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MACQUARIDRILUS: A NEW GENUS OF TUBIFICIDAE (OLIGOCHAETA) FROM MACQUARIE ISLAND

SUMMARY

A new monotypic genus of the family Tubificidae is described, with *Macquaridrilus bennettae* n. sp. as the type species. This represents the first record of the family from Macquarie Island, an isolated subantarctic island 1,000 kilometres southwest of New Zealand and 650 kilometres from the nearest land, the Auckland and Campbell Islands. The species is unique in the morphology of its male deferent apparatus and is the only tubificid with closed spermathecal diverticula.

Evidence is given that *Macquaridrilus*, or an ancestral form, is unlikely to have survived glaciation of the island. It is suggested that colonization occurred after amelioration of the last glaciation, possibly less than 11,000 years ago, the distribution of the species suggesting that it may only very recently have reached the island. Aspects of the zoogeography and ecology of the island which are relevant to *Macquaridrilus* are briefly discussed and the means of dispersal examined.

INTRODUCTION

The oligochaete fauna of Macquarie Island was monographed by Benham in 1922. The species then known from the island were three enchytraeids, *Lumbricillus werthi* (Michaelsen) 1905, *L. macquariensis* Benham 1915, and *Marionina antipodum* (Benham) 1905, together with a member of the Acanthodrilidae, *Microscolex macquariensis* (Beddard) 1896. Of these, only the acanthodrilid was endemic.

Microscolex contains two other species which are endemic on subantarctic islands and, like *M. macquariensis* which they closely resemble, are apparently euryhaline. The remaining two species of the genus are less similar cosmopolitan species. The three enchytraeids are clearly euryhaline, being found in fresh waters or terrestrially on the island and in the marine littoral. *L. werthi* occurs also on Kerguelen Island, *L. macquariensis* on the Auckland and Campbell Islands, and *Marionina antipodum* on Antipodes Island. No further species have subsequently been recorded from Macquarie Island, but *Microscolex macquariensis* was redescribed by Lee (1959).

In December 1965 the author had the opportunity of collecting oligochaetes on Macquarie Island while visiting biologist on the annual relief excursion to the Australian and New Zealand Research Expeditions station on the island. To the author's collections were added a large collection from all parts of the island made by Mr. K. Simpson (A.N.A.R.E. Technical Officer) and a small sample by Miss Isobel Bennett, a visiting biologist on the same expedition. Miss Bennett's material includes specimens belonging to the aquatic family Tubificidae, the peculiar morphology of which warrants recognition of a new genus and species. The present account will be restricted to consideration of this species, the first record of a tubificid from the island.

The author is indebted to the Antarctic Division, Department of External Affairs, for the opportunity to visit the island. Thanks are also due to the University of Queensland for contributing towards the cost of transportation.

ZOOGEOGRAPHICAL CONSIDERATIONS

The existence on Macquarie Island of a tubificid which is sufficiently distinct to be accorded generic rank is of interest in view of the extremely isolated location of the island. It poses a number of questions: whether the genus originated on the island and if so from what precursor; by what agency it or its precursor reached the island; and the source from which colonization occurred. These problems will be briefly discussed in relation to the geography and geological history of the island.

Macquarie Island, at 54°30'S. 158°57'E., is an oceanic island, 21 miles long by 3 miles wide, in the Southern Ocean. The nearest land masses are the Auckland and Campbell Islands approximately 650 kilometres to the northeast, with New Zealand a further 350 kilometres. Tasmania is 1,300 kilometres northwest and the Antarctic continent 1,450 kilometres south. The island probably originated in the early Tertiary, but there is evidence of its subsequent submergence to reappear in the Miocene (Mawson, 1943). It bears abundant evidence of Pleistocene glaciation and, although the extent of the icesheet which it then acquired is unknown, it is unlikely that its present flora and fauna predate glaciation. Lignite beds on the island have yielded pollens which indicate a preglacial flora quite different from the present one (Bunt, 1956) and evidence of the extent of glaciation of more northerly islands points strongly to glaciation of Macquarie Island sufficiently severe and extensive to have destroyed its oligochaete fauna. Thus the South Island of New Zealand was only partially glaciated and apparently supported patches of *Nothofagus* forest throughout the Pleistocene, some of which survives today (Willett, 1950). Further south, in the Auckland Islands, the snow-line extended below 1,000 feet at the glacial maximum (Willett, cited by Fleming, 1949), but a coastal strip of vegetation may have been retained, as is suggested by the presence of endemic earthworm species (Lee, 1959). Campbell Island, a Pliocene volcano, still further south but well to the north of Macquarie Island, was glaciated in the Pleistocene to 500 feet above sea level (Fleming, 1949) and correspondingly lacks endemic oligochaetes. It supports only one species of *Microscolex* (a circum-subantarctic genus) and two species of *Rhododrilus* (a genus endemic in the New Zealand region), all euryhaline species which were probably derived by rafting on the West Wind Drift from the Auckland Islands, on which they also occur. It may therefore reasonably be postulated that the ice-cap on Macquarie Island must have extended too near to sea level to have permitted survival of its oligochaete fauna.

There is good evidence for large-scale species diversification in the African Ocnerodrile earthworm genus *Pygmaeodrilus* since the Miocene-Pleistocene rifting (Jamieson, 1957), but the period since the last glaciation of Macquarie Island is unlikely to have been sufficient for evolution of *Macquaridrilus* from a tubificid colonizing the island after glaciation. There is evidence for glaciation of New Zealand as late as 20,000 years ago, and of the retreat of the ice-sheet from the Southern Indian Ocean only 15,000 years ago (Mellor, 1959). The validity of these dates is indicated by a corresponding date of about 18,000 years ago for the beginning of clearance of ice from the southern British Isles. However, Lee (1959) cites a radio carbon dating of the last (Mankato) glaciation of New Zealand at 11,000 years ago.

The apparent absence of *Macquaridrilus* from pools on the island similar to the one in which it was found, as indicated by the author's collections from the island, perhaps indicates that it has only very recently reached the island. Lee (1959) drew a similar conclusion from the restriction of *Microscolex* species to the shore and its vicinity on Campbell Island. A slight possibility exists that *Macquaridrilus bennettae* was introduced by man as there has been spasmodic settlement of the island in this and the last century. If colonization were recent this species may well occur elsewhere, possibly on the subantarctic islands of New Zealand which harbour two of the island's three enchytraeid species. Derivation from southern land masses without the agency of man must be considered, however. Three agents will be discussed.

