

SOME SPECIES OF *PYGMAEODRILUS* (*OLIGOCHAETA*) FROM EAST-AFRICA.

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INTRODUCTION.

IN 1936 Michaelsen pointed out the existence within his genus *Pygmaeodrilus* of a species-group distinguished from other members of the genus by a peculiar arrangement of the spermathecal diverticula. In this paper three species of this group, two of which were hitherto unknown, are described. The last generic description given by Michaelsen (1900) is based on only four species, and the only other description, that of Stephenson (1930), does not take into account the unusual features of *P. aequatorialis* Stephenson, and requires extension in other respects. I have therefore included an emended diagnosis together with a discussion of the comparative morphology of the genus.

Apart from a brief reference by Michaelsen (1903 *a*), there has been no previous discussion of the zoogeography of the genus. In the final section of this paper I have listed the localities of all species of the genus and have drawn attention to the remarkable homogeneity in the geographical distribution of the species-group mentioned above and to the fact that the distribution considered with the comparative morphology appears to show clearly that all species of the group arose by speciation of one geographically isolated ancestral species.

In the discussion particular emphasis is placed on those aspects which indicate the possible course of evolution of the genus and the inter-relationships of its species.

Genus *PYGMAEODRILUS* Michaelsen, 1890. Emended diagnosis. *

Small, limnic Ocnero-drilinae with spermathecal diverticula. Clitellum annular or saddle-shaped or both, lying between segments 12 and 20, not infrequently extending onto the former, only in one species onto the latter, and usually occupying between five and seven segments. Setæ lumbricine, closely paired; ventral setæ of segment 17 absent, not represented by penial-setæ.

One pair only of spermathecae, in segment 9, or one medially in each of segments 8 and 9 or in 9 only, each with a duct which may be long or very short opening to the exterior ventrally in the intersegmental-furrow anterior to the segment occupied, never much further laterally than setal-lines *b* †; diverticula opening in common with or via these ducts, one to many to each spermatheca: ampullae simple or deeply lobed sacs. No gizzard. One pair of chylous-pouches, the lumina of which are constricted or divided by folds of their walls, in segment 9.

* This diagnosis differs from previous descriptions mainly in regard to the occurrence of spermathecae in segment 8.

† In this paper the conventional terminology for the four setæ of each side (i.e. the lumbricine arrangement) is used, namely *a*, *b*, *c* and *d* for the respective setæ in order laterally from the midventral-line.

Holandric, or (in one species only) metandric; testes free (perhaps sometimes enclosed in testis-sacs); seminal vesicles sac-like to racemose, in segments 9 and 12, much less commonly in 12 only (perhaps also in segments 10 and 11 in some species), two or more in each segment. One pair of ovaries in segment 13, without ovisacs. Prostates one pair, tubular, with ducts which are almost always muscular and clearly distinguishable from the glandular parts, opening separately from or fused with the male pores in segment 17 (if separated from the latter, never widely) in or between setal-lines *b* and the midventral-line. Prostate ducts and vasa-deferentia, only the former, or only the latter, or neither pair distally thickened.

Type species *Pygmaodrillus quilimanensis* Michaelsen, 1890.

As is explained in the discussion of the comparative morphology of the genus, members of the species-group mentioned in the introduction are characterized in having the diverticula of each spermatheca arranged in an anterior and a posterior group. The apparent homogeneity of this group, which I have called group I, in this feature is paralleled by homogeneity in its geographical distribution (see discussion), and there seems no reason to believe that the grouping, first proposed by Michaelsen from a consideration only of the comparative morphology, is artificial. The species of the genus which do not have the peculiar arrangement of the spermathecal diverticula form a heterogeneous assemblage which for convenience I have called group II. The following key enables specific separation of the members of the homogeneous group. It must, however, be borne in mind that, apart from the portions dealing with the three species described in this paper, the key is based only on literature and that some of the features used for specific separation may in the light of future evidence prove invalid for this purpose.

Key to those species of Pygmaodrillus in which the diverticula of each spermatheca are arranged in an anterior and a posterior group.

- | | | |
|--|------------------------------|---------|
| Only one, median, spermathecal pore, in intersegmental-furrow 8/9 | <i>P. affinis</i> Michaelsen | |
| Spermathecal pores one pair, in intersegmental-furrow 8/9 | 1. | |
| 1. <i>a.</i> Prostate ducts and also the vasa-deferentia much thicker distally than elsewhere | <i>P. nabugaboensi</i> . | 451-456 |
| <i>b.</i> Not as <i>1a.</i> | sp. n. below pp | |
| 2. <i>a.</i> Spermathecae reniform | <i>P. worthingtoni</i> | |
| <i>b.</i> Spermathecae not reniform | sp. n. below pp | 456-458 |
| 3. <i>a.</i> Neither the prostate ducts nor the vasa-deferentia distally thicker. Spermathecal pores median to <i>a.</i> | 3. | |
| <i>b.</i> Only the vasa-deferentia slightly or moderately thickened distally | 4. | |
| 4. <i>a.</i> Ventral setae of segment 9 not developed; a black point in each of the two posterior angles of the spermathecal field. Male and prostate pores of each side opening just median to a small tubercle of which there is one on each side of the midventral-line. The tubercles lying within a roughly circular low wall which extends over the anterior and posterior borders and beyond <i>b</i> of segment 17 | 5. | |
| | <i>P. bipunctatus</i> | |
| | Michaelsen. | |

- b.* Ventral setae of segments 8 and 9 not developed ; no black points in the spermathecal field, which covers the ventral surface of these segments. Each prostatic pore lying on a tiny papilla of which there is one on each side lying roughly in *ab* on a transverse midventral cushion which extends beyond *b* and across the anterior and posterior borders of 17, almost to 15/16 and 18/19. A pair of papillae in the posterior and anterior regions respectively of segments 16 and 18 in *ab*. *P. bulduensis*,
Michaelsen.
5. *a.* Spermathecal pores in *ab*. 6.
b. Spermathecal pores median to *a*. *P. modestus*,
Michaelsen.
6. *a.* Male genital field glandular, bounded by an almost circular slightly raised wall ; extending onto segments 16 and 18, and in segment 17 laterally beyond *b* in which on each side it bears a stump-like outwardly inclined papilla. Spermathecal ducts coiled, at least as long as the ampulla from which they are poorly demarcated. *P. ngomanus*,
Michaelsen.
- b.* Male genital field deeply sunken, with three papillae on each side, lying transversely and all median to *b*, of which the median-most is largest, concavo-convex, and touches that of the other side at its median convexity. Male and prostatic pores immediately lateral to these median-most papillae. One pair of tubercula-pubertatis in each of intersegmental-furrows 16/17 and 17/18 lateral to *b*. Spermathecal ducts not coiled, approximately equal in length to the width of the ampullae from which they are abruptly demarcated. *P. bukobensis*,
Michaelsen. *
- c.* Male genital field with a conical papilla on each side in *ab* bearing the male and prostatic pores. Spermathecal ducts short and thick. Septa 6/7 and 7/8 slightly thickened. *P. cavalli*, Cognetti.

Pygmaeodrilus nabugaboensis sp. n.

Locality : N.W. shore of Lake Nabugabo, approximately 0° 21' S. 31° 52' E., Uganda, ten yards from the water's edge in the garden of a fishing-chalet, in crumbly-moist humus-rich leafmould near the base of a large tree, with *Dichogaster saliens*. Collector : B. Jamieson 26. iv. 1956.

