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A REVISION OF THE EARTHWORM GENUS *DIGASTER*

(Megascolecidae, Oligochaeta)

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(Figs. 1-7)

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SUMMARY

The account begins with a brief review and discussion of recent trends in the systematics of the Megascolecidae.

The genus *Digaster* Perrier 1872 is revised and *Perissogaster* Fletcher 1887 is united with it. The status of the digastric genus *Didymogaster* Fletcher 1886 is discussed and reasons are given for retaining the genus although Fletcher's definition no longer merits separation from *Digaster*.

A definition of *Digaster* s. lat. is followed by a key to all constituent species and a discussion of morphology and affinities in the genus.

Descriptions of six of the eleven species of the extended genus, based on new and/or type-material, are given, together with new information from the types of *D.* (= *Perissogaster*) *nemoralis*.

INTRODUCTION

This revision of *Digaster* stems from an identification, as *D. longmani*, of giant earthworms collected in Northern New South Wales by Miss E. Pope, of the Australian Museum. Before the taxonomic section is commenced, recent trends in the systematics of the Megascolecidae, the largest family of earthworms, and the only group of earthworms native to Australia, will be outlined.

Two recent events of major importance in the taxonomy of the Megascolecidae have been reduction in number of the Megascolecid subfamilies from four to two by Lee (1959), in his monograph of the earthworm fauna of New Zealand, and the elevation of the four subfamilies to family rank by Gates (1959). These conflicting actions reflect a common disenchantment among present-day oligochaetologists with the "*Notiodrilus* theory" adhered to so closely by Michaelsen (e.g. 1909) and by Stephenson in his great monograph (1930).

Followers of the *Notiodrilus* theory strove to arrange all Megascolecidae in a family tree springing from an Acanthodriline stem genus with the morphology of the extant *Notiodrilus*. To do this, generic definitions were limited to relatively few characters, mainly setae, location of male and prostatic openings and of spermathecal pores, number of gizzards, form of prostates and andry. The shortcomings of this system have been demonstrated by Gates (1959, 1958, 1942, etc.), who campaigned for more emphasis on somatic characters such as the blood vascular system, calciferous glands and other features of the alimentary canal, and also by Lee (1959), who gave a useful review of Michaelsen's classical work leading to the delimitation of the Megascolecid subfamilies, and by Jamieson (1963). The latter paper, and that of

Gates (1942), was an attempt to elucidate the classification of *Gordiodrilus* (Ocnodrilinae), a genus which exemplified the earlier authors' tendency to omit consideration of forms which did not conform with the accepted phylogeny and suggested the evolution of the Megascolecidae from a precursor anatomically very different from *Notiodrilus*.

In his re-classification of the Megascolecidae, Lee (1959) placed the Octochaetinae in the Acanthodrilinae and divided the Ocnodrilinae as follows: *Quechua* (i.e., *Quechuona* Gates 1941) was placed in the Megascolecinae, because of a supposed resemblance to *Plutellus*, and the remaining genera were placed in the Acanthodrilinae; *Gordiodrilus* was not referred to any subfamily. On the present evidence the author supports Gates (1939, 1959) in retaining the Ocnodrilinae as a distinct group, although not advocating their elevation to family rank. They form a satisfactorily homogenous and distinct group as defined by Gates (1959, p. 254) on the basis of intestinal origin and position of hearts. The restriction of hearts to segments x and xi appears to distinguish them from the Megascolecinae and Acanthodrilinae and clearly separates *Quechuona* from *Plutellus*. A consideration of the histology of the oesophageal diverticula of *Quechuona* (see Jamieson 1962, fig. 5) suggests that Ocnodrilinae and Megascolecinae diverticula are not always structurally homologous.

Lee (1959) extended the Megascolecinae to include all forms with the male and prostatic pores restricted to xviii, the megascolecin condition of classical terminology, and only such forms. ("Megascolecine" refers to subfamily and "megascolecin" to a condition of the male terminalia.) This represents an emphasis on the location of male terminalia relative to somatic characters which exceeds that of classical workers. Gates (1959) rejected Lee's classification for a number of reasons, notably the somatic identity of *Scolioscolides* (originally placed in the Megascolecinae, with male and prostatic pores on xviii) and the Octochaetine genus *Eutyphoeus* in which the pores lie in xvii, the microscolecin condition (Gates 1937). Similarly Jamieson (1962, p. 622) has added a new microscolecin species to the megascolecin *Quechuona* on the grounds of somatic similarity.

Gates (1959) restricted the Megascolecinae to species with racemose (i.e. *Pheretima*-type) prostatic glands. *Pheretima*-type prostates develop ontogenetically by peritoneal proliferation (i.e. are mesodermal) and acquire external openings by growth outward through the body wall (Stephenson and Ram 1919); tubular prostates are epidermal invaginations (Pickford 1937). On these grounds Gates considered gradual evolution from tubular to *Pheretima*-type prostates to be unlikely. The Megascolecinae, as thus restricted, were raised to family rank because the mesodermal origin of the prostates was considered to be "an evolutionary innovation of sufficient importance to justify more than subfamily status". Species with tubular prostates excluded from the Megascolecinae went into the Acanthodrilinae, if holonephric, and into the Octochaetinae, if meronephric, and these two subfamilies were given family status as each "seems to be entitled to the same rank as the Ocnodrilidae". Gates agreed with the later work of Michaelsen (1921, 1929) that the three groups showed close affinity, being roughly equivalent to the Acanthodrilidae of Michaelsen, but deferred formal taxonomic indication of this as scarcely worthwhile on present evidence.

Application of Gates' classification to Australian Megascolecids would have profound effects. *Notoscolex*, *Megascolex*, *Pheretima*, *Digaster* (including *Perissogaster*, see synonymy p. 87), *Didymogaster*, *Woodwardiella*, *Exxus* (Locality unknown, presumed by Gates (1959) to be Australian) and *Perionyx*, all genera with *Pheretima*-type prostates, would remain in the Megascolecidae, while *Diplostroma*, *Diporochaeta* and *Plutellus*, all with tubular prostates and holonephric nephridia, would go into the Acanthodrilidae.

Spenceriella and *Megascolides* would go into the Octochaetidae (a transfer effected by Gates 1940 for oriental species), a group not previously recorded from Australia but occurring in India and New Zealand.

The author agrees with Gates that certain Megascoleceines show Octochaetine affinities. A survey of the endemic Australian genus *Digaster* reveals that calciferous glands, partially or wholly developed, occur in all species of the genus except *D. minor* and possibly *D. lumbricoides*. Furthermore, an examination of the literature of the Australian fauna shows that calciferous glands occur frequently in other genera, including *Megascolex*, *Notoscolex* and *Megascolides*. It is remarkable that nowhere in the account of the Megascoleceinae, including sixteen genera, in Stephenson's monograph (1930) is the presence of calciferous glands, or even of intermediate structures approaching these, mentioned. On the other hand the development of "incipient" and fully formed calciferous glands in the Octochaetinae is discussed. Thus consideration of calciferous glands also suggests that the two subfamilies, as previously defined, overlap.

The question remains whether Gates' division of the Megascoleceidae of Stephenson on the basis of prostate form cuts across monophyletic groups and the possibility deserves consideration that the family would be better divided on the basis of calciferous glands and other somatic characters. Gates (1958) has constructed a satisfactory key to the genera of Octochaetinae solely on the basis of the number, location and structure of calciferous glands. The existence of prostates which are intermediate between the tubular and *Pheretima* ("lobate") type reported by Sweet (1900) would, if confirmed, remove Gates' distinction between Octochaetidae and Megascoleceidae. Lastly, it may be questioned whether the distinction between Acanthodrilidae and Octochaetidae according as nephridia are respectively holonephric or meronephric is valid. Holonephry appears to be ancestral to meronephry but the derivation may have occurred more than once, independently, in different lineages.

Only by continued attention to details of somatic anatomy, which has been characteristic of Gates' work, and the development of karyotypic studies, can a definitive classification of the Megascoleceidae be achieved. It is the author's belief that the Australian fauna, neglected for nearly thirty years, will contribute much to attainment of this objective.

SYSTEMATICS

Genus *Digaster* Perrier

- Digaster* Perrier 1872, *Nouv.Arch.Mus.Paris*, 8, 1872, pp. 94-96, illus. (Type-species *Digaster lumbricoides*; Australia, some from the neighbourhood of Port Macquarie); Michaelsen 1900, *Tierreich*, p. 196; Stephenson 1930, *The Oligochaeta*, p. 839.
- Digaster* (part.); Beddard 1895, *Monograph*, p. 484 (non *Didymogaster* Fletcher 1886 a, *Proc.linn.Soc.N.S.W.* (2), 1, pp. 554-559).
- Perissogaster* Fletcher 1887 a, *Proc.linn.Soc.N.S.W.* (2), 2, pp. 383-387 (Type-species *Perissogaster excavata*; Morpeth, and Hawkesbury River District, N.S.W.); Michaelsen 1900, *Tierreich*, p. 198; Stephenson 1930, *The Oligochaeta*, pp. 839-840.

Terrestrial worms ranging from slender forms little more than an inch long to inch-thick specimens over five feet in length. Number of segments less than 100 to over 300. Pigmentation of the integument present or absent. Prostomium very variable. Setae four pairs per segment. Clitellum ring-shaped or saddle-shaped,

embracing part of the region between intersegmental furrows 11/12 and 19/20. A pair of pores, each of the united prostatic duct and vas deferens of its side, present in segment xviii. Accessory puberty papillae frequently present in the vicinity of the male field or in the forebody. Female pores paired or united, presetal in xiv. Spermathecal pores two pairs, in 7/8 and 8/9 with sometimes (intraspecific variation¹) a third pair in 6/7. Position of the first dorsal pore variable but in most species either in 5/6 or in 11/12.

Two gizzards, in v and vi, or in vi and vii (perhaps in v and vii in the type-species); or three gizzards, in v, vi and vii; oesophagus usually highly vascularized and showing partial or complete development of calciferous glands; intestine commencing in xvii or xviii, exceptionally in xvi. Dorsal blood vessel single; last hearts in xii or rarely² in xiii. Nephridia meronephridia; some species with tufted enteronephric and/or exonephric nephridia formed by apposition of ducts of micromeronephridia; some species with megameronephridia posteriorly. Holandric or metandric; (always?) without testis-sacs. Prostates racemose with branched ducts within the gland. Vasa deferentia (always?) uniting entally with the prostate ducts. Spermathecae two pairs, in viii and ix, or three pairs, in vii, viii and ix, each (always?) with one or more diverticula.

Key to Species of *Digaster* s. lat.