Land connections

Oceanic depths at 12,000 feet or more in the Southern Ocean around Macquarie Island are too great to have permitted land connections with other regions by eustatic sea level changes. The last glaciation of New Zealand is believed to have resulted in a fall of sea level of only 350 feet (Fleming, 1962). Land connections, either as "bridges" or by virtue of continental drift, which Benham (1922) envisaged to explain the occurrence of oligochaetes on Macquarie Island, cannot therefore be considered relevant to post-glacial dispersal.

Rafting

Rafting by sea on vegetation (an agency refuted by Benham) deserves consideration as *L. macquariensis*, *L. werthi*, and *Marionina antipodum* are known to be truly intertidal (Kenny & Haysom, 1962), and *Microscolex* is also euryhaline (Lee, 1959) and presumably could survive rafting on, for instance, kelps. The apparent restriction of *Macquaridrilus* to fresh water high on North Head, and its absence from the marine littoral, may indicate that it is relatively stenohaline, however. Unless an organism were highly tolerant of submersion in sea water, the time for drift to the island would appear to be too long to permit survival. Costin (1965) estimates that rafting of a viable seed of *Caesalpinia bonduc* from South America to Macquarie Island could not have been accomplished in much less than a year. Drift from Kerguelen or Heard Islands would take approximately half this time and would not solve the problem of the ultimate origin of *Macquaridrilus* as these islands have permanent ice and were presumably less hospitable than Macquarie Island during the Pleistocene. Even drift from the subantarctic islands of New Zealand from which, by their distribution, *Marionina antipodum* and *Lumbricillus macquariensis* may well have originated, would be lengthy as it would be contrary to the prevailing West Wind Drift. Restriction to elevated freshwater pools on the island, if not due to its being stenohaline, would at least raise the possibility that *Macquaridrilus* reached the island by some agency other than the sea.

Avian transport

The possibility of aerial transport of *Macquaridrilus*, and conceivably of the other oligochaete species, to the island by birds deserves mention. Susceptibility of the worms or of their cocoons to desiccation would seem to offer little obstacle to

aerial dispersal in a latitude where precipitation is rarely interrupted for more than a few hours. Evans (1965) found larval stages of a circum-subantarctic freshwater copepod in the plumage and on the foot of a giant petrel on Macquarie Island at some distance from pools in which the copepod occurs and he suggested that birds were responsible for its introduction to the island. Birds have also been invoked as the dispersive agents of subantarctic mites (Dalenius & Wilson, 1958) and of the stenohaline land snail *Phrixgnathus* which is endemic in New Zealand and its subantarctic islands with a single species on Macquarie Island (Dell, 1964). Banding records indicating the speed of migration (e.g. Falla, 1960; Hitchcock & Carrick, 1959) of aquatic birds to and from Macquarie Island over great distances do not militate against the hypothesis of bird dispersal.

Origin

Irrespective of the means of dispersal it may be presumed from the distribution of other subantarctic oligochaetes that the region of origin of *Macquaridrilus* had a climate similar to that of Macquarie Island, that is to say a cool temperate maritime climate. If invasion were very recent the most likely origin would be the southern tip of South America and its neighbouring Magellanian Islands or the subantarctic islands of New Zealand, with the time factor for survival of the worms favouring the latter origin. The microdrile fauna of these regions is very little known and it is possible that *Macquaridrilus* still occurs in them.

ECOLOGICAL DATA

Climate

The climate of Macquarie Island is characteristic of the subantarctic or cool temperate zone in which it is situated. This zone lies between the Antarctic and Subtropical Convergences and includes the Magellanian Province of South America, Falkland Islands, Gough Island, Tristan da Cunha, Crozet Islands, Marion and Prince Edward Islands, St. Paul and New Amsterdam Islands, Kerguelen Islands, Auckland and Campbell Islands, and Macquarie Island. Precipitation, as rain, hail, or snow averages annually 1,029 millimetres (40.5 inches) spread over about 330 days of the year. The mean duration of sunshine per day is 1.8 hours ($\frac{1}{2}$-hour in June to 3 hours in February). Consistent high winds, predominantly from the west and northwest, blow with a mean annual velocity of 31 kilometres per hour (19.2 miles per hour), with gusts of gale force on 180 days of the year. The mean annual temperature is 4.5°C with a mean annual range of 3.0°C to 6.3°C and an extreme range of -8.3°C to 11.4°C. The mean monthly range in temperature varies between 2.6°C and 3.8°C. Mean monthly relative humidity varies from 86 per cent to 95 per cent (data from Macquarie Island Meteorological Station, situated on an exposed isthmus at an altitude of 7.6 metres).

Vegetation

The "herbfield" in which the pool containing *Macquaridrilus* occurs is characteristic of areas with a high water-table and moderate but not severe wind. It is dominated by the large herb *Pleurophyllum hookeri* (occurring elsewhere only on the Auckland and Campbell Islands). Other conspicuous plants with their distribution elsewhere are *Festuca erecta* (Kerguelen and Falkland Islands and Tierra del Fuego), *Carex trifida* (Auckland and Campbell Islands and New Zealand, Falkland Islands and Tierra del Fuego), and *Stilbocarpa polaris* (Auckland and Campbell Islands). On North Head herbfield occurs above 300 feet and is surrounded, at lower altitudes, by wet Tussock Grassland dominated by *Poa foliosa* (Auckland and Campbell Islands and New Zealand).

