Aquatic Oligochaetes Occurring in Forest Litter.—II

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Abstract

Five worms are recorded from beech litter. One new naidid species and two new phreodrilid species are described, the latter being placed in a new genus. All the worms reproduce asexually, the two phreodrilid worms by fragmentation and subsequent regeneration. The species are considered specially adapted to this ground habitat.

This paper deals with worms occurring in beech (*Nothofagus truncata*) litter collected from the western hills overlooking the Hutt Valley, near Silverstream. The worms have occurred fairly regularly in samples of litter collected monthly over a period of twelve months. They have been cultured and studied in the manner previously described (Stout, 1956).

The fauna consists of two aeolosomatid worms, a new species of naidid worm, and two new species of phreodrilid worms which I place in a new genus. Representatives of the first two families have been previously recorded from this type of habitat (Stout, 1956), but this is the first record of phreodrilid worms from forest litter.

Sixteen species of phreodrilid worms have been described. With the exception of one from Ceylon they are confined to the southern hemisphere and are circumpolar in distribution, occurring in Chile, Kerguelen Is., South Georgia, Campbell Is., New Zealand, Tasmania, Australia and South Africa. Although such a small family, two species often occur together as in the present litter. Thus two species are recorded from Campbell Is., two species from the Falkland Is., and two species in New South Wales (Australia) are ectocommensals of *Astacus*. The present species differ from those previously described by reproducing asexually. Asexual reproduction has not previously been recorded in the Phreodrilidae or in the closely related Tubificidae. It has been recorded, however, in the Lumbriculidae, another closely related family of microdrili which, in contrast to the Phreodrilidae, is confined to the Northern Hemisphere. These worms reproduce by fragmentation and subsequent regeneration in distinction to the budding of aeolosomatid and most naidid worms. In the present instance this method of reproduction may be connected with adaptation to life in forest litter.

Besides the aquatic oligochaetes, turbellarian and enchytraeid worms also occurred regularly in the cultures.

Description of the Fauna

Family AEOLOSOMATIDAE

Aeolosoma hemprichii Ehrenberg 1831.

Aeolosoma niveum Leydig 1865

Family NAIDIDAE

Pristina nothofagi n.sp. Figs. 1-3.

This is a very small, transparent worm in which the coelomocytes, white in reflected light, are the most conspicuous feature to the naked eye. Individual worms are about 1 mm in length and two zooids may be up to 2 mm. The breadth of the prostomium is about 100 mu,

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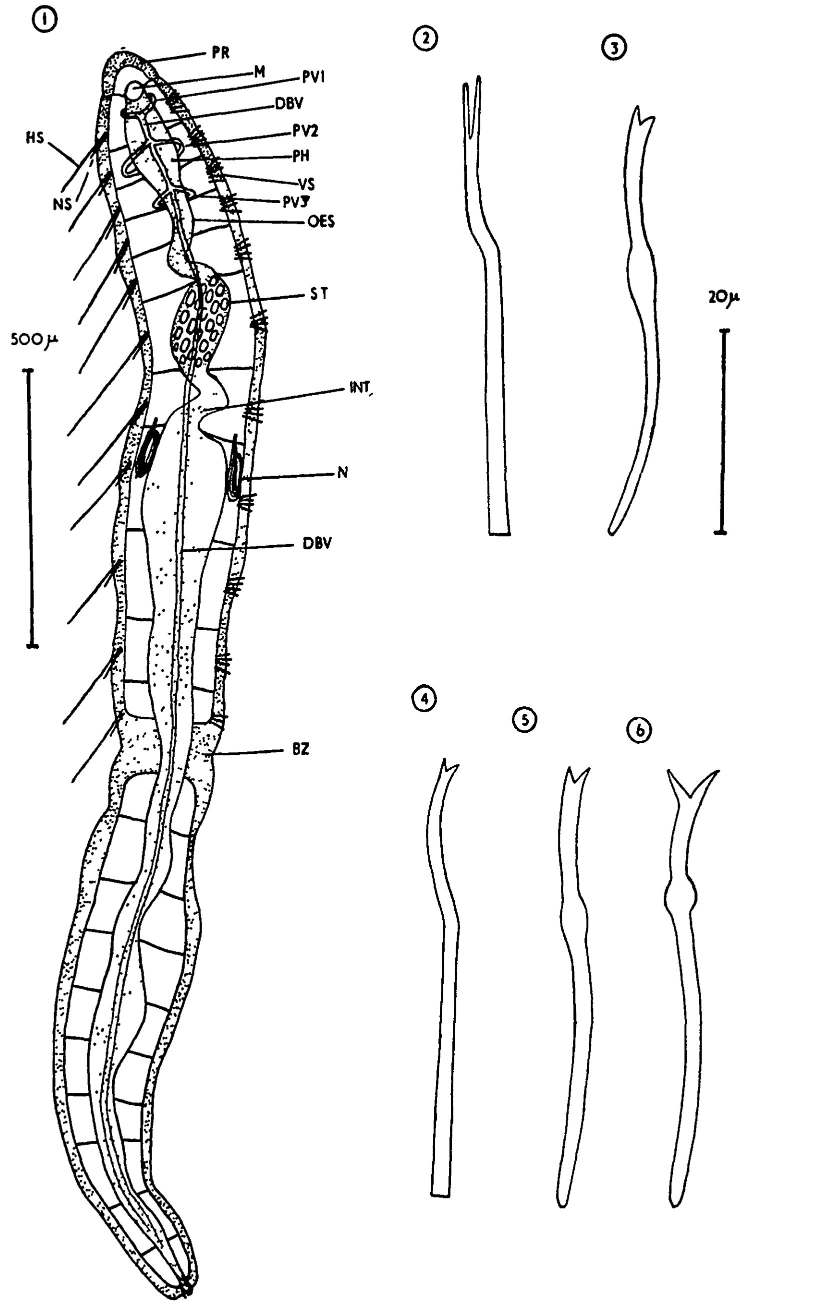


