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The Invertebrate Fauna of New Zealand:

Nemertea
(Ribbon Worms)

Ray Gibson

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Frontispiece. Colour paintings of unnamed species of nemerteans recorded from New Zealand. **A-C** from Schmarda (1859), **D-H** from Morton and Miller (1968) (reproduced with the kind permission of John Morton). **A.** *Cerebratulus macrostomus* (Schmarda, 1859). **B.** *Ischyronemertes heterophthalma* (Schmarda, 1859). **C.** *Cerebratulus macrorrhochmus* (Schmarda, 1859). **D.** "*Cerebratulus*" sp. **E.** "Unnamed nemertine" from Goat Island Bay, Leigh (= *Noteonemertes novaezealandiae*). **F.** "*Tubulanus*" sp. **G.** "Unnamed species" from mussels in pools from the North Island west coast. **H.** "*Amphiporus*" sp. from rocky shores in Waitemata Harbour. (Head region enlarged in **E-H**.)

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ABSTRACT

Marine nemerteans collected from various locations around North Island during August and September 1992 have been studied and seven species recorded. Among these the most widespread, found at several of the collection sites, was the cratenemertid monostiliferous hoplonemertean recently described as *Nipponnemertes sanguinea* Riser, 1998. The remaining six species are all new to science. Two of these, belonging in previously established monostiliferous hoplonemertean genera, are *Amphiporus mortonmilleri* sp. nov. and *Correanemertes gordoni* sp. nov. The remaining four species each prove to belong in new genera; these are the palaeonemertean *Sundbergia albula* gen. et sp. nov. (the first palaeonemertean taxon described from New Zealand), and the monostiliferous hoplonemerteans *Heilogonemertes cooki* gen. et sp. nov., *Noteonemertes novaezealandiae* gen. et sp. nov., and *Parischyronemertes mathesonensis* gen. et sp. nov.

Twenty-eight species of nemerteans, including freshwater and terrestrial taxa, have previously been recorded from New Zealand and its off-lying islands. For the sake of completeness, brief details of these forms are also covered in the present monograph and a key to the known nemerteans reported from New Zealand, now totalling 34 species, is provided. These comprise 24 species from marine habitats, 4 from fresh water, 4 from land, and 2 from supralittoral zones, one of which also occurs in terrestrial conditions. There are strong grounds for considering both supralittoral species (*Acteonemertes bathamae*, *Notogaeanemertes folzae*), two of the fresh water (*Campbellonemertes johnsi*, *Potamonemertes percivali*), and all three of the terrestrial *Antiponemertes* species as endemic forms. Far too little is known about the zoogeographic distribution of marine species, however, for any accurate estimates of endemism to be made. It is nevertheless interesting that among the marine taxa, 10 genera and 20 species are so far known only from New Zealand. One of these (*Arhynchonemertes axi*) is probably endemic, others may be.

Remarkably, 9 out of a world-wide total of 34 land and freshwater nemertean species (including terrestrial records of *Acteonemertes*) have been recorded from New Zealand (27% of the total). No other country can boast such a high percentage of these ecologically specialised taxa. However, at least one of these species (*Antiponemertes allisonae*) is seriously endangered, if not extinct, as a consequence of habitat loss.

Keywords: Nemertea, Palaeonemertea, Heteronemertea, Hoplonemertea, new genera and species, classification, distribution, marine, freshwater and terrestrial fauna, New Zealand.

INTRODUCTION

The phylum Nemertea (Nemertina, Nemertini, or Rhynchocoela) represents a poorly studied group of invertebrates. More than 1100 species are currently recognised (Gibson 1995), although many of these are either inadequately described or known only from single and often incomplete specimens. Most nemertean species live in marine habitats, though a few are found in fresh water and some live in terrestrial situations.

The principal morphological characteristics of members of the phylum are a ciliated alimentary tract with separate mouth and anus, a closed blood system composed of distinct vessels or lacunae, and an eversible muscular proboscis housed, when retracted, in a fluid-filled tubular chamber, the rhynchocoel, extending posteriorly above the gut (Fig. 1). Nemerteans also possess a well-developed nervous system with paired lateral longitudinal nerve cords extending from lobed cerebral ganglia, a ciliated epidermis, and, in most forms, a protonephridial excretory system. Long regarded as acoelomate, unsegmented worms ancestrally related to platyhelminthes, nemerteans now appear to be more closely related to protostome coelomates than to any acoelomate group (Turbeville & Ruppert 1985; Turbeville *et al.* 1992), and several interstitial forms are known with pseudo-segmental 'septa' crossing their bodies between adjacent 'segments' (Berg 1985a; Norenburg 1988). Zrzavý *et al.* (1998), amongst others, refer to the affinities between nemerteans and entoprocts in forming a unified clade of protostomes known as the Trochozoa.

The earliest report of a nemertean from New Zealand was Quoy and Gaimard's (1833) short account of a species they named *Borlasia novae-zelandiae*, found in the Bay of Islands, North Island. Schmarda (1859) subsequently illustrated and briefly described three further species, whilst Hubrecht's (1887) report on the nemerteans collected during the voyage of the *Challenger* included five new species from New Zealand waters and also provided the first histological details of nemertean anatomy. Dendy's (1895a, b) accounts of *Geonemertes novae-zealandiae* are the first record of a New Zealand terrestrial nemertean, two further species, no longer regarded as valid (Table 1) being described by Darbishire (1909). Between 1910 and 1980, despite numerous references to New Zealand nemerteans occurring in the literature, only five new taxa were reported from New Zealand and its off-lying islands; these were two terrestrial species (Southgate 1954; Moore 1973), one upper littoral to fully terrestrial form (Pantin 1961a), and two species from freshwater habitats (Moore & Gibson 1972, 1973). Many references to New Zealand nemerteans from many locations around both Islands provide neither generic nor species names (e.g., Batham 1958; Freed 1963; Morgans 1967a, b; Larcombe 1968; Poore 1968; Knox 1969; Rainer 1969, 1981; Gilmore & Trent 1974; Knight 1974; Anderson *et al.* 1978; Knox & Fenwick 1981; Jones 1983; Hayward *et al.* 1984, 1985; Bradstock 1985; Fleet 1986), but some refer to unidentified species of the palaeonemertean genus *Tubulanus* (Morton & Miller 1968; Gunson

- apical organ
- cephalic glands
- cephalic vascular loop
- cerebral sensory organ
- cerebral ganglion
- anterolateral diverticulum
- lateral blood vessel
- intestinal lateral diverticulum
- anterior proboscis chamber
- rhynchocoel
- stylet bulb region of proboscis
- posterior proboscis chamber
- gonad
- lateral nerve cord
- proboscis retractor muscle
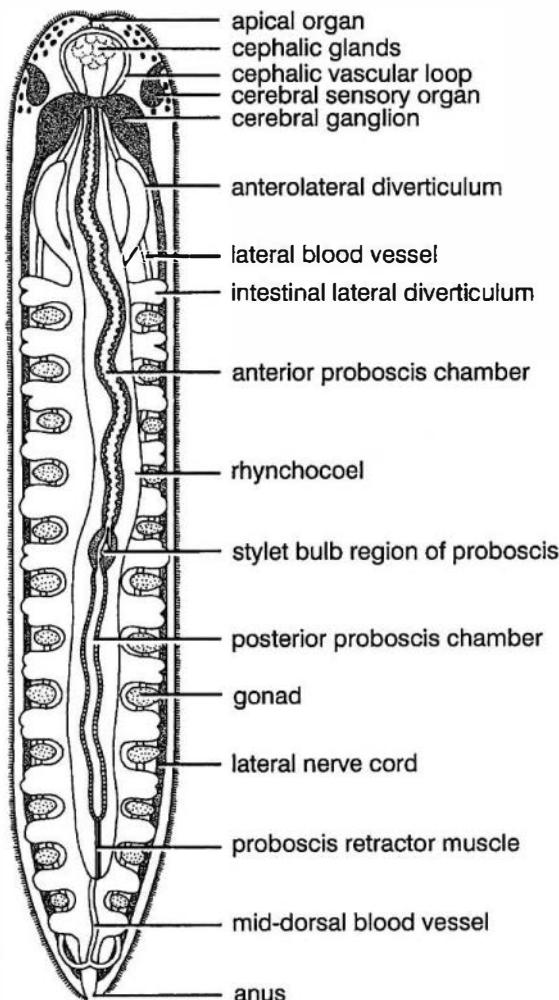- mid-dorsal blood vessel
- anus

Fig. 1. Schematic drawing to show some of the major anatomical features of nemerteans. The diagram is representative of a generalised monostiliferous hoplonemertean viewed from the dorsal surface. Modified from Gibson (1994).

Original name used	Habitat, current taxonomic status, and comments
ANOPLA	
Adenorhagas aurantiafrons Riser, 1990	Marine, currently valid.
Cerebratulus angusticeps Hubrecht, 1887	Marine, currently valid but inadequately described and of uncertain taxonomic affinities.
Cerebratulus macroren Hubrecht, 1887	Marine, currently valid but inadequately described; possibly synonymous with *Cerebratulus parkeri* Hubrecht, 1887 (Gibson 1995).
Cerebratulus parkeri Hubrecht, 1887	Marine, currently valid but inadequately described.
Craticulineus novaezealandiae Gibson, 1984	Marine, currently valid.
Eupolia australis Hubrecht, 1887	Marine, inadequately described but currently valid as *Baseodiscus australis* (Hubrecht, 1887).
Eupolia giardii Hubrecht, 1887	Marine, poorly described but currently valid as *Baseodiscus giardii* (Hubrecht, 1887).
Meckelia macrorrhochma Schmarda, 1859	Marine, inadequately described but currently valid as *Cerebratulus macrorrhochmus* (Schmarda, 1859).
Meckelia macrostoma Schmarda, 1859	Marine, inadequately described but currently valid as *Cerebratulus macrostomus* (Schmarda, 1859).
Micrura pleuropolia Cantell, 1994	Marine, currently valid.
Planaria sanguinea Rathke, 1799	Marine, currently valid as *Ramphogordius sanguineus* (Rathke, 1799).
Polia geniculata Delle Chiaje, 1828	Marine, currently valid as *Notospermus geniculatus* (Delle Chiaje, 1828).
Praealbonemertes whangateaunienses Cantell, 1993	Marine, currently valid.
ENOPLA	
Acteonemertes bathamae Pantin, 1961	Upper intertidal to fully terrestrial, currently valid.
Borlasia novae-zelandiae Quoy & Gaimard, 1833	Marine, inadequately described but currently valid as *Amphiporus novae-zelandiae* (Quoy & Gaimard, 1833); listed as a *nomen dubium* by Gibson & Crandall (1989).
Campbellonemertes johnsi Moore & Gibson, 1972	Freshwater, currently valid.
Geonemertes allisonae Moore, 1973	Terrestrial, currently valid as *Antiponemertes allisonae* (Moore, 1973).
Geonemertes caeca Darbishire, 1909	Terrestrial, an inadequately described species no longer recognised (Gibson, 1995).
Geonemertes dendyi Dakin, 1915	Terrestrial, currently valid as *Argonemertes dendyi* (Dakin, 1915).
Geonemertes novae-zealandiae Dendy, 1895	Terrestrial, currently valid as *Antiponemertes novaezealandiae* (Dendy, 1895).
Geonemertes pantini Southgate, 1954	Terrestrial, currently valid as *Antiponemertes pantini* (Southgate, 1954).
Geonemertes spirospermia Darbishire, 1909	Terrestrial, an inadequately described species no longer recognised (Gibson, 1995).
Meionemertepolygonimos Gibson, 1986	Marine, currently valid.
Nipponemertes sanguinea Riser, 1998	Marine, currently valid.

Original name used	Habitat, current taxonomic status, and comments
Notogaeanemertes folzae Riser, 1988	Supralittoral, currently valid.
Ommatoplea heterophthalma Schmarda, 1859	Marine, currently valid as *Ischyronemertes heterophthalma* (Schmarda, 1859), redescribed and transferred to this genus by Senz (1997).
Potamonemertes percivali Moore & Gibson, 1973	Freshwater, currently valid.
Stichostemma eilhardi Montgomery, 1894	Freshwater, currently valid as *Prostoma eilhardi* (Montgomery, 1894).
Tetrastemma graecensis Böhmig, 1892	Freshwater, currently valid as *Prostoma graecense* (Böhmig, 1892).
UNCERTAIN HIGHER TAXON	
Arhynchonemertes axi Riser, 1988	Marine, currently valid.

1983), the heteronemertean genera *Cerebratulus* (Powell 1947; Morton & Chapman 1968; Morton & Miller 1968; Heath & Dell 1971; Gordon & Ballantine 1976) or *Lineus* (Morton & Miller 1968; Doak 1971a, b; Morton [1981], or the monostiliferous hoplonemertean genera *Amphiporus* (Miller 1965; Miller & Batt 1973; Morton & Miller 1968; Morton [1981]; Gunson 1983), *Ototyphlonemertes* (Riser 1984), or *Zygonemertes* (Gibson et al. in press). Morton and Miller (1968) commented that nemerteans are often very common in both intertidal and shallow sublittoral habitats. In addition to their coloured illustrations of unidentified species of *Amphiporus*, *Cerebratulus*, and *Tubulanus*, and two forms for which no generic affiliations were indicated, Morton and Miller (1968) also recorded a dark brown *Lineus* species from a crevice habitat, and several other unnamed nemerteans from sandy beaches, mussel communities, or under boulders and stones on rocky shores. Colour photographs of several unidentified marine nemerteans are also given by Gibson et al. (in press). During recent years, several new taxa have been described from the region (Gibson 1984, 1986a; Riser 1988a,b, 1990, 1998a; Cantell 1993, 1994) and, including the fully terrestrial and freshwater forms, 28 valid species of nemerteans have previously been recorded from New Zealand and its offshore islands (Table 1). New Zealand clearly possesses a rich nemertean fauna that has yet largely to be investigated, Riser (1984: 242), for example, mentioning that, among the interstitial fauna, members of the hoplonemertean genus *Ototyphlonemertes* were "widely distributed, but never in adequate numbers to warrant the time required to distinguish species", and that cephalothricid palaeonemerteans "were present especially in very coarse substrates near rocks or against ledges, [although] small meiofaunal species belonging to the family were not encountered in the intertidal".

Compared with many invertebrate phyla, however, nemerteans remain one of the less well known groups, primarily because their identification and taxonomy depend upon studies of their internal morphology which require the use of time-consuming histological studies. Sublittoral species collected in dredge or grab samples are often damaged or incomplete, and many of the intertidal taxa fragment if handled too harshly; missing portions of the body such as the cephalic region or proboscis, both of which often contain features of taxonomic importance, frequently make certain identification impossible. It is hardly surprising, therefore, that so many references to 'nemertean sp.' appear in the literature, most zoologists evidently preferring to ignore the group completely or, at best, merely referring to them as unidentified nemerteans. All too frequently, even when generic or specific names have been given, their identification has been based entirely upon external features and comparatively few nemertean taxa can with certainty be identified without studies of their internal anatomy. As Riser (1989: 534) commented, for "almost half of the named species" of nemerteans there are few or no details of their internal morphology, many of the earlier genera and species being established entirely on the basis of their external features, before histological methods became routinely used in research on the group.

The present paper is primarily based upon a collection of nemerteans made around North Island by the author, Dr Alex Rogers, and Dr Steven de C. Cook, during August 1992 but, for the sake of completeness, also includes brief descriptions of those taxa previously reported from the region. Descriptions of long-established species provided in this article are not intended to be complete, nor should their generic affiliations or the arrangement of genera into families be taken as correct; there are still insufficient data on too many nemertean taxa for any useful, albeit necessary, revision of their systematic placement to be achieved.

Intensive field searches made during 1992 yielded several undescribed species, adding significantly to the number previously known from the region. There are thus now 34 nemertean species known from marine, terrestrial, or freshwater habitats of New Zealand.

MATERIALS AND METHODS

The numerous shores around North Island which were intensively searched for nemerteans during 1992 are indicated on Figure 2. Specimens were anaesthetised in 7.5% $MgCl_2$ and their external features examined before they were fixed in Bouin's solution. Examples of each species were subsequently sectioned at 6 μm in 56° C m.p. paraffin wax, and stained by the Mallory trichrome method. Type specimens of the new taxa are deposited in the NZOI collection at NIWA, Wellington.