Hydrology

Evans (1965) in a valuable unpublished study of Macquarie Island fresh waters draws attention to the similarity between the relative proportions of the major ions in these waters and the proportions in sea water, the ratio of Na:Cl being virtually

TABLE 1
Chemical composition of two pools on North Head, Macquarie Island (from Evans, 1965)
(In mg/litre unless otherwise indicated)

	Total Dissolved Solids	Na	K	Ca	Mg	Fe	Total Cations m.equ/litre	Ammoniacal Nitrogen mg/litre
North Pond 16/i/63	663	162.2	29.6	10.6	25.0	Trace	10.42	1.00
South Pond 1/ii/63	491	140.0	9.2	10.4	17.7	Trace	8.31	0.28

	Cl	SO_4	HCO_3	NO_2	SiO_2	Fe_2O_3	Al_2O_3	Total Anions m.equ/litre	Organic Nitrogen mg/litre
North Pond 16/i/63	320.0	11.2	41.5	0.06	40.6	11.3	9.7	9.91	2.67
South Pond 1/ii/63	280.0	20.3	8.5	0.03	1.6	1.0	1.3	8.45	1.76

	Ionic Proportions m. equ/litre % Total Cations or Anions							Total Dissolved Solids mg/litre	Dissolved Organic Matter (O₂ Absorbed) mg/litre
	Na	K	Ca	Mg	Cl	SO_4	HCO_3		
North Pond 16/i/63	68	7	5	20	91	2	7	663	31.7
South Pond 1/ii/63	73	3	6	18	93	5	2	491	22.6
World average fresh water	16	3	64	17	10	16	73		
Sea water Macquarie Island	76	2	4	18	90	9	1	34,912	
Precipitation Prion Lake	73	6	4	17	90	9	1	3,575	
Precipitation Isthmus	66	9	5	20	86	12	2	74	

identical (Table 1). This similarity is a reflection of the composition of the precipitation which, in the vicinity of one lake on the plateau (Prion Lake), had more than one-tenth of the total dissolved solids per litre which occur in sea water (i.e. 3,575 mg/litre against 34,912 mg/litre for Macquarie Island sea water) and did not differ significantly in relative proportions of major ions. Total dissolved solids in two ponds on North Head were 663 and 491 mg/l and in Prion Lake were only 93 mg/l. These figures suggest that the total concentration in rain water at Prion Lake must often be below that recorded, as does the much lower concentration of 74 mg/l recorded for precipitation on the isthmus which connects North Head with the main island. The ratio of Na:Cl in all these samples remained near 0.5. By condensing in the pools and contributing to run-off, frequent fogs on the island probably have some effect by diluting rain water contributed to the pools.

The pH of North Head pools varied between 6.8 and 8.6.

SYSTEMATICS
Genus MACQUARIDRILUS n.gen.

Setae 4 bundles per segment, beginning on segment 2; absent from segment 11; all bifid crochets without intermediate denticles; none modified as genital setae. Lateromuscular groove well developed. Male pores a pair posteriorly in 11. Spermathecal pores paired and lateral in 10. Nephridia each with a very large terminal rounded vesicle. Testes in 10. Ovaries in 11. Male ducts consisting of three consecutive regions: a coiled vas deferens; a long thin-walled atrium with which an elongated prostate communicates at intervals; and a stout muscular ejaculatory duct, at least as long as the segment, the cuticularized internal and external sheaths of which form a sperm canal which projects into a spherical chamber, the prostate vesicle, the latter debouching into a ventral chamber which is apparently evaginable as a penis. Posterior prostates present as low but well-developed masses enveloping the terminal bursa (prostatic vesicle and ventral chamber). Spiral muscle of the ejaculatory duct tightly coiled, internal to a high peritoneal epithelium. Spermathecae with blind stalked diverticula. Coelomocytes not obvious.

Monotypic.

Type species. Macquaridrilus bennettae n.sp.

Type locality. Macquarie Island, 54°30'S.158°57'E.

Remarks. Macquaridrilus is unique in the Tubificidae in possessing spermathecal diverticula. Its closest affinities seem to lie with a group of genera the limits and mutual interrelations of which have been the subject of much controversy, namely *Tubifex* Lamarck 1816, *Limnodrilus* Claparède 1862, *Isochaeta* Pointner 1911 and *Isochaetides* Hrabě 1966. Of these *Limnodrilus* appears closest but its atrium is relatively wider and more bulbous, its prostate gland smaller and more compact, its cuticular penis sheath is a more rigid structure than the apparently homologous cuticularized layers of the ejaculatory duct of *Macquaridrilus*, and its penial musculature forms a loose spiral outside the sheath; posterior prostate glands are absent. Sections through the penial apparatus of *Limnodrilus* (viz. *L. udekemianus* Clap. in Hrabě, 1966, Fig. 32 and *L. neotropicus* Černosvitov 1939, Fig. 94) show clearly two concentric epithelia between which is the single layer of the cuticular penial sheath and outside which (latter figure) are loosely arranged muscle fibres, a condition quite unlike that described below (see Fig. 6) for *Macquaridrilus bennettae*.

