/2aa, 1.0 mm, apart. Spermathecal pores 3 pairs, not externally visible, from internal examination in 6/7, 7/8 and 8/9, the last pair in ab.

Septa 8/9-10/11 the strongest, greatly thickened. Dorsal blood vessel single, continuous onto the pharynx. Last hearts in XIII, those in X-XIII latero-oesophageal. Gizzard very large, in V, ensheathed by the very thin septum 5/6 and deflecting several septa posteriorly. Calciferous glands 4 pairs, in X-XIII, sessile ventrolaterally
on the oesophagus and almost meeting midventrally. Intestine commencing with abrupt expansion in XV; with no appreciable typhlosole. Nephridia stomate vesiculate holonephridia; pretesticular nephridia have wide convoluted ducts each with a terminal swelling constituting a small but definite bladder; by XII the (lateral) bladder is very large and depressed subspheroidal; in the anterior intestinal region, e.g. XVII, the bladder is slightly smaller and is transversely elliptical; further posteriorly (XXXV) the bladder is drawn out medianly in the direction of its supplying duct and projects laterally beyond its excretory pore so that a short broad diverticulum may be considered to exist. Holandric; convoluted sperm funnels, lacking spermatozoal iridescence, in X and XI. Seminal vesicles in IX and XII; those in XII more strongly multiloculate including a greater development of minute bead-like loculi than those in IX. Ovaries not observed. Prostates racemose and deeply incised only in the holotype with some appearance of a compressed S-shape; limited to XVIII; duct long and muscular, although only a small fraction of the length of the gland; twisted in a loop in the paratype; entering the body wall in \( \text{ab} \) but nearer \( b \). Spermathecae 3 pairs, in VII, VIII and IX; each with a large thin walled ampulla, which is widest distal to its equator and is circumferentially pleated, and a very small, narrow muscular duct which is joined at its junction with the ampulla by a digitiform uniloculate diverticulum containing many iridescent sperm masses.

**Heteroporodrilus notatus** (Dyne, 1981)

(Fig. 18.25-18.27)
Platellus notatus Dyne, 1981: 102-104, Figs. 3A-E. Table 1.
Heteroporodrilus notatus; Blakemore, 1994b: 21.

Type Locality: 26° 25'S, 152° 55'E., Six Mile Creek, near Cooroy - Qld.
Holotype: AM W6648.
Paratypes: QM G8914-5.

Length 105, 85 mm. Width (midclitellar) 2.4-2.7 mm. Segments 232-262. Uniformly circular in cross-section throughout, pigmentless buff in alcohol, clitellum pinkish. Tanylobous, peristomium narrow. First dorsal pore 6/7. Setae a and b absent from XVIII; in XII, aa: ab: bc: cd: dd = 10.3: 5.1: 14.4: 12.4: 25.7. Nephropores distinctly visible; in II-IV in d, V-VI in c, VII in d, VIII slightly lateral of b, thereafter a regular alternation between d and b lines. Clitellum strongly developed, annular, embracing segments XIV-XVII; dorsal pores obscured, setae, intersegmental furrows distinct. Male pores situated on small papillae in conspicuous depressions, in ab. The papillae are separated by a slightly raised intervening strip, and surrounded by a thick rim of highly tumescent tissue which incorporates XIX, and slightly overhangs XX. This tumid area extends beyond b, and forms a rough ellipse, with the male pores approximating the foci. Genital markings: a single, highly tumescent swelling of bipartite appearance, the two portions with a central depressed 'dimple' region; this marking fills segment X longitudinally, extending laterally to b lines. Female pore unpaired, median, slightly presetal, in XIV. Spermathecae 2 pairs, opening in the midsegment of VIII and IX on small papillae, in b lines. The left set of pores open posterior to the furrow, whilst the right set open anteriorly.
Fig. 18.25. *Heteroporodrilus notatus* (Dyne, 1981). Genital field. Paratype QM G8914.
Fig. 18.26. *Heteroporodrilus notatus* (Dyne, 1981). Genital field. Holotype AM W6648.
Septa 7/8-10/ll. strongly thickened. Dorsal blood vessel single, continuous to the pharynx. Last hearts in XIII; supra-oesophageal vessel absent. Hearts in IX, XI-XIII apparently drain the lateral calciferous vessels directly, before the latter vessels fuse mid-dorsally as a contiguous loop. In X-XIII, there appears to be a further, much smaller connective to the dorsal vessel (from the dorso-ventral commissurals). Calciferous glands with a moderate vascularization only (though the entire vascular system is somewhat bleached). Commissurals diminish rapidly in size anteriad from X. Gizzard globular, slightly elongate, and highly muscular, (slightly compressible), in V. Oesophagus narrow, not vascular to any degree, excepting the final 5-6 segments. Four pairs of discrete ventrolateral calciferous glands in X-XIII, the individual glands of each pair virtually contiguous, and each with numerous, well-developed lamellae; the glands connected to the oesophagus by medium-length, stout, dorsolateral stalks, these appearing, at least superficially, to be more highly vascularized than the glands themselves. Intestine commences in XXI (or XVI), typhlosole and caeca absent. Nephridial ducts terminate in conspicuous ovoid bladders, which discharge through a wide tube to the exterior; the bladders themselves rather diaphanous and collapsed, with little variation in shape. Nephridial funnels and necks lie transversely in the segment preceding, in a-lines, the neck running transversely to b, then dipping into the setal line, and running posteriad through the septum to join the nephridial body. Holandric; 2 pairs of large, iridescent funnels and coagulated sperm masses, seemingly enclosed in a very thin membrane under the oesophagus, in X and XI. Seminal vesicles 2 prominent pairs, with large component loculi, in IX and XII, with a pair of smaller agglomerations just anterior to the funnels in XI. Vasa deferentia visible as single iridescent ducts on each side, not tortuously
Fig. 18.27. *Heteroporodrilus notatus* (Dyne, 1981). A: Right prostate in situ. B: Right spermatheca of IX. Right spermatheca of IX. Paratype QM G8914.
winding, joining the prostate gland at the point of insertion of the duct. Prostate glands roughly squarish lobes, conspicuously fissured, extending from XVIII into XIX. Duct long, narrow and muscular, somewhat coiled, entering the parietes in XVIII. Ovaries, comprising a racemose cluster of smallish oocytes, and a large folded funnel close to the nerve-cord on each side in XIII. The oviducal ducts are visible passing through septum 13/14, and fusing just prior to entering the parietes under the nerve-cord. Spermathecae 2 pairs in VIII and IX, discharging into the midsegment. Each comprises a conico-sacciform ampulla, and long, stout duct, which is bent through an acute angle before entering the body wall. From either side of the ental region of the duct arise 2 subequal, digitiform diverticula, each containing what appear to be a number of brightly iridescent sperm clusters Length right spermatheca of IX = 2.8 mm; ratio length spermatheca: length of duct = 2.3; ratio length of spermatheca: length diverticula (mean) = 2.75.

REMARKS

H. notatus has racemose prostate glands (as in Heteroporodrilus), in contrast to the tubular or tubulo-racemose organs found in the remainder of the genus Plutellus (as also in Paraplutellus) in which it was placed by Dyne (1991). This adds support to its placement in Heteroporodrilus by Blakemore (1994b).

**Heteroporodrilus oxleyensis** (Fletcher, 1889)

(Fig. 18.28-18.31)
Cryptodrilus oxleyensis Fletcher, 1889: 1537-1538.
Plutellus fletcheri (part.); Michaelsen, 1900: 173 (excluding Cryptodrilus fletcheri Beddard, 1887a).
Woodwardia oxleyensis; Michaelsen, 1907b: 162.
Heteroporodrilus oxleyensis; Jamieson, 1970a: 120-122, Fig. 3b-e, 5g, 9e, 10f,g ; Blakemore, 1994b: 29-31, Figs 5, 6.
Woodwardiella ashworthi Stephenson, 1933: 912-914, Fig. 11-13.
Non Heteroporodrilus ashworthi (part., Mt. Glorious); Jamieson, 1970a: 109 (see H. jamiesoni).

Type Locality: 27°33'S.152°59'E., Oxley - Qld.
Other Records: (Jamieson, 1970a) 27°31'S.152°50'E., Kholo Creek (QM) - Qld. 33°54'S.151°08'E., Marrickville, AM W3062 - NSW. (Blakemore, 1994b) 27°30'S.152°55'E., Brookfield, QMG210140. 27°53'S.153°14'E., Queensland University farm Mt. Cotton, QMG210141. 27°22'S.152°53'E., CSIRO Samford, lodged in Blakemore collection.

For H. ashworthi:

**TYPE LOCALITY:** (Stephenson, 1933) 27°28′S.153°01′E., Brisbane - Qld.

**TYPES:** BMNH 1932.5.5-6.

**OTHER RECORDS:** (Jamieson, 1970a). 27°20′S. 152°46′E., Mt. Glorious - Qld.

Length 70-183 mm. Width 4-6 mm. Segments 161-175. Secondary annulation minimal. Slight dorsal furrows in caudal segments. Colour: dorsum, especially in anterior and caudal segments, pigmented light yellowish-brown with slight iridescence or dark grey, ventrum pale; clitellum buff. Prostomium, pro-epilobous or closed epilobous, with distinct dorsal cleft (canalicula) extending from tip of prostomium through to 1/2 or 2/3; two grooves may be present, arising from the posterior angles of the prostomium diverge to 1/2. Pharynx may evert on preservation. Peristomium usually rugose. First dorsal pore 5/6-7/8. Setae 8 per segment from II; small and indistinct; a and b, or b only, absent from XVIII ; in XII, aa: ab: bc: cd: dd: u = 1.7-2: 1: 1.6-2.4: 1.4-2.3: 3-4.3: 0.23-0.3; thus lateral setal couples widely spaced, usually about twice the width of the ventral couples, and the dorsal interval (dd) only slightly greater than one quarter of the body circumference. Nephropores: in d lines in II-IV or also V, VI; then with irregular alternation into d, c or, in some specimens, b lines; regular alternation between b and d lines in IX-XIII posteriorly. In some
Fig. 18.28. *Heteroporodrilus oxleyensis*. Genital field. Marrickville specimen AM W3062. After Jamieson (1971e).
Fig. 18.31. *Heteroporodrilus oxleyensis*. Genital field. Kholo Creek specimen. After Jamieson (1971e).
specimens, nephropore alternations asymmetrical in $b$ and $d$ per side. Clitellum annular, moderately tumid, in 1/2XIII, XIV-2/3XVII, XVII interrupted ventrally in XVII; setae, nephropores, furrows (sometimes partly obscured) and dorsal pores retained. Male pores: on XVIII on slightly raised porophores, approximately in $b$ lines, filling the segment longitudinally or occupying most of the posterior two thirds; the two porophores linked by a transverse tumid band or flanking and mostly posterior to a median transversely elongated accessory genital marking. Female pores: on XIV a pair anteromedian to $a$ setae often in a common glandular field. Genital markings ventral unpaired slightly tumid patches filling their segments longitudinally, median to $b$ lines of X-XII and XVII and just including setae $b$ in XIX and XX, a rudiment of the former type of marking in XIII and possibly also XIV-XVI (Kholo Creek). Postclitellar markings in the Marrickville specimen are similarly distributed (with the addition of a marking in XVIII) but only that in XVII reaches the posterior border of its segment and those of XIX and XX do not include setae $b$; all bear indistinct glandular depressions which on those of XVII, XIX and XX show a tendency to pairing, preclitellar markings are indistinct, in VIII-XI. Accessory genital markings were not developed in the type-series (Fletcher, 1889a ). In Brookfield specimens: in some of VI-XI small closely paired, median pads, in XVII closely paired or elongate postsetal pads, XVIII-XX (and XXI in one unusual specimen) tumid, elongate, mostly presetal pads; in Mt. Cotton specimens in VII and VIII single or paired faint discs anterior to ventral setal couples, in IX and X closely paired discs between a setae, also in IX a smaller pair of markings just behind the spermathecal pores, in XVII a pair of postsetal pads, closely paired in common ventral tumid area and mostly presetal in each of XVIII-XX: elongate smooth pads sunken in otherwise
raised glandular areas; in Samford specimens in IX-XI small, ventrally paired discs, in XVII postsetally and presetal in XVIII-XX large, paired pads elongate from mid-ventrum to b lines. In Stephenson’s type of ashworthi, genital markings were reported for IX and those in XVII were postsetal. Spermathecal pores 3 pairs (Kholo Creek) or 4 pairs (Marrickville; Fletcher, 1889a; Blakemore, 1994b) in 5/6, 6/7-8/9 in b line, not always visible externally.

Septa 6/7-11/12, 12/13 slightly to strongly thickened. Gizzard strongly muscular, tubular to spherical muscular in V. Calciferous glands: three, ventrolateral pairs in XI, XII, and XIII: spherical glands with white lamellae in section; well demarcated from the oesophagus but sessile on it over a considerable arc or with short stalks. Intestine commencing, with abrupt or gradual expansion, in XV (in the Marrickville specimen posteriorly in the segment); typhlosole absent. Gut contents: mostly organic matter including woody (dead root) material, plus some fine and some coarser soil. Dorsal blood vessel single; commissurals from VI-X, hearts XI-XIII; at lest those of XII and XIII latero-oesophageal; suprooesophageal vessel there with small connective to dorsal heart valves and lateral branches attached to stout pink stalks that pass to dorsal centres of the calciferous glands on each side. The dorsal vessel from XIV has two small pairs of vessels in each segment that pass to each side of the alimentary canal.