- 1 Oesophageal gizzards three2
Oesophageal gizzards two, with rare intraspecific variation to three4
2. (1) Penial setae present, similar to those of *D. perrieri* (fig. 7). Male pores on slight elevations corresponding approximately to the ventral setal couples. A pair of papillae or a transverse ridge present in each of intersegmental furrows 16/17, 18/19, 19/20 and exceptionally 20/21. Spermathecae narrow cylindrical pouches with very short ducts, each with a small, lobed, knob-like diverticulum *D. nemoralis* Fletcher 1888.
Penial setae absent3
3. (2) First dorsal pore in 3/4. Spermathecal pores ventral to the setal rows. Accessory genital markings absent *D. queenslandica* Fletcher 1888.
Dorsal pores absent or present only posteriorly. Transverse depressions, reaching laterally nearly to the lateral setal rows, present anteriorly on xviii and less apparent on xix, xx and xxi *D. excavata* Fletcher 1887 a.
4. (1) Penial setae present5
Penial setae absent 6 to 11
5. (4) Penial setae as in fig. 2 *D. armifera*; p. 91
Penial setae as in fig. 7 *D. perrieri*; p. 107
6. (4) Large or giant worms. Clitellum brownish black. Male pores each situated on a low mound of which the median border only is clearly defined. Clitellar pigmentation absent between these papillae. Furrow 18/19 slightly backwardly dislocated between the ventral setal rows. Spermathecae sac-like with two convergent ovoid elongated diverticula, or a single diverticulum, sessile on the ectal end dorsally *D. longmani*; p. 101

¹*D. longmani*.

²*D. nemoralis* and *D. perrieri*.

7. (4) Large worms. Male genital field consisting of a pair of sucker-like depressions, or papillae, in furrow 17/18 and a similar unpaired structure on the left side in furrow 18/19, lying within a glandular area and slightly laterad of the male pores which are equatorial in xviii in the ventral setal rows. Spermathecal duct about half as long as the ampulla and mostly hidden by a large dorsal indistinctly lobed diverticulum arising towards its ectal end *D. lamingtonensis*; p. 98
8. (4) Small worms. Male pores equatorial on xviii in the ventral setal rows on minute papillae lying within a single lip-like ridge. A transversely oval pad with raised margins present in each of furrows 19/20, 20/21 and 21/22, reaching from the equator of the segment in front to that of the segment behind. Spermathecal ampulla spherical, almost sessile on the body wall, bearing ectally an ovoid several-chambered diverticulum..... *D. gayndahensis*; p. 96
9. (4) Small worms. Male pores on an oval patch on xviii in the ventral setal rows; a broad glandular patch present ventrally in xix. Spermathecae with relatively large ampulla and short duct bearing a lobed diverticulum at the ectal end; similar to those of *D. lamingtonensis* but smaller . . . *D. minor*; p. 105
10. (4) Fairly large worms. Male pores on papillae in the ventral setal rows; a transverse glandular region present equatorially in each of segments xvii, xix and xx and extending laterad of the ventral setal couples. Clitellum reaching furrow 19/20. Spermathecae large and sac-like, each with a very small double diverticulum..... *D. brunneus* Spencer 1900.
11. (4) Each male pore situated on a papilla adpressed to that of the other side and preceded and followed by a papilla. Spermathecae pear-shaped with short ducts; diverticula absent (?). *D. lumbricoides* Perrier 1872.

Synonymy of **Digaster** and **Perissogaster**

The genus *Digaster* Perrier 1872 is here extended to include the three trigastric species formerly placed in *Perissogaster* Fletcher 1887 *a*. Union of the two genera is necessitated, in the presence of close general similarity, by the discovery in the present investigation of intraspecific variation from two to three gizzards, in *D. perrieri* (p. 108). In this species the trigastric condition is not associated with abnormality in the distribution of other organs and the occurrence of it in two specimens of the small sample available suggests that it may be a common phenomenon in the species.

The following section deals with the morphology of *Digaster* s.lat. and serves also to indicate the basic similarity of *Digaster* s.strict. and *Perissogaster*.

Morphology of **Digaster** s.lat.

Both *Digaster* s.strict. and *Perissogaster* range in size from small worms less than 50 mm. long (*D. gayndahensis*, *D. minor* and *D. (= Perissogaster) nemoralis*) to large worms over 150 mm., i.e. 6 inches, long *D. brunneus*, *D. lamingtonensis*, *D. longmani*, *D. (= P.) excavata* and *D. (= P.) queenslandica*. *D. lamingtonensis* is known to reach a length of 273 mm., *D. (= P.) excavata* to reach 334 mm. with a width of 15 mm., a very large earthworm, and *D. longmani*, the type specimen of which was 520 mm. long, qualifies to be termed a giant earthworm, one living specimen from Kyogle in northern New South Wales (p. 102) measuring 5 feet 5 inches (1,625 mm.) with a width of 1 inch.

Secondary annulation of segments is common in the genus but reference to it is omitted from specific descriptions below because it appears to vary with the state of contraction on fixing.

Pigmentation is variable interspecifically and is sometimes, perhaps usually, absent. The setae are in eight rows but there are no setal distance ratios which are constant for the genus. Intraspecific variation in the ratios seems generally to be slight. In *D. longmani* the setae are so small relative to the bulk of the worm that they clearly do not function in locomotion. In *D. armifera* and *D. perrieri* the ventral setae of segment xviii are replaced by penial setae the presence and somewhat similar ornamentation of which tend to confirm that the two species, which have many points of close similarity, including the unique location of the gizzards in v and vi, are very closely related. The only other species with penial setae is *D.* (= *P.*) *nemoralis* which shows affinities with them in other respects (see below).

The clitellum usually embraces xiv to the anterior portion of xviii, but sometimes (*D. armifera*, *D. brunneus*) extends on to xii. The male pores are usually, therefore, immediately postclitellian but it is shown in the discussion of the status of *Didymogaster* below that the pores in *Digaster* are sometimes intraclitellian. The male genital field is associated with accessory genital markings on adjacent segments or intersegmental furrows in nine species of the genus, these markings being absent only from *D. longmani* and *D.* (= *P.*) *queenslandica*. The type-specimens of *D. queenslandica* were immature but a specimen examined by Michaelsen (1916) was clitellate and the absence of accessory genital markings in this suggests that they are normally lacking in this species. *D. longmani* conforms with other species of the genus in having glandular pads in some of the anterior segments (see Boardman, 1932). Genital markings possibly serve to secrete a mucous sheath around concopulants and, in some cases at least, to aid adhesion by acting as suckers. In the present revision of *D. armifera* and *D. lamingtonensis* it is shown that papillae associated with the male field can be invaginated to form sucker-like depressions.

The pre-setal location of the female pores in xiv is normal in the Megascolecidae but the diagonal orientation of the pores which is characteristic of *D. longmani* is unusual. Although spermathecal pores appear to lie in intersegmental furrows 7/8 and 8/9 and, in addition, in some specimens of *D. longmani* in 6/7, they probably always are situated on the extreme anterior border of the segment behind the furrow, i.e., the segment in which their spermathecae lie. All species of the genus excepting *D. lumbricoides* have been shown to possess spermathecal diverticula. The inadequate and contradictory nature of the type-description of the latter species suggests the possibility that they were overlooked.

The position of the first dorsal pore is believed to be important in determining relationships in the Oligochaeta. Gates' characteristically thorough examinations indicate that its position is constant intraspecifically; for instance, it was in 12/13 in 71 specimens of an Octochaetine species he examined (1961 p. 648). In the Lumbricidae, Muldal (1952) has shown that heterogeneity in location of the first dorsal pore is associated with significant genome differences and other morphological divergence. It is not unlikely that variation which exists in its location in *Digaster* is indicative of polyphyly. In *D. armifera* and *D. perrieri*, which resemble each other, and stand apart from the rest of the genus in several features, the first dorsal pore lies in 11/12. The location in *D.* (= *P.*) *nemoralis* is "after about segment x or xi" according to Fletcher (1888) and this species is morphologically very similar to the latter two species. It is the only other species of *Digaster* with penial setae. Re-examination of a paratype reveals that the latter resemble those of *D. perrieri* very closely. Furthermore it has tufted organs in iv, described by Fletcher as salivary glands, which appear in the re-examined type and paratype to be (enteronephric?)

nephridia. However, re-examination of the same paratype reveals a distinct dorsal pore in 10/11 and a possible rudiment in 9/10, though, owing to conspicuous secondary annulation and extreme indistinctness of setae, it is not possible to be certain of the location. Elsewhere in the genus the first dorsal pore lies in 11/12 only in *D. gayndahensis* which does not seem to be more closely related to these species than to other members of the genus, lacks penial setae and has the gizzards one segment behind those in *armifera* and *perrieri*.

“Duplication” of the gizzards was considered by Michaelsen and Stephenson to be derived from the monogastric condition of the “*Notiodrilus* ancestor” of the Megascolecidae. The author has elsewhere disputed the validity of the *Notiodrilus* theory and has presented evidence that a trigastric condition is perhaps primitive in the Megascolecidae (Jamieson, 1963).

A striking feature of *Digaster* is the tendency to complex folding of the internal walls of the oesophagus and to the development of segmental dilation of the latter so that structures which are morphologically very similar to calciferous glands are found in some species. Paired pouches are present in x to xiii, and less developed in xiv to xvi, in *D. perrieri* (p. 108). Fletcher (1888) has described “calciferous glands” in *D. (= P.) nemoralis* in x to xiv where they are “not quite so completely pinched off” as in other genera and this is confirmed in the re-examination of the holotype and paratype. Also vascularized dilation and plication of the oesophagus have been described for *D. armifera* (p. 93), *D. brunneus* Spencer 1900, *D. lamingtonensis* (p. 99), *D. longmani* Boardman 1932, *D. (= P.) excavata* Fletcher 1887 a and *D. (= P.) queenslandica* Fletcher *ibid.* Folding and vascularization without dilation is described for *D. gayndahensis* (p. 97). The condition in *D. lumbricoides* is undescribed, and in *D. minor* Spencer 1900 denies the presence of vascular swellings and of calciferous glands. The omission of reference to calciferous glands in the Megascolecinae by Stephenson (1930) has been alluded to in the introduction above.

Prostates in *Digaster* are usually of the *Pheretima*-type. Sweet (1900) states that the prostates of *Perissogaster* (now *Digaster*) *excavata* are intermediate between tubular and “lobate” (*Pheretima*-type) prostates, the conspicuous central lumen having in some cases only seven or eight side branches (for the significance of this see Introduction, above). Michaelsen (1916, pp. 22-23) has pointed out that the prostates of *Perissogaster queenslandica*, said by Sweet *ibid.* to be tubular in one specimen, are intermediate between those of *excavata* and those of Megascolecinae with typical *Pheretima*-type prostates.

No taxonomic significance can be attached at present to the segment of origin of the intestine in *Digaster*. In one species it is said to commence in xvi, in two species in xvii and in four species in xviii.

The last hearts lie in xii in nine species. The location in xiii, in *D. perrieri* (re-examination) and *D. (= P.) nemoralis* (confirmation of Fletcher 1888 from re-examination of the holotype and paratype), is interesting in view of their close similarity in other respects. The work of Gates (e.g. 1961, p. 653) indicates that the position of hearts is constant within single genera and perhaps suggests that these two species should be placed in a separate genus from *Digaster*. However, this would ignore the apparent close affinity between *D. perrieri* and *D. armifera* which has last hearts in xii. The usefulness of the vascular system in classification is thus, in this respect, still in doubt.