Within this group of genera, prostatic cells occur in the vicinity of the male apertures in some species of *Isochaetides* but never form the large masses seen in *Macquaridrilus*. Such posterior prostatic cells occur in the North American brackish water species *Isochaetides hamatus* (Moore, 1905), but the latter species has a much shorter atrium, possesses dorsal setae in 11, and apparently lacks the well-developed terminal bursa of *Macquaridrilus. Isochaetides lacustris* (Černosvitov, 1939) resembles *Macquaridrilus*
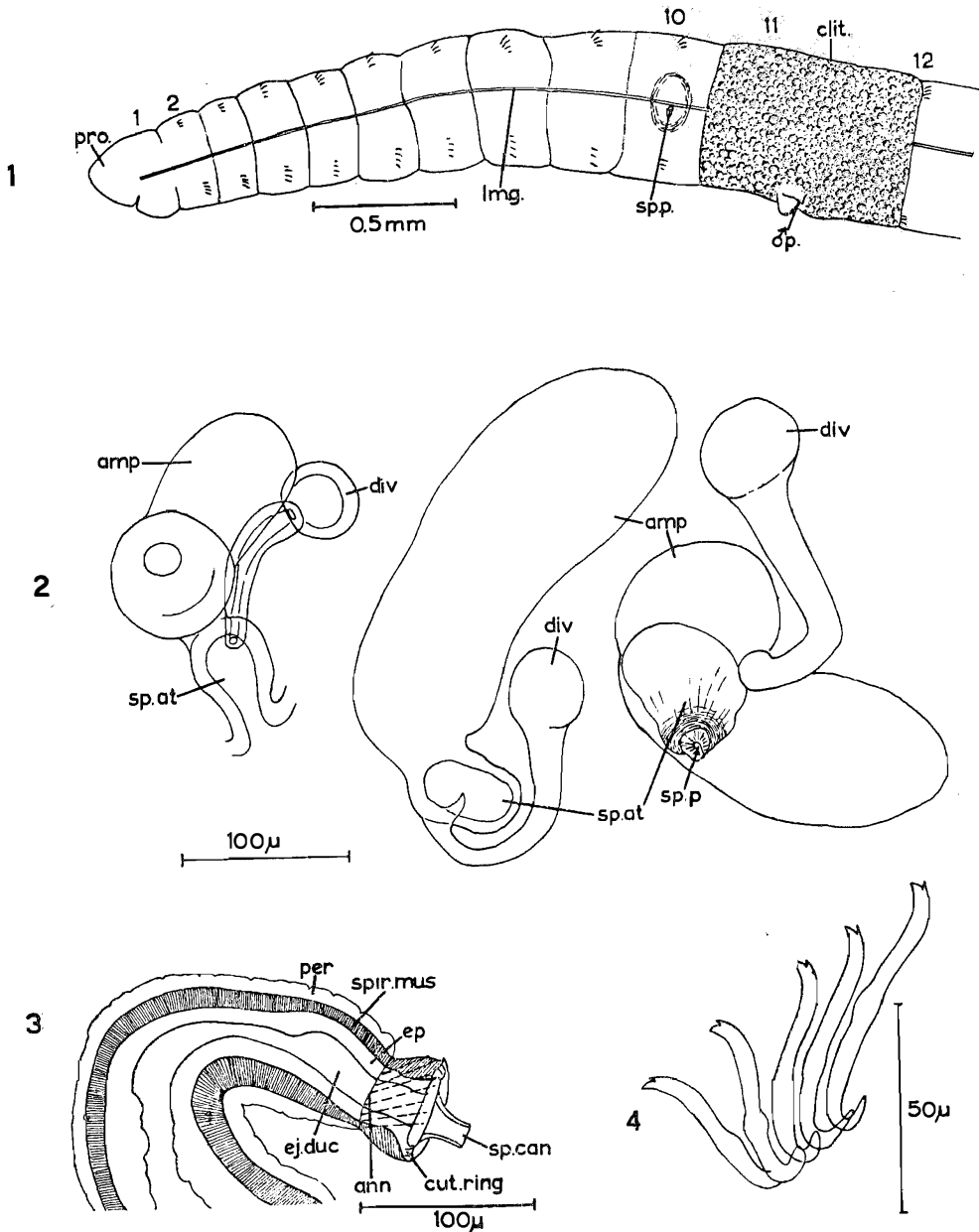
FIG. 1.—Lateral view of the holotype. FIG. 2.—Spermathecae from three paratypes. FIG. 3.—Ejaculatory duct and sperm canal of a paratype. FIG. 4.—A ventral setal bundle in segment 38 of a paratype. *Abbreviations:* amp, spermathecal ampulla; ann, annulus; clit, clitellum; cut. ring, cuticular ring; div, spermathecal diverticulum; ej. duc, ejaculatory duct; ep, epithelium; lmg, lateromuscular groove; ♂p, male pore; per, peritoneum; pro, prostomium, sp. at, ectal chamber or atrium of the spermatheca; sp. can, sperm canal; sp. p, spermathecal pore; spir. mus, spiral muscle.

in lacking all setae in segment 11, but its penial apparatus, although equipped with a few prostatic cells, differs significantly from that of *Macquaridrilus*, as does that of the other *Isochaetides* species.

MACQUARIDRILUS BENNETTAE n.sp.

Type locality. Macquarie Island; among submerged mosses with Enchytraeids in a shallow pool in herbfield at about 300 feet near the summit of Wireless Hill, North Head; collector Isobel Bennett, 12 December 1965. Numerous specimens, of which some 15 are clitellate. Two sagittal halves of the holotype, serial sections of a paratype, and a whole mount of a paratype have been lodged in the British Museum (Natural History) Registration Numbers, 1967.9.37/53. Longitudinal and transverse sections of a further paratype have been placed in the Queensland Museum. The remaining paratypes, including a further series of longitudinal sections, are in the author's collection.

Definition. Length 6.5 mm to 12.5 mm, width 0.5 mm to 0.6 mm, 40 to 49 segments. Form relatively stout, not filiform. Lateromuscular groove present. Clitellum annular, segments 11 to $\frac{1}{2}$12. Setae 4 bundles per segment beginning on segment 2; all simple bifid crochets; 4, sometimes 5, per bundle, with omissions commonest behind the clitellum; none modified as genital setae; absent from segment 11. Mamillary male porophores post-equatorial in 11 in line with the ventral bundles; male pores crescentic slits encircling their posterolateral aspects. Spermathecal pores lateral in the setal arc of segment 10, midway between the dorsal and ventral bundles. Buccal cavity in 1 and 2, pharynx in 3, gut dilated in 13 posteriad but chloragogue beginning in 6. No obvious ceolomocytes. Brain in segment 1. Nephridia micronephridiostomal holonephridia, commencing in segment 7; with very large terminal vesicle; nephridiopores immediately in front of the ventral bundles. Testes and funnels paired in 10. Vas deferens winding to septum 11/12 or further posteriad; continuing anteriad almost to septum 10/11 as a thin-walled unciliated atrium. An elongated, lobed prostate at least as long as segment 11 communicates with the atrium at intervals. Atrium continuous with a wide, tubular, muscular ejaculatory duct (resembling the penis of *Limnodrilus*) which occupies the length of segment 11. Cuticular sheath of the ejaculatory duct forming a spout-like sperm canal which is surrounded basally by a broad, hollow cuticular ring and projects into a spherical prostatic vesicle. The vesicle opens into a ventral chamber (eversible penis) which with it forms a terminal bursa opening at the male pore. This bursa invested by lobular posterior prostate glands. Ovaries anterior in 11. Ovisacs with separate large yolky ova extending into 12 and 13. Oviducal apparatus, including pores, unrecognizable. Spermathecae a pair in 10 with ampulla, ectal chamber, and a spherical diverticulum which communicates with the chamber by a slender duct.

