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## THE INDIGENOUS EARTHWORMS (MEGASCOLECIDAE: OLIGOCHAETA) OF LORD HOWE ISLAND

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#### SUMMARY

The known indigenous earthworms of Lord Howe Island are restricted to the subfamily Megascolecinae. They are assignable to six genera with ten species, Diporochaeta plutelloides sp. n., Plutellus hutchingsae sp. n., Paraplutellus insularis Jamieson, and Pericryptodrilus nanus gen. et sp. n. (Tribe Perionychini), Eastoniella gen. n. with E. howeana and E. modesta spp. n. (Tribe Dichogastrini) and Spenceriella (Austroscolex) subgen. n., with S. (A.) howeana, S. (A.) difficilis, S. (A.) hollowayi and S. (A.) saundersi spp. n., (Tribe Megascolecini). In addition to these 10 endemic species, the circummundane Amynthas diffringens Baird and the anthropochorous holarctic family Lumbricidae are recorded from the island. Diporochaeta and Spenceriella (Austroscolex) are otherwise restricted to Australia and (secondarily?) New Zealand, and Plutellus to Australia. Pericryptodrilus and Eastoniella are known only from the island but have strong Australian affinities. The earthworm fauna thus appears to be of Australian origin. Evidence for rifting of the Lord Howe Rise from Eastern Australia at ~80 million years before the present is noted but it is considered unlikely that the earthworm fauna dates from that period in view of catastrophic vulcanism on the island between  $\sim$  30 and 8 million years before the present. The zoogeography and evolution of the earthworms is discussed and a tentative hypothesis of origin of the predominantly Oriental genus Pheretima s. lat. from an Australian precursor of Spenceriella is advanced.

### INTRODUCTION

Lord Howe Island, 700 km NE of Sydney, Australia, at It. 31°31′S, long. 158°04′E, is one of several volcanic peaks on Lord Howe Rise, the others, with the exception of Ball's Pyramid 20 km away, being submerged. The Rise which joins the Coral Sea Platform in the north and the Campbell Plateau in the south on which New Zealand is situated, forms an easterly and northeasterly boundary of the Tasman Sea. The bed of the Tasman Sea is bisected by an extinct tectonic ridge (mid-ocean ridge), trending approximately north-west to south-east, the morphology of which is consistent with its having been the axis of origin of sea-floor spreading. Hayes and Ringis (1973) have brought the two oldest corresponding magnetic anomalies together (80 million years before the present), the one closest to the continental edge of east Australia, the other closest to the Lord Howe Rise, and state that because of the well developed magnetic pattern there is "not much uncertainty" as to the pre-rifted configuration of the two continental elements. Their reconstruction, bringing the Lord Howe Rise into contact with eastern Australia at 80 million years before the present, is of the greatest interest for zoogeography as it establishes that the primary faunistic affinities of the Lord Howe Island area must have lain with eastern Australia, of which it was a part. At that

Records of The Australian Museum, 1977, 30, 272-308, Figures 1-7.

time New Zealand, with which the island shows considerable biogeographic affinities, was, according to the reconstruction, very much closer to Australia (and Antarctica which this abutted) than at present. Nevertheless New Zealand seems to have had no direct land connection with Australia and the pre-rifted Lord Howe Island area.

To suggest that the Lord Howe Rise, and the island itself, originated by rifting from Australia in the Cretaceous and probably possessed an Australian flora and fauna is not, however, to suggest that Australian elements in the present fauna of the island necessarily represent a survival of that fauna. Even if the island has had a continuous history as an exposed land mass, above sea level, it is questionable that its fauna could have survived the formation of the oldest volcanics 30 m.y.B.P. or the catastrophic and very extensive late Miocene volcanics at about 8 m.y.B.P. (Standard, 1961; Game, 1969) which latter produced Mts Gower and Lidgbird and peripheral areas, since lost by erosion, of a much larger island. It is not unlikely that the contemporary fauna of the island is of post-Miocene origin and that the Australian elements of its terrestrial invertebrate fauna were therefore acquired from Australia when the island was only about one tenth nearer Australia than it is at present.

It is the aim of the present paper to describe the indigenous earthworm fauna of the island and to attempt to establish the taxonomic and zoogeographic affinities of this fauna.

Explanations of descriptive terminology are given in Michaelsen (1900), Stephenson (1930) and Jamieson (1974). In the lists of material examined "W" refers to the registration number of specimens in the Australian Museum, and "BJ" indicates that specimens are lodged in the author's collections. Unless otherwise stated, collections were made by Dr. P. Hutchings from 15-21 April 1971. Italicised numerals denote the collecting sites (see map, Fig. 1). Abbreviations for specimens are H (holotype) and P (paratype). Abbreviations used in illustrations are indicated under Fig. 2.

#### **SYSTEMATICS**

Eleven species assignable to the indigenous family Megascolecidae are present in the Lord Howe Island collections. They are described in alphabetical order under their genera which, in turn, are grouped according to the tribes to which they belong. Some members of the holarctic earthworm family Lumbricidae are also present but are beyond the scope of this work. A key to the eleven Megascolecidae follows. For correct identification, in view of the possibility of new species coming to light, agreement with illustrations and text should be checked.

### KEY TO THE MEGASCOLECID OLIGOCHAETES OF LORD HOWE ISLAND

1.		Setae 8 per segment	2
2.	<u>(1)</u>	Nephridia 2 per segment	} 5
3.		Nephropores on each side with definite alternation Nephridial bladders present	<b>1</b>
4.		Calciferous glands 1 sessile pair in segment XIII Gizzard absent	

5.	(2)	Gizzard in segment VIII Eastoniella howeana, Fig. 3B p. 281 Gizzard in segment IX Eastoniella modesta, Fig. 3C, D, p. 282
6.	(1)	Nephropores externally visible as 3 straight rows on each side, in line with the second, tenth and penultimate dorsal seta; the intermediate row more strongly developed than the others
		Nephropores very numerous but not externally recognizable
7.	(6)	Spermathecal pores 2 pairs, in 7/8 and 8/9. Gizzard rudimentary, in V. Intestinal caeca absent. Testis-sacs absent
		Spermathecal pores 4 pairs, in 5/6-8/9. Gizzard large, in segment VIII.  Intestinal caeca in segment XXVII. Testis-sacs present. (Holandric)
8.	(7)	In segment XII, setae more than 40; interval between dorsal setae (zz) less than 10% of body circumference. Interval between last spermathecal pores 0.1-0.2 of circumference
		of circumference
9.	(8)	In segment XII, setae more than 50; interval between ventral setae (aa) 3-4% of circumference. Accessory genital markings, when present, including paired post-spermathecal discs lateral of setal lines 6
		In segment XII, setae less than 45; interval between ventral setae (aa) 6% of circumference. Accessory genital markings including paired post spermathecal pads with porelike centres in setal lines 2-3
10.	(8)	In segment XII, setae 20 or less; interval between ventral setae (aa) 6-10% of circumference. Accessory genital markings, when present, including paired post-spermathecal discs in setal lines 2-5
		In segment XII, setae more than 20; interval between ventral setae (aa) 12-13% of circumference. Accessory genital markings unknown

Subfamily MEGASCOLECINAE Michaelsen, 1900 sensu Jamieson, 1971a TRIBE PERIONYCHINI Jamieson, 1971a Genus **Diporochaeta** Beddard, 1890, sensu Jamieson, 1975 **Diporochaeta plutelloides** sp. n. Fig. 1, 2A, 6C, 7A. Table 1.

 $1 = 110 \,\mathrm{mm}$ ; w (mid-clitellar) =  $3.2 \,\mathrm{mm}$ ; s = 188. Form dorso-ventrally depressed; clitellum lighter brown. Prostomium epilobous 1/2, open. Canalicula absent. First dorsal pore 4/5. Setae 8 per segment, commencing in II, in longitudinal rows all of which become slightly irregular posteriorly; setae a absent, b to d present, in XVIII.

Nephropores inconspicuous in c lines. Clitellum annular, weakly developed in XIII-XVII; dorsal pores and intersegmental furrows fainter than elsewhere; setae clearly visible. Male pores on XVIII, 0.88 mm, 0.11 body circumference, apart; each a transversely extensive slit centred in a, each pore surrounded by a transversely elliptical glandular genital marking

(porophore) which forms a depression but has a raised lateral margin, the two markings filling XVIII longitudinally and extending transversely from b lines to the ventral midline, where they merge; a small midventral elliptical accessory genital marking in 17/18 filling the space between the porophores and the anterior margin of XVIII; this accessory marking traversed by the intersegmental furrow. Female pores inconspicuous, one third of the distance between the setal arc and the anterior border of XIV in a lines. Spermathecal pores 3 pairs of small eyelike orifices, near but not at the posterior borders of VI, VII and VIII, their median borders in a lines; last pores 0.92 mm, 0.13 body circumference, apart.

No septa strongly thickened but 7/8, 8/9 and 9/10 moderately thickened, Dorsal blood vessel single, but bifurcating in III under the brain. Supra-oesophageal in IX-XIV, adherent to the roof of the oesophagus, from the vascular plexus of which it here receives vessels, but almost as wide as the dorsal blood vessel. Last hearts in XIII; those in X-XIII larger than the other commissurals and receiving each a wide connective from the dorsal and the supraoesophageal vessel (latero-oesophageal hearts); commissurals in VI-IX still considerable but dorsoventral only and decreasing in size anteriorly. Gizzard absent; pharyngeal glands forming a unified large mass concealing the gut as far posteriorly as VI; oesophagus moniliform and widened, with circumferential blood vessels forming a plexus, in IX-XIV and less so in the anterior half of XV; poorly vascularized and narrow in the posterior half of XV. The vascularized region with low internal blood filled rounded villi but calciferous glands absent. Intestinal origin XVI; muscular thickening, caeca and typhlosole absent. Holonephric with transition to meronephry; nephridia not demonstrable in II; small in III; increasing in size and number of separate tubules and forming sessile tufts to X; small and less complex in XI and XII; but again large and complex in XIII-XVII and only slightly smaller, but still forming tufts far into the intestinal region; a very large presental funnel demonstrated on each side from segment IX to the caudal extremity but possibly present more anteriorly; ducts only sporadically traceable; some in the caudal segments demonstrated entering the parietes in clines; the tufts in V appearing to send a (composite?) duct to the pharynx; bladders absent. Tufting in oesophageal and clitellar segments appears to have advanced to meronephry though the single presental funnel on each side of the gut is well developed. Holandric; compacted sperm masses and very large complexly convoluted iridescent sperm funnels in X and XI: testis-sacs absent; large compact racemose seminal vesicles in IX and XII. Prostates tubuloracemose, a pair of wide tubes in XVIII-XXII cross section elliptical, slightly variable in width; the exterior frequently though not deeply incised and not significantly lobulated; hooked entally and convoluted in XVIII but otherwise straight; the sinuous muscular duct in XVIII widening ectally and ensheathed in a thin layer of peritoneal connective tissue; vas deferens joining the gland shortly before this joins its duct. The prostates supplied by a large pair of parietal trunks passing posteriorly from beneath the oesophagus in XIII. Penial setae absent. Metagynous; ovaries very large palmate structures with many strings of large oocytes, and large pleated funnels in XIII; ovisacs absent. Spermathecae 3 pairs, in VII, VIII and IX, each with an ovoid ampulla and a short narrow duct which is joined medially, shortly ental of midlength, by a subspherical to stoutly clavate inseminated diverticulum; size uniform; length of right spermatheca of IX 1.1 mm; ratio of length spermatheca: length duct = 3.4; ratio of length: length diverticulum = 3.7.

MATERIAL EXAMINED: 6, 31°35′03½″S. 159°04′56″E. Mt. Gower ridge, close to stream; leaf litter in places, elsewhere dense moss covering trees; — Holotype (W6566).

REMARKS: The male genital field (with its combination of large, low almost contiguous porophores and median accessory marking at 17/18), the absence of a gizzard and the unusually extensive tufting of nephridia distinguish *D. plutelloides* from all other species of this genus.