Commissural vessels commence in vi in *D. brunneus*, *D. gayndahensis* and *D. lamingtonensis* but they commence in iv in *D. longmani*. The blood system is difficult to elucidate even in well-preserved material and it is possible that the commencement in iv in *longmani*, the great size of which facilitates investigation, is characteristic of the genus.

Holandry (testes and funnels in x and xi) is general in the genus but metandry (these organs in the posterior segment only) has been described for *D. brunneus* Spencer 1900 and *D. longmani* (p. 104). Such variation intragenerically is of common occurrence although it was once considered to merit generic separation (*Stuhlmannia* and *Eudriloides*, in the Eudrilidae, are still separated on this basis alone).

Meronephridia occur in all species, holonephridia being absent; pseudo-tufted nephridia formed by apposition of ducts of meronephridia occur in at least *D. armifera*, *D. perrieri*, *D. (= P.) excavata* (?), and (in both syntypes re-examined) in *D. (= P.) nemoralis*. Some of these are known to be enteronephric in *D. armifera* and probably are in *D. nemoralis*. Micromeronephridia in anterior segments in *D. lamingtonensis* are probably enteronephric and in the grouping of their ducts show a condition which approaches the pseudo-tufted nephridia of other species. The occurrence of "meganephridia", i.e. megameronephridia, in posterior segments is frequent in the Megascolecinae and they occur alongside micromeronephridia in *D. lamingtonensis* and *D. longmani*, which show close morphological affinities and are the only species of *Digaster* with the dorsal pores in 5/6, and in *D. (= P.) queenslandica*. They do not occur in *D. perrieri* and *D. armifera*. The ventral nephridia are said to be larger in *D. (= P.) nemoralis* by Fletcher (1888) but this is not confirmed from re-examination of the types where the apparent ventral enlargement is seen to be due to aggregation of micromeronephridia. The condition in other species is uncertainly known.

The Status of *Didymogaster*

Didymogaster, which contains the single species, *D. sylvaticus* Fletcher 1886 a, is the only remaining genus of the Megascolecinae with more than one oesophageal gizzard. Fletcher's definition of the genus (1886 p. 555):—

"Clitellum of about five segments from xiii or xiv to xviii; male pores on xviii; female pores on xiv; eight rows of setae; two gizzards"

was at the time of composition equally applicable to *Digaster* with the single exception, which is not now applicable, that the male pores were "intraclitellian" in the material referred to *Didymogaster* whereas in Perrier's account of the type-species, *Digaster lumbricoides*, they appeared to be "post-clitellian". Such a distinction is of questionable significance. Furthermore, in *Digaster longmani* (p. 102) the clitellum extends on to the segment behind the male pores and in *D. brunneus* Spencer 1900 and *Perissogaster* (now *Digaster*) *queenslandica*; Michaelsen 1916 reaches furrow 19/20. The three species thus show the intraclitellian condition.

Beddard (1895) argued for union of *Didymogaster* with *Digaster* but was not followed by Michaelsen (1900) or by Stephenson (1930). The author's reasons for supporting retention of *Didymogaster* as a separate genus, although Fletcher's definition no longer merits this, are outlined below.

The possession by *Didymogaster sylvaticus* of three pairs of spermathecae hitherto might have been used to distinguish *Didymogaster* from *Digaster* but variation from two to three pairs of spermathecae as a normal intraspecific character of *D. longmani* has been demonstrated in the present work and is known to occur intraspecifically in other Megascolecidae. Nevertheless, in *Didymogaster sylvaticus* the spermathecae open in ix, x and xi, two segments behind their ampullae, in a segmental position, and not as in *Digaster*, at the anterior border of the same segment, i.e. in furrows 7/8, 8/9 and sometimes also 6/7.

The dorsal blood vessel of *D. sylvaticus* is described by Stephenson (1932) as single, as in *Digaster*. Fletcher (1886) described a double "supra-intestinal trunk" from which the hearts arose (clearly the dorsal vessel). The two constituent parts,

he stated, were confluent at and for a short distance on either side of each septum. The author has observed bifurcation of the dorsal vessel in this way in a specimen of *D. sylvaticus* from Commodore Heights, Pittwater, New South Wales, used for karyotypic studies. This bifurcation, in conjunction with the presence of hearts in xiii, militates against union of *Didymogaster* and *Digaster*.

Stephenson (1932) noted testis-sacs in this species. These are unknown in *Digaster*.

The location of the first dorsal pore in 4/5 noted by Stephenson (1932) and confirmed by the author in the above-mentioned specimen, distinguishes *D. sylvaticus* from all species of *Digaster* except *D. lumbricoides*, the description of which is manifestly unreliable.

Didymogaster thus differs conspicuously from *Digaster* in features of the spermathecal, vascular and male genital systems which taken together appear to constitute sufficient grounds for continued separation of the two genera.

***Digaster armifera* Fletcher 1886**

Figs. 1-2

Digaster armifera Fletcher 1886, *Proc. linn. Soc. N.S.W.*, (2) i, pt. III, 947-951, Pl. 13, figs. 1-3.

Digaster armifera; Beddard 1895, Monograph, 486.

Digaster armifera; Michaelsen 1900, Tierreich, Lief. 10, 197.

Type-locality: The neighbourhood of Sydney, N.S.W., i.e. at Marrickville (3 under a stone, April [1886?]; 1 under a stone at the same spot, July, 1886) and at Auburn, near Parramatta (6 under logs and bark, August and September, 1886).

Material examined: (All except the last two lots were presented to the Australian Museum by J. J. Fletcher, November, 1924).

1. Australian Museum Reg. No. W. 1380; many specimens labelled "*D. armifera*", from Homebush, May 24, 1888; Ryde, June 4, 1887 and Oatley, October 30, 1886, March 3, 1887 and also an "original specimen" from Old Newington, June 25, 1887 (all near Sydney). These are not type-localities and the specimens, although labelled as types, cannot be regarded as such.

2. Australian Museum Reg. No. W. 1406; 11 specimens, labelled "*D. armifera*", from Penshurst (near Sydney), August 2, September 30, 1890.

3. Australian Museum Reg. No. W. 1501; 3 specimens, labelled "*Digaster*", from Oatley, October 19, 1889, and Sutherland, April 19, 1890 (both localities near Sydney).

4 and 5. Australian Museum Reg. No. W. 1527 and 1528; two specimens labelled "*D. armifera*", from Turrumurra to Thornleigh, October, 1892, and from Carlingford, July 8, 1893 (both localities near Sydney).

6. National Museum Melbourne, Reg. No. G.93; several surface-hardened specimens, labelled "*Digaster armifera*", Baldwin Spencer Collection. No locality given.

7. Australian Museum Reg. No. W. 3764; 3 clitellate and 5 aclitellate specimens from Galston Gorge (near Sydney); in rich black sandy soil amongst rocks in *Eucalyptus-Casuarina* woodland, May, 1962, collected by B. G. M. Jamieson.

Morphological Data

These data are derived mainly from the specimens from Galston Gorge. Of these, the clitellate specimens are referred to as W. 3764 a-c. A qualitative external examination of the five acitellate specimens from this locality, which range from 54 to 95 mm. in length, revealed no differences, other than those pertaining to the reproductive condition, from the clitellate specimens. Significant variation and some other information from specimens from other localities is also included.

Dimensions: Length 72 to 137 mm., with the mode at 100 mm. (11 specimens, W.1380, W.1406, W.1501, W.3764). Maximum width between 3 and 4 mm.—*Number of segments:* 105 to 241 (4 specimens, W.1380, W.1501, W.3764).—*Colour:* In life the specimens from Galston Gorge were pigmentless grey with the clitellum and forebody suffused with pink.—*Prostomium:* Epilobous ca. $\frac{1}{3}$ (7 specimens, W.1380, W.1406, W.1501, W.3764) with the dorsal tongue broad and blunt, or acute.—*Setae:* Apparently uniform. The following data are from specimens W.3764, a-c and W.1501, a. In segment ix *cd: ab* = 1.2-1.6 (mean = 1.4); *bc: aa* = 0.6-0.8 (mean = 0.7); *dd: u* = 0.5 (four specimens); in segment xxv *cd: ab* = 1.4-1.8 (mean = 1.7); *bc: aa* = 0.8-0.9 (mean = 0.8); *dd: u* = 0.6 (four specimens).

Clitellum: Annular but often indistinct ventrally, $\frac{1}{3}$ xiii, $\frac{1}{2}$ xiii to xvii, $\frac{1}{n}$ xvii, $\frac{1}{3}$ xviii, $\frac{1}{2}$ xviii (10 specimens, W.1380, W.1406, W.1501, W.3764).—*Male genital field:* This was examined in specimens from all localities and sources listed. Its considerable variability between specimens from different localities was found to be no greater than that within samples from a single locality. Where conspicuous variation occurred it seemed referable to the degree of maturity of the male field. The greatest development of the field was seen in a specimen from Penshurst, Australian Museum Reg. No. W.1406, a, (see fig. 1a) where it has the following characteristics:—

Segment xviii is filled longitudinally by a whitish tuberculum the rounded lateral extremities of which reach to mid *bc* on the right and on the left include seta *c*. The central region of the tuberculum is slightly constricted. The male pores are a pair of short transverse slits at the sites of the absent setae *ab* (the latter are replaced by penial setae). In mid *bc* on each side the tuberculum bears two elliptical sucker-like depressions, one in front of and the other behind the setal zone.

A smaller but similar tuberculum is present on each of segments xvii and xix, the anterior extending laterally to mid *ab*, the posterior including setae *a* and *b*. Each tuberculum has a pair of suckers which lie just median to seta *a*. A suggestion of a median unpaired sucker was observed on that of xix.

All the other Penshurst specimens showed the paired suckers laterad of the male pores and on segment xix, but only one of these possessed them (a pair) on the tuberculum of xvii.

Ten specimens, from all the other localities, have fields very similar to that of the specimen described above. The absence, from some, of the suckers, of the tubercula of xvii and (or) xix, and the presence in a few of two discrete papillae in place of a single tuberculum are probably due to lesser maturity of the fields.

One of the preserved specimens and a further living specimen, both from Galston Gorge, have elliptical elevations in place of suckers. It seems probably, therefore, that muscular depression of these elevations produces the suckers and that the latter aid in adhesion of concopulants.

Accessory genital markings: A midventral squarish glandular pad is present in each of segments xi and xii (fig. 1a) in all mature specimens. These pads reach to mid *ab* and in all but two of the eleven specimens examined they fill the segments

longitudinally. In the figured specimen (W.1406, fig. 1a) the posterior pad did not extend behind the setal annulus of xii. The centre of each pad usually has a sucker-like depression of irregular outline.

Female pores: minute, a pair anteromedially from setae *a* of xiv. (Specimen W.3764, a-c; W.1501, b; not seen in others.)

Spermathecal pores (fig. 1a): Visible as paired crescentic protrusions of viii and ix into intersegmental furrows 7/8 and 8/9 in line with or slightly laterad of setal lines *a* (Specimens W.3764 a-c; W.1380, a, b; W.1406, a; W.1501, a, b).