FIG. 1.—*Pristina nothofagi* n sp. semi-diagrammatic drawing. FIG. 2.—*Pristina nothofagi* n.sp. needle seta. FIG. 3.—*Pristina nothofagi* n.sp. ventral seta. FIG. 4.—*Pristina minutum* (Marcus) needle seta. FIG. 5.—*Pristina minutum* (Stephenson) needle seta. FIG. 6.—*Pristina osborni* (Walton) needle seta.

but the body broadens to about 180 mu. There may be up to 22 segments in a worm and n is always 12. The prostomium is small, rounded, with no proboscis development. The first seven body segments are generally smaller than the succeeding segments.

The setae commence on the second segment. They consist dorsally of a single unserrated hair seta and a single needle seta per bundle and ventrally of 6–2 bifid crotchets per bundle. The hair setae are simple and flexible and vary in length from 110–200 mu, increasing in length up to segment VII. The needle setae (Fig. 2) are bayonet shaped with a distinct kink but no nodulus. The kink occurs about one-third the length from the distal end. The setae are 35–50 mu in length, bifid, with slightly separated teeth about 6 mu long. The teeth are nearly equal in size, the proximal tooth being slightly larger than the distal. The ventral setae (Fig. 3) are sigmoid, from 30–40 mu in length, with a distinct nodulus about one-third the length from the distal end. The teeth are subequal and about 1.5 mu long.

The alimentary canal consists of a pharynx in segments I–III with a dorsal diverticulum in II–III; a narrow oesophagus IV–VI; a stomach with characteristic *Pristina* canals in VII; a short looped narrow intestine in VIII broadening in IX into a wide intestine, some 100 mu in width, which narrows again posteriorly. Chloragogen starts in IV.

There is a simple dorsal and a simple ventral blood vessel. The main commissure is in II and other perivisceral commissures in III and IV. The dorsal vessel is not attached to the alimentary canal in VIII but passes directly from the stomach in VII to the large intestine in IX.

Nephridia are paired in IX. They may occur in subsequent segments either paired or single In the posterior zooid they are generally single. They are similar in form to those of *P. taita* Stout, 1956, with a small nephrostome and double lumina. The nephridiophore opens ventrally just anterior to the ventral setae.

Pharyngeal, oesophageal, and septal glands occur in II–VI. Coelomocytes, black in transmitted light, are numerous throughout the body length and are up to 20 mu in diameter.

Budding is the only form of reproduction observed. There may be several fission zones, the intermediate zooids consisting always of a single segment.

TABLE I.

	P. osborni (Walton)	*P. nothofagi* n.sp.	*P. minutum* (Stephenson)	*P. minutum* (Marcus)
Hair setae Length μ	145	110–200	80–90	80–90 up to 120
Needle setae Type	Crotchet with nodulus (Fig. 6)	Bayonet-shaped (Fig. 2)	Crotchet with nodulus (Fig. 5)	Bayonet-shaped (Fig. 4)
Length μ	50	35–50	35	30–35
Ventral setae Length μ	40	30–40	30–40	30–40
Nephridia	?	Paired IX	Single IX, XI	Single IX, XI
Stomach	VIII	VII	VIII	VII ? or VIII ?
Length mm	1.6	1–2	2	1–2
n	?	12	12	12
s	15–16	22	17–19	?