Nephridia paired holonephridia with long convoluted tubes and large deflated, subspherical to elongate, terminal bladders, from at least V, corresponding in position to the nephropores. Testes, sperm funnels, hearts and nephridia of X and XI enclosed in a longitudinal peritoneal sheath which, with the transverse intersegmental septa, forms a testis-sac in each segment concentric with and enclosing the gut. Small, lobed testes and large convoluted iridescent male funnels free in X and XI; seminal vesicles
in IX and XII, racemose or lobulated. Prostates each a flattened lobe with frequent incisions, restricted to XVIII; the muscular duct approximately as long, or shorter, and receiving the vasa deferentia at its junction with the gland; an accessory prostatic lobe present at the junction in the Marrickville specimen. Penial setae absent. Ovaries compact with small funnels in XIII; individual ova not apparent; ovisacs absent; nebulous oviducts in posterior of XIII. Spermathecae three pairs (Kholo Creek) or four pairs (other localities) in VI, VII-IX; each with an ovoid to almost conical, sometimes annulated ampulla and a poorly to moderately well demarcated duct which is of equal length or is shorter by as much as one half and which bears medianly, near its ectal extremity, a single clavate to digitiform diverticulum; length of a spermatheca 0.94 (Kholo Creek, inseminated); length of a diverticulum 0.8 mm; ratio length spermatheca: length diverticulum = 1.2 respectively.

REMARKS
The original brief description by Fletcher (1889) was based on one aclitellate specimen (plus two incomplete specimens) from Oxley. Jamieson (1970a) described material from nearby Kholo Creek but also from Marrickville in New South Wales, and commented that a range from Sydney to Brisbane, was unusually large for the genus. Furthermore the possibility of synonymy with the Queensland species *Heteroporodrilus (=Woodwardiella) ashworthi* was raised. Blakemore described material from Brookfield, Mt. Cotton and Samford, all in the Brisbane environs. Despite some variation between the specimens from the three locations, he considered that all could be included in *H. oxleyensis*. He also concluded that Brookfield, Mt Cotton and Samford material agreed sufficiently with Stephenson's (1933) single
specimen of *Woodwardiella ashworthi* for the latter species to be included in *oxleyensis* as foreshadowed by Jamieson (1970a). However, he erected a new species, for Mt. Glorious material in which he included material from the same locality attributed by Jamieson (1970a) to *H. ashworthi*. Blakemore’s decision is supported here on the basis of the presetal location of the genital markings on segment XVII in *H. jamiesoni*, contrasting with the postsetal location in *H. oxleyensis*, a feature which Jamieson (1970a) noted as differentiating the Mt. Glorious specimen from Stephenson's material of *H. ashworthi*. The fact that material from Mt. Glorious, albeit a small sample, collected on separate two occasions had the presetal markings in XVII suggests that it is a real difference. Nevertheless, a detailed study of the large collections of *H. oxleyensis* listed above is required for this and other characters. The new material confirms the unusually large geographical range of this species (or species complex?) from Brisbane to Sydney.

As Blakemore (1994b) discusses, justification for synonymy of *H. ashworthi* in *H. oxleyensis* is that Stephenson (1933) omitted reference to the earlier description of *oxleyensis* yet Stephenson’s specimen from Brisbane agrees with every point in Fletcher's (1889) account of *H. oxleyensis* apart from those attributable to a difference in maturity. The specimens from Kholo Creek and Marrickville also concur with Stephenson's (1933) specimen except that they are slightly shorter, have dorsal pores in 5/6 or 6/7 (rather than 7/8), do not retain setae *a* of XVIII, one has three pairs of spermathecae (rather than four) and they have paired postsetal genital markings in XVII (rather than an analogue, Stephenson, 1933). The combination of three pairs of calciferous glands in XI-XIII, four (or three) pairs of spermathecae and postsetal genital markings in XVII are, as Blakemore states, unique to this species.
The *Heteroporodrilus oxleyensis* complex would be a good candidate for molecular investigations which might reveal cryptic genetic diversity.

**Heteroporodrilus raveni** (Jamieson and Nash, 1976)  
(Fig. 18.32, 18.33)

*Plutellus raveni* Jamieson and Nash, 1976: 50-52, Fig. 2H-J, 3, Table 1.  
*Heteroporodrilus raveni*; Blakemore, 1994b: 22.

**TYPE LOCALITY:** 27°08'S.152°57'E., near Forest Glen - Qld.  
**HOLOTYPE:** QM G8374.  
**PARATYPES:** QM G8375. BMNH 1976.1.1-2.

Length 56-77 mm. Width (midclitellar) 2.3-2.8 mm. Segments 127-212. Secondary annulation absent. Pigmentless in life. Prostomium epilobous 2/3 to 5/6 or tanylobous. First dorsal pore 6/7 or 7/8. Setae *a* and *b* absent in XVIII; in XII, 10.9: 7.5: 9.6: 9.8: 35.0. Nephropores in *d* lines in II-IV; in *c* lines in V and VI; in *c* or *d* (usually alternating between *c* and *d*) in VII-IX though with rare displacement to *bc*; alternating between *b* and *d* (or vice versa) in X posteriorly. All nephropores designated as being in *b* lie slightly lateral of *b* lines. Occasionally (and always unilaterally) displacement towards *c* is significant, the pore sometimes lying nearer *c* than *b*. Clitellum annular, XIV1/3XVII. Male pores equatorial on XVIII in *b* lines, minute points in dark glandular circular areas on raised tumescences extending from
Fig. 18.32. *Heteroporodrilus raveni*. Genital field. Holotype QM G8374. After Jamieson and Nash (1976).
mid-\(bc\) to \(b\) lines; separation of the pores 1.58-1.80 mm, 0.22-0.25 body circumference apart. All specimens have circular genital markings in XIX and XX viz. one on each side postsetally median to \(b\) in XIX and two on each side, transversely aligned, presetally in \(ab\) in XX. The two longitudinally aligned markings immediately lateral to the male pores are usually recognisable. Markings not constant for all specimens are one on each side immediately presetally in \(ab\) in VII and VIII (frequently) and variably in IX or a transverse pair equatorially well median of \(a\) lines in VII, VIII and IX; in XVII, one postsetally on the right side in \(ab\) or the left side median to \(a\) or median to \(b\); in XVIII, one on each side presetally in \(a\) and midventral, unpaired and postsetal; in XIX, one on each side presetally lateral of \(a\) and one on the left presetally in \(b\). Rarely with numerous scattered wart-like excrescences questionably to be considered accessory genital markings. Female pore unpaired or, less often, paired in XIV midventrally, midway between the setal arc and the anterior margin, in the centre of a dark elliptical field. Spermathecal pores inconspicuous, 3 pairs at the anterior margins of VII-IX in \(b\) lines; separation of the last pair of pores 1.63-1.96 mm; 0.23-0.25 body circumference apart.

Thickest septa 7/8 and 8/9, strongly thickened. Dorsal blood vessel closely adherent on the intestine, free on the oesophagus. Dorsoventral commissural vessels in VI-XIII, all valvular; those in X-XIII forming four pairs of moderately large latero-oesophageal hearts, each of which arises from and lies behind the corresponding calciferous vessel and receives a slender connective from the dorsal vessel. The two large calciferous vessels of each segment branch at the oesophageal end of the duct of the calciferous gland to give several vessels running longitudinally in the wall of the duct and further dividing in the lamellae of the gland. The two calciferous veins are
Fig. 18.33. *Heteroporodrilus raveni*. A: Left prostate. B: Right spermatheca of IX. C: Right calciferous gland of XII. Holotype QM G8374. After Jamieson and Nash (1976).
continuous across the roof of the oesophagus and a middorsal supra-oesophageal vessel joins the points of fusion in posterior X-XIII. A pair of suboesophageal vessels provides a branch on each side to the corresponding calciferous gland; the suboesophageal vessels are traceable at least as far forward as segment V, and in XIV diverge laterally to form a pair of longitudinal lateroparietal vessels which enter XVIII, after which they discontinue. Oesophagus thin-walled in IV; in V forming a moderately long cylindrical or anteriorly widening firmly muscular gizzard; thin-walled whitish and intersegmentally constricted in VI to IX and in each of X-XIII bearing a pair of long-stalked, reniform calciferous glands, the stalks of which join the oesophagus dorsolaterally. Intestine commencing, with abrupt expansion, at the anterior septum of XV. Nephridial bladders thin-walled irregularly subspherical or more often bilobed with the nephridial duct joining the median lobe. Testes and firm flocculent sperm masses attached to iridescent sperm funnels in X and XI; seminal vesicles approximately equal in size, in IX and XII, each with separate, relatively smooth-surfaced lobed portion and a very much divided racemose portion. Vas deferens joining the ectal end of the muscular prostate duct which is sinuous and terminally widened; glandular portion of prostate a depressed, marginally incised entally widening lobe lying transversely in XVIII, the epithelial duct bifurcating within the gland shortly ental of the emergence of the muscular external duct (racemose prostate); only these major branches with recognisable epithelium. Penial setae absent. Ovaries bushy, though flattened; small sacs on the anterior septum of XIV are doubtfully ovisacs. Spermathecae 3 pairs, discharging anteriorly in their segments, each with a subspherical ampulla and stout, though much thinner duct which ectally narrows abruptly but is not distinguishable into discrete ectal and ental
regions; a single (inseminated) digitiform to clavate uniloculate diverticulum joining the duct very shortly before this enters the parietes. Spermathecae slightly increasing in size posteriorly; length of right spermatheca = 1.3, 1.2 mm; ratio total length: length duct = 2.6, 2.1; ratio of total length: length diverticulum = 2.9, 2.5 (right spermathecae of VIII and IX respectively).

REMARKS

Differences between *H. raveni* and other species of the genus are given in the remarks on *H. incommodus.*

**Heteroporodrilus shephardi** (Spencer, 1900)

For synonymy, see subspecies.

**Heteroporodrilus shephardi shephardi** (Spencer, 1900)

(Fig. 18.34-18.36)

*Cryptodrilus shephardi* Spencer, 1900: 40-41, Pl. 6, fig. 28-30.

*Woodwardia shephardi*; Michaelsen, 1907b: 162.

*Heteroporodrilus shephardi*; Jamieson, 1970a: 122-124, Fig. 4c, d, 9f, 10i.

**TYPE LOCALITY:** 36°43'S.142°12'E., Horsham - Vic.

**LECTOTYPE:** NMV F4034.
PARALECTOTYPES: NMV F401409. Further (type?) specimen AM W1290.

Length 112 mm. Width 10 mm, (6 inches long, 1/2 inch broad, Spencer 1900). Segments 119. Prostomium proepilobous, longitudinal grooves on the peristomium, of which there are several, giving it a spurious appearance of being tanylobous. Dorsal pores commencing in 6/7 (confirmation) but in the paralectotype not perforate until 7/8. Colourless in alcohol with the exception of the pale pinkish brown clitellum. In XII, \(aa: ab: bc: cd: dd = 1.0: 1.0: 1.6: 1.1: 3.8; dd: u = 0.31\). Nephropores in II-IV in \(d\) lines; in V-VI in mid-\(bc\) on the left and \(c\) on the right; in VII in mid-\(bc\) on the left and \(d\) on right; in VIII in \(d\) on the left and mid-\(bc\) on the right; in IX reversing this situation; thereafter alternating regularly between \(d\) and \(b\) lines but asymmetrically disposed in each segment. Clitellum annular, strongly tumid though not wider than adjacent segments, in XIV-XVI, with weaker development in XIII to shortly in front of the setal arc and pretaxially in XVII in which it is interrupted ventrally; setal follicles and intersegmental furrows visible; dorsal pores occluded. Male genital field: a pair of very strongly protuberant mamma-like ventromedianly directed male porophores in XVIII, their bases immediately median to \(b\) lines of adjacent segments, setae \(b\) being absent in this segment, setae \(a\) visible immediately median to them in a depressed median area. This median depression extending the length of XVII and posteriorly of XVIII for a number of segments depending, apparently, on the degree of contraction. Accessory genital markings inconspicuous paired oval patches median to \(b\) and including setae \(a\) of VIII-XI and postsetal and median to \(a\) of XVII or (Spencer, 1900) on XVIII and XIX only. Female pores anteromedian of setae \(a\) of XIV: in the paralectotype in a deep transverse furrow which extends between setal
Fig. 18.34. *Heteroporodrilus shephardi shephardi*. Posterior genital field. Paralectotype NMV F401409. After Jamieson (1970a).
Fig. 18.35. *Heteroporodrilus shephardi shephardi*. Anterior genital field. Paralectotype NMV F401409. After Jamieson (1970a).
lines a. Spermathecal pores three pairs, in 6/7-8/9 immediately lateral of b lines, each a minute papilla largely or wholly concealed in the corresponding intersegmental furrow.

