

A REVIEW OF THE MEGASCOLECOID EARTHWORM GENERA
(OLIGOCHAETA) OF AUSTRALIA.

PART III—THE SUBFAMILY MEGASCOLECINAE

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ABSTRACT

This paper forms the final part of a review in which the earthworm family Megascolecidae has been redefined and its constituent genera have been arranged in new groupings. The subfamily Ocnodrilinae and its two tribes the Ocnodrilini and Malabarini represent no departure from the previous classification of Gates beyond their reduction from familial and subfamilial ranks, respectively, but the constitution of the remaining subfamilies here recognized, the Acanthodrilinae and Megascolecinae, differs significantly from that proposed by other workers. The subfamily Acanthodrilinae, which was treated in part II, was amended to include holonephric and meronephric forms in which the prostates varied in number but were never restricted to a pair near or combined with male pores on XVIII. The subfamily Megascolecinae, with which this paper deals, is reserved for worms with the pores of the single pair of prostates close to or combined with the male pores on XVIII and for those with the acanthodrilin arrangement (or an approximation to this) which have exonephric stomate nephridia median to micromeronephridia in posterior segments. The latter condition of the excretory system is diagnostic of the Tribe Dichogastrini. The Dichogastrini corresponds with the Octochaetinae (-idae) of some previous workers after transfer of *Octochaetus* and some other genera to the Acanthodrilinae as the Tribe Octochaetini. Tribes of the Megascolecinae recognized in addition to the Dichogastrini are the Perionychini, which possess holonephridia, and the Megascolecini which have various non-dichogastrin arrangements of meronephridia. The Megascolecinae, their tribes, and all constituent Australian genera are defined and check lists of the species of the latter genera are provided.

In part I of this review (Jamieson, 1971a) a new classification of the megascolecoïd earthworms of the world was advanced in synoptic form. In the present work fuller definitions of suprageneric taxa recognized within the subfamily Megascolecinae will be given,

and additional evidence for recognizing the proposed groupings will be advanced. The Australian genera will be defined in preparation for their revision and checklists of Australian species will be given. This paper completes a review of the 18 genera and listing of the 247 species comprising the known megascolecoïd fauna indigenous to Australia.

SYSTEMATICS

Subfamily MEGASCOLECINAE

Megascolecidae in which the prostates have a single, central lumen or a central lumen receiving lateral canals, and are externally tubular or (racemose prostates) the lumen is branched from its junction with the duct. Purely holonephric or meronephric, or with meronephridia in a varying number of segments anterior to holonephridia. If stomate nephridia are present median to micromeronephridia, no holonephridia are present. Male pores on XVIII or its homeotic equivalent; prostates a single pair with the pores on the same segment as the male pores, with which they are almost always united; or male terminalia acanthodrilin, with prostate pores 2 pairs, on XVII and XIX and male pores intermediate on XVIII; such acanthodrilin worms differing from the Acanthodrilinae in having stomate nephridia median to micromeronephridia in posterior segments and no holonephridia. Homeotic forms (*Tonoscolex*) with combined male and prostatic pores on XVII, differing from Acanthodrilinae with similarly located male terminalia in possessing racemose prostates. Calciferous glands, if present, not arranged as in the Ocnerodrilinae; intestine commencing in or behind XIV; last hearts rarely in XI.

TRIBES: Dichogastrini; Perionychini; and Megascolecini.

DISTRIBUTION: PALAEARCTIC: China, Korea; Japan. NEARCTIC: N. America; Queen Charlotte I. NEOTROPICAL: Mexico; Central and Tropical South America; West Indies; Cuba. ETHIOPIAN: Tropical Africa. ORIENTAL: India, Pakistan and northwards beyond Nepal; Ceylon; Andaman I.; Assam; Annam; Burma; Java; Sumatra; Philippines; Molluccas. AUSTRALIAN: Australia and Tasmania; Norfolk Island; New Guinea. NEW CALEDONIA. NEW ZEALAND and neighbouring islands including Chatham Island. SUB-ANTARCTIC ISLANDS: Auckland I.; Snares I.; Stewart I. FIJI. Endemicity over much of the Pacific, from the Mariannas, Bismarck Archipelago and the Solomons eastwards remains to be established. Some species peregrine, sometimes widely.

TYPE GENUS: *Megascolex* Templeton, 1844.

Tribe DICHOGASTRINI

Megascolecinae which are purely meronephric; with micromeronephridia anteriorly, often with bucco-pharyngeal nephridia; posteriorly with astomate micromeronephridia

together with, on each side in each segment, a median nephridium with one or more preseptal funnels, which frequently is enlarged as a megameronephridium. Prostates tubular or less commonly racemose or intermediate, one pair, their pores on XVII, XVIII or XIX, united with or rarely near the male pores; or two pairs, their pores on XVII and XIX, with the male pores intermediate on XVIII or sometimes nearer to or united with the anterior prostatic pores; exceptionally (*Hoplochaetella*) with intestinal enteronephry of the megameronephridia and with two pairs of prostatic pores combined with two pairs of male pores, on XVII and XIX or 17/18 and 18/19.

DISTRIBUTION: PALAEARCTIC: China (?). NEARCTIC: N. America. NEOTROPICAL: Mexico; Central and Tropical S. Africa; West Indies; Cuba. ETHIOPIAN: Tropical Africa. ORIENTAL: India, Pakistan and northwards beyond Nepal; Burma; Ceylon. AUSTRALIA. NEW ZEALAND. FIJI. Some species peregrine, sometimes widely, in warmer regions.

TYPE-GENUS: *Dichogaster* Beddard, 1889b.

GENERA: (see Jamieson, 1971a).

AUSTRALIAN GENERA: *Digaster* Perrier, 1872 (part, including the type-species?); *Didymogaster* Fletcher, 1887a; *Megascolides* (part) McCoy, 1878; *Notoscolex* (part, including the type-species?) Fletcher, 1887a, and *Spenceriella* (*S. gigantea* only?) Michaelsen, 1907a.

REMARKS: The author, in preparing a list of those genera of the Octochaetidae *s. Gates* which have both micromeronephridia and, posteriorly, megameronephridia or at least stomate meronephridia, found that precisely those genera (*Deinodrilus*, *Leucodrilus*, *Hoplochaetina* and *Octochaetus*) which Lee suspected of having their closest affinities with genera placed by Gates (1959) in the Acanthodrilidae stood apart in lacking these features, having neither megameronephridia nor median stomate nephridia though purely meronephric. The other genera of Gates's Octochaetidae were purely meronephric and in the hindbody had median stomate nephridia, often enlarged as 'meganephridia' (megameronephridia) in addition to closed 'micronephridia', with the exception of the two Indian genera *Octochaetona* and *Octochaetoides* which were significantly products of division of *Octochaetus*. The genera with median stomate nephridia comprise the Dichogastrini of the present work.

The homogeneity of the Dichogastrini is supported by Sims's computer analysis and by virtue of their being the core of Gates's Octochaetidae. Although the author recognized the existence of the tribe independently, its validity and delineation on the basis of the type of excretory system is supported by earlier work of Gates (1940b) who dispensed with the 'obsolescent' name Octochetinae and substituted the name '*Hoplochaetella* group' which comprised *Dichogaster* (from which *Millsonia* and *Benhamia* have since been resurrected),

Hoplochaetella, *Ramiella*, *Eutyphoeus*, *Scolioscolides*, *Barogaster*, *Eudichogaster*, *Lennogaster*, *Pellogaster*, *Rillogaster*, *Priodochaeta* and provisionally also *Priodoscolex*.

References attesting the coexistence of median stomate nephridia with micromeronephridia, with the dubious exceptions of *Priodoscolex* and *Trigaster*, for all genera of the Dichogastrini are set out below. In the examples bearing an asterisk, the median stomate nephridium is known to be enlarged as a megameronephridium. Bibliographic references in parentheses denote the source of information and only coincidentally refer to authors of taxa.

Bahlia: Nephridia are undescribed but the genus is said to be similar to *Eutyphoeus* q.v. (Gates, 1945). *Barogaster*: type-species, *B. barodensis** (Gates, 1939b, p. 158). *Benhamia*: type-species, *B. rosea** (Omodeo, 1958, p. 39); *B. liberiensis** (Omodeo, 1958, p. 45). *Calebiella*: type-species, *C. parva** (Gates, 1945, p. 244). *Celeriella*: in the type-species, *C. duodecimalis*, some meronephridia (four in a segment?) are enlarged almost to the appearance of holonephridia according to Michaelsen (1907a) but in *C. quadripapillata* a single median nephridium on each side, in the hindbody, has a preseptal funnel (Gates, 1958, p. 614). *Dichogaster*: type-species, *D. damonis** (Beddard, 1889a, p. 258); *D. bolau** (Gates, 1958, p. 619); *D. titillata** (personal observations of a type-specimen). *Didymogaster sylvaticus** (Horan, personal communication). *Digaster** (part (?), see p. 75); *Eudichogaster** (Gates, 1939b, p. 160). *Eutrigaster*: in the type-account (*E. oraedivitis* Cognetti, 1904) nephridia are merely described as diffuse but Omodeo (1955) considers it to belong to the *viridis*-group of *Dichogaster*. *Eutyphoeus*: *E. foveatus**, *E. nicholsoni** and *E. waltoni** (Bahl, 1942, p. 440). *Hoplochaetella*: *H. khandalensis** (Bahl, 1947, p. 122); this genus is exceptional in that the megameronephridia, instead of being exonephric, open into a pair of longitudinal excretory canals which run along the inner surface of the body wall, one on each side of the middorsal line, from segment XX to the anal end, each canal opening separately at the place where the outer body wall passes into the wall of the rectum, a first step in the direction of the enteronephric condition (see also Gates, 1940b). *Lennogaster*: type-species, *L. yeicus*, median stomate nephridium thickened but not enlarged (Gates, 1939b, p. 183). *Megascolides*: type-species, *M. australis** (Spencer, 1888, p. 22; Bahl, 1947, p. 121); *M. raglani** and *M. urewerae** have 'meganephridia' in addition to 'micronephridia' in the posterior segments (Lee, 1959) as do some Indian species (Stephenson, 1923); megameronephridia or median stomate nephridia are not described by Lee for other New Zealand species of this genus but no indication of examination of the posterior end is given. *Millsonia**: entire genus (always?) (Omodeo, 1955); details for *M. inermis** (Omodeo, 1955, p. 222); *M. anomala** shows an interesting approach to the condition in *Hoplochaetella khandalensis*: the large megameronephridia of each side (present in XXI posteriorly) are connected to a longitudinal duct which runs on each side of the nerve cord. This duct opens to the exterior regularly in each intersegment, medianly by a minute pore whereas in *Hoplochaetella* there are no pores in the course of the duct (Omodeo, 1955, p. 220). *Neogaster*: type-species, *N. americanus*, with two pairs of nephridia in each segment (mid-body only investigated), the ventral nephridia alone having funnels (Pickford, 1937, p. 608).

Notoscolex (part, including the type-species?): Fletcher's account of the type-species indicates merely that it has parietal (exonephric?) meronephridia. Both *Notoscolex ulla-dullae** and *N. attenuatus** (Australia) have tufts which in the former are probably and in the latter are certainly pharyngeal. They also have scattered parietal micromeronephridia and, coexisting with those in each of the hindermost segments, a (stomate?) megameronephridium on each side (Boardman, 1931). The Australian species *Notoscolex* (= *Megascolides*) *albertsi** Cagnetti, 1910, has enlarged (stomate?) ventral nephridia from segment XXX posteriorly. *Omodeona*: in the type-species, *O. proboscoides**, there is in each of the posterior segments, on each side, a large megameronephridium, shortly lateral of the nerve cord and below the gut. It has a large preseptal funnel and a wide duct which enters the parietes shortly in front of seta *c*. Lateral to the megameronephridium there are, on each side of the body, three or four very small micromeronephridia (personal observations of a syntype).