Material : Four mature specimens (the holotype and two paratypes, and one specimen not preserved), and one immature specimen.

Dimensions : The holotype British Museum (Nat. Hist.) Reg. No. 1957. 3. 8. 176, and the two paratypes British Museum (Nat. Hist.) Reg. No. 1957. 3. 8. 177 and 178 (part of latter on slide), are approximately 39 mm. long, and each has a greatest width, just in front of the clitellum, of approximately 1.75 mm. The number of segments in the holotype and second paratype are respectively 95 and 88 (the tail region of the first paratype was regenerating).

Colour : In life a pinkish grey ; colourless in alcohol.

Prostomium : Tanylobous, with broad dorsal-tongue ; appearing closed epilobous where intersegmental furrow 1/2 is indistinct.

Setae : Lumbricine, very closely paired.

* See Michaelsen 1892 *b* ; 1898 *c* ; and 1900, (p. 336).

Setal distance-ratios.

Segment 7.			
	aa : ab : bc : cd : dd	dd : u	bc : aa
Holotype	18 : 7 : 25 : 6 : 60	0.39	1.4
Immature specimen	21 : 5 : 21 : 4 : 60	0.42	1.0

Setal distance-ratios.

Segment 20.			
	aa : ab : bc : cd : dd	dd : u	bc : aa
Holotype	21 : 5 : 30 : 6 : 60	0.37	1.4
Immature specimen	22 : 5 : 29 : 5 : 60	0.37	1.3

It was not possible to measure the ratios in the other specimens with sufficient accuracy, owing to folding of the dorsal surface of the body.

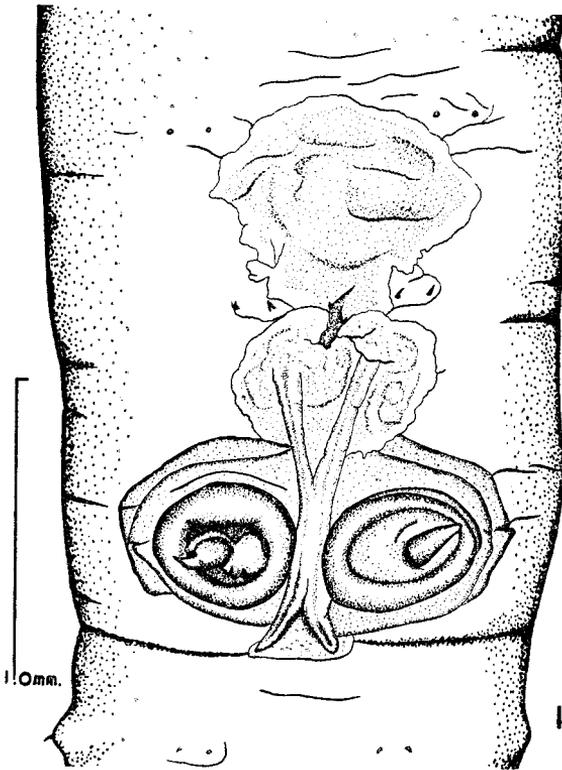
Clitellum : In the holotype the clitellum extends over segments $\frac{1}{2}$ 13–17 ; in paratype British Museum (Nat. Hist.) 1957. 3. 8. 177, 14–17 ; and in paratype British Museum (Nat. Hist.) Reg. No. 1957. 3. 8. 178 (slides), 13–18. In all three it is annular.

Male genital field (fig. 1) : The following description is based on an examination of the holotype, but unless otherwise stated applies to the other mature specimens.

Ventrally in segment 17 inclined antero-laterally to the midventral-line, and close to it, there is on each side a large oval, almost circular, papilla. This papilla has the form of an inflated tyre, and the small central region is filled by a pad approximately level with the general surface of the papilla. Just laterally to the centre of the pad there projects a ventro-laterally directed conical penis with an acute apex, the base of which, occupying about one quarter of the width of the pad, is in the holotype swollen into an almost spherical form, and is accompanied medially by a low swelling of the pad of similar area. Each papilla extends well beyond the setal-line *b* and medial to setal-line *a* (taking a line from the ventral setae of segment 18, those of 17 being absent). Each penis lies in line with the ventral seta pair of its side. The papillae lie in a slightly raised glandular (?), roughly oval field the long axis of which, lying transversely, is about twice the shorter axis ; it extends laterally to about $\frac{1}{4}$ *bc* and is bounded laterally and latero-anteriorly by a strip of similar appearance and outline reaching laterally to between $\frac{1}{2}$ and $\frac{3}{4}$ *bc*. The field with its bounding-strip extends along the whole median ventral line of segment 17.

From a small midventral patch lying across intersegmental-furrow 17/18, of similar appearance to the papilla-field, a seminal (?) -groove runs forward on each side of the mid-line and fuses with its fellow to form a white path filling the narrow space between the papillae. They diverge again on a whitish circular area, centrally somewhat sunken, of which the posterior edge borders the papilla-field and which anteriorly extends to the setal-zone of 16 where it joins a slightly larger but otherwise similar circular area. The latter extends anteriorly to a point just in

Fig. 1.



Pygmaeodrilus nabugaboensis sp. n.
1. Male genital field of the holotype.

front of setal-zone of segment 15, and laterally reaches or overlaps setal strip *ab*. Whereas the setae of segments 15 and 18 are in line with their counterparts in other segments, the ventral seta pairs of 16 are displaced towards the midventral-line, lying on each side of the waist formed by fusion of the circular areas.

Female pores : These lie, one on each side, just in front of seta *b* of segment 14 and have the appearance of short transverse slits.

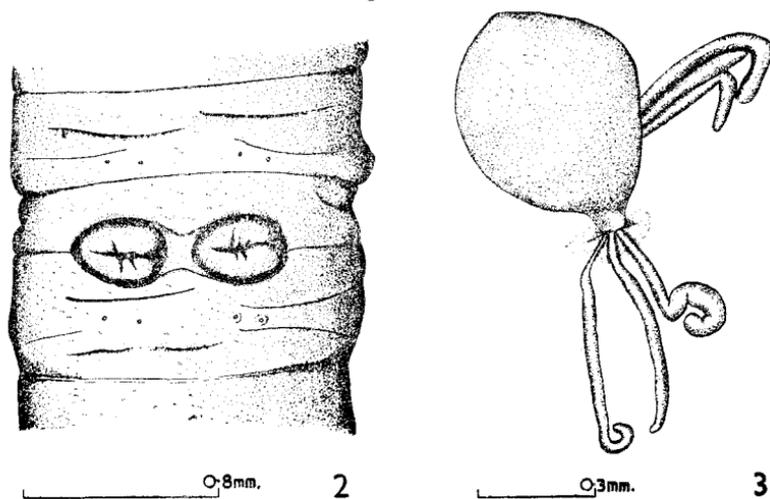
Spermathecal pores : (fig. 2) : In intersegmental-furrow 8/9 there lie

two large transversely oval protuberant papillae each bearing a slit-like spermathecal pore and each extending well laterally beyond setal-line *b* and medially of setal-line *a*. Apart from the slightly sunken area immediately surrounding the papillae, the ventral body surface is unmodified in segments 8 and 9.