Fig. 2. Beaches around North Island, New Zealand, visited during 1992 in the search for nemerteans. 1. Whangamumu Bay; 2. Taurikura, approach to Whangarei Harbour; 3. Leigh Cove, Whangateau Harbour, and Matheson Bay; 4. Whanga-paraoa; 5. Cheltenham Beach, Auckland, Devonport Beach, Torpedo Bay, Devonport, and Rangitoto Island; 6. Waitara Beach; 7. Pukerua Bay; 8. Lyall Bay, Wellington, and Greta Point, Wellington.
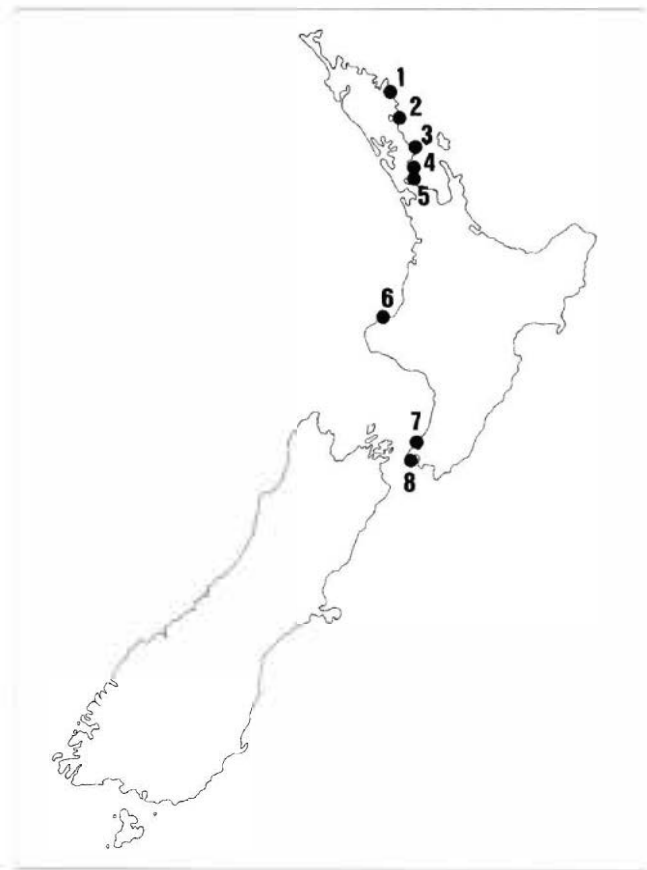
CLASSIFICATION OF THE NEMERTEA

Although the identification and classification of nemerteans has traditionally depended upon histological studies of their anatomy, the internal morphology of many species has either never been investigated or is inadequately described (Riser 1989). During the past 10–15 years the use of cladistic and molecular studies on nemerteans has led to several proposed systematic changes in the classification of the phylum (e.g., see Sundberg 1991; Sundberg & Hylbom 1994), at almost all taxonomic levels from species upwards and, beyond family level, there is at present no universally accepted classification for the phylum beyond the division into the two main classes, Anopla and Enopla. The classification of the higher taxonomic categories employed in the present monograph follows Sundberg's (1991) proposals, whereas the placement of genera into families accords with Gibson's (1985) scheme for the heteronemerteans and Gibson and Knight-Jones' (1995) arrangement for the remaining subclasses.

HIGHER CLASSIFICATION

Phylum NEMERTEA

Unsegmented, bilaterally symmetrical worms with a gut possessing separate mouth and anus, a blood vascular system, and (with the exception of the highly atypical New Zealand species *Arhynchonemertes axi*) an eversible muscular proboscis situated above the gut in an enclosed tubular chamber, the rhynchocoel.

Class ANOPLA (Fig. 3A)

Mouth below or posterior to the cerebral ganglia; central nervous system situated within the body wall (epidermis, dermis or body-wall musculature); proboscis not differentiated into three distinct regions and either not armed or provided with large numbers of rhabditoid epithelial barbs (the heteronemertean *Heteroenopleus enigmaticus* Wern, 1998, is exceptional in possessing a proboscis armed with two longitudinal rows of parastylets).
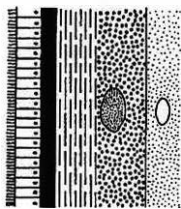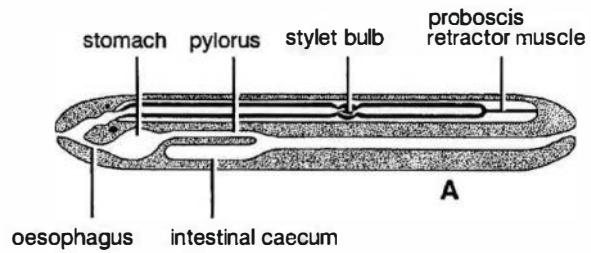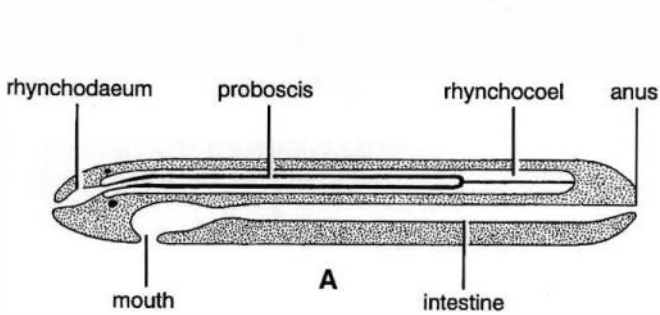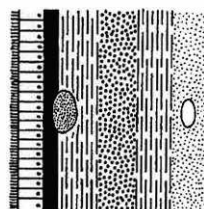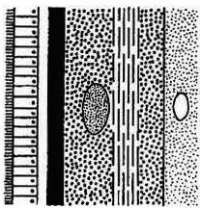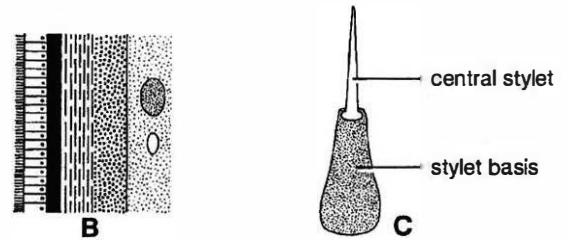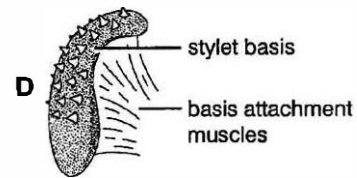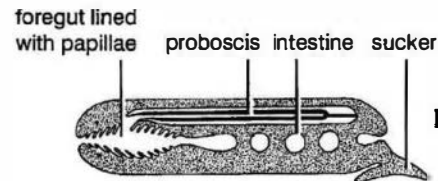
Fig. 3A. Schematic vertical longitudinal section to show the relationships between the gut and proboscis apparatus in the class Anopla. The smaller upper and larger lower solid black ovals at the rear of the rhynchodaeum represent the dorsal and ventral transverse cerebral commissures respectively. **B–D**. Diagrams to show the relationships of the epidermis, dermis, body-wall muscle layers, lateral nerve cords and lateral blood vessels in the anoplan subclasses Palaeonemertea (B, C) and Heteronemertea (D). All redrawn from Gibson (1972).

Fig. 4A. Schematic vertical longitudinal section to show the relationships between the gut and proboscis apparatus in a generalised monostiliferous hoplonemertean of the class Enopla. **B**. Diagram to show the relationships of the epidermis, dermis, body-wall muscle layers, lateral nerve cords and lateral blood vessels in the enoplan subclasses Hoplonemertea and Bdellonemertea. For explanation of symbols used see Fig. 3B–D. **C**. Drawing to show a single central stylet and its basis, characteristic of the proboscis armature in the hoplonemertean superorder Monostilifera. **D**. Drawing of a typical proboscis stylet apparatus of the enoplan superorder Polystilifera. **E**. Schematic vertical longitudinal section to show the relationships between the gut and proboscis in the enoplan subclass Bdellonemertea. All redrawn from Gibson (1972).

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Subclass PALAEONEMERTEA (Figs 3B, C)

Layers of body-wall musculature either two (outer circular, inner longitudinal) or three (outer circular, middle longitudinal, inner circular); dermis of hyaline connective tissue; central nervous system either in inner longitudinal muscle layer or external to body-wall muscles.

Subclass HETERONEMERTEA (Fig. 3D)

Body wall musculature primarily three-layered (outer longitudinal, middle circular, inner longitudinal), sometimes with additional inner circular and/or diagonal layers; dermis well developed and normally composed of fibrous connective tissues and gland cells; central nervous system situated between outer longitudinal and middle circular muscle layers.

Class ENOPLA (Fig. 4A)

Mouth anterior to cerebral ganglia; central nervous system internal to body-wall musculature, which is primarily two-layered (outer circular, inner longitudinal) though often with additional circular or diagonal layers; proboscis usually regionally differentiated and armed with one or more needle-like stylets mounted on a basis within middle region of proboscis.

Subclass HOPLONEMERTEA (Fig. 4B)

Proboscis armed with one or more stylets; intestine straight, mostly with paired lateral diverticula; no posterior ventral sucker.

Superorder MONOSTILIFERA (Fig. 4C)

Proboscis a single central stylet carried on a large cylindrical basis.

Superorder POLYSTILIFERA (Fig. 4D)

Proboscis armature a pad or shield bearing numerous small stylets.

Subclass BDELLONEMERTEA (Figs 4B, E)

Proboscis not armed with stylets; intestine sinuous and without lateral diverticula; foregut barrel-shaped and lined with longitudinal tracts of papillae; with posterior ventral sucker.

CLASSIFICATION OF NEW ZEALAND NEMERTEANS AND CHECKLIST OF SPECIES
(*new species and records described in this memoir)

Phylum **NEMERTEA**
Class **ANOPLA** Schultze, 1853
Subclass **PALAEONEMERTEA** Hubrecht, 1879

Family **HUBRECHTIDAE** Bürger, 1892
Sundbergia albula gen. et sp. nov.

Subclass **HETERONEMERTEA** Bürger, 1895

Family **CEREBRATULIDAE** Gibson, 1985
Adenorhagas aurantiafrons Riser, 1990
Cerebratulus angusticeps Hubrecht, 1887
Cerebratulus macroren Hubrecht, 1887
Cerebratulus macrorrhochmus (Schmarda, 1859)
Cerebratulus macrostomus (Schmarda, 1859)
Cerebratulus parkeri Hubrecht, 1887
Praealbonemertes whangataeaunienses Cantell, 1993

Family **LINEIDAE** McIntosh, 1873–74
Craticulineus novaezealandiae Gibson, 1984
Micrura pleuropolia Cantell, 1994
Notospermus geniculatus (Delle Chiaje, 1828)
Ramphogordius sanguineus (Rathke, 1799)

Family **VALENCINIIDAE** Hubrecht, 1879
Baseodiscus australis (Hubrecht, 1887)
Baseodiscus giardii (Hubrecht, 1887)

Class **ENOPLA** Schultze, 1853
Subclass **HOPLONEMERTEA** Hubrecht, 1879
Superorder **MONOSTILIFERA** Brinkmann, 1917

Family **AMPHIPORIDAE** McIntosh, 1873–74
Amphiporus mortonmilleri sp. nov.
Amphiporus novaezelandiae (Quoy & Gaimard, 1833)

Correanemertes gordoni sp. nov.
Ischyronemertes heterophthalma (Schmarda, 1859)
Noteonemertes novaezealandiae gen. et sp. nov.
Parischyronemertes mathesonensis gen. et sp. nov.

Family **CRATENEMERTIDAE** Friedrich, 1968
Nipponnemertes sanguinea Riser, 1998

Family **PLECTONEMERTIDAE** Gibson, 1994
Acteonemertes bathamae Pantin, 1961
Antiponemertes allisonae (Moore, 1973)
Antiponemertes novaezealandiae (Dendy, 1895)
Antiponemertes pantini (Southgate, 1954)
Argonemertes dendyi (Dakin, 1915)

Campbellonemertes johnsi Moore & Gibson, 1972
Potamonemertes percivali Moore & Gibson, 1973

Family **PROSORHOCHMIDAE** Burger, 1895
Heilogonemertes cooki gen. et sp. nov.
Notogaeanemertes folzae Riser, 1988

Family **TETRASTEMMATIDAE** Ehrenberg, 1828
Meionemertes polygonimos Gibson, 1986
Prostoma eilhardi (Montgomery, 1894)
Prostoma graecense (Böhmig, 1892)

UNCERTAIN HIGHER TAXON
Arhynchonemertes axi Riser, 1988

ABBREVIATIONS USED IN FIGURES

AC anterior caecum of intestine
AP anterior pouch of intestine

BC branch of foregut capillary blood network
BR brain lobes

CC ciliated cerebral canal
CF cephalic furrow
CG cephalic glands
CM circular muscle layer of body wall
CN circumferential neural ring of proboscis
CO cerebral sensory organ
CP ciliated cephalic epidermal pit
CV cephalic blood vessel

DC dorsal cerebral commissure
DE dermis
DG dorsal ganglionic lobe
DM diagonal muscle layer of body wall
DN dorsal nerve

EP epidermis
EX excretory tubule

FG foregut
FN foregut nerve

IC inner circular muscle layer
ICT inner connective tissue layer
ID intestinal lateral diverticulum
IL inner longitudinal muscle layer of body wall
IN intestine

LB bundle of longitudinal muscle fibres which forms part of the anteriorly divided longitudinal musculature of the body wall
LL lateral blood lacuna
LM longitudinal muscle layer of body wall
LN lateral nerve cord
LV lateral blood vessel

MV middorsal blood vessel

OC outer circular muscle layer
OCT outer connective tissue layer
OE oesophagus
OL outer longitudinal muscle layer of body wall
OV ovary
OV^1 immature ovum
OV^2 mature ovum

PB basophilic glands of proboscis epithelium

PC proboscis circular muscle layer
PE proboscis epithelium
PI proboscis inner lining
PIC proboscis inner circular muscle layer
PL proboscis longitudinal muscle layer
PN proboscis nerve
POC proboscis outer circular muscle layer
PP proboscis pore
PR proboscis
PY pyloric region of foregut

RC rhynchocoel
RD rhynchodaeum
RM retractor muscle of proboscis
RS rhynchodaeal circular muscle sphincter

SG subepidermal gland
SM submuscular gland
ST stomach
ST^1 stage 1 ovum
ST^3 stage 3 ovum

TS testis

VC ventral cerebral commissure
VG ventral ganglionic lobe

KEY TO THE SPECIES OF NEW ZEALAND NEMERTEANS

The following key is primarily intended for the field identification of living specimens, although for several of the New Zealand nemerteans there is no information on their appearance in life. Inadequately described taxa are indicated with an asterisk.

1   Found living in freshwater or terrestrial habitats ... 2
     Found living in marine or lower estuarine habitats   10

2   Freshwater species 3
     Terrestrial species 6

3   With 4–8, usually 6, eyes; adults typically coloured in shades of red, brown or orange, juveniles cream or pale yellowish; mostly up to 20–25 mm long, exceptionally to 35 mm 4
     Without eyes 5

4   With distinct, ciliated oesophagus; cephalic glands reaching back to brain; rhynchodaeal wall with longitudinal muscle layer *Prostoma graecense* (Böhmig, 1892)
     Oesophagus indistinct and unciliated; cephalic glands not reaching back to brain; rhynchodaeal wall without longitudinal muscle layer ....
           Prostoma eilhardi (Montgomery, 1894)

5   Up to about 30 mm long; white, with faint grey tinge to gut under higher magnification; readily fragments during collection ....
       Potamonemertes percivali Moore & Gibson, 1973
     Up to about 100 mm long, very slender; grey with single white middorsal stripe extending full length of body; does not readily fragment during collection ....
       Campbellonemertes johnsi Moore & Gibson, 1972

6   With 2-6 eyes 7
     With 20–30 eyes arranged in 4 groups; background colour cream marked with 2 brown dorsolateral stripes extending full body length ....
         Argonemertes dendyi (Dakin, 1915)

7   With 4-6 eyes 8
     With 2 eyes; body dorsally mottled in brown with clear longitudinal middorsal stripe above proboscis ....
         Antiponemertes allisonae (Moore, 1973)

8   With 4 eyes; general colour cream marked with 4 dark-brown longitudinal dorsal stripes, outer pair more slender than inner pair ....
       Antiponemertes novaezealandiae (Dendy, 1895)
     With 4-6 eyes; dorsal body surface either with 2 longitudinal stripes or bands of mottling, or uniformly coloured, no stripes or bands 9

9   With 4 eyes; general colour cream marked with 2 rich brown longitudinal dorsal stripes which are sometimes divided for all or part of their length; in some specimens the longitudinal stripes appearing as wide, mottled bands .... *Antiponemertes pantini* (Southgate, 1954)
     With 4, occasionally 6, eyes; either uniformly light grey overall without stripes or cream dorsally with 2 broad longitudinal chocolate-brown stripes separated by narrow pale line, ventrally pale (N.B., this species also lives in upper intertidal regions) ....
         Acteonemertes bathamae Pantin, 1961

10   With striking colour pattern, typically bright pea-green to dark green dorsally, sometimes dark brown or black, marked with 30 or more narrow white, cream or yellowish variably or regularly spaced transverse bands; anterior band on head forms forward-pointing shallow V-shape; with 40–50 eyes along each lateral margin of head .. *Notospermus geniculatus* (Delle Chiaje, 1828)
     Either without obvious colour pattern, or if with colour pattern, not as above 11

11   Body flattened, strap-like, dorsal colour red with median longitudinal white stripe extending full length, ventral surface pale red; pointed head with pair of eyes near its tip, then farther back on each side 7 eyes forming a longitudinal line followed by 3 eyes arranged in a triangle ..
     Ischyronemertes heterophthalma (Schmarda, 1859)
     Not as above 12

12   With obvious eyes on head in living specimens ... 13
     Without eyes or, if eyes present, not obvious in living specimens 21

13   With 4 large distinct eyes on head, which is distinctly shark-like in lateral view; anterior third of body dorsally pale brown, ventrally whitish-brown, posterior two-thirds of body pale or whitish ....
         Correanemertes gordoni sp. nov.
     With more than 4 eyes, arranged in lateral rows on either side of head or in distinct groups 14

14   Eyes arranged in 3 or 4 distinct groups on head .. 15
     Eyes arranged in single or double rows on either side of head 19

15   Eyes in 3 groups on head, single anterior group of 8–10 or more large eyes forming a forward-pointing V-shape, two posterior groups, each of 3 or 4 smaller eyes, above anterior margins of brain lobes; head bluntly pointed and darker brown than succeeding anterior third of body, which is reddish brown; remainder of body whitish with irregular, dark-grey transverse streaks or patches; ventral surface with pale longitudinal median region below greyish gut ... *Heilogonemertes cooki* gen. et sp. nov.
     Eyes in 4 distinct groups on head 16

16 General body colour whitish, pinkish or pale orange 17
Body dorsally dark brownish-purple, ventrally pale grey, dorsal and ventral coloration either sharply delimited or fading into each other; dorsal surface usually with slender, darker longitudinal median streak extending along body; head shaped almost like an equilateral triangle; head with 4 groups of 6–10 or more eyes in each group . . . . *Noteonemertes novaezealandiae* gen. et sp. nov.

