

A REVISION OF THE GENUS  
*GORDIODRILUS* BEDDARD  
(OLIGOCHAETA : MEGASCOLECIDAE)

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# A REVISION OF THE GENUS *GORDIODRILUS* BEDDARD (OLIGOCHAETA: MEGASCOLECIDAE)

By B. G. M. JAMIESON

## SYNOPSIS

*Nannodrilus* Beddard, 1894, and *Diaphorodrilus* Cognetti, 1910, are removed from the synonymy of *Gordiodrilus* Beddard, 1892, and *G. luykerleni* Michaelsen, 1913, and *G. overlaeti* Michaelsen, 1936, are transferred to the genus *Ilyogenia* Beddard. The restricted *Gordiodrilus* is divided into five species-groups: an *elegans* group of fifteen species and four monotypic groups, a *tenuis* group, a *robustus* group, a *pampaninii* group and a *papillatus* group.

The phylogeny of *Nannodrilus* and *Gordiodrilus* is discussed and it is suggested that the *Notiodrilus* ancestor of classical theory should be replaced by a sexprostatic form similar to that postulated by Gates (1942). Some evidence is presented for regarding an even more extensive series of prostates as the primitive condition in the Ocnerodrilinae (and perhaps the Megascolecidae as a whole).

Keys and definitions of the species-groups and species of the restricted *Gordiodrilus* are given.

## INTRODUCTION

"I CAN do nothing with this heterogeneous group", so wrote Stephenson (1930) of *Gordiodrilus* Beddard, 1892. The genus had already seemed heterogeneous to Beddard when he reviewed it in 1895. Beddard was of the opinion that *G. tenuis* Beddard, 1892, showed some claims to being regarded as a separate genus, that *G. robustus* Beddard, 1892, stood alone, linking *Gordiodrilus* with *Ocnerodrilus* Eisen, and that the four remaining species, *G. elegans* Beddard, 1892, *G. ditheca* Beddard, 1892, *G. dominicensis* Beddard, 1892, and *G. zanzibaricus* Beddard, 1894a, formed a distinct group.

In 1913 Michaelsen included *Nannodrilus* (then containing *N. africanus* Beddard, 1894b, *N. phreoryctes* Michaelsen, 1903, and *N. staudei* Michaelsen, 1897) with *Diaphorodrilus* (a monotypic genus established for *D. doriae* Cognetti, 1910) in *Gordiodrilus* because he considered that the male and prostatic terminalia of *Gordiodrilus elegans*, *G. luykerleni* Michaelsen, 1913, *Nannodrilus staudei*, *N. africanus* and *G. togoensis* Michaelsen, 1913 formed a continuous series. (He preceded the series with *Eukerria* which, however, he did not unite with *Gordiodrilus*.) Chiefly as a result of uniting the, in part, sexprostatic *Nannodrilus* with the previously quadriprostatic *Gordiodrilus*, Michaelsen included *Diaphorodrilus* which has three pairs of prostates.

Stephenson (1930) believed *Gordiodrilus* to be evolving along various lines and to be raw material from which many distinct genera were still to be produced.



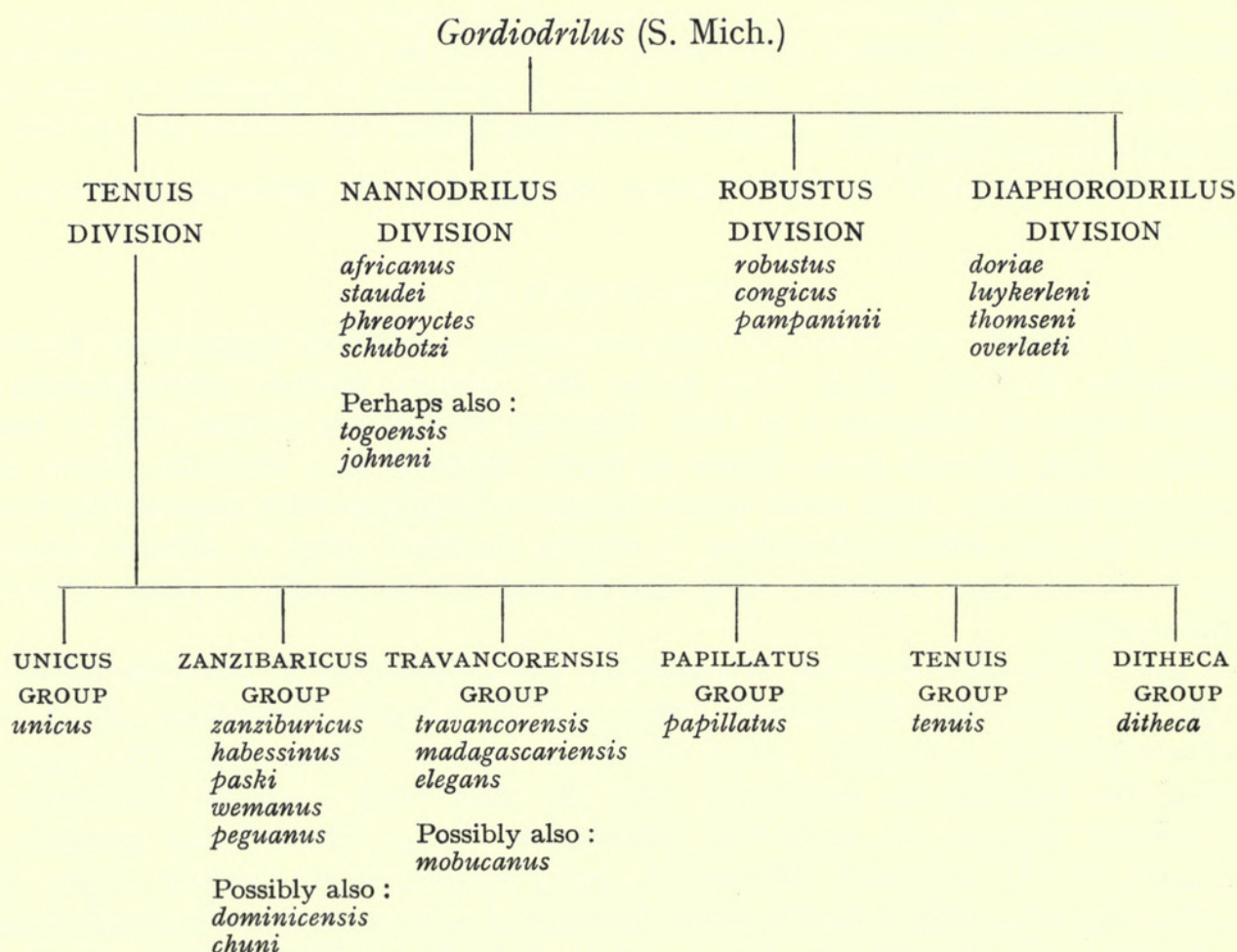
His diagnosis of *Gordiodrilus* (s. Mich.), which he admitted to be meaningless, is as follows :—

“Condition of male apparatus very various—incompletely or irregularly micro-scolecine, or showing a tendency to balantine reduction, or megascolecine. Two or one or no gizzards. A single oesophageal sac, or a pair, in ix. Holandric, metandric, or proandric (*G. chuni*). Spermathecae without diverticula on the duct, but sometimes with evaginations at the ectal end of the ampulla.”

Twenty species were known when this was written and nine have since been described.

Gates (1942) described *Gordiodrilus* as “one of the most difficult problems in Megadrilid taxonomy” and (1957) a “taxonomic waste-basket”. He divided the genus into “generic groups” (Table I) for which he gave definitions (1942). His examination of material was limited, however, to *Gordiodrilus peguanus* Gates, 1942, and he stated that it should not be considered that he had restricted the genus.

TABLE I.—Gates' (1942) Analysis of *Gordiodrilus*



Perhaps the most important aspect of this valuable paper was the suggestion (pp. 78, 80) that *Gordiodrilus* could be derived from sexprostatic forms. This released Megascolecoid taxonomy from the restrictions of the orthodox theory of



origin from the quadriprostatic acanthodriline *Notiodrilus* ancestor (see Phylogenetic Considerations, below).

The present review originated during a study of material of the Ocnerodrilinae. As the study progressed it became possible to suggest a solution to the problem of the classification of the genus. The new classification and the reasons for it are presented in this work.

#### MATERIAL AND ACKNOWLEDGMENTS

This work was made possible by grants from the Goldsmiths' Company of London and the Department of Scientific and Industrial Research.

The paper is based on part of a section on the Ocnerodrilinae in a doctorate thesis submitted to the University of Bristol in 1958. I am indebted to Professor J. E. Harris of Zoology Department, University of Bristol, Professor L. C. Beadle of Zoology Department, Makerere College, Uganda, and the Trustees of the British Museum (Natural History) for the facilities which they put at my disposal in these institutions and to Professor K. von Haffner for permitting me to examine material in the collections of the Zoological Museum, Hamburg. My special thanks are due to Dr. R. B. Clark of Zoology Department, University of Bristol, for his advice and helpful criticism throughout the progress of the work, and I also thank Mr. R. W. Sims, Mr. N. Tebble and Miss Angela Edwards of the British Museum (Natural History) for their valuable assistance. I am also grateful to members of the Museum staff, and to Dr. D. T. Anderson of Zoology Department, University of Sydney, for their critical appraisal of the manuscript.

#### SYSTEMATICS

Before discussing the genus *Gordiodrilus* in the sense which it is restricted here, the taxa which are removed and the reasons for their exclusion will be given.

**EXCLUSION OF *Nannodrilus*.** Michaelsen's series (see above) for the union of *Nannodrilus* and *Gordiodrilus* arose largely from consideration of the morphology of *G. luykerleni* Michaelsen, 1913. The series shows defects which, in my opinion, invalidate union of the two genera.

First, *G. luykerleni*, in which one pair of prostatic ducts discharges in common with the thickened male ducts, is seen by its male terminalia and paired oesophageal diverticula, in addition to complete somatic identity, to be an *Ilyogenia*. Michaelsen considered it to link those species of *Gordiodrilus* (s. Beddard) in which the ducts discharge separately and are unthickened (e.g. *G. elegans*) with *Nannodrilus* in which at least one pair of prostatic ducts always discharges in common with the constantly thickened male ducts.

Secondly, a survey of the six species here included in *Nannodrilus* suggests, as Gates (1942) has proposed, that *Nannodrilus* is basically sexprostatic (see pp. 320–321 below). Derivation of a sexprostatic *Nannodrilus* from an acanthodrilin quadriprostatic *Eukerria* is improbable and does not easily allow the construction of a series of the type which Michaelsen has advanced for the union of *Gordiodrilus* and *Nannodrilus*.



A consideration of somatic characters shows Michaelsen's series to be equally unacceptable. The stages in the series: *Eukerria*—*Gordiodrilus elegans*—*G. luykerleni* involve reduction of the pair of oesophageal diverticula of *Eukerria* to the single midventral sac of *Gordiodrilus* (s. Beddard) and a reversal of this reduction to give the pair of sacs of *luykerleni*—an unlikely sequence. *Nannodrilus* should, therefore, be reinstated as a separate genus.