Genus **Plutellus** Perrier, 1873 **Plutellus hutchingsae** sp. n. Fig. 1, 2B, 6H, 7E-I. Table 1

1=36 mm (H), 50 mm (Pl), w (midclitellar) = 2.3 mm, (post-clitellar = 3.1 mm), s = 127 (H), 137 (Pl). Form moderately stout, ventrally flattened in bb, lacking appreciable secondary annulation. Pigmentless buff in alcohol. Prostomium broad, epilobus, 1/2 (H, P2) to 5/6 (Pl), laterally demarcated by deep grooves, posteriorly by a faint groove (H) or open (P1, 2). First dorsal pore 4/5 (H, P1-3). Setae in 8 regular longitudinal rows, commencing on II; ab absent, bc present, in XVIII.

Nephropores conspicuous to poorly visible; anterior in their segments in more than one series on each side in the holotype in d lines in II; in c lines in III-V; in d in VI; in b in VII and thereafter alternating regularly from d to b. Paratype 1 shows precisely the same arrangement on the left side but on the right side alternation from b to d starts in V.

Clitellum developed in holotype only, annular, strongly tumid but narrow relative to adjacent segments, embracing XIV-XVII; dorsal pores and intersegmental furrows totally obliterated; setae and intersegmental furrows fainter than elsewhere. Male genital field; male pores equatorial on XVIII in ab slightly (H) or very much (P1-3) nearer a than b, minute points in oval depressed dark glandular areas each of which extends from approximately a to shortly lateral of mid ab; the pores 1.02, 0.58, 1.16 mm, 0.12, 0.08, 0.10 body circumference, apart (H, P1, P5). Accessory genital markings depressed oval glandular areas with porelike centres presetal, or extending slightly postsetally, a pair in each of XX and XXI with centre slightly median of mid ab; a pair of presetal glandular markings median to a lines and almost contiguous in the midline, in XIX; a pair of low oval prominences almost filling XI longitudinally, reaching b laterally and extending slightly median of a (H). The accessory genital markings of the paratype conform with those of the holotype with the exception that paratype 1 has a pair of markings in XII, in addition to those in XI, and in XIX apparently has a median unpaired rather than paired marking; and paratype 2 has an additional presetal marking in ab unilaterally, on the left, in XXII. Female pores a pair in XIV, midway between the setal arc and the anterior margin and very slightly median of, almost in, a lines (H, P1-3). Spermathecal pores inconscipuous, 5 pairs at the anterior margins of V-IX, in a lines; the last pair 0.66, 0.46, 1.12 mm, 0.10, 0.08, 0.10 body circumference apart (H, P1, P5).

Internal anatomy (Holotype; gross anatomy confirmed from paratype 1): Septa 5/6 and 6/7 slightly thickened; 7/8 and 8/9 moderately thickened; 9/10-12/13 strongly; 13/14 moderately; 14/15 very slightly thickened, the remainder thin. Last septal glands in IV. Dorsal blood vessel single; continuous onto the pharynx, closely adherent to the intestine; free on the oesophagus. Dorsoventral commissural vessels in VI-XIII, all valvular; those in X-XIII forming 4 pairs of moderately large latero-oesophageal hearts, each of which arises from and lies behind the corresponding calciferous vessel and also receives a connective from the dorsal blood vessel. The two large calciferous vessels of a segment branch at the oesophageal end of the long duct of the calciferous gland to give about 10 vessels running longitudinally in the wall of the duct and further dividing in the lamellae of the gland. Medianly the two calciferous veins are continuous across the roof of the oesophagus and a midventral supraoesophageal vessel joins the points of fusion, in XI-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 but are not visible further posteriorly. Subneural vessel absent.

Oesophagus thin-walled in IV; in V forming a short cylindrical, firmly muscular gizzard; thin-walled whitish and intersegmentally constricted in VI-XIV but in each of X-XIII bearing a pair of long-stalked, reniform calciferous glands, the stalks of which join the oesophagus

laterally. Intestine commencing, with abrupt expansion, at the anterior septum of XV; muscular thickening, caeca and typhlosole absent. Nephridia stomate, vesiculate exonephric holonephridia throughout, commencing in II. Each bladder anteriorly, e.g. in VI, a narrow and elongate expansion of the ectal nephridial duct; in the anterior intestinal region expanded over the pore but attenuated to one side where the ectal nephridial duct enters; in the caudal segments similar but less drawn out at the entrance of the duct; diverticula absent although the side of the bladder opposite the duct (intestinally and caudally) is suggestive of a rudimentary diverticulum.

(Testes?), and firm flocculent sperm masses attached to iridescent sperm funnels in X and XI; racemose seminal vesicles in IX and XII, the posterior pair the larger but only moderate-sized; vasa deferentia on each side double but in a common sheath, wide and conspicuously visible winding posteriorly, free in the coelom on the ventral body wall; the prostate duct having the appearance of an ectal expansion of the vasa deferentia, i.e. an atrium; the thickly tubular prostate gland, which is restricted to XVIII, joining the atrium by a slender, short duct. Penial setae absent. Ovaries, a few separate chains of oocytes, (H) and funnels in XIII; ovisacs absent (H, P1).

Spermathecae 5 pairs, discharging anteriorly in their segments, each with an ovoid ampulla and a long duct consisting of a wide portion ental to the elongate clavate diverticulum and a very short, narrow portion ectal to the diverticulum (H, P1). Size uniform; length of the right spermatheca of IX (H) = 0.65 mm; ratio of total length: length diverticulum = 1.6.

MATERIAL EXAMINED: 17, 31°34′52″S. 159°05′07″E. At the foot of the cliff at Mt. Gower. Dracophyllum fitzgeraldii — in leaf litter; — Holotype (W6567), 8, 31°35′05″S, 159°4′52″E. Mt. Gower ridge, in thick moss covering the ground; — paratype 6 (W6568); 20, 31°34′34″S, 159°05′03″E. Stream crossing in Erskine Valley; grass, Howea belmoreana, Cleistocalyx fullageri, Pandanus forsteri, Drypetes australasica; — P1-P3 (W6569), P4 (BJ), 2 (W6570). Camp site, Mt. Gower; — P5 (BJ); Lord Howe Island (no further data); collector Saunders — 3 (W1509).

REMARKS: Plutellus hutchingsae has very close affinities with the two other species of Plutellus s. strict. Jamieson, 1971b, viz. P. heteroporus Perrier (which is presumably Australian although stated by Perrier to be Pennsylvanian) and P. manifestus (Fletcher), from New South Wales. The restricted genus therefore remains very homogeneous. The three species nevertheless show clear specific differences. Some features which distinguish P. hutchingsae from the other two species are the disposition of the accessory genital markings; location of the spermathecal pores in a lines; and occurrence of the last hearts in segment XIII.

### Genus Paraplutellus Jamieson, 1972a Paraplutellus insularis Jamieson, 1972a

Paraplutellus insularis Jamieson, 1972a: 85-86, Fig. 1A-C, Table 4

TAXONOMIC NOTE: This species was previously known only from two specimens. The present series of forty-five identifiable specimens shows the species to be the commonest and most widely distributed earthworm in natural habitats on Lord Howe Island. Great variation in size is exhibited and the distribution of markings is variable but there is no evident correlation between the arrangement of markings and size-classes. There thus seems no reason to doubt that all specimens in the series are conspecific. The distribution of genital markings in the holotype remains the most extensive known for the species though an extra pair of markings, in intersegment 19/20 in ab, not seen in the types, occurs in three specimens. The distribution of genital markings in eighteen clitellate specimens compared

with the distribution in the holotype follows. The number of specimens, of these eighteen, with a given location of genital markings is given in parentheses following the location recorded for the holotype. All markings are paired, though occasionally only developed unilaterally. In VI, lateral of b (none); VII, lateral of b (4; in c to d); VIII (3; in bc to d); IX, presetal in ab (none); X and XI, presetal in ab (2); anterior margin of XVIII (17); anterior margin of XIX (18); intersegment 19/20, in ab (3; these markings absent from the types). Thus the most characteristic markings are those anteriorly in XIX which appear to be invariably present in sexual specimens. Those in XVIII, in front of the male porophores, though usually present, are often very indistinct.

MATERIAL EXAMINED: 2. 31°30′56"S. 159°02′55"E. Dense mixed forest: Howea forsterana dominant; leaf litter 1"-11/2" thick, sandy dark soil; — 3 (W6571); 5, 31°34'26"S, 159°04'39"E. Erskine Valley. Pandanus forsteri, Drypetes australasica, Howea sp., Cleistocalvx fullageri. Linociera quadristaminae. Moist dark soil under deep leaf litter — 1 (W6572); 6, 31°35'03½''S, 159°04'56"E. Mt. Gower ridge, close to stream; leaf litter in places, elsewhere dense moss covering trees; —4 (6573); 7, 31° 35′04″S, 159° 04′55″E. Mt. Gower ridge, in a layer of soil beneath moss on a tree trunk: — 1 (W6574): 8. 31°35′05″S. 159°04′52″E. Mt. Gower ridge, in thick moss covering the ground; — 1 (6575); 9, 31°35′06″S, 159°04′49″E. Mt. Gower ridge, under dense vegetation in ground with sparse leaf litter; — 1 (W6576); 10, 31°35'07"S, 159°04'48"E. Mt. Gower ridge, in leaf litter; — 4 (W6577); 12, 31°35'09"S, 159°04′46″E. Mt. Gower ridge, in dense moss on the ground and in fallen logs; — 3 (BJ); 13, 31°35′01″S, 159°04′49″E. At the foot of small stream running at right angles to Mt. Gower ridge, in the moss on the stones near the stream; other vegetation Dracophyllum fitzgeraldii; Passiflora edulis; tree ferns; — 5 (W6578); 15, 31°35′03″S, 159°04′53″E. Up stream running at right angles to Mt. Gower ridge, very dense vegetation, in aerial roots and in the base of fronds of the palm, Hedyscepe canterburyana; — 2 (6579); 15, 31°35′03″S, 159°04′53″E. Up stream running at right angles to Mt. Gower ridge, very dense vegetation, in aerial roots; — 1 (W6580); 19, 31°34′37″S, 159°05′06″E. Going down into Erskine Valley from Mt. Gower; Pandanus forsteri, Dracophyllum fitzgeraldii, mountain palms. Coprosma putida, in soil under leaf litter; — 2 (W6581); 28, 31°31′51″S, 159°04′40″E. Up towards Transit Hill. Woodland on coral sand; Drypetes australasica, Cryptocarya triplinervis, Ficus columnaris, Howea forsterana, H. belmoreana; — 1 (W6582); 30, 31°31′55″S, 159°04′52″E. Woodland lacking coral sand, Drypetes australasica, Cryptocarya triplinervis, Ficus columnaris, Howea forsterana, H. belmoreana, Cleistocalyx fullageri, Linociera quadristaminea, in leaf litter and soil; — 3 (W6583); 30, 31°31′55″Ś, 159°04′52″E. Woodland lacking coral sand, Drypetes australasica, Cryptocarya triplinervis, Ficus columnaris, Howea forsterana, H. belmoreana, Cleistocalyx fullageri, Linociera quadristaminea, in the base of palms, worms less abundant in this habitat than on Mt. Gower; — 3 (BJ); 35, 31°32′54″S, 159°05'44"E. Going up North Hummock, few palms, Howea forsterana and H. belmoreana. Xylosma ovatum, Elaeodendron curtipendulum; — 1 (W6584); 38, 31°33'27"S, 159°05'23"E, Up Smoking Tree Ridge. Open woodland with Howea forsterana; in leaf litter and in soil; — 4 (W6585); 39, 31°33′50″S, 159°05′39″E. At the top of Goat House, just around the ledge, Dracophyllum fitzgeraldii, Cassinia tenuifolia Tree-fern, Pimelea congesta, Olearia ballii, Metrosideros nervulosa; from pockets of soil or leaf litter between large boulders; a thin covering of moss on ground; — 4 (W6586); (no data). 8-9, 1966 — 10 (W6587); Lord Howe Island (no further data) — 4 (W4567).

### Pericryptodrilus n. gen.

DIAGNOSIS: (Perichaetine). Combined male and prostatic pores a pair on XVIII. Spermathecal pores pretesticular (and intersegmental). Gizzard (rudimentary) in V. Calciferous glands absent. Intestine lacking typhlosole, muscular thickening and caeca absent. Meronephric; pharyngeal or other enteronephric nephridia and tufted nephridia

absent; nephridia each with a bladder, in 3 longitudinal rows on each side; those of the intermediate series with preseptal funnels. (Holandric; metagynous). Prostates tubular. (Spermathecae diverticulate).