Three of the species of *Pristina* which have the same setal characteristics as this worm are distinguished by their very much larger size. These are *P. menoni*, *P. jenkini*, and *P. breviseta*, in which n is 19 or more. These worms have the stomach in VII. The remaining species, without a proboscis and with the same setal characters, is *P. minutum* (Stephenson). In this species Sperber (1948) includes worms described by Walton (1906) from North America, by Stephenson (1914) from India, and by

Marcus (1943) from Brazil. All these worms resemble each other, and the present worm in their very small size. However, there is a marked distinction between the North American and Indian worms on one hand, and the Brazilian and the New Zealand worms on the other. The needle setae are clearly figured by Walton (Fig. 6) and by Stephenson (Fig. 5) as bifid, sigmoid crotchets with a distinct nodulus. Marcus, figures a bayonet shaped seta (Fig. 4) without a nodulus, closely resembling the setae of my worm. Marcus' worm is not therefore *P. minutum.* The principal distinction between Marcus' worm and the New Zealand worm lies in the position of the stomach. Although Marcus (1943: 130) is ambiguous on this point, indicating either VII or VIII, he figures it in VIII. He also states that the sinuous intestine occurs in IX and the swollen intestine in X. Another difference, although not so important, is that the nephridia are single in the Brazilian and paired in the New Zealand worm. The hair setae are very much longer in the New Zealand worm. The relations between the four worms are summarised in Table I. As can be seen from this table there is insufficient information about *P. osborni* to identify it with *P. minutum* (Stephenson). They may well prove distinct species. The New Zealand worm is separated from the Brazilian by the position of the stomach. Accepting this distinction it will be necessary to give a new name to *P. minutum* (Marcus).

Family PHREODRILIDAE

Schizodrilus n.gen.

Dorsal setae single needle and two pectinate setae per bundle commencing in III; ventral setae paired uncinate, single tip or bifid, commencing in II; paired spermathecae, opening ventrally, in XI and sometimes XII; testes in IX: penial setae present; asexual reproduction by simple or multiple fragmentation and subsequent regeneration.

Type species *Schizodrilus nothofagi* n.gen., n.sp.

Key to the Species of *Schizodrilus*

1. Ventral setae similar . .. . *S. nothofagi* n.gen., n.sp
2. Ventral setae dissimilar ... . *S. major* n.gen., n.sp.

Schizodrilus nothofagi n.gen., n.sp. Figs. 7-16.

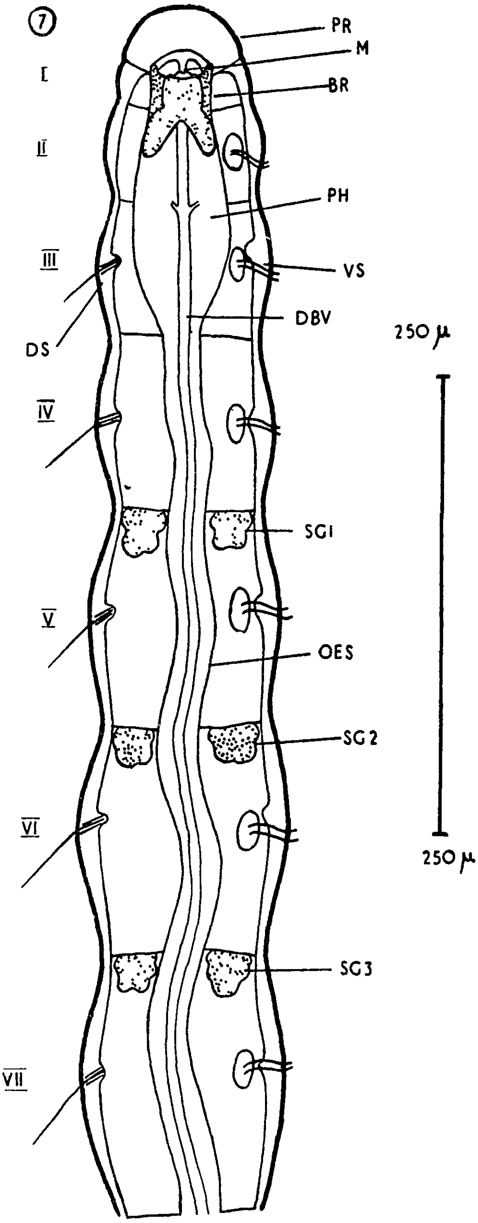
This is a small white worm closely resembling an enchytraeid worm in general appearance. It is closely annulated with a relatively firm and opaque body wall. Large specimens are less than 10 mm in length when fully extended and only about 150 mu broad. There are generally about 50 segments in a full grown worm, the anterior segments being somewhat smaller and shorter than succeeding segments. The prostomium is short and mobile.