Gates' (1942) *Nannodrilus* division was co-ordinate with his *tenuis*, *robustus* and *Diaphorodrilus* divisions, each of which was virtually a genus and was given a "generic" definition although he did not designate them genera. He excluded *G. togoensis* Michaelsen, 1913, and *G. johneni* Michaelsen, 1936, from the division because they lack gizzards. I do not consider this to invalidate their inclusion in *Nannodrilus* (Jamieson, 1962b, footnote p. 619) and have transferred them from *Gordiodrilus* to this genus.

**EXCLUSION OF *Diaphorodrilus*.** Gates regarded the species in his *Diaphorodrilus* division (*G. doriae* (Cognetti, 1910), *G. overlaeti* Michaelsen, 1936, *G. luykerleni* Michaelsen, 1913, and *G. luykerleni thomseni* Michaelsen, 1933, the latter regarded by Gates as specifically distinct) as having little in common, and was able to give only a brief diagnosis. The only feature which he could find to diagnose the group from all other Ocnerodrilinae was a constant segmental location of the spermathecal pores. As I have found these pores to be intersegmental in one apparently normal specimen of *luykerleni*, the character appears to be unreliable.

I propose that *overlaeti*, like *luykerleni*, should be transferred to *Ilyogenia*,<sup>1</sup> leaving only *doriae* in the *Diaphorodrilus* division. The sexprostatic *doriae* has a pair of oesophageal diverticula and has little in common with the quadriprostatic, unicaecal *Gordiodrilus*. I therefore propose to reinstate the genus *Diaphorodrilus* Cognetti, 1910, of which *doriae* is the type and sole species.

### THE RESTRICTED *Gordiodrillus*

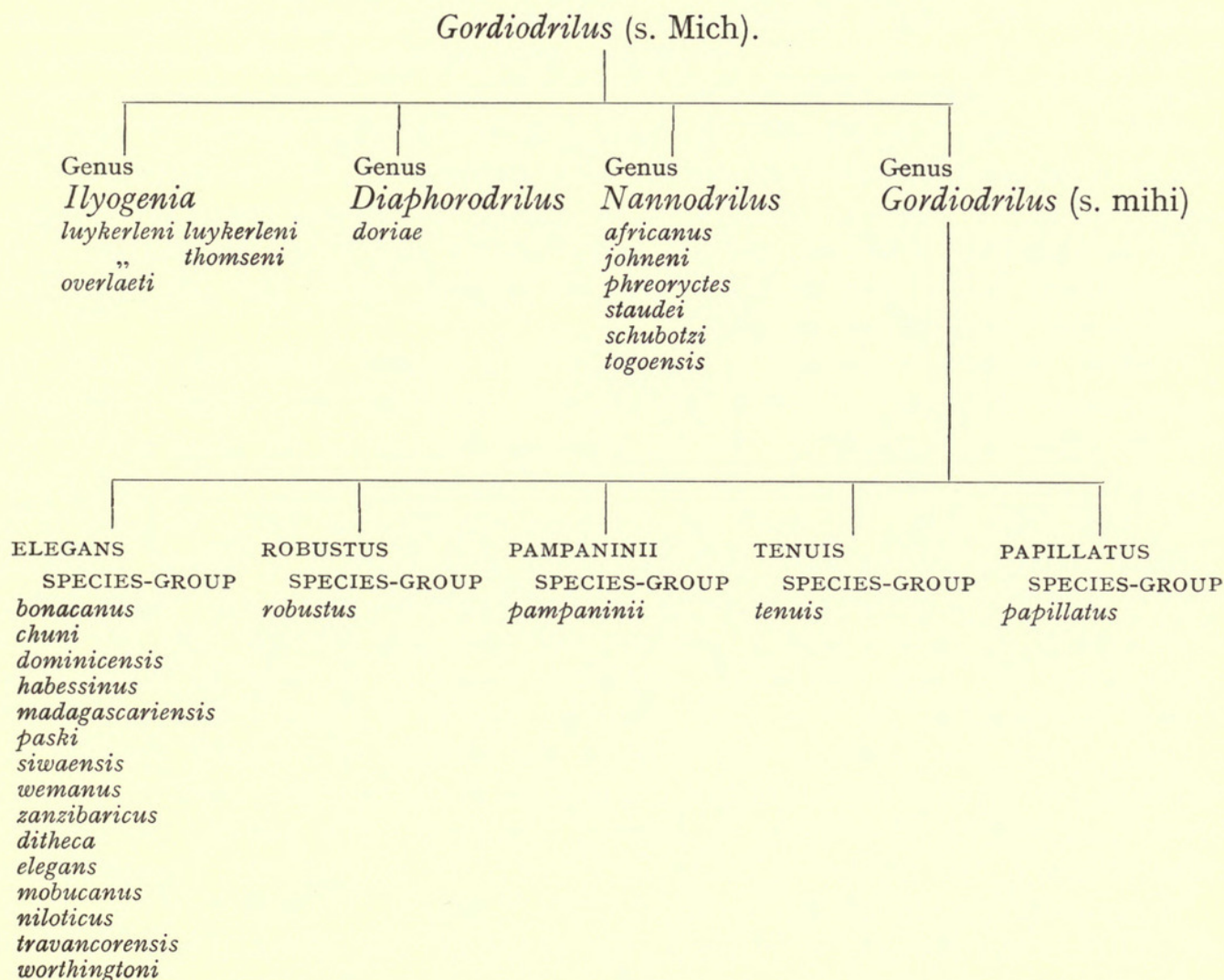
The restriction of *Gordiodrilus* (s. Mich.) proposed above (see also Table II) leaves only Gates' *tenuis* division (divided by Gates into six groups, Table I) and his *robustus* division (containing *G. robustus*, *G. pampaninii* and *congicus*) to be considered. The species they contain constitute *Gordiodrilus* (s. mihi) which is here divided into five species-groups: an *elegans* group of fifteen species and four monotypic species-groups, a *tenuis* group, a *robustus* group, a *pampaninii* group and a *papillatus* group. The grounds for recognizing these species-groups are best shown by a discussion of Gates' two divisions.

The species of Gates' *tenuis* division (Table I) share with his *robustus* division a quadriprostatic condition, with the prostatic pores at the termini of the seminal grooves in which lie the male pores in an intermediate position, but differ in lacking

<sup>1</sup> *Ilyogenia luykerleni* (Mich.) is intermediate between most species of *Ilyogenia*, which have the male and prostatic pores on xvii (with, in one case, *I. limicola*, a further pair of prostatic pores on xviii) and *I. chubbi* and *I. overlaeti* (Mich.) which have male and prostatic pores on xix with a further pair of prostatic pores on xx. *I. luykerleni* has pores on xviii (and additional prostatic pores on xix in *I. l. luykerleni*). It is the only member of *Ilyogenia* with two pairs of spermathecae. That *I. overlaeti* is distinct from *I. chubbi* is very doubtful.



a gizzard. Gates stated that *G. tenuis* should be regarded as a specialized representative of the species placed in the *tenuis* division because it maintains the gordiodrilin approximation to an acanthodrilin condition of the male terminalia. Its affinities with these species seem doubtful and I share with Beddard (1895) the view that *tenuis* has some claims to being regarded as generically distinct. Peculiar features of *G. tenuis* are the far posterior position of its male and prostatic pores (xx to xxi),

TABLE II.—*Present Analysis of Gordiodrilus*

the great length of the clitellum (xiv to xxvii) and the possible metandry. The extraordinary length of the clitellum seems not to be explicable merely by its having been drawn out in response to backward movement of the prostatic and male pores for, in *G. papillatus*, where the pores are in xix and xx, the anterior limit of the clitellum is xviii. For the present *tenuis* becomes the sole representative of a *tenuis* species-group within the restricted *Gordiodrilus*.

The remaining groups into which Gates split his *tenuis* division may now be considered. The *unicus* group is no longer valid as *unicus* has been synonymized with *paski* (see Jamieson, 1962a). The *zanzibaricus* group (prostates in xvii and



xviii) and the *travancorensis* group (prostates in xviii and xix) are here united as the *elegans* group. Although their separation probably has some phylogenetic basis (see p. 321), it seems possible that in some cases the variation in location of the pores occurs intraspecifically. Thus the separation of *G. bonacanus* Cernosvitov, 1942, with prostates in xvii and xviii, and *G. travancorensis* Michaelsen, 1910, with prostates in xviii and xix, is questionable (Jamieson, 1962c; both occur outside Africa and may be peregrine forms of the same species). A similar variation occurs intraspecifically in *Ilyogenia christyi* Stephenson, 1928.

Of the species which Gates considered to belong only doubtfully to his *tenuis* division, i.e. *G. ditheca*, *dominicensis*, *mobucanus*, *chuni* and *papillatus*, the first four appear to be members of the *elegans* species-group. *G. ditheca* is probably a variant of *G. elegans*, as Michaelsen (1933) believed; *G. dominicensis* need not be excluded because it is athecal; *G. mobucanus* is a normal member of the group except in the reported post-setal location of its female pores, an observation requiring confirmation; *G. chuni* is referable to the group, its bithecal condition appearing to be an expected reduction, but the extraordinary length and attenuation of the spermathecal ducts, seen elsewhere only in *robustus*, *tenuis* and *papillatus*, may indicate that it should be separated.

I follow Gates in referring *G. papillatus* to a distinct, monotypic group. The combination of characters which distinguishes *papillatus* from other members of the restricted *Gordiodrilus* is: the far posterior position of the male genital field (prostatic pores in xix and xx), the presence of genital markings, the setal disparity and, most important, the presence of bursae copulatrices. Gates recognized the distinct position of *papillatus* and mentioned that there is a remote possibility that it provides a transition between his *travancorensis* group and *tenuis* group; alternatively, he stated that if gizzards and prostates opening into the bursae copulatrices had been overlooked, *papillatus* could be included in *Nannodrilus*. I have suggested (p. 302 and 1962b) that the absence of gizzards need not exclude a species from *Nannodrilus*; nevertheless, the absence of prostates opening into the bursae taken with the intersegmental position of the male pores and the presence of seminal grooves does seem to exclude *papillatus*. The possible phylogenetic relationships of the species are discussed below under Phylogenetic Considerations.

The main diagnostic characteristics of Gates' "generic" definition of the *robustus* division (i.e. the presence of gizzards, the unusually long spermathecal ducts and the presence of genital markings behind the male genital region) mark off the division from other gordiodrilids. But phylogenetic considerations (p. 321 below) suggest that *robustus* (including *congicus*) and *pampaninii* should each be regarded as typical of a separate group within *Gordiodrilus* (s. mihi).

It seems unnecessary to follow Gates' suggestion that, if Beddard's statement were correct and one specimen of *G. robustus* had paired oesophageal sacs, this species would have to be referred to a distinct genus. Pairing, to a lesser extent, in this species has been reported by Michaelsen (1936) and by myself (1963) and does not seem to be of a type which would give rise to paired sacs of the type seen in genera which normally show pairing. The sacs remain ventral and sessile and retain the appearance of a bifurcated gordiodrilid or nannodrilid sac.