DISTRIBUTION: Lord Howe Island.

TYPE-SPECIES: Pericryptodrilus nanus sp. n. (Monotypic genus).

REMARKS: Pericryptodrilus agrees with Cryptodrilus Fletcher (1887) in having meronephridia with bladders, a condition unrecorded in other genera of the Megascolecidae in Australia but described by Gates (1943) for Pleionogaster Michaelsen (1892), a genus from the Philippines and Moluccas. It differs from Cryptodrilus in being perichaetine, a condition now known to be of little significance, and notably in that whereas in Cryptodrilus the medianmost nephridium, only, may have a preseptal funnel, it is the intermediate nephridium which is stomate in Pericryptodrilus.

### Pericryptodrilus nanus n. sp. Fig. 1, 3A, 6A, 7J, K. Table 2

1 = 25 mm (P2) - 32 mm (H) (P1, posterior amputee); w (mid-clitellar) = 1.0 (P2), 1.2, (H), 1.5 mm (P1); s = 111 (H) - 123 (P2). Form slightly depressed dorsoventrally; secondary annulation absent but setae on circumferential annuli. Prostomium broadly epilobous >1/3 < 1/2. First dorsal pore 6/7 (H, P2) or 10/11 (P1). Setae commencing on II; numbers per segment 34, 30 on XII; 34, 31 on XX; 43, 32 fifteen segments from the posterior end (H, P2 respectively) as a clearly recognizable interruption in the setal circle; setae a and b absent in XVIII; no setae notably enlarged.

Nephropores 3 straight series on each side, in line with the penultimate setae (y), in approximately the tenth setal row and in line with the second setae (b), at the anterior margins of their segments, the dorsal and ventral series discernible only with difficulty and not certainly continuous to the anterior end; the intermediate series (in s.1.10) conspicuous from intersegmental furrow 1/2 posteriorly. Clitellum annular, slightly protuberant, embracing 1/2 XIII (P1, 2), XIV (H) — XVI (H, P1, 2); nephropores and setae retained; dorsal pores and intersegmental furrows obscured. Small slit-like combined male and prostatic pores a pair in XVIII approximately in b on prominent papillae which when well developed (Holotype) occupy about one third of the length of the segment, their lateral borders indistinct, in bc; a midventral depression present in the holotype, but not in the paratypes, between them; the pores 0.30, 0.58 mm, 0.08, 0.16 body circumference apart (H, P2). Accessory genital markings 2 midventral presetal circular glandular areas, with indistinct porelike centres, one in XX, the other in XXI (H). Female pore unpaired, midventral on XIV, midway between the setal arc and 13/14, surrounded by an oval glandular area; spermathecal pores 2 pairs, in 7/8 and 8/9, between the third and fourth setal rows (H, P1, 2), The last spermathecal pores 0.66, 0.72 mm, 0.24 body circumference apart (H, P2).

Septa: 5/6 — 7/8 slightly thickened; 8/9 — 10/11 moderately thickened (9/10 the strongest); the remainder thin (schizoparatype). Dorsal blood vessel single, continuous onto the pharynx. Latero-oesophageal hearts 3 pairs, in X-XII; no dorsoventral commissural vessels recognizable in IX anteriorly (H, P2). Supra-oesophageal vessel in VIII (P2), IX (H) — XII, weakly developed. Oesophagus not enlarged, but moniliform and of uniform width in IV-VII, the wall in V seen in the schizoparatype to possess considerable muscular thickening and warranting recognition of a rudimentary gizzard. Oesophagus narrow and tubular in VIII; intersegmentally constricted and somewhat vascularized in IX-XIV; strongly dilated in XIII (H) or XIII and XIV (P2), internally rugose; calciferous glands at least extramurally absent; oesophageal walls with well developed sinus in IX posteriorly; this wide sinus continuous in the intestinal walls to XVII; a narrower sinus present posteriorly

(schizoparatype); oesophagus narrower in XV; intestine commencing with abrupt expansion in XVI (H, P2), origin not certainly determinable in the schizoparatype; typhlosole, muscular thickening and caeca absent.

Nephridia: 3 subspherical slightly bilobed nephridial bladders present on each side per segment, those in the tenth setal lines, large and conspicuous; the upper in y lines small; those in b lines still smaller. The nephridia of the intermediate series each with a preseptal funnel near the nerve cord; no funnels demonstrable for the dorsal and ventral series, the nephridial tubules of which are short and discernible only with difficulty. Pharyngeal, or other enteronephric nephridia, and tufted nephridia absent (H, P2). Location of bladders confirmed in transverse sections of posterior half of P3.

Testes, large firm sperm masses and iridescent sperm funnels in X and XI; racemose seminal vesicles in IX and XII, the posterior the larger. Only the anterior sperm funnels iridescent in P2 and only the posterior funnels sperm-carrying in the schizoparatype. Small tongue-like ovaries, lacking evident oocytes and moderate-sized funnels in XIII (H, P2). Large multiloculate ovisacs in XIV (H, P2). Prostates thickly tubular, in XVIII and extending into XIX; ducts median, slender (H, P2); vas deferens joining each gland at its junction with the duct (H). Penial setae absent. Spermathecae discharging anteriorly in VIII and IX; each with a subspherical ampulla, conical, entally almost equally wide and a large clavate inseminated lateral diverticulum which joins the duct at midlength; the diverticulum (H) with or without a subsidiary less well developed or knoblike diverticulum of similar width at its base or (P2) all simple; size approximately uniform; length of left spermatheca of IX (H) = 0.40 mm; ratio total length spermatheca: length duct = 1.6; ratio total length: length diverticulum = 1.2.

MATERIAL EXAMINED: 6, 31°35′03½″S, 159°04′56″E. Mt. Gower ridge, close to stream; leaf litter in places, elsewhere dense moss covering trees; under leaf litter; — Holotype (W6588); 15, 31°35′03″S, 159°04′53″E. Up stream running at right angles to Mt. Gower ridge, very dense vegetation, in leaf litter; — Paratypes 4, 5 (W6589). Summit of Mt. Gower; collector J. Dysney, 1 Aug. 1971 — P1 (BJ), P2, 3 (W4561), 2 (6590 ex W4561); (no data), 8-9, 1966 — P6 (BJ).

REMARKS: *Pericryptodrilus nanus* is exceptionally small for a megascolecid oligochaete. The median accessory genital markings and three rows of nephropores readily distinguish it from the other oligochaetes of the island.

### Eastoniella n. gen.

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; the 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 n. sp.

OTHER SPECIES: E. modesta n. sp.

REMARKS: The presence in caudal segments of a stomate nephridium with preseptal funnel, median to astomate meronephridia places *Eastoniella* in the tribe Dichogastrini in which location of the gizzard in VIII or IX renders it unique. Elsewhere in the Megascolecidae the most posterior known location of the gizzard is VIII, in *Pheretima* and *Pleionogaster*, genera which show no close relationship to *Eastoniella*. The multilipped funnels of some of the stomate nephridia are a further peculiarity.

For a discussion of relationships of Eastoniella see p. 294

### **Eastoniella howeana** n. sp. Fig. 1, 3B, 6D, 7D, L. Table 1

1 = 80 mm, w (midclitellar) = 9 mm, s = 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 ½, 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. 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 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; typhlosole, 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, recemose, in XI only, dependent from the anterior septum. 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.

MATERIAL EXAMINED: 6, 31°35′03½″S, 159°04′56″E. Mt. Gower ridge, close to stream; leaf litter in places, elsewhere dense moss covering trees; under leaf litter; — Holotype (W6591).

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** n. sp. Fig. 1, 3C-E, 6G. Table 1

Length = 100, 90 mm, w (midclitellar) = 5, 10 mm, s = 144, 119 (H, P). Circular in cross section. Pigmentless in alcohol. Prostomium tanylobous (?), extending to the posterior border of the first annulation (H); broadly epilobous (P). Canalicula and dorsal pores absent. Setae 8 per segment, in regular longitudinal rows excepting posteriorly where d line is very slightly irregular (H, P). Seta a (H) or a and b (P) absent in XVIII. Nephropores not externally recognizable. Clitellum not discernible (H) imperfectly developed with limits not certainly discernible but clitellar modification apparently embracing XIII-XXI (P). 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 (H, P), 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 (H) or transverse segmental papilla (P) 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 (P) or into ab (H); in H, segment XVII slightly tumid from the pad to intersegmental furrow 16/17. Female pores distinct minute pits shortly anteromedian of setae a of XIV (H, P). 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 (H, P).

Septa 9/10-12/13 very strongly thickened; 10/11 and 11/12 the thickest (H, P). Dorsal blood vessel single, continuous onto the pharynx (H, P). 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 (H) but visible in XIII, though weakly developed and not certainly continuous in XI and XII (P). Dorsoventral commissurals in VI-XIII (P); those in X (H), XI (P)-XIII (H, P) each receiving a slender connective from the dorsal vessel and from the middorsal line of the oesophagus (H) or from the distinguishable supra-oesophageal vessel (P); the hearts large in XIII, moderate-sized in XII and slender in X and XI (H) or all unusually slender (P); slender commissurals in IX anteriorly dorsoventral only; subneural not demonstrable (H, P). Gizzard barrel-shaped, very large, and strongly muscular (H) or thinner walled and slenderly fusiform (P) in IX; its location in this segment clearly indicated by the intervention of a section of narrow oesophagus which is short (H) or half the length of the segment (P) 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 (H, P). 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 (H, P); 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 (H). Oesophagus behind the gizzard virtually supressed 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 (H, P). Nephridia as for G. howeana but multilipped funnels smaller in H though similar in size in P. Holandric; large sperm funnels, with spermatozoal iridescence, in X and XI; testis-sacs absent; multiloculate seminal vesicles paired in IX and XII (H, P) that in XII extending through septum 12/13 into XIII (H). Metagynous (from disposition of pores in XIV); ovaries, oviducal funnels and ovisacs not demonstrable (H) or funnels only seen (P). 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 (H, P); the ducts entering an internal glandular mass corresponding with the external genital marking in XVIII (P); slender vas deferens joining the duct shortly ental of the midlength of the latter (H). Penial setae absent (H, P). 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 (H, P).

MATERIAL EXAMINED: Lord Howe Island (no further data) — Holotype (W6592 ex W4567); lowlands — paratype, (W4564).

REMARKS: Location of the gizzard in segment IX in Eastoniella modesta appears to be the sole 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.

### Tribe Megascolecini Jamieson, 1971a Genus **Spenceriella** Michaelsen, 1907, emended definition

DIAGNOSIS: (Perichaetine). Combined male and prostatic pores a pair on XVIII. Spermathecal pores pretesticular (and intersegmental). (Accessory genital markings intrasegmental). Gizzard in V, (large or rudimentary). Calciferous glands 3 or 4 pairs dorsolateral in X, XI-XIII, or absent. Intestine lacking caeca. Meronephric; pharyngeal tufts present or absent; oesophageal nephridia astomate or stomate; caudal nephridia stomate (and astomate?); nephridia in regions in which they are stomate (always?) with multiple discrete intrasegmental, not preseptal, nephrostomal funnels per segment (excluding S. (S) tasmanica which has preseptal rudiments?) excepting the medianmost ventral nephridium which (always?, including tasmanica) has a preseptal funnel. Intestinal enteronephry present in at least some species. (Holandric; metagynous). Prostates racemose or tubuloracemose. (Spermathecae diverticulate).

DISTRIBUTION: Australia: Victoria, South Australia, New South Wales, Queensland, Tasmania; Lord Howe Island; Norfolk Island, New Zealand.

TYPE-SPECIES: Diporochaeta notabilis Spencer, 1900.

OTHER SPECIES: See Jamieson (1974b) and S. (Austroscolex), below.

Subgenus Spenceriella Michaelsen, 1907 sensu Jamieson, 1974b

DIAGNOSIS: Gizzard large. Three or four pairs of dorsolateral calciferous glands, in X, XI-XIII. Pharyngeal meronephric tufts present. Multiple intrasegmental nephrostomes (always?) present but caudal only (?).

### Subgenus Austroscolex n. subgen.

DIAGNOSIS: Gizzard rudimentary. Extramural calciferous glands absent. Pharyngeal meronephric tufts absent; multiple intrasegmental nephrostomes in intestinal and (always?) oesophageal segments.