Septa 4/5 and 5/6 very thin, 6/7 moderately thickened, 7/8-13/14 strongly thickened, 10/11-12/13 being very strongly and about equally thickened, 14/15 slightly thickened, the succeeding thin. Dorsal blood vessel single, continuous onto the pharynx. Supraoesophageal vessel traced into VII, ending posteriorly at the calciferous glands of XIII, receiving a transverse vessel from each calciferous gland. Last hearts in XIII, those of X-XIII, which are stout, originating from the calciferous vessels and receiving slender connectives from the dorsal vessel. Dorsoventral commissurals, apparently lacking supra-oesophageal connectives, in V-IX, those in IX, though slender, thicker than the preceding commissurals, valvular, and apparently constituting hearts. Hearts of X-XIII unbranched below their origins, those of IX each giving off a lateral vessel to the parietes near their ventral ends. Subneural vessel absent. Pharynx in III anteriorly with a low glandular investment; pharyngeal or septal glands not, however, present posteriorly of III. Gizzard broad, glossy, fairly easily compressible, in V. Oesophagus unmodified in IX, bearing ventrolateral broadly sessile extramural calciferous glands in X-XIII. The lumen of each gland almost occluded by numerous deep narrow lamellae which are radial and at the same time obliquely vertical relative to the axis of the oesophagus, the two glands of a segment almost in contact midventrally at their origins from the oesophagus. Oesophagus short, narrow and chloragogenous in XIV. Intestine beginning with abrupt expansion to full width in XV; typhlosole absent. Nephridia with large subspherical terminal vesicles, though in a few of the anteriormost segments the vesicles are smaller and are
Fig. 18.36. *Heteroporodrilus shephardi shephardi*. A: Prostate. B: Right spermatheca of VIII. Paralectotype NMV F401409. After Jamieson (1970a).
hidden in the loose longitudinal musculature of the body wall. Large compacted sperm masses (testes ?) filling segments X and XI and investing delicate petaloid, much dissected sperm funnels. Seminal vesicles fairly large, and much-divided but compact, in IX and XII. Prostate glands large dorsoventrally depressed lobes in XVII-XIX, each almost completely divided into an anterior and a posterior section at its equator and each of these portions more or less deeply incised; the surface distinctly but not deeply mammillate; the glossy muscular duct forming a loop with thick ectal and thinner less muscular ental limbs; the wide double vas deferens joining the duct at its junction with the gland but separable by dissection almost to the ectal end of the ental limb. Penial setae absent. Ovaries and funnels in XIII. Spermathecae three pairs discharging anteriorly in their segments; the abruptly demarcated muscular, ectally widening duct about one and a half times the length of the flaccid ampulla the ectal border of which overhangs the ectal end of the duct. Abruptly widening clavate diverticulum less than half the length of the duct arising from the latter shortly ectal of its middle, its base reflexed to open posteriorwards into the duct; length of a spermatheca 3.2 mm.

REMARKS
A textual reference in Spencer's description (1900) to occurrence of accessory genital markings "on segments 18 and 10" is clearly a lapsus for XVIII and XIX in which they are shown to lie, presetally and median to a lines, in his Fig. 28. It is probable that, as in the paralectotype, the anterior pair was in fact postsetal in XVII. Spencer did not observe the additional series of markings in the forebody. He gives the
location of hearts as VII-XIII and records no additional commissurals; the supraoesophageal vessel is said to occupy IX-XIII.

**Heteroporodrilus shephardi armatus** Jamieson, 1974b  
(Fig. 0.11, 18.37-18.38)

*Heteroporodrilus shephardi armatus* Jamieson, 1974b: 85-87, Fig. 2B, 10B, 11A, 13, Table 3.

**TYPE LOCALITY:** 37°28'S.140°49'E., 11 km S. of Penola. 36°37'S.140°42'E., 37 km from Bordertown. 36°59'S.140°44'E., 2 km S. of Naracoorte.  
**HOLOTYPE:** AM W6083.  
**PARATYPES:** BMNH 1978.21.4. SAM E1567.

Length 113-132 mm. Width (midclitellar) 7-8 mm. Segments >109 (amputee). Form angular in cross section the periphery being straight between adjacent setal lines. Pigmented greyish brown but pale ventrally in alcohol. Prostomium protanylobous, with a transverse furrow at 0/I or epitanylobous with a transverse furrow at 1/4 I; the peristomium with several longitudinal furrows so that extension of a dorsal prostomial tongue to 1/2 is questionable. Canalicula absent. First dorsal pore 6/7. Setae 8 per segment, in regular longitudinal rows throughout; setae $a$ and $b$ absent, replaced by penial setae, in XVIII; in XII, $aa: ab: bc: cd: dd = 1.4: 1.0: 1.5: 1.7: 3.3; dd: u = 0.25$. Nephropores conspicuous, anterior in their segments in the holotype in II(?) II-V in $d$ lines; in V-IX alternating from $d$ to mid $bc$ (commencing in V in $a$ on the right and
mid bc on the left); thereafter alternating from d to b (in X in b on the right and d on the left); the nephropores symmetrically disposed in paratype 1: in II-IV in d lines, in V and VI in mid bc; in VII-IX alternating from d to mid bc; in X backwards alternating from b to d. Clitellum annular, XIV-1/3 XVII; dorsal pores occluded in 14/15-16/17; intersegmental furrows fainter dorsally; setae and nephropores clearly visible. Male pores on XVIII in b, each on a slender papilla strongly protuberant from an indistinct low circular prominence. Accessory genital markings: transverse oval to oblong pads with porelike centres in VI (unilateral, right), VII and VIII (paired) filling ab and with centres at or slightly behind the setal arc; similar but larger pads almost filling the segments longitudinally and with centres immediately presetal in ab paired in XI and XII and unilateral, right, in XXII; paired deep pits in ab in 17/18 and immediately behind 18/19, a small indistinct eylike marking present posterolaterally to each pit. In the four type specimens paired pads in ab, which do not include the anterior portions of their segments, are present in VI, VII and VIII in H (right), P2 and P3. A liplike swelling extending to the preceding setal arc is present in these segments in front of each spermathecal pore in P1-3. An unpaired midventral circular postsetal marking with porelike centre is present in each of segments VI, VII and VIII in H or in VIII only in P3. Paired pads median to setae b and occupying much of the length of the segment are present in X in P1 and P3, in XI in H and P1 and 3, and in XII in H, P2 and P3. Paired pits in ab lie in intersegment 17/18 and immediately behind 18/19 in H, P1, 2 and 3. Paired oval pads in ab occur in XXII in P2 but there is only one, unilateral pad in H(R), P1 (right) and P3 (left). Indefinite tumid areas may be present in the vicinity of the paired pits of 17/18 and 18/19, i.e. ill defined eylike markings posterolateral to the pits in XVIII and XIX in H or posteromedian to the pits in XVIII.
in P1 and P3 and in XIX also in Pl. Female pores inconspicuous midway between the setal arc and anterior border of XIV, shortly median of a. Spermathecal pores 3 pairs in 6/7, 7/8 and 8/9, in b lines (and with inconspicuous elliptical lips, or shortly lateral of b lines and preceded by a semicircular swelling which fills the posterior third of the previous segment.

Septa 8/9-11/12 strongly thickened. Dorsal blood vessel single, continuous onto the pharynx. Supra-oesophageal vessel traced into VIII, not demonstrable in VII, ending posteriorly in XIII, receiving a transverse vessel from each of the calciferous glands, in X-XIII. Last hearts in XIII, those in X-XIII, which are stout, originating from the calciferous vessels and receiving slender connectives from the dorsal vessel (latero-oesophageal hearts); commissurals in VII-IX more slender, dorsoventral only and, unlike the latero-oesophageal hearts, with parietal branches but nevertheless valvular, vessels from the dorsal vessel in V and VI branching on the gut. Gizzard broad, glossy, strong but fairly easily compressible or elongate and firm, the preceding oesophagus, in IV, forming a wide flaccid proventriculus. Oesophagus unmodified in IX, bearing 4 pairs of ventrolateral broadly sessile extramural calciferous glands, in X-XIII, the lumen of each gland almost occluded by numerous radial lamellae. Oesophagus short, narrow and chloragogenous in XIV. Intestinal origin XV, typhlosole absent. Holonephric; nephridia with moderately large subspherical terminal vesicles, which are readily visible in the posterior intestinal region, are less well developed in the anterior intestinal region and not apparent in the forebody; preseptal funnels large, in ab irrespective of position of bladder (first demonstrated in XIV). Compacted sperm masses surrounding iridescent sperm funnels in X and XI; seminal vesicles racemose, in IX and XII. Large racemose prostates a pair, in XVI-
Fig. 18.38. *Heteroporodrilus shephardi armatus*. Right spermatheca of IX. Holotype AM W6083. After Jamieson (1974b).
XXI, a U-shaped muscular duct passing medianly from the middle region of the gland; the duct bifurcating at its ental extremity to receive ducts from the anterior and posterior portions of the gland: vas deferens joining the duct near its ectal end. Penial setae slender, sinuous, almost filiform, the ectal region, viewed from either side, ornamented with irregular, approximately transverse to oblique rows of a few (P1) to several triangular flattened scales which, except at their bases, are free from the setal surface but point towards the ectal extremity of the seta; the scales in the holotype with single, bifid or trifid points and in two or three groups, each group corresponding approximately with one of the coarser scales of paratype l; total number of scales counted in a longitudinal line approximately 21 (in 0.21 mm) and 37 (in 0.44 mm) in two setae of the holotype; each seta tapering to a rounded but delicate point; length of a fully developed seta 2.9-3.7 mm; width of the most strongly ornamented region 20-27. Ovaries, when observable, with numerous egg strings, and funnels in XIII; ovisacs absent. Spermathecae three pairs discharging anteriorly in their segments; ampulla subspherical, slightly shorter than the stoutly fusiform muscular glossy duct; an abruptly widening clavate diverticulum less than one third the length of the duct arising from the median aspect of the duct shortly ectal of the ampulla.

REMARKS

*Heteroporodrilus shephardi armatus* agrees with *H. shephardi* alone in the genus in alternation of nephropores between *d* and mid *bc*, rather than the usual *d* to *c* and was therefore included in *H. shephardi* as by Jamieson (1974b) as a subspecies although it shows differences, including the distribution of genital markings and the presence of penial setae, which might be considered to warrant separate specific status. Whether
or not it be reproductively isolated from the nominate subspecies it is unquestionably, from its morphology, more closely related to *H. shephardi* than to any other taxon in *Heteroporodrilus*. *H. shephardi* belongs to a group of species with four pairs of calciferous glands, the other members of which are *H. canaliculatus* and *H. mediterreus*, *H. incommodus*, *H. raveni*, *H. bongeen*, *H. thompsoni*, and *H. notatus*. The geographically closest species, *H. canaliculatus* and *H. mediterreus*, occur terrestrially in upper reaches of the Murray-Darling river system while *H. shephardi* occurs on the Wimmera River.

**Heteroporodrilus sloanei** (Fletcher, 1889)

*Cryptodrilus sloanei* Fletcher, 1889: 1536-1537.
*Platellus sloanei*, Michaelsen, 1900: 172.

**TYPE LOCALITY:** 31º16'S.149º17'E., Coonabarabran - NSW.
**SYNTYPES?**: AM W1317 (part.)

Length 52-71 mm. Width 5 mm. Segments 135-150. Epilobous, almost tanylobous. Setae cd very far apart. Clitellum not developed. Male pores on conspicuous papillae on XVIII, in b. Spermathecal pores three pairs, in b lines. Calciferous glands three pairs, in XI-XIII more or less underlying the gut. Seminal vesicles in IX and XII. Spermathecae each with two diverticula.
REMARKS
The description of this species is grossly inadequate but the presence of paired spermathecal diverticula, together with three pairs of calciferous glands limits consideration of possible synonyms to *H. canaliculatus* and *H. lamingtonensis*. Fletcher (1889) distinguished *H. sloanei* from *canaliculatus* solely by its fewer segments and the absence of a dorsal canalicula and of accessory genital markings. The latter distinction may be invalid, as the type-series comprised immature individuals, but the difference in numbers of segments, though of doubtful significance, at present precludes synonymy. Agreement in numbers of segments with *lamingtonensis* is close and both species lack canaliculi. However, conformity of the description of *sloanei* with that of *lamingtonensis* is of questionable significance in view of the brevity of the former account, and the sole known difference, presence of conspicuous male papillae in *sloanei*, suggests that further distinctions may be found at such time as new material of *sloanei* becomes available.

**Heteroporodrilus thompsoni** Blakemore 1994b

*Heteroporodrilus thompsoni* Blakemore 1994b: 32-33, Fig. 7.