17 Head without obvious oblique cephalic furrows, colour whitish or very pale orange, occasionally with a slight pinkish tinge 18
Dorsoventrally flattened head with two pairs of oblique dorsal cephalic furrows, anterior pair extending to ventral surface and meeting to form forward-pointing V-shape, posterior pair meeting in midline dorsally to form backward-pointing V-shape; 2 groups of 4–6 eyes close to anterolateral margin of head in front of anterior cephalic furrows, 2 groups of about 8 eyes dorsolaterally about midway between the 2 pairs of furrows; general body colour pale pink . . . . *Amphiporus mortonmilleri* sp. nov.

18 Anterior and posterior groups of eyes on head not widely separated, each anterior group with 5–9 eyes, each posterior group with 3–6 smaller eyes situated close in front of brain; overall colour creamy-white with a slight pinkish tinge, body anteriorly suffused with tan which varies in intensity between individuals . . . . *Notogaeanemertes folzae* Riser, 1988
Anterior and posterior groups of eyes on head widely separated, each group containing 4 or 5 eyes; general colour translucent white to very pale orange, but with distinct pale blue-grey hue on upper surface of head and on either side of gut in anterior half of body . . . . *Parischyronemertes mathesonensis* gen. et sp. nov.

19 Eyes in a single regular row on each side of the head 20
Eyes on each side of head arranged into 1 or 2 more or less irregular rows of about 20 eyes; body shape very variable, short, fat and wide or slender, elongate and flattened; general colour vivid orange to pale yellowish, dorsal surface usually somewhat darker than ventral; bright red blood cells make lateral blood vessels very obvious, especially when viewed ventrally, on either side of intestine . . . *Nipponnemertes sanguinea* Riser, 1998

20 Colour overall chalk white; body cigar-shaped, tapered at both ends; with 2–4 eyes on each side of head arranged in single row; head without cephalic furrows . . . . *Arhynchonemertes axi* Riser, 1988
Colour varying with age and size, transparent white or cream with reddish brain region in juveniles to overall reddish-brown, greenish-brown, brownish-black, or dull mid-brown, posterior and ventral surface usually rather paler, intestinal region often marked by variable number of widely spaced pale annulations; body long and slender; with 3–7 eyes on each side of head in dorsal wall of lateral cephalic furrows . . . . *Ramphogordius sanguineus* (Rathke, 1799)

21 Head with distinct lateral horizontal cephalic furrow on each side 22
Head without lateral horizontal cephalic furrows 30

22 Head distinctly pointed or sharply tapering 23
Head bluntly rounded 25

23 Body with a solid consistency, only slightly flattened dorsoventrally; ventral mouth forming a gaping, longitudinal slit; overall colour greenish with a dark-blue tinge . . . . *Cerebratulus macrostomus* (Schmarda, 1859)
Body distinctly dorsoventrally flattened, at least in intestinal region 24

24 Lateral body margins acute, sharp; ventral mouth distinct and moderately large; overall colour dull yellow with a darker middorsal longitudinal stripe . . . . *Cerebratulus angusticeps* Hubrecht, 1887
Lateral body margins rounded; ventral mouth small and slit-like; overall colour olive-brown, inner surface of cephalic furrows blood red . . . . *Cerebratulus macrorrhochmus* (Schmarda, 1859)

25 Posterior end of body terminating in slender but distinct caudal cirrus 26
Posterior end of body without caudal cirrus, or cirrus present but minute, papilla-like and easily missed in living specimens 27

26 Overall colour dark brown, lateral body margins and tip of head pale grey; a yellowish-white anterior patch present in each lateral cephalic furrow; on either side of the head up to 5 structures which resemble eyes but completely lack pigment . . . . *Micrura pleuropolia* Cantell, 1994
Overall colour variable, typically white in anterior half, pink to pinkish-brown posteriorly, larger examples often dorsally and ventrally streaked with green in posterior regions; posterior region may vary in colour depending upon gut contents . . . . *Praealbonemertes whangateaunienses* Cantell, 1993

27 General body colour dull yellowish, cream-brown or brownish, sometimes with darker brown tinge on upper surface of the head; lateral horizontal cephalic furrows short; tip of head without vivid orange patch . . . 28
Colour varying from overall chalk-white to white with a middorsal longitudinal orange stripe in individuals more than 10 mm long, to overall dirty orange dorsally in examples above 18 mm in length, but in all forms tip of head marked by vivid orange cap or patch; caudal cirrus minute and papilla-like . . . . *Adenorhagas aurantiafrons* Riser, 1990

28 Appearance in life not known; preserved colour dull brown to pale creamish-brown overall; ventral mouth small, indistinct . . . . *Craticulineus novaezealandiae* Gibson, 1984
Overall colour dull yellowish, tinged brown on dorsal surface of head 29

29 Efferent excretory duct leads from extreme posterior of main collecting tubule; single nephridiopore on each side of body ..... *Cerebratulus macroren* Hubrecht, 1887
Excretory system with 2 efferent ducts leading from mid-region of each collecting tubule; 2 nephridiopores on each side of body ... *Cerebratulus parkeri* Hubrecht, 1887

30 General colour translucent or opaque white to off-white or very pale brown 31
Overall colour reddish-brown dorsally, somewhat darker in midline, yellowish ventrally; head heart-shaped, distinctly marked off from body by constriction, from rear of which extend several short streaks of intense reddish-brown colour; lateral blood vessels and intestinal diverticula visible through body surface ....
.. *Amphiporus novaezelandiae* (Quoy & Gaimard, 1833)

31 Body stout, width 10–15% of length 32

Body long and very slender, width only 1 or 2% of length; overall colour translucent white; head diamond-shaped, with more or less distinct median longitudinal dorsal ridge or lobe, on either side of which is an elongate white patch .... *Sundbergia albula* gen. et sp. nov.

32 Mouth and proboscis pore separate, mouth ventral, situated close behind head 33
Mouth and proboscis pore united; appearance in life unknown; preserved colour off-white to very pale brown .... *Meionemertes polygonimos* Gibson, 1986

33 Anterior tip of head with short transverse and vertical furrows in form of cross, in centre of which is proboscis pore .... *Baseodiscus giardii* (Hubrecht, 1887)
Anterior tip of head with neither transverse nor vertical furrows .... *Baseodiscus australis* (Hubrecht, 1887)

DESCRIPTION OF THE SPECIES

Class ANOPLA Schultze, 1853
Subclass PALAEONEMERTEA Hubrecht, 1879
Family **HUBRECHTIDAE** Bürger, 1892

Sundbergia gen. nov.

DIAGNOSIS: A single pair of short, shallow lateral horizontal cephalic furrows; body-wall musculature mainly consisting of outer circular and inner longitudinal layers, but in posterior intestinal region with additional outer longitudinal coat external to circular musculature; rhynchocoel extending almost to posterior end of body; proboscis short, regionally differentiated and asymmetrically developed, anterior region with outer circular and inner longitudinal muscle layers, posterior region with additional inner circular layer; cerebral ganglia and anterior regions of lateral nerve cords situated between epidermal basement membrane and body wall circular muscle layer, but in posterior intestinal region lateral nerve cords located between circular and outer longitudinal muscle layers; foregut with longitudinal somatic musculature; post-cerebral blood system with single middorsal and 2 lateral vessels, lateral vessels developed into vascular plexus around posterior foregut, middorsal vessel penetrating rhynchocoel floor; caudal cirrus absent; head with small, dorsal ciliated (sensory?) pits; cephalic glands present, situated in cephalic blood lacunae; eyes absent; excretory system absent; cerebral sensory organs present, post-cerebral; sexes presumed separate.

TYPE SPECIES: *Sundbergia albula* sp. nov.

ETYMOLOGY: The genus is named in honour of Professor Per Sundberg, Göteborg University, Sweden, as a tribute to his studies on palaeonemertean phylogeny. The specific epithet comes from the Latin *albulus* (= whitish) and refers to the translucent white colour of the species in life.

Sundbergia albula sp. nov.   (Figs 5–10)

TYPE SPECIMEN: Holotype, immature female, complete set of transverse sections, 82 slides, NIWA H-772, deposited in Wellington.

TYPE LOCALITY: Torpedo Bay, Auckland (Fig. 5), under rock buried in black, sulphide-rich, muddy sand, lower midshore, found by Dr Alex Rogers, 22 August 1992.

DESCRIPTION: *External features:* A long, very slender species, about 0.5 mm in maximum width but varying in length from 20–30 mm up to 50–60 mm depending upon degree of contraction or extension. Diamond-shaped head with more or less distinct longitudinal median dorsal lobe, an elongate opaque white patch on either side (Fig. 6). No eyes. Tail bluntly rounded. Overall colour translucent white. When disturbed, coiling spirally into tight knot.
Body wall, musculature and parenchyma: Near tip of head, epidermis dorsally ~ 30 μm tall, whereas ventrally no more than about 5 μm deep. Basement membrane thin but distinct; below this a tissue layer, at most 10–12 μm thick, corresponding with what Hylbom (1957: 559) described in *Hubrechtella dubia* Bergendal,
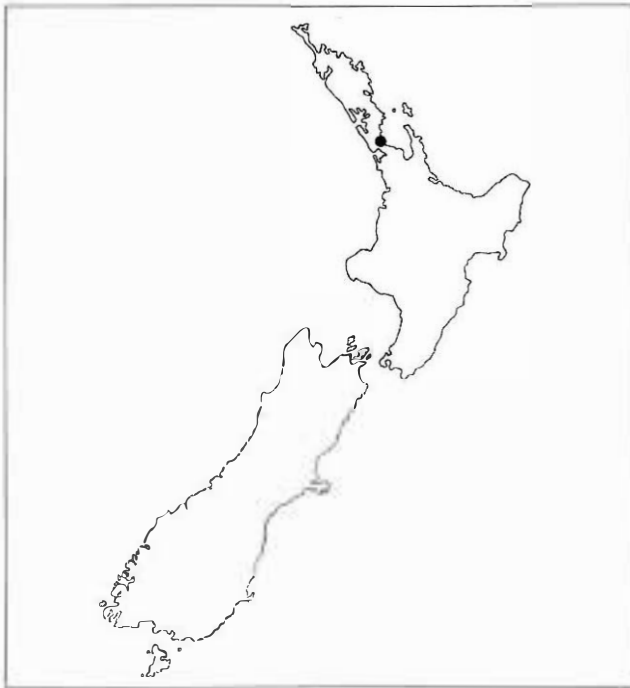
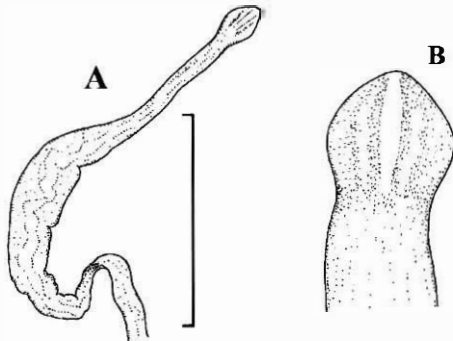**Fig. 5.** *Sundbergia albula* gen. et sp. nov. Recorded distribution in New Zealand.

Fig. 6. *Sundbergia albula* gen. et sp. nov. **A.** Drawing of anterior region of body, based on sketches made of the living specimen. **B.** Enlargement of the head viewed from the dorsal aspect. Scale bar = 2 mm (refers to A only).

1902, as "a kind of nervous layer"; in present specimen this layer dorsally and ventrally separated from epidermis by basement membrane, but laterally the 2 tissues seeming to merge and no trace of basement membrane distinguishable. Whether or not neural elements contribute to the layer could not be determined. In brain region dorsal epidermis 75-80 μm tall, this zone appearing to correspond with longitudinal cephalic ridge visible in living animal, but ventrally no more than 25-30 μm deep. The forward "nervous layer" in the head not visible in brain region. Behind brain, epidermis becoming much more uniformly developed on all sides of body, reaching a height of 50–60 μm in foregut region but becoming gradually reduced to only some 12–15 μm in posterior region of body. Just in front of mouth a dense proximal zone of strongly acidophilic and coarsely granular gland cells appearing in dorsal half of body, these appearing to represent Type 3 glands described by Hylbom (1957: 558–559). Behind mouth the glands spreading to all body margins, filling proximal half of epidermis and comprising the dominant gland type in this region, although scattered Type 1 basophils distinguishable between them. Towards rear of foregut, Type 3 glands disappearing dorsally but extending back a short distance ventrally before disappearing from there too. These glands thus effectively form a 'band' obliquely encircling body in foregut region. Hylbom's Type 2 glands dominating epidermis in intestinal regions of body, though Type 5 can also be distinguished in smaller numbers; both gland types reduced in density more posteriorly.

Musculature in head weakly developed, although both outer circular and inner longitudinal layers distinguishable. Both layers better developed dorsally and respectively about 3 μm and 15–20 μm thick. Circular musculature ventrally reduced to only 1 or 2 fibre thicknesses and not always evident. In foregut region outer circular and inner longitudinal muscle layers about 6–8 μm and 15–30 μm thick respectively. Also a thin but distinct somatic layer of longitudinal muscle fibres, mostly 3-4 μm thick, encircling foregut. This somatic layer extending back into anterior region of the intestine, but progressively reduced to form an increasingly narrower longitudinal plate between rhynchocoel and dorsal gut wall; the plate reaching some distance back into intestinal region. In posterior half of body are 3 muscle layers (Fig. 7), an outer longitudinal muscle coat up to about 30 μm thick outside circular musculature; longitudinal nerve cords in this part of body run in this layer rather than immediately below epidermis. Subepidermal gland cells scattered between muscle fibres of this outer longitudinal layer. Among the 4 known hubrechtid genera, an outer longitudinal muscle layer has been reported only in *Tetramys* (Iwata 1957) but this monospecific taxon also has an inner circular musculature not found in the present specimen. No evidence of the so-called 'zigzag and longitudinal' differentiation described for some species of *Hubrechtella* distinguishable in either of the 2 longitudinal muscle layers of the present specimen, or evidence of dorsoventral muscle bundles in the intestinal region.

Parenchymatous connective tissues exceedingly sparingly developed in all parts of body and mainly restricted to slender layers investing the various body organs.
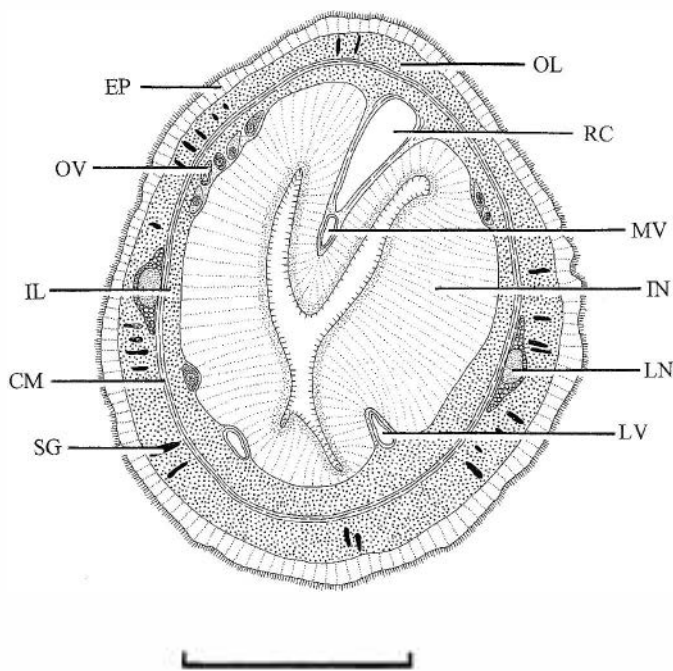
Fig. 7. *Sundbergia albula* gen. et sp. nov. Camera lucida drawing through the posterior intestinal region to show the organisation of various body structures. Scale bar = 250 μm.

Proboscis apparatus: Proboscis pore opening ventrally and just subterminally into large rhynchodaeum whose anterior epithelium, up to 15 μm thick, consists predominantly of pale-staining basophilic tissues identical in appearance to glandular masses in cephalic blood lacunae. Farther back, however, rhynchodaeal wall is only about 5–6 μm thick, unciliated, and without glands.

Proboscis insertion situated in anterior brain region. Rhynchocoel extending almost to posterior tip of body; among other hubrechtids a long rhynchocoel found only in *Tetramys* (Iwata 1957). Wall of rhynchocoel containing separate circular- and longitudinal-muscle layers, the former in places 15–20 μm or more thick, particularly towards portion where retractor muscle attached to wall. In foregut and anterior intestinal regions the rhynchocoel about 50% or more of body width, but more posteriorly becoming greatly reduced to less than 5% of body diameter, and its walls very much thinner. A similar situation was described for *Tetramys* by Iwata (1957).