DESCRIPTION: Terrestrial. Body circular or depressed in cross section. Prostomium epilobous to tanylobous; peristomium sometimes bisected by a longitudinal furrow ventrally. First dorsal pore 4/5-6/7. Setae numerous in each segment, absent between the male pores. A pair of combined male and prostatic pores on XVIII. Clitellum annular, embracing 3 or more segments, always including XIV-XVI, maximally XIII-XVII; its dorsal pores and intersegmental furrows obscured at maturity but at least some setae visible. Segmental accessory genital markings present. Female pores inconspicuous, paired anteromedian of setae a or unpaired midventral, in XIV. Spermathecal pores 2 pairs, in intersegmental furrows 7/8 and 8/9.

Dorsal blood vessel single, continuous onto the pharynx. Last hearts in XII, those in X posteriorly latero-oesophageal, each arising from the short (postgizzard) supraoesophageal vessel and from the dorsal vessel. Subneural vessel absent. Gizzard rudimentary in V. Oesophagus with internal almost lamellar villi but lacking extramural calciferous glands. Intestine commencing in XVI; typhlosole, caeca and muscular thickening absent. Excretory system meronephric. Pharyngeal tufts absent; micromeronephridia numerous, in transverse parietal bands commencing in II; several to many nephrostomes present on each side in each segment in the intestinal region and (always?) the oesophageal regions, the funnel in the same segment as the body of the nephridium; caudally (always?) with, in addition, a preseptal funnel on the ventralmost median nephridium. Intestinal enteronephry present (?). Testes and funnels in X and XI; testis-sacs absent; seminal vesicles in IX and XII.

Ovaries and funnels in XIII; ovisacs usually present. Prostates racemose; (sometimes tubuloracemose?); vasa deferentia joining the glands near their muscular ducts. Spermathecae each with a clavate, uniloculate diverticulum.

DISTRIBUTION: Australia: Queensland; New South Wales; Lord Howe Island; Norfolk Island, New Zealand.

TYPE-SPECIES: Austroscolex howeana n. sp.

#### CHECKLIST OF SPECIES

- 1. Austroscolex difficilis n. sp. (Lord Howe Island)
- 2. Austroscolex hollowayi n. sp. (Lord Howe Island)
- 3. Austroscolex howeanus n. sp. (Lord Howe Island)
- 4. Perichaeta newcombei Beddard, 1887 (Queensland, New South Wales, New Zealand) (syn. Megascolex laingii Benham, 1903).
- 5. Austroscolex saundersi n. sp. (Lord Howe Island).

REMARKS: The genus Spenceriella Michaelsen, 1907a, has recently been redefined (Jamieson, 1974b) to include two new South Australian species; seven species from Victoria previously placed in other genera, in addition to the type-species; a Tasmanian species, and five species incertae sedis from Victoria and New Zealand. This entire group of species (with the possible exception of the species incertae sedis) now becomes the subgenus Spenceriella with no emendment of the description. The nephridial arrangement given in the diagnosis of S. (Spenceriella) above (caudal nephridia with postseptal nephrostomes but medianmost ventral nephridium with large presental funnel) is confirmed in the present study for paratypes of the South Australian species S. imparicystis and S. penolaensis but was not demonstrable in S. (S). tasmanica though this has stomate medianmost nephridia. (Jamieson, 1974a). In all three species intestinal enteronephry with longitudinal supraintestinal ducts has been demonstrated. The nephridia of the type-species are little known and those of the remaining species remain to be investigated. In the closely examined S. (S), imparicystis and S. (S), penolaensis nephrostomes are absent from the nephridia of the anterior intestinal and oesophageal regions, or at least are not demonstrable on diligent examination. Presence of anterior nephrostomes thus constitutes, as far as is known, a distinction of S. (Austroscolex) from S. (Spenceriella). This important distinction contains with additional distinctions — the reduced gizzard, absence of calciferous glands and of pharyngeal tufts — to clearly distinguish S. (Austroscolex) from S. (Spenceriella) and may later be considered to warrant separate generic status for Austroscolex. At present, however, Austroscolex seems satisfactorily accommodated as a subgenus in Spenceriella.

The enlarged genus is redefined, in a diagnosis, above. No one character is diagnostic but the possession of nephrostomes in the same segment as their meronephridial bodies is exceedingly rare in the Oligochaeta, being known in only the Megascolecidae and there in only *Spenceriella* and *Pheretima* s. lat. The affinities of *Spenceriella* with Australian and Oriental pheretimoids are further discussed on p. 294

Gemascolex, from South Australia and Victoria, shows close affinities with Spenceriella but is clearly distinguished by the preseptal location of the nephrostomal funnels, in addition to those of the medianmost ventral nephridia, in the segment in front of the corresponding nephridial bodies. The intersegmental location of accessory genital markings in Gemascolex further contrasts with their segmental location in Spenceriella.

### **Spenceriella (Austroscolex) difficilis** n. sp. Fig. 1. Table 2

1 = 152 (H), 224 (P) mm, w (midclitellar) = 4.5 mm, s=84+ (H, posterior amputee), 120 (P). Circular in cross section. Pigmentless buff in alcohol. Prostomium tanylobous (H), or epilobous 1/3 (P), not canaliculate. First dorsal pore: 4/5 (imperforate, H) or 3/4 and 4/5 imperforate (P), 5/6 (perforate). Setae commencing on II; numbers per segment 26, 21 on XII; 32, 27 on XX; 40, 31, fifteen segments from posterior end (H, P respectively); aa and zz broad interruptions of the setal circlet in the forebody; recognizable but narrow posteriorly; setae a and b (and c?) absent in XVIII (H, P). Nephropores not visible. Clitellum annular, indistinctly developed, in 1/2 XIII-XVI. Male pores a minute pair in XVIII, not on papillae, between setal lines 2 and 3 relative to adjacent segments, 2.0, 2.8 mm, 0.17, 0.23 circumference, apart (H, P). Accessory genital markings not developed (incompletely mature?). Female pores minute, a pair at about 1/3 (H), 1/5 (P), the distance from the setal arc to the anterior margin of XIV, about 1/2 (H), 2/3 (P) aa apart. Spermathecal pores 2 pairs, in 7/8 and 8/9, in setal lines 3-4, short transverse slits on small but conspicuous papillae (P) or with level whitish margins (H); 2.8, 3.28 mm, 0.24, 0.31 circumference apart (H, P respectively).

Septa 7/8-13/14 strongly thickened, 12/13-13/14 the strongest. Gizzard rudimentary in V, concealed in the last septal glands. Intestinal origin 1/2 XVI. Nephridia lateral parietal bands of very numerous avesiculate stomate micromeronephridia, a transverse series of postseptal nephrostomal funnels demonstrable in the oesophageal and intestinal regions. Holandric: iridescent sperm funnels in X and XI; large racemose seminal vesicles of approximately equal size, and not transversely elongate, in IX and XII. Ovaries, large webs with many large oocytes, and funnels in XIII, large multiloculate ovisacs in XIV. Prostates each in the form of a flattened, lobulated S, the muscular external duct arising from the anterior 2 of the 3 portions and shown by dissection to give three or more branches immediately within the gland, being, therefore, racemose; vas deferens joining the anterior lobe of the gland near but not at the junction with the external duct. Penial setae absent. Spermathecae 2 pairs, in VIII and IX, those in IX one and a half (P) to twice (H) the length of those in VIII; each with an ovoid ampulla, short poorly demarcated duct and wide clavate dorsolateral diverticulum. (All previous data for H and P). Total length of right spermatheca of IX (H) = 2.7 mm; ratio total length: length duct = 9.0; ratio length: length diverticulum = 3.8.

MATERIAL EXAMINED: Lord Howe Island (no further data) — Holotype (W4563), paratype 1 (BJ).

REMARKS: S. (A). difficilis differs from S. (A) newcombei in the paired female pores and questionably in a smaller number of setae per segment (reaching 32 in XX whereas 35 are reported by Gates, 1965, for post-clitellar segments in newcombei). It also lacks the

accessory genital markings described for newcombei so far as is known from the imperfectly clitellate available material. It is distinguished in the key from the other species of the subgenus on Lord Howe Island.

### **Spenceriella (Austroscolex) hollowayi** n. sp. Fig. 1, 4B, C, 6B, 7C. Table 2

1 = ?(postclitellar amputee), w (midclitellar) = 4.8 mm, s = ?. Pigmentless in alcohol. Prostomium tanylobous, parallel sided, bisected by median furrow. First dorsal pore 4/5. Setae irregularly spaced, slightly more closely spaced laterally than dorsally and ventrally: numbers of setae per segment 43 in XII (H); 39, 41, 42 in XX (H, P1, 2); 41, 40, fifteen segments from the caudal end (P1, 2); a and z lines approximately straight until near the caudal extremity where they become very irregular; anteriorly with wide and approximately equal ventral and dorsal interruption of the setal circlet; no appreciable interruption caudally; setae a and b absent in XVIII. Clitellum annular, 1/3 XIII (ventrally), 2/3 XIII (dorsally) — XVII, intersegmental furrows strongly indicated; setae less distinct than elsewhere; dorsal pores obscured. Male pores in XVIII, considerable transverse slits, each on a low but distinct transversely elliptical porophore, filling the equatorial third of the segment, centred very slightly lateral of b lines of adjacent segments; 1.48, 1.24, 1.50 mm, 0.10, 0.11, 0.12 circumference apart (H, P1, 2). Accessory genital markings: a pair of dome-shaped papillae, slightly wider than long, in X, XI and XII, each papilla occupying the setal annulus and anterior third of the segment, the setae traversing its posterior flank, and with a dark porelike centre in c line (X), bc (XI) or b (XII). Similar but smaller markings in XXI and XXII, with centres in ab and a respectively, (right side only in XXII, H). Paratype 1 has the paired postclitellar accessory genital markings in XXI only (amputee with forebody to XVI missing); paratype 2 has paired markings in XX and XXI but has also a pair (similarly conjoined) in XVII, with presetal centres approximately in a lines (forebody to XVI missing). Female pores an inconspicuous pair in XIV, shortly anteromedian to setae a. Spermathecal pores 2 pairs, in 7/8 and 8/9, each a small transverse slit in bc on an inconspicuous papilla; 1.24 mm, 0.10 circumference apart (H).

Septa 7/8-12/13 strongly thickened; 9/10 strongest. Dorsal vessel single, not traceable (broken?) in front of segment VI. Dorsoventral commissurals in VI-IX very slender, though valvular, and each giving off a lateral branch before the junction with the ventral vessel. Hearts in X-XII thicker than preceding commissurals but not large.

Gizzard in V, wide but short, compressible and only moderately muscular. Oesophagus virtually suppressed in VI; moniliform (segmentally widened) in VII-XIV, with circumferential vascular striae and internal rugae which in XII are almost lamellae, but no extramural calciferous glands; narrow and covered with yellowish chloragogue in XV and 1/2 XVI. Intestinal origin 1/2 XVI; typhlosole, muscular thickening and caeca absent. Nephridia astomate (?) avesiculate, exonephric micromeronephridia commencing in II, forming a parietal band in transverse single file in each segment, approximately 15 on each side in the posterior region of the oesophagus; no tufted nephridia present. In the postprostatic region, at least, each nephridium has a minute nephrostomal funnel which lies in the same segment as the body of the nephridium (H). Caudally 15 nephrostomes counted on each side per segment, lying shortly behind the anterior septum; no preseptal funnels demonstrated. Ventral nephridia forming an exonephric (?) group of several on each side but no megameronephridia present. Dorsal nephridia adherent to the intestine and apparently individually enteronephric; no longitudinal ureters demonstrable (P2).

Holandric; large iridescent sperm funnels in X and XI; very small racemose seminal vesicles, with few loculi, on the posterior septa of IX and X and the anterior septum of XII. Ovaries, plicate webs with many chains of large oocytes, and funnels in XIII; ovisacs absent.