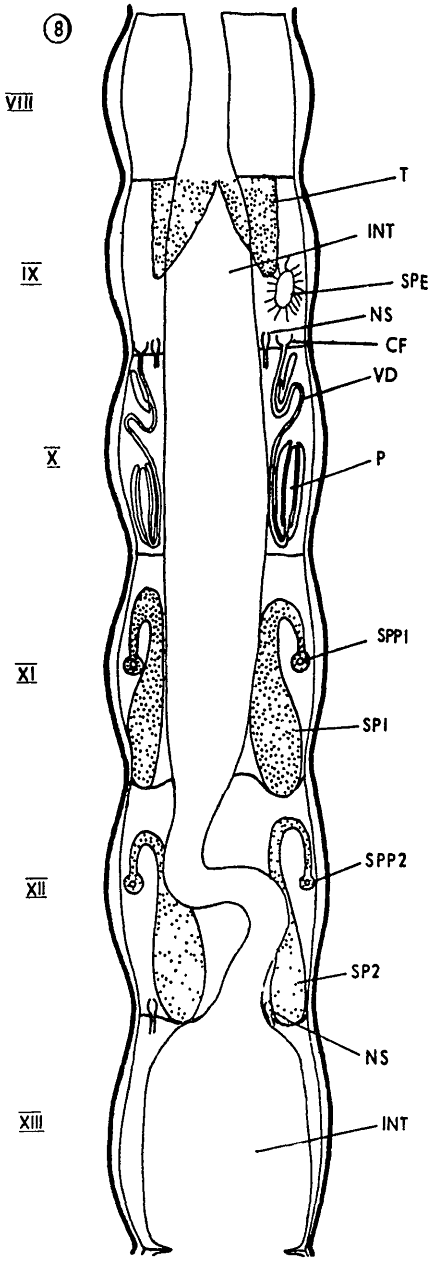
Ventral setae (Fig. 14) commence in II and consist of two per bundle. The setae are similar, each a bifurcate sigmoid seta with a well defined nodulus about one-third the length from the distal end. The proximal tooth is slightly larger than the distal. The setae range in length from 50–60 mu, and the width at the nodulus is about 5 mu.

The dorsal setae (Figs. 13, 15) commence in III and consist of a single needle and two pectinate setae per bundle. The needle setae (Fig. 15) consist of a broad flattened shaft within the setal follicle and an attenuated hair-like distal extremity set at a slight angle to the shaft and projecting beyond the body wall. These setae vary in length from 80–100 mu and the setae of the first seven or eight segments are typically shorter than those of succeeding segments. The length of the shaft is about 50 mu and its width about 3–4 mu.

The pectinate setae (Fig. 13) are minute bristles about 25–30 mu in length and 2 mu broad lying within the body wall close to the shaft of the needle setae and therefore difficult to observe in the living worm. There are two surfaces, one is smooth and convex, the other is fluted and slightly concave at the distal extremity. This distal extremity is rhomboidal in outline and some 2 by 2 mu in size.

The alimentary canal (Figs. 7, 8) consists of a pharynx in II-III, a winding oesophagus in IV-IX which broadens in IX into an intestine. The intestine narrows into a loop in XII and broadens again, almost filling the coelom, in XIII. Towards the posterior end of the body the intestine narrows again. It is commonly constricted by the septa. The gut is ciliated and as is the case in aquatic worms, the anal cilia are well developed. The transition from





FIGS. 7–16.—*Schizodrilus nothofagi* n.gen. n.sp. FIGS. 7, 8.—Semi-diagrammatic drawing.