Septa : 5/6–10/11 thickened : 5/6, 9/10, 10/11 moderately ; 6/7–8/9 greatly.

Alimentary canal : The slender intersegmentally constricted oesophagus gives rise ventrolaterally, in a posterior extension of segment 9, to a pair of separate ovoid or digitiform chylous-pouches with short stalks. In longitudinal sections the lumen of each pouch is seen to be reduced by the presence of folds of the wall, but it is not possible to see whether or not it is actually divided. The wide mid-gut begins in segment 13.

Fig. 2-3.



Pygmaeodrilus nabugaboensis sp. n.

2. Spermathecal pores of the holotype. 3. Right spermatheca of paratype British Museum (Nat. Hist.) Reg. No. 1957. 3. 8. 177 ; the ampulla has been turned forward to expose the posterior group of diverticula.

Anterior male organs : In each of segments 10 and 11 there is pair of large shining seminal funnels, lying ventrally on the posterior septum of the segment, each with its mouth directed anteriorly. The testes, of which there is a pair almost filling each of these segments, appear in dissection to be free, but in longitudinal sections a membrane is visible separating them from the septa. It is possible that the membrane encloses the testes in discrete sacs. On each side the sperm ducts meet in segment 12 and run backwards in a common sheath, in contact with the body wall.

There is a pair of large distended sac-like seminal vesicles attached to septum 11/12 lying in segment 12, and a much smaller pair attached to

septum 9/10 lying in segment 9. In sections it appears that there may be a pair of small seminal vesicles in segment 11, but this is not certainly established.

Posterior male organs : The following description is based on observations of the fresh mature specimen which was not preserved. The prostates were very long, extending backwards tortuously to segment 31 ; and the transition from the glandular part to the narrow muscular duct was abrupt. The ducts were short and fairly straight, occupying three segments, and each was distally thickened in the shape of a spindle the ectal tip of which was applied to the median border of an internal tumescence together, just posteriorly, with the ectal tip of the similarly shaped thickening of the vas-deferens. The spindle of the vas-deferens was at right-angles to its duct which even in segment 17 appeared double, and was overlain by the backwardly projecting thickening of the prostate duct which was about one and a half times as thick. From longitudinal sections, paratype British Museum (Nat. Hist.) Reg. No. 1957. 3. 8. 178 appears similar.

Paratype British Museum (Nat. Hist.) Reg. No. 1957. 3. 8. 177 was opened for measurements which are as follows :

Width of glandular part of prostates.....	≈ 350 μ.
Width of ducts of prostates.	≈ 100 μ.
Length of duct of prostates.	≈ 430 μ.
Width of distal thickening of duct of prostates.	≈ 200 μ.
Width of distal thickening of vasa-deferentia.	≈ 130 μ.

This specimen is abnormal in that the prostates have crossed ducts and run forward to segment 13 and then back to end in 17, but otherwise appears normal and similar to the other specimen described. (This forward direction and crossing of the prostates has been observed to occur erratically in other megascolecid.)

In longitudinal sections of paratype British Museum (Nat. Hist.) Reg. No. 1957. 3. 8. 178 the outlet duct of the prostate glands and of the vasa-deferentia of each side can be followed separately almost to the body surface, but it is not possible to make out whether or not they open separately or by a common pore on the penis.

Female organs : An ovary lies on each side of the gut ventrally on the anterior septum of segment 13.

Spermathecae : (fig. 3) : There is a pair of spermathecae in segment 9. The ampullae which are egg-shaped are very large, about 570 μ wide, and extend backwards through about three-quarters of the length of the segment from their short narrow ducts. The ducts, which are about 100 μ wide, are transparent, and this with their shortness gives the spermathecae the appearance of being sessile.

The diverticula of each spermatheca are simple tubes, straight or distally coiled in one plane, of fairly uniform size, about 100 μ wide and narrowing distally, and are arranged in an anterior and a posterior group, three in each group. They open to the exterior on the surface of the

spermathecal papilla in common with the spermatheca but do not actually enter its duct. The anterior group is separated from the spermathecal duct by septum 8/9 and extends into segment 8. It is possible that the number of three in each group observed in paratype British Museum (Nat. Hist.) Reg. No. 1957. 3. 8. 177, is variable in the species. The diverticula are white and shiny and contain sperm whereas none is detectable in the spermathecal ampulla or its duct.

Remarks: It is possible that these specimens were truly, though secondarily, terrestrial.

Pygmaeodrilus worthingtoni sp. n. *

Locality: Lake George, (approx. 00° 00' 30". 10¹E.). Collected by E. B. Worthington, 1931; originally registered at the British Museum (Nat. Hist.) as *Pygmaeodrilus* sp. British Museum (Nat. Hist.) Reg. No. 1933. 2. 10. 3-4, (re-registered as 1957. 3. 8. 180-183).

Material: Four softened specimens; one (British Museum (Nat. Hist.) Reg. No. 1957. 3. 8. 180), (taken as holotype) already opened and fragmentary appears mature internally; the others are too badly macerated to be dissected.

Dimensions :	Length	Greatest width	No. of segments
B.M. (N.H.) Reg. No. 1957.3.8.180 (Holotype)	27 mm.	1.25 mm.	77
„ „ „ 1957.3.8.181 (paratype)	27 mm.	1.0 mm.	99
„ „ „ 1957.3.8.182	28 mm.	1.0 mm.	68
„ „ „ 1957.3.8.183	27 mm.	1.0 mm.	99

Colour: In alcohol, a dark golden-brown.

Prostomium: In all the specimens the prostomium is epilobous with the open dorsal tongue extending posteriorly for one half to two thirds of the peristomium.

Setæ: Lumbricine, closely paired.

Setal distance-ratios.

Segment 7.

	aa : ab : bc : cd : dd	dd : u	bc : aa
1957.3.8.181.	13 : 5 : 18 : 5 : 45	.39	1.4
1957.3.8.182.	20 : 6 : 22 : 6 : 55	.38	1.1
1957.3.8.183.	17 : 6 : 25 : 5 : 60	.40	1.5

Mean

.39

1.3

Segment 20.

	aa : ab : bc : cd : dd	dd : u	bc : aa
1957.3.8.181.	10 : 5 : 20 : 5 : 50	.42	2.0
1957.3.8.182.	12 : 5 : 25 : 5 : 50	.38	2.1
1957.3.8.183.	15 : 5 : 27 : 5 : 70	.44	1.8

Mean

.41

2.0

* Named after the collector, Dr. E. B. Worthington.

The holotype, having been opened, was not measurable. The measurements were made on whole specimens (not on epidermal strips) and are therefore only approximate. Keeping within the accuracy of the measurements it can be said for the species that :

$dd \simeq 0.4 u$ in segments 7 and 20.

$bc \simeq 1.3 a$ in segment 7.

$bc \simeq 2.0 aa$ in segment 20.

Clitellum : Not distinguishable.