## THE NEW CLASSIFICATION

## Family MEGASCOLECIDAE

## Subfamily OCNERODRILINAE

Genus *GORDIODRILUS* Beddard, 1892

*Gordiodrilus* Beddard, 1892. *Ann. Mag. nat. Hist.* (6) **10**: 93–94.

*Gordiodrilus*: Beddard, 1895. A Monograph of the Order Oligochaeta. Oxford. Clarendon Press: 506–507.

*Gordiodrilus*: Michaelsen, 1900. *Das Tierreich*, Lief. **10**, Vermes, Oligochaeta: 373.

*Gordiodrilus* (part.): Michaelsen, 1913. *Zoologica*. Stuttgart, **68**: 3–5.

*Gordiodrilus* (part.): Stephenson, 1930. The Oligochaeta. Oxford: 863.

*Gordiodrilus* (part.): Gates, 1942. *Bull. Mus. comp. Zool. Harvard*, **89**, no. 13: 75–85.

[non] *Nannodrilus* Beddard, 1894b. *Proc. zool. Soc. Lond.* **1894**: 388.

[non] *Diaphorodrilus* Cognetti, 1910. *Ann. Mus. civ. nat. Genova*, (3) **4**: 107.

TYPE-SPECIES: *Gordiodrilus elegans* Beddard, 1892<sup>1</sup>. *G. elegans* is here designated the type-species of *Gordiodrilus* because it was the first species to be described in the largest species-group in the genus. Descriptions of *G. tenuis* and *G. robustus* preceded it in Beddard (1892) but each of these is placed in the present work in a monotypic species-group which has claims to being regarded as a genus.

DEFINITION. Fairly small, usually limnic, worms. Number of segments of the order of 100. Prostomium usually epilobous, sometimes pro-epilobous, or zygotobous. Setae lumbricine, closely paired, one or more of each ventral pair often absent in the prostatic segments. Genital, but not penial, setae sometimes developed;  $dd = 0.4$  to  $0.5$   $u$ . Clitellum ring-shaped or saddle-shaped, or a combination of the two, usually extending from a part or the whole of xiii (or xii) to part or the whole of that behind the last prostatic pores, rarely more extensive, the most posterior limit xxvii. Prostatic pores paired in xvii and xviii or less frequently in xviii and xix, rarely in xix and xx or xx and xxi, abnormally (?) in xviii only; a seminal groove probably always present, connecting the pores of each side. Male pores, one in each seminal groove, in or near the intersegmental furrow between the corresponding prostatic pores. Female pores anterior to the setal zone of xiv, exceptionally near the posterior margin of this segment. Spermathecal pores usually two pairs, one in each of intersegmental furrows  $7/8$  and  $8/9$  or rarely  $6/7$  and  $7/8$ , sometimes one pair behind (or in ?)  $7/8$ ; sometimes absent.

Septal glands anterior to and including vii or viii. Oesophagus usually without a gizzard; exceptionally with a well-developed gizzard in vii or with a vestigial gizzard in this segment and a well-developed gizzard in viii; the oesophagus always bearing midventrally in ix a sessile unpaired or rarely paired<sup>2</sup> oesophageal pouch, which has at most a small lumen, the thick apparently syncytial walls of which are permeated by numerous, perhaps intracellular, chylous canals and by blood vessels. Intestine usually commencing in xiii, apparently sometimes in xii, xiv or xv; typhlosole only rarely present. Hearts paired in x and xi. Holonephridial. Holandric

<sup>1</sup> Professor Gates informs me, in correspondence, that he has designated *G. elegans* the type-species in MS.

<sup>2</sup> This variation occurs only intraspecifically, in *G. robustus*.



or exceptionally, but not certainly, metandric; testis-sacs apparently sometimes present; seminal vesicles a pair in each of ix and xii or in xii only, sometimes present in x and xi in addition to one or both of these. Prostates tubular, two pairs, the glandular parts lined by a single layer of cells. Ovaries and their funnels situated in xiii, exceptionally (abnormally?) in xii. Spermathecae with or without diverticula; each restricted to the segment behind its pore.

DIAGNOSTIC CHARACTERS. The combination of the possession of a single mid-ventral oesophageal pouch and the presence of two pairs of prostatic pores on two consecutive segments with the male pores in or near the intermediate furrow.

#### KEY TO SPECIES-GROUPS WITHIN *Gordiodrilus* (s. mihi)

	Gizzard present	. . . . .	1
	Gizzard absent	. . . . .	2
1a	Gizzard in viii	. . . . .	<b>robustus</b> species-groups, pp. 317
1b	Gizzard in vii only	. . . . .	<b>pampaninii</b> species-group, pp. 319
2a	Vasa deferentia discharging through bursae copulatrices		<b>papillatus</b> species-group, pp. 319
2b	No bursae copulatrices	. . . . .	3
3a	Prostatic pores paired in xvii and xviii or xviii and xix or in xviii only		<b>elegans</b> species-group, pp. 306
3b	Prostatic pores paired in xx and xxi	. . . . .	<b>tenuis</b> species-group, pp. 316

#### **ELEGANS** SPECIES-GROUP (see Jamieson, 1962b)

Representative species *Gordiodrilus elegans* Beddard, 1892; the type-species.

DEFINITION. Small to medium-sized worms with 80 to 125 segments. Prostomium epi-, proepi-, or zygo-lobous. Setae uniform. Clitellum embracing part or the whole of xii or xiii or xiv to part or the whole of xvii or xviii or xix, usually commencing on xiii and ending on xviii or xix. Prostatic pores paired in each of xvii and xviii or xviii and xix, exceptionally<sup>1</sup> (abnormally?) a pair in xviii only. Female pores anterior to the setal zone of xiv, exceptionally<sup>2</sup> posterior in this segment. Spermathecal pores paired in intersegmental furrows 7/8 and 8/9, or exceptionally<sup>3</sup> one pair in (?) or just behind furrow 7/8, or none. No genital markings present. Dorsal pores at least sometimes present.

Gizzards absent. Oesophageal pouch not known to be paired; typhlosole absent (?). Holandric; testis-sacs apparently sometimes present. Spermathecal ducts only exceptionally very long and slender.

DIAGNOSTIC CHARACTERS. The combination of the absence of a gizzard, with a pair of prostate pores in xvii and xviii or xviii and xix.

REMARKS. The *elegans* species-group appears to be a natural one although it is not homogeneous in some respects. It includes *G. bonacanus*, *chuni*, *dominicensis*, *habesinus*, *madagascariensis*, *paski*, *siwaensis*, *wemanus* and *zanzibaricus*, with prostatic

<sup>1</sup> *G. ditheca*.    <sup>2</sup> *G. mobucanus*.    <sup>3</sup> *G. chuni*.



pores in xvii and xviii; *G. ditheca* with prostates in xviii only; and *G. elegans*, *mobucanus*, *niloticus*, *travancorensis* and *worthingtoni* with prostatic pores in xviii and xix.

Until more extensive collections of this species-group are available it seems unlikely that the full synonymy of its species will be convincingly established. Nevertheless, recourse to type material has shown *G. unicus* and *G. peguanus* to belong in the synonymy of *G. paski* (see Jamieson, 1962a). Far wider synonymy probably exists. It has been suggested (Jamieson, 1962b) that *G. niloticus*, *G. worthingtoni* and *G. bonacanus* may belong in *G. travancorensis* and a possibility of their synonymy with *G. paski* is indicated by the suggestion of Cernosvitov (1942) that *unicus* (now in *paski*) *madagascariensis*, *travancorensis*, *bonacanus* and *dominicensis* may represent a single species and the placing by Gates (1954) of *bonacanus* in the synonymy of *peguanus* (now in *paski*).

Acceptance of all these synonymies would reduce the *elegans* species-group from fifteen to nine species and, by reducing the importance attached to certain characters for specific separation, would probably necessitate further suppression. Such extensive changes require more evidence than is yet available and in the present work only the synonymy of *peguanus* and *unicus* with *paski* is accepted.

KEY TO SPECIES OF THE *ELEGANS* SPECIES-GROUP

- |     |  |                                     |
|-----|--|-------------------------------------|
| 1a  | Prostatic pores two pairs . . . . .  | 2                                   |
| 1b  | Prostatic pores one pair (in xviii) . . . . .  | <i>G. ditheca</i> , p. 309          |
| 2a  | Prostatic pores in xvii and xviii . . . . .  | 3                                   |
| 2b  | Prostatic pores in xviii and xix . . . . .   | 10                                  |
| 3a  | Spermathecal pores absent . . . . .  | <i>G. dominicensis</i> , p. 309     |
| 3b  | Spermathecal pores one pair, in viii . . . . .   | <i>G. chuni</i> , p. 308            |
| 3c  | Spermathecal pores two pairs . . . . .   | 4                                   |
| 4a  | Clitellum saddle-shaped . . . . .  | <i>G. bonacanus</i> , p. 308        |
| 4b  | Clitellum ring-shaped . . . . .  | 5                                   |
| 5a  | A greatly raised tuberculum pubertatis present between the seminal grooves . . . . .   | <i>G. siwaensis</i> , p. 313        |
| 5b  | No tuberculum between the seminal grooves . . . . .  | 6                                   |
| 6a  | Ventral surface of viii and of the anterior half of ix thickened and glandular . . . . .   | <i>G. zanzibaricus</i> , p. 316     |
| 6b  | Ventral surface of viii neither thickened nor glandular . . . . .  | 7                                   |
| 7a  | Spermathecal ducts with diverticula . . . . .  | 8                                   |
| 7b  | Spermathecal ducts without diverticula . . . . .   | 9                                   |
| 8a  | Septa 5/6 to 9/10 thickened, 6/7 to 8/9 very strongly . . . . .  | <i>G. habessinus</i> , p. 310       |
| 8b  | Septa never very strongly thickened . . . . .  | <i>G. paski</i> , p. 312            |
| 9a  | Prostatic pores in setal lines <i>b</i> ; the male genital field protuberant as an almost square area at fullest development from 16/17 to 18/19 . . . . . | <i>G. wemanus</i> , p. 315          |
| 9b  | Prostatic pores just lateral to setal lines <i>b</i> ; field not as above . . . . .  | <i>G. madagascariensis</i> , p. 311 |
| 10a | Spermathecal pores absent . . . . .  | <i>G. niloticus</i> , p. 312        |
| 10b | Spermathecal pores two pairs . . . . .   | 11                                  |
| 11a | Spermathecal duct with diverticula . . . . .   | 12                                  |
| 11b | Spermathecal duct without diverticula . . . . .  | 13                                  |
| 12a | Prostatic pores in setal lines <i>b</i> . . . . .  | <i>G. worthingtoni</i> , p. 315     |
| 12b | Prostatic pores median to setal lines <i>a</i> . . . . .   | <i>G. elegans</i> , p. 310          |
| 13a | Female pores presetal in xiv . . . . .   | <i>G. travancorensis</i> , p. 314   |
| 13b | Female pores post-setal in xiv . . . . .   | <i>G. mobucanus</i> , p. 311        |



***Gordiodrilus bonacanus* Cernosvitov, 1942**

*Gordiodrilus bonacanus* Cernosvitov, 1942. *Proc. zool. Soc. Lond.*, 1941 (B), **111**: 215-217, text-fig. 53-57.