Prostates, a pair in XVIII-XIX, superficially racemose, the left one trilobed, the right one bilobed by deep transverse incisions (H), or irregular in outline but linear (P1); the very slender, long muscular duct arising considerably posterior to the anterior limit of the gland (H, P1); vas deferens joining at its junction with the duct. Serial sections show only a single very narrow (eccentric) lumen in each lobe; this has a distinct lining epithelium; side branches are not visible but, from the great thickness of the surrounding glandular tissue, are presumably present; continuity of the lumina between the different lobes was not demonstrated but in view of their single nature this appears more probable than separate origin of each lumen from the muscular duct; the gland therefore is taken to be tubuloracemose, as the linear form in P1 also suggests. Penial setae absent. Spermathecae 2 uniform pairs, in VIII and IX; ampulla ovoid, wider than long; duct less than half as wide though stout, joined dorsolaterally at its junction with the ampulla by a wide stalked, clavate, inseminated diverticulum which in the four spermathecae is curved around the duct; length of right spermatheca of IX = 1.5 mm; ratio total length: length of duct = 2.6; ratio length: length of diverticulum = 1.5 (H).

MATERIAL EXAMINED: Summit of Mt. Gower, Lord Howe Island; collector G. Holloway, Oct 1971 — Holotype, paratype 1 (W6598), paratype 2 (BJ).

REMARKS: S. (A). hollowayi differs from S. (A). newcombei in the greater number of setae per segment, in the paired female pores and in the configuration of the accessory genital markings. It is distinguished in the key from the other species of the subgenus on Lord Howe Island.

### **Spenceriella (Austroscolex) howeana** n. sp. Fig. 1, 4A, 6E, 7D. Table 3

1 = 24-35 mm (mean 31.6 mm); w (midclitellar) = 1.5-2.0 mm (mean 1.6 mm), s = 84-97 (mean 89) (H, 4 paratypes). Form dorsoventrally depressed. Lacking appreciable secondary annulation. Purplish pigmentation present dorsally (H, 9 paratypes). Prostomium epilobous, varying from 1/2-5/6, usually with a faint middorsal groove (H, 6 paratypes). First dorsal pore 5/6 (H, 5 paratypes, within H and P8 an imperforate rudiment in 4/5). Setae commencing on II; numbers per segment 17, 19, 16, 18, 20 on XII; 21, 22, 17, 19, 20 on XX; 17, 19, 23, 22, 20 at fifteen segments from posterior end (H, P1, 17-19); aa a clearly recognizable interruption in the setal circle ( $\doteqdot$  2 ab); zz a very wide interruption, so wide in the forebody that only setae y and z are visible dorsally, zy being here much wider than in the hindbody although zz  $\doteqdot$  2zy throughout the body; setae a, b (and c?) absent in XVIII; a and z lines approximately straight; the two dorsal setae (yz) on each side conspicuously enlarged in IV or V to IX or rarely to X, the other setae of each segmental circle decreasing in size ventralwards. Lengths and greatest widths of seta z (P1); 290 μm, 36 μm (V); 360 μm, 50 μm (VII); 430 μm, 50 μm (VIII); 400 μm, 50 μm (VIII); 360 μm, 50 μm (IX); and of seta x in IX 300 μm, 32 μm; scattered cicatricing well developed on the enlarged setae, less apparent on normal setae.

Nephropores not visible. Clitellum annular, tumid but not protuberant, embracing XIII, 1/2 XIII-1/n XVII, 1/2 XVII or XVII; dorsal pores and intersegmental furrows obscured at full development; small slit-like combined male and prostatic pores a pair on XVIII slightly lateral of s.1.2 on papillae which occupy the length of the segment but are indistinctly demarcated laterally (H, 5 paratypes) pores 0.90 mm, 0.20 circumference, apart (H); means for 5 specimens (H, P1, 17-19), 0.93 mm (range 0.84-1.08 mm), 0.18 circumference (range 0.15-0.20). Accessory genital markings (holotype) indistinct presetal pits or circular glandular patches lateral of setal lines 3 in IX and X (P5); lateral of s.1.2, 3 or 4 in XI (H, P5, 6, 9); near s.1.2 or 3 in XII (H, P6, 9); between s.1.1 and 2 or in s.1.2 in XVII (H, P2, 3, 4,9); in or lateral of s.1.2 in XIX (P4, 9); and between s.1.2 and 3 and in s.1.2 in XX (H, P4) or no genital markings apparent. Female pores small but moderately conspicuous shortly in front of the setal arc of XIV and almost contiguous midventrally to almost as far laterally as s.1.1 (H, 7 paratypes).

Spermathecal pores 2 pairs, in 7/8 and 8/9, minute and visible only when the intersegmental furrow is held open, very slightly lateral of s.1.3 or in 4 (H, P2, 3, 5-8) or lateral of s.1.2 (P9); the last pores 0.94 mm, 0.23 body circumference, apart (H); means for 5 specimens (H, P1, 17-19) 1.18 mm (range 0.94-1.28 mm), 0.26 circumference (range 0.20-0.36).

Internal anatomy (Holotype, P1 and, where mentioned, schizoparatype).

Septa 5/6 and 6/7 thin; 7/8 slightly thickened; 8/9 and 9/10 moderately strong; 10/11-14/15 and to a lesser extent several succeeding septa appreciably thickened. Last pharyngeal glands, large paired masses in VI investing the dorsoventral commissural vessels. A slender subneural vessel apparently present, adherent to the parieties but not demonstrated with certainty. A pair of large latero-parietals originating from the vascular plexus of the floor of the oesophagus in XIII and extending posteriorly to the vicinity of the prostate glands.

Gizzard moderately large but readily compressible, in V. Oesophagus in IV narrower and not modified as a proventriculus. Oesophagus swollen and with circumferential vascular striae in XI and XII, especially so in XIII and XIV; internally with vascular rugae in XI-XIV, which are thin and high in XIII in P1, but extramural calciferous glands absent; narrower and less vascular in XV. In the schizoparatype the oesophagus is not especially enlarged in XIII but in XIV is greatly distended dorsally and has a very wide blood sinus in the dorsal wall and lesser sinuses in the ventral wall; these sinuses are not present elsewhere in the oesophagus; the floor of the dilatation in XIV is rugose, but not more so than in other segments, while the roof is internally smooth. Intestine beginning, with definite oesophageal valve, in XVI; in this segment and XVII wider than but otherwise morphologically similar to the oesophagus; typhlosole and caeca absent. Nephridia avesiculate micromeronephridia throughout, commencing in II; numerous in each segment; in caudal segments with a presental funnel on each side near the ventral nerve cord, additional funnels detectable on lateral nephridia in paratype 1; nephridia in the intestinal region attached to septa; pre-intestinal nephridia integumentary; pharyngeal nephridia absent; no enteronephry demonstrable but absence requiring confirmation from appropriately preserved material. Testes, sperm masses and large iridescent sperm funnels free in X and XI; racemose seminal vesicles in IX and XII, the posterior pair the larger. Ovaries, large folded thick laminae with many large oocytes, and funnels in XIII; racemose ovisacs in XIV. Prostates racemose, i.e. dorsoventrally depressed elongate structures, the posterior portion of which is joined to the anterior portion by a narrow neck and is approximated to it in such a way that the gland as a whole appears superficially to form a broad rectangle; the surface not notably lobulated but the external curved muscular duct is seen in the schizoparatype to bifurcate within the gland. Penial setae absent. The intracoelomic portion of each enlarged seta in the forebody invested in a conspicuous glandular mass. Spermathecae 2 pairs, discharging anteriorly in VIII and IX, each with an ovoid ampulla and slightly shorter ectally tapering duct which receives a single lateral clavate diverticulum at midlength, the diverticulum embracing the oesophagus and visible dorsally; size of spermathecae approximately uniform; length of left spermatheca of IX (holotype) = 0.68 mm; ratio total length: length duct = 2.3; ratio total length: length diverticulum = 1.8.

MATERIAL EXAMINED: 6, 31°35′03½″S, 159°04′56″E. Mt. Gower ridge, close to stream; leaf litter in places, elsewhere dense moss covering trees; — Holotype and paratype 1 (W6593); 7 31°35′04″S, 159°04′55″E. Mt. Gower ridge, in a layer of soil beneath moss on a tree trunk; — P20 and 5 further specimens (W6594); 11 31°35′08″S, 159°04′47″E. Mt. Gower ridge, in the leaf of a short palm, Hedyscepe canterburyana, 1 metre off the ground; — P2-4, 10-18 (W6595); 13, 31°35′01″S, 159°04′49″E. At foot of small stream running at right angles to Mt. Gower ridge, in the base of fronds of the palm Lepidorrhachis; other vegetation Dracophyllum fitzgeraldii, Passiflora edulis; tree-ferns; — P5-8 (BJ); 14, 31°35′02″S,

159°04′50″E. Up stream running at right angles to Mt. Gower ridge, dense vegetation, damp conditions; in leaf litter; — P9 (W6596); Lord Howe Island (no further data) — P19 (4560), P21-23 (W4565); Lord Howe Island, collector Saunders — 1 (W6597 ex W1509).

REMARKS: Spenceriella (Austroscolex) howeana is distinguishable from the other species of the subgenus by the very large setal interval zz (13 to 26% of the circumference in 5 measured specimens), the conspicuous enlargement of setae yz, and the configuration of the genital markings.

### Spenceriella (Austroscolex) saundersi n. sp. Fig. 1, 5A, B, 6F, 7B. Table 3

1 = 65, 105 mm; w (segment XV) = 5.3, 6.2 mm; s = 110, 109 (H, P1). Greyish brown (pigmented) in alcohol with clitellum (P3) light brown. Slightly flattened ventrally. Prostomium epilobous, open (?), ½, not canaliculate. Peristomium bifid (H) or (P1) not bifid ventrally. First dorsal pore 4/5 (?) (H, P1). Setae commencing on II; 53,55 on XII, 56,61 on XX; 42, 49, fifteen segments from posterior end (H, P1); aa and zz only a narrow break in the setal circlet (= 2ab and 2zy, respectively); aa narrower but a just appreciable break; zz an inappreciable break, caudally; setae 1-6 (a-f) absent in XVIII; a and z lines approximately straight; no setae notably enlarged; setal intervals progressively increasing dorsalwards. Nephropores not visible. Clitellum developed (H) or (P1, 2) rudimentary; annular in XIV-XVII but possibly more extensive when fully developed; well developed in ½ XIII-XVII in P3. Combined male and prostatic pores a pair of small but distinct orifices on XVIII in setal lines b relative to adjacent segments; with marginal tumescence which only in the holotype constitutes a porophore though then indistinct; pores 2.16, 2.28 mm, 0.16, 0.16, body circumference apart (H, P1, 2). Small disclike accessory genital markings basically in an inner and an outer ventral series, that is, 4 longitudinal rows, in IX-XII; the outer row approximately in setal lines 7, the inner row in setal lines 2-3, the markings post setal in IX in which only that of the outer row is present on the left and only that of the inner row on the right; in X pre- and post-setal in the outer row but only presetal in the inner row, that of the right inner row being transversely duplicated, that of the left inner row single but accompanied by an anterior supernumerary marking between it and the outer row; in XI pre- and post-setal in the outer row and presetal only, in the inner row; in XII, presetal only, in the outer and inner row (H). The accessory genital markings restricted in P1 to a pair of postsetal disclike markings in X, in setal lines 7 and in XI in setal lines 9-10 with a suggestion of similar markings posteriorly in XVIII, immediately posteromedian to the male pores; accessory genital markings absent in P2 and 3. Female pores inconspicuous, a pair immediately median to a lines, midway between the setal arc and anterior border of XIV. Spermathecal pores 2 pairs, in 7/8 and 8/9, each a minute orifice with a crescentic anterior lip forming a half-papilla concealed in the intersegmental furrow, in setal lines 6 or 7 (H, P1) last pores 1.8, 2.56 mm, 0.19, 0.20 body circumference apart (H, P1).

Septa 8/9-13/14 strongly thickened; 10/11 (H), 11/12 (P1) — 13/14 the strongest. No subneural demonstrable.