**Type Locality:** 27°30'S.152°55'E., Lower Savages Rd. and near Gold Creek, Brookfield - Qld.

**Holotype:** QMG210142.

**Paratypes:** P1-6, QMG210143-210146.
Length 210-270 mm. Mass: 21.5 g. Width, midclitellar 11-13 mm. Segments: 181-235. Faint secondary annulation, especially after the clitellum; sometimes with marked dorsal furrow (i.e. canaliculate) in the latter half of its body. Colour unpigmented, grey in alcohol; clitellum darker pink-grey and faintly iridescent. Prostomium closed epilobous to pro-epilobous with definite furrow that bisects prostomium and extends to 2/3 as a groove. Peristomium rugose. First dorsal pore: not clearly detectable in deep furrows but seen in 10/11 and 13/14 at least, and again from 17/18. Setae 8 per segment, from II, dark tipped, ab absent from XVIII; in XII aa: ab: bc: cd: dd: u = 1.7:1.0:1.5:2.5:3.8:0.26. Nephropores at anterior margin of segment almost in furrow, obvious on clitellum. The most common arrangements: II/D, III/D, IV/C or D, V/C, VI/C, VII/C, VIII/C or D, IX/D or C, X/B, XI/D, XII/B, XIII/D, XIV/B, XV/D, XVI/B, XVIII/D, XVIII/B, XIX/D, XX/B, XXI/D, etc. Several specimens had irregular pore distributions to the above scheme, one had the opposite arrangement from X, another two had asymmetrical alternations within a segment (i.e. a pore in B and one in D). Clitellum annular and tumid XIV-XVII, setae and nephropores retained often in deep dimples. Male pores: in XVIII in site of b setae on slightly raised porophore. Female pores on XIV variously closely paired anteromedian to aa, sometimes concealed in a lateral groove, alternatively a single pore on a slightly tumid pad anteromedian to aa setae. Spermathecal pores: two pairs in 7/8 and 8/9 almost hidden in furrows in b line but visible under traction as small eye-shaped stomata. Genital Markings in X: a distinct pair of circular, tumid pads occupying the longitudinal width of the segment and encompassing the ventral setal pairs. In XVIII, the areas of the missing ventral setal couples are generally tumid with
a midventral hollow and in XIX is a similar glandular area which extends as far as the
limit of the ventral setae.

Septa 4/5-7/8 moderately thickened, 8/9-12/13 becoming progressively much
thicker, then, after 13/14, thinning. Dorsal blood vessel single continuous on pharynx;
commissurals in VII-IX, large hearts X-XIII; from IX or X to XIV or XV large dorsal
bladders dominate the dorsal vessels, in XV the enlarged dorsal vessel has two pairs
of ventrally directed vessels which surround the oesophageal valve. Bifurcate ventral
blood vessels form a pair of hairpin loops under gizzard before moving anteriorly.
Gizzard: large, muscular and barrel shaped in V with slight anterior rim, compressing
septa 5/6 onto 6/7 and reaching as far back as VII. Calciferous glands: four pairs in X-
XIII, the anterior pair the smallest, as spherical, white, ventral pouches sessile on
oesophagus each with numerous fine lamellae internally. A pair of suboesophageal
blood vessels run between the lobes of each pair of glands. Intestine origin (caeca,
typhlosole): abrupt in XV or XVI, no typhlosole. Nephridia: holonephric with large,
subspherical to elongate, flattened bladders corresponding in position with external
nephropores. Male organs: holandric: large paired, iridescent sperm funnels free (or
sometimes appearing to be in testis sacs) in X and XI. Seminal vesicles medium to
small size, paired and racemose in IX and XII (the latter lobulated on anterior
septum). In IX white coagulum, the same texture as in seminal vesicles, frequently
seen. Ovaries a small pair of egg-string tufts anteriorly in XIII, and paired diaphanous
oviducts on posterior ventrum. Prostates confined to XVIII, a pair of compact,
squarish, racemose glands with short, bent duct joined entally by vasa deferentia. In
section the prostates appear solid without obvious central lumina. Spermathecae two
pairs in VIII and IX; large, bulbous but slightly deflated or deflected subspherical
ampullae with fine concertina-like corrugations, attach to shortish ducts bearing several (2-6), small digitiform or bi-, tri-, or multi-lobed diverticula encircling the duct near the ectal end. Stalks (and occasionally termina) of several diverticula with spermatozoal lustre. Gut contents: mostly reddish silt with some grits and sometimes organic debris including woody remains (geophagous/detritivorous).

REMARKS
The combinations of four pairs of calciferous glands and two pairs of polydiverticulate spermathecae identify *H. thompsoni*. This species was rightly considered by Blakemore (1994b) to have close affinities with the similarly large *H. tryoni*, also collected from the type locality. It differs from *H. tryoni* in having one less pair of calciferous glands, one less pair of spermathecae, different setal ratios and in having a distinct pair of genital markings in X. *H. tryoni* usually has a pair or trio of tortuous diverticula on each of its three pairs of spermathecae, often with sessile seminal chambers. Blakemore (1994b), notes that Boardman's (1932) description for *H. youngi* (syn. *H. tryoni*) has compound diverticula similar to those described for *H. thompsoni*, but has three pairs of spermathecae and is placeable, as Jamieson (1970a) indicated, in *tryoni*. This similarity, combined with general similarity of the two taxa, and the fact that spermathecal numbers and even numbers of calciferous glands, are known, albeit rarely, to vary in good megascolecid species, are here considered to cast doubt on the specific status of *H. thompsoni*. Molecular studies would aid resolution of its status.
Heteroporodrilus tryoni (Fletcher, 1890)
(Fig. 0.33A, 18.39-18.41)

Cryptodrilus tryoni Fletcher, 1890: 994-996.
Platellus tryoni; Michaelsen, 1900: 171.
Woodwardia (?) tryoni; Michaelsen, 1916a: 62.
Woodwardiella tryoni; Boardman, 1932: 127-128.
Woodwardiella youngi Boardman, 1932: 128-130, Fig. 2.
Heteroporodrilus tryoni; Jamieson, 1970a: 125-129, Fig. 5b, c, 8c, d, 9g, h, 10j; Blakemore, 1994b: 32-33, Fig. 7.

TYPE LOCALITY: Milton, 27°28'S.153°01'E. - Qld.
TYPES: Lost.
OTHER RECORDS: (Boardman, 1932) c. 27°28'S.153°01'E., Brisbane suburbs; as holotype and paratype of W. youngi, QM G783, now G 3574 and 3575, and 5 slide mounted specimens; as W. tryoni, two slides of specimens mounted in glycerine jelly; one slide of 3 spermathecae and one slide of penial seta, QM G964. Slide labelled with old collection number Don 14373. (Blakemore, 1994b) 27°30'S.152°55'E., Adavale St. and Lower Savages Rd., Brookfield, QMG210147-49. (Jamieson, 1970a) 27°30'S.152°55'E., Mt. Elphinstone, 28°12'S.153°11'E., Binna Burra (BJ). 27°20'S.152°46'E., Mt. Glorious (QM 5305).
27°05'S.152°47'E., Mt. Mee (BJ). 26°38'S.152°58'E., Nambour (BJ). 27°24'S.152°49'E., Jolly's Lookout, QM G1106. 27°07'S.152°33', Somerset Dam, QM G 3576 - Qld.
Fig. 18.40. *Heteroporodrilus tryoni*. Genital field. Mt Elphinstone specimen, QM G5447. After Jamieson (1970a).
Length 250-460 mm (-580 mm, Boardman). Width 11-24 mm. Segments 123-237. Usually unpigmented in alcohol with the exception of the pigmented brown, grey or greenish clitellum; dorsal dark purple-grey pigmentation present segmentally but absent from intersegmental bands in some specimens. Prostomium prolobous (?) proepilobous or closed epilobous, often with a slight dorsomedian longitudinal groove which may be visible throughout the body and with or without other parallel grooves. First dorsal pore in 5/6, 6/7; or 7/8. Setae inconspicuous; in XII, \(aa: ab: bc: cd: dd: ud\) = 2.0-2.8 : 1.0 : 1 3-1.8 : 2.6-3.5 : 3.7-5.1 : 0.22-0.29. Nephropores at anterior margins of segments, in setal lines \(d, c\) and \(b\); the pores of II, III and IV in \(d\). At V or VI alternation from \(c\) to \(d\) commences (though Blakemore observed both pores in \(c\), on V) and the last segment in which \(c\) is occupied is IX-XII; this alternation is usually regular but in some specimens two or three consecutive openings occur in the same setal line. Nephropores do not open in \(b\) lines in VII, VIII nor IX as these positions are occupied by the spermathecal pores. Setal lines \(b\) begin to be occupied by XI-XIV, alternation from \(b\) to \(d\) occurring in consecutive segments thenceforth (however, Blakemore observed nephropores in \(b\) and \(d\) in VI in specimens in which alternation between \(b\) and \(d\) otherwise occurred in XII); locations of nephropores on the left and right sides of the body may or may not correspond and occasionally pores of a side are in the same line in two successive segments. In the specimen which Boardman identified as \(tryoni\), \(c\) line was occupied by IV (or V) otherwise agreement with the above generalization was exact. Clitellum annular and tumid: 1/2XIII, XIV-XVII but interrupted ventrally on XVII by genital markings. Setae and nephropores retained. Male genital field: large oval combined male and prostatic porophores a pair in XVIII; at full development extending laterally of \(b\) lines, sometimes almost to \(c\) lines,
and medianly to mid-\(ab\); male pores in or shortly median to \(b\) lines. Ventral setal couples absent in XVIII or (Toowong specimen) a slightly elongated penial (?) seta projecting from the male pore in or slightly median to \(b\) lines (probably dehiscent). (Setae \(b\) present or absent in \(youngi\) according to Boardman). Accessory genital markings; the ventral acilitellar region of XVII may be more or less tumid and may form a sucker like transverse pad on each side of the midline. Low sucker-like pads may also be present in XIX, or XIX and XX, and less commonly in XXI-XXIV anteriorly in each segment, laterally just including, and extending more or less far behind, the ventral setal couples. Similar patches may be present in X and XI. Female pores inconspicuous, a pair anteromedial from setae \(a\) of XIV midway between the setal arc and intersegmental furrow 13/14; sometimes in a common transverse groove. Spermathecal pores 3 pairs, in 6/7, 7/8 and 8/9, visible as minute rosette-like papillae, with central pores, at the extreme anterior margins of segments VII-IX, almost or wholly concealed in the intersegments in \(b\) lines (slightly dorsal of \(b\) (\(youngi\) (v. Boardman)).

Septa 2/3-4/5 delicate, 5/6 thin; 6/7, 7/8 to 12/13 or 13/14 strongly thickened; 8/9 and especially 9/10-12/13 very strongly; 14/15 slightly thickened; the succeeding septa thin. Dorsal blood vessel continuous on to the pharynx; receiving a pair of wide vessels from the gizzard in V; in VI-XIII sending commissurals to the ventral vessel. In VI-IX the commissurals are slender though increasing in diameter and posteriorwards each ventrally sends a slender lateral branch to the corresponding nephridia and is valvular above the branch. In IX-XIII the commissurals; which also increase in diameter posteriorwards and lack branches, are large enough to be termed hearts; each heart of X-XIII has two roots, one from the dorsal vessel, the other from
Fig. 18.41. *Heteroporodrilus tryoni*. A: Prostate. B: Right spermatheca of VIII. Mt Elphinstone specimen, QM G5447. After Jamieson (1970a).
the transverse vessel from the corresponding calciferous gland. Supraoesophageal vessel extending from XIII, where it arises from the calciferous vessels of that segment, anteriorly to as far as VIII or IX in which it becomes vestigial. Dorsal vessel in XIV receiving a pair of vessels from the oesophagus and in XV, posteriorly, two pairs of vessels in each segment. Suboesophageal vessel (Mt. Mee specimen) paired in XIV anteriorly and traceable at least as far forwards as VIII; each supplying two or more vessels in each segment to the calciferous gland of its side, the posterior vessel on each side in each segment continuous beyond the calciferous gland onto the adjacent septum. In segment IX, a thick latero-oesophageal vessel, median to the commissurals, joins the left suboesophageal (presence of a corresponding vessel on the right side not verified). Pharynx in III anteriorly, with only low investing glandular masses but many posteriorly directed tendons. Oesophagus in IV simple. Gizzard a large truncated, almost parallel sided cone, base forward, in V, only moderately firm and lacking a muscular sheen. Paired ventrolateral sessile calciferous glands five pairs in IX-XIII; internally with many lamellae; oesophagus in XIV simple and narrow. Intestinal origin variable, in XV or in XVI; ingesta mainly plant remains including large woody husks and small leaf skeletons. Typhlosole absent. Nephridia with large subspherical, though often collapsed, transparent ectal vesicles lacking diverticula. Testes and large convoluted iridescent male funnels free in X and XI; vasa deferentia running backwards beneath the ventral peritoneum. Seminal vesicles racemose, relatively small in IX and XII. Large paired racemose septal pouches on the anterior face of XIII, thin walled (corpuscle producing?) septal pouches at the septa where they are penetrated by the dorsal vessel in XVI posteriorly. Prostates tongue shaped (kidney shaped youngi, v. Boardman), not especially
depressed, coarsely lobulated but not deeply incised organs confined to XVIII; the vas deferens joining the middle or the ectal end of the short, straight, non glossy duct, or (Gold Creek Road specimen) the gland externally appearing elongate and almost tubular. Penial setae absent (dehisced) or (Toowong specimen) present. Ovaries extensive transverse ribbons, or tufts, composed of longitudinal chains of oocytes several deep dorsoventrally. Funnels large, rather simple and relatively delicate. Ovisacs absent. Spermathecae three pairs, in VII-IX, discharging anteriorly in their segments; ampulla conical with rounded ectal end, or rounded at both ends with a narrower waist, both conditions sometimes present in a single specimen (Toowong); duct much shorter, well demarcated (2/3 as long in youngi (Boardman)), base of ampulla often with sessile hemispheroidal seminal chambers (present or absent in same individual); diverticula tortuous blind tubes arising from the duct ectally or entally, one on each side or sometimes two laterally, each diverticulum simple or bifurcate or trifurcate; alternatively a simple clump of three to five tubes, closely bound together (one simple or bifurcate or trifurcate diverticulum, or three or four closely apposed sometimes bifurcate diverticula in youngi (Boardman)); the diverticula often with spermatozoal iridescence. Length of a spermatheca (Mt. Elphinstone specimen) 2.3 mm.