External morphology

Dimensions. Length 6.5 mm to 12.5 (mean 11.8) mm, width 0.5 mm to 0.6 (mean 0.5) mm, 40 to 49 (mean 44) segments (8 specimens).

Prostomium. Prolobous but only faintly demarcated from the peristomium.

Form. Short and relatively stout, for a tubificid; often contorted after fixation but rarely forming a coil. Longitudinal lateromuscular groove (lateral line) well developed, located midway between the ventral and dorsal bundles of setae; clearly visible from the posterior limit of the prostomium to the clitellum, less distinct or unrecognizable behind this (Fig. 1).

Setae. Commencing on the segment behind the peristomium, i.e., on segment 2; 4 bundles per segment with the exception of segment 11 from which all setae are
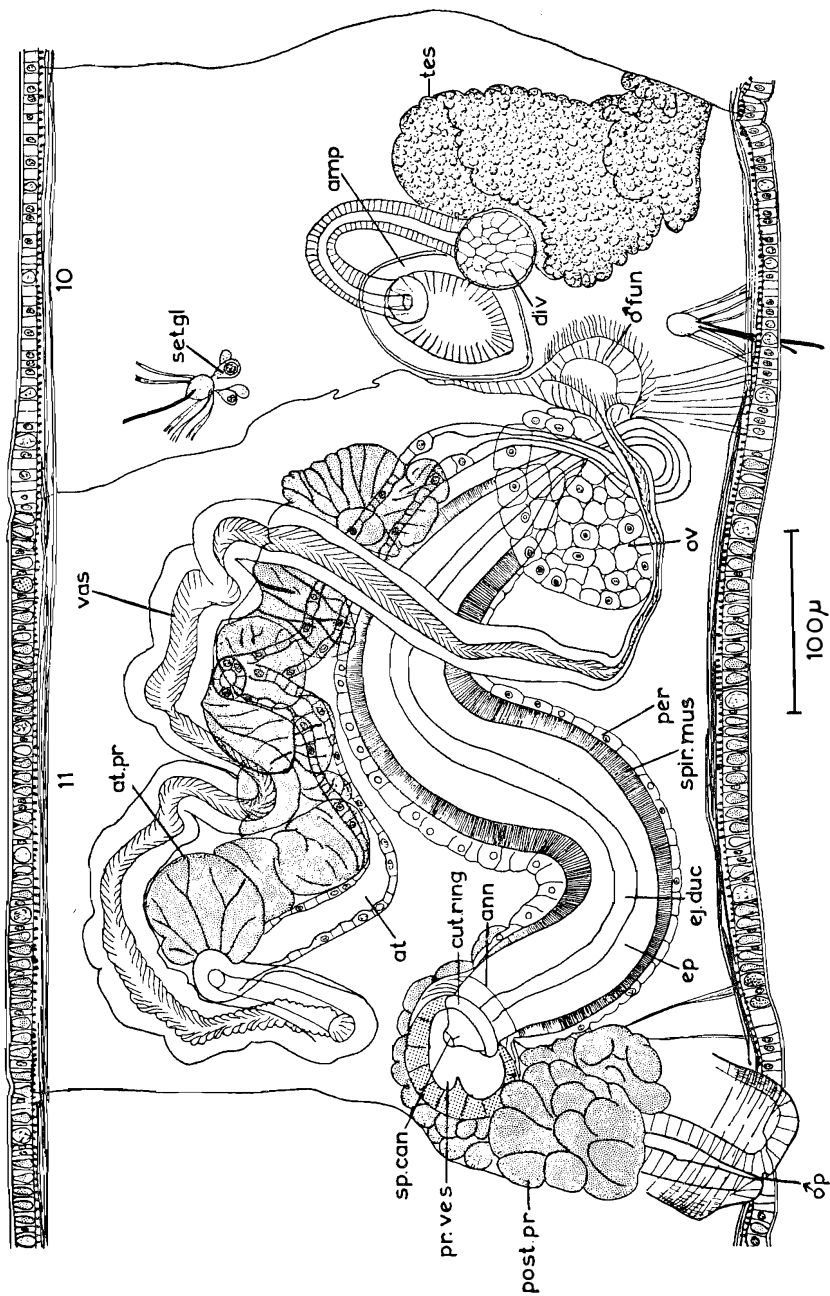
Fig. 5.—Sagittal section of the spermathecal and male segments (10 and 11) of the holotype.

Abbreviations: amp, spermathecal ampulla; ann, annulus; at, atrium; at. pr, atrial prostate; div, spermathecal diverticulum; ej. duc, ejaculatory duct; ep, epithelium; ♂f, male funnel; ♂p, male pore; ov, ovary; per, peritoneum; pr. ves, prostatic vesicle; post. pr, posterior prostate; set. gl, setal gland; sp. can, sperm canal; spir. mus, spiral muscle; tes, testis; vas, vas deferens.

absent. Throughout the body the setae are bifid sigmoid crochets with the upper tooth only about one-third as wide as the lower tooth, and have a well-developed node (Fig. 4). In segments 2 to 10 the total number of setae per segment varies in one paratype from 14 to 17, the average per bundle in each segment being 4 setae. The number in each bundle varies from 3 to 5, with 4 the commonest count; in the ventral bundles omissions are less frequent and supernumeraries, giving a count of 5, the more common. Omissions appear normal and supernumeraries exceptional in segment 10, the spermathecal segment, but the setae are unmodified. Behind the clitellum the full complement of 16 setae per segment is rarely attained; counts per bundle-site in order of decreasing frequency are 3, 4, (2, 5, 1, 0). (Uncommon or rare counts in parentheses.)

Clitellum (Fig. 1). Annular, not appreciably protuberant, appearing glandular and more opaque than the general body wall which is transparent; embracing 11 to $\frac{1}{2}$ 12; furrow 11/12 almost or completely obliterated.

Male porophores (Fig. 1). A pair of short mamma-like protuberances, each with a male orifice forming a crescentic slit on its posterior and posterolateral aspect at a variable distance above its base. The porophores lie behind the equator of segment 11, approximately in line with ventral bundles of adjacent segments.

Female pores. Undetectable.

Spermathecal pores (Fig. 1). One pair, strictly lateral in the setal arc of segment 10, immediately below the lateromuscular grooves, each a small orifice surrounded by an oval mound or slight papilla.