*Gordiodrilus bonacanus*; Jamieson, 1962c. *Ann. Mag. nat. Hist.*, (13), **5**: 47-49.

*Gordiodrilus peguanus* (part.); Gates, 1954. *Bull. Mus. comp. Zool. Harvard*, **111**, no. 6: 246.

TYPE-LOCALITY: Bonaco Island, "16° 30' N. 85° 55' W."

DEFINITION. Length 40 to 42 mm., diameter at the anterior end 1 mm., number of segments 85 to 91. Setae uniform; in vii and xxxi to xxxv,  $dd = 0.5 u$ ,  $bc = 1.2 aa$ . Clitellum saddle-shaped, embracing  $\frac{1}{2}$  xiii to  $\frac{1}{2}$  xix, the ventral surface in this region to a lesser degree glandular. Prostatic pores paired in xvii and xviii at the sites of the absent setae *b*, each on an almost circular, slightly raised papilla which extends laterally beyond setal line *b* and medially just includes seta *a* of its side; the pores on each side connected by a fine, distinct seminal groove which is straight or perhaps slightly curved towards the midline and is intersected by three transverse medially unbroken furrows; the first of these furrows posteriorly limiting the anterior prostate porophores, the second intersegmental and the third anteriorly limiting the posterior prostate porophores. Male pores probably at the intersection of the seminal grooves and intersegmental furrow 17/18, certainly not far removed from this situation; the whole genital field distinctly protuberant. Female pores in setal lines *b*, or a little median of this, anterior in xiv. Spermathecal pores a pair in each of intersegmental furrows 7/8 and 8/9 in setal lines *b*; each pore almost as wide as a setal couple.

Intestine commencing in xiii. Holandric with a pair of seminal vesicles in xii. Prostates with imperceptibly demarcated ducts. Spermathecae paired in viii and ix; the efferent duct, which has a width in the middle region of 0.09 to 0.14 mm., distinctly demarcated from the subspherical ampulla, the width of which varies from 0.18 to 0.24 mm. The duct narrow, tubular, distally tapering and without diverticula; or distinctly spindle-shaped with a minute knob-like diverticulum on each side of the equator.

***Gordiodrilus chuni* Michaelsen, 1913**

*Gordiodrilus chuni* Michaelsen, 1913: *Zoologica*. Stuttgart, H. **68**: 7-9, text-fig. 3, Taf. II, fig. 17.

*Gordiodrilus chuni*; Jamieson, 1963. *Mitt. naturh. Mus. Hamburg*. **60**, Dec, 1962: 43-55.

TYPE-LOCALITY: Kandahar Island, some kilometres above the Victoria Falls, Rhodesia.

DEFINITION. Length 35 mm., diameter 1.1 mm., 87 to 95 segments. Setae:  $dd$  slightly less than  $0.5 u$ ,  $bc$  about equal to  $aa$ ; one or both members of each ventral couple present in xvii and xviii. Clitellum saddle-shaped with the ventral borders approximately in setal lines *b*, embracing xiii to xvi ventrally and xii to xvii dorsally. Prostatic pores paired in xvii and xviii, those of a side situated at the opposite ends of a conspicuously raised, longitudinally oval, glandular thickening of the skin. This extends from before the setal zone of xvii to behind that of xviii and is separated from its fellow of the other side by a region of similar width; each



thickening symmetrically cleft by a longitudinal seminal groove which connects the prostate pores and which lies just lateral to setal line *b* of the adjacent segments. Male pores each on a minute papilla at the intersection of the seminal and intersegmental furrows 17/18. Female pores somewhat lateral of setal line *b*, a little in front of the setal zone of xiv. Spermathecal pores a single pair just median to setal lines *c* and approximately midway between intersegmental furrow 7/8 and the setal zone of viii, or in the furrow and setal line *b*.

Holandric, with seminal vesicles in ix and xii. Prostate ducts unusually slender and abruptly demarcated. Ovaries (abnormally ?) in xii, oviducts normally situated. Bithecal; spermathecae consisting of an ampulla, 0.68 mm. long, made up of a proximal small spherical appendage which opens through a short duct into an inflated though slightly depressed region, 0.27 mm. wide, one side of which is faintly lobed, and a slender abruptly demarcated duct, 0.41 mm. long and 0.04 mm. wide, into which the latter opens; the proximal part of the lobed region extending below the appendage; or consisting in a thin-walled, tubular, sac-like ampulla which is slightly longer than the tubular bent duct from which it is clearly demarcated.

### *Gordiodrilus ditheca* Beddard, 1892

*Gordiodrilus ditheca* Beddard, 1892. *Ann. Mag. nat. Hist.* (6), **10**: 90–91, Pl. VII, fig. 8.

*Gordiodrilus ditheca*; Beddard, 1895. *A Monograph of the Order Oligochaeta*: 509.

*Gordiodrilus ditheca*; Michaelsen, 1900. *Das Tierreich*, Lief. **10**, Vermes, Oligochaeta: 374.

TYPE-LOCALITY: Lagos, West Africa (?). Found in Kew Gardens, England.

DEFINITION. Clitellum embracing xiii to xvii. Spermatheca a single pair, without diverticula, opening in intersegmental furrow 7/8 (?); prostate glands a single pair opening in xviii. Otherwise as *G. elegans*.

### *Gordiodrilus dominicensis* Beddard, 1892

*Gordiodrilus dominicensis* Beddard, 1892. *Ann. Mag. nat. Hist.* (6): **10**, 91–93, 94, 95, Pl. VI, fig. 2–3.

*Gordiodrilus dominicensis*; Beddard, 1895. *A Monograph of the Order Oligochaeta*: 509.

*Gordiodrilus dominicensis*; Michaelsen, 1900. *Das Tierreich*, Lief. **10**, Vermes, Oligochaeta: 374.

*Gordiodrilus dominicensis*; Beddard, 1901. *Proc. zool. Soc. Lond.* 1901, **1**: 364.

*Gordiodrilus dominicensis*; Jamieson, 1962c. *Ann. Mag. nat. Hist.* (13), **5**: 50.

[non] *Gordiodrilus dominicensis*; Michaelsen, 1914. *Mitt. naturh. Mus. Hamburg*, **31**: 109–110 (vide *G. niloticus*).

TYPE-LOCALITY: Dominica, West Indies (?). Found at Kew Gardens, England.

DEFINITION. Length 26 mm., diameter at the head end 1 mm., about 80 segments. Setae uniform; the ventral pairs absent from xvii and xviii. Clitellum xiii to xviii; spermathecal pores absent; prostate pores paired in xvii and xviii, borne on two projecting (longitudinal?) folds of epithelium. Intestine commencing in xiii. Holandric. No spermathecae.



***Gordiodrilus elegans* Beddard, 1892**

*Gordiodrilus elegans* Beddard, 1892. *Ann. Mag. nat. Hist.* (6), **10**: 84-90, 94, 95, Pl. VI, fig. 1, Pl. VII, fig. 6A, 7.

*Gordiodrilus elegans*; Beddard, 1895. *A Monograph of the Order Oligochaeta*: 508-509.

*Gordiodrilus elegans*; Michaelsen, 1900. *Das Tierreich*, Lief. **10**, Vermes, Oligochaeta: 374.

*Gordiodrilus elegans*; Jamieson, 1962c. *Ann. Mag. nat. Hist.* (13), **5**: 53.

TYPE-LOCALITY: Lagos, West Africa (?). Found at Kew Gardens, England.

DEFINITION. Length ca. 40 mm. Setae uniform; *a* and *b* of xviii (?) and xix (?) absent at maturity. Clitellum saddle-shaped, embracing xiii to xviii. Prostate pores paired in xviii and xix; a male pore lying in intersegmental furrow 18/19 in line with, or perhaps just median to, and midway between those of each side. All three pores appreciably median to setal line *a* of the adjacent segments and situated near the lateral edges of a raised rectangular area, which extends anteriorly and posteriorly almost to the borders of xviii and xix and laterally approximately to setal lines *a* of the adjacent segments. The centre of this region is abruptly sunken so as to be surrounded by a ridge bearing the pores. Spermathecal pores paired in intersegmental furrows 7/8 and 8/9.

Holandric with seminal vesicles in ix to xii. Prostate ducts abruptly demarcated. Spermathecae paired in viii and ix, rarely both pairs in viii; each with a round or oval thin-walled ampulla and a narrow duct with a pair of rudimentary diverticula at their junction.

***Gordiodrilus habessinus* Michaelsen, 1913**

*Gordiodrilus habessinus* Michaelsen, 1913. *Zoologica*. Stuttgart, H. **68**: 5-7, Taf. II, fig. 30-31, text-fig. 2.

*Gordiodrilus habessinus*; Michaelsen, 1915. *Wiss. Ergebn. zw. dtsh. zent. Afr. Exped.* Band **1**, Zool. **1**, Teil. **1**, Lief. **8**, Oligochaeta: 218-219.

*Gordiodrilus habessinus*; Jamieson, 1963. *Mitt. naturh. Mus. Hamburg*. **60**, Dec. 1962: 43-55.

TYPE-LOCALITY: Abyssinia.

OTHER LOCALITIES: Source of the River Shari, Fort Crampel, "ca. 7° N. 19° 20' E.," Gribingi, French West Africa.

DEFINITION. Length 30 to 36 mm., maximum diameter 1 to 1.4 mm., ca. 80 to 110 segments. Setae: *dd* slightly smaller than  $\frac{1}{2}$  *u*, *bc* ca. = 1.3 *aa*; setae *b* and sometimes some of setae *a* absent from xvii and xviii; setae *a* closer together in these segments than elsewhere. Clitellum ring-shaped, embracing segments  $\frac{1}{3}$  xiii to  $\frac{1}{3}$  xix. Male genital field at maturity strongly raised in the form of a right-angled cushion, wider than long, which extends over the entire lengths of xvii and xviii and laterally over setal lines *b*. The angles of the field each filled by an indistinct transverse papilla. Prostate pores paired in xvii and xviii at the sites of the absent setae *b* or just lateral to setal lines *b*; those of each side interconnected by an almost straight seminal groove, which ends on the papilla of its side or, in the absence of the papillae (perhaps when less mature) connected by a laterally somewhat convex seminal groove rimmed by slight ridges surrounding the prostate pores. Male pores in the seminal grooves approximately where these are intersected by intersegmental furrow 17/18. Female pores anterior in xiv, just lateral to setal lines *b* which their



median ends reach. Spermathecal pores paired in intersegmental furrows 7/8 and 8/9 just lateral to or in setal lines *b*.