Male genital field : It is not possible to discern this in the holotype. In paratype British Museum (Nat. Hist.) Reg. No. 1957. 3. 8. 183, there is a transversely oval whitish area in the setal-zone of segment 17 between the setal-lines *a*. In paratype British Museum (Nat. Hist.) Reg. No. 1957. 3. 8. 182, the field is more clearly developed but even here is faint (fig. 4). There is a very slightly raised pale transversely oval area in the midventral-line in the setal-zone of segment 17 not reaching as far as the setal-line *a* laterally. It lies in a dark-brown field which has four rectangular extensions set diagonally, the angles of which lie approximately in setal-line *ab*, and which reach almost as far as the setal-zones of segments 16 and 18 respectively. A pale line, narrowing laterally, runs from the lateral borders of the median oval area across the field to beyond setal-line *b*.

Female pores : Not detectable.

Spermathecal pores : (Fig. 5) : These are apparent as a pair of transverse slits ventrally in intersegmental-furrow 8/9, separated by a narrow median strip, and laterally extending approximately to setal-line *a*. Anteriorly each appears to be at the summit of a very slight semi-circular elevation of the body surface.

Internal characteristics : (from a study of the holotype only).

Septa : It is not possible to make out the distribution of septal thickening.

Alimentary canal : The slender intersegmentally constricted oesophagus gives rise laterally in segment 9 to a pair of separate, rather stout, ovoid chylous-pouches.

Anterior male organs : One pair of seminal vesicles in segment 9 and one pair in segment 12 ; flimsy and much divided. Testes represented by flocculent sperm masses the segmental situations of which are indeterminate.

Posterior male organs : (from a study of a mounted fragment of the holotype). The prostates are very long and straight and the glandular part of each opens to the exterior by a well-defined, long, thin, muscular, shining duct in the position of the absent setæ *a* of segment 17 or perhaps just median to this. The ducts are not distally thickened. Those dimensions of the prostate glands which it is possible to measure are as follows :—

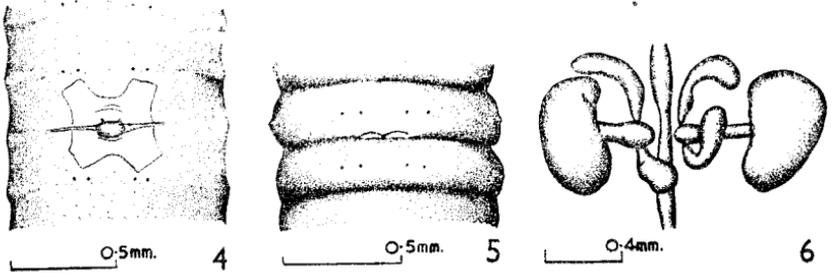
Width of glandular part of prostates	$\simeq 250 \mu$.
Width of ducts of prostates	$\simeq 70 \mu$.
Length of duct of prostates.	$\simeq 1.2 \text{ mm}$.

What appear to be the distal ends of the vasa-deferentia, but may be merely thickening of the skin, are seen to run well medial to the prostate ducts after curving round them posteriorly. They do not appear to be notably thickened and have widths of approximately $49\ \mu$.

Female organs: Not distinguishable.

Spermathecae: (fig. 6). The spermathecae, of which there is a single pair in segment 9, are of a form peculiar to this species. Each ampulla is

Figs. 4-6.



Pygmaeodrilus worthingtoni sp. n.

4. Male genital field of paratype British Museum (Nat. Hist.) Reg. No. 1957. 3. 8. 182.
 5. Spermathecal pores of the same. 6. Spermathecae and diverticula in the "in situ" position with the ventral nerve cord between them.

very large (approximately $400\ \mu$ transversely), simple and reniform, with a long slender but strong duct, (approximately $125\ \mu$ wide), projecting transversely from the median hylus to open, via a distal swelling, to the exterior. In front and behind, a stout, bent, tubular, almost, club-shaped diverticulum (the thinnest approximately $150\ \mu$ wide proximally) enters the body-wall in contact with the swollen end of the duct.

Pygmaeodrilus affinis Michaelsen, 1892. Emended description.

Pygmaeodrilus affinis Michaelsen, (1892a): Mitt. naturh. Mus. Hamburg, **9**, 2, pp. 6-8, Taf. fig. 3, Michaelsen, (1900): Tierreich, Lief. 10, Vermes, Oligochaeta, 396-387.

Ocnodrilus affinis, Michaelsen, (1898a): Deutsch-Ost-Afrika, **4**, Thierwelt, Regenwürmer, p. 40.

Ocnodrilus (*Pygmaeodrilus*) *affinis*, Eisen, (1900): Proc. Calif. Acad. Sci., series 3, **2**, p.112.

Locality: (All latitudes and longitudes given are from maps and only approximate). *Previously collected specimens*: (Michaelsen, 1892), *Lake Victoria*: Bukoba, $1^{\circ} 20' S. 31^{\circ} 55' E.$, Tanganyika, collected by Stuhlmann, 28. ix. 1890. *Present specimens*: (Collector B. Jamieson), *Lake Victoria*: Lake Nabugabo (virtually in connection with the former lake by swampy ground), north-west shore, $0^{\circ} 21' S. 31^{\circ} 54' E.$, Uganda, abundant in moist organic sand containing much leafy debris, at water's edge, very near *P. nabugaboensis* and *Dichogaster saliens*, 26. iv. 1956 British Museum (Nat. Hist.) Reg. No. 1957. 3. 8. 28/35; Kazi (south of the yacht club), $0^{\circ} 12' N. 32^{\circ} 36' E.$, Uganda, abundant in moist shelly laterite-shingle, 1. xii. 1955 British Museum (Nat. Hist.) Reg. No. 1957. 3. 8. 105/113; Napoleon Bay, $0^{\circ} 24' N. 33^{\circ} 12' E.$, just north of the

Ripon-Falls, source of the Victoria-Nile, (shortly before the disappearance of these caused by the closing of the Owen-Falls Dam), Uganda, frequent in red, coarsely particulate mud bearing Hippopotamus spoor and

TABLE I.—*Pygmaeodrilus affinis*: Table to show the numbers of specimens collected from each locality, their sexual maturity, lengths and numbers of segments.

Locality	Length of specimens in mm.					
	20-25	26-30	31-35	36-40	41-45	46-50
<i>Lake Nabugabo.</i> 8 specimens.						
Immature	2	3	—	—	—	—
Mature	1	1	1	—	—	—
Segments	79-80	94-95	93	—	—	—
<i>Kazi.</i> 9 specimens.						
Immature	1	6	—	—	—	—
Mature	1	—	—	—	—	—
Segments	79-85	91-98	—	—	—	—
<i>Napoleon Bay.</i> 3 specimens.						
Immature	—	—	—	—	—	—
Mature	1	1	—	—	—	—
Segments	67	78	—	—	—	—
<i>Namasagali.</i> 47 specimens.						
Immature	—	—	—	—	—	—
Mature	1	7	17	4	—	—
Segments	102	87-99	89-111	93-103	—	—
<i>Butiaba.</i> 22 specimens						
Immature	—	—	—	—	—	—
Mature	1	3	8	6	1	—
Segments	99	96-120	104-118	117-130	123	—
<i>Kasenyi.</i> 5 specimens.						
Immature	—	—	—	1	—	—
Mature	—	—	—	2	—	1
Segments	—	—	—	101-111	—	117

almost in suspension owing to lapping water, 25. xii. 1955 British Museum (Nat. Hist.) Reg. No. 1957. 3. 8. 191/121.