Pellogaster: type-species, *P. bengalensis**, (Gates, 1939b, pp. 200, 203). *Priodochaeta**: 'meganephridia' with funnels extending to the posterior end; posterior extent of 'micronephridia' uncertain (Gates, 1940a). *Priodoscolex*: Gates (1940b) was uncertain whether this genus should be included in his '*Hoplochaetella* group'. It appears from his account of the genus that each of the posterior meronephridia, rather than merely the medianmost one, is stomate. The description is as follows: Excretory organs: two pairs of closed, exonephric (?) micronephridia (or clusters of micronephridia) on the parietes of III (?), one pair of large clusters on the parietes of IV (?), two pairs of large clusters close to the ventral parietes in IV and V, paired clusters of micronephridia on the anterior faces of the septa in VI–IX (and X–XI?) and XII–XIII; from XIV posteriorly a transversely placed, preseptal band of closed, exonephric micronephridia on each side, the band of two rows; in the posteriormost segments a single transversely placed row of 10–12 small, exonephric micronephridia on each side with a corresponding row of preseptal funnels.

Ramiella: (Gates, 1958, p. 610); *R. parva* and *R. pachpaharensis* (Bahl, 1942, p. 441; contrary to Stephenson who found no septal connections or funnels). The small number of meronephridia, the absence of pharyngeal and of other enteronephry (Bahl, 1942, p. 441) and the absence or rudimentary condition of calciferous glands in *Ramiella* appear to be primitive features and suggest that with the partly holonephric *Howascolex* (Indian section), *Ramiella* is a little-changed representative of the ancestral stock of the Indian and other genera of the Dichogastrinae. *Neogaster americanus*, like the type-species, *Ramiella bis-hambari*, has only 2 pairs of meronephridia per segment (including the median stomate nephridia) but has well developed calciferous glands.

Ramiellona: like *Ramiella*, this genus lacks enteronephric nephridia. There are several ranks of meronephridia on each side, the median nephridium on each side in posterior segments having a preseptal funnel, *vide R. guatemala*, *R. balantina*, *R. strigosa* and *R. mexicana*, in all of which the median stomate nephridium is not enlarged (Gates, 1962c, pp. 198, 203, 207, 211) and *R. irpex*, in which the median stomate nephridium is described

as a meganephridium. (Pickford, 1937, p. 607). *Rillogaster**: (Gates, 1939b, p. 207); Bahl (1942, p. 446) drew attention to the similarity of the excretory systems of *Scolioscolides*, *Barogaster*, *Eudichogaster*, *Lennogaster*, *Pellogaster* and *Rillogaster*.

Scolioscolides: type-species, *S. bergtheili** (Gates, 1937, p. 309; Bahl, 1942, p. 446). *Spenceriella* (part, excluding the type): *S. gigantea** (Lee, 1959, p. 344).

Trigaster: the condition in this genus is not entirely certain. Gates (1962b) states that the nephridia of *T. cavernicola* form at least six longitudinal ranks posteriorly; those of the median rank are larger than the others but funnels are not mentioned and he queries that they may be composite. *Wegeneriona*: Pickford (1937, p. 608) who placed *W. michaelsoni* in *Howascolex*, states that this species has two or three pairs of nephridia in each segment of the middle region of the body which she examined, and that the ventralmost nephridium appeared to have a septal attachment though she was unable to state definitely that a septal funnel was present.

Median stomate nephridia also occur in some genera of Gates's Megascolecidae, and the condition presumably indicates phylogenetic relationship with the Dichogastrini, but in the 'megascolecoid' genera the stomate nephridia discharge into the intestine, with the notable exception of some species of *Notoscolex* and of *Didymogaster sylvatica*. In these species they remain exonephric and in view of the reduction in significance of the racemose condition of prostates, demonstrated in the present work there seem no barriers to placing them in the Dichogastrini. This step resolves yet another anomaly to which Sims (1966) drew attention, clustering of *Notoscolex* with the octochaetine genera.

The position of *Hoplochaetella* deserves special mention. It alone of the Dichogastrini has intestinal enteronephry of the posterior stomate megameronephridia. This might appear to necessitate placing it in the Megascolecini but the close affinity to octochaetine genera and isolation from 'megascolecoid' genera demonstrated by Sims (1966) suggests that there is more justification in grouping it in the Dichogastrini. Its highest coefficient of similarity (16.3%) was with the dichogastrin genus *Lennogaster* in Sim's analysis, the low figure indicating its relatively isolated position. Its two pairs of openings of the male ducts is unique in the megascolecoid earthworms and exceedingly rare in megadrile oligochaetes.

Genus **Digaster** Perrier, 1872, emend. Jamieson, 1963

Terrestrial worms ranging from slender forms little more than an inch long to inch-wide specimens over 5 feet in length. Segments less than 100 to over 300. Pigmentation of the body wall present or absent. Prostomium very variable. Setae 4 pairs per segment, rather widely to closely paired. Clitellum annular or saddle-shaped, embracing part of the region between intersegments 11/12 and 19/20. A pair of pores, each of the united prostatic duct,

and sperm duct of its side, present in XVIII. Accessory puberty papillae frequently present in the vicinity of the male pore segment or in the forebody. Female pores 1 pair, or single and median, presetal in XIV. Spermathecal pores 2 pairs, in 7/8 and 8/9 with sometimes (intraspecific variation in *D. longmani*) a third pair in 6/7. Position of the first dorsal pore variable, usually in 5/6 or 11/12.

Two gizzards, in V and VI, or in VI and VII (perhaps in V and VII in the type-species); or 3 gizzards, in V, VI and VII; oesophagus usually highly vascularized and showing partial or complete development of calciferous glands; intestine commencing in XVII and XVIII, exceptionally in XVI. Dorsal blood vessel single; last hearts in XII or less commonly in XIII. Meronephric; some species with tufted enteronephric and/or exonephric nephridia formed by apposition of ducts of micromeronephridia; some species with megameronephridia in addition to micromeronephridia posteriorly. Holandric or metandric; (always?) lacking testis-sacs. Prostates racemose with branched ducts within the gland. Sperm ducts (always?) uniting entally with the prostate ducts. Spermathecae 2 pairs, in VIII and IX, or 3 pairs, in VII, VIII and IX, each (always?) with 1 or more diverticula which are never long tubes.

DISTRIBUTION: Australia: New South Wales, Queensland and Victoria.

TYPE-SPECIES: *Digaster lumbricoides* Perrier, 1872.

SPECIES (All Australian):

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| 1. <i>Digaster anomala</i> Jamieson, 1970b | 8. <i>Digaster longmani</i> Boardman, 1932 |
| 2. <i>Digaster armifera</i> Fletcher, 1887a | 9. <i>Digaster lumbricoides</i> Perrier, 1872 |
| 3. <i>Digaster bradburyi</i> Jamieson, 1970b | 10. <i>Digaster minor</i> Spencer, 1900 |
| 4. <i>Digaster brunneus</i> Spencer, 1900 | 11. <i>Perissogaster nemoralis</i> Fletcher, 1889a |
| 5. <i>Perissogaster excavata</i> Fletcher, 1888a | 12. <i>Digaster perrieri</i> Fletcher, 1889a |
| 6. <i>Digaster gayndahensis</i> Spencer, 1900 | 13. <i>Perrisogaster queenslandica</i> Fletcher, |
| 7. <i>Digaster lamingtonensis</i> Michaelsen, 1916 | 1889a |

REMARKS: The trigastric genus *Perissogaster* Fletcher, 1887a, was included in *Digaster* (Jamieson, 1963) because of the demonstration of intraspecific variation from two to three gizzards in *D. perrieri* and because of general similarity of the two genera. The author (Jamieson, 1970b) demonstrated the dichogastrin condition of posterior nephridia in *Digaster anomala* (a species closely resembling the type-species, *D. lumbricoides*), in *D. bradburyi* and in *D. armifera* and previously demonstrated megameronephridia occurring alongside exonephric micromeronephridia, although funnels were not demonstrated for the megameronephridia, in *D. lamingtonensis*, *D. longmani* and *Perissogaster queenslandica* (vide Jamieson, 1963). On the other hand the latter paper showed the type-species of *Perissogaster*, *P. excavata*, and also *P. nemoralis*, to lack stomate nephridia having only

dense astomate (exonephric?) micromeronephridia in posterior segments. It thus appears that the latter two species should be placed in a re-established *Perissogaster*, a genus which, from its excretory system, appears to belong in the Megascolecini. Resurrection of *Perissogaster* will be deferred pending further revision of the *Digaster-Perissogaster* complex.

Genus **Didymogaster** Fletcher, 1887

Setae 8 per segment, rather widely paired, all ventral, none penial. Clitellum occupying XIII–XVIII. Prostates 1 pair, with small lobules, their pores (combined with the male pores?) anterior on XVIII. Genital markings present. Female pores paired, median to *a* lines, in XIV. Spermathecal pores conspicuous, 3 pairs intrasegmental in IX, X and XI. First dorsal pores in 4/5.

Gizzards 2, moderately developed in VI and VII. Calciferous glands absent. Intestine commencing in XVII. Dorsal blood vessel single; or double only intrasegmentally. Mero-nephric with stomate exonephric megameronephridia median to micromeronephridia posteriorly; tufted nephridia absent. Holandric; paired testis-sacs present, confluent medianly and intersegmentally. Seminal vesicles in IX and XII. Ovaries and funnels in XIII. Spermathecae in VII, VIII and IX, 2 segments in front of their pores; each with a small diverticulum.

DISTRIBUTION: Australia: New South Wales. New Zealand (?).

TYPE-SPECIES: *Didymogaster sylvaticus* Fletcher, 1887a.

OTHER SPECIES: None known.

REMARKS: Lee (1959) rightly considered the New Zealand record to be dubious. The type-species was redescribed by Stephenson (1933) and distinction from *Digaster* was upheld by Jamieson (1963). Stephenson did not observe stomate nephridia but these have been demonstrated in this laboratory and in a configuration which indicates that *Didymogaster* must be transferred to the Dichogastrini from the Megascolecidae s. Gates though remaining isolated in the extremely unusual location of the spermathecal pores.

This unusual worm is common in the Audley National Park and in adjacent regions of New South Wales where *Livistona* palms occur.

Genus **Megascolides** McCoy, 1878

Setae 8 per segment. Clitellum developed over at least four segments between XII and XIX, usually annular. Male pores 1 pair, on XVIII, combined with the pores of a pair

of tubular prostates, not always on papillae. Female pores on XIV; paired, ventrolateral, or unpaired, median ventral. Spermathecal pores 1–5 pairs, anterior to 9/10. Gizzard single, in V, or VI or VII; calciferous glands present or (typically) absent. Dorsal vessel usually unpaired, occasionally paired; 2–5 pairs of hearts, the last in XII or XIII. Meronephridia numerous in each segment; usually in lateral bands, occasionally concentrated in ventrolateral tufts. The median nephridium on each side in each posterior segment typically possessing a preseptal funnel. Holandric; testis-sacs absent. Seminal vesicles in any or all of IX, X, XI, XII. Penial setae present or absent. Spermathecae diverticulate.