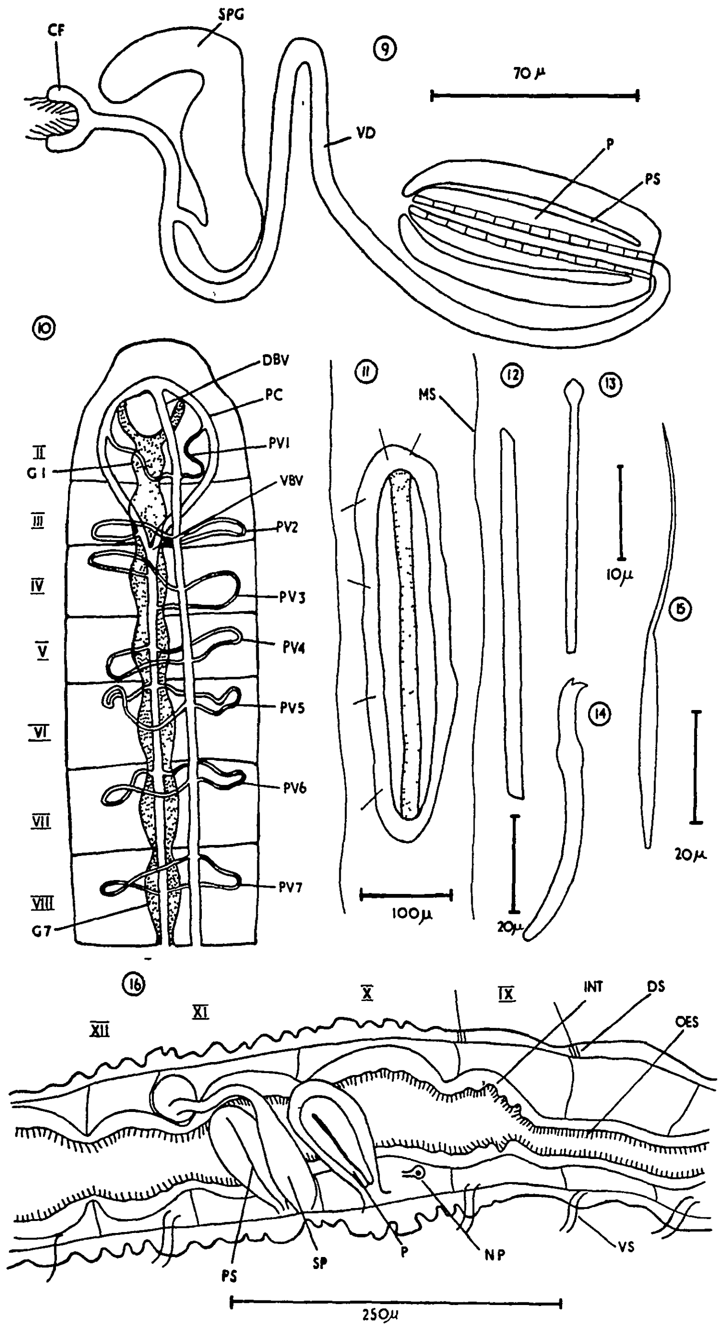


FIG. 9.—Sperm duct and efferent organ. FIG. 10.—Vascular system. FIG. 11.—Section of worm in mucous sheath following multiple fragmentation. FIG. 12.—Penial seta. FIG. 13.—Pectinate seta. FIG. 14—Ventral seta. FIG. 15.—Needle seta. FIG. 16.—Lateral view of type specimen.

oesophagus to intestine is slight, being marked by a slightly broader lumen, a thicker gut wall and longer cilia. In fixed material the distinction is cleaıer than in the living worm (Fig. 16).

The vascular system is ıllustrated in Fig. 10. The ventral loop unites in III and in all the anterior segments is joined to a single dorsal vessel by a pair of commissures in each segment. This arrangement closely resembles that of *Tubifex* (Dixon, 1915) and is simpler than that described by Beddard (1891) for *Phreodrilus subterraneus* which has two dorsal vessels. The nervous system was not specially studied.

The nephridia are tubificid in structure (*cf.* Dixon, 1915), much coiled and with a small diamond-headed nephrostome. The nephridiopore opens ventrally in line with the ventral setae near the anterior margin of the segment The nephridia occur either paired or single. In the latter case they occur on alternate sides. Typically they occur paired in X and XIII, although occasionally alternate nephridia occur in these two segments. They are present in a number of subsequent segments either paired or single

Besides the nephridia and reproductive organs, the coelom, especially of the anterior segments, contains gland cells which are often aggregated into septal glands in V-VII but may also lie freely in the coelom. The setal follicles of the stout ventral setae and their muscles are relatively large and project well into the coelom. Those of the dorsal setae are much smaller. Chloragogen commences in VII.

Only a few worms have been observed with reproductive organs, and these show considerable variation not only from the typical phreodrilid arrangement but even between ındividuals. This is doubtless associated with the unusual form of asexual reproduction characteristic of the species A similar variation is recorded for *Lumbriculus variagatus* which also reproduces by multiple fragmentation (Stephenson, 1930, p. 789)

Female organs have not been observed. The testes are found in IX, and the sperm masses lie freely in the coelom (Fig. 8). There are no seminal vesicles. The sperm duct and efferent organ, or penis, occur in X. They are paired. The ciliated funnel of the sperm duct opens in IX close to the site of the nephrostome. The sperm gland, or prostate, is an elongate body joining the sperm duct just posterior to the IX/X septum. The penis (Fig. 9) is a simple evertible organ lined with large cells. It opens ventrally, and is strongly muscular. A fine penial bristle, about 80 mu in length, may occur in XI (Fig. 12, 16). A pair of large spermathecae occur in XI. A second pair may occur in XII. The spermathecae open ventrally, in line with the ventral openings of the penis. They are elongate bodies and may be coiled on themselves within their segments or may protrude backwards into the succeeding segments.