Dorsal pores: First dorsal pore in 11/12 (W.3764, a-c; W.1501, a).

Internal characteristics:—

Septa: In sections of W.1380, a, 6/7 to 12/13 are thickened, 7/8 to 11/12 very thick, 6/7 and 12/13 about half as thick though still fairly strong, the remainder thin; septum 3/4 is the most anterior septum recognizable.—*Alimentary canal*: A strong-walled spherical gizzard lies in each of v and vi. In segments vii to xiv the oesophagus is highly vascularized and pouch-like on each side. Transection reveals that, although the walls of the oesophagus are complexly folded, it has no diverticula. The intestine

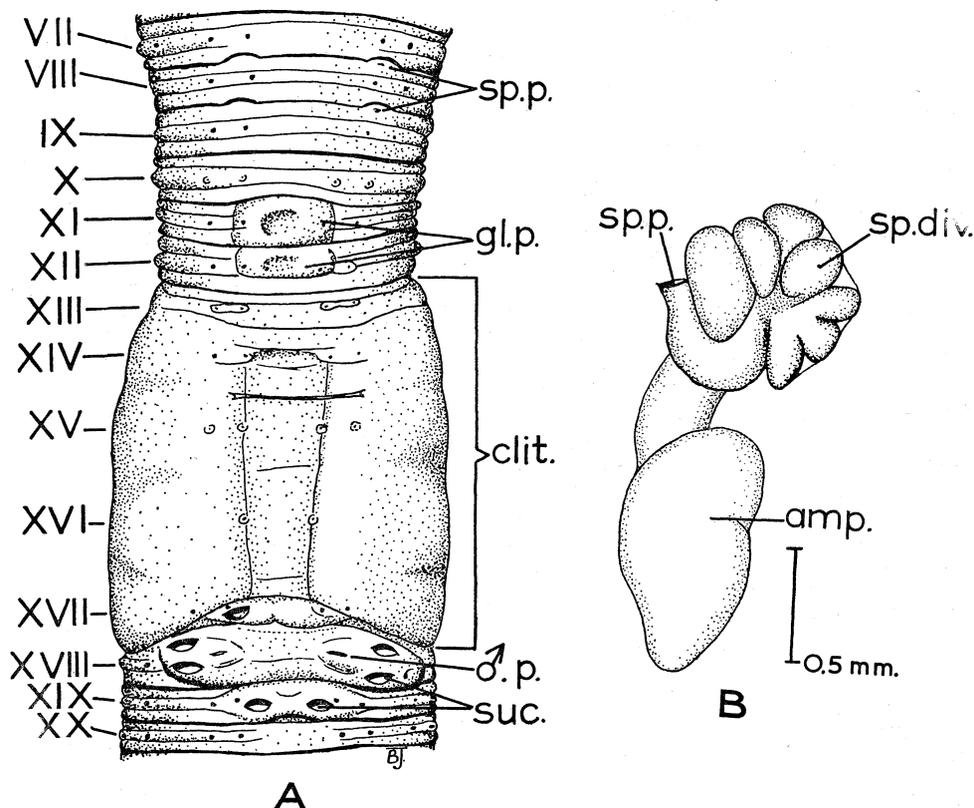


Fig. 1: A, *Digaster armifera* ventral surface in the region of the genital pores (specimen W.1406 a, from Penschurst). B, ventral view of right posterior spermatheca of same specimen. amp., spermathecal ampulla; clit., clitellum; gl.p., glandular pads; ♂ p., male pore; sp.div., spermathecal diverticulum; sp.p., spermathecal pore; suc., suckers.

commences in xvii (W.3764, a; W.1406, a). Transection in xviii reveals no typhlosole. In longitudinal sections (W.1380, a) it can be seen that each plication of the oesophageal wall consists of a single layer of cubical epithelium overlying a very large blood sinus.

Blood vascular system: The dorsal vessel is single and is greatly enlarged on the intestine. In xi to xii it gives off a pair of commissural vessels in each segment. Those in xi are very slender; the remainder are large. In xv and posterior segments the dorsal vessel gives off a vessel on each side to the laterodorsal wall of the alimentary canal. In xiii and xiv the wall is vertically striated by blood vessels but the paired vessels are not detectable (W.3764, a).

Nephridia: A pair of tufted enteronephric nephridia formed by apposition of the ducts of meronephridia is present in each of segments v and vi, their ducts passing forward to enter the alimentary canal in the region of the junction of pharynx and buccal cavity. Tufted nephridia in vii, and micromeronephridia in more posterior segments, are confined to the segment of origin and probably discharge through the parietes. (W.3764, a, and sections of W.1380, a.)

Anterior male organs: Shining sperm funnels and free sperm masses lie in x and xi. Large racemose seminal vesicles project into ix and xii from the posterior and anterior septum respectively; the posterior are the larger (W.3764, a). In the sections (W.1380) well-developed testes and funnels are present in x and xi and large racemose seminal vesicles in xii only.

Posterior male organs: Broad racemose prostate glands discharge in xviii and pass posteriorly through three segments (W.3764, a). The vas deferens of each side runs back to join the prostate duct at the ental end of the latter (W.1406, a; W.1380, b). It then runs with the prostate duct in a common muscular sheath and is distinguishable by its anterior position and its ciliation. The lumina of the two ducts unite only ectally near their common pore through which the penial setae project. Branching of the prostate duct within the gland is visible (W.1380, a, sections).

Penial setae (fig. 2): Removal of the right penial setal follicle of two specimens (W.1406, a, and W.3764, a) revealed three penial setae in each follicle. Each curves gradually from near the base so that the ectal end subtends a right angle or less with the basal portion. The ectal end is slightly thickened and bears somewhat irregular circlets of minute spines. The extreme tip is free of spines and forms a web (fig. 2, c). The lengths of the three penial setae of the right follicle of specimen W.1406, a, are 1.1, 1.5 (fig. 2, c) and 1.9 mm., with a width ental to the ornamented part of 20 μ . The two setae mounted from the right follicle of W.3764, a (fig. 2, a and b) are respectively 1.3 and 1.7 mm. long and of the same width as in the other specimen.

Female organs: A pair of ovaries in xiii (W.3764, a; W.1380 sections).—*Spermathecae* (fig. 1b): Paired in viii and ix. The spermatheca figured is from specimen W.1406, a, the male field of which is shown in fig. 1a. Each spermatheca is about 2 mm. long, has an ovoid ampulla and a wide duct into which a many chambered diverticulum opens ectally (W.1406, a; W.1501, a; W.3764, a). In sections (W.1380) the duct appears to contain a spermatophore.

Remarks

The above account extends and largely confirms the type-description of Fletcher (1886). The re-examination necessitates, however, considerable emendment of the description of the male genital field and of the penial setae, both characters of great taxonomic value. Fletcher described the two pairs of the sucker-like organs, here described (fig. 1a), as pores, either of accessory glands or for the protrusion of penial setae. He considered similar structures on xix to be, possibly, pores. The male genital field is illustrated for the first time in the present account.

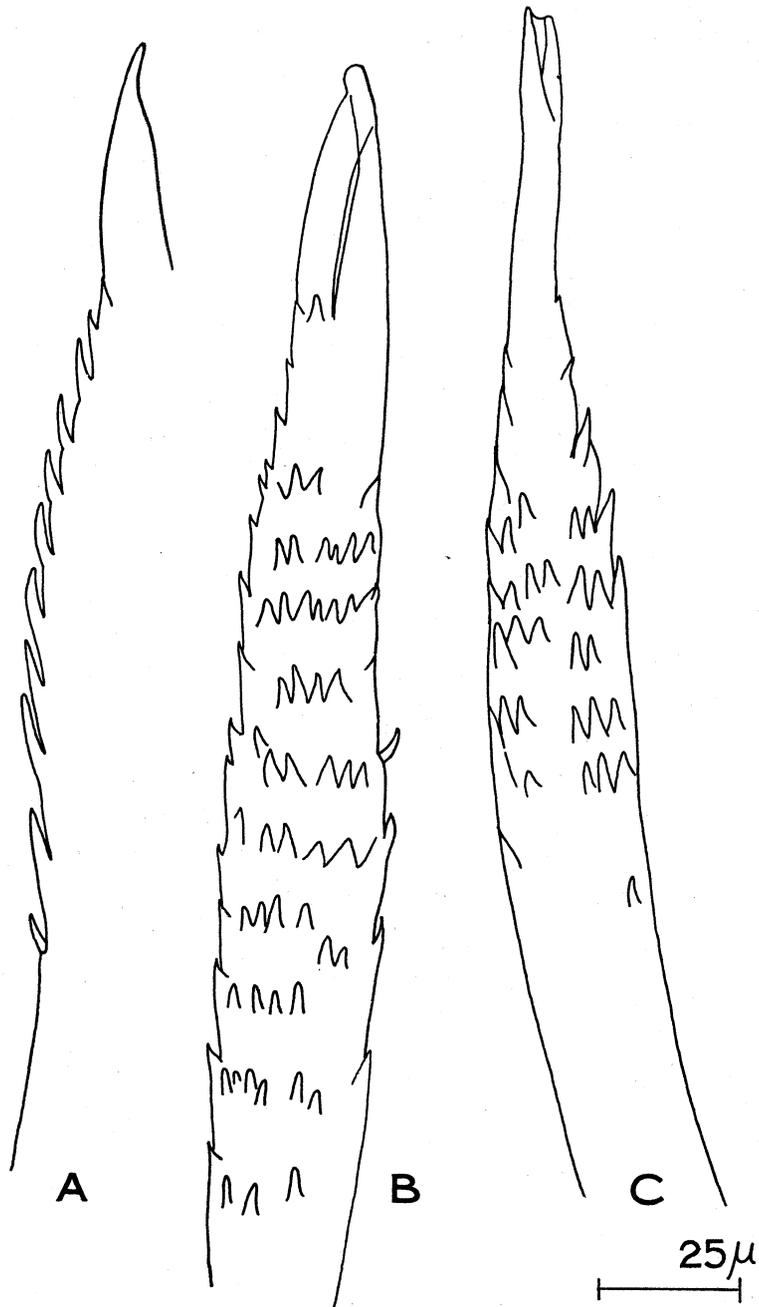


Fig. 2: *Digaster armifera*, A and B, ectal ends of two penial setae from the right follicle of specimen W.3764 a, from Galston Gorge. C, intermediate of three penial setae from the right follicle of specimen W.1406 a, from Penshurst.

Fletcher (*ibid.*) described the penial setae as chelate. Reference to his illustration of a penial seta and examination of penial setae of new material and material which was in Fletcher's possession indicates, however, that he mistook a web-like expansion of the apex of the seta, with thickened edges, for bifurcation (see fig. 2c, above).

This species, recorded from numerous localities in the vicinity of Sydney, was clearly one of the commoner species of the Sydney region. Most of the localities where it was found by Fletcher have now been built over and it will be interesting to investigate whether the populations sampled have survived human settlement, cultivation, and the inevitable introduction of lumbricids. The species is still common in the relatively undisturbed *Casuarina-Eucalyptus* woodland of the Galston Gorge reserve.