Victoria-Nile: Namasagali on the east bank, just north of the Stanley's berth, 1° 1' N. 32° 57' E., Uganda, abundant in decaying leaf-debris in moist black mud at water's edge, 15. v. 1956. British Museum (Nat. Hist.) Reg. No. 1957. 3. 8. 36/82. (Slides 130/150).

Lake Albert: Butiaba promontory, Uganda side, 1° 50' N. 31° 18' E., Uganda, abundant in and under moist decaying reed-debris washed up

on the sloping stone quay-side, at the water's edge, 16. v. 1956 British Museum (Nat. Hist.) Reg. No. 1957. 3. 8. 83/104 (Slides 122/129); Kasenyi, 1' 22° N. 300' 27° E., Belgian Congo, abundant in black moist mud composed largely of decaying plant-debris amongst reeds, at the water's edge, with *Alma*, 17. v. 1956. British Museum (Nat. Hist.) Reg. No. 1957. 3. 8. 114/118 (Slides 151/153).

Material : (see Table I). The specimens included in the table were identified by comparison of the appearance of the male genital field with that described by Michaelsen (1892a and 1900). The maturity of the specimens was judged by the degree of development of the spermathecal pore in conjunction with that of the male genital field. Those specimens which are damaged so as not to be of use in the table are included only in the total counts given in the left-hand column.

Dimensions : (see Table I). In mature specimens under examination the lengths range from 22 to 50 mm. as compared with 35 to 60 mm. given by Michaelsen (1892a, 1900); the widths from approximately 1.25 to 2 mm. (1 to 1½ mm., Michaelsen, *ibid.*); and the numbers of segments from 67 to 130 (72 to 106, Michaelsen, *ibid.*).

Colour : In life the specimens were an orange-red; in alcohol they are whitish to pale-brown (pigmentless, yellowish-grey, Michaelsen, *ibid.*); only in the Butiaba specimens is the clitellum of a colour (dark-brown) distinguishable from the general body colour.

Prostomium : Epilobous, with the closed, or less frequently open, narrow dorsal-tongue extending posteriorly for one third to one half of the length of the peristomium. The form appears to be the same for all specimens.

Setæ : Lumbricine, closely paired; in my specimens the setæ can be seen to project well from the body-surface. Michaelsen has not given any setal distance-ratios, but I have given measurements of these, in specimens from all localities, on page 461. Though the table is not an adequate statistical analysis, it may be concluded that the setal distance-ratios for different localities do not vary significantly.

Clitellum : Segments 13 to 18, annular (Michaelsen 1892a, 1900; and present examination). In my material it is almost always indistinct and is best seen in the Butiaba specimens where it is distinguishable by its colour.

Male genital field : (fig. 7). This does not appear to vary significantly from one locality to another, and the considerable individual variations are ascribable to differences in the degree of sexual-maturity. In the least mature specimens there is a transversely elongated tubercle of spindle-shaped outline in the midventral-line and setal-zone of segment 17, reaching anteriorly and posteriorly nearly to the intersegmental-furrows 16/17 and 17/18 respectively. This tubercle is divided into right and left halves by a deep median furrow, and usually in more mature specimens there is a second furrow, incomplete laterally, at right-angles to the other, which also divides the tubercle symmetrically. At the intersection of these furrows, or in a slight widening halfway along the median furrow if

Setal distance-ratios.

Locality	Segment 7.						Segment 20.								
	aa :	ab :	bc :	cd :	dd :	dd : u bc : aa	aa :	ab :	bc :	cd :	dd :	dd : u bc : aa			
LAKE ALBERT	Kasenyi	20 :	9 :	25 :	7 :	70	0.42	1.3	19 :	7 :	30 :	6 :	60	0.38	1.6
		22 :	10 :	25 :	9 :	60	0.35	1.1	18 :	6 :	30 :	8 :	60	0.36	1.6
		27 :	9 :	28 :	8 :	70	0.37	1.0	22 :	8 :	32 :	10 :	70	0.36	1.5
	Mean					0.38	1.1						0.37	1.6	
	Butiaba	24 :	8 :	30 :	7 :	65	0.36	1.3	25 :	8 :	42 :	10 :	65	0.31	1.7
25 :		7 :	26 :	6 :	65	0.35	1.0	20 :	8 :	32 :	7 :	65	0.31	1.6	
24 :		7 :	23 :	7 :	60	0.32	0.96	22 :	9 :	30 :	9 :	70	0.37	1.4	
35 :		10 :	30 :	9 :	75	0.36	0.86	26 :	9 :	45 :	9 :	75	0.33	1.7	
25 :	6 :	30 :	8 :	70	0.38	1.2	20 :	8 :	28 :	9 :	70	0.39	1.4		
Mean					0.35	1.1						0.34	1.6		
VICTORIA-NILE	Namasagali	28 :	8 :	26 :	8 :	70	0.38	0.92	24 :	9 :	35 :	9 :	65	0.33	1.5
		25 :	9 :	24 :	9 :	75	0.41	0.96	20 :	8 :	32 :	10 :	70	0.41	1.6
		25 :	8 :	26 :	8 :	65	0.37	1.0	22 :	8 :	35 :	8 :	65	0.34	1.6
		20 :	7 :	25 :	8 :	60	0.37	1.25	21 :	9 :	35 :	9 :	60	0.32	1.7
Mean					0.38	1.0						0.35	1.6		
LAKE VICTORIA	Napoleon-Bay	25 :	6 :	24 :	6 :	60	0.38	0.96	21 :	8 :	30 :	8 :	55	0.33	1.5
		22 :	8 :	20 :	7 :	50	0.35	0.91	17 :	7 :	27 :	6 :	50	0.34	1.6
	Mean					0.37	0.94						0.34	1.6	
	Kazi	25 :	8 :	21 :	7 :	60	0.38	0.84	20 :	7 :	30 :	9 :	55	0.33	1.5
		22 :	7 :	25 :	8 :	65	0.38	1.1	20 :	7 :	25 :	8 :	60	0.38	1.3
	Mean					0.38	0.97						0.34	1.4	
	Lake Nabugabo	19 :	8 :	24 :	8 :	60	0.36	1.3	22 :	9 :	30 :	7 :	50	0.31	1.4
22 :		9 :	25 :	7 :	60	0.36	1.1	21 :	7 :	30 :	7 :	65	0.37	1.4	
22 :		6 :	25 :	6 :	55	0.36	1.1	17 :	7 :	27 :	6 :	55	0.35	1.6	
21 :		6 :	23 :	7 :	55	0.37	1.1	20 :	5 :	28 :	6 :	57	0.36	1.4	
Mean					0.36	1.1						0.35	1.5		
Mean of 20					0.37	1.1						0.35	1.5		

it only is present, there is a small conical papilla. Four rounded or, more frequently, pointed papillae develop on the tubercle which often by the time the furrows have developed has assumed a roughly quadratic or oval form with one of the papillae at each corner and with lateral extensions still connecting it to the body-surface. The lateral borders of the tubercle lie just medial to setal-line *a*.