REMARKS
*H. tryoni* is often reported from the greater Brisbane area, where its large size attracts attention, occurring in decomposing leaf litter in suburban gardens in addition to natural locations.
19. *Hiatidrilus* Jamieson 1994


**DIAGNOSIS**

Setae 8 per segment. Male pores in XVIII. Genital markings present. Spermathecal pores 2 pairs, the last at anterior limit of IX. Gizzard in V. Oesophageal vascularization in the vicinity of the hearts, usually with development of extramural calciferous glands in XI and XII. Intestine commencing in XIV, XV or XVI. Nephridia stomate holonephridia, with or without bladder-like ducts, in straight rows. Holandric or metandric. Ovaries in XIII. Prostates coiled tubular (or tubuloracemose?). Penial setae present (or absent?). Spermathecae each with 1 or 2 sometimes biloculate diverticula.

**DESCRIPTION**

Setae 8 per segment. Dorsal pores present. Clitellum annular or saddle-shaped, in the vicinity of XIII, XIV-XVII, XVIII. Male pores in XVIII, median to or lateral of b lines. Segmental and intersegmental genital markings present. Spermathecal pores 2 pairs, in or immediately behind 7/8 and 8/9 in line with the ventral setae couples. Female pores anteromedian or anterior to setae a of XIV. Last hearts in XII. Gizzard weak to strong, in V. True extramural, pyriform, dorsolateral or ventrolateral calciferous glands two pairs, in XI and XII; or oesophagus segmentally dilated and
vascular, with large internal villi in IX-XIII but lacking calciferous glands. Intestine commencing in XIV, XV or XVI. Nephridia stomate, holonephridia; ducts discharging in \(c\) to \(cd\) lines, slender or wide and bladder-like. Testes in X and XI or XI only. Ovaries and funnels in XIII; ovisacs absent; pseudovesicles absent or present in XIV. Prostates elongate tubular, in XVIII and XIX or as far as XXII. Penial setae present (or, \(zacharyi\), absent?. Spermathecae each with 1 or 2 clavate, sometimes bifid, diverticula.

**DISTRIBUTION**
Eastern Subregion: Bunya Mountain and Ban Ban Springs near Gayndah (South-east Queensland); Bongeen and on the Clarence River (New South Wales).

**TYPE-SPECIES:** *Diporochaeta bunya* Jamieson, 1976b.

**REMARKS**
The name *Hiatidrilus* referred to the fact that the two species for which the genus was erected, both previously referable to *Diporochaeta*, occurred in the southern region of the very large geographical hiatus which separated *Diporochaeta*, in Victoria and Tasmania, from the North Queensland species of *Diporochaeta* since transferred to *Terrisswalkerius*. Three additional species, from the same geographic area, are here included in the genus.

A highly distinctive and unifying feature of *Hiatidrilus bunya*, *H. angus* and *H. bongeeni*, relative to most *Diporochaeta* species is the possession of true extramural calciferous glands, in XI and XII, although extramural glands occur in the type-
species of *Diporochaeta, D. intermedia*, in X and XI. Extramural glands do not occur in *H. semicinctus* and *H. zacharyi*. These two species are distinctive in having a saddle-shaped clitellum. *H. semicinctus* is distinguished in being metandric.

**CHECKLIST OF SPECIES OF HIATIDRILUS**
1. *Sebastianus angus* Blakemore, 1997
2. *Hiatidrilus bongeeni* Blakemore, 1997
3. *Diporochaeta bunya* Jamieson, 1976b
4. *Cryptodrilus semicinctus* Fletcher, 1890
5. *Zacharius zacharyi* Blakemore, 1997

**KEY TO THE SPECIES OF HIATIDRILUS**

1  a. Well developed extramural calciferous glands present in XI and XII. Clitellum annular or weakly developed ventrally  
   b. Extramural calciferous glands absent. Clitellum saddle-shaped  

2(1a) a. Spermathecae each with a single diverticulum  
   b. Spermathecae each with two diverticula  

3(2b) a. Genital markings two pairs of raised glandular pads in XVII and XIX; three pairs of ventral swollen papillae presetally in XVIII, XIX and XX. Midventral markings in XI and XII.  

   H. *bongeeni*
b. Genital markings include a midventral transverse glandular pad extending longitudinally from 1/2XVII-1/2XVIII and laterally to include setae b of XVII, bearing on each side, a circular whitish genital marking in b posteriorly in XVII, and a further one median to setal lines a at 17/18; circular genital markings at the anterior border of XIX behind the latter pair, median of a lines.  Midventral markings in XI and XII.

4(1b)  a. Metandric, with male funnels in XI only.  
      b. Holandric, with male funnels in X and XI.

_Hiatidrilus angus_ (Blakemore, 1997)


**TYPE LOCALITY:** 25°42’S, 151°47’E., Ban Ban Springs, near Gayndah - Qld. 
**HOLOTYPE:** ANIC:RB.94.1.1.  
**PARATYPES:** P1 ANIC:RB.94.1.2; P2 ANIC:RB.94.1.3. P3 ANIC:RB.94.1.4, P4 RB.94.1.5.

Body slender, anterior slightly bulbous, wider in XVII-XVIII. Length 35-45 mm. Width 1.5 mm. Segments 86-94, without secondary annulation. Colour white in life with pink anterior and orange-pink clitellum; unpigmented, transparent in alcohol with faint blue tinge. Prostomium open epilobous. First dorsal pore: in 7/8, 8/9 (in 11/12 in one specimen), indistinct anteriorly, occluded on clitellum, more pronounced posteriorly. Setae minute, eight per segment in longitudinal rows from II; ab replaced
by long, sigmoid penial setae on XVIII; aa: ab: bc: cd: dd: u = 2.3: 1.0: 2.2: 1.2: 5.5: 0.33. Nephropores not seen, lateral? (nephridia in mid-bc). Clitellum XIV-XVIII, weakly tumid, interrupted ventrally by genital markings. Male pores on small tumid mounds on XVIII coincident to the tips of paired penial setae in ab lines. Genital markings faint, paired, between ventral setal couples in VIII, IX-XI; large tumid pad postsetally distending ventral aspect of XVII encompassing 17/18, containing two lateral rows of 4-6 small translucent discs; similar ventral pad below male pores in XVIII distending 18/19 with 2-4 discs and, in two specimens, faint pad posteriorly in XX with five discs; these tumid pads forming depressions with raised borders on preservation. Female pores a pair anterior to a setae on XIV. Spermathecal pores 2 pairs, in 7/8 and 8/9, close to a lines, with raised tumid borders.

Septa: 4/5 membranous, 5/6 weak and displaced by gizzard, 6/7-13/14 not especially thick, thereafter thin. Dorsal blood vessel single, continuous onto pharynx in IV, distended in XIII. Commissurals in VI-IX; hearts in X-XII. Gizzard: in V, weakly muscular and compressible. Calciferous glands two extramural pairs in XI and XII, ventrally pendant as subspherical glands, each with about ten internal lamellae, terminal on long curved ducts which enter oesophagus laterally; oesophagus in this region also has internal rugae. Intestine commences abruptly in XIV, and maintains same width through clitellar region; typhlosole not found. Gut contents fine red/yellow soil, large quartz grains and some organic matter. Nephridia avesiculate holonephridia in straight series on each side in mid-bc, without obvious preseptal funnels. Small, iridescent 'testis-sacs' seen on anterior septa in X and XI; racemose seminal vesicles in IX and XII. Ovaries paired ventrally in XIII, palmate with relatively large ova. Prostates paired elongate tubular glands on thin flaccid ducts in
XVIII, extending dorsally to XXI, XXII; large, gracefully curved penial setae overlie ducts. Spermathecae 2 pairs in VIII and IX; small blunt ampulla on stout duct each with single, long-stalked diverticulum with iridescent bulb branching midlength.

**REMARKS**
Features which Blakemore (1997) considered to warrant placing this species in a distinct genus are also seen in *Hiatidrilus* to which it is here transferred: lumbricin setae, avesiculate holonephridia, here considered plesiomorphies, and two pairs of extramural calciferous glands in XI and XII, a notable synapomorphy. The supposedly tubular condition of the prostates against the tubuloracemose condition in *Hiatidrilus bunya* does not appear to constitute a valid generic distinction in view of the other similarities. The monodiverticulate spermathecae, though contrasting with the bidiverticulate condition in the type-species, is shared with *H. semicinctus*.

As Blakemore notes, the region of Gayndah is notable for being the type locality for several other species (e.g. *Diplotrema fragilis*, *Spenceriella minor*, *Digaster minor*, *D. brunnea* and *D. gayndahensis*, all of Spencer, 1900).

**Hiatidrilus bongeeni** Blakemore, 1997


**TYPE LOCALITY:** 27°34'S, 151°27'E., Bongeen - NSW.

**HOLOTYPE:** ANIC:RB.94.2.1.
Length 50 mm. Width 2.8 mm. Segments 96-99, the first twelve segments smooth then with much secondary annulation often obscuring the true intersegments. Unpigmented almost transparent in alcohol with faint blue tinge. Prostomium open epilobous. First dorsal pore rudimentary, in 10/11, more developed on clitellum. Setae minute, eight per segment in longitudinal rows from II; ab replaced by penial setae on XVII; mean aa: ab: bc: cd: dd: ud = 2: 1: 2.2: 1:4: 5: 0.33. Nephropores: not seen (nephridia in mid-bc). Clitellum not developed. Male pores: on XVIII, minute, on small raised poropores in b lines (by dissection). Genital markings two pairs of raised glandular pads with translucent centres in line with the male pores in XVII and XIX; three pairs of ventral swollen papillae presetally in XVIII, XIX and XX, those in XIX within generally tumid band extending between b setal lines; rudimentary genital markings, midventral in XI and XII. Female pores minute, on anterior annulus of XIV in raised tumid band anteromedian to setae a. Spermathecal pores 2 pairs, in 7/8 and 8/9 lateral in b lines as obvious ellipsoid openings.

Septa 4/5 and 5/6 membranous, 6/7 weak, 7/8-9/10 moderately thickened. Dorsal blood vessel: single, continuous on pharynx in IV. Hearts in X, XI and XII or XIII. Gizzard in V, spherical and muscular (appearing in VI as septum. 5/6 is membranous and compressed near 6/7). Calciferous glands two extramural pairs in XI and XII, pendant from short ducts which combine on each side to enter the oesophagus dorsolaterally through common opening; oesophagus internally rugose in this region. Intestinal origin XV; typhlosole absent. Gut contents mainly fine soil coagulurn with a few organic remains. Nephridia: avesiculate holonephridia in straight series on each
side in mid bc, without obvious preseptal funnels. Testes in X and XI; seminal vesicles small in IX and XII. Ovaries paired ventrally in XIII, palmate and compact. Paired elongate tubular prostates in XVIII-XIX, overlying long thin muscular ducts; vasa deferentia attaching at junction of duct and gland; small penial setae converge with duct at body wall. Spermathecae 2 pairs, in VIII and IX, ampulla subspherical sharply demarcated from equally long ducts each bearing opposed digitiform diverticula.

REMARKS
This species again has the synapomorphy of *Hiatidrilus*, extramural calciferous glands in XI and XII, and is not here considered to warrant separate generic status. As noted by Blakemore (1997), this species occurs only 80 km from the type locality of *H. bunya* (the type-species of *Hiatidrilus* which it closely resembles), but its distribution is significant in that these earthworms were not confined to the refugium of the Bunya Mountains National Park and were surviving, albeit in pockets, in the cultivated soils of the Darling Downs. It was found in association with *Heteroporodrilus bongeen* Blakemore, 1994b.

**Hiatidrilus bunya** (Jamieson, 1976b)
(Fig. 19.1, 19.2)

*Diporochaeta bunya* Jamieson, 1976b: 18-20, Fig. 1, 11A, 13E., 15E., Table 1.

*Hiatidrilus bunya*; Jamieson, 1994:
TYPE LOCALITY: 26°57'S.151°35'E., Bunya Mts., near Festoon Falls - Qld.
HOLOTYPE: QM G8336.