Gizzard recognizably differentiated but no wider than the adjacent oesophagus and with rudimentary muscularization, in V, concealed in the penultimate last septal glands. Last septal glands in VI. Oesophagus in IV equally wide and forming a proventriculus. Oesophagus simple in VI, segmentally widened in VIII-XIV; not especially vascular in VII and VIII but with obvious circumferential vascular striae and conspicuous internal radial lamellae in VIII-XIV, though extramural calciferous glands are absent, and chloragogenous in XV-½ XVI; intestine originating at ½ XVI, here and in XVII moniliform and resembling the oesophagus but only villous, not lamellate internally; typhlosole, muscular thickening and caeca absent. Nephridia avesiculate micromeronephridia throughout, commencing in II;

dense lateral bands of moderately to very numerous tubules in II and III but neither tufting nor enteronephry demonstrable, lateral bands also especially dense in XIV-XVIII; numerous intrasegmental nephrostomal funnels demonstrable on each side in each segment in IV posteriorly, in both the oesophageal and intestinal regions. Testes and large convoluted sperm funnels free in X and XI, only the funnels in X iridescent, transversely elongate tortuous racemose seminal vesicles with many discrete loculi, in IX and XII, the anterior pair the larger. Ovaries rudimentary (H) or moderate-sized webs with several conjoined strings of large oocytes, (P1); funnels in XIII (H, P1); loculate sacs (ovisacs?) near the oviducts on the anterior septum of XIV (P1) or absent (H). Prostates racemose, the muscular duct branching on entering the gland each gland restricted to XVIII and consisting of a subrectangular, flattened anterior lobe and a more slender, elongate irregular posterior lobe, the two lobes meeting at the muscular duct from which a branch passes into each lobe; the two lobes separate, or conjoined by connective tissue. Vas deferens joining the gland at the junction of this with the muscular duct; penial setae absent; no glandular masses associated with somatic setae (H, P1). Spermathecae 2 pairs, discharging at the anterior margin of VIII and IX, each with a subspherical ampulla and a slightly shorter moderately slender well demarcated tubular duct which is joined slightly ectal of its midlength by a single lateral (inseminated) clavate diverticulum, the stalk of which is almost as wide as the spermathecal duct; the diverticulum projecting laterally, not embracing the oesophagus; size of spermathecae uniform; length of left spermatheca of IX = 0.95, 0.85 mm ratio total length: length duct = 1.9, 2.9; ratio length: length diverticulum = 0.7, 1.1 (H, P1 respectively).

MATERIAL EXAMINED: Lord Howe Island (no further data) — Holotype (W6599 ex W4560); Lord Howe Island, collector Saunders — P1 (BJ ex W1509), P2, 3 (W6600 ex W1509); 7 (W6601 ex W4563); Lord Howe Island, collectors "E.J. & W." — P4 (W4562).

REMARKS: S. (A). saundersi differs from S. (A). newcombei in the greater number of setae per segment, in the paired female pores and in the configuration of the accessory genital markings when these are developed. It is distinguished in the key from the other species of the subgenus on Lord Howe Island.

The five specimens (W4563, no data) are excluded from the above description of *S.* (*A*). saundersi though they agree with it in all stated respects excepting the following. They are larger (in a selected specimen 1 = 172 mm, w (XV) = 8.0 mm, s = 131). Although setae 1-6 are absent in XVIII, as in saundersi, the male pores are consistently in setal lines 4 as are the spermathecal pores, this difference occurring despite similar numbers of setae (54 on XII, 58 on XX and caudally). The ventral distance between the male pores though greater (2.48 mm) is a smaller proportion of the circumference (0.11) than in saundersi and the same is true for the spermathecal pores (3.12 mm, 0.14 circumference apart). Spermathecae are larger (length 1.6 mm; ratio length: length duct 1.4; ratio length: length diverticulum = 2.3). Differences in the setal ratios are doubtfully significant. As the spermathecal diverticula are inseminated, the absence of a clitellum is presumably due to post-copulatory regression.

A further specimen (W4562, no data) excluded from the type-series of saundersi resembles these five specimens in size, in location of male and spermathecal pores in setal lines 4, and has even larger spermathecae (length 2.3 mm, ratio length: length duct 3.0; length: length diverticulum 1.9). It agrees closely with 5. (A). saundersi in setal ratios, however, and is probably conspecific with the type-series.

The ratio of separation of male pores to the circumference (2.52 mm, 0.13 circumference, apart) in this specimen is intermediate between the saundersi and the five W4563 specimens and its spermathecal pore ratio (3.04 mm, 0.13 circumference, apart) is close to both series. This specimen links S. (A). saundersi and the five specimens and suggests that the latter represent a population which, though morphologically somewhat distinct from the type-series, is conspecific with it. Separate specific status cannot be ruled

out with certainty on present evidence, however, expecially as the possibility exists of a distribution of accessory genital markings different from *saundersi* if the specimens had been clitellate.

### Genus Amynthas Kinberg, 1867 Amynthas diffringens (Baird, 1869)

Megascolex diffringens Baird, 1869: 40

Pheretima heterochaeta. — Michaelsen, 1909: 189

Pheretima divergens var. yunnanensis Stephenson, 1912: 274

Pheretima mirabilis. — Gates, 1934: 260 (fide Gates, 1972)

Pheretima diffringens. — Gates, 1972: 177

Amynthas diffringens. — Sims & Easton, 1972: 214

TAXONOMIC NOTE: Synonyms of this frequently recorded and almost cosmopolitan species are listed above. The account of Gates (1972) is the most comprehensive. Sims and Easton (1972) in their excellent computer analysis of Pheretima justify transfer of diffringens to a reinstated Amynthas and give an exhaustive list of nominal species which they include in a diffringens group. The single specimen in the material from Lord Howe Island under investigation conforms to genus Amynthas in the key to the genera of the Pheretima complex of species given by Sims and Easton in having a cylindrical body with evenly distributed setae, intestinal caeca arising at the anterior margin of segment XXVII and no copulatory pouches (but here no prostates) at the male pores. It agrees with the diffringensgroup in the key to species and nominal species-groups of Amynthas in having 4 pairs of inter-segmental spermathecal pores, in 5/6-8/9, and in being holandric. The following account of the excretory system, in so far as it can be elucidated in the single somewhat macerated specimen, appears to be the first description with any detail for this species. Nephridia all avesiculate; pharyngeal tufts (? specimen anteriorly macerated); in the oesophageal region with numerous, scattered, astomate parietal micromeronephridia which are especially numerous and densely crowded in the clitellar segments; anterior intestinal nephridia numerous, rather large (enteronephric?), dependent from the posterior face of the septum and each (?) with a presental nephrostomal funnel the long, very slender neck of which extends far in front of the septum (at least 12 funnels counted on one side in a selected segment); minute parietal micromeronephridia also present in these intestinal segments, each apparently corresponding with a setal follicle and with its duct entering the body wall presetally. By XXV, or possibly more anteriorly, nephridia are added on the anterior faces of the septa with funnels in the same segment as the nephridial bodies, in addition to the post septal nephridia which retain their presental nephrostomes. In caudal segments the presental nephridia continue to have funnels on the same side of the septum but the postseptal nephridia, which seem more sparsely developed, have postseptal nephrostomes, the arrangement of these two sets of (enteronephric?) septal nephridia therefore being as described by Bahl (1919) for Metaphire posthuma. A difference from M. posthuma is that at least some of the parietal (exonephric) nephridia in caudal segments have funnels.

MATERIAL EXAMINED: 40, 31°33′15″S, 159°05′57″E. On the track to Boat Harbour, by a creek; Pandanus forsteri, Guioa coriacea, Howea forsterana, H. belmoreana, Linociera quadristaminae; —3 (W6602).

### ZOOGEOGRAPHIC AFFINITIES AND EVOLUTION OF THE EARTHWORMS OF LORD HOWE ISLAND

The indigenous earthworms of Lord Howe Island, all of which are assignable to the family Megascolecidae, are morphologically and, it is inferred, phylogenetically more closely related to the Australian fauna than to that of any other region. One genus, Diporochaeta has its type-species in New Zealand but the genus is predominantly Australian. It represents the sole link between Lord Howe Island and other regions, excepting the widely transported Oriental species, Amynthas diffringens. The six indigenous genera of the island are all members of the subfamily Megascolecinae. They are Diporochaeta, Plutellus, Paraplutellus, Pericryptodrilus (Tribe Perionychini), Eastoniella (Tribe Dichogastrini) and Spenceriella (Tribe Megascolecini?).

### PARAPLUTELLUS AND PLUTELLUS

Despite their undoubted Australian affinities, three of the six genera (Paraplutellus, Pericryptodrilus and Eastoniella) are known only from the island. Of these, Paraplutellus is exceedingly close to, yet satisfactorily distinct from, Plutellus s. strict, which has only three known species, one in rainforest in coastal New South Wales, one on Lord Howe Island, and one of doubtful origin. The discovery of an endemic species of Plutellus on the island in the present study raises the possibility of evolution of the two species, Plutellus hutchingsae and Paraplutellus insularis on the island from a common ancestor, or speciation there of one from an isolated population of the other. The alternative would be to accept separate invasion of the island by each species or by two distinct ancestral species. Unless these plutelloids have a special propensity for transoceanic dispersal the probability of the double invasion when many species from eastern mainland Australia have failed to invade would seem low. The North American plutelloid genus Argilophilus has a salt tolerant species A. marmoratus in estuarine conditions in New South Wales (personal observations) and all earthworms from so small an oceanic island as Lord Howe Island must presumably have greater salt tolerance than is usual in earthworms. But even if such salt tolerance were presumed for the plutelloids of Lord Howe Island, a double landfall on so small an island would seem improbable. Whether the two species have speciated from a common ancestral species or not, and whether such speciation occurred on the island or elsewhere, their very close relationship is unquestionable. Which is the more primitive (plesiomorphic) is difficult to ascertain. The more widely distributed, more numerous, and in most habitats presumably more efficient Paraplutellus appears the more derived: it has lost the gizzard; the oesophagus has extended by one segment (intestinal origin in XVI as against XV in Plutellus); and anterior nephropores are in d lines in segments II-IV whereas they are in d only in II of these segments, in Plutellus hutchingsae (though alternation from d to b occurs in V or VI posteriorly). Occurrence of pores in d is here considered a modification of location in c which is the basic or common condition in Australian perionychins. In this respect modification has proceeded further in Paraplutellus insularis than in Pl. hutchingsae. Restriction of calciferous glands to a single pair in XIII in Paraplutellus, in contrast with four pairs, in X-XIII, in Plutellus and three to five pairs ending in XIII in the related Heteroporodrilus, may also be a reduction from a previously more extensive series. It is here suggested that Paraplutellus is, in Hennig-Brundin terms, the apomorph sister-group of Plutellus and that it evolved on the island from a stock which, contrary to the principles of those workers, would have been itself assignable to Plutellus.

#### **PERICRYPTODRILUS**

The monotypic genus *Pericryptodrilus* appears on initial examination to be no more than a perichaetine (multisetose) form of the eastern Australian and Tasmanian genus *Cryptodrilus* but restriction of nephrostomes to the intermediate rather than the ventral

row of nephridia, in addition to the perichaetine condition, at present warrants generic status. Its affinities nevertheless lie with the Australian rather than any other fauna.

#### **EASTONIELLA**

The genus Eastoniella is, likewise, known only from Lord Howe Island while having undoubted Australian affinities. Location of the oesophageal gizzard in its two species as far back as segments VIII or IX is a highly evolved condition, the gizzard having reached segment VIII elsewhere in the Megascolecidae in the Oriental genera Pleionogaster and Pheretima s. lat., which show only distant affinities with Eastoniella. The multi-lipped, and sometimes exceptionally large, paired nephrostomal funnels in Eastoniella add to its distinctiveness but the posterior caudal nephridia and general anatomy in the genus are those of an Australian dichogastrin and its descent from a form placeable in the eastern Australian Megascolides is easily envisaged.

#### **DIPOROCHAETA**

The genus *Diporochaeta* is represented on Lord Howe Island by a single species which is unknown elsewhere. The genus is restricted to New Zealand and Australia with doubtful representation in Southern India. It is the dominant genus in Tasmania (23 species), though its largest representation is in Victoria (33 species, synonymy to be investigated), and it has some representation on high ground in New South Wales (3 species on Mt. Kosciusko of which one also occurs in Victoria) and a few northerly outliers, in North Queensland (7 species), mostly in the Cairns-Atherton Tableland area, this area being regarded as a refuge area. Affinities of the Lord Howe Island species appear to lie with the southeastern Australian species. In New Zealand most species are restricted to the west coast and there seems a possibility of relatively recent invasion from Australia. Lee (1959) considers that most species have probably had their present distribution in New Zealand only since the end of the Pleistocene glaciation. Occurrence on Lord Howe Island may be due to the same transoceanic dispersal and it will be interesting to investigate whether Australian members of the genus are euryhaline.