Externally there are few signs of sexual maturity. The clitellum is not distinguishable in living worms but in fixed material there is an obvious thickening of the body wall in X, XI and XII, and to a lesser extent in IX and XIII (Fig. 16). The dorsal setae are typically absent from X-XIII and the ventral setae from X–XI, the penial bristles occurring in XI, posterior to the spermathecal openings.

This arrangement of the reproductive organs agrees with the phreodrilid pattern generally, and in particular in the posterior position of the spermathecae. It differs chiefly in the anterior displacement of the principal organs—viz., the testes, efferent organ and spermathecae, which are usually in XI, XII and XIII respectively. Beddard, however, recorded an individual of *Phreodrilus albus* in which the organs were displaced one segment forwards and in *P. zeylanicus* the efferent organ opens in XIII and the spermathecal pores in XIV, i.e., they are displaced one segment further back (Stephenson, 1913). The exact location of these organs is then of less significance than the posterior relation of the spermathecae to the other organs. The present species is unusual in having occasionally two pairs of spermathecae.

Despite the presence of reproductive organs in some worms I have observed no evidence of sexual reproduction. Reproduction appears to take place chiefly asexually by a process of fragmentation and subsequent regeneration. Typically the worm secretes a mucous sheath within which the process of fragmentation takes place. It may break up into ten or more fragments, the smallest consisting of only three or four segments (Fig. 11). The most anterior and posterior segments lose their setae and are thickened terminally, the alimentary canal being, for a time, a closed tube. Only the first fragment, with the original head, and the last fragment, with the original tail, are exceptions to this, and in these two cases the activity of the cilia of the alimentary canal is inhibited. Within a week to a fortnight the worm develops a head and a tail and very rapidly regenerate a large number of segments, so that by the end of a month the separate parts are identical with the original worm. Long before regeneration is complete, however, the worms will move actively through the culture.

Asexual reproduction is commonly correlated with remarkable powers of regeneration. In some experiments with this worm it was found that amputated fragments would regenerate, following the closure of the original wound, in very much the same way as the naturally occurring fragments.

This asexual method of reproduction and the great capacity for regeneration of damaged fragments of this worm closely parallels *Lumbriculus variegatus,* another aquatic worm in which sexually mature individuals are very rare and which reproduces asexually by a similar process (Stephenson, 1930, p. 538). Like the present species *L. variegatus* belongs to a family, the Lumbriculidae, in which sexual reproduction is the rule and asexual reproduction by budding does not occur. The only other worms for which fragmentation and regeneration have been recorded all belong to the Naididae, a group in which asexual reproduction, typically by budding (i.e., regeneration prior to separation) is the rule.

Schizodrilus major n.gen., n.sp. Figs. 17-22.

This is a small, white, very soft bodied worm, generally tubificid in appearance, with a delicate transparent body wall which is highly contractile but not strongly annulated. There are up to 120 segments in a large worm which may measure almost 20 mm when fully extended. They are about 250–350 mu broad. The prostomium is rounded and flexible and about 150–200 mu broad.

Ventral setae commence in II and dorsal setae in III. The ventral setae consist of two per bundle; both are sigmoid setae, but one is single pointed, the other bifurcate (Figs. 19, 20). The single pointed seta is about 100–170 mu in length with a well defined nodulus between a-half and one-third the length from the distal extremity. The bifurcate seta is the same length with a nodulus between a quarter and a fifth the length from the distal extremity The proximal tooth is slightly larger than the distal tooth.

The dorsal setae consist of a single (or rarely two) needle setae per bundle, and sometimes one or two pectinate setae. The needle setae and the pectinate setae resemble those of the previous species but differ in size. The needle setae (Fig. 22) are 200–300 mu in length and the length of the shaft about 60–120 mu and its breadth about 10 mu. The pectinate setae (Fig. 21) are 55–75 mu in length and almost 5 mu in breadth. In the anterior segments and in regenerating segments the setae are shorter.

The alimentary canal consists of a pharynx in II–IV, a winding oesophagus in V–IX which broadens into the intestine in X. The intestine which nearly fills the coelom is partially constricted by the septa. Chloragogen commences in V.