In having the gizzards in v and vi *D. armifera*, with *D. perrieri*, differs from all other species of *Digaster* s. strict., in which the gizzards are in vi and vii. In trigastric specimens of *D. perrieri* each of segments v to vii contains a gizzard, as in the former genus *Perissogaster*, and the condition in *D. armifera* need not, therefore, be considered to indicate polyphyly in *Digaster* s. lat.

***Digaster gayndahensis* Spencer 1900**

Digaster gayndahensis Spencer 1900, *Proc. roy. Soc. Victoria*, 13, (new series), 13, pt. 1, p. 67, fig. 106, 107, 108.

Type-locality: Gayndah, Queensland (see Material Examined, below).

Material Examined: 2 clitellate specimens, one of which had previously been dissected and had had the male genital field excised, from "scrub behind Gayndah, Oct. '91". National Museum, Melbourne, registration, *Digaster gayndahensis*, No. G.99.

There is no reason to doubt that this is type-material, that the dissected specimen is the holotype and the undissected specimen a paratype.

Morphological Data

Unless otherwise indicated, these data are from the paratype.

Dimensions: Length 44 mm.; maximum width (forebody) 4 mm.—Number of segments: 95.—*Colour*: Pigmentless buff in alcohol with the clitellum darker in the holotype.—*Prostomium*: Epilobous, $\frac{1}{2}$, with narrow, open, dorsal tongue.—*Setae*: Small, uniform, difficult to discern on the clitellum; in segment ix $cd: ab = 1.3$; $bc: aa = 0.8$; $dd: u = 0.6$; in segment xxv $cd: ab = 2.2$; $bc: aa = 1.1$; $dd: u = 0.7$ (paratype).

Clitellum: Ring-shaped and thick; embracing xiv to xviii and possibly part of xiii.

Male genital field (fig. 3a): The male pores are situated equatorially and in setal lines *ab* in xviii, each being visible as a transverse slit in a minute papilla. The two papillae lie within a single lip-like ridge which reaches a little laterad of setal lines *b*. Medially the anterior and posterior lips so formed almost meet. Accessory genital markings are present in intersegmental furrows 19/20, 20/21 and 21/22. Each consists of an oval pad with the long axis transverse to the long axis of the body. The boundary of each pad is raised into a lip so that the pad has a sucker-like appearance. Each pad extends antero-posteriorly between the setal zones of the adjacent segments and laterally to midway between setal lines *a* and *b*.

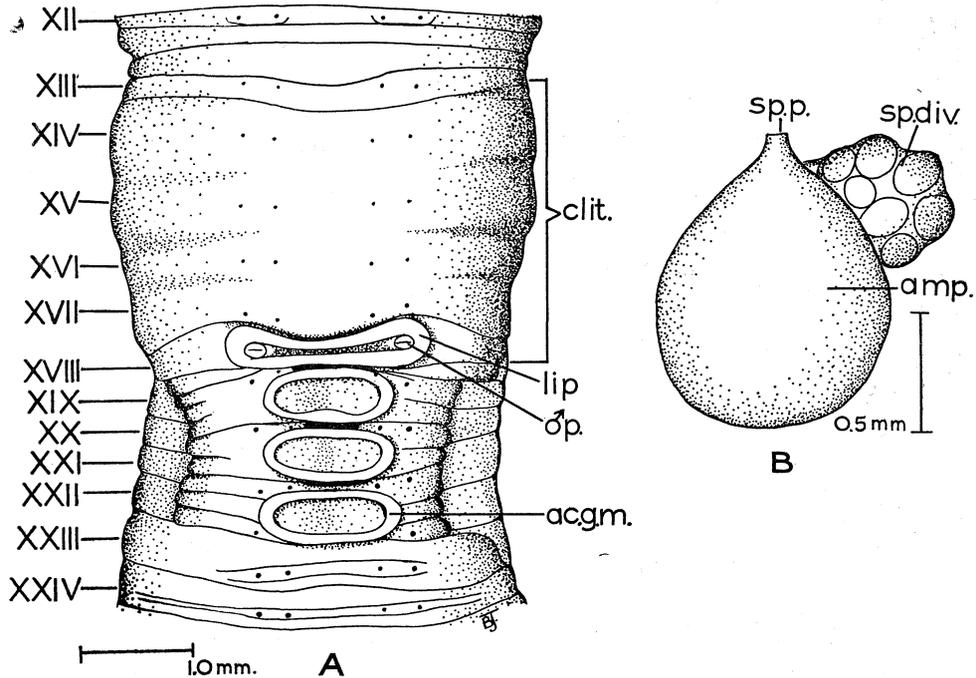


Fig. 3: *Digaster gayndahensis*, A, male genital field of paratype; B, dorsal view of right spermatheca of holotype. a.c.g.m., accessory genital marking; clit., clitellum; lip, lip surrounding male pores; ♂p., male pore.

Female pores: Not visible.

Spermathecal pores: Paired in intersegmental furrows 7/8 and 8/9, which they cause to protude forwards in their immediate vicinity.

Dorsal pores: The first visible were in 11/12.

Internal characteristics:—

Septa: Septa 3/4 to 8/9 very delicate; 9/10 thin; 10/11 to 13/14 moderately thickened and somewhat funnel-shaped, 14/15 thin; the rest delicate.

Alimentary canal: The pharynx and associated glandular tissue is situated in front of septum 3/4. A large, strong-walled, approximately spherical gizzard lies in each of vi and vii, a fairly long region of thin-walled oesophagus intervening between the two. In ix and x the oesophagus has a deep dorsal fold which is perhaps not normally present. Transection of the oesophagus in ix and xiv reveals folding of the walls as in other *Digasters*. The intestine begins in xviii but does not immediately reach its full width.

Blood vascular system: The dorsal vessel was traced anterior of the gizzard in vi. Paired commissural vessels were observed running ventrally from the dorsal vessel in vi to xii only. In x to xii these were large and heart-like.

Nephridia: From the segment containing the brain (iii?) posteriorly micromeronephridia are fairly common. They appear to be attached to the integument and not to the septa, but contraction of the specimen and the necessity to maintain it as intact as possible rendered examination difficult. No enteronephric nephridia were seen.

Anterior male organs: Thick, convoluted bodies on the anterior faces of septa 10/11 and 11/12 are probably sperm funnels. Sperm funnels were seen in these positions in the holotype on re-examination. Seminal vesicles were seen on the posterior faces of these septa in both specimens.

Posterior male organs: A racemose, ovoid prostate gland with several closely applied lobes opens to the exterior by a very short duct on each side in xviii. Vasa deferentia were not seen.

Penial setae: Absent.

Spermathecae (fig. 3b): In the holotype there is a pair of spermathecae in each of segments viii and ix. Each spermatheca has a spherical ampulla, approximately 1 mm. wide, which is almost sessile on the body wall. An ovoid diverticulum, 0.4 mm. wide, opens into the ectal region of the ampulla. The diverticulum lies lateral to the ampulla and is partly hidden by the latter *in situ*; it appears to contain several sperm chambers.

The left anterior spermatheca has a diverticulum on each side. The spermathecal ampullae of the paratype fragmented very readily and released large numbers of what appeared to be nematodes. Description of them is therefore excluded from this account because of the possibility that they are abnormally developed.

Remarks

The above description of the two remaining syntypes of *D. gayndahensis* greatly extends and partly emends the brief type-description of Spencer (1900). Points of divergence of the present account are: the first dorsal pore is shown to lie in intersegmental furrow 11/12, not 37/38, thus conforming with *D. armifera*; the gizzards are shown to lie in vi and vii, not vii and viii, and the intestine appears to commence in xviii, not in xvii; paired commissural vessels are described in vi to xii, being large and heart-like in x and xii, whereas Spencer noted hearts in ix to xiii.

***Digaster lamingtonensis* Michaelsen 1916**

Fig. 4

Digaster lamingtonensis Michaelsen 1916. Kungl. Svenska Vetenskapakad. Handlingar, 52, no. 13, pp. 20-22, taf. 1, fig. 1, 2.

Type locality: South Queensland, Glen Lamington (November, 1911. 1 specimen).

Material examined: 13 acitellate specimens in alcohol, of which two have distinguishable genital apertures, from Nordlington Farm, Tyalgum Creek, Tweed River, Queensland, presented by E. M. Embury, September 16, 1938. Australian Museum Registration No. W.3425.

Morphological Data

Only the two specimens which show male orifices are described below. For each character the two specimens are dealt with in the same order. Where no distinction is made the character is the same for the two specimens.

Dimensions: Length 265 mm., 273 mm.; maximum width (in the forebody) 5.5 mm., 7 mm.

Number of segments: 306, 295.

Colour: Pale straw colour in alcoholic preservation.

Prostomium: Tanylobous but giving an illusion of an epilobous condition because the peristomium is unusually short antero-posteriorly.

Setae: Lumbricine, all very small, fairly closely paired. In segment ix *cd*: *ab* = 1.3-1.5; *bc*: *aa* = 0.8-1.2; *dd*: *u* = 0.6-0.7; in segment xxv *cd*: *ab* = 1.6-1.7; *bc*: *aa* = 0.7-0.8; *dd*: *u* = 0.6-0.7 (two specimens).

Clitellum: Not present.

Male genital field (fig. 4a): The male pores are two equatorial transverse slits in xviii, at the sites of the absent ventral setae, and are slightly less in extent than a ventral setal couple. In the first specimen each pore is situated on a small dome-shaped papilla and the two papillae lie in a glandular area which includes two sucker-like depressions in intersegmental furrow 17/18 and a similar, unpaired depression in 18/19 on the left side (see discussion). The median limit of each sucker is approximately in the same longitudinal line as the male porophore of its side and laterally each extends to midway between setal lines *b* and *c*. The other specimen shows only slight glandular modification of the epidermis around the male pores in xviii. It is improbable that it is in the breeding condition.

Female pores: Visible only in the second specimen as a pair of minute pores 0.17 mm. apart (i.e., less than the width of a setal couple) and situated in a circumsegmental furrow in front of the setal zone of xiv.

Spermathecal pores: A pair in each of viii and ix very near the anterior border in or very slightly lateral to setal lines *a*. Each pore visible as a crescentic area the convexity of which pushes the anterior intersegmental furrow slightly forward.

Dorsal pores: Clearly visible; the first in intersegmental furrow 5/6 (specimen 2; this region damaged in the other).

Internal characteristics:—

The following data derive solely from dissection of specimen a. Septa: 5/6 thin; 6/7 moderately thickened; 7/8 and especially 8/9 to 12/13 thick and funnel-shaped; 13/14 to 17/18 successively thinner and transverse, 17/18 being flimsy. Behind this the septa are thin.

Alimentary canal: The pharynx and tendinous glandular material adherent to it extend back to septum 5/6. A large, strong-walled gizzard in the form of a truncated cone with the narrow end posterior lies in each of segments vi and vii. The oesophagus is slender in viii and ix. In x to xvii it is wider and a reticulum of what appear to be blood sinuses is visible on its surface. The gut expands abruptly as the intestine in xviii.