DISTRIBUTION: Australia including Tasmania. New Zealand (restricted to northern North Island). North America.

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

AUSTRALIAN SPECIES:

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|--|---|
| 1. <i>Megascolides australis</i> McCoy, 1878
(synonym <i>Notoscolex gippslandicus</i>
Fletcher, 1888b) | 3. <i>Megascolides nokanenaensis</i> Michaelsen,
1907b |
| 2. <i>Megascolides diaphanus</i> Spencer, 1900 | 4. <i>Cryptodrilus polynephricus</i> Spencer, 1895
5. <i>Cryptodrilus tenuis</i> Fletcher, 1889a |

REMARKS: The genus is a congeries which requires revision. Separation from *Spenceriella* solely by possessing eight rather than many setae per segment is unsatisfactory. The type-species differs further from that of *Spenceriella* in lacking calciferous glands and in having the last hearts one segment further posteriorly, in XIII, and it remains to be seen whether additional and more significant features separate the two genera. *Megascolides* was distinguished from *Notoscolex* by Michaelsen (1907b) by the unbranched condition of the central canal of the prostates. Earlier (Michaelsen, 1900) he had distinguished it from *Notoscolex* by possession of a pair of 'meganephridia' in addition to 'diffuse' nephridia in the hindbody and ignored the condition of the prostates which were stated to be tubular or racemose in each genus, though the existence of racemose prostates in *Megascolides* was questioned. The nephridia of the type-species of *Notoscolex* are described as small tufts of glandular tubes attached to the coelomic wall and most conspicuous in some anterior segments (Fletcher, 1887a) but there is no certainty that the *Megascolides*-condition of the nephridia is not found posteriorly, as it is in some *Notoscolex* species and revision of the two genera should be made *paru passu*. The type-species of the *Notoscolex* differs from *Megascolides australis* in possessing calciferous glands but the significance of this difference, at least in Australian earthworms, is uncertain as glands may be present or absent in closely similar species of *Megascolex* (personal observations).

Apart from *M. australis* (the type-species) only *M. nokanenaensis* qualifies for inclusion in *Megascolides*, and in the Dichogastrini, in having megameronephridia in addition to

micromeronephridia in posterior segments. Of the remaining species, *M. diaphanus*, *Cryptodrilus tenuis* and *C. polynephricus* have, respectively, two, three and five (stomate?) nephridia on each side in each segment and their affinities are uncertain. They probably have affinities with the Perionychini.

Twenty-two New Zealand species, nearly half of the generic total, are described by Lee (1959). Very few of them are known to have median stomate nephridia and their affinities appear to lie with the Megascolecini as is suggested, though not unequivocally, by the dendrogram given by Lee (in press). It is therefore noteworthy that Gates (1940a) divided the Indian species of *Megascolides* among the genera *Scolioscolides*, and *Barogaster* (*Dichogastrini s. mihi*) and *Travoscolides* (*Megascolecini s. mihi*) and considered affinities of the Assamese species *M. antrophyes* Stephenson, 1924, to lie with the *Tonoscolex-Nelloscolex* group (also *Megascolecini s. mihi*).

N. American species are described by Smith (1937) and Macnab and McKey-Fender (1948).

Genus *Notoscolex* Fletcher, 1887a

Setae 8 per segment; prostates 1 pair, with branched system of ducts, externally racemose or sometimes appearing tubular, their pores (always?) combined with the male pores, on XVIII. Female pores in XIV. Spermathecal pores 1-3 pairs, the last in furrow 8/9 (in certain abnormal species in 7/8).

Gizzard in V or VI. Calciferous glands lacking or one to at least six pairs in the region of XI-XVII. Intestinal origin in one of XV-XIX. Micromeronephridia only present (species to be transferred to the Megascolecini), or (*Dichogastrini*) these associated with megameronephridia.

DISTRIBUTION: Australia. New Zealand (1 species). South India and Ceylon.

TYPE-SPECIES: *Notoscolex camdenensis* Fletcher, 1887a. (New South Wales).

AUSTRALIAN SPECIES:

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|---|---|
| 1. <i>Megascolides albertsi</i> Cognetti, 1910 | 6. <i>Cryptodrilus campestris</i> Spencer, 1895 |
| 2. <i>Notoscolex attenuatus</i> Boardman, 1931 | 7. <i>Cryptodrilus dubius</i> Spencer, 1892a |
| 3. <i>Notoscolex brancasteriensis</i> Michaelsen, 1910b | 8. <i>Cryptodrilus fastigatus</i> Fletcher, 1889a |
| 4. <i>Notoscolex camdenensis</i> Fletcher, 1887a | 9. <i>Notoscolex grandis</i> Fletcher, 1887a |
| 5. <i>Megascolides cameroni</i> Spencer, 1892a | 10. <i>Notoscolex hortensis</i> Michaelsen, 1907b |
| | 11. <i>Megascolides hulmei</i> Spencer, 1892 |

12. *Megascolides illawarrae* Fletcher, 1889a
13. *Cryptodrilus illawarrae* Fletcher, 1889a
(homonym)
14. *Megascolides insignis* Spencer, 1892a
15. *Cryptodrilus irregularis* Spencer, 1895
16. *Notoscolex jenolanensis* Michaelsen, 1907c
17. *Notoscolex leai* Michaelsen, 1910b
18. *Notoscolex leios* Jackson, 1931
19. *Notoscolex maecenatis* Michaelsen, 1907b
20. *Cryptodrilus mediocris* Fletcher, 1889a
21. *Notoscolex modestus* Michaelsen, 1907b
22. *Cryptodrilus mudgeanus* Fletcher, 1889a
23. *Megascolides obscurus* Spencer, 1892a
24. *Cryptodrilus officeri* Spencer, 1895
25. *Notoscolex prestonianus* Michaelsen,
1907a
26. *Megascolides* (?) (*Notoscolex*) *pygmaeus*
Fletcher, 1889a
27. *Cryptodrilus queenslandica* Spencer, 1900
28. *Notoscolex rubescens* Michaelsen, 1907b
29. *Cryptodrilus rusticus* Fletcher, 1887a
30. *Cryptodrilus saccarius* Fletcher, 1887b
31. *Megascolides simsoni* Spencer, 1895
32. *Cryptodrilus simulans* Fletcher, 1889b
33. *Cryptodrilus singularis* Fletcher, 1889a
34. *Megascolides sinuosus* Spencer, 1892a
35. *Notoscolex* (*Trinephrus*) *suctorius*
Michaelsen, 1907b
36. *Notoscolex ulladullae* Boardman, 1931
37. *Megascolides victoriensis* Spencer, 1892a
38. *Cryptodrilus wellingtonensis* Spencer,
1895

REMARKS: The above definition is based on Stephenson (1930) and a discussion of the genus by Gates (1960), who removed *N. pumila* (Stephenson, 1931) as the type of *Lenno-scolex*. Gates rightly states that *Notoscolex* is a congeries with no geographical justification and that it is not based on the over-all similarity which is to be expected in species so closely related as to belong in one genus. No attempt can be made here to revise this large genus.

The genus was placed in the Megascolecidae *s. strict.* by Gates (1959) and was retained in the Megascolecinae *s. strict.* by Sims (1966) despite the fact that the example he considered (*N. lunatus* Gates, 1929) showed its closest affinities to lie with *Eudichogaster* (Octochaetidae *s. Gates*; Dichogastrini *s. mihi*). As some Australian species have megameronephridia median to micromeronephridia in posterior segments they must, despite their racemose prostates, be referred to the Dichogastrini, a transfer supported by Sims's computer analysis. The condition of the nephridia in the hind body in the type-species is unknown but its similarity to the dichogastrin *Notoscolex ulladullae* suggests that the two species are strictly congeneric.

Tribe PERIONYCHINI

Male and prostatic pores coincident, or (*Diplotrema* part, New Caledonia) near together, on XVIII; sometimes with a single median combined male and prostatic pore. Prostates one pair, tubular to racemose. Purely holonephric, or with meronephridia in a varying number of segments anterior to holonephridia; never (?) with intestinal enteronephry.

DISTRIBUTION: NEARCTIC: N. America; Queen Charlotte I. NEOTROPICAL: Guatemala; Northern S. America. ORIENTAL: India; Ceylon; Burma. AUSTRALIA (including Tasmania).

NEW ZEALAND (and Chatham I.). NEW CALEDONIA. SUBANTARCTIC ISLANDS: Auckland I.; Snares I.; Stewart I.

Pontodrilus circummundane on sea shores in the warmer parts of the world, including the PALAEARCTIC.

TYPE-GENUS: *Perionyx* Perrier, 1872. (India).

GENERA: (see Jamieson, 1971a).

AUSTRALIAN GENERA: *Diporochaeta* Beddard, 1890; *Fletcherodrilus* Michaelsen, 1891; *Heteropodrilus* Jamieson, 1970a; *Plutellus* Perrier, 1873; *Pontodrilus* Perrier, 1874; *Pseudoperichaeta* Jamieson, 1970a and *Woodwardiella s. strict.*

REMARKS: *Perionyx* and *Woodwardiella* were the only genera of Gates's Megascolecidae which possessed holonephridia. *Perionyx* Perrier, 1872, restricted by Gates (1960) to oriental species, includes some species in which there are several holonephridia (?) per segment which are not, in Gates's view, to be considered meronephridia as all are stomate. The affinity of these requires further investigation. Where there is a pair of holonephridia, the pores are in a single series on each side or alternate and nephridial vesicles (bladders) are sometimes present. The type-species, *P. excavatus*, lacks vesicles and has nephropores in a rather irregular, approximately midlateral rank on each side.

Comarodrilus Stephenson, 1915 (Cochin, India) is here placed in the Perionychini as it has a pair of 'meganephridia' (presumably holonephridia, a term not employed at that date) in each segment behind XII. In II to XII it possesses parietal and septal micromeronephridia. The nephridia have not been reinvestigated since Stephenson's original description of the type-, and only, species, *C. gravelyi*, and absence of meronephridia behind XII requires confirmation.

With regard to *Diporochaeta*, the nephridia of *Diporochaeta davallia* were described by Jamieson (1970a). It is found, like the closely similar *Pseudoperichaeta smithi*, to have anterior meronephric tufted nephridia with composite ducts but, whereas those of *smithi* are limited to a single segment, those of *D. davallia* extend from segment II for about one third of the length of the intestine; stomate holonephridia are present further posteriorly. Lee (1959) records only holonephridia (with large ovoidal vesicles) for the type-species, *D. intermedia* (Beddard, 1888) which is doubtfully congeneric with *D. davallia*.