Proboscis (Fig. 8) regionally differentiated, much shorter than rhynchocoel, its retractor muscle being attached about one-third along length of rhynchocoel to its ventral margin. Anterior portion (Figs 8A, B), extending back to anterior intestinal region when retracted, up to some 210–250 μm in overall diameter, comprising a glandular epithelium 30–80 μm tall, a

very thin outer circular-muscle layer, an inner longitudinal-muscle coat 10-12 μm in maximum thickness, and a flattened inner lining. Circular-muscle layer not distinguishable in short, extreme anterior part of proboscis (Fig. 8A). Throughout most of anterior region, epithelium developed asymmetrically (Fig. 8B), on one side forming longitudinal 'ridge' with somewhat mushroom-like shape in transverse section, whilst
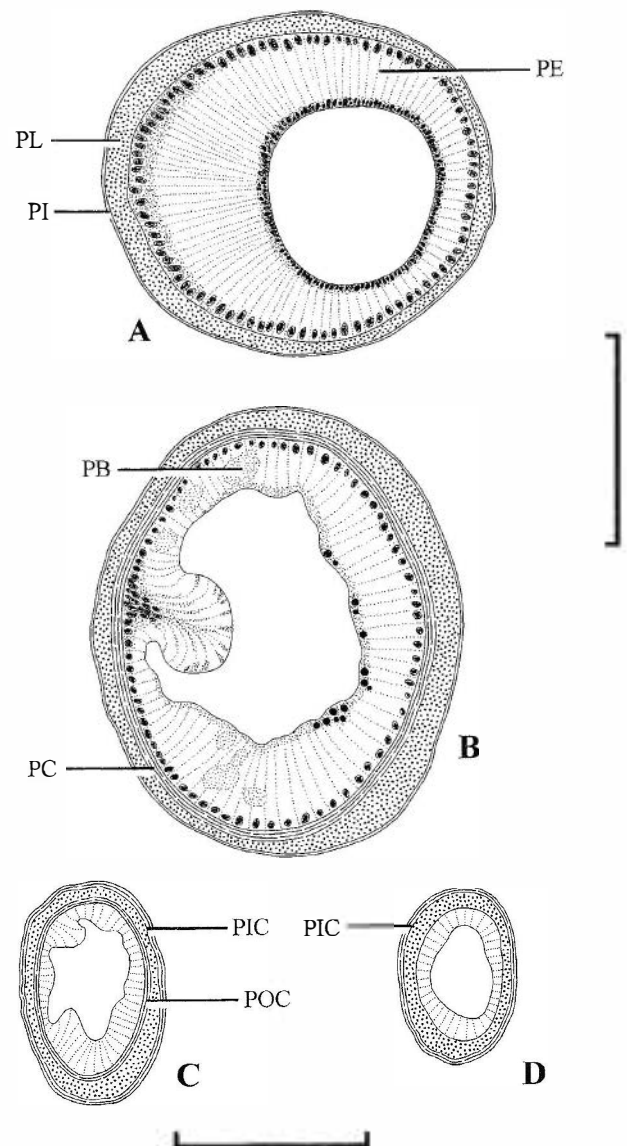

Fig. 8. *Sundbergia albula* gen. et sp. nov. Camera lucida drawings to show the organisation of the proboscis in its different regions. **A**, **B** = the anterior region, the most anterior being shown in A, the major part of the anterior region being represented by B; **C** = posterior portion of the proboscis with three muscle layers; **D** = extreme posterior portion of the proboscis, with no outer circular muscle layer. Scale bars: A, B = 100 μm, C, D = 200 μm.

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on opposite side distal epithelial zone packed with acidophilic globules. In brain region no basophilic glands distinguishable in proboscis epithelium, but as stomach region is approached large basophilic glands filled with homogeneous cytoplasm mainly disposed on either side and at right angles to longitudinal ridge (Fig. 8B). In this part of proboscis, longitudinal-muscle layer also asymmetrically developed, being some 15 μm on side opposite ridge, but only about half this thickness below ridge. Asymmetrical proboscis epithelial development, though unusual, is not unknown in nemerteans and has been illustrated, for example, in species of heteronemerteans from Australia by Gibson (1978). Farther back, in intestinal region of body, a third muscle layer, an inner circular zone about 3 μm thick, begins to appear between innermost lining layer and longitudinal musculature (Fig. 8C). This inner circular-muscle layer appears to originate from fibres that emerge from outer coat and pass through longitudinal-muscle layer, as outer circular-muscle zone disappears more posteriorly, commensurate with proboscis epithelium losing its asymmetrical development (Fig. 8D). Posterior portion of proboscis with overall diameter of about 135–165 μm, with glandular epithelium 30-45 μm tall in which at least 3 types of cells distinguishable—an outer longitudinal-muscle layer no more than 15–16 μm thick, a thin inner circular coat, and an internal lining layer. Towards posterior end, proboscis narrows even more and longitudinal muscle coat leads directly into proboscis retractor muscle.

In several parts of proboscis, hints of what might be neural tissues are distinguishable between epithelial basement and outermost muscle layer, but no definite neural supply discernible.

Alimentary canal: Ventral mouth appearing about 80 μm behind end of cerebral sensory organs, forming a narrow median slit, 100–110 μm long, leading into buccal cavity lined by richly glandular epithelium up to 45 μm or more tall in which basophilic glands predominate. Buccal epithelium bulging anteriorly in front of mouth, reaching almost to cerebral organs, to displace ventrolateral margins of lateral blood lacunae. Anterior portion of stomach forming wide, dorsoventrally compressed curved tube lying below rhynchocoel, its dorsal epithelium only about 15 μm thick in contrast to that of ventral side which is 45 μm or more deep. At first, somatic longitudinal-muscle fibres ventrally abutting directly against body-wall longitudinal muscles but, more posteriorly, lateral blood lacunae extending ventrally below stomach, the latter gradually becoming narrower and more slender. Posterior portion of stomach epithelium almost completely lacking basophilic gland cells and ventrally progressively reduced to maximum thickness of only

about 20–25 μm. Relative to total length of alimentary tract, foregut comprising only very small proportion, its overall length only about 1 mm (i.e., at most 5% of total body length).

At its rear, foregut merging imperceptibly into anterior portion of intestine, recognisable by its longer and more sparsely distributed cilia. First part of intestine comprising a simple, dorsoventrally compressed tubular canal with no lateral diverticula, but farther back shallow lateral pouches beginning to appear, curving dorsolaterally around sides of rhynchocoel. Somatic muscle layer of foregut continuing back to enclose tubular part of intestine, but, as muscles become increasingly restricted to form median longitudinal plate, intestine widens and begins to develop diverticula. For most of its length intestine with shallow, unbranched but densely crowded lateral diverticula, gastrodermal thickness varying considerably but maximally about 60 μm. Anus opening almost at posterior tip of body.

Blood system: In tip of head, in front of proboscis pore, a single large, thin-walled median blood lacuna (Fig. 9A) divided into 2 spacious lateral cephalic lacunae by dorsoventral extension of rhynchodaeum at proboscis pore (Fig. 9B). Behind proboscis pore the 2 lacunae continuing posteriorly (Fig. 9C), gradually narrowing towards beginning of brain lobes; becoming somewhat compressed between ventrolateral rhynchocoel wall and brain (Fig. 9D), extending ventrally and meeting below rhynchocoel to form U-shaped ventral lacuna. This continuing for only short distance before dividing into 2 ventrolateral branches close in front of ventral cerebral commissure, the 2 branches continuing posteriorly over ventral commissure (Fig. 9E) then beginning to expand dorsally towards cerebral sensory organs, these bathed by lacunae. Between brain and mouth lateral lacunae again expanding dorsally to form pair of large channels on either side of rhynchocoel (Fig. 9F), becoming ventrally restricted where walls of buccal chamber bulging anteriorly and upwards. Above mouth a small flattened middorsal vessel about 15 μm wide protruding through ventral rhynchocoel wall. Origin of this vessel not traceable; it continues posteriorly in rhynchocoel lumen for approximately 300 μm before passing back through rhynchocoel wall, its structure somewhat intermediate in form between a heteronemertean rhynchocoelic villus and a hoplonemertean vascular plug. For most of foregut region, lateral lacunae forming spacious, thin-walled dorsolateral channels, but in posterior stomach region extending ventrally to meet below foregut. In this part of blood system, lacunae irregularly subdivided by connective-tissue strands, forming what is similar to foregut vascular plexus described for many heteronemerta taxa. This condition continuing pos-
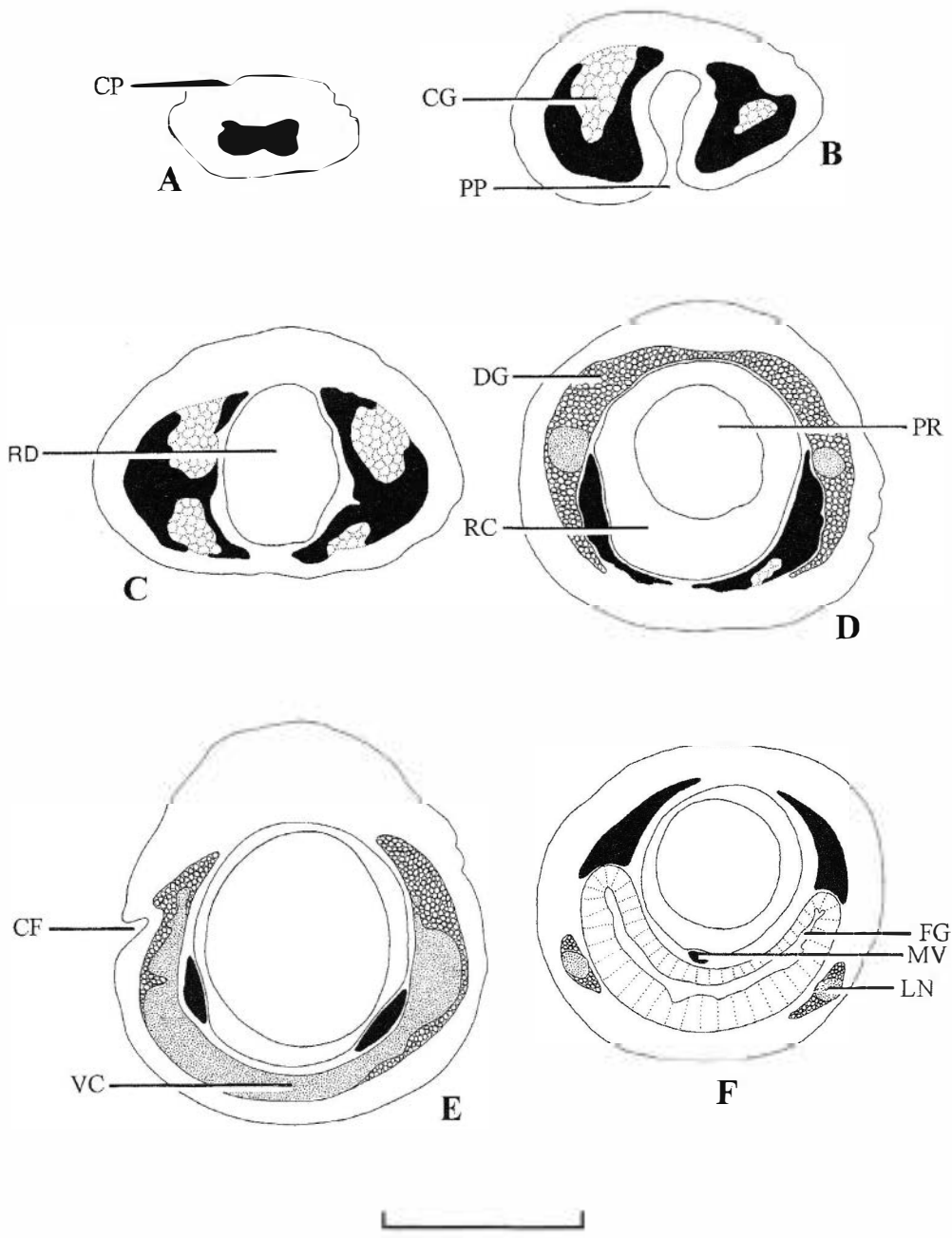
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Fig. 9. *Sundbergia albula* gen. et sp. nov. Schematic diagrams through the anterior regions of the body, drawn to emphasise the blood system (solid black). **A**, through the tip of the head in front of the proboscis pore; **B**, through the proboscis pore; **C**, through the rhynchodaeum about midway between the proboscis pore and proboscis insertion; **D**, through the anterior brain region; **E**, through the ventral cerebral commissure; **F**, through the foregut region not far behind the mouth. Scale bar = 200 μm (A–E), 315 μm (F).

teriorly around anterior, tubular, portion of intestine, but as intestinal diverticula begin to appear lateral lacunae again becoming increasingly restricted to dorsolateral position on either side of rhynchocoel. As they continue backwards lateral lacunae gradually moving to ventrolateral position adjacent to main intestinal channel, their walls like that of middorsal vessel, becoming thicker (Fig. 7). For most of body length, therefore, are 3 thick-walled longitudinal blood vessels with no transverse connectives between them. All 3 vessels, particularly in most posterior end of body, often dilated though remaining thick walled, apparently

joined posteriorly by supraintestinal connective.

Nervous system: Brain lobes situated immediately below epidermal basement membrane, with thin but distinct outer neurilemma but no inner neurilemma or neurochord cells. Dorsal lobes both extending in front of and wider apart than ventral. Slender dorsal cerebral commissure, about 15 μm thick, located above proboscis insertion far anterior to ventral commissure. Ventral cerebral commissure transversely linking ventral brain lobes about 30 μm thick, located behind posterior extent of dorsal lobes (Fig. 9E). From rear of dorsal commissure a thick median

nerve running directly back through neuroganglionic tissues, emerging behind commissure to form origin of median dorsal nerve running immediately outside body-wall circular-muscle layer (Fig. 10); this nerve traceable back into anterior intestinal regions of body but beyond this not traceable. Hind end of dorsal lobes continuing as short, thick nerve leading to cerebral sensory organs. From rear of ventral commissure a thick nerve (Fig. 10) leading backwards towards mouth, dividing as buccal epithelium begins to bulge inwards to form 2 foregut nerves, their ultimate fate not traced. From rear of ventral brain lobes, lateral nerve cords continuing posteriorly between epidermal basement membrane and body-wall outer circular-muscle layer. No neurochords in lateral nerves. In posterior intestinal part of body, however, after outer longitudinal-muscle layer has been established, lateral nerve cords extend to hind end of body immediately outside circular musculature (Fig. 7), displacing fibres of outer longitudinal layer; nerve cords meeting posteriorly by subintestinal commissure.

Apart from suggestions of neural involvement in subepidermal cephalic layer (see above) no other components of nervous system distinguishable.

Apical organ and cephalic glands: No obvious apical organ distinguished, but close to tip of head a number of small, ciliated pits extend across dorsal surface (Fig. 9A). Epithelium lining these pits not containing gland cells, unlike adjacent epidermis; these structures may correspond to apical organ of other nemerteans.

Irregular tissue masses somewhat resembling typical nemertean cephalic glands first appearing as single accumulation hanging down in cephalic blood lacunae on each side (Fig. 9B). These masses continuing back in lacunar lumen as far as proboscis insertion, dividing on each side into dorsal and ventral accumulations (Fig. 9C); similar tissues occur in anterior wall of rhynchodaeum. Whether or not these glandular structures discharge to exterior via dorsal epidermal pits not discernible.

Sense organs: Towards rear of brain on each side of body a short, horizontal cephalic furrow, about 100 μm in length, extending along lateral margin (Fig. 9E). From its posterior end a short ciliated cerebral canal, some 20 μm in diameter, turns inwards, passes through epidermal basement layer and meets acidophilic glandular tissues of cerebral sensory organ. Cerebral organ nerve essentially forming a posterior extension of dorsal cerebral lobes, running ventrally below glands. Ciliated canal then turns through 90° to run back along outer lateral margin of cerebral organ. Cerebral organs (Fig. 10) egg-shaped, about 90 μm long, 85 μm in height, 45 μm wide, lying in lumen of lateral blood vessels immediately behind brain.
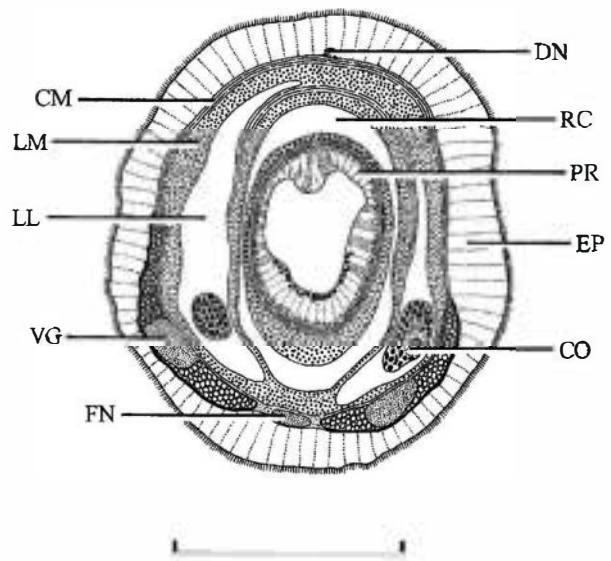

Fig. 10. *Sundbergia albula* gen. et sp. nov. Camera lucida drawing through the posterior cerebral region to show the cerebral sensory organs situated in the lateral blood lacunae. Scale bar = 250 μm.