Length 34 mm. Width (midclitellar) 3.4 mm. Segments 103. Pigmented purplish grey in alcohol. Circular in cross section generally but dorsoventrally depressed in the vicinity of the male field. Prostomium prolobous; peristomium not shortened, nor grooved midventrally; canaliculi absent. First dorsal pore 6/7 (? clearly visible only caudally). Setae 8 per segment, in regular longitudinal rows throughout; a and b absent in XVIII; all setae absent from the last two segments. Nephropores sporadically and faintly visible in c lines, anterior in their segments. Clitellum annular, strongly protuberant, XIV-1/2XVII. Male pores on small firm, conical papillae in XVIII in ab, nearer b, relative to adjacent segments; the pores 1.68 mm, 0.13 body circumference apart. Genital markings a midventral transverse glandular pad occupies the region in front of the male pores, extending longitudinally from 1/2XVII-1/2XVIII and laterally to include setae b of XVII, bearing on each side, a circular whitish genital marking in b posteriorly in XVII, and a further one median to setal lines a at the site of the obliterated intersegment 17/18; a further similar pair of circular genital markings present at the anterior border of XIX behind the latter pair, median of a lines, each of this pair on an elliptical tumescence extending longitudinally from 1/2XVIII to include setae ab of XIX, furrow 18/19 persistent and separating off its anterior region; each ellipse conjoined with that of the other side to form a transverse pad narrowed in the midline. A transversely elliptical tumid pad present midventrally in each of XI and XII filling the segment and including setae a,
Fig. 19.1. *Hiatidrilus bunya*. Genital field. Holotype QM G8336. After Jamieson (1976b).

*Hiatidrilus (=Diporochaeta) bunya*
each pad with a pair of circular genital markings median to \( a \), the marking on the right in XII may be transversely duplicated. Female pores an inconspicuous pair shortly anteromedian of setae \( a \) of XIV. Spermathecal pores two pairs, at the anterior margins of VIII and IX, in \( b \) lines; each on a small transversely elliptical papilla; the pores of IX 1.82 mm, 0.28 body circumference apart; the left posterior spermathecal pore abnormally duplicated transversely well lateral of \( b \) line.

Thickest septa 8/9 and 9/10, moderately strongly thickened. Last hearts in XII; those in X-XII latero-oesophageal each with a well developed connective from the dorsal vessel and a further connective from a paired circum-oesophageal vessel, adherent to the gut, well ventral of the connection of this vessel with its fellow middorsally on the gut; presence of a supra-oesophageal vessel not ascertained.

Gizzard large, barrel-shaped but wider than long; appearing to be in VI but the exceedingly delicate (and incomplete?) septum 5/6 adherent to and probably containing it; preceded by an almost equally large region of the oesophagus. True extramural calciferous glands two pairs, in XI and XII; each gland pyriform or bluntly fusiform, arising from the dorsolateral face of the oesophagus by its narrow tapering end but lacking a distinct duct; the gland curving ventralwards around the oesophagus having in the order of 10 thick radial septa which meet axially and almost occlude the lumen but are not axially united. Intestine commencing in XV but pushing septum 14/15 forward so as to appear spuriously to commence in XIV. Nephridia simple stomate, avesiculate holonephridia; slender ducts discharging in \( c \) lines or, in the preclitellar region, occasionally in \( cd \); postseptal ducts visible in II posteriorly but small preseptal funnels only sporadically demonstrated though presumably present. Iridescent sperm funnels in X and XI; testis-sacs absent; seminal vesicles in IX (large,
Fig. 19.2. *Hiatidrilus bunya*. A: Right prostate. B: Right spermatheca of IX. Holotype QM G8336. After Jamieson (1976b).
racemose) in XII (small sacciform). Ovaries, large bunches of oocytes, and funnels in XIII; ovisacs and pseudovesicles absent. Prostates fairly thickly and irregularly tubular (tubuloracemose?), much-coiled in XVIII and XIX; the muscular duct once-bent. Penial setae present; ectally gently curved and finely tapering, slender but not filiform; ornamentation?. Spermathecae two pairs, opening anteriorly in VIII and IX; ampulla large, sacciform; duct stout but tapering; two clavate inseminated diverticula joining the junction of ampulla and duct, one on each side; size uniform; length of right spermatheca of IX = 1.1 mm; ratio total length: length duct = 2.2; ratio length: length diverticulum = 3.1.

REMARKS
Presence of two spermathecal diverticula, on opposite sides of the duct, separates *Hiatidrilus bunya* from species now or formerly in the *Diporochaeta + Vesiculodrilus* complex, excepting the Tasmanian *Scolecidrilus scolecoidea*. The latter species differs significantly in being strongly perichaetin and in having racemose prostates. A supernumerary diverticulum in series with the usual diverticulum occasionally occurs in *V. hobartensis* (Tasmania), and the diverticulum is doubled in *D. willsiensis* (Victoria) but although these two species also have basically eight setae per segment, they have five pairs of spermathecae.

*Hiatidrilus semicinctus* (Fletcher, 1890)
(Fig. 19.3)
Cryptodrilus semicinctus Fletcher, 1890: 996-997.
Megascolides semicinctus Beddard, 1895: 494.
Plutellus semicinctus; Michaelsen, 1900: 170; Jamieson, 1971c: 88.
Hiatidrilus semicinctus; Jamieson, 1994: 175.

Type Locality: 29°41'S.152°56'E., Grafton, Clarence River - NSW.
Syntypes: AM W1312 (3 specimens; a fourth is in fact a Heteroporodrilus).

Length 38-54 mm. Width (midclitellar) 2.5-3 mm. Segments 97. Pigmentless buff in alcohol with the exception of the clitellum which is pigmented pinkish brown. Prostomium broadly epilobous 1/2, with a faint dorsal groove for two thirds or the whole of the peristomium. First dorsal pore 12/13 (18/19, Fletcher). Setae prominent in 8 regular longitudinal rows throughout; ab absent in XVIII; in XII, aa: ab: bc: cd: dd = 2.06: 1.00: 1.38: 1.30: 5.95; dd = 0.4. Nephropores not visible. Clitellum saddle-shaped, 1/3, 1/2 XIII-XVII, dorsal of b lines; setae present but indistinct, intersegmental furrows and dorsal pores obscured. Male pores a pair in XVIII, very slightly lateral of b lines, each on a large dome-shaped strongly protuberant papilla which extends transversely from well median of a line nearly to c line. Genital markings at fullest development small circular boss-like prominences, each surrounded by an elliptical glandular field, unpaired and midventral in 13/14; paired between setae a in 14/15, 15/16, and 16/17, those in 14/15 almost contiguous medially, those in the next two intersegments further apart to that those of 16/17 are shortly median of setae a; a small marking present on each side in front of and behind the male porophore, lateral of b lines, at the posterior and anterior limits of XVII and
Fig. 19.3. *Hiatidrilus semicinctus*. A: Prostate. B: Right spermatheca of VIII. Syntype AM W1312. (Jamieson, 2000).
XIX respectively; paired markings almost contiguous medianly in 19/20 accompanied by a marking in \( ab \) (the left one bearing a boss); and an unpaired median marking in 20/21. Further genital markings present in the vicinity of the spermathecal pores in or lateral of the lines of ventral setal couples: post-setal in VII and VIII, presetal in IX and X, those on the right side transversely duplicated in VII and triplicate in VIII; an additional equatorial marking present on this side in VIII. In the other two specimens the posterior genital field (XIII posteriorly) is similar though several of the markings are at least unilaterally absent. Constant in the three specimens are the paired markings at 14/15, 15/16, 16/17, posterior XVII and anterior XIX. The anterior genital markings may be absent or substantially similar to those described. Female pores a pair of small slits shortly in front of setae \( a \) of XIV in a common transverse glandular field which fills \( bb \). Spermathecal pores 2 pairs of small slits in \( b \) lines, in 7/8 and 8/9.

Septa 8/9-10/11 very strong. Last septal glands in IV. Dorsal blood vessel single, continuous on the pharynx; dorsoventral commissural vessels in VI-XII, slender though widening posteriorly, in VI-X; forming 2 pairs of large latero-oesophageal hearts in XI and XII; commissurals in VI-IX dorsoventral only; those in X apparently also lacking connectives to the supra-oesophageal vessel; this vessel well developed in X-XII, weakly developed in IX and 1/2XIII. Subneural vessel absent. Nephridia (stomate?) simple holonephridia throughout, the postseptal bodies commencing in II; the ectal duct widening to form an approximately straight, or bent, wide-tube which might be considered tubular bladders; all penetrating the parietes in \( c \) lines. A moderately muscular narrow proventriculus in IV. Gizzard large, globose and strongly muscular in V. Oesophagus segmentally dilated and vascular, with large internal villi.
in IX-XIII; narrow elsewhere. Intestine commencing, with abrupt expansion, in XVI; muscular thickening, caeca and typhlosole absent. Metandric: testes, iridescent large sperm masses free in XI (absent from X); a pair of very large racemose seminal vesicles in XII. Prostates tubular, the gland much and compactly wound in XVIII and XIX, the strongly muscular duct bent in an s-shape; the wide vas deferens joining the junction of duct and gland. Penial setae each very slender, sharply pointed and curved; ornamentation absent; length of a well developed seta 0.8 mm, width of the untapered region of the shaft 16 µm. Ovaries (very large laminae with numerous, peripherally large oocytes) and funnels in XIII; ovisacs absent; a racemose mass anteriorly in XIV on each side of and partly encircling the oesophagus does not appear to be an ovisac. Spermathecae uniform, 2 pairs, opening anteriorly in VIII and IX, each with an almost spherical ampulla and a longer, clearly demarcated spindle-shaped duct which bears at its ectal end a lateral and a median clavate inseminated diverticulum about as long as the ampulla; length of the right spermatheca of VIII = 1.96 mm, ratio total length: length duct = 1.9; ratio total length: length diverticulum = 3.2.

**Hiatidrilus zacharyi** (Blakemore, 1997)


**TYPE LOCALITY:** 29°28'S, 153°12'E., Woodburn Is., Maclean, on Clarence River - NSW.
Length 38 mm. Width 1.5 mm. Segments 102, some secondary annulation posterior to the clitellum. Unpigmented or light brown in alcohol; clitellum buff. Prostomium small, pro-epilobous or closed epilobous with dorsal furrows reaching almost to 1/2, giving tanylobous appearance. First dorsal pore not found in anterior (possibly obscured by deep intersegmental furrows) but noted from 12/13, retained on clitellum. Setae: small, eight per segment from II; ab absent on XVIII. (Ratio on XII: aa: ab: bc: cd: dd: u = 4.4: 1.0: 1.8: 1.6: 12.0:0.50). Nephropores not seen (near c lines?). Clitellum 1/2XIII-XVII, saddle-shaped with distinct ventral flare. Male pores on XVIII, minute on small raised porophores in b lines. Genital markings faint, intermittently paired genital markings as small circular papillae presetal and almost in line with spermathecal pores in VIII-XIII; in XIII two distinct pairs of papillae anteromedian to each ventral seta within generally tumid pad; in XVII paired postsetal papillae in b lines and, obscuring 17/18, large ventrally raised glandular pad that bears a row of five small papillae; in 18/19 a fainter repetition of glandular area in 17/18 but with only two pairs of papillae. Female pores on XIV in raised tumid band, minute anteromedian to setae a. Spermathecal pores in 7/8 and 8/9 in b lines as swollen ellipsoid openings.

Septa 5/6 membranous to base of gizzard, 6/7-11/12 only slightly thickened, otherwise delicate. Dorsal blood vessel single, continuous onto pharynx in IV; ventral blood vessel bifurcates under gizzard. Hearts in X-XII, small (dorsal blood vessel enlarged in XIII and XIV). Gizzard in V, muscular and amphora-shaped with anterior rim, tapering to oesophagus. Calciferous glands not found, but oesophagus in XIII and XIV.
less so in XIV contracts and has pink coloration with internal rugae; in XV-XVII the intestine dilates and has increased dorsal vascularization but is not internally lamellate. Intestinal origin abrupt in XV and XVI then narrowing slightly to accommodate prostates; acaecate; no distinct typhlosole but from about XXXVIII a low wide dorsal ridge is present. Gut contents fine silt plus large quartz grains (0.5 x 0.25 mm) and some fibrous plant material. Nephridia avesiculate holonephridia in straight series on each side in mid-bc, without obvious preseptal funnels, as simple coiled tubes closely associated with anterior septa; tufted nephridia not detected anteriorly in the pharyngeal mass which extends to V or VI. Holandric; iridescent funnels in X and XI; small paired racemose seminal vesicle in XII (not detected in IX although VIII-XI filled with coagulum). Ovaries paired ventrally in XIII, palmate and compact, each consisting of several egg strings. A pair of convoluted S-shaped tubuloracemose prostates (central lumen not found in section) with thin muscular ducts, occupying XVIII-XXI; penial setae not found. Spermathecae two pairs in VIII and IX; ampullae sub-spherical each with equally long duct from which blunt iridescent diverticulum on a short stalk branches medially.