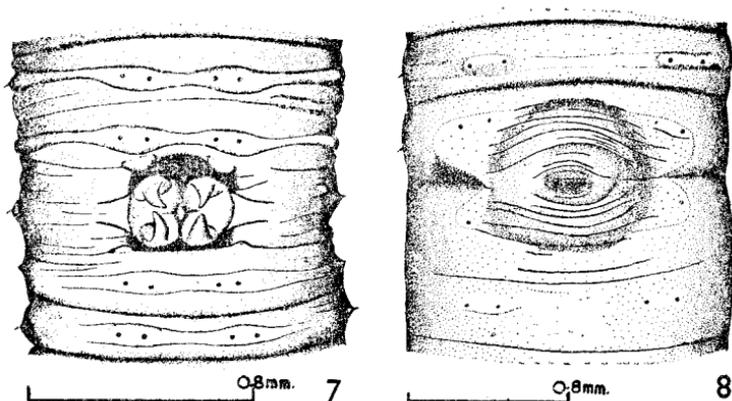
In some specimens (taken to be more mature) the ventral body-surface, bounded by the posterior border of segment 16 and the anterior border of segment 18 and laterally by the setal-lines *ab* of segment 17, has become sunken so that the tubercle lies in a square pit and often has lost the lateral connections with the body-surface. Specimens in this condition have a papilla-like thickening of the borders of the pit approximately in

setal-line *ab* in each corner ; or only the anterior or none may be present.

In many specimens which appear mature, the small median conical papilla is hidden in the median furrow.

As shown in fig. 9 (Butiaba specimen British Museum (Nat. Hist.) Reg. No. 1957. 3. 8. 122/129 slides) a vas-deferens opens just medially to and in common with the prostate of its side, on the floor of the slit, each side of this papilla. The conditions described above conform well with the description given by Michaelsen (1892*a*) except for the fact that in describing the fully mature condition only, he described the sunken tubercle as a field at the bottom of the genital-hollow and stated that the prostate ducts open by a common mid-ventral pore on the median conical papilla, and that the

Figs. 7-8.



Pygmaeodrilus affinis, Michaelsen, 1892.

7. Male genital field of a Butiaba specimen. 8. Spermathecal pore.

male pores were probably lateral to this. In his later (1900) account which was not a description of new material, he stated that the male pores open on each side of this papilla in the bottom of the hollow, did not mention the prostate pores, and described only papillae in setal-lines *ab* of segment 17.

Female pores : Not observed ; said by Michaelsen (1892*a*) to be in front of the ventral setæ of segment 14.

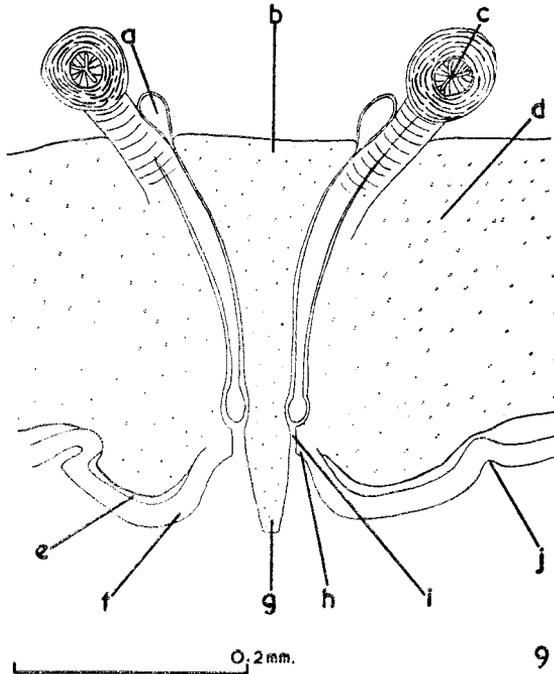
Spermathecal pore : (fig. 8). As described by Michaelsen (1892*a*), there is a single mid-ventral narrow but transversely extensive slit in intersegmental-furrow 8/9, at the summit of a glandular thickening of the skin. This thickening is wart-like, concentrically grooved, and when fully developed occupies most of the ventral surface of segments 8 and 9 at which stage one or more of the ventral setæ of these segments may be obscured.

Septa : These were not described by Michaelsen. Even in specimens from a single locality the distribution of septal-thickening as determined by

dissection seems variable. The arrangement appears to be: 5/6, 6/7 to 10/11, 11/12 thickened; 5/6, 11/12 if thickened, only slightly; 10/11 often only slightly; 6/7 to 9/10 moderately.

Alimentary canal: The slender intersegmentally-constricted oesophagus bears laterally in segment 9 a pair of separate ovoid to digitiform chylous-pouches. In a transverse sagittal section of one of these from a Kasenyi

Fig. 9



Pygmaeodrilus affinis, Michaelsen, 1892.

9. Transverse section of the male openings in Butiaba specimen British Museum (Nat. Hist.) Reg. No. 1957. 3. 8. 122-129 (slides); a, lumen of the vas deferens of the right side; b, longitudinal muscle block; c, lumen of the prostate duct of the left side; d, longitudinal and vertical muscle, e, circular muscle of the body-wall, f, epidermis, g, conical papilla, h, lip of i, common opening of the prostate and vas deferens of the left side, j, limit of raised tubercle.

specimen the lumen was seen to be divided by six longitudinal septa which radiate from a central axis.

Anterior male organs: Michaelsen (1892a) described the seminal vesicles as being compact pear- or bulb-shaped organs in segments 9 and 12; but he stated that he could not clearly make out the arrangement of these and other anterior male organs, so it is possible that his description of the seminal vesicles is not correct. In all my specimens they are divided almost to the extent of being racemose; one pair in each of segments 9 and 12, of which the posterior sometimes are more diffuse.

Posterior male organs : The tubular prostates are usually very long (1.2 cm. in one Kasenyi specimen) and have well-defined thin, muscular, shining ducts. Their arrangement is very variable. In my specimens they may be entirely anterior or entirely posterior to their pores in segment 17, or may run forward first and then backwards, and have been seen to extend as far posteriorly as segment 38. They may run straight or cross and recross, and may be complexly coiled and intertwined at some point along their lengths. Proximally there is a thinner region which at its extremity is often reflexed forward. The measurements of the prostates for one mature specimen from each locality are :

	Nabugabo	Kazi	Napoleon Bay	Namasagali	Butiaba	Kasenyi
Widths of glandular parts of prostates.	290 μ	220 μ	220 μ	240 μ	300 μ	225 μ
Widths of ducts of prostates.	97 μ	95 μ	80 μ	110 μ	96 μ	125 μ
Length of ducts of prostates.	1.3 mm.	—	1.25 mm.	0.75 mm.	1.2 mm.	2 mm.

I find that the measurements show remarkably little relationship to the size of the specimens or the time of year at which they were collected. The lengths of the specimens range from 20 to 50 mm., and although it seems probable that a statistical analysis of a large number of specimens would show that the size of the prostates is maximal in the largest specimens, it nevertheless seems probable that within certain fairly narrow limits the size of the glands is uniform throughout mature specimens. The vas-deferens of each side only occasionally shows a slight distal thickening at the point where it reaches the anterior surface of the unthickened prostate-duct before entering the body-wall, in contact with it, near the midventral-line. Michaelsen did not describe any variation in the form of the prostates.

Female organs : In segment 13 on each side of the gut ventrally, almost hidden by it, there is a large ovary, attached to the anterior septum and extending backwards to its large funnel on the posterior septum.