No eyes; no other sensory structures identified.

Excretory system: No evidence found of any part of excretory system. Amongst previously known hubrechtid genera an excretory system has been reported only from *Hubrechtia*.

Reproductive system: The single individual found was an immature female. Ovaries are located in posterior intestinal portions of body, appearing squeezed between gut wall and body-wall musculature on dorso- and ventrolateral margins of body (Fig. 7).

DISCUSSION: Fifteen genera of palaeonemerteans are presently known (Gibson 1995; Gibson & Sundberg 1999), although three of these (*Cephalothrix, Cephalotrichella, Procephalothrix*) were, until the phylogenetic studies of Sundberg and Hylbom (1994), separated as a separate taxon, the Archinemertea. Although family diagnoses within the nemerteans are mostly in need of careful revision, five of the paleonemertean genera (*Coeia, Hubrechtella, Hubrechtia, Parahubrechtia, Tetramys*) have been placed in the family Hubrechtidae and some of the major anatomical features used to distinguish between these are summarised in Table 2. Bürger (1895: 530–531) originally established the family Hubrechtidae for *Hubrechtia*, defining the family as nemerteans with "ball-shaped cerebral sensory organs which lie deep in the head and project into the lateral blood vessels. The brain and lateral nerve cords lie below the epidermal basement membrane. The epidermis is low and contains numerous

flask-shaped glands instead of packet glands. The basement layer is reticulate and contains scattered gland cells, reminiscent of the dermal gland cell region of heteronemerteans. Both lateral and dorsal blood vessels are present. The nephridia consist of a profusely branched canal system" (author's translation). Hylbom (1957: 557) expressed caution about including the genus *Hubrechtella* in the Hubrechtidae: "In view of the differences between the two genera *Hubrechtia* ... and *Hubrechtella* .. it is only with hesitation that [I include] *Hubrechtella* in the family". Among the anatomical features which have been traditionally used to group palaeonemertean genera into families, the position of the brain and lateral nerve cords in relation to the various body wall layers has been regarded as of major importance. In all the previously known hubrechtids the neural components are situated between the epidermal basement membrane and the body-wall outer circular-muscle layer (Table 2), although this arrangement is by no means unique to these taxa (Sundberg & Hylbom 1994: table 2). Two other features which have been widely regarded as typical of hubrechtids are the organisation and position of the cerebral sensory organs and the presence of a middorsal vessel in the blood system. Well-developed cerebral organs, closely attached to the rear of the brain and posteriorly protruding into the lateral blood vessels, are found in the palaeonemerteans only in hubrechtid genera (Table 2), although *Parahubrechtia* completely lacks cerebral organs (Gibson & Sundberg 1999) and in *Tetramys* the organs run alongside instead of penetrating the blood vessels. A middorsal blood vessel is also typical of hubrechtid taxa, although none is found in *Parahubrechtia*, and one other palaeonemertean species is reported to possess this feature (*Procephalothrix kiliensis* Friedrich, 1935). Table 2 shows that the present species from New Zealand shares many characters in common with at least some of the known hubrechtid genera but can

Table 2

Summary of some of the anatomical features which can be used to distinguish between the palaeonemertean genera at present included in the family Hubrechtidae. Data obtained from Bürger (1895), Takakura (1922), Iwata (1957), Sundberg and Hylbom (1994), Gibson and Sundberg (1999) and the present paper.

Taxon	1	2	3	4	5	6	7	8
Coeia	+	1	1	O	O	O	2	+
Hubrechtella	+	1	1	O	O	O	2, 3	+
Hubrechtia	+	3	1	+	O	+	2	+
Parahubrechtia	O	3	1	+	O	O	2	O
Tetramys	+	2	1	O	+	O	3	+
Sundbergia gen. nov.	+	4	2	O	+	O	4	+

1 Cerebral sensory organs present (+) or absent (O).

2 Body-wall musculature comprising outer circular and inner longitudinal layers (1), outer circular, outer longitudinal, inner circular and inner longitudinal layers (2), outer circular, middle longitudinal and inner circular layers (3) or outer circular, inner longitudinal anteriorly, outer longitudinal, middle circular, inner longitudinal posteriorly (4).

3 Brain and lateral nerve cords situated between epidermal basement membrane and outer circular musculature (1) or as above anteriorly but posteriorly lateral nerve cords run in outer longitudinal muscle layer (2).

4 Excretory system present (+) or absent (O).

5 Rhynchocoel short (O) or long (+).

6 Eyes present (+) or absent (O).

7 Proboscis with two (2) or three (3) muscle layers or with outer circular and inner longitudinal layers present anteriorly which reverse their position posteriorly, short middle region with three layers (4).

8 Middorsal blood vessel present (+) or absent (O).

be distinguished from all of them by the organisation of its body wall and proboscis musculature, and by the posterior position of its lateral nerve cords in relation to the body-wall muscle layers. It is thus concluded that although the well-developed cerebral sensory organs penetrating the lateral blood vessels, the presence of a middorsal blood vessel, and the position of the brain and lateral nerve cords in the anterior regions of the body justify the taxon being included in the family Hubrechtidae, it cannot be placed in any of the previously known genera and is thus named *Sundbergia albula* gen. et sp. nov.

Subclass HETERONEMERTEA Bürger, 1895
Family **CEREBRATULIDAE** Gibson, 1985

Adenorhagas Riser, 1990

TYPE SPECIES: *Adenorhagas aurantiafrons* Riser, 1990

DIAGNOSIS: A single pair of short, shallow lateral horizontal cephalic furrows; proboscis unbranched, with outer longitudinal, middle circular and inner longitudinal muscle layers, and one muscle cross; rhynchocoel extending to posterior end of body, its circular muscles not interwoven with adjacent body-wall longitudinal muscles; dorsal fibre core of cerebral ganglia forked only at rear into upper and lower branches; brain lobes with neither distinct outer neurilemma nor neurochord cells; foregut with neither somatic muscles nor subepithelial gland cell zone; longitudinal muscle plate between rhynchocoel and foregut missing; lateral blood vessels developed into a vascular network around foregut; dermis without connective-tissue layer separating glandular region from body-wall outer longitudinal musculature; caudal cirrus present; apical organ consisting of three sensory pits; frontal glands present, small and in four groups; eyes absent; excretory system absent; sexes presumed separate.

Adenorhagas aurantiafrons Riser, 1990
(Figs 11–12)

ORIGINAL DESCRIPTION: Riser, 1990: 597–605, figs 1–10.

ADDITIONAL LITERATURE RELATING TO NEW ZEALAND RECORDS: Gibson 1995, in press; Gibson *et al.* in press (all as *Adenorhagas aurantiafrons*).

DESCRIPTION: *External features:* Largest individual found was 24 mm long and 1.1 mm diameter when fully extended. Body uniformly cylindrical throughout its length, and bluntly rounded both anteriorly and pos-

teriorly (Fig. 11). A minute, papilla-like, caudal cirrus present at posterior end but difficult to distinguish in life. Lateral cephalic furrows on either side of head short, shallow, easily overlooked; extending back as far as level of tiny, ventral mouth. General colour overall chalky-white with a bright orange cap at tip of head. In most specimens exceeding 10 mm long, however, a median, dorsal, orange stripe extends to end of body, whilst in examples over 18 mm long entire dorsal surface a dirty orange hue except for bright orange cephalic tip. No eyes.

Internal anatomy: Genus monospecific, hence major internal characters as given in generic diagnosis above, although Riser (1990: 597) noted that "The species is characterised by presence of a large number of gland cells in the lateral cephalic fissures, extensive development of sensory cells posteriorly in the cephalic fissures, and the absence of an excretory system."

OCCURRENCE: So far known only from New Zealand, *Adenorhagas aurantiafrons* was originally found in a holdfast of the kelp, *Lessonia variegata*, washed up on the shore at Kaikoura, South Island. Other specimens have been found in a stranded holdfast of *Ecklonia radiata* on Goat Island Beach, Leigh, North Island (Fig. 12). Riser (1990) suggested that because most of the specimens found at both locations were immature, the holdfasts were being used as a 'nursery' rather than as a permanent habitat niche.

Cerebratulus Renier, 1804

TYPE SPECIES: *Cerebratulus marginatus* Renier, 1804

Fig. 11.
Adenorhagas aurantiafrons. Drawing of a complete mid-sized specimen, viewed dorsally, based on the description given by Riser (1990).
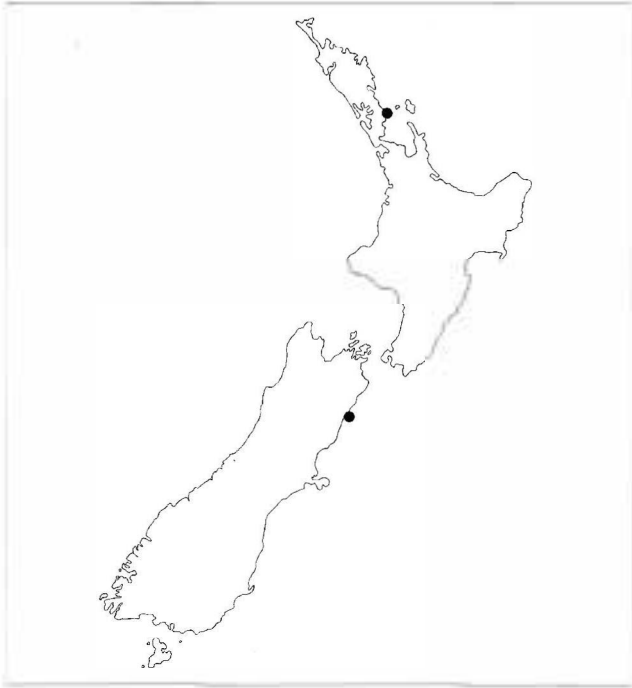Scale bar = 5 mm.

Fig. 12. *Adenorhagas aurantiafrons*. Recorded distribution in New Zealand.

DIAGNOSIS: A single pair of horizontal lateral cephalic furrows; proboscis with 3 muscle layers (outer longitudinal, middle circular, inner longitudinal), and 0–2 muscle crosses; rhynchocoel-wall circular musculature not interwoven with adjacent body-wall muscle fibres; dorsal fibrous core of cerebral ganglia forked only at rear into upper and lower branches; nervous system with neurochords and neurochord cells; foregut enclosed by layer of longitudinal somatic-muscle fibres; dermis variable, either comprising distinct outer glandular and inner connective tissue zones or with gland-cell region abutting directly against body-wall outer longitudinal muscles and without intervening connective-tissue layer; body-wall musculature usually with diagonal layer; caudal cirrus present; dorsoventral muscles, especially in intestinal region, ususally powerfully developed; cephalic glands usually well developed; most species with apical organ; eyes present or absent; sexes separate. Generally large animals, often with sharpened lateral body margins and able to swim actively with sinuous up and down movements.

Cerebratulus angusticeps Hubrecht, 1887

(Figs 13–14)

ORIGINAL DESCRIPTION: Hubrecht, 1887: 44–45, pl. 1, fig. 15, pl. 14, figs 1, 6, pl. 15, fig. 4.

ADDITIONAL LITERATURE RELATING TO NEW ZEALAND RECORDS: Hamilton 1896; Murray 1896; Hutton 1904; Bürger 1904; Gibson 1995, in press; Gibson *et al.* in press (all as *Cerebratulus angusticeps*).

DESCRIPTION: *External features:* Reported as similar in shape to *Cerebratulus angulatus*, the head acutely pointed, with a pair of distinct horizontal lateral cephalic furrows (Fig. 13). Intestinal region dorsoventrally flattened, up to about 4.5 mm wide, with sharp lateral margins. Ventral mouth distinct and moderately large. Colour dull yellow, with darker middorsal stripe (Hubrecht 1887).

Internal anatomy: Hubrecht's (1887) original account of *Cerebratulus angusticeps* is far from complete and Gibson (1995: 329), whilst including it as a valid species, commented that it is "an inadequately described form whose taxonomic affinities [are] uncertain". Among the few anatomical features referred to or illustrated in the original description are the large dorsal cerebral ganglionic lobes and the well-developed cerebral sensory organs surrounded by blood lacunae.

OCCURRENCE: So far recorded only from New Zealand waters; first found 27 June 1874 in Queen Charlotte Sound, South Island (41°4'0"S, 174°19'0"E), at about 30 m in mud. A second specimen was subsequently obtained from 2200 m in blue mud southeast of North Island (40°28'0"S, 177°43'0"E) (Fig. 14).
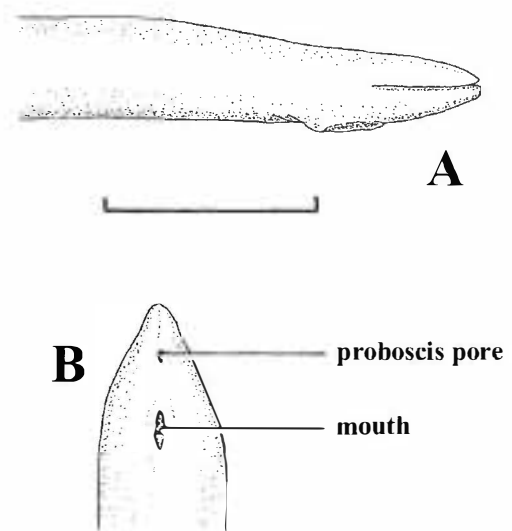

Fig. 13. *Cerebratulus angusticeps*. **A**. Lateral view of anterior end of specimen taken from approximately 2200 m depth. **B**. Ventral view of head. Both redrawn from Hubrecht (1887). Scale bar = 10 mm (refers to A only).
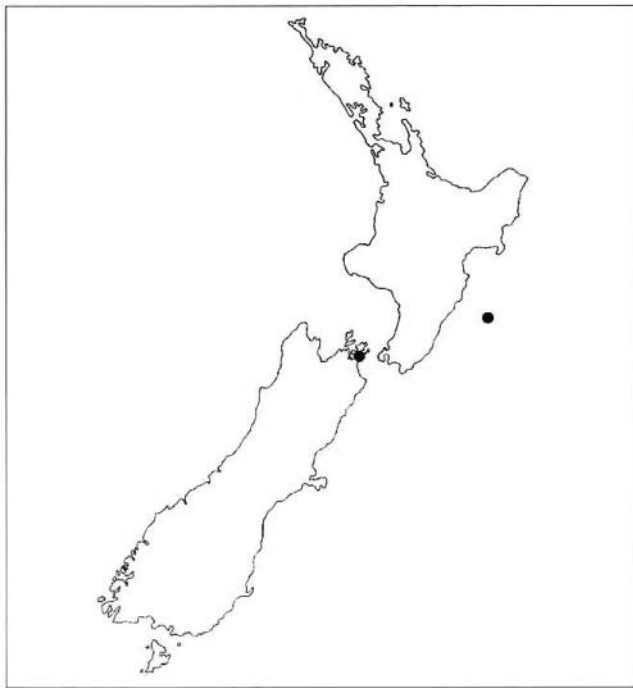
Fig. 15. *Cerebratulus macroren*. **A**. Lateral view of anterior end of body. **B**. Ventral view of head. Both redrawn from Hubrecht (1887). Scale bar = 2 mm.

Fig. 14. *Cerebratulus angusticeps*. Recorded distribution in New Zealand.

Cerebratulus macroren Hubrecht, 1887 (Figs 15–16)

ORIGINAL DESCRIPTION: Hubrecht, 1887: 46–47, textfig. 4b, pl. 1, figs 13, 14, 18, 19, pl. 10, figs 8, 9, pl. 11, fig. 11, pl. 12, figs 1, 2, 7, 8, pl. 13, figs 7–9, pl. 14, figs 7, 8, 11, pl. 15, figs 2, 3, 19.

ADDITIONAL LITERATURE RELATING TO NEW ZEALAND RECORDS: Hamilton 1896; Bürger 1904; Hutton 1904; Mallach 1930; Gibson 1995, in press (all as *Cerebratulus macroren*).

DESCRIPTION: *External features:* Hubrecht (1887: 46) noted that there was "no possibility of giving outwardly visible distinctive features of colour or shape" to distinguish it from *Cerebratulus parkeri*. *Cerebratulus macroren* is described as being of a dull yellowish hue, somewhat brownish on dorsal surface anteriorly. Head bluntly rounded (Fig. 15), with pair of lateral horizontal cephalic furrows which, in the Japanese specimen, were "perhaps comparatively a little longer than are those of *Cerebratulus parkeri* ... although the New Zealand representative ... is again very similar, even in this respect, to *Cerebratulus parkeri*" (*ibid.*). Body narrowing posteriorly from behind head, the ventral mouth minute. No indication of size was given for either individual.