Blood vascular system: The single, median, anteriorly narrowing dorsal vessel was traced forward as far as the cerebral ganglia. It gives off a commissural vessel on each side in each of segments vi to vii. In viii and posteriorly the commissural vessels were shown to connect with the ventral blood vessel; demonstration of the connection in the more anterior segments was not achieved. Only in ix to xii do the commissural vessels attain the thickness of the dorsal vessel. In vi to viii a vessel which is smaller than the commissural vessel runs from the wall of the gut and joins the latter vessel ventrally, but whether the lumina become confluent was indeterminable. A dorsal (paired?) vessel runs antero-posteriorly along, and imbedded in, the dorsal surface of the gut in ix to xii. It appeared possible that this vessel is not continuous through the septa. It gives off a vessel on each side which passes downwards around the oesophagus and is barely discernible from the numerous lacunae of the oesophageal sinus. These perioesophageal intramural

vessels are equatorial in x to xii but are anterior in ix. In xii a connection between the upper extremity of the right commissural vessel and the dorsal intramural vessel was demonstrated. In xiii, where there are no commissurals, a pair of dorsal intramural vessels originates from the anterior wall of the segment (from the commissural vessels of xii) and the two vessels diverge backwards and equatorially pass ventrally around the gut as intramural vessels. In xiv and the succeeding segments there are no dorsal intramural vessels and the pair of equatorial intramural periesophageal vessels in each segment connects by free roots to the ventral face of the main dorsal vessel. The mottling of the wall of the gut in xiii to xvii becomes less obvious and is not visible on the intestine.

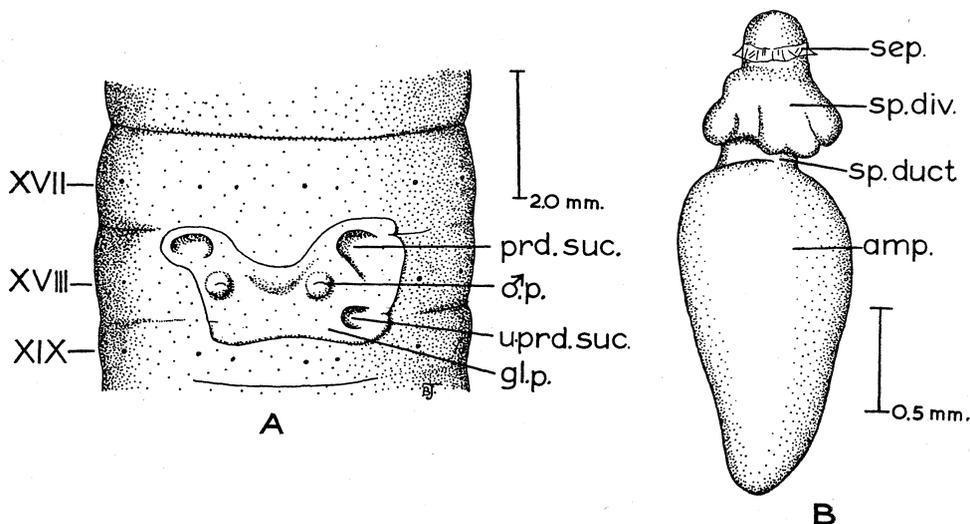


Fig. 4: *Digaster lamingtonensis*, A, male genital field of specimen W.3425 a. gl.p., glandular pad; u-prd.suc., impaired sucker; ♂p., male pore; prd.suc., paired sucker. B, dorsal view of right spermatheca of the same. amp., spermathecal ampulla; sep., septum; sp div., spermathecal diverticulum; sp.duct, spermathecal duct.

Nephridia: Micro-meronephridia are densely grouped in iii (i.e. the segment containing the cerebral ganglia and the anterior part of the subpharyngeal ganglion) to v. At least the ventral nephridia of the anterior segment have very long ducts which run in parallel rows anteriorly and medianwards to the region of the buccal cavity in this segment. It is probable that these nephridia are enteronephric. Behind v the nephridia are sparse and approximately equatorial and appear to be closed integumentary micro-meronephridia. In the hindbody, however, the median-most nephridium on each side is large and constitutes a mega-meronephridium, but again no funnel is detectable.

Anterior male organs: Holandric. A pair of sperm funnels was seen on the posterior wall of each of x and xi. A compact lobulated seminal vesicle lies on each side in ix and xii, flattened against the posterior and anterior septum respectively.

Posterior male organs: The pair of prostate glands opens to the exterior in xviii. The glandular part of each is compact, flattened and racemose with several major lobes. The duct is short and stout. The very thin, apparently single, vas deferens on each side runs to the ental end of each prostate duct where it becomes hidden by the base of the glandular part.

Penial setae: Absent.

Female organs: A pair of well-developed ovaries projects from septum 12/13 into xiii. Oviducts were not seen.

Spermathecae (fig. 4b): Paired in viii and ix. The right posterior spermatheca is 2.4 mm. long and has an ovoid, ectally tapering ampulla 0.93 mm. wide and a fairly stout duct which entally attains its maximum diameter of 0.38 mm. and is about half as long as the ampulla. Approximately the ectal third of the duct appears to be anterior to the septum which bounds its segment anteriorly. From the duct immediately behind the septum arises a large, dorsal, indistinctly lobed diverticulum which hides most of the duct. The other spermathecae are similar.

Remarks

The above account is based on hitherto undescribed material of *D. lamingtonensis* from the Tweed River. The description of the male genital field accords closely with that of Michaelsen (1916) for the single type-specimen which was also from South Queensland. The similarity extends even to the asymmetrical development of a single puberty marking, on the left side, behind the male pores. Michaelsen described the puberty markings as lying posteriorly in xvii and xviii, however, whereas in a mature specimen of the new material they are sucker-like depressions, in 17/18 and 18/19. It seems likely that in this species, as in *D. armifera*, the "suckers" are formed by muscular depression of papillae and that they aid in cohesion of concopulants.

Points of difference of the two accounts are generally minor. The oviducts opened by a single midventral pore in the holotype but discharged by two separate very closely paired pores in a Tweed River specimen. In both they are anterior in xiv. The setal distance ratios are not in accordance. Bifurcation of the prostate glands into two distinct lobes is shown not to be a constant feature of the species.

Digaster longmani Boardman 1932

Fig. 5

Digaster longmani Boardman 1932. *Mem. Queensland Mus.*, 10, pt. 2, pp. 125-127, fig. 1.

Type-locality: Tambourine Mountain, South Queensland (holotype and four fragments, including a head end, Queensland Museum, Reg. No. G.684). Not seen.

Material examined:—

1. Australian Museum Reg. No. W.3643. Five badly softened fragmenting specimens, the largest 4 feet 11 inches in alcohol, bull-dozed from soil in Kyogle State Forest, northern New South Wales, September, 1956, donated by Axel Poignant.

2. Australian Museum Reg. No. W.3644. One fine clitellate specimen, 4 feet 1 inch long, of which the male field had been destroyed by a ventral incision. From Kyogle State Forest, collected in early 1950's by W. T. Jones.

3. Australian Museum Reg. No. W.3669. 11 clitellate and 17 a clitellate specimens (complete); 8 clitellate and 4 a clitellate specimens (lacking the tail end). From a spur above Oaky Creek, Richmond Range State Forest, May 20, 1957; bull-dozed from red soil, Kyogle, and from the Toonumbar State Forest, spur above Iron Pot Creek, Kyogle, collector E. Pope (see Abs. Proc. Linn. Soc. N.S.W. 82, pt. 3, no. 385, May, 1957, p. 368 and August, 1957, p. 370, where Miss Pope gives ecological and other notes on these specimens).

Observations on what were perhaps specimens of *D. longmani* are given by Fleay (1956) in "Talking of Animals", Jacaranda Press, Brisbane, pp. 6-7.

Morphological Data

These data are derived from the specimens collected by Miss Pope which bear the Australian Museum Registration Number W.3669.

Dimensions (Table 1): Length 860 to 1,025 mm. (2 feet 10 inches to 3 feet 5 inches) but a length of 1,625 mm. (5 feet 5 inches) has been recorded by Miss Pope (*in litt.*) in a live specimen suspended by the tail.

Table 1

Specimen	Length (mm.)	Greatest width (mm.)	Number of segments
W.3669, a	860	25	309
b	925	25	357
c	1,025	25	282
d	1,025	25	378
e	937	25	334
f	1,025	25	382

Number of segments (Table 1): 282 to 382.

Secondary annulation: Variable and probably dependent on the degree of contraction on fixation.

Colour: Darkish buff with the clitellum brownish black.

Prostomium: Broad and zygotobous (5 specimens) with sometimes a faint transverse furrow making it probolous (specimen 3).

Setae: Minute relative to the size of the worm and presumably functionless.

In segment ix *cd*: *ab* = 1.3-1.8 (mean of six = 1.6); *bc*: *aa* = 0.4-0.5 (mean of six = 0.4); *dd*: *u* = 0.6-0.8 (mean of six = 0.7); in segment xxv *cd*: *ab* = 1.3-1.7 (mean of five = 1.5); *bc*: *aa* = 0.4-0.8 (mean of five = 0.6); *dd*: *u* = 0.7-0.8 (mean of five = 0.7).

In the tail region the ratio *bc*: *aa* increases though it does not reach unity.

Clitellum: Poorly developed and recognizable only by its brownish black colour and swelling round the dorsal pores, which are perhaps occluded in this region; embracing half or less of xiii to half or less of xix (specimens a-d, f). It is ring-shaped but is paler ventrally in xiv. In one specimen (e) it shows no ventral pigmentation, embraces xiv to $\frac{1}{2}$ xix, and is perhaps saddle-shaped.

Male genital field: The male pores are equatorial (specimens a, b, e, f) or sometimes (specimens c, d) just presetal on segment xviii in setal lines *a* (specimen b) or *b* (specimen d) or between these (specimens a, c, e, f). Usually each pore lies on a low mound of which only the median border is clearly defined. Clitellar pigmentation is lacking between these papillae and the existence of a male field is indicated by slight backward dislocation of furrow 18/19 between the ventral setal lines.

Female pores: A pair of female pores lies about half way between the setal zone of xiv and the anterior border of this segment. In four specimens (a-d) the right pore lies well anterior to the left, in one (f) the pores are obscured in a median pit, and in another specimen (e) they seem to be in the same transverse line.

Spermathecal pores: Two specimens (a, d) have three pairs of pores, in intersegmental furrows 6/7, 7/8 and 8/9, while the other four specimens have two pairs of pores, in furrows 7/8 and 8/9. The pores in all lie in setal lines *a*.

Dorsal pores: The first dorsal pore lies in intersegmental furrow 5/6 in five specimens. In a single specimen (e) the first detectable pore was in 6/7.

Internal characteristics (the following data are derived from specimen W.3669, a):—

Septa: The first visible, 4/5, is poorly developed and is fused to the pharynx. 5/6 and 12/13 are strong, 6/7 to 11/12 are very thick and the succeeding septa are thin. The septa back to 17/18 are funnel-shaped and the remainder transverse. Successive thickened septa are united by tendons.