Spermathecae : According to Michaelsen (1892a) the single spermatheca opens mid-ventrally in intersegmental-furrow 8/9 and has an irregularly sac-like ampulla bent over to one side of the midventral-line, and a thick muscular duct into the base of which anteriorly and posteriorly open, in each position, two long, tubular, irregularly constricted diverticula. The duct is described as having a trace of median glandular folding suggesting the fusion of two lateral spermathecae. In the later (1900) account he described the constrictions as causing the diverticula to appear almost beaded. This description conforms in most respects with

the appearance of the spermathecae in my specimens ; in these the ampulla often has a pleated appearance and may be on either side of the mid-line ; but in all cases the duct consists of a short proximal region the walls of which are similar in texture to those of the ampulla, and a distal dorsally convex muscular part into the cavity of which this leads and which opens to the exterior. The diverticula open one antero-laterally and one postero-laterally on each side into the spermathecal pore at the base of this distal part of the duct ; they are usually simple blind tubes about as long as the ampulla, reflexed proximally, or appearing two- or three-lobed at their extremities owing to folding within their sheaths.

DISCUSSION.

(a) *The comparative morphology of the genus :*

The gizzard and chylous-pouches : The Ocnerodrilinae are exceptional within the Megascolecidae in being mainly limnic or amphibious. They are also unusual in that the majority of genera lack the oesophageal gizzard ascribed to the *Notiodrilus*-like ancestor. It seems probable that the absence of a gizzard is a derived condition associated with the invasion of a limnic habitat. The reduction of the number of chylous-pouches from a pair in each of segments 9 and 10 to a single pair in the more posterior segment which appears to have occurred in several genera, seems to be independent of the reduction of the gizzard and may have no connection with the invasion of more aqueous habitats.

The spermathecae : *Pygmaeodrilus* is unique in the subfamily, with the exception of certain species of *Gordiodrilus*, in possessing spermathecal diverticula. The evidence supplied by *Pygmaeodrilus aequatorialis* Stephenson (1930a) is here brought forward in support of Stephenson's contention (1930b p. 862) that although *Pygmaeodrilus* appears morphologically to be an *Ilyogenia* which has developed diverticula of the spermathecae, this cannot be its true origin as the incompletely microscolecine condition of the male pores of many species of *Pygmaeodrilus* could not have been derived from the completely microscolecine condition found in all species of *Ilyogenia*. Of both genera, *P. aequatorialis* is the only species which possesses a spermatheca in segment 8 as well as in segment 9, thus showing that this species and such other species as can be considered monophyletic with it cannot be descended from *Ilyogenia*.

Stephenson (1930a p. 493) points out that the anterior spermatheca of *P. aequatorialis* may be in the process of being lost as it would appear that there are no prostates to supply it with sperm ; if this is so, it would seem good evidence that this species has only recently lost a pair of prostates in segment 18, and that perhaps the acanthodriline condition of the male openings has only recently been lost.

I have divided the species of *Pygmaeodrilus* as follows, into a homogeneous and, for convenience, a single heterogeneous group according to whether or not the diverticula of each spermatheca are divided into an anterior and a posterior group.

GROUP I. (Homogeneous): Species in which the diverticula of each spermatheca are arranged in one anterior and one posterior group.

Species.	No.	Arrangement,		Form,	Position of opening. *
		ant.	post.		
<i>P. affinis</i>	4	2	2	Simple tubes	X
<i>P. bipunctatus</i>	3	2	1	" "	Y
<i>P. budduensis</i>	4	?	?	" "	Y
<i>P. bukobensis</i>	2 or 4	1-2	1-2	" "	X
<i>P. cavalli</i>	5 or 6	?	?	" "	Y
<i>P. modestus</i>	4-6	2-3	2-3	" "	X
<i>P. nabugaboensis</i>	6	3	3	" "	X
<i>P. ngomanus</i>	3	1	2	" "	Y
<i>P. worthingtoni</i>	2	1	1	" "	X

GROUP II. (Heterogeneous): Species in which the diverticula are not arranged as above.

<i>P. aequatorialis</i>	7	Bound to ampulla. one or two freer		Simple tubes	?
<i>P. arasionensis</i>	1	Lying in seg. 8.		Sac (like ampulla)	Y
<i>P. grawerti</i>	6	Wreath round ampulla duct		Lobed tubes	Y
<i>P. kiwuensis</i>	7	Hidden under ampulla		Lobed tubes	Y
<i>P. moeroensis</i>	6	2 groups, coiled mass round long ampulla-duct		Simple tubes	Y
<i>P. montanus</i>	5-7	Hidden under ampulla		Simple tubes	X
<i>P. neumanni</i>	3	On walls of ampulla-duct		Tiny sacs	Y
<i>P. paulae</i>	2 ?	Wreath round ampulla-duct		Simple tubes	Y
<i>P. quillimanensis</i>	Many.	Wreath round ampulla-duct		Club-shaped	Y
<i>P. rhodesiensis</i>	2-3	Hidden under ampulla		Simple tubes	Y

The homogeneous group was first reported by Michaelsen (1936) in his description of *P. ngomanus* and he noted that it belonged to a group including *P. affinis* Michaelsen (1892a); *P. bipunctatus* (Michaelsen, 1898 b); *P. budduensis* Michaelsen (1910 a); *P. bukobensis* Michaelsen (1892 b); *P. modestus* Michaelsen (1910 b); and probably *P. moeroensis* Michaelsen (1915) which are all characterized by the possession of a small number of spermathecal diverticula in the form of simple blind tubes divided into two groups as mentioned and projecting from the ectal end of the spermathecal duct. He questioned the inclusion of *P. moeroensis*, and a study of his figure of its spermathecae (Michaelsen, 1915) shows that it does not belong to this species-group. The two new species here described belong to this group as does *P. cavalli* Cognetti (1906 and 1909). In these three species and in *P. affinis* the diverticula enter the body-wall independently of the ampulla-duct before opening to the exterior by its pore. This condition was shown to be present in

* In the last column an X indicates that the diverticula enters the body-wall independently of the ampulla-duct though always opening to the exterior by the same pore as the latter; a Y indicates that the diverticula are described as entering the ampulla-duct and not as at first entering the body-wall. Where the Y is underlined the opening of the diverticula into the ampulla-duct is given as distal.

P. modestus by Michaelsen (1910 *b*) and I believe may on re-examination prove to be characteristic of all species of the homogeneous group. To the heterogeneous group belong *P. aequatorialis* Stephenson (1930 *a*); *P. arausionensis* Michaelsen (1910 *e*); *P. grawerti* Michaelsen (1910 *c*); *P. kiwuensis* Michaelsen (1910 *d*); *P. moeroensis* Michaelsen (1915); *P. montanus* Michaelsen (1907); *P. neumanni* Michaelsen (1903 *b*); *P. paulae* Michaelsen (1913 *a*); *P. quilimanensis* Michaelsen (1890); and *P. rhodesiensis* Michaelsen (1913 *b*).

The variation in the position of the spermathecal pores in all species of the genus, drawn from the original and later descriptions, is shown below; the evidence of other genera indicates that the more median position of the pores is derived from the more lateral.

Positions of the spermathecal pores.