Holandric with seminal vesicles in ix and xii or (probably only when immature) in xii only; sperm masses in x and xi perhaps in vesicles also. Prostate glands unusually thin and with the duct about half the thickness of the glandular part. Ectal ends of the vasa deferentia unthickened. Spermathecae consisting of an ellipsoidal almost spherical ampulla and a sharply demarcated fairly stout cylindrical or spindle-shaped duct about as long as the ampulla; the duct bearing at different points three (or four?) diverticula which are embedded in the glandular investment of the duct and are hardly visible externally.

***Gordiodrilus madagascariensis* Michaelsen, 1907**

*Gordiodrilus madagascariensis* Michaelsen, 1907. Reise in Ostafrika in den Jahren 1903–1905, von A. Voeltzkow. Ergebn., II, Syst. Arb., H.2: 46–47.

*Gordiodrilus madagascariensis*; Jamieson, 1963. Mitt. naturh. Mus. Hamburg. 60, Dec. 1962: 43–55.

TYPE-LOCALITY: Madagascar: Fénérive (30 miles N. of Tamatave, 18° 8' S. 49° 22' E.) and Ambodifotra (16° 55' S. 49° 52' E.), Sainte Marie.

DEFINITION. Length 38 mm., diameter 1 mm., 115 segments. Setae uniform; *bc* slightly smaller than *aa* only in the first setigerous segment elsewhere larger; especially behind the clitellum where *bc* ca. =  $\frac{7}{5}$  *aa*; *dd* a little smaller than 0.5 *u*; ventral setae of xvii and xviii present. Clitellum ring-shaped, apparently less developed ventrally, embracing  $\frac{1}{2}$  xiii to xix. Prostate pores paired in xvii (?) and xviii (?), the anterior immediately behind and the posterior just in front of the setal zone lateral to setal line *b*. Male pores immediately behind intersegmental furrow 17/18, roughly in line with the prostate pores. Female pores in front of setae *b* of xiv. Spermathecal pores a pair in or close behind each of intersegmental furrows 7/8 and 8/9, a little lateral to setal lines *b*.

Intestine commencing in xiv. Holandric with seminal vesicles in ix and xii. Prostate ducts not sharply demarcated. Ectal ends of the vasa deferentia not thickened. Spermathecae without diverticula, consisting of a large almost spherical ampulla and a long, thin, sharply demarcated duct of which the ectal end, running within the body wall, is sharply bent.

***Gordiodrilus mobucanus* Cognetti, 1907**

*Gordiodrilus mobucanus* Cognetti, 1907a. Boll. Mus. Zool. comp. Torino, 22, No. 551: 4.

*Gordiodrilus mobucanus*; Cognetti, 1907b. Il Ruwenzori: 383–384, Taf. III, fig. 43.

TYPE-LOCALITY: Mt. Ruwenzori, Mobuco Valley, East Africa.

DEFINITION. Length (immature) 65 mm., width 1.5 mm., 120 segments. Setae uniform; in the midbody *bc* ca. = 1.3 *aa*, *dd* = 0.5 *u*. Prostate pores paired in xviii and xix in the setal zones a little lateral of setal lines *b*; those of each side connected by a long, narrow, straight seminal groove which is bounded by a marked tumescence. Male pores in the seminal grooves at the posterior margin of xvii. Female pores at the posterior margin of xiv in setal strip *ab*, like the prostate pores



not externally visible. Spermathecal pores paired in intersegmental furrows 7/8 and 8/9 a little lateral of setal lines *b* on small tubercles.

Intestine commencing in xv. Holandric with seminal vesicles in ix and xii. Vasa deferentia of each side running close together and uniting near the male pore. Spermathecae almost tubular, a little dilated entally; without diverticula; paired in viii and ix.

### *Gordiodrilus niloticus* Jamieson, 1962

*Gordiodrilus niloticus* Jamieson, 1962b. *Proc. zool. Soc. Lond.* **139**: 608.

(= *G. dominicensis*; Michaelsen, 1914. *Mitt. naturh. Mus. Hamburg*, **31**: 109–110; [non].

*G. dominicensis* Beddard, 1892).

TYPE-LOCALITY: 9° 30' N. 31° E., on the White Nile, Tongo, Upper Nile Province, Sudan.

DEFINITION. Length 28 to 50 mm., maximum diameter 1 to 1½ mm., 87 to 125 segments. Setae fairly delicate and uniform (with the exception of those of xii which may be elongated?); setae *b* absent from xviii and xix, where the distance between setae *a* is only two-thirds of that in xx; in xii *dd* ca. = 0.4 to 0.5 *u*, *bc* ca. = 1.3 to 1.5 *aa*. Clitellum saddle-shaped, anteriorly very protuberant; embracing xiii, ¾ xiii, ½ xiii to ½ xix, xix (minimally 6½ segments). Prostate pores paired in xviii and xix at the sites of the absent setae *b*, each on a transversely oval papilla which extends laterally well beyond setal line *b* and medially just includes seta *a* of its side. The pores of each side connected by a fine, distinct seminal groove which is intersected by three transverse medially unbroken furrows; the first of these posteriorly limiting the anterior prostate porophores, the second intersegmental, and the third anteriorly limiting the posterior prostate porophores. Male pores at the intersection of seminal grooves and intersegmental furrow 18/19. Spermathecal pores absent.

Intestine commencing in xiii (?). Holandric with seminal vesicles in xii. Prostates with abruptly demarcated very narrow ducts. Vasa deferentia entering the body wall just behind septum 18/19.

### *Gordiodrilus paski* Stephenson, 1928

*Gordiodrilus paski* Stephenson, 1928. *Ann. Mag. nat. Hist.* (10), **1**: 1–4, text-fig. 1.

*Gordiodrilus unicus* Stephenson, 1931. *Proc. zool. Soc. Lond.* 1931, **1**: 79–81, text-fig. 25.

*Gordiodrilus peguanus* Gates, 1942. *Bull. Mus. comp. Zool. Harvard*, **89**, No. 3: 85–90.

*Gordiodrilus peguanus* (part.); Gates, 1954. *Bull. Mus. comp. Zool. Harvard*, **111**, No. 6: 246 (excluding *G. bonacanus*.)

*Gordiodrilus paski*; (including *G. unicus* and *G. peguanus*) Jamieson, 1962a. *Ann. Mag. nat. Hist.* (13), **4**: 519–527.

TYPE-LOCALITY: Kigoma Harbour (4° 52' S. 29° 38' E.), Lake Tanganyika.

OTHER LOCALITIES: Bhamo (24° 5' N. 97° 5' E.), Burma (Stephenson, 1931); Bangalore (12° 58' N. 77° 35' E.), India, and numerous localities in Burma (Gates, 1942); Rio Piedras, Porto Rico (Gates, 1954).

DEFINITION. Length 35 to 47 mm., width 1 to 1.5 mm., about 98 segments. Setae uniform; in vii *dd* = 0.5 *u*, *bc* ca. = 1.1 *aa*; in xxv *dd* ca. = 0.4 *u*, *bc* = 1.3 *aa*;



ventral setae of the segments bearing the prostate pores all absent (merely obscured?) or some of them present. Clitellum ring-shaped except sometimes in xvii and xviii, embracing  $\frac{1}{2}$  xiii, xiv (?) to xviii, 1/n xix, 1/n xx. Prostate pores paired in xvii and xviii in the setal zones in the immediate neighbourhood of the sites of the ventral setae, those of each side connected by a seminal groove which is straight or curves slightly outwards and which is often covered by the cuticle of the general body surface. The borders of the grooves sometimes very slightly raised especially at the extremities. The whole male genital field protruding as an approximately square area or consisting of a dumb-bell-shaped area bearing each groove and raised more noticeably at the pores than elsewhere. Male pores apparently situated at the intersection of the seminal grooves with intersegmental furrow 17/18. Female pores just lateral to setal lines *b* immediately behind intersegmental furrow 13/14. Spermathecal pores paired transverse slits in intersegmental furrows 7/8 and 8/9, the centres of which lie in or near setal lines *b*.

Intestine commencing in xii. Holandric with seminal vesicles in xii and sometimes also in ix and possibly testis-sacs in x and xi. Vasa deferentia on each side passing a little lateral of the prostate pores and entering the body wall midway between the corresponding prostates; at least posteriorly single. Ducts of prostates more slender than the glandular parts but not sharply demarcated. Spermathecae paired in viii and ix, each with the form of an almost tubular sac which is bent a few times. The ental end of the sac may be swollen into a definite ampulla and is markedly swollen over a short region immediately ental to the fairly distinct remaining region which constitutes the duct. The walls of this swollen region (always?) possess two to eight small chambers or diverticula. Length ampulla 0.2 mm., width ampulla and the swollen part of the duct 0.1 mm., width of the spermatheca ental to and ectal to the swollen portion 0.07 mm.

### *Gordiodrilus siwaensis* Jamieson, 1962

*Gordiodrilus* sp. Michaelsen, 1937 (1938). *Proc. zool. Soc. Lond.* (B), **107**, pt. 4: 509.

*Gordiodrilus siwaensis* Jamieson, 1962b. *Proc. zool. Soc. Lond.* **139**: 612.

TYPE-LOCALITY: Siwa Oasis, ca. 29° N. 26° E., Egypt.

DEFINITION. Length 37 mm., maximum diameter (at the clitellum) 1.3 mm., 90 segments. Setae apparently uniform; in ix *dd* ca. = 0.5 *u*, *bc* ca. = 1.5 *aa*; setae *b* of xvii and xviii absent, setae *a* closer together here than elsewhere. Clitellum ring-shaped, xiii (?),  $\frac{1}{2}$  xiii to  $\frac{1}{2}$  xix, anteriorly not protuberant, but recognizable by its brownish colour. Prostatic pores paired in xvii and xviii. A greatly raised tuberculum pubertatis lies ventrally in xvii and xviii, its rounded anterior and posterior ends pushing the setal ridges of these segments respectively anteriorly and posteriorly but just including setae *a*; its lateral borders flanked by straight seminal grooves which lie in line with setae *a* of adjacent segments (not with those of xvii and xviii) and are terminated by the prostate pores. A low papilla fills each of the angles subtended by the border of the tuberculum and the bounding setal ridges and extends laterally to approximately midway between setal lines *b* and *c*. Male pores at the intersection of the seminal grooves and intersegmental furrow 17/18 (?). Female



pores each on a small purplish, protuberant, transversely oval papilla, approximately as wide as a setal couple, the centre of which lies very slightly lateral to setal line *b* and a little nearer the setal zone of xiv than that of xiii. Spermathecal pores paired in intersegmental furrows 7/8 and 8/9; each pore a transverse slit slightly wider than a setal couple, its centre just lateral to setal line *b*. The ventral surface of viii bearing a clitellum-like thickening which reaches laterally to setal lines *c*.