### SPENCERIELLA AND THE ORIGIN OF PHERETIMA SPENCERIELLA (AUSTROSCOLEX)

Inclusion of the subgenus Austroscolex, erected for three species from Lord Howe Island and a fourth from Queensland, in the south-eastern Australian and Tasmanian genus Spenceriella represents a further, major link between Lord Howe Island and Australia. The structure of the excretory system in both subgenera of Spenceriella raises the possibility of relationship of this (wholly?) Australian genus with the predominantly Oriental genus Pheretima s. lat., however. Bahl (1947: 131), in his impressive review of excretion in the Oligochaeta, states that in the (septal) nephridia of Pheretima the funnel and body lie in the same segment whereas in all other earthworms the funnel is preseptal. The only other demonstration of such intrasegmental nephrostomes appears to be that for Spenceriella (v. Jamieson, 1974b), confirmed in the present study. The excretory system in Pheretima differs from that in Spenceriella in location of those nephridia having intrasegmental funnels on the anterior and posterior septa of the intestinal segments whereas in Spenceriella the stomate nephridia are parietal. The shared possession of intrasegmental nephrostomes would not be sufficient to suggest a closer relationship between the overwhelmingly extra-Australian Pheretima (with only one described indigenous Australian species) and Spenceriella. It may, nevertheless, reflect a special relationship as the external facies of some S. (Austroscolex) species are remarkably like those which have been thought distinctive of Pheretima. Gates (1965) in redescribing S. (A), newcombei (as Megascolex) remarked that it "appeared externally to be referable to Pheretima", a reference, presumably, to the perichaetine condition, median unpaired female pore, and short clitellum, on XIV-XVI. Pheretima s. lat. differs significantly from Spenceriella in the far more complex arrangement of the various types of nephridia, described by Bahl (1919) for Metaphire posthuma, in location of the gizzard in VIII, both derived characters, and origin of the intestine in XV or XVI rather than constant origin in XVI of Spenceriella. Of the pheretimoid genera, Metapheretima most closely approaches Spenceriella in lacking intestinal caeca. Its nephridia, too, are closer to those of Spenceriella for an examination, in the present study, of non-indigenous Queensland material of Metapheretima elongata reveals, caudally, parietal (not septal) nephridia located anterior and posterior to the setal arc which have intrasegmental funnels. No intestinal enteronephry is demonstrable though this requires additional investigation in more and better preserved specimens. The stomate nephridia of Metaphire posthuma are septal and enteronephric and, as there is a row on both faces of each intestinal septum, intrasegmental funnels occur on both faces of the septum. This arrangement is here confirmed for further available non-indigenous Queensland material of the genus, Metaphire javanica. The nephridia of Amynthas (=Pheretima) diffringens are briefly described above in the taxonomic note on the species.

Spenceriella thus appears more than any other megascolecid oligochaete to deserve consideration as a representative of the ancestral stock from which *Pheretima* s. lat. arose.

The possibility of an Australian or at least Gondwanaland origin of *Pheretima* from a *Spenceriella*-like stock would raise the question of how *Pheretima* might have taken up its predominantly oriental distribution. The possibility that the oriental pheretimoid fauna is the result of a Tertiary invasion of the Oriental Region by Australian pheretimoids as the Indo-Australian tectonic plate brought Australia into its vicinity deserves consideration. The existence of an endemic pheretimoid, *Metaphire queenslandica*, in a Pleistocene refuge area of northern Queensland, together with the generic and specific diversification of pheretimoids in New Guinea, point to a long sojourn of pheretimoids in Australia and New Guinea. If *Spenceriella* is representative of an ancestral pheretimoid stock, its restriction to Australia militates against the alternative view that *Pheretima* first entered Australia from S.E. Asia, though such an origin of Australia's peregrine pheretimoids, such as *Amynthas diffringens*, is here accepted.

With regard to the four species of Austroscolex here recorded from Lord Howe Island, it is tempting to speculate that these have speciated on the island from a single ancestral species. The alternative, multiple invasion of the island, is not difficult to conceive but poses the question why numerous other species of the adjacent mainland were unable to colonise if Spenceriella was able to do so four times. The four species show close relationship in their very homogeneous internal anatomy and if accessory genital markings are absent (and no markings are known for difficilis) the species can only be separated on detailed comparison of such characters as setal counts, ratios of intersetal distances, distances between male and spermathecal pores and ratio of these to the circumference, a situation approaching that for Drosophila sibling species in the thoroughness of analysis necessary for discrimination of species, albeit in this case morphospecies.

### **DISTRIBUTION PATTERNS**

Sampling on Lord Howe Island by Dr. Hutchings, though necessarily not exhaustive in the time available, has been extensive and the distribution patterns for the earthworm fauna which emerge must be considered real, with the reservation that only a single sample was taken from Mt. Lidgbird. The chief characteristic of the distribution is the apparent restriction of five species to the vicinity of the summit of Mt. Gower, one of the more natural and most isolated parts of the island. This restricted distribution contraindicates recent introduction of the species concerned, by transportation or otherwise, to the island. The

restricted Mt. Gower distribution is seen in Diporochaeta plutelloides, Pericryptodrilus nanus, Eastoniella howena, Spenceriella (Austroscolex) howeana and S. (A). hollowayi. Plutellus hutchingsae extends from Mt. Gower onto the saddle between this and Mt. Lidgbird, while Paraplutellus insularis, which we have seen could conceivably have originated from the ancestral stock of Pl. hutchingsae, is widespread on the island. Eastoniella modesta is known from an unspecified lowland area and an unrecorded locality. The distribution of Spenceriella (A). saundersi on the island is unknown. Amynthas diffringens, found in the vicinity of the boat harbour, is almost certainly introduced. Finally Lumbricidae, a holarctic family which it is not the purpose of this paper to identify, have been recorded from three localities (stations 22, 25 and 34) in or closely adjacent to cultivated areas.

The following abbreviations are used in the figures in this Record: \$, female pore; g.m., accessory genital marking; 3, male pore, 3po, male porophore; np, nephropore; pr.d, prostate duct; pr.g, prostate gland; sp.p, spermathecal pore; y.d, yas deferens. Clitellum shaded. All by camera lucida.

**Table 1 Intersetal Distances** 

		As % of circumference								
	aa	ab	bc	dc	dd	dc	cb	ba	u	
Diporochaeta plutelloides										
XII Holotype	9.5	8.2	12.2	13.5	24.5	13.6	11.3	7.3	7.36	
XX Holotype	8.4	7.4	9.9	11.2	33.5	12.3	9.9	7.4	8.07	
Plutellus hutchingsae										
XII Holotype	9.7	8.3	12.6	12.6	20.4	14.1	13.1	9.2	7.23	
Paratype 1	9.2	8.0	13.5	12.3	24.5	11.7	13.5	7.4	5.72	
Paratype 5	8.7	8. <i>7</i>	13.6	12.4	22.3	13.0	12.7	8.7	12.92	
mean	9.2	8.3	13.2	12.4	22.4	12.9	13.1	8.3	8.62	
XX Holotype	8.3	8.0	15.0	13.6	23.3	10.7	13.1	8.0	8.24	
Paratype 1	8.7	6.9	15.0	11.6	26.0	12.7	12.1	6.9	6.92	
Paratype 5	<i>7</i> .5	5.5	15.4	13. <i>7</i>	25.3	13.3	12.5	6.8	11.70	
mean	8.1	6.8	15.1	12.9	24.9	12.2	12.6	7.3	8.95	
Eastoniella howeana										
XXV Holotype	8.5	5.0	10.6	10.4	38.7	9.7	11.1	5.8	29.50	
Eastoniella modesta										
XX Holotype	15.1	6.2	10. <i>7</i>	10. <i>7</i>	34.4	7.6	8.9	6.5	14.55	
XXV Paratype	9.6	5.5	10.0	7.9	44.3	7.4	9.8	5.5	26.14	
mean	12.4	5.9	10.3	9.3	39.3	7.5	9.4	6.0	20.35	

**Table 2 Intersetal Distances** 

		As % of circumference					
		aa	ab	bc	zy	ZZ	u
Peric	ryptodrilus nanus						
	Holotype	6.9	3.3	3.3	3.6	4.8	3.30
	Paratype 2	7.3	4.7	4.4	3.5	4.4	3.16
	mean	7.1	4.0	3.9	3.5	4.6	3.23
XX	Holotype	7.5	3.8	3.8	3.8	6.9	3.20
	Paratype 2	8.4	4.2	3.9	4.5	5.6	3.58
	mean	8.0	4.0	3.9	4.2	6.3	3.39
Spen	ceriella (A) difficilis						
	Holotype.'	13.0	3.3	3.4	2.9	12.3	11.05
	Paratype	11.9	3.3	4.0	4.0	10.2	12.12
	mean	12.5	3.3	3.7	3.4	11.3	11.59
XX	Holotype	10.2	2.0	2.0	3.4	9.5	11.80
	Paratype	10.4	2.4	1.8	3.6	10.0	12.30
	mean	10.3	2.2	1.9	3.5	9.8	12.05
Spen	ceriella (A) hollowayi						
	Holotype	5.92	2.5	2.0	2.8	5.4	12.16
	Holotype	6.5	1.9	2.2	2.7	5.7	13.94
	Paratype 1	10.3	2.2	2.8	3.1	5.5	11.64
	Paratype 2	9.2	1.9	2.4	3.5	4.7	12.60
	mean	8. <i>7</i>	2.0	2.4	3.1	5.3	12.72

**Table 3 Intersetal Distances** 

	As % of circumference						
	aa	ab	bc	zy	ZZ	u	
Spenceriella (A) howeana							
XII Holotype	9.8	<b>5.8</b>	5.4	8.3	19.6	4.08	
Range (H, P1, 17, 18, 19) minimum	5.6	2.6	3.0	4.1	13.1	4.08	
maximum	9.8	5.8	5.4	9.0	25.5	6.40	
mean	7.6	3.9	4.1	7.4	19.0	5.01	
XX Holotype	9.6	3.9	3.3	5. <i>7</i>	16.2	4.56	
Range (H, P1, 17, 18 19) minimum	8.0	2.6	3.0	5.6	10.0	4.32	
maximum	10.2	3.9	4.0	9.3	19.4	6.36	
mean	9.0	3.3	3.6	6.8	13.4	5.26	
Spenceriella (A) saundersi							
XII Holotype	4.0	1.5	1.6	2.7	9.5	10.08	
Range (H, P1-3, W4562, 6601) minimum	3.2	1.2	1.2	1.5	3.1	10.08	
maximum	4.9	1.8	1.6	2.7	9.5	23.50	
mean	3.8	1.5	1.4	2.1	6.0	15.83	
XX Holotype	3.9	1.5	1.3	1. <i>7</i>	4.8	13.4	
Range (H, P1-3, W45062, 6601) minimum	3.0	1.1	1.2	1.6	2.8	12.7	
maximum	5.5	1.8	1.4	2.5	<i>7.</i> 5	19.8	
mean	4.2	1.5	1.3	1.9	4.2	16.0	

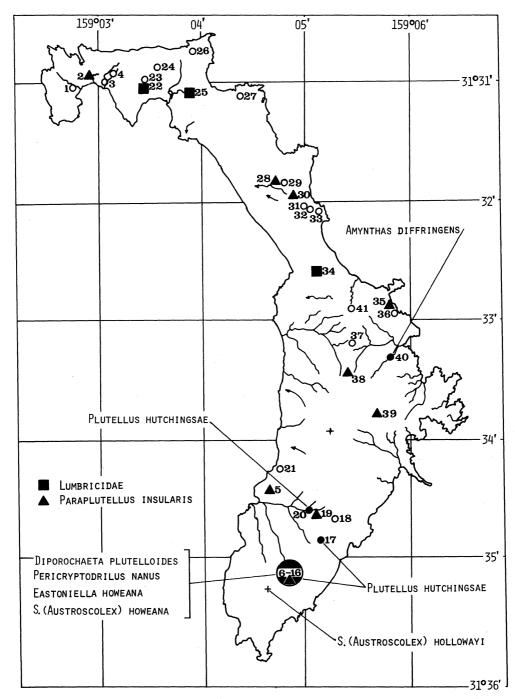


FIGURE 1. — Known distribution of earthworms (Megascolecidae and Lumbricidae) on Lord Howe Island. ● Present ○ Absent or unidentifiable (immature or incomplete).