Fletcherodrilus Michaelsen, 1891, here separated from *Plutellus* with which it was synonymized by Michaelsen, 1910a, p. 22, has holonephridia only. The form and arrangement of the nephridia and features such as the single median male pore indicate that the

type-species, *F. unicus*, is not congeneric with the type-species of *Plutellus*, *P. heteroporus*. In a specimen of *F. unicus* from the Numinbah Valley, Queensland, examined by the writer, the first nephridial bladder opens to the exterior anteriorly in III. In III–VIII, the terminal bladder is a bilobed sac, with ental and ectal chamber, the terminal tubule of the nephridium entering the ental chamber. In segment IX the ectal chamber is beginning to elongate as a diverticulum or caecum. By XV the diverticulum reaches its maximum size, this being almost twice the longitudinal extent of the segment. In XX posteriorly the diverticulum is an only slightly elongate sac and is joined ectally by the widened, bladderlike end of the terminal tubule. The nephropores form a single series on each side, in *d* lines. The prostrate glands are thick, tortuous, short tubes with a wide central lumen. The nephridia of *Heteropodrilus* are stomate holonephridia the postseptal portions of which commence in II and are equipped with very large subspherical vesicles. The pores show a peculiar alternation which is remarkably constant in the ten species of the genus. *Woodwardiella*, the genus in which *Heteropodrilus* was previously included, appears from an examination of the type-species which, however, requires confirmation, to have tufted (meronephric?) nephridia in some anterior segments in addition to avesiculate stomate holonephridia and the nephropores are apparently in a single series on each side. A very close relationship between *Heteropodrilus* and *Plutellus manifestus* has been demonstrated (Jamieson, 1970a). The latter species has subspherical vesicles as in *Heteropodrilus* but the alternation of pores differs in detail from that in the latter genus and agrees exactly with that described by Perrier (1873) for the type-species of *Plutellus*, *P. heteroporus*. Despite a difference in the arrangement of calciferous glands, the last glands being in XIII in *manifestus* and XII in *heteroporus*, the two species are evidently congeneric, very closely related, and constitute *Plutellus s. strict.* in the present work. Inclusion of *Heteropodrilus* and *Plutellus* in the same tribe is therefore justified.

Pontodrilus is totally holonephric and its nephridia commence in the region of the clitellum. Nephropores are in a single row on each side (see p. 89). In no species have nephridial vesicles been reported.

Pseudoperichaeta has a pair of anterior meronephric tufts with composite ducts followed in the succeeding segments by stomate, avesiculate holonephridia.

A series thus exists in the Perionychni, though it is not suggested that it is an actual evolutionary lineage, in the direction of increasing development of meronephry. It commences with total holonephry, as in *Perionyx* (most species), *Plutellus*, *Fletcherodrilus*, *Heteropodrilus*, and supposedly the type-species of *Diporochaeta*, and proceeds to modification of the first pair of nephridia as exonephric (astomate?) meronephric tufted nephridia in *Pseudoperichaeta*, to several pairs of (meronephric?) tufts in *Woodwardiella s. strict.*, and finally to development of astomate tufted nephridia through many anterior segments in *Diporochaeta davallia*. This entire series occurs in Australian species. Australia thus harbours the most primitive known megascolecines. Although *Pontodrilus* (circummundane) is totally holonephric, absence of preclitellar nephridia could conceivably have been

preceded by the development of meronephry in that region. This seems unlikely, however, in view of apparent affinities with *Plutellus* and the demonstration by Hague (1923) of anterior holonephridia in juveniles of *Sparganophilus* (Glossoscolecidae) which similarly lacks preclitellar nephridia in the adult and is similarly amphibious. If Stephenson's account of *Comarodrilus* is correct, this Indian genus stands apart from the Australian genera which also have partial meronephry in lacking tufted nephridia.

It may be necessary, when knowledge of the Megascolecinae is more complete, to subdivide the Perionychini into further tribes as association on the presence of holonephridia may represent a grade rather than a clade. However, as the holonephric condition is evidently primitive relative to the meronephric condition, it is reasonable to conclude that the genera of the Perionychini are cladistically more closely related one to the other than they are to exclusively meronephric species. We have seen that some genera are morphologically or phenetically closely linked and that other genera appear to be closely similar. Thus *Heteroporodrilus* and *Plutellus s. strict.* are almost congeneric; *Pseudoperichaeta* and at least one species of *Diporochoeta* and apparently *Woodwardiella s. strict.*, are mutually close. These two groups are sufficiently similar for constituent genera to have been confused in the 'classical' work of Michaelsen and Stephenson. *Pontodrilus* is generally considered to have affinities with *Plutellus s. lat.* *Fletcherodrilus* is near enough to *Plutellus* to have been synonymized with it by Michaelsen while showing a number of remarkable similarities with *Perionyx* (flattened form of the body; an extreme condition of the tendency of male pores to approach the ventral midline; reddish pigmentation; irregularity of posterior setae as a possible prelude to the perichaetine condition in the latter genus). *Perionyx* in turn is closely similar (Sims, 1966) to *Diporochoeta*. Knowledge of *Plutellus s. lat.*, *Diporochoeta*, *Perionyx* and *Woodwardiella* and of most genera of the Megascolecini is very rudimentary, however, and changes in the internal classification of the Megascolecinae must be expected.

Genus **Diporochoeta** Beddard, 1890, emend. Michaelsen, 1900

Setae, at least in the mid and hind body, numerous (more than 8) per segment Clitellum developed over at least 3 segments, between XIII and XVII; annular for most or all of its length. Male pores 1 pair, on XVIII, combined with the pores of the single pair of prostates, ventrolateral, not always on papillae. Female pores 1 pair, on XIV, ventrolateral. Spermathecal pores paired, or unpaired and midventral in 2-5 intersegments, anterior to 9/10 Nephropores in a single sometimes irregular series on each side. Calciferous glands present or absent. Gizzard sometimes absent; if present, single, in V, VI or VII. Dorsal blood vessel unpaired; hearts 2, 3 or 4 pairs, the last in XI, XII or XIII. Holandric or metandric; testis-sacs absent. Prostates externally tubular or racemose or intermediate but (always?) with a central lumen which may or may not have side branches. Penial setae and copulatory muscles usually absent. Spermathecae with or without diverticula. Possessing holonephridia and with or without anterior tufted exonephric nephridia with composite ducts. Holonephridia with (e.g. type-species) or without terminal vesicles.

DISTRIBUTION: Australia: Victoria, Tasmania, Queensland. New Zealand, including Stewart, Chatham, Auckland and Snares Islands. South India.

TYPE-SPECIES: *Perichaeta intermedia* Beddard, 1888. (New Zealand).

AUSTRALIAN SPECIES:

- | | |
|--|--|
| 1. <i>Perichaeta alsophila</i> Spencer, 1892b | 22. <i>Perichaeta lochensis</i> Spencer, 1892b |
| 2. <i>Diporochaeta apiocystis</i> Stephenson, 1933 | 23. <i>Diporochaeta manni</i> Spencer, 1900 |
| 3. <i>Diporochaeta arnoldi</i> Spencer, 1900 | 24. <i>Diporochaeta mediocincta</i> Spencer, 1900 |
| 4. <i>Perionyx</i> (<i>Diporochaeta</i>) <i>athertonensis</i> Michaelsen, 1916 | 25. <i>Perichaeta moroea</i> Spencer, 1895 |
| 5. <i>Perichaeta barronensis</i> Fletcher, 1887b | 26. <i>Diporochaeta nemoralis</i> Spencer, 1900 |
| 6. <i>Perichaeta bakeri</i> Fletcher, 1888b | 27. <i>Perichaeta obscura</i> Spencer, 1892b |
| 7. <i>Perichaeta canaliculata</i> Fletcher, 1888a | 28. <i>Perionyx</i> (<i>Diporochaeta</i>) <i>phalacrus</i> Michaelsen, 1916 |
| 8. <i>Perichaeta copelandi</i> Spencer, 1892b | 29. <i>Megascolex pritchardi</i> Spencer, 1900 |
| 9. <i>Diporochaeta davallia</i> Spencer, 1900 | 30. <i>Diporochaeta richardi</i> Spencer, 1900 |
| 10. <i>Perichaeta dendyi</i> Spencer, 1892b | 31. <i>Perichaeta richea</i> Spencer, 1895 |
| 11. <i>Perichaeta dicksonia</i> Spencer, 1892b | 32. <i>Perichaeta scolecoidea</i> Spencer, 1895 |
| 12. <i>Perichaeta dilwynnia</i> Spencer, 1895 | 33. <i>Diporochaeta sedecimalis</i> Michaelsen, 1907c |
| 13. <i>Perichaeta dubia</i> Spencer, 1892b | 34. <i>Perionyx</i> (<i>Diporochaeta</i>) <i>sigillatus</i> Michaelsen, 1916 |
| 14. <i>Perionyx</i> (<i>Diporochaeta</i>) <i>erici</i> Michael- sen, 1916 | 35. <i>Diporochaeta spenceri</i> Michaelsen, 1907a |
| 15. <i>Diporochaeta euzona</i> Spencer, 1900 | 36. <i>Pericheata tanjilensis</i> Spencer, 1892b |
| 16. <i>Diporochaeta faucium</i> Michaelsen, 1907b | 37. <i>Diporochaeta telopea</i> Spencer, 1900 |
| 17. <i>Diporochaeta frosti</i> Spencer, 1900 | 38. <i>Perichaeta</i> (?) <i>terraereginae</i> Fletcher, 1889b |
| 18. <i>Diporochaeta grandis</i> Spencer, 1900 | 39. <i>Perichaeta walhallae</i> Spencer, 1892b |
| 19. <i>Perichaeta irregularis</i> Spencer, 1895 | 40. <i>Perichaeta yarrensensis</i> Spencer, 1892b |
| 20. <i>Perionyx lacustris</i> Stephenson, 1924 | |
| 21. <i>Diporochaeta lindti</i> Spencer, 1900 | |

REMARKS: The most recent account of *Diporochaeta* is that of Lee (1959) who described the ten New Zealand species, bringing the total for the genus to approximately 63 species. *D. pellucida* (Bourne, 1894) was transferred by Gates (1940a) to a new genus, *Priodochaeta*. Michaelsen (1900) established *Diporochaeta* in its present form but later (1916, 1924a) combined it with *Perionyx*, at the latter date as a subgenus. Stephenson (1923) separated the two genera, while suggesting a close relationship. Gates (1959) placed *Diporochaeta* in the Acanthodrilidae and *Perionyx* in the Megascolecidae but the two genera are here placed in the same tribe of the subfamily Megascolecinae for reasons given on p. 82.

Morphological heterogeneity in the 40 Australian species is sufficient to suggest that revision of the genus will necessitate establishment of several new genera. Jamieson (1970a) reported the existence of anterior exonephric tufted nephridia in *D. davallia* although the

genus is defined by Stephenson (1930) as 'purely meganephridial', the sole supposed distinction from *Spenceriella*. Transfer of *D. davallia* to *Spenceriella* is, however, insupportable as the latter genus is meronephric throughout the body. Some species currently placed in *Plutellus* also have anterior tufts and their distinction from species of *Diporochaeta* which have the same condition solely because their setal arrangement is lumbricine is questionably valid. Revision of *Diporochaeta* requires consideration of such species of *Plutellus* and both genera are concomitantly being reviewed in this laboratory. It appears that *Perionychella* must be resurrected for the type-species *Perichaeta dendyi*.

Genus **Fletcherodrilus** Michaelsen, 1891, emend.

Medium to large terrestrial worms (85–325 mm) with less than 160 segments. With strong purplish parietal pigmentation. Prostomium slightly epilobous. Body not canaliculate. First dorsal pore 4/5 or 5/6. Setae in 8 longitudinal rows throughout or *cd* irregular posteriorly; some posterior segments occasionally with one or two supernumerary setae. Ventral setal couples (*ab*) widely paired; dorsal couples (*cd*) distant, further apart than the two couples of a side ($cd > bc$); dorsal median intersetal distance (*dd*) equal to half of the circumference; $dd > 4cd$. Penial setae absent. Nephropores in *d* lines throughout. Clitellum annular, occupying 4 to 5 segments beginning on XIII or XIV. The combined opening of the male and prostatic ducts unpaired, midventral on a conical penis-like papilla. Accessory genital markings absent. Female pores anteromedial to setae *a* of XIV, inconspicuous. Spermathecal pores unpaired, midventral, 4 or 5, commencing at 4/5 or 5/6.