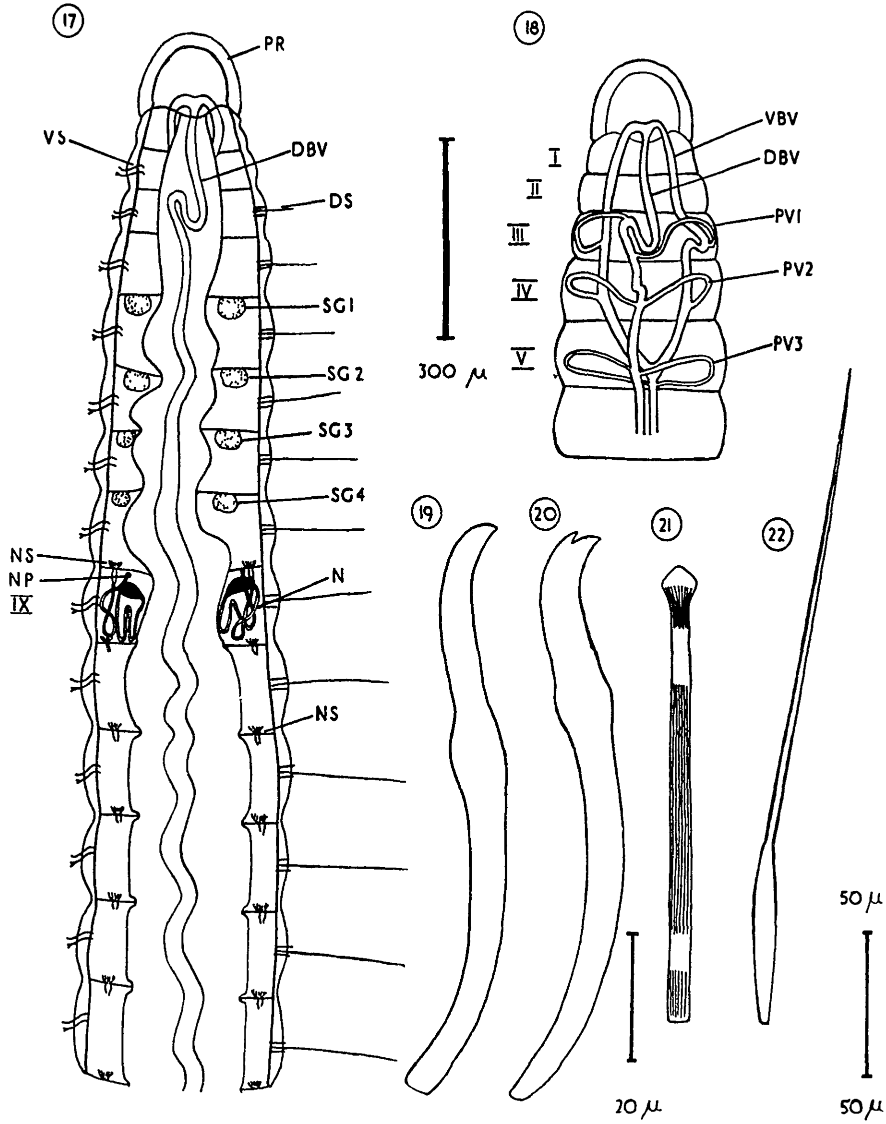
The vascular system presents some unusual features (Fig. 18). The dorsal vessel, closely apposed to the gut, shows a remarkable double loop in III. From the anterior portion of the second loop the first left commissural vessel arises, while the right commissural vessel arises from the posterior part of the loop just anterior to the septum. The ventral vessel is double in the first five segments, the two parts uniting just before the junction of the commissural vessels in V.

Nephridia generally occur paired in IX, and are either paired or single (and then alternate) in subsequent segments. The nephridia consist of closely apposed coils with double lumina There is a small nephrostome with a slightly swollen base leading into the succeeding segment. Here, after several coils, the tube leads into a swollen body or ampulla and then to the ventral nephridiopore.

Septal glands occur in V-VIII Coelomocytes up to 20 mu in diameter occur throughout the coelom.

No reproductive organs have been observed in any of the worms even when the same worm has been observed regularly over a period of ten months. No instance of multiple fragmentation has been observed, but a number of small fragments—of about 12 segments—have been observed. These fragments regenerate a head and ultimately increase in size, by the addition of further segments. Further, like the previous worm, there are very great powers of regeneration of mutilated fragments. I believe, therefore, that this worm reproduces by a process of simple fragmentation and regeneration. In this case it appears that only a single posterior fragment becomes detached, and consequently it is very difficult to observe the actual process of fission

To support this interpretation a number of experiments were carried out in which a worm was cut into two and in one case, into three parts. In every instance all the parts regenerated quite satisfactorily. Briefly the process falls into the following stages: first, the closure of the wound; secondly, the regeneration of a small pros-



FIGS. 17–22.—*Schizodrilus major* n.gen , n.sp. FIG. 17.—Semi-diagrammatic drawing. FIG 18—Vascular system FIG 19, 20—Ventral setae. FIG. 21.—Pectinate seta. FIG. 22.—Needle seta.