Internal anatomy

Septa. All thin; 3/4 present only dorsally, 4/5 to 9/10 transverse; 10/11 to 12/13 displaced forwards centrally; the remainder transverse.

Septal glands. Paired, ventral to the gut in segments 3 to 5.

Alimentary canal. The slender buccal cavity occupies segments 1 and 2 and the pharynx, which has a thick ventral floor, segment 3. The oesophagus in segments 4 to 12 is intersegmentally constricted and in 6 posteriad is invested by enlarged peritoneal cells which are rendered opaque by abundant large pigment granules (chloragogen cells). The intestine appears to commence in segment 13, where the gut enlarges (holotype and sectioned paratype), but might be considered to originate in segment 6 if the presence of chloragogue were used as a criterion. The internal epithelia of both the oesophagus and the intestine bear long cilia. The gut contents are diatoms and filamentous algae.

Blood vascular system. Dorsal and ventral blood vessels well developed, the dorsal vessel traceable onto the ventral aspect of the brain. A pair of tortuous dorso(-ventral?) commissurals extending far laterally occurs in each of segments 1 to (10?). A subneural vessel is absent.

Nervous system. The brain lies in the peristomium immediately behind and dorsal to the mouth; the "suboesophageal" ganglion lies in segment 2 and is thus in fact sub-buccal.

Nephridia (Fig. 7). Micronephridiostomal holonephridia, the first postseptal bodies in segment 7; preseptal duct projecting well in front of the septum, postseptal duct widened and looping ventrally before coiling many times in a compact mass and opening to the exterior through a very large terminal vesicle which extends well into the body cavity and about equals the coiled portion in size. From sections the nephridiopores are situated shortly anterior to the ventral setal bundles.
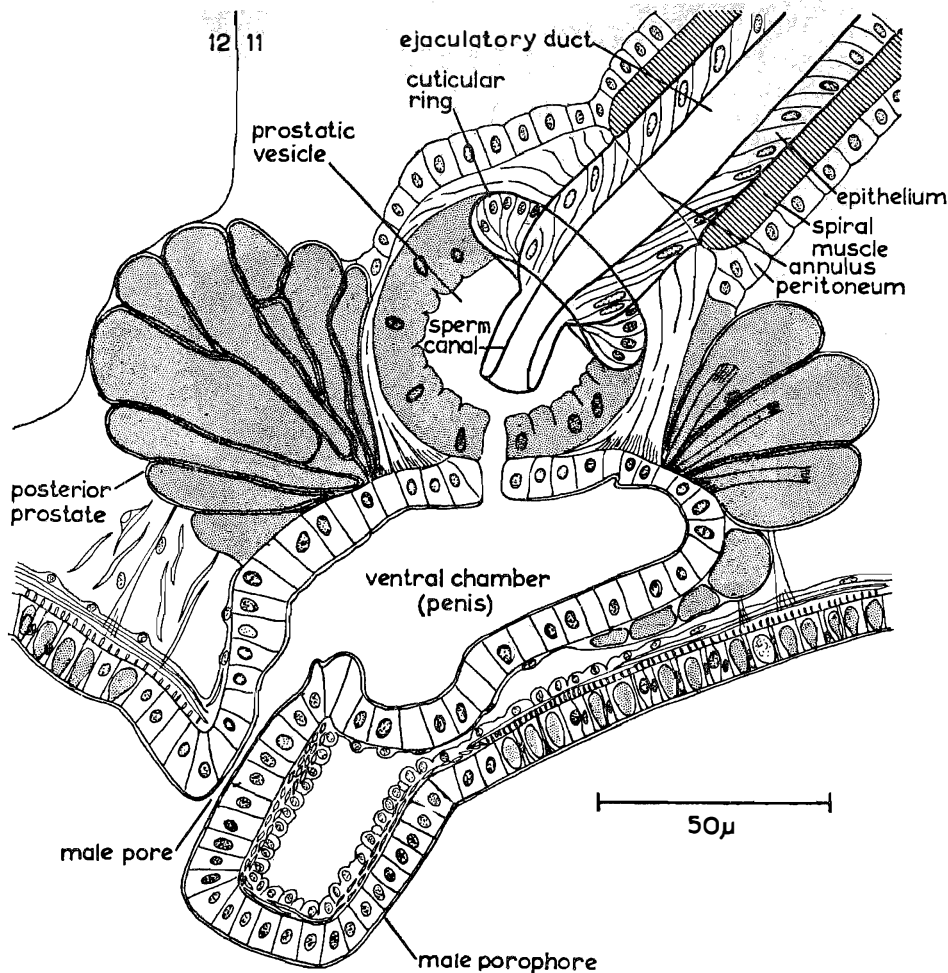
FIG. 6.—Penial apparatus of a paratype. Slightly diagrammatic reconstruction from several longitudinal sections.

Male genital system (Figs. 3, 5, 6, 9). Testes very large lobed masses in segment 10 arising from the junction of septum 9/10 and the ventral body wall. Sperm funnels large, not convoluted, with long cilia, on the posterior wall of 10. The male duct rises to the anterodorsal region of segment 11, traverses the length of the segment three times, opening to the exterior (in terms of internal septation) via a terminal bursa near septum 11/12. The three longitudinal traverses of segment 11 correspond with three main morphological regions of each male duct which are as follows:

(1) the *vas deferens:* a tortuous portion, running posteriorly the length of the segment, which consists of a single layer of ciliated epithelium and appears internally annulated because of the form and regular arrangement of its cells.

(2) the *atrium* (in conventional terminology) which consists of an anteriorly running thin-walled, only slightly bent section composed of a single layer of low, poorly defined, unciliated cells which are longer than high and surround an irregular lumen which is generally somewhat wider than that of the vas deferens. An elongated, tortuous, lobed prostate passes from the anterior end of the segment to the junction

of the vas deferens and atrium, being supported between and closely adpressed to the two sections. It sends minute ductules into the atrium at intervals along the length of the latter. These ductules appear composite, and it is probable that each prostate cell contributes secretion directly to the atrium as in *Monopylephorus aucklandicus* Benham. The deferent ducts differ markedly from those of *Monopylephorus*, however. The atrium connects with section (3) by a slender non-muscular tubular portion which conventionally, and it appears inappropriately, would be termed the ejaculatory duct.