Lateral to setal-line <i>b</i> .	In setal-line <i>b</i> .	In setal-strip <i>ab</i> .	Median to setal-line <i>a</i> .	In midline.
<i>P. quilimanensis</i> .	<i>P. grawerti</i>	<i>P. arausionensis</i> .	<i>P. bipunctatus</i> .	<i>P. aequatorialis</i>
<i>P. rhodesiensis</i> .	<i>P. kiwuensis</i> .	<i>P. bukobensis</i> .	<i>P. budduensis</i> .	<i>P. affinis</i> .
	<i>P. montanus</i> .	<i>P. cavalli</i> .	<i>P. modestus</i> .	
	<i>P. paulae</i>	<i>P. moeroensis</i> .	<i>P. worthingtoni</i> .	
		<i>P. nabugaboensis</i> .		
		<i>P. neumanni</i> .		
		<i>P. ngoraensis</i>		

The male-organs : In no species has it been proved that the testes are enclosed, but this has been suggested in *P. montanus* (see Michaelsen, 1907) and in *P. nabugaboensis*. The restriction of the seminal-vesicles to segment 12 in *P. montanus* is correlated with its metandrism, and the occurrence of this restriction in *P. neumanni* and *P. arausionensis* in which the testes are large in segments 10 and 11 may indicate that metandrism is incipient in the genus. But it may indicate merely that maturation of sperm can occur efficiently in the absence of distinct seminal-vesicles (as in *Ocnerodrilus*).

Throughout the genus, a microscolepine condition of the male-openings exists in so far as the prostate pores and male pores open in segment 17; and every stage is seen from relatively wide separation to fusion of the male and prostate pores of each side. Also there appears to be a tendency for movement of the pores of each side towards the midventral-line independently of the movement of the spermathecal pores. This trend is furthest developed in *P. affinis*.

In all species with the exception of *P. arausionensis*, *P. cavalli* and *P. modestus*, the thin muscular duct of each prostate is well differentiated from the glandular region. The distal end of this duct, like that of each vas-deferens, may be distally thickened into a spindle-shape or, in *P. paulae*, may widen gradually. Most commonly only the vas-deferens or neither of the ducts is thickened, but in *P. nabugaboensis* and *P. paulae* both are thickened, and in *P. neumanni* alone only the prostate duct is thickened.

The presence of a spermatheca in segment 8 in *P. aequatorialis* in which there is also a median spermatheca in segment 9, and the more usual pairing of spermathecae (in segment 9 only) in other species,

suggests that the stem-form of the genus *Pygmaeodrilus* possessed a pair of spermathecae in each of segments 8 and 9. As has been indicated above, these probably opened laterally to the ventral setæ. The spermathecae would also be associated with diverticula. Other characteristics of the stem-form which can be surmised from the above discussion are that it possessed one pair only of chylous-pouches, and no gizzard, in segment 9; that it was holandric, and that the prostate pores and male pores, which on each side were separate, opened in segment 17; it is also, as has been mentioned, possible that there was a pair of prostates in segment 18. These characteristics were ascribed by Stephenson (1930 *b* pp. 855-856) to the "Primitive *Ocnerodrilus*" ancestor of *Ocnerodrilus*, *Liodrillus* and *Ilyogenia* (sub-genera of *Ocnerodrilus*) and of *Pygmaeodrilus*, with the exception that his "Primitive *Ocnerodrilus*" did not have spermathecal diverticula and possessed prostates in segment 17 only. As *Pygmaeodrilus* differs from the three sub-genera in still having (in one species) spermathecae in segment 8 and in being in some of its species incompletely microscoleicine, it is here suggested that it is in fact the more primitive genus.

(b) *The geographical distribution of the genus and its relation to the geological past :*

It can be seen from the list below that the homogeneity in the morphology of the spermathecae of the species of group I is paralleled in their geographical distribution; they are all restricted to what I have called the Albert-Victoria drainage-system (including Lakes Albert, Victoria, Edward, George and, see below, Kivu; together with connecting rivers and associated regions drained) and are the only species of the genus which are known from Lake Victoria. The distribution of species (group II) not belonging to this species-group is given for comparison and it can be seen that they, too, show certain geographical groupings. It may be noted in passing that these groupings are again in some species reflected in segregation of morphological features.

It is important to note, in connection with the distribution of group I species, that though Lake Kivu drains into Lake Tanganyika and does not now belong to the Albert-Victoria drainage system, there is abundant evidence that until geologically very recent times it flowed into Lake Edward and had no connection with the then effluentless Lake Tanganyika (see Moore 1903).

For clarity the details of the localities have been omitted but where necessary brief details have been included in brackets.

GROUP I SPECIES (Homogeneous with regard to the spermathecal diverticula).

<i>P. affinis</i>	L. Victoria ; Victoria-Nile ; L. Albert.
<i>P. bipunctatus</i>	L. Albert.
<i>P. budduensis</i>	L. Victoria (Buddu Forest).
<i>P. bukobensis</i>	L. Victoria.
<i>P. cavalli</i>	L. Victoria.

<i>P. modestus</i>	L. Kivu ; L. Karago * ; L. Mohasi * ; . . . Belgian Congo.
<i>P. nabugaboensis</i>	L. Victoria (L. Nabugabo).
<i>P. ngomanus</i>	L. Kivu.
<i>P. worthingtoni</i>	L. George.

GROUP II SPECIES (Heterogeneous with regard to the spermathecal diverticula).

<i>P. aequatorialis</i>	L. Albert.
<i>P. arausionensis</i>	Orange River ; Groot-Fontein.
<i>P. grawerti</i>	L. Tanganyika.
<i>P. kiwuensis</i>	L. Kivu (and west of this).
<i>P. montanus</i>	Mt. Kilimanjaro ; Mt. Meru.
<i>P. moeroensis</i>	L. Mweru.
<i>P. neumanni</i>	L. Stefanie . . . Abyssinia. †
<i>P. paulae</i>	Zambezi.
<i>P. quilimanensis</i>	Zambezi (Coast, near mouth).
<i>P. rhodesiensis</i>	Zambezi.
<i>P. sp. Michaelsen '38</i>	Siwali Oasis.

There is abundant evidence that when the Albertine Rift was formed (probably in the Middle-Pleistocene) the more easterly headwaters of the Congo were severed from the main river and that these then reversed their flow and participated in the formation of Lake Victoria with its outflow the Victoria-Nile via the north end of Lake Albert (King, 1942). The present-day distribution of *Pygmaeodrilus* points to the existence of the stem-form of the genus or of its descendants in the Congo headwaters before the faulting occurred and it seems possible that it was on the formation of the Albertine Rift that segregation of the worms into fairly discrete groups occurred.

The nine group I species appear to be the products of the speciation of a progenitor isolated, though not of course by impassable barriers, within the Albert-Victoria drainage-system at some period after the formation of the Rift. It is not yet possible to decide between the alternatives that this progenitor had the structure of the stem-form and gave rise to those species in the system which lack the double grouping of the spermathecal diverticula ; that it was cut off, but not necessarily contemporaneously, with species of the latter type ; or that it was the product of their earlier isolation. Combinations of these alternatives are also possible and no solution can be given at least until more adequate collecting is done.

The Lake Kivu species could have reached it after its separation from the system but probably reached it before. Indeed, like any other part of the system this lake could have been the original focus of group I speciation.

* Probably erratic.

† The other localities, all in Abyssinia, have been omitted.

It will have been noted that the new, Lake George, species forms a link between the Lake Kivu and Lake Albert species of group I, and that the localities of *P. affinis* given in this paper illustrate the spreading of species from one part of the Albert-Victoria drainage-system to another.

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