Internal anatomy: Hubrecht (1887) separated this species from *Cerebratulus parkeri* on the basis of differences in the position and number of their nephridiopores; in *Cerebratulus macroren* the efferent excretory
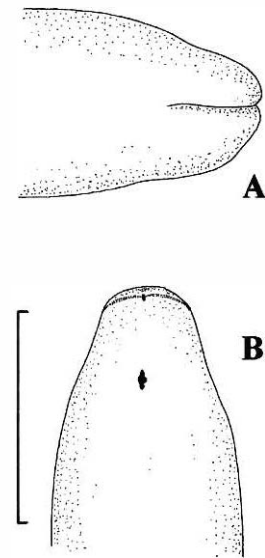
longitudinal collecting tubule on each side of the body leads to a single nephridiopore, whereas in *Cerebratulus parkeri* there are 2 efferent ducts and nephridiopores on each side of the body, leading from the mid-region of each collecting tubule. Hubrecht did consider the possibility that these differences might merely be a consequence of size (i.e., growth) but dismissed this suggestion as improbable. Other anatomical features described or illustrated for *Cerebratulus macroren* include dermis with no separate connective-tissue layer, middorsal blood vessel formed into a distinct rhynchocoelic villus, gonads opening dorsolaterally and proboscis containing 3 muscle layers (outer and inner longitudinal and middle circular) and 2 muscle crosses, although farther back the organ comprising only a longitudinal muscle layer in which the 2 proboscis nerves are distinct. Coe (1895: 489) noted that Hubrecht's (1887: pl. 15, fig. 3) illustration of the posterior proboscis depicts a structure similar to that found in the anterior proboscis of *Cerebratulus lacteus*, commenting that 'It would be surprising if the anterior end of the proboscis in one species should correspond to the posterior end in another species of the same genus'; other cerebratulids are known, however, in which the proboscis is anatomically differentiated into 3 distinct regions (e.g., see Cantell 1988a, on *Cerebratulus hepaticus*) such that Coe's implied criticism must be regarded as unjustified. Gibson (1995) noted that this species may be synonymous with *Cerebratulus parkeri*; if both are indeed the same form, then *Cerebratulus parkeri* should be the valid name on the grounds of priority, its description appearing before

that of *Cerebratulus macroren* in Hubrecht's (1887) publication.

OCCURRENCE: Known from only two specimens, the first obtained from blue mud at about 1280–1290 m north-east of East Cape, North Island (37°34′ S, 179°22′ E) (Fig. 16), the second from shallower (630–635 m) green mud in the Sagami Sea south of Honshu, Japan (35°11′ N, 139°28′ E).

Fig. 16. *Cerebratulus macroren.* Recorded distribution in New Zealand.

Cerebratulus macrorrhochmus (Schmarda, 1859)
(Frontis., fig. C; Fig. 17)

ORIGINAL DESCRIPTION: Schmarda, 1859: 43, textfig. p. 43, pl. 11, fig. 96 (as *Meckelia macrorrhochma*).

ADDITIONAL LITERATURE RELATING TO NEW ZEALAND RECORDS: As *Meckelia macrorrhochma* (Diesing 1862; Hutton 1879); as *Cerebratulus macrorhochmus* (Hutton 1904); as *Cerebratulus macrorrhochmus* (Bürger 1904; Gibson 1995, in press; Gibson *et al.* in press); for other synonyms see Gibson (1995).

DESCRIPTION: *External features:* Described entirely on basis of external features (Fig. 17): dorsoventrally flattened body, with long, pointed head bearing obvious horizontal lateral cephalic furrows, these blood red in life. General body colour dark olive-brown; no eyes. Ventral slit-like mouth situated just behind head, proboscis pore round, terminal. Schmarda (1859) commented that he was unable to determine whether

or not the proboscis was armed, but the separate mouth and proboscis pore and nature of the cephalic furrows indicate that the form is almost certainly a heteronemertean.

Internal anatomy: There is no information on the internal anatomy of this inadequately described species and neither its generic placement nor specific validity can yet be confirmed.
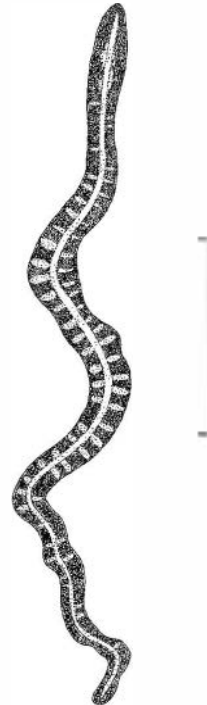

Fig. 17. *Cerebratulus macrorrhochmus.* Complete specimen viewed from dorsal aspect. Redrawn from Schmarda (1859). Scale bar = 20 mm.

OCCURRENCE: Schmarda (1859) merely recorded this species from the coast of New Zealand without giving further particulars. He also noted that a species from South Africa was very similar in shape and the appearance of the head, but differed in possessing a reddish middorsal stripe and incomplete white transverse streaks. Diesing (1862) uncertainly identified the South African form as a separate species, *Meckelia capensis*, but Bürger (1904) regarded both the South African *capensis* and New Zealand *macrorrhochmus* as different varieties of *Cerebratulus macrorrhochmus*. The two taxa are, in all probability, separate and may not even be congeneric.

Cerebratulus macrostomus (Schmarda, 1859)
(Frontis., fig. A; Figs 18–19)

ORIGINAL DESCRIPTION: Schmarda, 1859: 42, textfig. p. 42, pl. 11, fig. 92 (as *Meckelia macrostoma*).

ADDITIONAL LITERATURE RELATING TO NEW ZEALAND RECORDS: As *Meckelia macrostoma* (Diesing 1862; Hutton 1879); as *Cerebratulus macrostomus* (Bürger 1904; Hutton 1904; Gibson 1995, in press; Gibson *et al.* in press).

DESCRIPTION: *External features:* A solid-bodied nemertean, up to 200 mm long and 8 mm in maximum width, slightly flattened dorsoventrally and gradually narrowing posteriorly to end in a blunt, pointed tail with no caudal cirrus (Fig. 18). Sharply tapering head with pair of wide lateral horizontal cephalic furrows but apparently no eyes. Mouth forming on ventral surface, a gaping longitudinal opening, just in front of which is the proboscis pore. General colour greenish, with very dark blue tinge.

Internal anatomy: Only anatomical detail known for this species is the proboscis, described by Schmarda (1859: 42) as ending in a point which forms a kind of bowl provided with 4 large elevations in which long stinging filaments are set ('Die Spitze des Rüssels bildet eine Art Napf mit vier grossen Erhöhungen, in welchen lange Nesselorgane stecken'). Although transferred to *Cerebratulus* by Diesing (1862), in which it is currently contained, Schmarda's description of the proboscis *could* refer to an enoplan armed form, the 'lange Nesselorgane' referring to accessory stylets being contained in 4 accessory stylet pouches; several monostiliferous hoplonemertean species are known in which 4 or more such pouches are situated in stylet bulb portion of proboscis. In absence of other anatomical data, however, it is impossible to determine its systematic position, although the close-set ventral mouth and proboscis pore could represent the condition known in such benthic polystiliferous hoplonemertean genera as *Paradrepanophorus* and *Punnettia* (Gibson 1994).
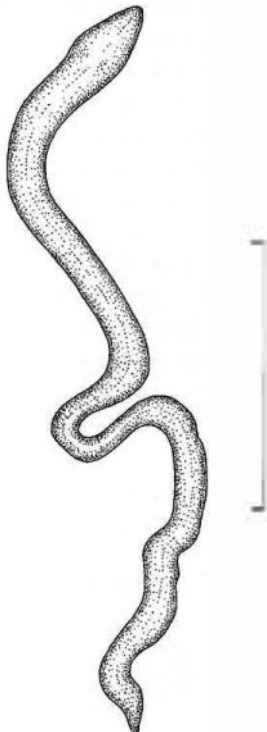

Fig. 18. *Cerebratulus macrostomus.* Complete specimen viewed from dorsal aspect. Redrawn from Schmarda (1859). Scale bar = 40 mm.

OCCURRENCE: Recorded only from Auckland, North Island (Fig. 19); no data on species habitat or distribution.

Fig. 19. *Cerebratulus macrostomus.* Recorded distribution in New Zealand

Cerebratulus parkeri Hubrecht, 1887 (Figs 20–21)

ORIGINAL DESCRIPTION: Hubrecht, 1887: 43–44, textfig. 4a, pl. 14, fig. 5, pl. 15, figs 5, 16.

ADDITIONAL LITERATURE RELATING TO NEW ZEALAND RECORDS: Hamilton 1896; Bürger 1904; Hutton 1904; Gibson 1995, in press; Gibson *et al.* in press (all as *Cerebratulus parkeri*).

DESCRIPTION: *External features:* Known from only a single specimen, body more or less rounded anteriorly, about 7 mm in maximum diameter, somewhat dorsoventrally flattened posteriorly (Fig. 20). Anterior body fragment 34 mm long but total length not recorded. Bluntly rounded head with pair of short, lateral horizontal cephalic furrows and slight median anterior notch, not demarcated from trunk. Ventral mouth small. A dull yellowish colour overall, tinged brown on dorsal surface of head.

Internal anatomy: Hubrecht (1887) noted internal anatomy of this species very similar to that of *Cerebratulus macroren*, differing essentially only in arrangement of excretory system. In *Cerebratulus parkeri*, longitudinal collecting tubule on either side of body with 2 efferent ducts, emerging about midway along length of each tubule, in contrast to single posterior efferent
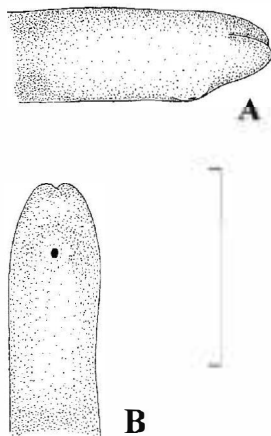
Fig. 20. *Cerebratulus parkeri.* Lateral (A) and ventral (B) views of the head of the only known specimen. Both redrawn from Hubrecht (1887). Scale bar = 10 mm.

duct found in *Cerebratulus macroren*. Ventral brain lobes in *Cerebratulus parkeri* linked by normal thick transverse cerebral commissure, as in other nemerteans, but close behind this are several slender pseudometameric transverse connectives between outer neurocellular layer of ganglia. Paired oesophageal nerves also transversely joined by 3 close-set connectives; cf. similar arrangement recorded for other species of *Cerebratulus* (e.g., Thompson 1908). Only known specimen of this species a mature female, its intestinal regions packed with large numbers of ova.

Fig. 21. *Cerebratulus parkeri.* Recorded distribution in New Zealand.

OCCURRENCE: Dredged from mud at about 20 m, Queen Charlotte Sound, South Island (41°4′ S, 174°19′ E) (Fig. 21).

Praealbonemertes Cantell, 1993

TYPE SPECIES: *Praealbonemertes whangateaunienses* Cantell, 1993

DIAGNOSIS: A single pair of lateral horizontal cephalic furrows; proboscis unbranched, with outer longitudinal, middle circular, and inner longitudinal muscle layers and 2 muscle crosses; rhynchocoel circular musculature in oral region interwoven with adjacent body-wall longitudinal muscles and also forming crossovers with outer circular musculature; dorsal fibre core of cerebral ganglia forked only at rear into upper and lower branches; brain lobes enclosed by distinct outer neurilemma; foregut with circular somatic muscles; dermis without connective-tissue layer separating glandular region from body-wall outer longitudinal musculature; caudal cirrus present; apical organ present; cephalic glands well developed; eyes absent; sexes separate.

Praealbonemertes whangateaunienses Cantell, 1993 (Figs 22–23)

ORIGINAL DESCRIPTION: Cantell, 1993: 63–69, figs 1–11.

ADDITIONAL LITERATURE RELATING TO NEW ZEALAND RECORDS: Gibson 1995, in press; Gibson *et al.* in press (all as *Praealbonemertes whangateaunienses*).

DESCRIPTION: *External features:* Body 130–335 mm long, about 2 mm maximum width. Bluntly rounded head with single pair of lateral horizontal cephalic furrows but no eyes, posteriorly demarcated from adjacent body region by distinct narrowing just behind cerebral ganglia; the ganglia visible as reddish patches through dorsal body surface (Fig. 22). Body terminates posteriorly in distinct caudal cirrus. Body colour somewhat variable; anterior half typically white, posterior pink to pinkish-brown, but rear half also white in some individuals and colour in this region to some extent depending upon food in gut. Larger specimens sometimes posteriorly streaked with green both dorsally and ventrally.

Internal anatomy: Described and illustrated by Cantell (1993): major features include regionally differentiated proboscis with 3 muscle layers and 2 muscle crosses in its wall, dermis with no separate connective-tissue region, an anterior blood system developed as plexus, caudal cirrus, no neurochord cells, and no foregut subepithelial gland-cell zone.
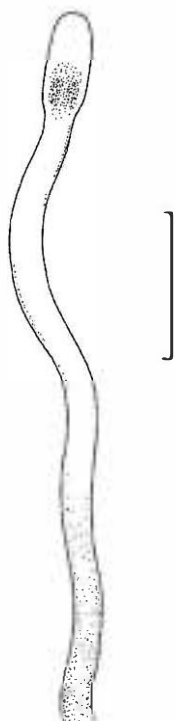
Fig. 22. *Praealbonemertes whangateaunienses.* Drawing of anterior body region, viewed from dorsal aspect. Based on Cantell (1993). Scale bar = 5 mm.
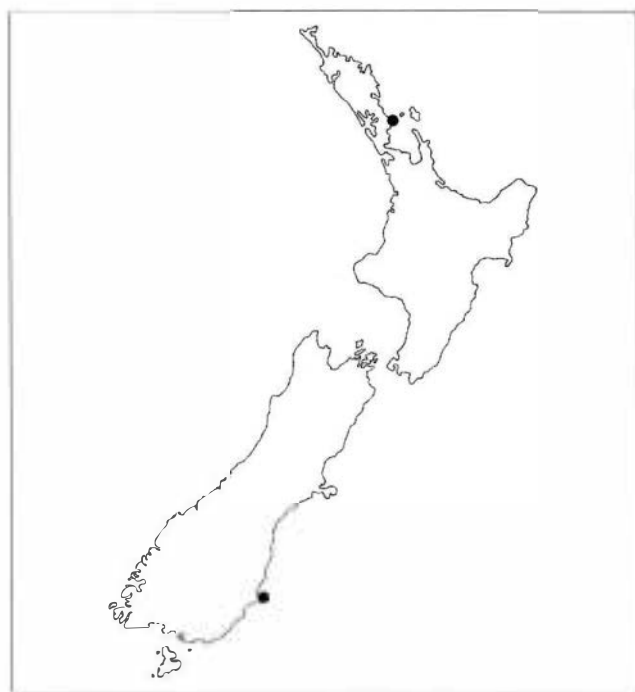

Fig. 23. *Praealbonemertes whangateaunienses.* Recorded distribution in New Zealand.

OCCURRENCE: A lower-shore eulittoral species, first found in sand mixed with mud at Whangateau Harbour, North Island (type locality), but also occurring under stones outside the Portobello Marine Biological Station, South Island (Fig. 23).

Family **LINEIDAE** McIntosh, 1873-1874
sensu Gibson, 1985

Craticulineus Gibson, 1984

TYPE SPECIES: *Craticulineus novaezealandiae* Gibson, 1984

DIAGNOSIS: A single pair of horizontal lateral cephalic slits; caudal cirrus absent; proboscis for most of its length with 2 muscle layers (outer circular, inner longitudinal) but in anterior regions with 2 additional blocks of outer longitudinal fibres, no muscle crosses; rhynchocoel-wall circular musculature partially interwoven with adjacent body-wall inner longitudinal muscles; dorsal fibrous core of cerebral ganglia posteriorly forked into upper and lower branches; nervous system without neurochords and neurochord cells; foregut without subepithelial gland-cell zone, but with circular somatic muscle layer; extremely well developed median longitudinal-muscle plate present between rhynchocoel and foregut, posteriorly extending into anterior intestinal regions; body wall without diagonal muscle layer; dermis divisible into outer glandular and inner connective-tissue zones; blood system with single median cephalic lacuna and 3 post-cerebral longitudinal vessels not linked by pseudo-metameric transverse connectives; excretory system extending throughout most of foregut region, discharging into foregut and without external nephridiopores; cephalic glands poorly developed, scattered.

Craticulineus novaezealandiae Gibson, 1984
(Figs 24–25)

ORIGINAL DESCRIPTION: Gibson, 1984: 78–87, figs 1–20.

ADDITIONAL LITERATURE RELATING TO NEW ZEALAND RECORDS: Gibson 1995, in press; Gibson *et al.* in press (all as *Craticulineus novaezealandiae*).

DESCRIPTION: *External features:* Unknown in life. Both preserved individuals were about 18 mm long and 2 mm in maximum diameter, their bodies rounded in cross-section and sharply tapering posteriorly to bluntly pointed tip with no caudal cirrus (Fig. 24). Blunt, rounded head with a pair of short lateral horizontal cephalic furrows. Ventral mouth small and indistinct. Neither specimen showed evidence of colour

pattern, preserved colouration varying from dull uniform brown to pale creamish-brown.
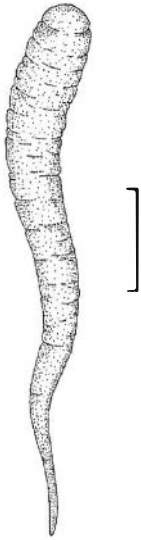

Fig. 24. *Craticulineus novae-zealandiae.* Drawing of the holotype to show how the body is sharply tapered posteriorly. Redrawn from Gibson (1984). Scale bar = 3 mm.

Internal anatomy: Fully described by Gibson (1984), Anatomical features include partial interweaving between rhynchocoel circular and adjacent body-wall inner longitudinal musculature — an unusual hetero-nemertean character found only in a few other genera (*Micrurides, Micrurinella* and *Paramicrurinella*) (Cantell, 1988b). In these, however, interweaving restricted to intestinal region of body, whereas in *Craticulineus* it occurs in foregut region. Internally opening efferent excretory tubules of *Craticulineus* also an unusual feature, although in some species of *Baseodiscus* the excretory tubules also opening into foregut.