Some preclitellar septa thickened. Gizzard well developed, in VI but the post-gizzard oesophagus may not commence until anterior VIII or IX. Calciferous glands lateral, sessile pouches in XIII, XIV and/or XV with laminate internal folds but no partitions. Intestine commencing in XVIII; typhlosole and caeca absent. Dorsal blood vessel continued onto the pharynx. Dorsoventral commissural vessels in VII–XII; those of X–XII forming latero-oesophageal hearts which are unbranched ventrally; those of VII to IX slender, with dorsal but no supra-oesophageal connectives and giving off parietal branches ventrally. Supra-oesophageal vessel in IX (and further forward?)–XII. Subneural vessel absent. Nephridia stomate holonephridia; post-septal bodies commencing in II; each with a fairly large elongate bladder which, after the first few, bears a lateral diverticulum. Testes and funnels free, in X and XI; seminal vesicles 2 to 4 pairs the last on the anterior face of XII. Ovaries and funnel in XIII; ovisacs absent. Prostates thickly tubular with large central lumen; vasa deferentia joining their ducts at mid-length. Spermathecae unpaired, each discharging anteriorly in its segment; duct shorter than the ampulla and bearing, ectally, two (sometimes one) digitiform diverticula.

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

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

SPECIES (All Australian):

1. *Plutellus affinis* Stephenson, 1933
2. *Cryptodrilus* (?) *unicus* Fletcher, 1889a
3. *Cryptodrilus fasciatus* Fletcher, 1889b

REMARKS: *Fletcherodrilus* was placed by Michaelsen (1910a) in the synonymy of *Plutellus* because he had found an Indian species, supposedly belonging to the latter genus, in which the spermathecal pores were unpaired. The genus is here re-established as the type-species is clearly not congeneric with the type-species of *Plutellus* (*P. heteroporus*) or its congener *P. manifestus*. The generic account has been augmented from the author's study of material of *F. unicus* from the Numinbah Valley and of *F. fasciatus* from Binna Burra, Queensland. Highly distinctive features of *Fletcherodrilus* are the straight series of nephropores, the presence of diverticula of the nephridial vesicles; the indefinite, lateral calciferous glands and the large ratio $dd:u$.

Four species of the genus have been described three of which (*F. unicus* (Fletcher, 1889a); *F. purpureus* (Michaelsen, 1889) and *F. fasciatus* (Fletcher, 1889b)) were first assigned to *Cryptodrilus*. Michaelsen (1891) considered these to be 'varieties' with a new variety, *pelewensis*, of one species *F. unicus*. Later (1900) he placed *purpureus* in the synonymy of '*F. unicus typicus*' and *pelewensis* in *F. unicus fasciatus*. The author agrees that *purpureus* is a synonym of *unicus* but considers that *fasciatus* should be reinstated as a distinct species as the material from Binna Burra, examined in the present study differs from *unicus* in having the gizzard more posteriorly situated and no calciferous glands in XV, two differences noted also by Fletcher in the type-description of *fasciatus*. Michaelsen's var. *pelewensis*, with gizzard in VI and calciferous glands in XIII–XV presumably belongs in *unicus*. It is hoped to settle the question of specific status for *fasciatus* in a separate publication based on additional material which has been acquired since this paper was commenced.

The third valid species, *Plutellus affinis* Stephenson, 1933, differs from the others in having a single diverticulum only to each spermatheca.

Genus **Heteroporodrilus** Jamieson, 1970a

Moderate-sized to large terrestrial worms (52–580 mm long) with less than 300 and usually less than 200 segments. With or without brownish pigmentation. Prostomium variable from prolobous to tanylobous. Body with or without a narrow dorsal groove. First dorsal pore in 5/6 or 6/7 (variable intraspecifically) or rarely in 7/8 or 8/9 (?), exceptionally with a rudimentary pore at 4/5. Setae in 8 regular longitudinal lines, commencing with II. Ventral setal couples widely paired to distant (aa equal to or $< 2.5 ab$); setae of the dorsal couples (cd) widely separated, always further apart than those of each ventral couple and usually a greater interval, rarely slightly smaller, than the interval between the couples of a side ($cd > ab$ and $>$ or rarely slightly $< bc$); dorsal median intersetal distance (dd) < 0.3

of the circumference. Setae *b* and often setae *a* absent in XVIII; *b* rarely replaced by penial setae. Nephropores conspicuous at the anterior borders of their segments, in *d* lines in II–IV or V, in *c* lines for a few segments, then alternating in successive segments between *d* and *c* (or exceptionally mid *bc*) until in X, or less commonly within a segment or two of this, alternation between *b* and *d* commences and is continued to the posterior extremity. Clitellum annular, well developed on XIV–XVI, frequently extending through whole or part of XIII and XVII, rarely impinging on XVIII. A pair of combined male and prostatic pores on XVIII, in *b* lines or less commonly in *ab*. At maturity, accessory genital markings always present in the vicinity of the male pores and frequently in the fore-body, sometimes forming continuous longitudinal series; integumentary only, not represented by intracoelomic glands. Female pores a pair anteromedial to setae *a* of XIV, inconspicuous, though sometimes in a common glandular field. Spermathecal pores 2–4 pairs in or very slightly lateral to *b* lines, the last in intersegment 8/9.

Some preclitellar septa strongly thickened, gizzard vestigial to strong in V. Well developed paired sessile ventrolateral extramural calciferous glands, 3 to 5 pairs, the last always in XIII; the two members of each pair almost contiguous midventrally; the lumen of each gland divided by numerous transverse lamellae. Intestine commencing in XV or, rarely, XVI; typhlosole and caeca absent. Dorsal blood vessel (always?) continued onto the pharynx. Dorsoventral commissural vessels in VI (sometimes V?) to XIII; those of X, or (*oxleyensis*) XI, to XIII with connectives from a pair of efferent vessels which arise from the oesophagus or from its calciferous glands in each of these segments; the efferent (calciferous) vessels discharging thence into a paired or single supra-oesophageal vessel. Commissurals (hearts) of X–XIII differing from those more anteriorly situated in lacking ventral branches. A paired or single suboesophageal vessel between the calciferous vessels continuous to the anterior end of the body as a pair of ventrolatero-oesophageal vessels running median to the hearts. Nephridia stomate holonephridia, their postseptal portions commencing in II; the duct of each with a very large subspherical, thin walled muscular vesicle which lacks diverticula; nephropore with a small sphincter. Testes and funnels in X and XI, free or in unpaired pericardiac testis-sacs; seminal vesicles in IX and XII, rarely (*mediterraeus*) in XI and XII. Ovaries and funnels in XIII; ovisacs absent; septal pouches exceptionally present in XIII. Prostates one pair, racemose, sometimes (intraspecific variation) externally approaching a tubular form; vasa deferentia joining their short muscular ducts entally to ectally. Spermathecae discharging anteriorly in their segments; each with a distinct duct, shorter than or slightly longer than the ampulla, bearing one, or less commonly, two or more diverticula which sometimes are branched.

DISTRIBUTION: Australia: In the basins of the Murray-Darling (in the vicinity of the Gwydir, Barwon, Castlereagh, Lachlan and Darling Rivers); of the Wimmera River (southern Victoria); and of some Eastern coastal rivers (Brisbane R., Paramatta R. and headwaters of Mary R. and Albert R.).

TYPE-SPECIES: *Cryptodrilus tryoni* Fletcher, 1889b.

SPECIES (All Australian):

- | | |
|---|--|
| 1. <i>Woodwardiella ashworthi</i> Stephenson, 1933 | 7. <i>Cryptodrilus mediterreus</i> Fletcher, 1888b |
| 2. <i>Cryptodrilus canaliculatus</i> Fletcher, 1889a | 8. <i>Cryptodrilus oxleyensis</i> Fletcher, 1889a |
| 3. <i>Cryptodrilus cooraniensis</i> Spencer, 1900 | 9. <i>Cryptodrilus shephardi</i> Spencer, 1900 |
| 4. <i>Woodwardiella dioecia</i> Stephenson, 1933 | 10. <i>Cryptodrilus sloanei</i> Fletcher, 1889a |
| 5. <i>Cryptodrilus fletcheri</i> Beddard, 1887 | 11. <i>Cryptodrilus tryoni</i> Fletcher, 1889b |
| 6. <i>Heteroporodrilus lamingtonensis</i> Jamieson, 1970a | (synonym <i>Woodwardiella youngi</i> Boardman, 1932) |

REMARKS: This is undoubtedly a natural assemblage closely related to *Plutellus s. strict.* (see Jamieson, 1970a).

Genus *Plutellus* Perrier, 1873

Seatae 8 per segment. Male pores united with or near the pores of the single pair of tubular prostates on XVIII. Holonephric; nephridia present in front of the clitellum. Female pores a pair, or sometimes single, on XIV. Spermathecal pores paired or single, in one to five intersegments, the last in 8/9.

Gizzard well developed to vestigial, in V–VII; sometimes in two segments, V–VI or VI–VII. Calciferous glands absent or 2–5 pairs present in the region of X–XVI. Intestinal origin in XIV–XIX; typhlosome present or absent. Hearts in X–XI, XII or XIII. Holandric or meroandric; testis-sacs present or absent. Ovaries a single pair, in XIII. Penial setae present or absent. Spermathecae with one or more diverticula.

DISTRIBUTION: Australia, including Tasmania; New Caledonia; New Zealand; Auckland Is.; Queen Charlotte I.; the Pacific coastal strip of the United States; Guatemala; northern South America; India; Ceylon; Burma.

TYPE-SPECIES: *Plutellus heteroporus* Perrier, 1873. (Pennsylvania (?)).

AUSTRALIAN SPECIES:

- | | |
|--|--|
| 1. <i>Plutellus asymmetricus</i> Michaelsen, 1907b | 9. <i>Cryptodrilus ellisi</i> Spencer, 1895 |
| 2. <i>Megascolides attenuatus</i> Spencer, 1892a | 10. <i>Megascolides eucalypti</i> Spencer, 1900 |
| 3. <i>Megascolides bassanus</i> Spencer, 1895 | 11. <i>Cryptodrilus frenchi</i> Spencer, 1892a |
| 4. <i>Plutellus blackwoodianus</i> Michaelsen, 1907b | 12. <i>Cryptodrilus gippslandicus</i> Spencer, 1892a |
| 5. <i>Plutellus candidus</i> Jackson, 1931 | 13. <i>Cryptodrilus hobartensis</i> Spencer, 1895 |
| 6. <i>Plutellus carneus</i> Michaelsen, 1907b | 14. <i>Megascolides incertus</i> Spencer, 1892a |
| 7. <i>Plutellus dalgarangae</i> Jackson, 1931 | 15. <i>Cryptodrilus insularis</i> Spencer, 1895 |
| 8. <i>Plutellus decatheca</i> Michaelsen, 1910b | (homonym, see <i>Pontodrilus</i>) |
| | 16. <i>Cryptodrilus intermedius</i> Spencer, 1892a |