tomium and peristomium; thirdly, the intercalation of new segments immediately posterior to the new head; fourthly, the reorganisation of the body to a reduced size and the addition of further segments posteriorly. The rate of regeneration, as with the previous species, is rapid. The posterior half of a worm cut into two parts shows regeneration of a "stub" prostomium in seven days, and regeneration of the whole head within a fortnight, although the setae take longer to develop. The severed tail of the anterior half regenerates a new anus just as quickly. When the worm was cut into three parts the centre section consisted of only 12 segments. In less than a week a head was developing on both the posterior parts, and in less than three weeks the middle section had developed a head, six new segments immediately behind the peristomium and sixteen new posterior segments. In other words it had trebled the initial number of segments in three weeks, and this included the differentiation of a new head. Besides these experimentally mutilated worms there occurred occasionally in the cultures individuals which were regenerating a new anus and also an individual without a head. The course of regeneration in these worms was similar to that of the experimental worms. Besides regenerating worms there also occurred in one of the cultures a worm in which dedifferentiation had taken place. This worm was only 3 mm long and had no setae, nephridia, mouth or anus.

The present classification of the Phreodrilidae is based wholly on the character of the spermathecae and in particular the position of the spermathecal pores. Four genera are recognised by Michaelsen and Stephenson: *Hesperodrilus* (9 spp.) with spermathecae opening ventrally, *Phreodrilus* (5 spp.) with spermathecae opening dorsally, *Gondwanaedrilus* (a single sp.) with spermathecae opening into the male pore, *Phreodriloides* (a single sp.) with no spermathecae. I do not believe that this represents in any way a natural classification of the family, as it does not accord well with their distribution, and it suffers from the serious defect that immature worms, or those without reproductive organs, cannot be classified and are left as species incertae sedis. Michaelsen (1923) so treats *Hesperodrilus zelanicus, Phreodrilus mauiensis,* and *Tasmaniaedrilus tasmaniensis.* In the other families of microdrili much more attention is paid to the character of the setae, and indeed it is by the character of their setae that the Phreodrilidae are separated from other families. It is unfortunate, therefore, that in describing the various species of Phreodrilidae few of the authors have given any adequate description of the setae, for it is clear from what evidence is available that the species could be separated very conveniently by this character, and it has the great advantage that it permits poorly preserved and immature specimens to be identified. The three species rejected by Michaelsen can all be distinguished from other species by this character. It is obvious that species which reproduce asexually will rarely show any sexual characters and that even when they are present they are capable of considerable variation within the species (Gates, 1956). For this reason alone the taxonomy of any group of worms including asexually reproducing species should never be based on the character of the reproductive organs alone unless no other characters are available. In the Phreodrilidae, however, the setae provides an admirable criterion for specific diagnosis, and it is to be hoped that further study of these worms will be directed to a detailed study of these structures largely unknown for about half the described species.

The two species described in the present paper differ from other phreodrilids in the character of the dorsal setae, which consist of needle and pectinate setae. The only other species in which a hair-like needle seta is recorded is *H. litoralis,* but Michaelsen does not figure or describe its form. Pectinate setae, although common in tubificids, have not previously been recorded from phreodrilids, although I suspect that the "minute bristles" of *P. beddardi* referred to by Benham (1904), the "reserve setae" of *P. subterraneous* referred to by Beddard (1891), and the "ersatzborsten" of *H. crozetensis* referred to by Michaelsen (1905) might all prove to be pectinate setae. None of these authors describe or figure these structures.

The differences in the position of the reproductive system I do not consider of very great significance, but the occurrence of asexual reproduction is a further distinction.

The two species can be separated from each other by the character of their ventral setae.

Slides of the new species of worms described in this paper and of *Pristina taita* Stout, 1956, have been deposited at the Dominion Museum, Wellington.

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BR, brain.
BZ, budding zone.
CF, ciliated funnel of sperm duct.
DBV, dorsal blood vessel.
DS, dorsal seta.
G 1, 7, nerve ganglions.
HS, hair seta.
INT, intestine.
M, mouth.
MS, mucous sheath.
N, nephridium.
NP, nephridiopore.
NS, nephrostome (Figs. 8, 17) or needle seta (Fig. 1).
OES, oesophagus.
P, penis.
PC, peristomal loop.
PH, pharynx.
PR, prostomium.
PS, penial sac (Fig. 9) or penial seta (Fig. 16).
PV 1, 2, 3, etc., perivisceral connectives.
SG 1, 2, 3, etc., septal glands.
SP 1, 2, spermathecae.
SPE, sperm mass.
SPG, spermiducal gland.
SPP 1, 2, spermathecal pores.
ST, stomach.
T, testis.
VBV, ventral blood vessel.
VD, vas deferens.
VS, ventral seta.