REMARKS
This species was found in irrigated alluvial massive earth or prairie soil intergrade, under 'trash' from sugar cane cultivation, in association with numerous, exotic *Eukerria saltensis* earthworms of the family Ocnerodrilidae.
20. Hickmaniella Jamieson, 1974a

_Hickmaniella_ Jamieson, 1974a: 300

**DIAGNOSIS**
Perichaetin; setae numerous per segment. Combined male and prostatic pores a pair on XVIII. Calciferous glands, typhlosole and intestinal caeca absent An oesophageal gizzard in V and an intestinal gizzard in XIX-XX, XXI?. Nephridia few exonephric avesiculate meronephridia per segment; the medium nephridium with preseptal funnel. Prostates tubuloracemose. Penial setae present. Spermathecae 1 or 2 pairs.

**DESCRIPTION**
Terrestrial. Form circular in cross section, anus terminal. Dorsal pores present. Setae numerous in each segment (> 30-40 in posterior segments); ventral gap large; dorsal gap recognizable anteriorly, inappreciable caudally (zz ca = zy). Nephropores not externally visible. Clitellum annular; anterior to the male porophores. Combined pores of the vasa deferentia and a pair of tubuloracemose prostates one pair on XVIII. Female pores a pair on XIV. Spermathecal pores 1 or 2 pairs, in intersegments 7/8 and 8/9 or 8/9 only.

Last hearts in XII (latero-oesophageal). Subneural vessel absent. Oesophageal gizzard in V. Extramural calciferous glands absent. Intestine commencing in the vicinity of the prostate glands; with a very thick-walled intestinal gizzard in XIX-XX,
XXI?; typhlosole and caeca absent. Few, exonephric, avesiculate meronephridia per segment, the median nephridium in oesophageal and intestinal regions with preseptal funnel (not examined in *H. gogi*); tufting and enteronephry absent. Holandric; gymnorchous; seminal vesicles in IX and XII. Metagynous; ovisacs absent. Penial setae present. Spermathecae 1 or 2 pairs, with clavate but internally multiloculate diverticulum.

**DISTRIBUTION**
Northwest Tasmania

**TYPE-SPECIES:** *Hickmaniella opisthogaster* Jamieson, 1974a

**CHECKLIST OF SPECIES OF Hickmaniella**
2. *H. opisthogaster* Jamieson, 1974a

**REMARKS**
*Hickmaniella* differs from *Nexogaster* in being perichaetin with tubuloracemose prostates, an intestinal gizzard in XIX-XX and absence of a typhlosole (Blakemore and Kingston, 1997).

*Hickmaniella* and *Nexogaster* are almost unique in the known Megascolecidiae in possessing an intestinal gizzard. (the Oriental *Pleionogaster* has 3 or 4 such gizzards.) This feature is characteristic of the Oriental family Moniligastridae (in which, however, Gates (1962) states the gizzards are actually oesophageal though
post-ovarian), the holarctic family Lumbricidae and the Palaeartic, Neotropical and Ethiopian subfamily Alminae of the non-Australian family Glossoscolecidae. The Moniligastridae (Order Moniligastrida) differ from Megascolecids in many significant respects, including the single-layered clitellum, large-yolked eggs, presence of intra-septal testis sacs, location of one or two pairs of male pores in the next segment or segments respectively and absence of an anterior gizzard. The Lumbricidae are distinguished by the absence of an oesophageal gizzard, location of the male pores in or in front of segment XV, location of the clitellum far behind these pores, the exclusively lumbricine setae and in other respects. In contrast, the Glossoscolecidae, while showing their closest affinities with the Lumbricidae (vide Jamieson 1971d), show notable resemblances to the Megascolecidae which may indicate that they are more closely related to the latter than is any other family with the exception of the Eudrilidae. The intestinal gizzard of Hickmaniella constitutes a further link between the Megascolecidae and the Glossoscolecidae. Like many other common features of the two families the intestinal gizzard may have been independently acquired in each but sufficient similarities exist to suggest that if this be the case we have here a case of parallelism in evolution stemming from a common, though remote, ancestry rather than convergence in relatively unrelated lineages of the Metagynophora. These similarities include the following (in addition to general characteristics of the non-alluroidid Lumbricina of Brinkhurst and Jamieson 1971): progression from the lumbricine to the perichaetin arrangement of setae; presence of prostate-like glands in some Glossoscolecidae which resemble the prostates of the Megascolecidae; frequent presence in both families of oesophageal gizzards and the mutual possession of intestinal gizzards; location of the male pores in XVIII in some Glossoscolecidae,
as in most Megascolecidae; location of these pores on the clitellum in some Megascolecidae as in many Glossoscolecidae and finally replication of the nephridia, in Tritogenia, as in many Megascolecids. While inclusion, on the one hand, of the Glossoscolecidae and Lumbricidae in the superfamily Lumbricoidea and, on the other hand, of the Megascolecidae and Eudrilidae in the superfamily Megascolecidae is here upheld, the above-mentioned similarities between the parent families Megascolecidae and Glossoscolecidae bring the two families closer.

KEY TO THE SPECIES OF HICKMANIELLA

a. Spermathecal pores 2 pairs, in 7/8 and 8/9
   H. opisthogaster
b. Spermathecal pores 1 pair, in 8/9
   H. gogi

Hickmaniella gogi Blakemore and Kingston, 1997

Hickmaniella gogi Blakemore and Kingston, 1997: 1690-1693; Fig. 1.

TYPE LOCALITY: 41°29’S.146°27’E., Gog Range; 41°42’S.146°18’E., Little Fisher River, Lake Rowallan; 41°42’S.146°15’E., Dublin Creek, Lake Rowallan; 41°52’S.146°03’E., Pelion Gap; 41°37’S.146°16’E., Snake Creek Road, Mole Creek; 41°26’S.146°14’E., O’Neils Road, Gowrie Park - Tas.

HOLOTYPE: QVM:14:3328.
Body stout hardly tapering to tail, first segment compressed. Length 60-75 mm. Width ca 7 mm. Segments 70-103. Unpigmented in alcohol, clitellum buff. Prostomium tapering epilobous, faintly furrowed dorsally. Clitellum 1/2XIII, XIV-XVII, 1/2XVIII. Dorsal pores rudimentary in 2/3, open from 3/4. Nephropores not found. Setae numerous, 40-48 per segment, ventral couples *ab* in regular rows, other rows sinuous; dorsal setal gap ca 1/2 *aa*. Female pores widely paired on XIV. Male pores paired on XVIII on flat, irregular pads with two or three penial setae protruding. Genital markings: include median troughs in *bb* in 10/11, or 13/14 and/or 16/17; two pairs of ill-defined hollow disks joined by median troughs in 17/18 and 18/19 wider apart than the male pores; elongate, depressed pads in *bb* in 19/20 same width as male. Spermathecal pores 1 pair, in 8/9 in *a* or *ab* lines within tumid area.

Septa 7/8-12/13 thickened, 9/10/11/12 peripherally adpressed (as pericardiac testis-sacs?). A muscular but compressible oesophageal gizzard in V; large muscular intestinal gizzard in XIX-XX and perhaps part of XXI also modified; externally with lateral bands of muscle fibres, internally with longitudinal striations, wall ca 0.5 mm thick (thicker than that of oesophageal gizzard). Oesophagus not especially dilated. Nephridia avesiculate meronephridia, five or six tubules per side equatorially connected by mesentery; larger anteriorly but not tufted; funnels 'not found'. Dorsal blood vessel single; hearts XI-XII, with connectives to supra-oesophageal vessel in
VII-XIV. Iridescent testes [funnels?] in mucus in X and XI; small racemose seminal vesicles in IX and XII. Ovaries compact, in XIII. Prostates tubularacemose in XVIII, gland folded over itself, overlain by long penial setal sheaths and tendons; [form of penial setae not described]. Intestinal origin XVIII, dilated and thin-walled on either 'side' of gizzard in XVIII and in XXI, spiralling from XXII; typhlosole absent; gut containing soil with numerous quartz grits and sand. Spermathecae 1 pair in IX; ampulla saccular, smooth or irregular in outline, on thick duct bearing small clavate diverticulum with numerous iridescent chambers internally.

REMARKS
The definition of *Hickmaniella* of Jamieson (1974a) was emended to accommodate this bithecate species. Specific differences that further separate *Hickmaniella gogi* from *H. opisthogaster* are the position of the first dorsal pore and the form and arrangement of the genital markings (Blakemore and Kingston, 1997).

**Hickmaniella opisthogaster** Jamieson, 1974a

(Fig. 0.18(64-66), 20.1, 20.2)

*Hickmaniella opisthogaster* Jamieson, 1974a: 301-302, Fig. 4, 18A, 32C, D, Pl. 64-66.

*Hickmaniella opisthogaster* Jamieson, 1974a: Blakemore and Kingston, 1997: 1693-1695, Fig. 2.

**Type Locality:** 41°20'S.145°35'E., Parrawe. 41°20'S.145°35'E., Hellyer Gorge. 41°00'S.145°45'E., Table Cape - Tas.

**Holotype:** TM K360.


Length 45-70 mm. Width 5-5.5 mm. Segments 80-90. Prostomium epilobous or canaliculate, tanylobous. First dorsal pore 3/4 (sometimes a rudiment), 4/5. Setae ca 30-50 per segment; aa regular throughout or becoming irregular posteriorly; anteriorly aa 5 ab; caudally aa 3 ab; zz varying from 2-2.5 zy, anteriorly, to 1-1.5 zy caudally. Nephropores not externally visible. Clitellum annular, XIII, 1/2XIII-1/2XVII. Male pores approximately in a lines of XVIII, each median to a penisetal pore, on prominent dome-shaped medianly almost contiguous papillae which expand the segment longitudinally. Accessory genital markings paired, medianly conjoined oval glandular prominences with papillate or pore-like centres in approximately b lines in intersegments 11/12, on some of 10/11, 14/15-16/17 and 19/20-22/23, resembling the male porophores in appearance; sometimes unilateral. Female pores paired, anterior to setae a on XIV. Spermathecal pores 2 inconspicuous pairs, in 7/8 and 8/9, in a or ab lines.
Septa 6/7-12/13 thickened. Last hearts in XII; hearts in X-XII latero-oesophageal, with connective from dorsal and supra-oesophageal vessel; supra-oesophageal vessel recognizable in 1/2VII-1/2XIV, -XVII?. Oesophageal gizzard moderate to large but not strong, in V. Extramural calciferous glands absent. Intestine commencing in XVIII in which it is thin-walled and crop-like; a very large, extremely thick-walled intestinal gizzard in XIX and XX or both; typhlosole absent; intestine spiralled from XXII. Few, exonephric, avesiculate meronephridia per segment, commencing in II; 3 on each side in the intestinal region; median nephridium with preseptal funnel in intestinal and at least the posterior oesophageal segments; tufting and enteronephry absent. Holandric; gymnorchous; seminal vesicles in IX and XII. Metagynous; ovisacs absent. Prostates tubuloracemose, extending laterally in, and restricted to, XVIII; With very narrow central lumen which bears narrower epithelium-lined side branches. Penial setae (holotype) 2 mature and I completely developed on each side; when functional 1.6-I.7 mm long, general width of shaft 31 µm; gently or strongly curved, widened basally, the ectal tip flattened, usually curved, and with margins slightly inrolled; the ectal region of the shaft, but not the inrolled region, ornamented by numerous short, transverse minutely serrated linear markings of which there are 4 or more across the width of the seta; this ornamentation readily visible under the higher powers of the light microscope without recourse to oil immersion. Spermathecae 2 pairs, in VIII and IX; a single clavate but internally multiloculate diverticulum, the duct with a large dorsal swelling.
REMARKS
Blakemore and Kingston (1997) have considerably expanded the known range of this species. Although they did not find nephridial funnels, the notoscolecin (‘dichogastrin’) arrangement (a single median funnel on each side caudally) of these was unequivocally demonstrated by Jamieson (1974a) for the type-species.

**DIAGNOSIS**
Setae 8 per segment, the dorsal couple only about 1.5 times the width of the ventral couple. Nephropores in *b* lines. Clitellum annular. Male pores in XVIII. Eye-like genital markings absent. Female pores paired, shortly anterior to or anteromedian to setae *a* of XIV. Spermathecal pores 2 pairs or unpaired, in 7/8 and 8/9.

Last hearts in XIII, those in X-XIII latero-oesophageal. Gizzard small and globose in V. Calciferous glands absent. Intestinal origin apparently XIX or XX; typhlosole absent, though a rudimentary middorsal ridge may occur. Nephridia stomate avesciculate holonephridia; small tuftlike structures on the body wall, in IV and V may be tufted nephridia. Holandric; seminal vesicles large, racemose, with many large discrete loculi, in IX and XII. Penial setae present. Metagynous; true ovisacs in XIV.