Intestine commencing in xiii. Holandric with seminal vesicles in xii (and ix?). Prostate ducts not sharply demarcated from the tapering glandular parts. The double vas deferens of each side entering the body wall midway between the anterior and posterior prostate pores. Spermathecae paired in each of viii and ix, each consisting of an ovoid ampulla 0.24 mm. wide and 0.32 mm. long and a stout, strongly curved, slightly shorter duct distally 0.11 mm. wide; the duct swollen and spindle shaped owing to the presence of at least three evaginations of its walls, which are not externally visible because of a uniform (glandular?) covering of the duct; each evagination apparently with the form of a narrow-based diverticulum and, like the ampulla, containing sperm.

### *Gordiodrilus travancorensis* Michaelsen, 1910

*Gordiodrilus travancorensis* Michaelsen, 1910a. *Abh. naturw. Ver. Hamburg*, **19**, H.5: 98–100.

*Gordiodrilus travancorensis*; Stephenson, 1923. *Fauna of British India, Oligochaeta*, London: 482–483.

*Gordiodrilus travancorensis*; Jamieson, 1963. *Mitt. naturh. Mus. Hamburg*, **60**, Dec. 1962: 43–55.

TYPE-LOCALITY: Nedumangad, 10 miles NE. of Trivandrum, 8° 29' N. 76° 58' E., Travancore, S. India.

DEFINITION. Length 32 mm., maximum diameter  $\frac{2}{3}$  mm., 84 segments. Setae: in the forebody *dd* ca. =  $\frac{1}{2} u$ ; *bc* slightly smaller than *aa*; setae *b* of xviii and xix apparently absent. Clitellum saddle-shaped, or at least less well-developed between setal lines *a*, embracing  $\frac{1}{4}$  xiii to xix (=  $6\frac{1}{2}$ , *sic* Michaelsen) though much less developed in xix. Prostate pores paired in xviii and xix at the sites of the apparently absent setae *b*; each on a transversely oval, almost circular papilla which extends laterally beyond setal line *b* and medially just includes seta *a* of its side. The pores of each side connected by a fine distinct seminal groove which is intersected by three transverse medially unbroken furrows; the first of these posteriorly, limiting the anterior prostate porophores, the second intersegmental, and the third anteriorly, limiting the posterior prostate porophores. Male pores probably at the intersection of the seminal grooves and intersegmental furrow 18/19, certainly not far removed from this situation. Female pores anterior to setae *ab* of xiv. Spermathecal pores paired in each of intersegmental furrows 7/8 and 8/9 in setal lines *b*.

Intestine commencing between xii and xiii. Holandric, with seminal vesicles in xii. Prostate ducts little thinner than the glandular parts from which they are not abruptly demarcated. Vasa deferentia entering the body wall midway between the anterior and posterior prostate pores. Spermathecae in viii and ix, each consisting of a sac-like ampulla and a narrow duct of approximately the same length, or (only



when immature ?) of an entally blind tube 0.27 mm. long and 0.09 mm. wide, the ental fourth of which forms a spherical ampulla marked off from the duct, which anteriorly tapers to about half the general width, by a faint constriction.

***Gordiodrilus wemanus* Michaelsen, 1937**

*Gordiodrilus wemanus* Michaelsen, 1937. *Bull. Mus. comp. Zool. Harvard*, **79** : 446–449, fig. 8, 9.  
*Gordiodrilus wemanus*; Jamieson, 1963. *Mitt. naturh. Mus. Hamburg*, **60**, Dec. 1962 : 43–55.

TYPE-LOCALITY : Wema, “ca. 02° 30' S. 40° E.”, Ngatana District, Tana River, Kenya.

DEFINITION. Length 35 to 45 mm., width 1.0 to 1.5 mm., segments 92 to about 120. Setae :  $dd = 0.4$  to  $0.5 u$ ,  $bc$  greater than  $aa$  ; towards the clitellum the setae are apparently very slightly shifted ventralwards and moderately large, the ventral slightly larger than the lateral ; setae  $b$  of xvii and xviii apparently are always absent. Clitellum ring-shaped, embracing xii, xiii, xiv to xviii (?),  $\frac{1}{4}$  xix, xix ; sometimes saddle-shaped behind the seminal grooves. Prostate pores paired in xvii and xviii in the setal zones and setal lines  $b$ , each at the centre of a more or less distinct circular porophore, those of each side connected by a straight or outwardly curving seminal groove, which is often covered by the cuticle of the body surface, and is bordered by lateral walls. The whole male genital field when fully developed projects as a squarish area extending between intersegmental furrows 16/17 and 18/19, and distinctly bordered on each side by a smooth, longitudinal, sometimes whitish elevation which lies slightly lateral of setal line  $b$ . Male pores in the seminal grooves at or very near the intersection with intersegmental furrow 17/18 and visible only in prepared sections. Spermathecal pores paired in intersegmental furrows 7/8 and 8/9 in setal lines  $b$  or slightly lateral of this, not visible externally ; or transverse slit-like openings with swollen margins forming an ellipse.

Intestine commencing in xiii. Holandric, with seminal vesicles in ix and xii. Testis-sacs perhaps present. Vasa deferentia attenuated, those of each side uniting before opening through the male pore. Prostate ducts not abruptly demarcated from the glandular parts, but perceptibly narrowing and distinguishable by their muscular sheen. Spermathecae paired in viii and ix, each consisting of a small oval or inverted pyriform ampulla and a narrower, rather sharply demarcated duct which in the ental two-thirds is about half as wide as the ampulla and in the ectal third gradually narrows to the exterior. The lumen of this duct is a simple, narrow, straight canal only in the narrower ectal third ; in the ental two-thirds it meanders slightly and forms irregular convolutions. There are no diverticula. Length of ampulla 0.21 mm., width of ampulla 0.27 mm., length of duct equal to that of the ampulla or two or three times as great, greatest width of the duct 1.14 mm.

***Gordiodrilus worthingtoni* Jamieson, 1962**

*Gordiodrilus worthingtoni* Jamieson, 1962b. *Proc. zool. Soc. Lond.* **139** : 615.

TYPE-LOCALITY : Lake Baringo, 00° 45' N. 36° 10' E., from a stream running into Lake Hannington, Tanganyika.

DEFINITION. Length ca. 55 mm., maximum diameter (at the clitellum) ca. 1.5 mm., ca. 100 segments. Setae uniform ; in segment 7  $dd = 0.5 u$ ,  $bc = 1.1 aa$  ;



in xviii and xix, setae *a* present, setae *b* apparently absent. Clitellum distinctly saddle-shaped, embracing xiii to  $\frac{1}{2}$  xix, indistinctly delimited posteriorly, its longitudinal borders just median to setal lines *a*. Male genital field differing from that described for *G. niloticus* only in the more tumescent borders of the seminal grooves; sites of the male pores not known. Female pores a pair in setal lines *b* just behind intersegmental furrow 13/14. Spermathecal pores a pair of small elliptical slits in each of intersegmental furrows 7/8 and 8/9 in setal lines *b* or perhaps very slightly median to this.

Intestine commencing in xiii. Holandric, with seminal vesicles in xii (not seen in ix or xi). Prostates with abruptly demarcated ducts. Spermathecae paired in viii and ix, each consisting in a large, irregular, sac-like, thin-walled ampulla and much narrower, although still fairly stout, abruptly demarcated duct of approximately the same length. The duct may be tortuous entally; it bears, embedded in the cellular investment of the spermatheca, two or more pouch-like, narrow-stalked diverticula at about the ental quarter. The length of these diverticula is approximately equal to the width of the more ectal widest region of the duct; the lumina of some of the diverticula are branched and all communicate with the lumen of the duct. Greatest width of the ampulla 0.3 mm., length of the duct (not extended) 0.43 mm., greatest width of the duct 0.07 mm.

### ***Gordiodrilus zanzibaricus* Beddard, 1894**

*Gordiodrilus zanzibaricus* Beddard, 1894a. *Quart. J. micr. Sci.*, N.S. **36**: 252-254.

*Gordiodrilus zanzibaricus*; Beddard, 1895. *A Monograph of the Order Oligochaeta*, 509-510.

*Gordiodrilus zanzibaricus*; Michaelsen, 1900. *Das Tierreich*, Lief. **10**, Vermes, Oligochaeta, pp. 374-375.

*Gordiodrilus mathewsi* Beddard, 1895: *ibid.*: 453 [*Lapsus calami* for *G. zanzibaricus*, see Beddard, 1901, *Proc. zool. Soc. Lond.* 1901, **1**: 364, footnote].

*Gordiodrilus zanzibaricus*; Jamieson, 1962c. *Ann. Mag. nat. Hist.* (13), **5**: 51-52.

TYPE-LOCALITY: Zanzibar.

DEFINITION. Length ca. 25 mm. Setae all ventral; *bc* = *aa*; setae *a* (?) of xvii and xviii absent. Clitellum annular,  $\frac{1}{2}$  xiii to  $\frac{1}{4}$  xix?, xix. Prostate pores paired in xvii and xviii, those of each side connected by a seminal groove with raised somewhat folded margins. Male pores in intersegmental furrow 17/18 (?). Female pores immediately lateral to and at least sometimes (probably always) in front of setae *b* of xiv. Spermathecal pores paired in intersegmental furrows 7/8 and 8/9 a little lateral to setal lines *b*. The ventral surface of viii and that of the anterior half of ix modified, the epidermal cells being tall and glandular.

Intestine commencing in xiii. Holandric, with seminal vesicles in xii. Prostate ducts short and about half as wide as the glandular parts. Spermathecae a pair in each of viii and ix each with a peg-shaped ampulla from which a relatively much thinner duct penetrates the body wall.

### ***TENUIS* Species-group**

Monotypic, containing *G. tenuis* Beddard, 1892.

DEFINITION. As for the species.



DIAGNOSTIC CHARACTERS. The far posterior position of the male and prostatic pores (xx and xxi) and the great length of the clitellum (xiv to xxvii).

REMARKS. (See also p. 303.) These characters taken with the possible metandry and the setal disparity suggest that *tenuis* should be given generic rank. The setal disparity is shared with the *papillatus* species-group.

### *Gordiodrilus tenuis* Beddard, 1892

*Gordiodrilus tenuis* Beddard, 1892. *Ann. Mag. nat. Hist.* (6), **10** : 75–82, 94, 95, Pl. VII, fig. 6C.  
*Gordiodrilus tenuis*; Beddard, 1895. *A Monograph of the Order Oligochaeta* : 507–508.  
*Gordiodrilus tenuis*; Michaelsen, 1900. *Das Tierreich*, Lief. **10**, Vermes, Oligochaeta : 373.  
*Gordiodrilus tenuis*; Jamieson, 1962c. *Ann. Mag. nat. Hist.* (13), **5** : 53–54.

TYPE-LOCALITY : Asaba, 75 miles E. of Benin, 6° 10' N. 5° 38' E., West Africa (?). Found at Kew Gardens.

DEFINITION. Length 90 mm., width 1 mm. The lateral setae about one fourth of the size of the ventral setae; setae *a* rather larger than setae *b*; the ventral setae present in the genital segments. Clitellum, visible only in prepared sections, saddle-shaped, embracing xiv to xxvii. Prostate pores paired in xx and xxi behind the setal zones. Male pores in front of the setal zone of xxi just lateral of setal lines *b*.