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| 17. <i>Plutellus levis</i> Michaelsen, 1907b | 31. <i>Cryptodrilus tanjilensis</i> Spencer, 1892a |
| 18. <i>Cryptodrilus lucasi</i> Spencer, 1892a | 32. <i>Notoscolex tasmanianus</i> Fletcher, 1888b |
| 18a. <i>Cryptodrilus macedonensis</i> Spencer, 1892a | 33. <i>Plutellus termitophilus</i> Michaelsen, 1907b |
| 19. <i>Cryptodrilus manifestus</i> Fletcher, 1889a | 34. <i>Megascolides tisdalli</i> Spencer, 1900 |
| 20. <i>Megascolides manni</i> Spencer, 1892a | 35. <i>Notoscolex tuberculatus</i> Fletcher, 1888b |
| 21. <i>Plutellus mendilai</i> Michaelsen, 1907b | 36. <i>Plutellus uncinatus</i> Stephenson, 1933 |
| 22. <i>Cryptodrilus minor</i> Spencer, 1892a | 37. <i>Plutellus varicystis</i> Jackson, 1931 |
| 23. <i>Plutellus murrayensis</i> Michaelsen, 1907b | 38. <i>Cryptodrilus victoriae</i> Spencer, 1892a |
| 24. <i>Cryptodrilus narrensis</i> Spencer, 1892a | 39. <i>Megascolides volvens</i> Spencer, 1900 |
| 25. <i>Megascolides roseus</i> Spencer, 1892a | 40. <i>Megascolides warragulensis</i> Spencer, 1900 |
| 26. <i>Cryptodrilus rubens</i> Fletcher, 1888a | 41. <i>Plutellus wellingtonensis</i> Michaelsen, 1907b |
| 27. <i>Plutellus schumanni</i> Michaelsen, 1907b | 42. <i>Plutellus whistleri</i> Michaelsen, 1935b |
| 28. <i>Cryptodrilus semicinctus</i> Fletcher, 1889b | 43. <i>Cryptodrilus willsiensis</i> Spencer, 1892a |
| 29. <i>Megascolides steeli</i> Spencer, 1900 | 44. <i>Plutellus woodwardi</i> Michaelsen, 1907b |
| 30. <i>Plutellus strelitzi</i> Michaelsen, 1907b | |

REMARKS: The above description considerably augments that of Stephenson (1930) but serves to demonstrate a morphological heterogeneity which is unacceptable, whether on phylogenetic or phenetic grounds, within a single genus. The characters which all species of *Plutellus* supposedly have in common are italicised at the beginning of the description but it should be noted that not even these are applicable to all species currently included in *Plutellus*. Thus Gates (1962c, p. 187) mentions species in which the prostates open to the exterior in XIX or XX, and *P. macedonensis* (Spencer, 1892a) has anterior tufted micromeronephridia (Horan, personal communication).

The Australian members of the genus are at present under revision in this laboratory and it is hoped that subdivision among discrete genera of approximately 105 species making up the global record will soon be practicable. Gates (1961) has already suggested that the oriental species, which differ from the type-species in lacking calciferous glands, should be placed in a separate new genus, though he has postponed this step until better characterization of the type-species becomes possible.

If, as in *Heteroporodrilus*, the nephropore arrangement seen in *Plutellus heteroporus* and *P. manifestus* is taken as a generic character, it appears that none of the Australian species other than *manifestus* can be included in *Plutellus*. Oriental *Plutelli*, all of which lack calciferous glands, must presumably be excluded. Whether the American *Plutelli* include species which are congeneric with the supposedly Pennsylvanian *heteroporus* is not known.

The supposedly Pennsylvanian origin of *P. heteroporus* has been queried by Gates (1961, p. 428). In view of the close similarity of *manifestus* (from New South Wales) it now seems likely that the type-species is Australian. Two lots of specimens were mixed in the

bottle in the Paris museum containing the types and Perrier described Australian specimens of other genera in the same collections.

Genus **Pontodrilus** Perrier, 1874

Small to moderately large littoral (mainly marine) worms. Pigmentless. Prostomium epilobous, rarely prolobous. Dorsal pores absent. Setae 8 per segment, commencing on II, in regular longitudinal rows or posteriorly irregular. Nephropores inconspicuous, in *b* lines (sometimes in *a* or *c* lines?) throughout the body. Clitellum annular, on XII, XIII–XVII, XVIII. Combined openings of a pair of tubular prostates and male ducts on XVIII, in *ab* or *b*; a male duct joining each prostate gland at its junction with its duct, where the lumina unite, or running in the gland to open into the ental end of the latter. Accessory genital markings present behind the male pores. Female pores a pair on XIV, anterior to setae *a*. Spermathecal pores 2 pairs, in 7/8 and 8/9, in *b*.

Gizzard rudimentary or absent, in front of the testis-segments. Intestine commencing in XIV (?) to XX; calciferous glands, intestinal caeca and typhlosome absent. Dorsal vessel single, complete; dorso-ventral commissural vessels in V–XIII; those of X–XIII (always?) with supra-oesophageal connectives; paired extraoesophageal vessels passing onto the oesophagus in XII–XIII and uniting midventrally in XIV–XV. Supra-oesophageal vessel typically (always?) present. Subneural vessel absent. Nephridia all avesciculate holonephridia; absent from the preclitellar region. Testes and funnels in X and XI; seminal vesicles in XI and XII. Penial setae absent (unless *lacustris* be included). Ovaries in XIII. Spermathecae diverticulate.

DISTRIBUTION: Circummundane on seashores in the tropics and warmer temperate regions (extending into the freshwater littoral in Lake Chilka, India). The lacustrine *P. lacustris* (New Zealand) and the terrestrial *P. agnesae* (India) are excluded from the above definition.

TYPE-SPECIES: *Lumbricus litoralis* Grube, 1855. (Southern France).

AUSTRALIAN SPECIES:

1. *Pontodrilus litoralis* (Grube, 1855)
2. *Pontodrilus bermudensis* Beddard, 1891

REMARKS: The above description augments that of Stephenson (1930).

The following four species can unequivocally be assigned to *Pontodrilus*:

- (1) *P. litoralis* (Grube, 1855) (syn.: *P. marionis* Perrier, 1874; *P. crosslandi* Beddard, 1905; *P. albanyensis* Michaelsen, 1907b, Jackson, 1931 (SW. Australia)).

- (2) *P. bermudensis* Beddard, 1891 (recorded from the Great Barrier Reef by Stephenson, 1931) (syn.: *Pontoscolex arenicola* Schmarda, 1861 (part); *Cryptodrilus insularis* Rosa, 1891; *Pontodrilus arenae* Michaelsen, 1892; *Pontodrilus hesperidum* Beddard, 1894; *Pontodrilus michaelsoni* Eisen, 1895; *Pontodrilus ephippiger* Rosa, 1898 (recorded from SW. Australia by Michaelsen, 1907b); *Pontodrilus laccadivensis* Beddard, 1903).
- (3) *P. matsushimensis* Iizuka, 1898 (syn.: *Pontodrilus chathamianus* Benham, 1901).
- (4) *P. gracilis* Gates, 1943.

Two further species are only doubtfully assignable to *Pontodrilus*, namely the terrestrial *P. agnesae* Stephenson, 1915, (India) and the lacustrine *Plutellus lacustris* Benham, 1903, (New Zealand) which was referred to *Pontodrilus* by Michaelsen, 1907b. Michaelsen (1922, 1928a) included *Pontodrilus* as a subgenus in *Plutellus* but Stephenson (1930) retained the two genera. Although *Pontodrilus* may have affinities with some species currently included in *Plutellus*, accordance with a restricted *Plutellus* (p. 88) is small and separation of the two genera is here endorsed.

Pontodrilus lacustris shows the following departures from the four *Pontodrilus* species from which the generic definition above has been drawn: it has four pairs of spermathecal pores; the last hearts are in XII; seminal vesicles are in IX and XI and penial setae are present. Each of these features is known to vary intragenerically in other genera but the combination sets *lacustris* apart from the four marine littoral species as does its habitat deep in a glacial lake. On the other hand, Lee (1959) states that '*Plutellus*' *parvus* Lee, 1959, is more similar to *lacustris* than it is to the two other New Zealand species assigned to *Plutellus*. Several features, including presence of calciferous glands in XIII separate *parvus* from *lacustris*, however, and while *parvus* could justifiably be made the type of a new genus, it is questionable that *lacustris* could be placed in the latter. *Pontodrilus lacustris* must therefore be regarded, until *Pontodrilus* and *Plutellus* are revised, as a species *incertae sedis*. The above conclusions are endorsed by the computer dendrogram given by Lee (in press). In it *P. lacustris* clusters with the core of *Rhododrilus* while *Pontodrilus matsushimensis*, a true *Pontodrilus*, clusters with Megascolecini *s. strict.*, *Plutellus parvus* clusters with another group of *Rhododrilus* species which have a high but apparently not generic affinity with the typical cluster. The *Rhododrilus* affinities of *Pontodrilus lacustris* and *Plutellus parvus* may suggest that there are exceptional members of the Acanthodrilini in which association of male and prostatic pores has occurred on XVIII rather than, as in *Rhododrilus*, on XVII but the present definition of the Acanthodrilini will be retained pending further evidence.

Pontodrilus agnesae is too poorly known to be placeable with certainty either in *Pontodrilus* or in the Indian section of *Plutellus s. lat.* and must, again, be regarded as *incertae sedis* at least until the type-series in the British Museum is re-examined.

Genus **Pseudoperichaeta** Jamieson, 1970a

Typically moderate-sized terrestrial worms (<150 mm) with less than 200 segments; tanylobous; dorsal pores commencing in or anterior to 4/5. Setae 8 per segment; some rows irregular posteriorly; the ventral couples widely paired, the dorsal setal couples closely paired but translocated far dorsally so that the dorsal median intersetal distance is less than *cd*. Nephropores in a single series which is slightly oblique relative to the setal lines, on each side. Clitellum annular, occupying approximately 4 whole segments and anterior to a pair of combined male and prostatic pores which are situated on XVIII in *ab*. Accessory genital markings present in the forebody and in the vicinity of the male pores. Female pores antero-medial to setae *a* of XIV. Spermathecal pores 4 pairs, the last in 8/9.

Some anterior septa moderately thickened. Gizzard in V. Extramural calciferous glands absent but oesophagus vascularised and swollen in the region of XIII–XVI. Intestine commencing in XIX. Dorsoventral commissural vessels in V–XII; hearts in X–XII, latero-oesophageal. Nephridia holonephridia (stomate and avesiculate) with the exception of the first pair which are tufted meronephridia, each tuft having a composite duct. Testes and funnels in X and XI, free; seminal vesicles in IX and XII. Prostates racemose. Ovaries and funnels in XIII. Spermathecae diverticulate.

DISTRIBUTION: The Yarra Basin, Victoria.

TYPE-SPECIES: *Cryptodrilus smithi* Fletcher 1889b. (Synonym *Megascolides punctatus* Spencer, 1900).

OTHER SPECIES: None known.

REMARKS: The genus shows affinities with *Woodwardiella s. strict.* and with *Diporochaeta davallia* (see Jamieson, 1970a).

Genus **Woodwardiella** Stephenson, 1925, emend. Jamieson, 1970a

Small to moderate-sized terrestrial worms (20–80 mm) with less than 150 segments. With or without parietal pigmentation. Prostomium variable from proepilobous to tanylobous. Body rarely (*tesselatus*) canaliculate dorsally. First dorsal pore in (3/4) 5/6 or 6/7, exceptionally (*callichaeta*) postclitellar. Setae in 8 longitudinal rows throughout or (*tesselatus*) some rows irregular; ventral setal couples widely paired; setae of the dorsal couples (*cd*) widely separated, little if at all closer together than the two couples of a side; dorsal intersetal distance <0.3 of the circumference. Penial setae present in XVIII or exceptionally (*tesselatus*) absent. Nephropores in a single series on each side. Clitellum annular on (XIII) XIV–XVII (XVIII). A pair of combined male and prostatic pores on XVIII in *a* or *ab*.