Alimentary canal: The large ovoid pharynx ends against septum 4/5, with which it is fused, and sends numerous muscle bands and tendons to septum 5/6. In v the gut is thin-walled and pouch-like. A large strong-walled gizzard in the form of a truncated cone with the narrow end posterior lies in each of segments vi and vii. The anterior base of the cone is thin-walled. Only a very small length of oesophagus intervenes between the two gizzards and it is hidden in septum 6/7. The oesophagus is slender in segments viii to xii and bears no oesophageal diverticula. In xiii it is swollen and vascularized and transection in this segment shows that its wall is thin but is thrown internally into numerous discontinuous folds which, especially ventrally, appear to contain blood sinuses. The oesophagus in xiv is also internally ridged but is less vascularized and less swollen than in xiii.

Blood vascular system: The single, median, anteriorly narrowing dorsal vessel was traced forward on to the pharynx. It gives off a commissural vessel on each side in each of segments iv to xii but not in xiii and more posterior segments. In all these vessels the commissural vessels were seen to connect the dorsal vessel with the ventral vessel. In vi a slender vessel was seen to run forward from the lateral wall of the oesophagus to join the base of the commissural vessel on each side near the junction of the latter vessel with the ventral vessel. In vii a median vessel arising from a plexus on the floor of the oesophagus was present in addition to the lateral vessel and joined the commissural vessel at the same point. Supra-oesophageal vessels are present on the dorsal surface of the gut in viii to xiii. Their arrangement was particularly clearly seen in viii and ix where it seemed, with the exceptions noted below, to be typical. In each of the latter segments, three longitudinal vessels are present; the median of these runs through the entire length of the segment, that of viii being continuous with that of ix, while the vessel on each side arises from the median vessel posteriorly in the segment and runs the length of the segment but possibly ends at the anterior septum. From each of the paired supra-oesophageal vessels there arises an intra-mural peri-oesophageal vessel and, nearer the base, a vessel which connects with a ventrolatero-oesophageal vessel which runs on each side of the gut through segments iv (where it disappears in the posterior face of the pharynx) to x. In x the branch from each of the paired supra-oesophageals to the ventrolatero-oesophageal vessel appears to constitute the origin of the latter vessel which is not represented further posteriorly. In xii and xiii, in the absence of the ventrolatero-oesophageals, the branches from the paired supra-oesophageals which supply them in the more anterior segments send conspicuous branches to the posterior septa. The supra-oesophageals have connections with the dorsoventral commissurals in xi and xii. Here each commissural vessel has two roots, one from the dorsal vessel and the other from the paired supra-oesophageal vessel. In xii the latter root is the larger. In v and vi, at least, the ventrolatero-oesophageals receive vessels from the gut wall. In xiv posteriorly, in each segment, the dorsal vessel receives ventrally two pairs of vessels from the gut.

Nephridia: Septum 4/5 was dissected away from the pharynx and found to be clothed on its anterior face with dense clusters of robust meronephridia. Two bands of meronephridia were seen anterior to this; the posterior band appeared to belong also to septum 4/5 and the anterior and to the vestigial septum 3/4. Thus nephridia apparently begin in iii. The anterior face of septum 5/6 is densely clothed with coiled closed mero-nephridia only where the septum meets the parietes; nephridia are absent from the body wall and from the posterior face of septum 4/5. The conditions vi to xi is similar but in xi the nephridia impinge on the body wall adjacent to the posterior septum more than elsewhere. In xii and posteriorly this trend is taken further; there are no nephridia on the septa, the nephridia appearing sparsely in a band on the parietes posteriorly. By xiv the nephridia have become equatorial. At the posterior end of the body micro-meronephridia occur in a single equatorial band in each segment, except ventrally near the nerve cord where there is a patch of several on each side. In front of the latter in each segment there is a megameronephridium on each side.

Anterior male organs: No testes, sperm masses, sperm funnels or vasa deferentia were seen. A very large finely divided mass dependent on each side from the posterior face of septum 11/12 and filling xii anteroposteriorly appears to be a seminal vesicle and, in the absence of vesicles in ix or elsewhere, perhaps indicates metandry.

Posterior male organs: The prostate glands open to the exterior in xviii. The glandular portion is discoidal and its surface is much divided although there are no distinct lobes. The duct is short and stout. Transection of the gland entally shows that the greater part is a spongy mass with no macroscopic lumen but ectally reveals several macroscopic ducts.

Penial setae: Absent.

Female organs: Not visible.

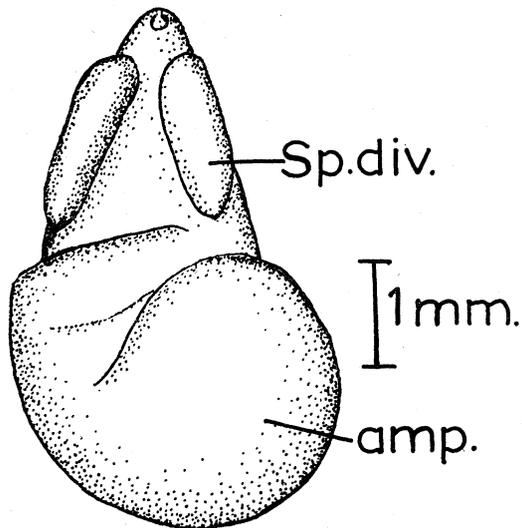


Fig. 5: *Digaster longmani*. Right hand spermatheca from segment viii of specimen W.3669 a. amp., spermathecal ampulla; sp. div., spermathecal diverticulum.

Spermathecae (fig. 5): A pair in each of vii, viii and ix (only the last two in most specimens, see above). Each has the form of a flattened sac tapering to the pore. The tapering portion constitutes a duct which is fairly clearly demarcated from the rounded ental region, the ampulla, of the spermatheca. The ectal third of the duct is attached ventrally to the body wall. The duct bears dorsally two approximately ovoid elongated diverticula, one on each side, which adhere to the duct through almost its whole length and converge towards the pore. The six spermathecae show a similar form. Each is ca. 5 mm. long.

Remarks

The above account, based on new material, largely confirms the type-description of Boardman (1932). Some points of divergence of the specimens examined from the types are as follows: they display gigantism, exceeding 5 feet in length; the prostomium is usually zygalobous; setal distance ratios are generally confirmed but $bc:aa$ averages 0.4 in the fore-body, not 0.8, and $cd:ab$ averages 1.5 behind the clitellum, not 2.3; the clitellum is longer, extending onto xiii and xix; the genital field is less clearly defined; accessory genital markings in viii to xii are not developed; the female pores are sometimes diagonally orientated; and two out of six specimens examined have an extra pair of spermathecal pores, in furrow 6/7.

On p. 90 affinities of *D. longmani* with *D. lamingtonensis* are discussed.

Digaster minor Spencer 1900

Fig. 6

Digaster minor Spencer 1900. *Proc. roy. Soc. Victoria*, 13 pt. 1, pp. 65-66, fig. 100, 101, 102.

Type locality: Gayndah, Queensland (see material examined, below).

Material Examined: Approximately 13 badly preserved fragments, of which four are head ends. Three of the latter had been severed by an intraclitellar cut and showed no male fields. The missing fields were not detected in other fragments. The fourth head end included segment xviii and had been previously dissected. National Museum, Melbourne, registration: "*Digaster* sp. 2 Q", scrub behind Gayndah, Queensland, October, 1891, No. G.100, W. Baldwin Spencer Collection.

These specimens were labelled at the National Museum consecutively to specimens which appear to be typical material of *G. gayndahensis*. They accord with the type description of *G. minor* Spencer 1900 and entered Spencer's collection from the type locality of this species before publication of the type description. They do not conform with the type description of *G. brunneus* Spencer 1900, the types of which are missing, and they are here regarded as typical material of *D. minor*. The previously dissected specimen is probably the holotype.

Morphological Data

Unless otherwise indicated, these data are from one of the previously undissected head ends only.

Dimensions: Greatest width (in the forebody) 3.2 mm.

Secondary annulation: Slight, or absent from all specimens.

Colour: Pigmentless straw colour in alcohol with the clitellum pigmented light brown.

Prostomium: Epilobous, almost tanylobous, the peristomium being very short.

Setae: Black and distinctly visible, although not large. Apparently uniform. Some were not discernible in ix and ratios were taken from vii.

In segment vii $cd:ab = 2.2$; $bc:aa = 1.3$; $dd:u = 0.6$ (one specimen).

Clitellum: Annular except in xiii where it is developed only dorsally, between setal lines *b*. In the previously dissected specimen it embraces xiii to xvii. Ventrally in xiv it shows a whitish area (a female genital field?) which extends from the anterior border to the equator of this segment and just includes the ventral setae.

Male genital field: Present only in the previously dissected specimen. A depression on each side at the site of the absent ventral setae of xviii appears from internal examination to mark the position of the prostate pores. In front of them a slight glandular development of the ventral surface of the segment is visible as a whitish area extending as far as intersegmental furrow 17/18.

Female pores: Not seen. Presumably on the glandular field in xiv described above.

Spermathecal pores: Not visible.

Dorsal pores: The first distinct pore is in furrow 7/8 but there is perhaps a suggestion of a pore in 6/7.

Internal characteristics:—

Septa: 6/7 fairly thin; 7/8 to 11/12 slightly thickened; 12/13 thinner. The condition of the more anterior septa is indeterminable.

Alimentary canal: Muscular, antero-posteriorly rather short gizzards are present in vi and vii. The gut otherwise is not sufficiently well preserved to provide useful data.

Blood vascular system: Indeterminable.

Nephridia: Micromeronephridia are visible in some anterior segments at least as far forward as the brain.

Anterior male organs: Well-developed racemose seminal vesicles lie on the anterior face of septum 9/10 and the posterior face of septum 11/12. No testes or funnels are visible.

Posterior male organs: Missing from the specimen examined. In the previously dissected specimen they are racemose with short ducts.

Penial setae: Absent.

Female organs: Septum 12/13, the posterior septum present, shows no gonads.

Spermathecae (fig. 6): In viii and ix, consisting of an ovoid ampulla and a sharply differentiated though fairly short duct, about a third as long, which bears ectally a many-lobed dorsal diverticulum.

Remarks

The above account, based on the syntypes, confirms and greatly extends Spencer's type-description. The accessory glandular patch in xix, noted by Spencer, was not seen in the re-examination, however. It is clear that Spencer erroneously interchanged the words "posterior" and "anterior" in his description of the seminal vesicles.