Intestine without typhlosole. Metandric (?). Seminal vesicles in x to xiii approximately. Vas deferens single on each side of the body, opening to the exterior not far behind the anterior septum of xxi after running closely adherent to the body wall. Prostates with rather short muscular ducts. Spermathecae paired in viii and ix, large and oval, each narrowing abruptly to form a very slender duct of considerable length; without diverticula.

### *ROBUSTUS* Species-group

Monotypic, containing *G. robustus* Beddard, 1892.

DEFINITION. As for the species.

DIAGNOSTIC CHARACTERS. The possession of a gizzard in viii, of an unpaired genital marking in xix, and of spermathecae in vii.

REMARKS. The reasons for restricting this group to *G. robustus* alone and for retaining it in *Gordiodrilus* are given on pp. 304 and 321.

### *Gordiodrilus robustus* Beddard, 1892

*Gordiodrilus robustus* Beddard, 1892. *Ann. Mag. nat. Hist.* (6), **10** : 82–84, 94, 95, Pl. 7, fig. 4, 5, 6B.

*Gordiodrilus robustus*; Beddard, 1895. *A Monograph of the Order Oligochaeta* : 508.

*Gordiodrilus robustus*; Michaelsen, 1900. *Das Tierreich*, Lief. **10**, Vermes, Oligochaeta : 374.

*Gordiodrilus robustus*; Beddard, 1901. *Proc. zool. Soc. Lond.* 1901, **1** : 363–365.

*Gordiodrilus robustus*; Michaelsen, 1910b. *Wiss. Ergebn. dtsch. zent. Afr. Exped.*, **3**, Zool. 1, Lief. **1** : 114.

*Gordiodrilus robustus congenericus* Michaelsen, 1936. *Rev. Zool. Bot. Afr.*, Tervueren, **29** : 47–52.

*Gordiodrilus robustus*; (suppressing *congenericus*) Jamieson, 1963. *Mitt. naturh. Mus. Hamburg.* **60**, Dec, 1962 : 43–55.



TYPE-LOCALITY: Lagos, West Africa (?). Found at Kew Gardens, England.

OTHER LOCALITIES: Lagos (Beddard, 1901); from between Warri,  $32^{\circ}$  N.  $5^{\circ}$  44' E., and Sapela (28 miles N. of Warri), and also at Benin,  $6^{\circ}$  10' N.  $5^{\circ}$  38' E., Nigeria, and from Debundscha,  $4^{\circ}$  7' N.  $8^{\circ}$  58' E., at the foot of the Cameroon Mountains (Michaelsen, 1910); Leopoldville, "ca.  $4^{\circ}$  47' S.  $15^{\circ}$  16' E.", Belgian Congo (Michaelsen, 1936).

DEFINITION. Length 32 to 72 mm., greatest width 2.0 mm., 90–125 segments. The posterior extremity, for about nine segments (always?) swollen so that the hind end appears club-like. Unmodified setae, in front of v, 0.18 mm. long and 0.01 mm. thick, distinctly S-shaped with prominent node somewhat distal of the middle; those of v to viii, or some of these segments, enlarged, as are those of the club-shaped region of the hind end, reaching 0.55 mm. in length and 0.03 to 0.04 mm. in width, the largest being the ventral setae of the last eight or nine segments; the lateral setae of these segments very slightly smaller. The enlarged setae slightly S-shaped, with indistinct node somewhat ectal from the middle, their ectal ends slightly depressed in one plane and the terminal eighth ornamented with irregular scalloped tracts. The ventral setae of xii and xiii also enlarged, three or four times as large as the lateral setae of their segments, ca. 0.5 mm. long and 0.04 mm. thick; similar in form and ornamentation to the other enlarged setae but perhaps less curved; markedly shifted ventralwards, the skin in their vicinity apparently glandular; the ventral setae of xi also surrounded by a glandular region slightly if at all displaced. In vii  $dd = 0.4$  to  $0.5 u$ ,  $bc = 0.8$  to  $1.0 aa$ , the distance between the setal pairs several times that between the members of a pair, e.g.  $aa : ab$  usually is about equal to 5; in the third segment from the posterior end,  $dd = 0.5 u$ ,  $bc = 0.7$  to  $1.0 aa$ , the distance between the setal pairs being maximally twice that between the members of a pair, e.g.  $aa : ab$  is about equal to 2. Clitellum saddle-shaped and protuberant, embracing  $\frac{1}{2}$  xiii,  $\frac{1}{4}$  xiii, xiv to xvi,  $\frac{1}{2}$  xvii,  $1/n$  xvii, xvii ( $= 3\frac{3}{4}$  to  $4\frac{1}{2}$ ), with its straight, distinct, ventral margins just lateral to or including setal lines  $b$ . Prostate pores paired in xvii and xviii just lateral to and sometimes slightly behind setae  $b$  on diffuse low porophores which include the ventral setae, those of each side connected by a seminal groove which curves slightly medianwards and which runs approximately in setal lines  $b$ . Male pores in the seminal grooves just behind intersegmental furrow 17/18. A median tuberculum pubertatis longitudinally fills the anterior half of xix, reaches laterally slightly beyond setal lines  $a$  and anteriorly projects slightly over its anterior border. Female pores a pair of transverse slits of little extent lying midway between the setal zone of xiv and its anterior border, immediately lateral to setal lines  $b$ . Spermathecal pores minute, paired in intersegmental furrows 6/7 and 7/8 a little lateral of setal lines  $a$ .

Oesophagus with a well-developed gizzard in viii and (always?) a rudimentary gizzard in vii; a wholly or partly paired oesophageal sac dependent midventrally from the oesophagus in ix; intestine commencing apparently in xii, possessing a typhlosole from approximately xvii posteriorly. Holandric, with seminal vesicles in xi and xii. Prostates frequently confined to the segments in which they open, the duct imperceptibly demarcated. Spermathecae paired in vii and viii; each



consisting of a crumpled sub-spherical ampulla and an extraordinarily long and thin, anteriorly running duct which is sometimes coiled. There are no spermathecal diverticula. Width ampulla 0.35 to 1.5 mm., length duct 1.35 to 1.75 mm., width duct 0.03 to 0.05 mm.

### **PAMPANINII** Species-group

Monotypic, containing *Gordiodrilus pampaninii* Baldasseroni, 1913.

DEFINITION. As for the species.

DIAGNOSTIC CHARACTERS. Restriction of the gizzard to vii.

REMARKS. The phylogenetic basis for exclusion of the single species of this species-group from Gates' *robustus* division is discussed on p. 322. The fact that the group is monotypic makes it impossible, as with the *robustus* species-group, to distinguish between group and specific characters.

### **Gordiodrilus pampaninii** Baldasseroni, 1913

*Gordiodrilus pampaninii* Baldasseroni, 1913. *Monit. Zool. It. Firenze*, 24: 127-129.

TYPE-LOCALITY: Tarhuna (40 miles SE. of Tripoli, 32° 52' N. 13° 12' E.), Tripolitania.

DEFINITION. Length 37 mm., width 1.7 mm., 84 to 87 segments. Setae uniform;  $dd = 0.5 u$ ,  $bc$  less than  $aa$ . Clitellum saddle-shaped, embracing xiii to xix, very prominent dorsally; the longitudinal margins in setal lines  $b$ . Prostate pores not visible externally, paired in xviii and xix; those of each side connected by a distinct seminal groove which runs in setal line  $b$  in xvii to xix on a marked tumescence. Male pores not externally visible, one lying in each seminal groove at the posterior margin of xviii. Female pores also not seen, situated in xiv in line with the ventral setae. Spermathecal pores clearly visible in intersegmental furrows 7/8 and 8/9. Three midventral pairs of very swollen papillae with whitish centres present in xx, xxi and xxii, extending over the posterior borders of these segments; the posterior pair absent in one of the two syntypes.

Oesophagus with a well-developed gizzard in vii. Holandric, with seminal vesicles in x, xi and xii. Prostates greatly elongated with the ducts much narrower than the glandular part. Spermathecae two pairs, in viii and ix. Those of viii small and pear-shaped with long, very slender, muscular ducts; those of ix larger, spherical with crumpled surfaces, opening by similar ducts; without diverticula.

### **PAPILLATUS** Species-group

Monotypic, containing *Gordiodrilus papillatus* Beddard, 1901.

DEFINITION. As for the species.

DIAGNOSTIC CHARACTER. The presence of bursae copulatrices.

REMARKS. This monotypic group is similar to the *robustus* and *pampaninii* species-groups in having genital markings behind the prostatic segments and in the form of the spermathecae. It is unique within the restricted *Gordiodrilus* in having bursae copulatrices and this, combined with the setal disparity in each segment,



suggests relationship with *Nannodrilus*. It is retained in *Gordiodrilus* because of the arrangement of the male and prostatic pores. The affinities of *G. papillatus* are discussed on p. 321.

***Gordiodrilus papillatus* Beddard, 1901**

*Gordiodrilus papillatus* Beddard, 1901. *Proc. zool. Soc. Lond.* 1901, 1: 358–363, text-fig. 88.

TYPE-LOCALITY: The neighbourhood of Lagos, 6° 29' N. 3° 30' E., West Africa.

DEFINITION. Length 63 mm., diameter 1.5 to 2.8 mm. (the latter measurement at the clitellum). The ventral setae much more marked than the lateral, especially in the five segments in front of the male genital pores, where they appear as strong hooks to the naked eye, and to a lesser extent in the last body segments; one member of each ventral couple absent in the genital region. Clitellum annular (?), embracing xviii (?) to xxii (?). Prostate pores paired in xix (?) and xx (?) which are swollen relative to the other segments; those of each side connected by, and terminating, a straight terminally somewhat widened seminal groove, ca. 1.8 mm. long. Each groove is bounded by tumid lip-like areas, ca. 3.3 mm. long, which are rounded anteriorly and posteriorly and narrow midway between the pores. Four pairs of small whitish papillae, each with a dark centre, lie immediately median to the tumid areas, the pairs lying in single file. A midventral papilla is present in each of three consecutive segments which are separated from the posterior prostate segment by four segments. The male pores open midway between the prostate pores.

Holandric, with seminal vesicles in ix, x and xi. Prostate ducts short and narrow. Vasa deferentia of each side uniting a segment or two before they enter a large spherical muscular terminal bulbus. Spermathecae paired in viii and ix, each with an oval sac-like ampulla and an unusually long, very slender duct.

PHYLOGENETIC CONSIDERATIONS

Stephenson (1930) accepted Michaelsen's suggestion that *Notiodrilus* (Acanthodrilinae) represents the ancestor of the Megascolecidae. *Notiodrilus* (since suppressed) is quadriprostatic with a pair of prostate pores in each of the segments xvii and xix with the male pores intermediate in xviii.