(3) the *penis* and *penis-sheath* (conventional terminology): a wide, muscular, sigmoid portion running from the anterior to the posterior limit of segment 11. This region is here termed the *ejaculatory duct*. The walls of the ejaculatory duct consist of three layers: a high external peritoneum; an internal unciliated columnar epithelium with basal nuclei; and a thick intermediate layer of muscle fibres which are wound in a spiral around the internal epithelium. In cross-section each muscle fibre appears narrowly wedge-shaped with its narrow edge applied to the internal epithelium and its outer, wider edge in contact with the peritoneum. Each radial intercellular boundary of the peritoneum coincides with the centre of the edge of a muscle fibre. The fibres are transversely striated. The internal and external surfaces of the internal lining epithelium of approximately the ectal third of the ejaculatory duct are heavily cuticularized. As shown in Figures 6 and 9, the inner and outer cuticular layers are confluent at the ectal end of the ejaculatory duct and form a narrow spout which projects into the dorsal of two chambers which comprise the terminal bursa. The formative cells of the spout are no longer present. This spout appears to be the equivalent of the penis stylet of turbellarian platyhelminthes. It is here termed the sperm canal. The rounded terminal end of the cuticularized ejaculatory duct is encircled by and fused with a wide, hollow, cuticular ring in which formative cells are visible. The muscular sheath of the duct ends at a line (Fig. 6, annulus) encircling the duct shortly ental to this cuticular ring. From this annulus originate muscle fibres which ensheath, and insert on, the dorsal chamber of the terminal bursa. The fibres pass obliquely on to the bursa, those above and below the terminal portion of the duct being mutually at right angles; the spiral arrangement of the musculature ental to the annulus is thus also evident in the fibres ensheathing the bursa. At the ental end of the ejaculatory duct a similar, though less evident annulus terminates the muscular sheath and is the origin of spirally orientated fibres which extend beyond the limits of the duct and insert on neighbouring structures.

The male orifice opens into the capacious ventral chambers of the terminal bursa. The walls of this chamber consist of a single layer of large epithelial cells and a low external peritoneum. An interruption in the roof of the chamber places it in communication with the spherical dorsal chamber (Fig. 6). The dorsal chamber is lined by an unciliated cuboidal epithelium the cells of which contain numerous eosinophil granules. This epithelium is surrounded by musculature from the ejaculatory duct and partially by high peritoneum continuous with that of the latter. Most of the bursa is invested by lobular masses of prostate cells with eosinophil contents similar to those of the epithelium of the dorsal chamber which they presumably supply. These prostatic masses may be termed the posterior prostates, and the dorsal chamber of the terminal bursa is to be regarded as a prostatic vesicle, a further analogy with turbellarian morphology.

The following functions of the male apparatus are here postulated and have largely determined the terminology employed in the present account. Section (2) of the male duct, which is clearly the homologue of the region termed the atrium in *Limnodrilus*-systematics, probably functions as a sperm reservoir as its flaccid, unciliated walls and relatively wide lumen suggests, the secretion of the prostate probably serving to nourish the stored sperm. The term seminal reservoir was used by Moore (1905) for the "atrium" of *Limnodrilus hoffmeisteri* (=*L. subsalsus* s. Moore) but unfortunately was not adopted by subsequent authors. The term atrium has been
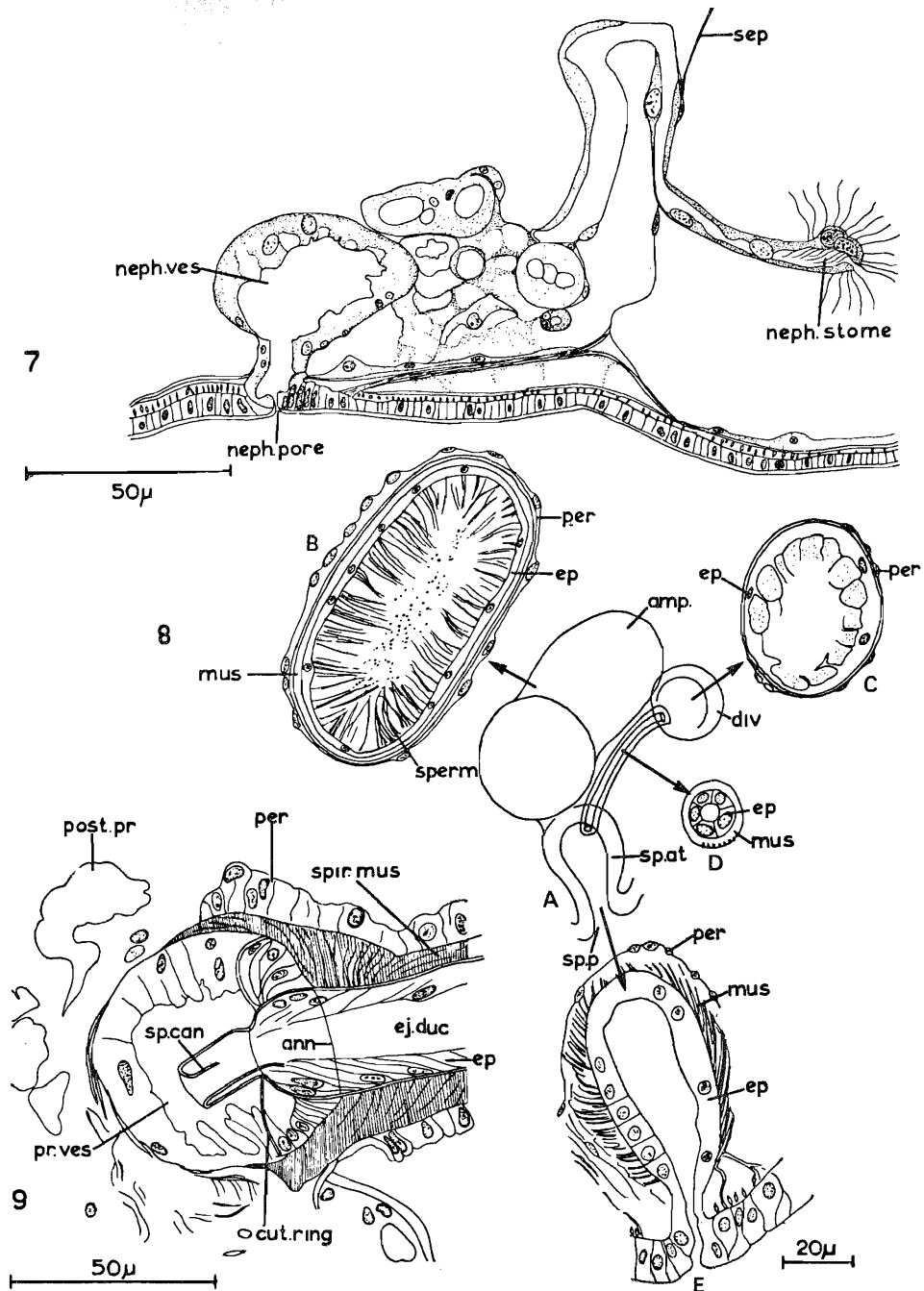
FIG. 7.—Longitudinal section through the ciliated funnel and terminal vesicle of a nephridium. FIG. 8.—*A*, outline of a spermatheca of a paratype; *B*, longitudinal section of the ampulla; *C*, section of the bulb of a diverticulum; *D*, transverse section of the stalk of the diverticulum; *E*, longitudinal section through the spermathecal atrium. FIG. 9.—Penial apparatus of a paratype showing histological detail.