**DESCRIPTION**
As for the single species.

**DISTRIBUTION**
Western Subregion: Kangaroo Island, off the South Coast of South Australia
TYPE-SPECIES: *Perionychella (Perionychella) inconstans* Jamieson, 1974b (Monotypic)

REMARKS
The single known species, *Kangaridrilus inconstans*, differs from species of *Diporochaeta*, in which it was previously placed, in location of nephropores in *b* lines and in that the setal interval *cd* is not as large relative to *ab*. Nephropores are more dorsally located in *Diporochaeta*, occupying *c* lines in the lumbricin species referred to *Vesiculodrilus* (as in Australian acanthodriles). The genital markings of *inconstans* are also highly distinctive; the presence of only two pairs of spermathecae is an infrequent condition in *Diporochaeta* and *Vesiculodrilus*, and their tendency to be unpaired is there unknown, though typical of *Fletcherodrilus*. Location of last hearts in XIII is reported in *Vesiculodrilus* only in *V. decatheca*. These differences, together with its insular, semi-aquatic habitat, indicate that *D. inconstans* is phylogenetically distinct from *Diporochaeta* and *Vesiculodrilus*. The most similar genus is *Hiatidrilus*, the type-species of which was also formerly placed in *Diporochaeta*, and, like *Kangaridrilus*, has two pairs of spermathecal pores. *Hiatidrilus* also differs from *Kangaridrilus* in the location of the nephropleure, lying in or above mid *bc*. Erection of a separate genus for *D inconstans* appears justified and is endorsed by its discrete geographical location. Its phylogenetic affinities within the other holonephric Megascolecinae are obscure. Etymology: *Kangari* reflecting its occurrence on Kangaroo Island, and *drilus*, a worm. Gender masculine.
Kangaridrilus inconstans (Jamieson, 1974b)
(Fig. 21.1, 21.2)

*Perionychella (Perionychella) inconstans* Jamieson, 1974b: 83-85, Fig. 6C, 10A, Table 2. *Diporochaeta inconstans*; Jamieson, 1976b: 4.

**Type Locality:** 35°56'S. 136°44'E., in soft, waterlogged earth, bonded with grass and grass roots, on the banks of Rocky River, about 1.6 km N. of Rocky River Homestead, Kangaroo Island-SA.

**Holotype:** AM W6079.

**Paratypes:** P2-4 AM W6080-6082. P1, 5, 6 BMNH 1978.21.1-3. SAM E1566.

Length 63-77 mm. Width (midclitellar) 2 mm. Segments 122-131. Pigmentless in alcohol with the exception of the reddish brown clitellum. Form attenuated; circular in cross section. Prostomium epilobous 2/3, acute, closed; not canaliculate. Peristomium not bisected ventrally. Setae 8 per segment, in regular longitudinal rows throughout or c and d irregular posteriorly; a and b absent in XVIII; in XII aa: ab: bc: cd: dd = 1.9: 1.0: 2.1: 1.5: 10.2; dd: u = 0.47. Nephropores sporadically visible, on and behind the clitellum, anteriorly in their segments in b lines. Clitellum annular, almost fusiform, very conspicuous owing to strong tumescence and its reddish colour, clearly demarcated in XIII-2/3XVIII, but some clitellar modification and pinkish pigmentation present throughout XII and XVIII dorsally, i.e. extent XII-XVIII (= 7 segments); intersegments 13/14-17/18 totally obliterated dorsally. Male pores equatorial in a lines of XVIII on strongly protuberant, subcircular papillae which fill all but a small anterior part of the segment, the lateral borders of the papillae less
clearly demarcated than the median borders. The papillae lie in a whitish glandular field which interrupts the clitellum from shortly presetally in XVII, laterally beyond \( b \) in XVII and XVIII, and which extends posteriorly to include or just precede the setal arc of XX. The setal annulus of XVII to shortly lateral of \( b \) forms a transverse ventral ridge. Distinct accessory genital markings are not recognizable in the male field but there may be a weakly developed transverse pad from mid \( ab \) to lateral of \( b \) on each side filling the anterior third of XVIII. An unpaired, midventral, circular genital marking with depressed central area and porelike centre almost fills the length of two or more of segments VII, VIII (constant), and IX and extends laterally to \( a \) or into \( ab \). Female pores paired, shortly anterior to or anteromedian to setae \( a \) of XIV, in a common glandular field which fills \( bb \) and longitudinally extends from 13/14 posteriorly to just include the ventral setal couples. Spermathecal pores 2 pairs, in 7/8 and 8/9, each on an inconspicuous papilla almost concealed in the intersegment, unpaired midventral or paired median to \( a \) lines.

Thickest septa 7/8-9/10, moderately strongly thickened. Dorsal blood vessel single, continuous onto the pharynx. Last hearts in XIII, those in X-XIII latero-oesophageal, each receiving a connective from the dorsal vessel and from the supra-oesophageal vessel. The latter vessel extends from 1/2 VIII-XIV, 1/2 XV and except at its extremities, is larger than the dorsal vessel. No subneural vessel detectable. Gizzard small and globose in V, its posterior limit being at 1/2 VI; muscular but easily compressed. Oesophagus moniliform but not evidently vascularized in VI-VIII, in IX-XIV moniliform and apparently with increased vascularization (especially vascular in IX), in XV-XVII-XIX tubular and only slightly vascularized, in XVIII similar to that in XVII but globose. Intestinal origin apparently XIX where the wall is thinner or XX
Fig. 21.2. *Kangaridrilus inconstans*. Right spermatheca of IX. Holotype AM W6079. After Jamieson (1974b).

Kangaridrilus inconstans

Spermatheca
Right, seg.
IX, Holotype

=Perionychella (P.) inconstans

=Diporochaeta inconstans
with oesophageal valve at 19/20, not reaching full width until XXI; typhlosole absent, though a rudimentary mid-dorsal ridge is observable in paratype 1; muscular thickening and caeca absent. Nephridia holonephridia first recognizable in XI or XIII but 2 pairs of small tuftlike structures on the body wall, in IV and V may be tufted nephridia (the extreme narrowness of the worm rendering dissection very difficult); each holonephridium with a large preseptal funnel and narrow duct discharging presetally in b line. Holandric, testes and iridescent funnels in X and XI; seminal vesicles large, racemose, with many large discrete loculi, in IX and XII. Penial setae present, their follicles extending from XVIII into XX, filiform. Metagnynous (ovaries consisting of a few irregular chains of very large oocytes and funnels in XIII); true ovisacs, each with several very large oocytes, in XIV. Prostates a pair of thick short tortuous tubes restricted to XVIII or their ental ends just entering XIX; muscular ducts straight or slightly curved, not sinuous. Spermathecae in VIII and IX, each with a sacciform, narrow-stalked ampulla and a digitiform-clavate (inseminated) diverticulum joining the base of the duct and longer than the duct plus ampulla. The spermathecae are unpaired, discharging beneath the ventral nerve cord, or are paired, discharging median to a lines; the ampulla may be doubled.

*Megascolides*(part., Type-species only); Beddard, 1895: 487-488; Spencer, 1888: 3-60, Pl 1-6; Michaelsen, 1907b: 161; Jamieson, 1971c: 76-77; Blakemore and Kingston, 1997: 1685.

**DIAGNOSIS**
Setae 8 per segment. Combined male and prostatic porophores a pair on XVIII. A single gizzard, in V. Meronephric, with numerous exonephric stomate nephridia median to which caudally are exonephric astomate micromeronephridia; caudal micro- and mega-meronephridia connected to a longitudinal ureter on each side of the ventral nerve cord; the ureter also opening to the exterior in each segment. Prostates truly tubular, much coiled. Spermathecal diverticula small, multiloculate, consisting of several longitudinal chambers which are multiloculate. Spermatozoa stored in the spermathecal ampulla in addition to the diverticula.

**DESCRIPTION**
As for the single species.

**DISTRIBUTION**
Eastern Subregion, Kosciuskan Division: Victoria.

**TYPE-SPECIES:** *Megascolides australis* McCoy, 1878
REMARKS

*Megascolides* is here limited to the type-species. Its closest relationship appears to be with *Austrohoplochaetella* from which it differs notably in the much coiled tubular prostates, as opposed to tubuloracemose to racemose prostates, and, it appears (see van Praagh, 1995), in storing spermatozoa not in the spermathecal diverticula but in the ampulla.

**Megascolides australis** McCoy, 1878
(Fig. 22.1-22.4)

*Megascolides australis* McCoy, 1878: 21, Fig. a-d, Pl. 7.
*Megascolides australis*; Fletcher, 1886a: 573; Spencer, 1888: 1-60, Pl. 1, fig. 1-4, Pl. 2, fig. 5-9, Pl. 3, fig. 10-17, Pl. 4, fig. 18-20, Pl. 5, fig. 21-25, Pl. 6, fig. 26-30; Beddard, 1895: 495-496; Sweet, 1900: 112; Bage, 1910: 231-233, Pl. 45, figs 12, 13; Pl. 46, 14, 15; Barrett, 1938: 66-70, 5 figs; Van Praagh *et al*., 1989: 197-201; Van Praagh, 1995: 489-507.

*Notoscolex gippslandicus*; Fletcher, 1887b: 603-607.
*Lumbricus australis*; Vaillant, 1889: 163.

**TYPE LOCALITY:** Gippsland - Vic.
**SYNTYPES:** Lodgement unknown.
**OTHER RECORDS:** (Spencer, 1888) 38°10'S.145°56'E., Warragul. 38°06'S.145°55'E., (Barrett, 1938) Brandy Creek. (Van Praagh, 1995) 38°S.21°S.145°44E., Loch. (Fletcher, 1887b) 38°10'S.145°56'E., Warragul AM W1253-1262 - Vic.

Length in life 1400-1800 mm, mean 1100-1200 mm. Width 6.25 mm. Segments 300-500 (Spencer). Colour dirty pinkish flesh colour, with dark purple clitellum; body wall not transparent. Prostomium?. First dorsal pore about 14/15? Setae 8 per segment in regular longitudinal rows; minute relative to the size of the worm, and difficult to see, especially in the forebody, although the protuberance around each seta may be clearly visible; cd > ab; setae a and b absent in XVIII. Clitellum XIII-XXI. Male pores on 2 slight papillae within the second genital marking, at the sites of the absent setae ab. Genital markings, 3 or 4 pale transverse midventral bands, extending into ab, in 17/18, 18/19, 19/20, and sometimes 20/21. Female pores immediately anterior to and slightly ventral of setae a of XIV. Spermathecal pores 2 pairs, very slightly in front of 7/8 and 8/9, approximately in ab.; each pair surrounded by a slight superficial line-marking.

Septa forming deep cups in the first 14 segments, becoming gradually thinner in XIV-XIX, after which they are membranous. Dorsal vessel single, continuous onto the pharynx. Hearts in VI-XIII. Gizzard in V. Calciferous glands absent but oesophagus with vascular dilatations in XII-XVIII. Intestine apparently commencing in XIX; typhlosole absent. Nephridia: buccopharyngeal ("peptonephridia") in I-IV; thereafter numerous astomate, exonephric micromeronephridia the ducts of which are interconnected to form a network which is continuous ventrally. In approximately the posterior half of the body, on each side, exonephric micromeronephridia are
Megascolides australis

Redrawn (modified) from Spencer, 1888.
(Cilitellum added from account)

Fig. 22.1. *Megascolides australis*. Genital field. Redrawn (and modified) from Spencer (1888).
Fig. 22.2. Previous page. *Megascolides australis*. A mature worm, dissected from the dorsal surface. The seminal vesicles are depicted on the posterior septa of XI, XII, XIII and XIV (XII, XIII and XIV in the legend) but are said by van Praagh (1995) to lie on the anterior septa of XI-XIV, itself an unusual disposition for the Megascolecidae. The fullest development known in Australian megascolecines of the tubular type of prostate is seen. After Spencer (1888).
accompanied (through as many as 220 segments in worms with 500 segments) by a ventral, preseptally stomate exonephric megameronephridium, the micromeronephridia interconnected with each other and across the middorsum (but not midventrally); they and the megameronephridia connecting in each segment to a longitudinal duct (ureter) on each side of the ventral nerve cord; the ureter also opening to the exterior in each segment (see details in Spencer, 1888; Bage, 1910). Testes in X and XI with occasionally an extra pair in XII; seminal funnels in X and XI; (Spencer, 1888; Van Praagh, 1995). Seminal vesicles racemose, on the anterior (correction of Spencer) walls of XI-XIV; all may show spermatogenic stages and it is suggested (Spencer, 1888) that these reach the vesicles of XIII and XIV via the septal foramen surrounding the ventral nerve cord. The two vasa deferentia on each side running completely separately of each other throughout their lengths, one above the other, beneath the body wall peritoneum, and joining the straight ectal portion of the prostate duct. Prostates a pair in XVIII; each a large mass consisting of a much coiled slenderly tubular gland and an ectal duct of which the ental portion is also said to be coiled and surrounded by a great development of circular and longitudinal muscle fibres, while the ectal part, receiving the vasa deferentia, is straight. The gland consisting of an inner and outer layer; the inner layer a single layer of cells, forming a columnar epithelium, with no apparent nuclei; the outer layer more than twice as thick as the inner layer with many cells, each cell in the form of a unicellular gland and reaching to various heights so that the gland appears multilayered; some connective tissue and blood vessels may be present between the two layers. Penial setae absent. Ovaries and funnels in XIII. Spermathecae 2 pairs, in VIII and IX; each with an ampulla varying in form from a sac with a pointed ectal extremity and a swollen ectal
Fig. 22.3. Previous page. *Megascolides australis*. A semidiagrammatic longitudinal section of the anterior part of the body. There is supposedly a third pair of testes, in XII. After Spencer (1888).