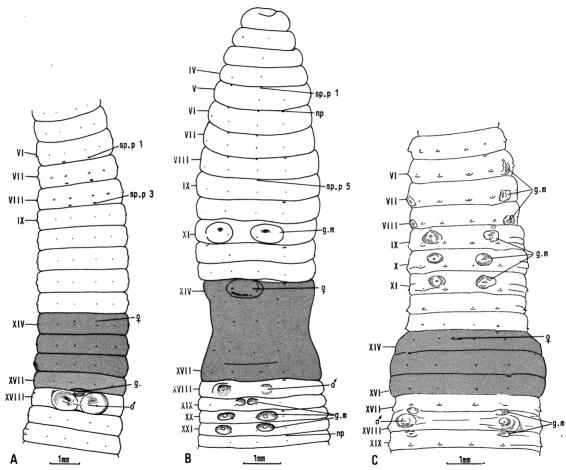


FIGURE 2. — Genital fields of: A, Diporochaeta plutelloides, holotype. B, Plutellus hutchingsae, holotype. C, Paraplutellus insularis (redrawn from Jamieson, 1972).

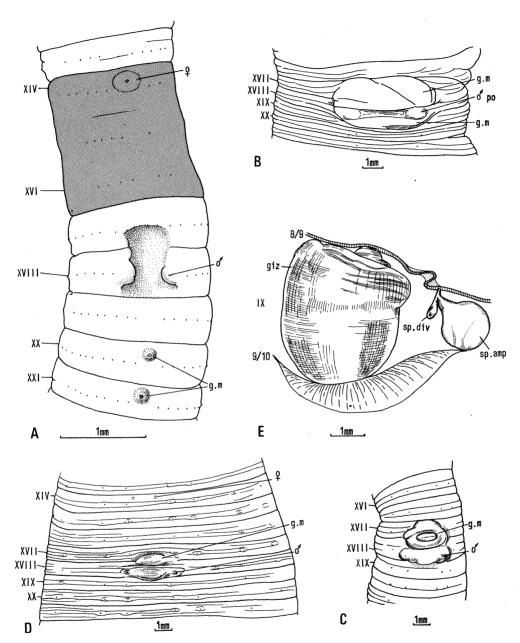


FIGURE 3. — Genital fields of: A, *Pericryptodrilus nanus*, holotype. B, *Eastoniella howeana*, holotype. C-E, *Eastoniella modesta*, C, holotype. D, paratype (opened and flattened), E, gizzard and right spermatheca *in situ*, holotype.

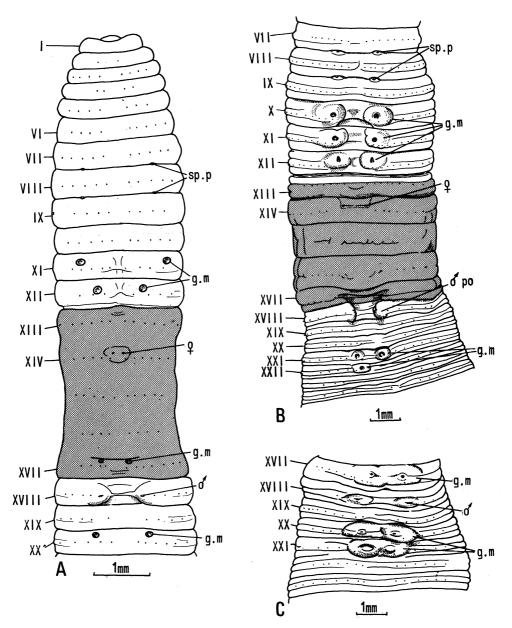


FIGURE 4. — Genital fields of: A, Spenceriella (Austroscolex) howeana, holotype. B, C, S. (A). hollowayi, B, holotype, C, paratype 2.

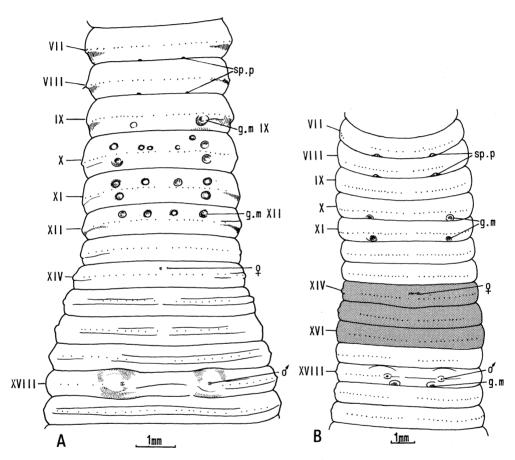


FIGURE 5. — Genital fields of Spenceriella (Austroscolex) saundersi, A, holotype, B, paratype 1.

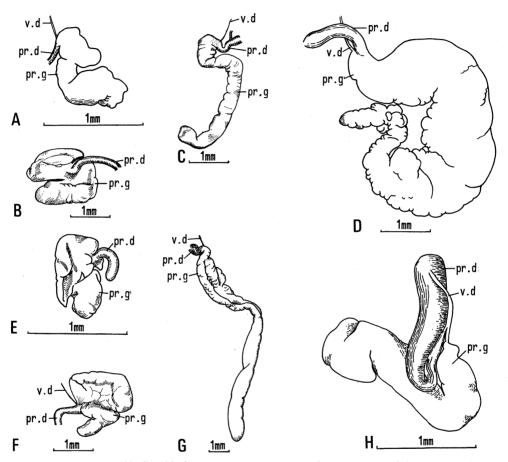


FIGURE 6. — Prostate glands (of holotypes or, F, paratype 1) of: A, Pericryptodrilus nanus (right). B, Spenceriella (Austroscolex) hollowayi (right). C, Diporochaeta plutelloides (left). D, Eastoniella howeana (right). E, Spenceriella (Austroscolex) howeana (left). F, S. (A). saundersi (right). G, Eastoniella modesta (right). H, Plutellus hutchingsae (right).

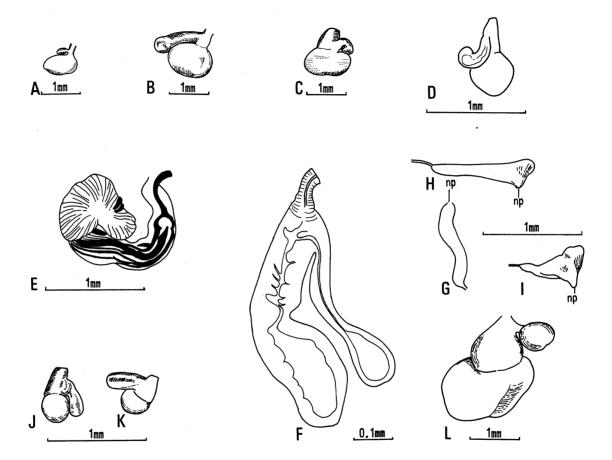


FIGURE 7. — A-D, Spermathecae (of holotypes or, B, paratype 1) of: A, Diporochaeta plutelloides (right IX). B, Spenceriella (Austroscolex) saundersi (left IX). C, S. (A). hollowayi (right IX). D, S. (A). howeana (left IX). E-I, Plutelloides hutchingsae, holotype, E, left calciferous gland of XII, F, spermatheca (right IX), G-I, nephridial bladders, G, of VI, H, of anterior intestinal region, I, of a caudal segment. J, K, Spermathecae of Pericryptodrilus nanus, holotype, J, right VIII, K, left IX. L, Eastoniella howeana, holotype, right spermatheca of IX.

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#### REFERENCES

- Bahl, K. N., 1919. On a new type of nephridia found in Indian earthworms of the genus *Pheretima*. Q. Jl microsc. Sci. 64: 67-119.
- ---- 1947. Excretion in the Oligochaeta. Biol. Rev. 22: 109-147.
- Baird, W., 1869. Description of a new species of earthworm (Megascolex diffringens) found in North Wales. Proc. zool. Soc. Lond., 1869: 40-43.
- Beddard, F. E., 1887. Observations on the structural characters of certain new or little-known earthworms. *Proc. R. Soc. Edinb.* 14: 156-176.
- ——— 1890. Contributions to the anatomy of earthworms with descriptions of some new species. Q. Jl. microsc. Sc. 30: 421-479.
- Benham, W. B., 1903. On a new species of earthworm from Norfolk Island. Trans. N.Z. Inst. 35: 273-274.
- Fletcher, J. J., 1887. Notes on Australian earthworms. Part I. Proc. Linn. Soc. N.S.W. 1: 523-574.
- Game, P. M., 1970. Petrology of Lord Howe Island, Pt. 1: The younger volcanics. Bull. Br. Mus. Nat. Hist. 2: 223-284.
- Gates, G. E., 1934. Notes on some earthworms from the Indian Museum. Rec. Indian Mus. 36: 233-277.
- ——— 1943. On some American and Oriental earthworms. Ohio J. Sci. 43, 3: 99-116.
- ——— 1965. On an Australian species of the earthworm genus *Megascolex* Templeton, 1844. *Aust. Zool.* 13, 2: 213-215.
- ——— 1972. Burmese earthworms. Trans. Amer. philos. Soc. (n.s.) 62, 7: 1-326.
- Hayes, D. E. and J. Ringis, 1973. Seafloor spreading in the Tasman Sea. Nature. 243: 454-458.
- Jamieson, B. G. M., 1971a. A Review of the Megascolecoid Earthworm Genera (Oligochaeta) of Australia. Part 1 — Reclassification and Checklist of the Megascolecoid Genera of the World. Proc. R. Soc. Qd. 82, 6: 75-86.
- ——— 1971b. Descriptions of the type-species of the earthworm genera *Plutellus* and *Digaster* (Megascolecidae: Oligochaeta). *Bull. Mus. Hist. Nat., Paris*, 2e ser. 42 (6): 1300-1310.
- ——— 1972a. The Australian earthworm genus Spenceriella and description of two new genera (Megascolecidae: Oligochaeta). Mem. natn. Mus. Vict. 33: 73-87.
- ——— 1974a. The indigenous earthworms (Megascolecidae: Oligochaeta) of Tasmania. Bull. Br. Mus. nat. Hist (Zool.) 26, 4: 203-328, 102 plates.
- ——— 1975. The earthworm genus *Diporochaeta* (Megascolecidae: Oligochaeta) in Queensland. *Zool. Verh.* (In press).
- Kinberg, J. G. H., 1867. Annulata nova. Ofvers. K. Vetensk Akad. Förh. 23: 97-103.
- Lee, K. E., 1959. The earthworm fauna of New Zealand. New Zealand Dept. of Scientific and Industrial Research. Wellington. *Bull. N.Z. Dep. Scient. Ind. Res.* 130: 1-486.

- Michaelsen, W., 1892. Terricolen der Berliner zoologischen Sammlung ii. Arch. Nat. 58, 2: 209-261.
- ——— 1900. Das Tierreich, Vermes, Lief 10, Oligochaeta, Friedländer, Berlin.
- ——— 1907. Oligochaeta, in: Die Fauna Südwest-Australiens. Bd. 1. Lief. 2: 117-232. Gustav Fischer, lena.
- ——— 1909. The Oligochaeta of India, Nepaul, Ceylon, Burma and the Andaman Islands. *Mem. Indian Mus.* 1: 103-253.
- Perrier, E., 1873. Etude sur un genre nouveau de lombriciens (Genre Plutellus E.P.) Archs. Zool. exp. gen. 2: 245-268.
- Sims, R. W. and E. G. Easton, 1972. A numerical revision of the earthworm genus *Pheretima* auct. (Megascolecidae: Oligochaeta) with the recognition of new genera and an appendix on the earthworms collected by the Royal Society North Borneo Expedition. *Biol J. Linn. Soc.* 4: 169-268.
- Spencer, W. B., 1900. Further descriptions of Australian earthworms, Part I. Proc. R. Soc. Vict. 13 (n.s.), 1: 29-67.
- Standard, J. C., 1963. Geology of Lord Howe Island. J. Proc. R. Soc. N.S.W. 96: 107-121.
- Stephenson, J., 1912. Contributions to the fauna of Yunnan based on collections made by J. Coggin Brown 1909-1910. Part VIII. Earthworms. Rec. Indian Mus. 7: 273-278.
- Stephenson, J., 1930. The Oligochaeta. Oxford.