Accessory genital markings always present at maturity within the region of segments X–XIV and sometimes in the vicinity of the male pores. Female pores anteromedial to setae *a* of XIV, inconspicuous. Spermathecal pores 2 pairs, in *a* or *ab* lines, in intersegmental furrows 7/8 and 8/9.

Some preclitellar septa moderately thickened. Gizzard well developed, in V. Extramural calciferous glands absent. Intestine (always?) commencing in XVII or XVIII; typhlosole and caeca unknown. Last hearts in XII, commissurals at least sometimes beginning in VI. Supra-oesophageal vessel present (?). Nephridia holonephridia becoming tufted but apparently remaining exonephric in III and IV (*callichaeta*); vesicles unrecorded. Testes and funnels in X and XI; seminal vesicles in IX and XII or in XII only. Ovaries and funnels in XIII; ovisacs unknown. Prostates racemose; vasa deferentia joining the prostate ducts entally. Spermathecae each with a single diverticulum; the duct shorter than the ampulla.

DISTRIBUTION: Southwestern Australia (Swan and Serpentine River Basins); Tasmania (Mt Olympus and, *mortoni*, Dee Bridge); Victoria (Healesville by the Yarra), if *W. healesi* be included.

TYPE-SPECIES: *Woodwardia callichaeta* Michaelsen, 1907b.

SPECIES (All Australian):

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|---|---|
| 1. <i>Woodwardia affinis</i> Michaelsen, 1907b
(synonym <i>Woodwardiella magna</i>
Jackson, 1931) | 3. <i>Woodwardia libferti</i> Michaelsen, 1907b |
| 2. <i>Woodwardia callichaeta</i> Michaelsen, 1907b | 4. <i>Woodwardia molaeleonis</i> Michaelsen,
1907b |
| | 5. <i>Cryptodrilus tesselatus</i> Spencer, 1895 |

Species inquirenda

- | | |
|---|--|
| 6. <i>Woodwardia healesi</i> Michaelsen, 1923 | 7. <i>Cryptodrilus mortoni</i> Spencer, 1895 |
|---|--|

REMARKS: Species 1–4 occur in southwestern Australia and are undoubtedly closely related. The Tasmanian *W. tesselatus* appears to have close affinities with the latter species but knowledge of all species is insufficient for conclusive demonstration that *tessalatus* is congeneric. To avoid erection of inadequately characterized genera, Jamieson (1970a) included the Victorian *W. healesi* and Tasmanian *W. mortoni* as *species inquirenda*.

Tribe MEGASCOLECINI

Male and prostatic pores coincident on XVIII (rarely XVII); prostates one pair, racemose or (less commonly) tubular. Purely meronephric; median stomate nephridia, if present, opening into the intestine.

DISTRIBUTION: PALAEARCTIC: China; Korea; Japan. ORIENTAL: India; Ceylon; Andaman Is.; Assam; Burma; Annam; Java; Sumatra; Philippines; Moluccas. AUSTRALIAN: Australia and Tasmania; Norfolk Island; New Guinea. NEW CALEDONIA. NEW ZEALAND. Endemicity from the Mariannas, Bismarck Archipelago, the Solomons, and eastwards across the Pacific Ocean remains to be established. Some species (*Pheretima*, *Lampito*) widely peregrine.

TYPE-SPECIES: *Megascolex* Templeton, 1844.

GENERA: (see Jamieson, 1971a).

AUSTRALIAN GENERA: *Digaster* Perrier, 1872 (part only, excluding the type-species?); *Megascolex* Templeton, 1844; *Notoscolex* Fletcher, 1887a (part, excluding the type-species?); *Pheretima* Kinberg, 1866.

REMARKS: The tribe Megascolecini has been delimited so as to include only non-dichogastrin genera of the Megascolecinae which totally lack holonephridia, that is, in which total meronephry has supervened. Again although close mutual similarity of some genera can be discerned, the tribe possibly represents a grade (acquisition of total meronephry) rather than a single clade or monophyletic group and it is noteworthy that from Sims's computer analysis some genera appear to be morphologically closer to Perionychini or Dichogastrini than they are to other genera of the Megascolecini. Nearest neighbours of genera considered in Sims's analysis as shown in the matrix of coefficients of similarity were as follows (D=Dichogastrini, P=Perionychini, M=Megascolecini): *Pheretima-Lampito* (both M); *Didymogaster* (D)-*Heteroporodrilus* (P); *Lampito* (M)-*Heteroporodrilus* (P); *Plutellus s. lat.* (P)-*Acanthodrilus* (but the type-species of *Plutellus* is unquestionably close to *Heteroporodrilus*). Unfortunately the type-genus *Megascolex* was not considered and it appears that it was rarely feasible to use type-species for the various genera. Of the twelve genera of the Megascolecini, six form a group (a *Pheretima*-group) which is unified by a combination of characteristics of the excretory system. The 6 genera are: *Megascolex* (a *campestris*-group of species, excluding the type-species); *Pheretima* (East Asia, including China and Japan; Indonesia; Australia and widely spread); *Lampito* (India); *Nellogaster* (Ceylon, S. India?); *Plionogaster* (?) (Philippines and Moluccas); and, hitherto placed in the Octochaetidae, *Travoscolides* Gates, 1940a (India). In all of these there are tufts of astomate micromeronephridia (with either composite or common ducts) opening into the foregut ('pharyngeal nephridia') together with stomate meronephridia opening into the intestine and consisting of one to many pairs per segment, the intestinal enteronephric nephridia of separate segments being interconnected by one or two longitudinal excretory ducts. In addition a pair to many exonephric micromeronephridia, which in *Travoscolides* and some species of *Megascolex* (e.g. *M. cochiniensis*) form tufts, are always present anteriorly and in all but *Travoscolides* extending into the intestinal region (Bahl, 1926b, 1946, 1947; Gates, 1940a, 1943, 1945; Vidya Vati, 1947). Inclusion of *Plionogaster* in the group is

questionable as pharyngeal nephridia have not been demonstrated. Despite the unity of the *Pheretima*-group and its distinction in these nephridial characters from the remainder of the genera here included in the Megascolecini, it does not at present seem advisable to separate it taxonomically from the residue.

With regard to the remaining genera, Gates (1939a) suggests that *Tonoscolex* has arisen directly from *Nellosolex* by constriction off of extramural calciferous pouches, and Bahl (1947) places *Tonoscolex* in a morphological sequence culminating with *Travoscolides*. Thus inclusion of *Tonoscolex* and *Nellosolex* in the group of genera here termed the Megascolecini has considerable justification. *Megascolex caeruleus* (the type-species) and *M. templetonianus* which lack intestinal enteronephry may be integrated with such a sequence as primitive (simplified?) forms. If *M. caeruleus* were placed in a separate tribe the tribe containing *Pheretima* would require renaming. Of twenty four species of *Megascolex* which have been closely examined, 19 species have pharyngeal nephridia and intestinal enteronephry, while 5 species, including the type-species, are purely exonephric in the intestinal region but have pharyngeal enteronephry (Bahl, 1942, 1946, 1947; Vidya Vati, 1947). This suggests a basis for restriction of this very large genus to species lacking intestinal enteronephry. The reader is referred to Bahl (1947) for details of the series of progressively more highly developed enteronephry from *Megascolex sarasinorum* etc., through *Tonoscolex*, *Megascolex cochinchensis*, *Megascolex campester* to *Pheretima*, in turn, and thence to *Travoscolides*. In *Travoscolides* the two longitudinal suprainestinal canals of *Pheretima* are represented by a single canal which is no longer suprainestinal but has become embedded in the typhlosole. The enteronephric nephridia commence in segment XV, number 20-24 per segment, have preseptal funnels and, in contrast to *Pheretima*, are not accompanied by exonephric nephridia. A pair of pharyngeal tufts, each with a common, not composite, duct is situated in segment V, and in each of eight segments behind this is a pair of similar but exonephric tufts. Several species of *Megascolex*, including *M. cochinchensis*, have a similar arrangement of one pair of pharyngeal tufts followed by 8 or 9 pairs of exonephric tufts though with composite ducts.

The excretory system of *Lenoscolex* (type-species *Woodwardiella pumila* Stephenson, 1931) is meronephric and lacks nephrostomes. Behind the clitellum there is a pair of clusters of 4-6 small exonephric nephridia in each segment (Gates, 1960). This small South Indian genus stands apart from the *Pheretima*-group.

Genus *Megascolex* Templeton, 1844

Setae, at least in the middle and hinder parts of the body numerous (more than 8) in each segment. Prostates 1 pair, racemose, their pores on XVIII or, exceptionally, an adjacent segment; sometimes associated with penial setae. Female pores paired or exceptionally unpaired. Spermathecal pores usually 1-5 pairs, between IV and IX (the exceptions are the few cases where the pores are fused in the midline, or where they are numerous on each side in each segment). One gizzard in V, VI, or VII. Calciferous glands present or absent.

Meronephric, with or without enteronephric nephridia. Holandric, rarely metandric; testis-sacs present or absent. Ovaries in XIII. Spermathecae with or without free diverticula.

DISTRIBUTION: Ceylon and India. Australia. New Caledonia. New Zealand. Norfolk Island. Annam.

TYPE-SPECIES: *Megascolex caeruleus* Templeton, 1844.

AUSTRALIAN SPECIES:

1. *Megascolex albanensis* Michaelsen, 1907b
2. *Megascolex albidus* Jackson, 1931
3. *Megascolex andersoni* Spencer, 1900
4. *Perichaeta attenuata* Fletcher, 1889a
5. *Perichaeta australia* Fletcher, 1887a
6. *Trichaeta australis* Spencer, 1900 (homonym)
7. *Perichaeta austrina* Fletcher, 1887b
8. *Megascolex bistichus* Michaelsen, 1907b
9. *Megascolex colliensis* Michaelsen, 1907b
10. *Perichaeta coxi* Fletcher, 1887a
11. *Megascolex crateroides* Boardman, 1943
12. *Perichaeta dorsalis* Fletcher, 1888b
13. *Perichaeta enormis* Fletcher, 1889a
14. *Perichaeta exigua* Fletcher, 1888a
15. *Megascolex fardyi* Spencer, 1900
16. *Megascolex fecunda* Fletcher, 1888a
17. *Perichaeta fielderi* Spencer, 1892b
18. *Megascolex fletcheri* Michaelsen, 1907
19. *Megascolex fletcheri* Shannon, 1920 (homonym)
20. *Perichaeta frenchi* Spencer, 1892b
21. *Perichaeta frosti* Spencer, 1892b
22. *Megascolex fuscus* Michaelsen, 1916
23. *Megascolex galei* Michaelsen, 1907b
24. *Perichaeta goonmurk* Spencer, 1892b
25. *Perichaeta gracilis* Fletcher, 1887b
26. *Perichaeta halli* Spencer, 1892b
27. *Perichaeta hamiltoni* Fletcher, 1888a
28. *Megascolex harveyensis* Michaelsen, 1907b
29. *Megascolex heterochaetus* Michaelsen, 1916
30. *Perichaeta hoggi* Spencer, 1892b
31. *Megascolex jenolanensis* Boardman, 1943
32. *Megascolex illidgei* Spencer, 1900
33. *Megascolex imparicystis* Michaelsen, 1907b
34. *Perichaeta indissimilis* Fletcher, 1889a
35. *Megascolex inermis* Stephenson, 1933
36. *Megascolex larpentensis* Spencer, 1900
37. *Perichaeta lateralis* Spencer, 1892b
38. *Megascolex lobulatus* Spencer, 1900
39. *Megascolex longicystis* Nicholls and Jackson, 1926
40. *Perichaeta macleayi* Fletcher, 1889a
41. *Perichaeta macquariensis* Fletcher, 1889b
42. *Megascolex mediaeviae* Michaelsen, 1907b
43. *Megascolex minor* Spencer, 1900
44. *Megascolex mjobergi* Michaelsen, 1916
45. *Megascolex monostichus* Michaelsen, 1907b
46. *Megascolex montanus* Spencer, 1900
47. *Perichaeta monticola* Fletcher, 1888a
48. *Megascolex newcombei* Beddard, 1887
49. *Megascolex parvus* Michaelsen, 1916
50. *Megascolex purpurascens* Michaelsen, 1907b
51. *Perichaeta raymondiana* Fletcher, 1888a
52. *Megascolex rodwayi* Stephenson, 1931
53. *Perichaeta rubra* Spencer, 1892b
54. *Perichaeta steeli* Spencer, 1892b
55. *Perichaeta stirlingi* Fletcher, 1888a
56. *Megascolex swarbricki* Nicholls and Jackson, 1926