Abbreviations: mus, musculature; neph. pore, nephropore; neph. stome, nephrostome; neph. ves, nephridial vesicle; sep, septum; sperm, spermatozoa (?). Other abbreviations as before.

used in oligochaete systematics to denote the terminal muscular section of the male duct, as in the Alluroididae, or the tubular prostate glands of megascolecoids, or the terminal region of the spermatheca in eudrilids in addition to the thin-walled expansion of the sperm ducts in the Tubificidae, despite the lack of homology between these structures.

The cuticular lining of portion (3) of the male duct of *Macquaridrilus* would conventionally be termed a penis sheath. This portion is termed the ejaculatory duct in the present account because it is doubtful that it can be extruded and because it has the appropriate musculature for sperm ejaculation. The anatomy of the terminal bursa (Fig. 6) suggests that the ventral chamber is eversible as a penis. Eversion would bring the dorsal chamber (prostatic vesicle) into the vicinity of the external pore of the evaginated penis. Contraction of the musculature investing the vesicle would have the effect of thrusting the spout-like cuticular sperm canal through the penial orifice while simultaneously ejecting the secretion of the posterior prostates from the vesicle into the apposed spermathecal pore of a concopulant. The form of the cuticular ring surrounding the ental end of the ejaculatory duct is consistent with its having the function of compressing the vesicle and acting as a point d'appui for contraction of the duct, while preventing prolapse. Muscles passing from the ventral chamber of the bursa to the ventral body wall which could bring about evagination of the penis are not strongly developed and it seems probable that increase in the hydrostatic pressure of the coelomic fluid in segment 11 would play an important part in erection of the penis. The spiral muscle of the ejaculatory duct if undergoing a wave of contraction in an ental-ectal direction, and acting on the thinly if at all cuticularized ental epithelium, would serve to eject sperm forcibly through the sperm canal at the tip of the penis. The spiral form of the musculature presumably allows a single sheath of fibres to subserve the functions of both circular and longitudinal muscles which occur in the ducts of many other animals. The function of the external male porophore may well be insertion in the spermathecal orifice of the concopulant before erection of the penis. After erection it would be forwardly deflected to give additional anchorage of the two animals. As the male pores are ventral and the spermathecal pores lateral it would appear, if the above views are correct, that both spermathecae are not simultaneously inseminated. If the entire ejaculatory duct were extruded as a penis simultaneous apposition of both male pores with both spermathecal pores would present little difficulty, but the above considerations militate against this. The author has recently described an alluroidid with males and spermathecal pores similarly disposed in which paired apposition is certainly impossible.

Female genital organs (Fig. 5). The ovaries are a pair of large compact masses each situated on the anterior septum of segment 11 on the back of the male funnel and immediately above the slender portion of the vas deferens which emerges from the septum. In the holotype a few oocytes lie ventral to the vas. In no specimens is any trace of ovarian funnels or oviducts detectable. The normal tubificid location for the funnels is the posterior wall of segment 11 with the ducts opening to the exterior in segment 12. One to a few large ova filled with yolk granules fill the body cavity dorsolaterally to the gut in segments 12 and 13; they do not form morulae. These eggs are invested in a thin membrane, with well-spaced nuclei, forming an unpaired middorsal ovisac. This is clearly a posterior evagination of septum 11/12 for, in longitudinal sections of two paratypes, it contains in segment 12, in addition to the eggs, portions of the vas deferens and of the prostate.

Spermathecae (Figs. 2, 8). A pair in segment 10; each with an oblong-ovoid or bulbous ampulla and a smaller terminal ectal chamber (spermathecal atrium) debouching at the lateral spermathecal pore. Unique in the Tubificidae is the presence of a spermathecal diverticulum. This consists of a spherical bulb which is about equal in width to the terminal chamber, into the ental region of which it opens via a long slender duct. The histology of the spermatheca is shown in Figure 8. The terminal

chamber (Fig. 8*E*) is lined by a cuboidal epithelium outside which is a thick muscular layer and an attenuated peritoneum. Layering of the ampulla is similar, but the peritoneum is higher, and (perhaps because of distension) the muscular layer is thinner, while the epithelial lining is lower and lacks recognizable cell boundaries. Adjacent to the internal epithelium of the ampulla, and orientated at right angles to it, are numerous almost straight filaments (Fig. 8*B*) which are presumably spermatozoa, though their stiff appearance and apparent absence of a distinct head causes some doubt as to their nature. The bulb of the diverticulum consists of a single layer of cells, which in surface view form a remarkably regular mosaic resembling a pavement epithelium (Fig. 8*C*). External to them is an attenuated peritoneum. The narrow lumen of the duct of the diverticulum is surrounded by an epithelium consisting of a few cells each of which is almost filled by a large nucleus. This epithelium is invested in a muscular sheath of approximately equal thickness; an external peritoneum is not apparent (Fig. 8*D*).

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