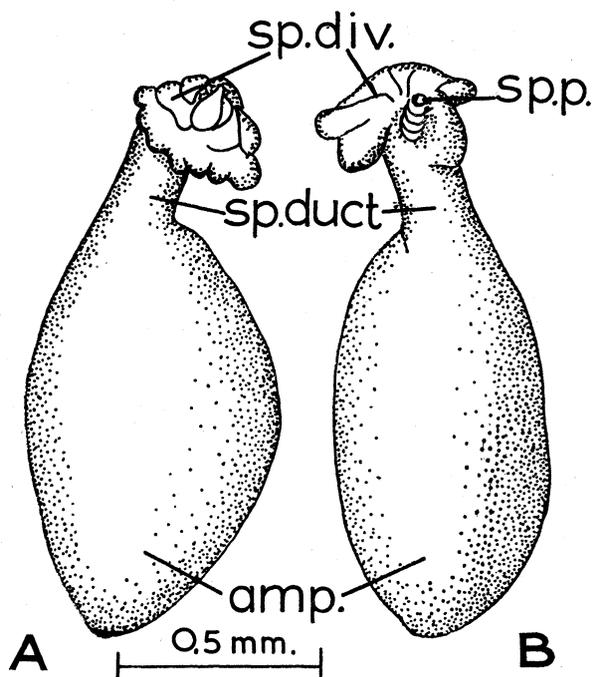


Fig. 6: *Digaster minor*. A spermatheca of a syntype. A, dorsal. B, ventral view. amp., spermathecal ampulla; sp.div., spermathecal diverticulum; sp.duct, spermathecal duct; sp.p., spermathecal pore.

***Digaster perrieri* Fletcher 1888**

Fig. 7

Digaster Perrieri (sic) Fletcher 1888. Notes on Australian Earthworms. Part V. *Proc. Linn. Soc. N.S.W.*, 3, (2), pp. 1,530-1,532.

Digaster perrieri; Michaelsen 1900. *Das Tierreich*, Lief. 10, p. 197.

Type-locality: Springwood, Blue Mountains, N.S.W. (25 spirit specimens, see Material Examined, below).

Material examined: Approximately 25 worms labelled "*Digaster Perrieri* (Valley Heights and Springwood)", Australian Museum Reg. No. W.1325. Most of the specimens are clitellate and are either surface-hardened and shrunken or badly softened. Of seven well-preserved acitellate specimens, four were opened and were found to conform with Fletcher's description of *D. perrieri*, as did a single clitellate specimen which was examined. Presumably this material is the type-series.

Morphological Data

Unless otherwise stated, these data are derived from a single specimen, W.1325, a.

Dimensions: Length 45 mm., greatest width (midbody) 3.5 mm.

Number of segments: 154.—*Colour*: Pigmentless buff.

Prostomium: Epilobous 1/3.

Setae: Apparently uniform, the lateral pair more widely spaced than the ventral pair.

In segment ix *cd: ab* = 1.7; *bc: aa* = 0.8; *dd: u* = 0.5; in segment xxv *cd: ab* = 1.4; *bc: aa* = 1.0; *dd: u* = 0.6 (one specimen, W.1325, 1).

Clitellum: Not developed.

Male genital field: This consists of three transverse ridges or tubercula pubertatis. The middle ridge occupies the setal annulus of xviii while the anterior and posterior ridges extend from this annulus almost to the setal zones of segments xvii and xix respectively. The three ridges extend laterally to mid *bc*. The anterior and posterior ridges are thus intersegmental. They bifurcate at their lateral extremities but the intersegmental furrow is otherwise absent from their surfaces. Setae *a* are present on the middle ridge, and at the site of the absent seta *b* on each side there is a dark point which is the penial seta projecting at the male pore. The anterior and posterior ridges bear a transverse linear series of minute white points the nature of which is obscure.

Female pores: Not visible.

Spermathecal pores: These are visible as paired small wart-like whitish swellings just laterad of setal lines *a* on the extreme anterior border of segments viii and ix and projecting into intersegmental furrows 7/8 and 8/9.

Dorsal pores: The first pore lies in intersegmental furrow 11/12 (specimens a and b).

Internal characteristics:—

Septa: Septa 2/3 to 5/6 are visible though very thin, and perhaps only 5/6 is complete; 6/7 to 11/12 are fairly thick and the remaining septa become successively thinner.

Alimentary canal: There is a gizzard in each of segments v and vi. In specimen a there are three gizzards, the anterior one being short and less well developed. Two further specimens, b and c, have gizzards only in v and vi, while a fourth specimen, (W.1325, d; prepared longitudinal sections placed in the Australian Museum) has three well-developed gizzards, in v, vi and vii. The latter specimen was identified as *D. perrieri* conclusively by examination of the general morphology and of the penial setae (see fig. 7 and remarks).

In specimen a the oesophagus in x to xiii has paired lateral pouches, each of which is highly vascularized and is supplied with a vessel from the dorsal vessel. Horizontal transection of these pouches in xi and xii revealed thick walls formed by folding of the wall of the pouch in such a way that numerous laterally radiating chambers are formed. These chambers appeared to be in some cases isolated by fusion of the inner extremities of the folds. In x a similar but less pronounced folding of the walls of the pouches is present while in xiii the walls were thick and possessed numerous constricted lumina. In xiv to xvi, although pouches are present, their lumina are not isolated from the oesophagus and only those in xiv show folding of the walls. The intestine does not conspicuously enlarge until xix but it begins to broaden anterior to this.

In specimen b the oesophagus, although vascularized, has no diverticula.

Blood vascular system: Hearts are present in xi to xiii and the dorsal blood vessel is unpaired.

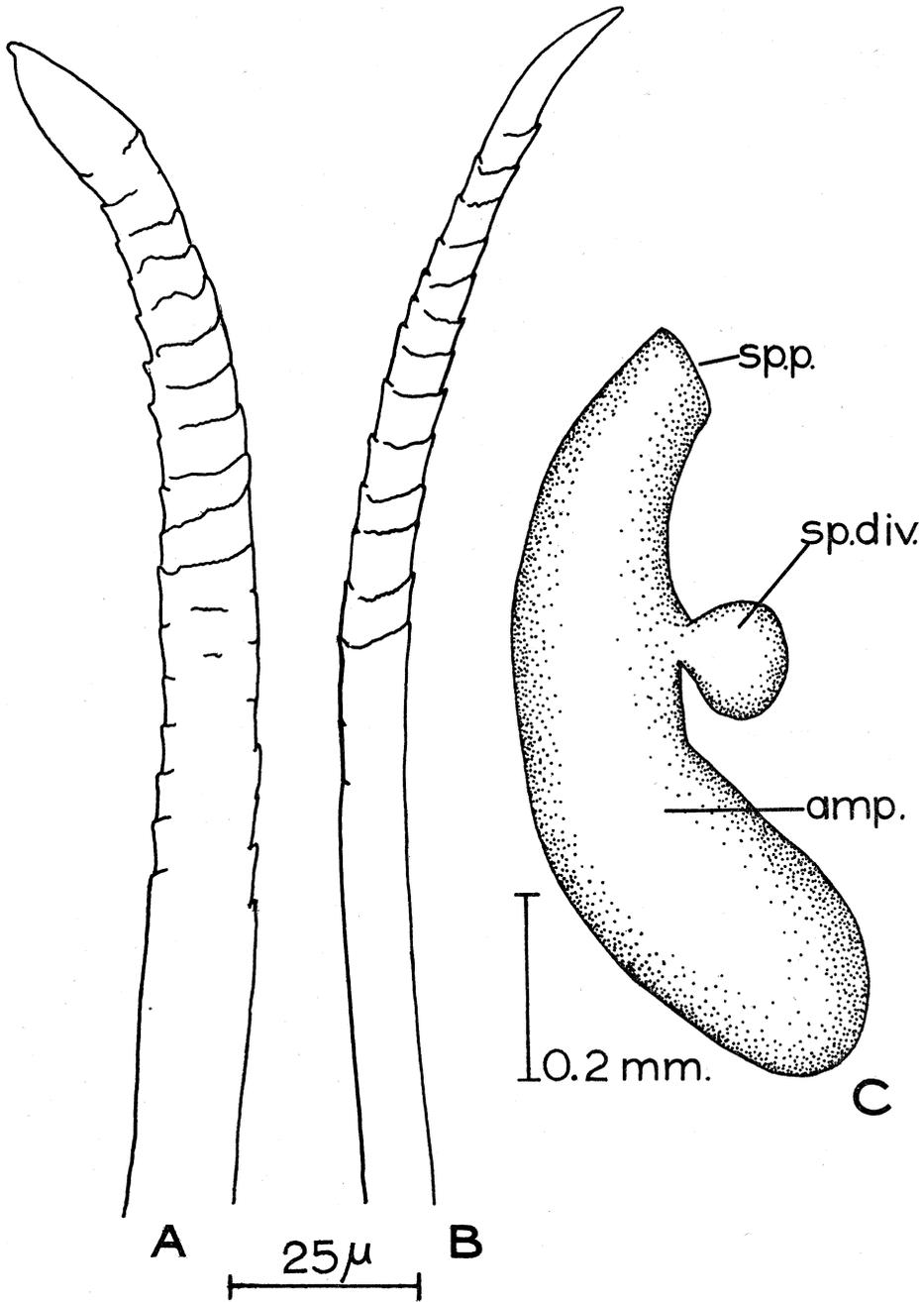


Fig. 7: *Digaster perrieri*. Ectal end of penial seta. A, of a digastric syntype, W.1325 b; B, of a trigastric syntype. C, right posterior spermatheca of specimen W.1325 b, *in situ*.

Nephridia: Micromeronephridia occur as far forward as iii. They are sparse in the forebody except in this segment in which they are apparently associate to form tufted nephridia. Behind xviii they are fairly numerous and are integumentary. An examination of the hindbody revealed no megameronephridia but about five micromeronephridia were seen on each side.

Anterior male organs: Shining seminal funnels were seen in x and xi and well-developed racemose seminal vesicles with very distinct lobes in xi and xii. No seminal vesicles occur in ix.

Posterior male organs: A racemose tongue-shaped prostate gland in xviii discharges to the exterior on each side by a slender shorter duct. What appeared to be a male duct was seen joining the ental end of the right prostate duct.

Penial setae: In specimen W.1325, b, and in the trigastric specimen a right penial seta is slightly curved in a single plane at the extremities. The ectal end tapers gradually to a point and bears a series of irregular encircling ridges except at the tip.

Length 0.9 mm., 0.6 mm., width ental to the ornamentation 15 mm. and 13 mm. respectively.

Female organs: Undeveloped.

Spermathecae (fig. 7): The spermathecae have each the form of an elongated sac the ectal portion of which constitutes a poorly demarcated duct. The duct bears a single finger-like diverticulum towards the ental end (W.1325, a). The spermathecae of W.1325, b, are fairly similar but the part of the duct ectal to the more rounded diverticulum is longer (fig. 7). Spermathecae in the specimens dissected from other localities are similar.

Remarks

Fletcher gave only a very brief account of this species which, he stated, agreed with *D. armifera* in general characters. The above account, based on material which almost certainly belongs to the type-series, confirms the similarity to *D. armifera*, except in the position of the last hearts. The penial setae are described and figured for the first time. Affinities between it and *D. armifera* and *D. nemoralis* are discussed on p. 88.

The significance of the occurrence in two specimens of three gizzards is discussed on p. 87. That both specimens conform with *D. perrieri* in general features and identity was conclusively demonstrated in one by examination of the penial setae. A sagittal half, a penial seta, and longitudinal serial sections of the latter trigastric specimen are in the collections of the Australian Museum.

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