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|---|---|
| 57. <i>Perichaeta sylvatica</i> Spencer, 1892 | 63. <i>Megascolex whistleri</i> Michaelsen, 1907b |
| 58. <i>Megascolex syndetoporus</i> Jackson, 1931 | 64. <i>Megascolex wiburdi</i> Boardman, 1943 |
| 59. <i>Perichaeta tasmanica</i> Spencer, 1895 | 65. <i>Perichaeta wilsoniana</i> Fletcher, 1888a |
| 60. <i>Perichaeta tenax</i> Fletcher, 1887b | 66. <i>Megascolex zietzi</i> Michaelsen, 1907c |
| 61. <i>Megascolex terangiensis</i> Spencer, 1900 | |
| 62. <i>Megascolex torbayensis</i> Michaelsen, 1907b | |

REMARKS: An attempt is made above to augment the brief description given by Stephenson (1930) but this very large genus remains one of the major problems in oligochaete taxonomy. It is clearly a polyphyletic congeries in need of extensive revision. The type species is from Ceylon. It has 2 pairs of spermathecal pores, in 7/8 and 8/9; the gizzard in V; no calciferous glands; is holandric, though with seminal vesicles in XII only; no penial setae; and each spermatheca has a very small diverticulum concealed in the duct.

Gates (1938) reinstated the genus *Lampito* which Michaelsen (1900) and Stephenson (1930) considered inseparable from *Megascolex*.

Indian species are described by Stephenson (1923, 1924, 1925a, b) and Aiyer (1929); from Ceylon by Michaelsen (1900, 1909a, 1910a) and Gates (1941); from Assam by Stephenson (1922); from Australia by Spencer (1900), Michaelsen (1907b, c; 1916), Shannon (1920), Nicholls and Jackson (1926), Jackson (1931), Stephenson (1933), Boardman (1943); and from New Zealand by Lee (1959).

Some species, for instance the Eastern Australian *Megascolex dorsalis* (Fletcher, 1888b), are very closely similar to the genus *Pheretima*.

Genus *Pheretima* Kinberg, 1866

Digestive system without suprainstestinal and calciferous glands (calciferous tissue in low ridges that are not lamelliform in region of XIII?) but with gizzard that develops in VIII. Vascular system with unpaired dorsal, ventral and supraoesophageal trunks, a sub-neural adherent to the parietes, paired extra-oesophageal trunks median to hearts, (latero-?) oesophageal hearts in some of segments X–XIII. Excretory system meronephric; paired clusters of astomate nephridia in IV–VI with ducts opening into the pharynx; astomate exonephric, very small, V-shaped parietal nephridia numerous in each segment back from III; larger stomate nephridia with funnels in the same segment as body of tubule, on both sides of septa from XVI posteriorly, joining postseptal canals that pass to longitudinal suprainstestinal excretory ducts opening at frequent intervals into gut. Setae numerous, in a circle at the equator of each segment from II posteriorly. Ovaries fan-shaped and with several egg-strings. Male pores postclitellar. (Female always intracitellar?). Testes and

male funnels enclosed in testis-sacs; seminal vesicles postseptal. Spermathecae diverticulate and pregonadial. Prostates racemose, of mesoblastic origin, with ducts joined entally by vasa deferentia.

DISTRIBUTION: Andaman Islands. The mainland of Asia from the Chindwin-Irrawaddy axis of Burma east through Yunnan and Szechuan provinces of China, including Korea and Japan, thence south into New Guinea, Java and Sumatra. Endemicity from the Marianas, Bismarck Archipelago, the Solomons, and New Caledonia eastwards remains to be established. Peregrine species throughout the world but none yet recorded from Alaska, Greenland, the Sahara, or Arabia.

TYPE-SPECIES: *Pheretima montana* Kinberg, 1866.

AUSTRALIAN SPECIES:

1. *Perichaeta queenslandica* Fletcher, 1887b

REMARKS: The writer is indebted to Professor G. E. Gates for the above, hitherto unpublished generic description.

Several peregrine species have been found in Australia and Sims and Easton are currently studying these as part of a taxonomic revision of the genus. *Pheretima queenslandica* (Fletcher, 1887b) is questionably indigenous in Australia. In the author's experience introduced species of *Pheretima* are now the most commonly found of all earthworm species where ground has been cultivated or natural vegetation removed.

Pheretima is distinguished from *Megascolex* by the location of the gizzard. It is expected that the revision by Sims and Easton will provide more substantial differences. The Australian *Megascolex dorsalis* despite its more anterior gizzard appears to the author to have closer affinities with *Pheretima* than with the type-species of *Megascolex*. *Pheretima* is the largest genus in the Oligochaeta, with some 800 recorded species, a number which will be very greatly reduced by synonymy in the above-mentioned revision. The anatomy of *Pheretima posthuma*, including that of the excretory system, has been described in great detail by Bahl (1926a). Gates (1960) after many years of study of a large number of species found no departure in the excretory system from the *posthuma*-type but it remains to be seen whether the whole genus is uniform in this respect.

Michaelsen (1928b, 1934) recognized six subgenera as follows (slightly modified):

Archipheretima: No distinct creeping-sole on the ventral surface of the body. Clitellum occupying more than 3 segments. Intestine without caeca. Holandric. Spermathecae not multiple. Borneo, Philippines.

Pheretima: No distinct creeping-sole. Clitellum restricted to XIV–XVI. Intestine usually with caeca. Holandric with or without copulatory bursae. Spermathecae only exceptionally multiple. Southeast Asiatic and Malayan regions.

Metapheretima: No distinct creeping-sole. Clitellum restricted to XIV–XVI. Metandric. No copulatory bursae. New Guinea, New Britain, North Queensland.

Parapheretima: No distinct creeping-sole. Clitellum restricted to XIV–XVI. Intestine with or without caeca. Holandric. Copulatory bursae present, into which open glands with muscular walls. New Guinea.

Planapheretima: A distinctly differentiated creeping-sole on the ventral surface marked by an extremely dense crowding of setae. Clitellum occupying more than three segments. Intestine without caeca. Holandric. No copulatory bursae. Spermathecae not multiple. Borneo.

Polypheretima: No distinct creeping-sole. Clitellum restricted to the three segments XIV–XVI. Intestine without caeca. Holandric. Copulatory bursae present or absent. Spermathecae multiple, in pairs of transverse groups of 2 or more. Caroline Islands, Sangir Islands (introduced?). Celebes. Borneo. Malay Peninsula. Lombok. Aru Islands (introduced?). New Guinea.

The validity of these subgenera seems somewhat questionable.

Genus *Spenceriella* Michaelsen, 1907b

Prostomium zygotobous, prolobous or epilobous. Setae more than 8 per segment throughout the body or in the postclitellar region; where multiplied, 12–72 per segment. Penial setae absent. Clitellum annular or saddle-shaped, occupying 3–6 segments in XIII–XVIII. Genital markings present. Prostates 1 pair, tubular though often with lateral canaliculi from the central lumen, their pores combined with the male pores on XVIII. Female pore unpaired, midventral, or paired, in XIV. Spermathecal pores 1–3 pairs, in 6/7, 7/8–8/9, or 7/8 only. Dorsal pores (always?) present; location of the first pore variable.

Gizzard large, in V. Discrete (but not stalked?) calciferous glands 4 pairs, in X–XIII, or forming a single or somewhat intersegmentally constricted dilatation on each side in 2–3 of segments XI–XIV; always present in XIII. Intestine commencing in XVI or (*maplestoni*) XVII. Hearts 3–7 pairs, the last in XII or XIII. Supra-oesophageal vessel (always?) present. Meronephridia in broad or narrow lateral parietal bands; pharyngeal nephridia present in Australian species only. Holandric or metandric; testis-sacs absent. Seminal vesicles IX and XII, XI and XII or XII only. Ovaries and funnels in XIII. Spermathecae each with (*notabilis*) a long tubular diverticulum or with 1 or 2 small diverticula.

DISTRIBUTION: Australia: Victoria. New Zealand: northern districts and neighbouring coastal islands.

TYPE-SPECIES: *Diporochaeta notabilis* Spencer, 1900.

AUSTRALIAN SPECIES:

1. *Diporochaeta maplestoni* Spencer, 1900
2. *Diporochaeta notabilis* Spencer, 1900

REMARKS: Michaelsen (1907b) erected *Spenceriella* for four species formerly placed in *Diporochaeta* but distinguishable by their meronephry, viz. *D. notabilis* and *D. maplestoni* (Australia), both of Spencer, 1900, and *D. gigantea* and *D. shakespeari* (New Zealand), both of Benham, 1906. His tentative inclusion of *Perichaeta lateralis* Spencer, 1892b, appears unwarranted as it has 'leaf-shaped' prostates which, though branching of the ducts is not recorded, seem to necessitate inclusion in *Megascolex* as at present defined. Subsequently (1907b) he added an Indian species, *S. duodecimalis*. *S. shakespeari* was shown by Lee (1962) to be a synonym of *S.* (= *Megascolex*) *antarctica* Baird, 1871. Michaelsen (1916) transferred the New Zealand species to *Megascolex* because of lateral branching of the central prostatic lumen in *S. shakespeari*. Stephenson (1923) accepted this change but later (1930) again included the New Zealand species. Gates (1958) erected *Celeriella* for the Indian species, a genus retained in the present work. Lee (1959) was unaware of Gates's paper and retained the Indian species in *Spenceriella* while adding two further New Zealand species, *S. argillae* and *S. pallida*. His definition of the genus is partly erroneous with regard to the Australian species and a new definition of the genus has therefore been given above.

S. gigantea (Benham, 1906) from New Zealand, is known to have median megamero-nephridia posteriorly and thus qualifies for inclusion in the Dichogastrini. It may be placeable in a perichaetine section of *Megascolides*.

Even after exclusion of *S. gigantea*, *Spenceriella* shows more heterogeneity than seems acceptable in a single genus and clearly requires revision. The type-species is unique in the diverticulate form of its calciferous glands and both Australian species differ from the New Zealand species in their shorter clitellum, significantly smaller numbers of setae per segment (maximally 14 and 24) and, if Spencer's account be correct, in possessing enteronephric pharyngeal nephridia.

Affinities with *Diporochaeta* and *Megascolides* are discussed under those genera.

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