OCCURRENCE: Trawled from 95 m approximately 140 miles east of Christchurch, South Island, between 43°22′ S, 175°20′ E and 43°24′ S, 175°15′ E (Fig. 25).

Micrura Ehrenberg, 1828

TYPE SPECIES: *Micrura fasciolata* Ehrenberg, 1828

DIAGNOSIS: A single pair of lateral horizontal cephalic furrows, posteriorly enlarged to form wide bays from which ciliated cerebral canals emerge ventrally; pro-boscis unbranched, with outer circular and inner longitudinal-muscle layers and 0–2 muscle crosses; rhynchocoel circular musculature not interwoven with adjacent body-wall muscles; dorsal fibre core of cerebral ganglia forked only at rear into upper and lower branches; nervous system with neither neurochords or neurochord cells; cerebral ganglia usually without outer neurilemma; foregut with or without somatic
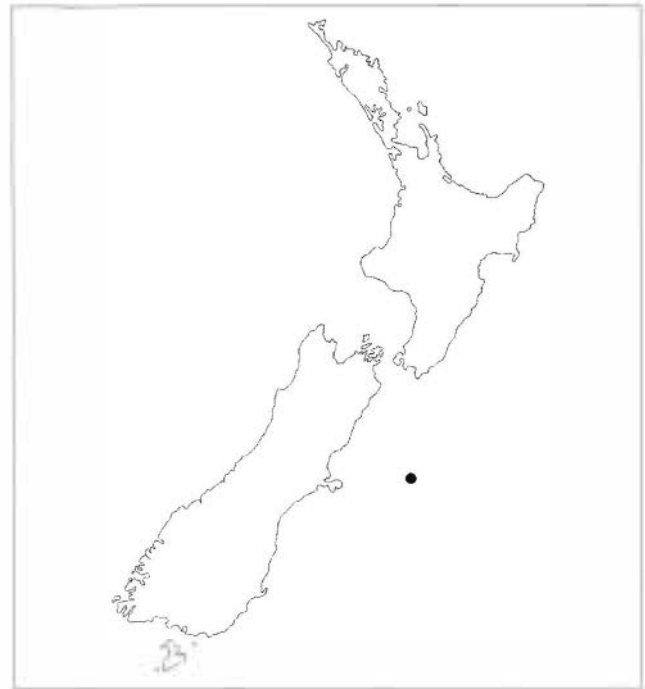

Fig. 25. *Craticulineus novaezealandiae.* Recorded distribution in New Zealand.

muscles, if present, variably longitudinal and / or circular; dermis variable, with or without connective-tissue layer separating glandular region from body-wall outer longitudinal musculature; caudal cirrus present; apical organ usually present; cephalic glands normally well developed, sometimes weak or absent; eyes present or absent; sexes separate.

Micrura pleuropolia Cantell, 1994   (Figs 26–27)

ORIGINAL DESCRIPTION: Cantell, 1994: 24–31, figs 1–11.

ADDITIONAL LITERATURE RELATING TO NEW ZEALAND RECORDS: Gibson 1995, in press; Gibson *et al.* in press (all as *Micrura pleuropolia*).

DESCRIPTION: *External features:* Body 8–80 mm long, 5–15 mm wide, oval in cross-section with rounded margins. Bluntly rounded head with a single pair of lateral horizontal cephalic furrows, anteriorly a yellowish-white patch in each (Fig. 26). Up to 5 struc-tures resembling eyes, but lacking pigmentation, on either side of head. General body colour an overall dark brown, but lateral margins and tip of head tinged with pale grey. Younger individuals tending to be paler ven-trally. On dorsal cephalic surface cerebral ganglia externally visible as reddish patches, the oblong mouth distinct ventrally. Body ending in caudal cirrus up to 6 mm long at posterior tip.

Fig. 26. *Micrura pleuropolia.* Drawing to show the appearance of the anterior portion of the body. The position of the brain lobes is indicated by the darker pigmentation on the head. Redrawn from Cantell (1994). Scale bar = 1 mm.

Internal anatomy: Described and illustrated by Cantell (1994): significant features include proboscis containing 2 muscle layers and 2 muscle crosses, dermis with no separate outer connective-tissue zone, no neurochord cells in nervous system, foregut blood supply developed into vascular plexus, no outer neurilemma surrounding brain lobes, isolated circular-muscle fibres of rhynchocoel wall in region of the brain and cerebral sensory organs slightly interwoven with body-wall inner longitudinal muscles ventrally, and caudal cirrus.

OCCURRENCE: The type locality is near the Leigh Marine Laboratory, North Island, at 8 m depth on shell gravel, but the species has also been found on a similar substratum at 11.5 m depth at the entrance to Otago Harbour, South Island (Fig. 27).

Fig. 27. *Micrura pleuropolia.* Recorded distribution in New Zealand.

Notospermus Huschke, 1830

TYPE SPECIES: *Notospermus geniculatus* (Delle Chiaje, 1828)

DIAGNOSIS: A single pair of deep lateral horizontal cephalic furrows; proboscis unbranched, with 3 muscle layers anteriorly (outer longitudinal, middle circular, inner longitudinal) and 2 muscle crosses, but outer longitudinal-muscle layer missing from posterior region; rhynchocoel circular musculature partially interwoven with adjacent body-wall longitudinal muscles; dorsal fibre core of cerebral ganglia forked only at rear into upper and lower branches; nervous system with neither neurochords nor neurochord cells; cerebral ganglia enclosed by distinct connective tissue outer neurilemma; foregut with loosely disposed longitudinal somatic muscles; dermis separated from body-wall outer longitudinal musculature by well developed connective-tissue layer; posterior tip of body sharply pointed but not developed into a caudal cirrus; no apical organ; no cephalic glands; eyes present; sexes separate.

Notospermus geniculatus (Delle Chiaje, 1828)
(Figs 28–29)

ORIGINAL DESCRIPTION: Delle Chiaje, 1828: 177, pl. 43, fig. 10 (as *Polia geniculata*).

ADDITIONAL LITERATURE RELATING TO NEW ZEALAND RECORDS: Riser 1991; Gibson 1995, in press; Gibson *et al.* in press (all as *Notospermus geniculatus*); for other synonyms see Gibson (1995).

DESCRIPTION: *External features:* Reported to attain lengths of 300–600 mm and widths of 5–8 mm (Bürger 1895), although most examples found in New Zealand less than 100 mm long (Riser 1991). Body rounded in cross-section, gradually tapering posteriorly. Head bluntly rounded, rather flattened, narrower than succeeding trunk regions, with a single pair of lateral horizontal cephalic furrows expanding posteriorly to form deep bays. Some 40–50 eyes extending along each lateral cephalic margin, both above and below cephalic furrows. Body strikingly patterned, typically bright pea-green to dark green dorsally, less often dark brown or black, with up to 30 or more narrow whitish to creamish or yellowish transverse bands variably or regularly spaced (Fig. 28). Anterior band situated on head, typically forming forward-pointing shallow V-shape. Ventral colour alternating with transverse bands paler than dorsal colour, varying from pale yellowish to diffuse bluish-green. In some individuals the pale transverse bands visible only in anterior body regions, the posterior portions uniformly pigmented with no trace of banding. The bright greenish colour-

30

ation typical of smaller individuals darkening with increase in size and age. Inner surfaces of cephalic furrows and brain lobes pinkish, the lateral blood vessels often visible in paler posterior parts of body because of the red corpuscles in blood fluid. Posteriorly body often acutely pointed and pale in colour, but no caudal cirrus.

Internal anatomy: Fully described by Gibson (1981) (as *Micrura tridacnae*) and Riser (1991): taxonomically important features include a regionally differentiated proboscis with 3 muscle layers and 2 muscle crosses in anterior region, whereas posterior portion with only 2 muscle coats and no outer longitudinal layer, circular rhynchocoel muscles partially interwoven with adjacent body-wall longitudinal musculature, and absence of both apical organ and cephalic glands.

OCCURRENCE: Reported by Riser (1991: 427) as "The most common heteronemertine present in kelp holdfasts examined ... during February to May 1986", the species was obtained from the holdfasts of *Lessonia variegata* at Kaikoura, South Island, and from "*Amphioxus*" sand at 22 m depth at Sponge Flats, off Goat Island, Leigh, North Island (Fig. 29). This heteronemertean has a wide geographic distribution, occurring from the lower intertidal to sublittoral depths of 30 m or more in kelp holdfasts, under stones or boulders in sand or muddy sand, or in rock and coral crevices. It has been recorded from the Black Sea, Mediterranean (coasts of France, Italy, Greece and Malta), the Canary Islands, the Gulf of Guinea (West Africa), Japan, Australia, and the western coasts of tropical America (Baha California, Panama and Peru). Gibson (1995) commented that Wheeler's (1934) report of this species from Annobón, Gulf of Guinea, is of uncertain validity.
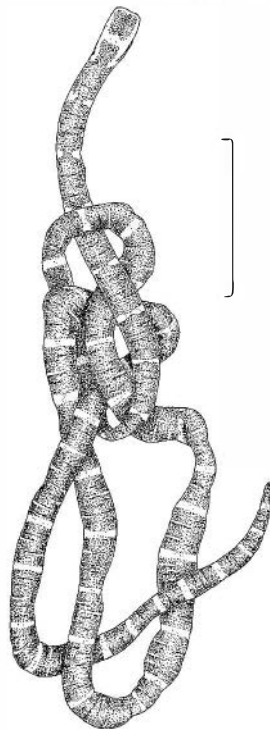
Fig. 28. *Notospermus geniculatus.* Drawing to show the typical colour pattern and general appearance of a complete specimen. Scale bar = 20 mm.
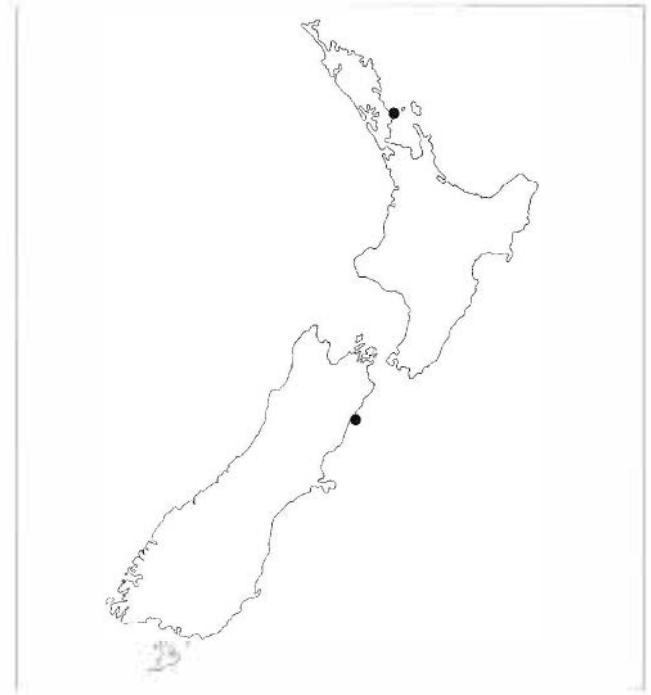
Fig. 29. *Notospermus geniculatus.* Recorded distribution in New Zealand.

Ramphogordius Rathke, 1843

TYPE SPECIES: *Ramphogordius lacteus* Rathke, 1843

DIAGNOSIS: A single pair of lateral horizontal cephalic furrows; proboscis unbranched, with 2 muscle layers (outer circular, inner longitudinal) and 2 muscle crosses; rhynchocoel circular musculature not interwoven with adjacent body-wall musculature; dorsal fibre core of cerebral ganglia forked only at rear into upper and lower branches; nervous system with neither neurochords nor neurochord cells; body-wall musculature with diagonal layer; dermis without connective-tissue layer separating glandular region from body-wall outer longitudinal musculature; blood system forming vascular plexus around foregut; foregut with sub-epithelial gland-cell layer and longitudinal somatic muscles; caudal cirrus absent; with 3 apical organs; cephalic glands present; head with 4–6 pairs of eyes; sexes separate; asexual reproduction by multiple fission.

Ramphogordius sanguineus (Rathke, 1799)

(Figs 30–31)

ORIGINAL DESCRIPTION: Rathke (1799: 83) (as *Planaria sanguinea*).

ADDITIONAL LITERATURE RELATING TO NEW ZEALAND RECORDS: As *Myoisophagos sanguineus* (Riser 1994; Gibson 1995; Gibson *et*

al. in press); as *Ramphogordius sanguineus* (Gibson in press); for other synonyms see Gibson (1995).

DESCRIPTION: *External features:* Attaining lengths of 100–200 mm but slender body about 1.2 mm in diameter during normal movement. General colour varying with age and size; smaller individuals (less than about 15 mm long) transparent whitish or cream with red brain region, older specimens ranging from bright overall reddish-brown to greyish-green, brownish-black or dull mid-brown. The posterior and ventral regions often somewhat paler than remainder of body, a variable number of widely spaced pale annulations throughout much of intestinal region (Fig. 30A). On each side of bluntly rounded head 3–7 eyes in dorsal wall of cephalic furrows; number of eyes on each side frequently differing, occasionally the same. Worm contracting in tightly coiled spiral when disturbed (Fig. 30B).

Internal anatomy: Described by Bürger (1895) (as *Lineus nigricans*), Coe (1931) (as *Lineus vegetus*), Coe (1943) (as *Lineus socialis*), and Riser (1994) (as *Myoisophagos sanguineus*), among others. Features of significance including a dermis with no connective-tissue layer separating gland cells from body-wall outer longitudinal-muscle layer, a proboscis with 2 muscle crosses and a slender diagonal muscle layer in the body wall.
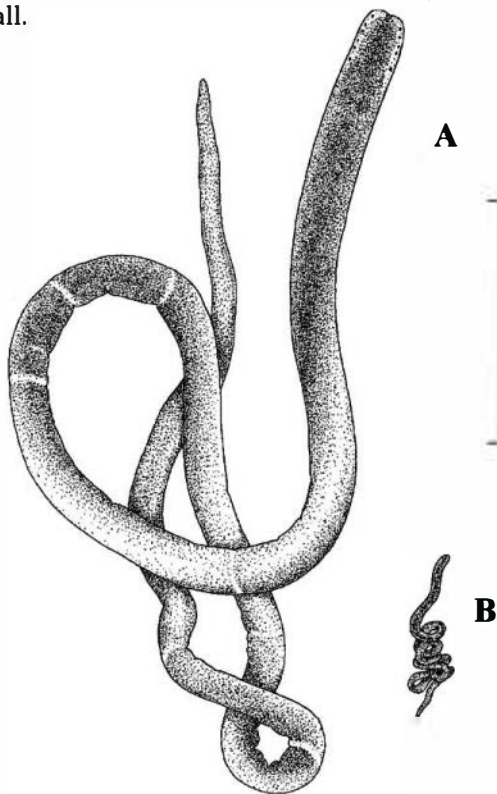

A

B

Fig. 30. *Ramphogordius sanguineus.* **A**. Drawing to show the general appearance of a complete specimen. **B**. A fully contracted individual, showing the characteristic tight spiral coiling of the body. Scale bar = 10 mm (refers to A only).

OCCURRENCE: Riser (1994: 548) found clumps of this species "beneath rocks on the reef just seaward of the rubble beach along the outer face of the Kaikoura Peninsula", South Island (Fig. 31). He described it under the name *Myoisophagos sanguineus*, but subsequently (Riser 1998b: 154) commented that the name *Myoisophagos* was "an invalid generic name" and reassigned the taxon to the genus *Ramphogordius*. *Ramphogordius sanguineus*, under one or another of its synonyms, has been widely reported in the northern hemisphere, with a distribution extending from the White Sea, Russia, the European coasts of Sweden, Belgium, the British Isles, France and Italy, and westwards to Atlantic, Gulf and Pacific coasts of North America; Isler's (1902) record of the species (as *Lineus nigricans*) from Chile refers to a different taxon (Riser 1994) and the Kaikoura specimens are the only ones so far known from the southern hemisphere. It is typically found under rocks and stones embedded in muddy substrata, often in muds blackened through the effects of decaying organic matter, or amongst algae. Riser (1994) noted that the species is a temperate-water taxon tolerant of gradual thermal and salinity fluctuations.

Fig. 31. *Ramphogordius sanguineus.* Recorded distribution in New Zealand.

Family **VALENCINIIDAE** Hubrecht, 1879
sensu Gibson 1985

Baseodiscus Diesing, 1850

TYPE SPECIES: *Baseodiscus delineatus* (Della Chiaje, 1825)

DIAGNOSIS: No horizontal lateral cephalic slits, some species with shallow oblique grooves; proboscis with 2 (outer longitudinal, inner circular) muscle layers and no muscle crosses; rhynchocoel short, rarely more than one-third of body length; rhynchocoel-wall circular musculature not interwoven with adjacent body-wall muscles; dorsal fibrous core of cerebral ganglia forked only at rear into upper and lower branches; nervous system with neither neurochords nor neurochord cells; foregut with distinct subepithelial gland-cell layer, usually at least in part separated from epithelium by delicate longitudinal, circular and/or oblique muscle strands; dermis well developed, with separate outer glandular and inner connective-tissue zones; caudal cirrus absent; cephalic glands extensively developed, extending post-orally among outer body-wall longi-tudinal muscle fibres; single apical organ present; excretory system mostly with external nephridiopores, but some species with efferent ducts discharging into lumen of foregut; eyes present, small and numerous; sexes separate.