Gates (1942, p. 66) in discussing characters of the alimentary canal in the Ocnerodrilinae, concluded that there are grounds for regarding the Ocnerodrilinae as more primitive than the Acanthodrilinae. Moreover, by presenting evidence in support of the derivation of his *zanzibaricus* and *travancorensis* groups and *Nannodrilus* and *robustus* divisions of *Gordiodrilus* from a sexprostatic form, he further discredited the *Notiodrilus* theory.

In view of the importance of any evidence which contradicts the classical *Notiodrilus* theory a short discussion of *Gordiodrilus* and *Nannodrilus* as defined in this revision seems desirable. Conclusions from a survey of the six species here included in *Nannodrilus* support Gates' contention that it is primarily sexprostatic. The genus is remarkably homogeneous: interspecific variation in the male and prostatic terminalia is no greater than that which occurs intraspecifically, as in *N. schubotzi*



and *N. stauderi*, and homogeneity in the somatic systems is as striking as that in the genital systems. Thus *johneri*, *phreoryctes*, *schubotzi* and *togoensis* are all described as exhibiting a disparity in the size of the setae in each segment, the ventral being much larger than the lateral. Only in *N. africanus* is the existence of this setal disparity questionable; it is not mentioned for *stauderi* but the latter species is said to differ from *schubotzi* only in certain non-setal characters. The size of setae is not mentioned in any description of *N. africanus* and I find the type-specimens to have uniform setae, but all are immature. In all species except *africanus* the spermathecae are a pair in each of segments viii and ix or in viii only, and in all except *togoensis* and *johneri* a gizzard is present in vii and viii.

It is here tentatively suggested that the ancestral *Nannodrilus* had a pair of prostates opening to the exterior approximately equatorially in each of segments xvii, xviii and xix, the middle pair of which communicated with the exterior through or in common with the muscular bursae of the vasa deferentia; possessed a strong gizzard in each of segments vii and viii; spermathecae in each of segments viii and ix; and exhibited setal disparity throughout the body. There was perhaps also a pair of spermathecae in vii, as is questionably the case in *N. africanus*.

The ancestral *Nannodrilus* here postulated does not seem too speculative. From it all known species of the genus can be derived by morphological variation which is evident in the extant species, and these species it closely resembles.

It is generally accepted (Stephenson, 1930, p. 820, 832) that fusion of male pores with prostatic pores is secondary to their separation. The ancestral *Nannodrilus* may, therefore, have been preceded by a form in which the male and prostatic pores in xviii were separate. Conditions prevailing in the Ocnerodrilinae suggest that these pores were situated equatorially in their segment rather than intersegmentally. This pre-*Nannodrilus* form may have possessed male ducts with unthickened ends. (Variation from thickened to unthickened ducts occurs among species of *Pygmaeodrilus*, *Nematogenia*, *Ilyogenia*, *Quechuona* (?) and *Malabaria* (?).) Such a form, with unthickened ducts, could give the arrangement of terminalia seen in Gates' *zanzibaricus* group by "elimination of the prostates of xix and dislocation anteriorly of the male pores to points midway between the remaining prostatic apertures" and in his *travancorensis* group by "suppression of the prostates in xvii and the dislocation posteriorly of the male pores", the changes advanced by Gates (1942) when he derived these groups from his (undefined) sexprostatic ancestor. Concomitant with these changes would be loss of the spermathecae of vii and of the gizzards. (For reasons for combining these groups in the *elegans* species-group see p. 304.)

*G. papillatus*, which shares with *Nannodrilus* the possession of bursae copulatrices and setal disparity may be closer to *Nannodrilus* than it is to *Gordiodrilus*, the absence of gizzards and the presence of the gordiodriline arrangement of terminalia being possibly convergent similarities. Prostates in xix and xx cannot be explained, however, without additional hypotheses.

*G. robustus* may be derived from a pre-*Nannodrilus* form with unthickened male terminalia by changes similar to those producing *zanzibaricus* group species but with loss, this time, of the spermathecae of ix and retention of the gizzard in vii



and viii; and *G. pampaninii* by changes like those producing *travancorensis* group species but with retention of the gizzard in vii. *G. tenuis* could be derived from the same form but, like *papillatus*, it has the male terminalia outside xvii to xix (and setal disparity) and its origins are obscure.

The existence in the Ocnerodrilinae of prostates or prostate-like organs in xix and xx, in *G. papillatus*; xx and xxi in *G. tenuis*; xvii and xx in *Malabaria paludicola* Stephenson, 1924; xvii, xix and xx in *Thatonia parva* Gates, 1945; xvii, xix, xx and xxi in *Eukerria peguana* Gates, 1942, and in *Deccania alba* Gates, 1949; and xvi, xvii and xviii in *Diaphorodrilus doriae* suggests that we may have to consider the possibility of origin of the Ocnerodrilinae, and probably of the Megascolecidae as a whole, from forms with a more extensive series of prostates even than has been postulated by Gates and myself in the sexprostatic precursors of *Gordiodrilus* and *Nannodrilus*. Certainly the validity of *Notiodrilus* or a similar quadriprostatic form as an ancestor of these species, and therefore of the family, is highly suspect.

#### REFERENCES

- BALDASSERONI, V. 1913. Lombrichi della Tripolitania. *Monit. zool. Ital. Firenze*, **24**: 127-130.
- BEDDARD, F. E. 1892. On a new genus of Oligochaeta comprising five new species belonging to the family Ocnerodrilidae. *Ann. Mag. nat. Hist.* (6), **10**: 74-97.
- 1894a. A contribution to our knowledge of the Oligochaeta of Tropical Eastern Africa. *Quart. J. micr. Sci. (New Series)*, **36**: 201-270.
- 1894b. On two genera, comprising three new species of earthworms from Western Tropical Africa. *Proc. zool. Soc. London*, 1894: 379-390.
- 1895. *A Monograph of the Order Oligochaeta*, Oxford, Clarendon Press.
- 1901. On some earthworms from British East Africa, etc. *Proc. zool. Soc. London*, 1901, **1**: 336-365.
- CERNOSVITOV, L. 1942. Oligochaeta from various parts of the world. *Proc. zool. Soc. London*, 1941 (B), **111**, 1942: 197-236.
- COGNETTI DE MARTIIS, L. 1907a. Spedizione al Ruwenzori di S.A.R. Luigi Amedeo di Savoia Duca degli Abruzzi. Diagnosi preliminari. *Boll. Mus. Zool. comp. Torino*, **22**, No. 551, 1907: 127-130.
- 1907b. *Il Ruwenzori*, 383-384.
- 1910. Lombrichi Africani. *Ann. Mus. civ. nat. Genova* (3), **4**.
- GATES, G. E. 1942. Notes on various peregrine earthworms. *Bull. Mus. comp. Zool. Harvard*, **89**, No. 3: 63-144.
- 1945. On some Indian earthworms. *Proc. Ind. Acad. Sci.* **21** B: 208-258.
- 1949. On some Indian Ocnerodrilids. *Proc. Ind. Acad. Sci.*, **30** B (5), 1949: 279-283.
- 1954. Exotic earthworms of the United States. *Bull. Mus. comp. Zool. Harvard*, **111**, No. 6: 219-258.
- 1957. Contribution to a revision of the earthworm family Ocnerodrilidae. The genus *Nematogenia*. *Bull. Mus. comp. Zool. Harvard*, **117**, No. 4: 427-445.
- JAMIESON, B. G. M. 1962a. A redescription of *Gordiodrilus paski* Stephenson (Oligochaeta). *Ann. Mag. nat. Hist. Ser. 13*, **4**: 519-527.
- 1962b. Some new species of Ocnerodrilinae (Oligochaeta). *Proc. zool. Soc. London*, **139**: 607-626.
- 1962c. Material of *Gordiodrilus* (Oligochaeta) in the British Museum (Natural History). *Ann. Mag. nat. Hist.*, (13), **5**: 47-55.
- 1963. Material of *Gordiodrilus* (Oligochaeta) in the Zoological Museum, Hamburg. *Mitt. naturh. Mus. Hamburg*, **60**, Dec. 1962: 43-55.



- MICHAELSEN, W. 1897. Neue und wenig bekannte afrikanische Terricolen. *Mitt. naturh. Mus. Hamburg*, **14**, 2 : 1-71.
- 1900. Das Tierreich, Lief. **10**, *Vermes Oligochaeta*, Berlin.
- 1903. Westafrikanische Oligochaeten, gesammelt von Herrn. Prof. Yngve Sjöstedt. *Arkiv. Zool.* **1** : 157-169.
- 1907. Oligochaeten von Madagaskar, den Comoren und anderen Inseln des westlichen Indischen Ozeans. *Reise in Ostafrika* v. A. Voeltzkoew, Bd. 2, Stuttgart, 1907 : 39-50.
- 1910a. Die Oligochätenfauna der vorderindisch-ceylonischen Region. *Abh. naturw. Ver. Hamburg*, **19**, H.5 : 1-108.
- 1910b. Die Oligochäten des inneren Ostafrikas und ihre geographischen Beziehungen. *Wiss. Ergebn. dtsch. zent. Afr. Exped.* **3**, Zool. **1**, Lief. **1** : 1-90.
- 1913. Oligochäten vom tropischen und südlich-subtropischen Afrika. II. *Zoologica*, Stuttgart, Heft. 68 : 1-63.
- 1914. Oligochaeten vom tropischen Afrika. *Mitt. naturh. Mus. Hamburg*, **31** : 81-127.
- 1915. Oligochäten in, *Wiss. Ergebn. zw. dtsch. zent. Afr. Exped.*, Band **1**, Zool. **1**, Teil **1**, Lief. **8**.
- 1933. Opisthopore Oligochäten aus dem mittleren und dem südlichen Afrika hauptsächlich gesammelt von Dr. F. Haas während der Schomburgh-Expedition 1931-32. *Abh. senk. nat. Ges.* **40**, H.4 : 411-433.
- 1936. Oligochäten von Belgisch-Kongo, III. *Rev. Zool. Bot. Afr.*, Tervueren, **29** : 213-225.
- 1937. Scientific results of an expedition to rain forest regions in Eastern Africa. VIII. *Oligochaeta. Bull. Mus. comp. Zool. Harvard*, **79** : 433-477.
- 1938. On a collection of African Oligochaeta in the British Museum. *Proc. zool. Soc. London (B)*, **107**, pt. 4, 1937 : 501-528.
- STEPHENSON, J. 1924. On some Indian Oligochaeta, with a description of two new genera of Ocnerodrilinae. *Rec. Ind. Mus.* **25**, pt. IV : 317-365.
- 1928. Oligochaeta from Lake Tanganyika (Dr. C. Christy's Expedition, 1926). *Ann. Mag. nat. Hist. (10)*, **1**, No. **1** : 1-17.
- 1930. *The Oligochaeta*. Oxford.
- 1931. Oligochaeta from Burma, Kenya, and other parts of the world. *Proc. zool. Soc. London*, 1931, **1** : 33-92.







Jamieson, Barrie G M. 1963. "A revision of the genus *Gordiodrilus* Beddard (Oligochaeta: Megascolecidae)." *Bulletin of the British Museum (Natural History) Zoology* 9, 297–323.

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