Baseodiscus australis (Hubrecht, 1887)

(Figs 32–33)

ORIGINAL DESCRIPTION: Hubrecht, 1887: 13–14, pl. 1, fig. 6, pl. 7, figs 1–3, 7 (as *Eupolia australis*).

ADDITIONAL LITERATURE RELATING TO NEW ZEALAND RECORDS: As *Eupolia australis* (Hamilton 1896; Hutton 1904); as *Baseodiscus australis* (Bürger 1904; Gibson 1995, in press).

DESCRIPTION: *External features:* Known only from single, incomplete, male specimen about 19 mm long and 2 mm maximum width. Body was rounded in front, tapered posteriorly. Conical head, with no trace of cephalic furrows, was partially retracted into trunk (Fig. 32); typical of many *Baseodiscus* species after preservation; ventral mouth situated a short distance behind anterior tip of the body. Hubrecht (1887: 13) commented that species was "Another type of a whitish colour", but whether this referred to colour in life or after preservation is unclear.
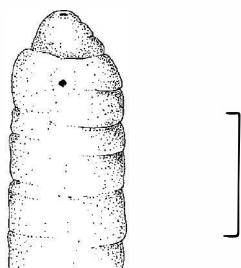

Fig. 32. *Baseodiscus australis.* Ventral view of head. Re-drawn from Hubrecht (1887). Scale bar = 2 mm.

Internal anatomy: Although incompletely described, is distinguishable from other New Zealand member of genus, *Baseodiscus giardii*, by epidermal basement membrane being very much thicker than connective-tissue layer between dermal connective tissue and body-wall outer longitudinal muscles.

OCCURRENCE: Known from only a single location, dredged at 1280 m in blue mud at 37°34′0″ S, 179°22′0″ E, east of central North Island (Fig. 33).
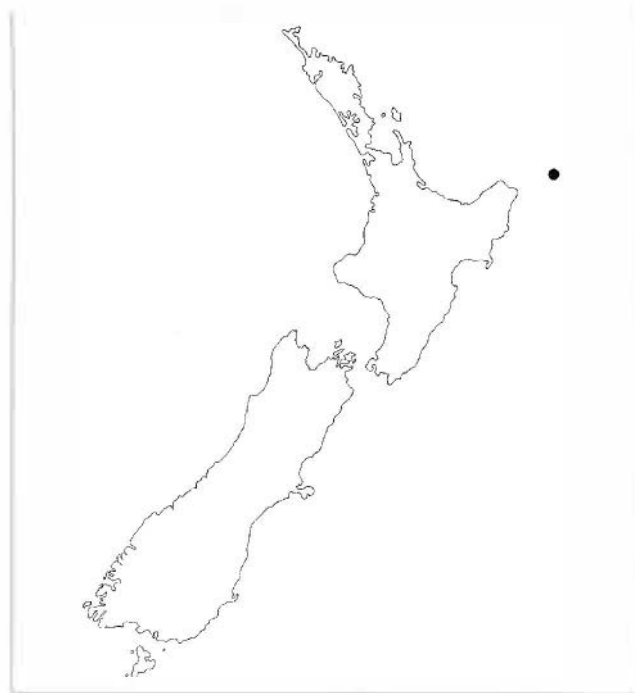

Fig. 33. *Baseodiscus australis.* Recorded distribution in New Zealand.

Baseodiscus giardii (Hubrecht, 1887)   (Figs 34–35)

ORIGINAL DESCRIPTION: Hubrecht, 1887: 11–13, pl. 1, figs 7–9, pl. 5, figs 1–9, pl. 6, figs 4–11, pl. 7, figs 4, 5, 8, pl. 10, fig. 6, pl. 11, fig. 12 (as *Eupolia giardii*).

ADDITIONAL LITERATURE RELATING TO NEW ZEALAND RECORDS: As *Eupolia giardii* (Hamilton 1896; Hutton 1904); as *Baseodiscus giardii* (Bürger 1904; Baylis 1915; Gibson 1995, in press); for other synonyms see Gibson 1995).

DESCRIPTION: *External features:* Hubrecht's (1887) des-cription of external features based on preliminary notes by W.C. McIntosh: body was about 40 mm long and 6.5 mm maximum diameter, bluntly rounded at either extremity, colourless. At anterior tip of head traces of transverse and vertical furrows form a cross, in centre of which is proboscis pore (Fig. 34). Head marked off from trunk by well-developed fold ventrally not quite

reaching mouth. Baylis' (1915) female specimen was described as about 60 mm long, 6 mm wide, with no trace of colour. Head slightly tapered, tail "conically pointed, thicker than the head".

Internal anatomy: Body-wall circular muscle layer thick, strongly developed around foregut, rhynchocoel small, with wall containing only slender layers of circular and longitudinal-muscle fibres.
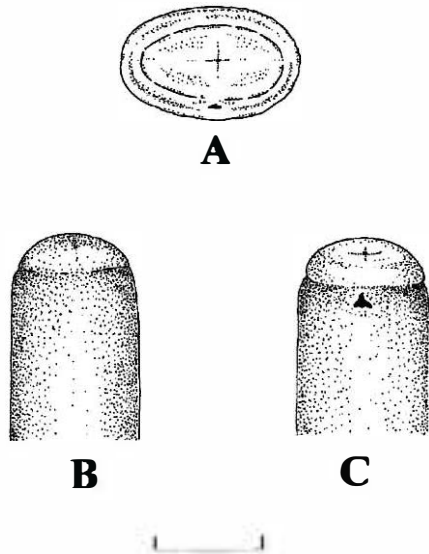

Fig. 34. *Baseodiscus giardii.* **A.** The anterior tip of the head, viewed from the front. **B.** Dorsal view of head. **C.** Ventral view of head. All redrawn from Hubrecht (1887). Scale bar = 5 mm.

Fig. 35. *Baseodiscus giardii.* Recorded distribution from New Zealand.

OCCURRENCE: Originally dredged from 1280 m in blue mud at 37°34'0"S, 179°22'0"E, east of central North Island, but subsequently also collected from 548 m on rock at Summit, Great King, Three Kings Islands, New Zealand (Baylis 1915) (Fig. 35).

Class ENOPLA Schultze, 1853
Subclass HOPLONEMERTEA Hubrecht, 1879
Superorder MONOSTILIFERA Brinkmann, 1917

Family **AMPHIPORIDAE** McIntosh, 1873-74

Amphiporus Ehrenberg, 1831

TYPE SPECIES: *Amphiporus lactifloreus* (Johnston, 1828)

DIAGNOSIS: Usually 2 pairs of transverse cephalic furrows; rhynchocoel extends to, or almost to, posterior end of body, with wall composed of separate circular and longitudinal-muscle layers; proboscis generally well developed; dermis development variably thick or thin; body-wall musculature generally well developed, with or without diagonal muscle layer between circular and longitudinal muscles; longitudinal muscle stratum in anterior body regions either a single layer or, less commonly, divided into 2 in some species by parenchymatous wedge; dorsoventral muscles present but usually few in number and restricted to intestinal regions; nervous system with neither neurochords or neurochord cells; apical organ present; cephalic glands usually few in number and small; cerebral sensory organs anterior to cerebral ganglia, variably developed according to species; blood vascular system with 3 longitudinal vessels, middorsal vessel with single vascular plug; excretory system positioned between rear of cerebral ganglia and foregut; intestinal caecum present, with a pair of anterior diverticula as well as lateral pouches; eyes normally numerous and distributed in groups, occasionally few or none; sexes separate (Gibson: 1994: 120).

Amphiporus mortonmilleri sp. nov.   (Figs 36-42)

TYPE SPECIMEN: Holotype mature male, complete set of transverse sections, 191 slides, H-785 deposited in the NZOI collection at NIWA, Wellington.

TYPE LOCALITY: Matheson Bay (Fig. 36), lower shore under flat, clean rock, collected 24 August 1992, one specimen.

ETYMOLOGY: The species is named in honour of John Morton and Michael Miller, whose book *The New Zea-*

land Sea Shore, which I read extensively during my visit to New Zealand in 1992, was an invaluable source of information.

Fig. 36. *Amphiporus mortonmilleri* sp. nov. Recorded distribution in New Zealand.

DESCRIPTION: *External features*: In life with a typical 'amphiporid' shape (Fig. 37A), during normal movement varying in length from 25–35 mm with maximum width of about 2 mm. Rhynchocoel and proboscis, visible through pale pink general body colour, extending to bluntly rounded posterior tip. Head strongly dorsoventrally flattened, with 2 pairs of oblique dorsal cephalic furrows (Fig. 37B); anterior pair extending to ventral cephalic surface to meet in rather elongate forwardly projecting V-shape that ends close behind median ventral epidermal head groove, whereas posterior pair meet medially and dorsally to form backwards-pointing V-shape; brain lobes visible below posterior furrows. Four groups of eyes comprising an anterior row of 4–6 ocelli close to each anterolateral margin, with 2 groups of about 8 ocelli lying dorsolaterally about midway between the 2 pairs of cephalic furrows (Fig. 37B). Orange lateral intestinal diverticula also visible through body wall. During collection, clouds of white spermatozoa discharged by specimen.

Body wall, musculature and parenchyma: Epidermis in cephalic region 35-45 μm tall ventrally and dorsally, somewhat thicker (55–60 μm) on lateral margins. Behind foregut region a gradual decrease in epidermal height posteriorly to minimum of about 15 μm dorsally and ventrally, 35–40 μm on either side. Epidermal glands mainly confined to distal half of layer and nowhere particularly dense, apparently mostly mucous and bacillary in terminology of Norenburg (1985). Epidermal basement lamina and basal-cup zone, though not always clear, resembling the arrangement depicted by Norenburg (1985). Dermis mostly only 3-4 μm thick but distinct.
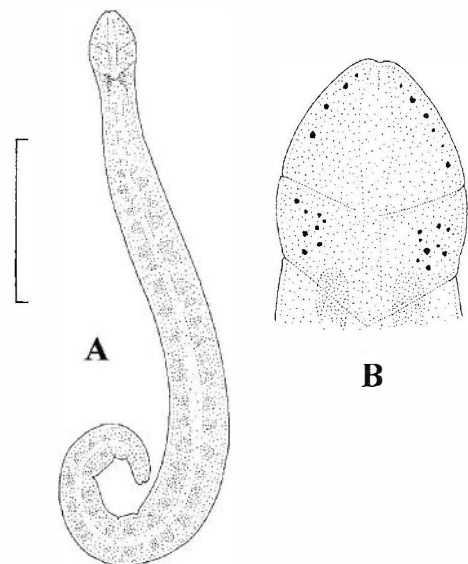

Fig. 37. *Amphiporus mortonmilleri* sp. nov. **A**. General view of the holotype, based on sketches made from life. **B**. Enlargement of the head, viewed from the dorsal aspect, to show the distribution of the eyes and cephalic furrows. Scale bar = 5 mm (refers to A only).

The body-wall musculature mainly comprising outer circular and inner longitudinal layers, but no diagonal layer, as found in many hoplonemerteans, distinguishable between them (Fig. 38). In posterior foregut region of body circular layer mostly 5–10 μm thick, the longitudinal coat 15-60 μm or more, depending upon local contraction. In general, longitudinal layer thickest on lateral body margins, but both layers gradually thinning posteriorly. In foregut region a thin inner circular-muscle layer, at most only about 3–4 μm deep, extending around body (Fig. 38). Fibres leading from this inner layer extending around foregut and on dorsolateral margins isolated strands leading dorsally, passing through longitudinal musculature and merging with outer circular coat.

Running forwards in brain region longitudinal musculature becoming incompletely divided into thin inner (5–10 μm) and thicker outer (15–30 μm) zones by connective-tissue membranes (Fig. 39). In front of brain inner longitudinal fibres becoming thicker (up to about 15 μm or more), ventrally enclosing oesopha-

gus below and just in front of ganglia. Only inner longitudinal fibres contributing to proboscis insertion, i.e., no cerebral septum in Kirsteuer's (1974) terminology. Both outer circular and longitudinal layers reduced in thickness in head, though both reaching anterior tip of body. Cephalic retractor muscles apparently derived only from outer portion of body-wall longitudinal muscle layer.

Parenchymatous connective tissues sparsely developed in all parts of body.

Proboscis apparatus: Proboscis pore opening ventrally and subterminally from rear of median ventral epidermal furrow approximately 125 μm behind tip of head leading into a rhynchodaeum; latter at first thin-walled, unciliated, without glands. Farther back, however, at level where ciliated cerebral canals opening from anterior cephalic furrows, rhynchodaeum becoming somewhat constricted, its epithelium thicker (up to about 7-8 μm) and enclosed by well-developed layer of circular muscles 15–30 μm across forming sphincter close in front of proboscis insertion; this situated some distance in front of brain lobes, approximately level with glandular region of cerebral organs.

Rhynchocoel extending almost to hind end of body, its wall containing separate circular and longitudinal muscle layers.

Proboscis large, well developed, as long as or longer than body; a short anterior portion extending from proboscis insertion to rear brain region; anteriormost region 90–200 μm diameter, comprising thin inner and outer linings sandwiching longitudinal muscle layer >15–30 μm thick in which the 13 proboscis nerves already well established. The longitudinal fibres distinctly fasciated (cf. Crandall 1993) in bundles enclosed by connective tissue. No circular-muscle layer distinguishable. First traces of proboscis epithelium appearing at about midbrain level, here about 10–12 μm thick, not organised into papillae, and no gland cells (Fig. 39). Circular-muscle layer established soon after, with epithelium acquiring a papillate appearance; overall diameter of proboscis here about 250 μm. Main anterior region of proboscis longest portion by far, extending back to between half and two-thirds of body length; for much of its length 0.2-0.3 mm in overall diameter, comprising a glandular epithelium arranged into narrow papillae 45 μm or more tall, outer circular-muscle layer 7–12 μm thick, an inner longitudinal muscle layer 15-25 μm across and delicate inner lining (Fig. 40). Connective-tissue membranes between the 2 muscle layers and longitudinal musculature and inner lining at first thin but distinct; farther back, however, a thick connective-tissue coat, up to 15–20 μm or more across, found immediately below epithelium. Gland cells predominantly acidophilic, though scattered basophilic glands distinguishable in posterior half of main region, forming the major type
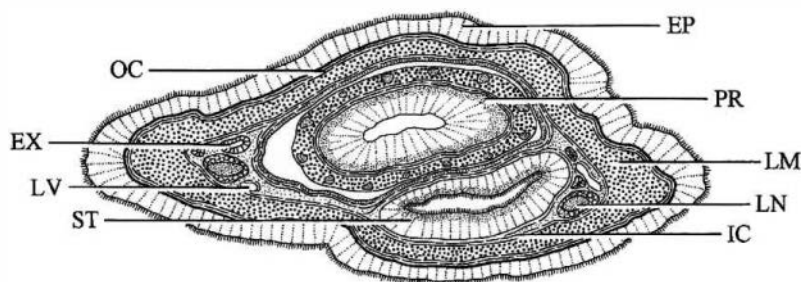
Fig. 38. *Amphiporus morton-milleri* sp. nov. Camera lucida drawing to show the arrangement of the different body structures in the anterior stomach region of the body. Scale bar = 500 μm.
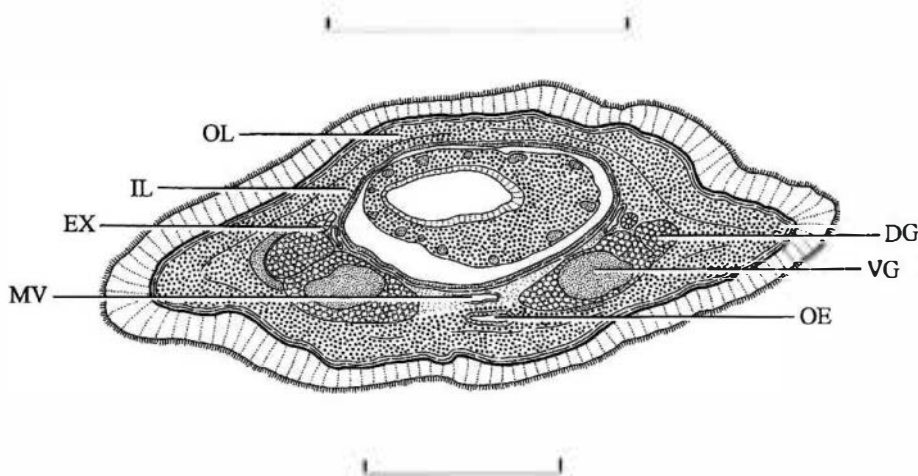

Fig. 39. *Amphiporus morton-milleri* sp. nov. Camera lucida drawing through the posterior brain region, showing the rear portions of the dorsal ganglia extending above the ventral lobes where these merge into the lateral nerve cords. Note the body-wall longitudinal-muscle layer incompletely divided into inner and outer portions by connective-tissue membranes. Scale bar = 250 μm.

just before origin of stylet bulb region. Towards its posterior region main chamber gradually narrowing to overall diameter of about 200 μm.

Muscular stylet bulb region, housing the stylet apparatus, some 350 μm in overall diameter, for much of its length containing well-developed peripheral layer of orange-staining gland cells. Three accessory stylet pouches, each containing 2 or 3 reserve stylets in various stages of styletogenesis. Stylet basis massive, tapering, conical, up to 90 μm in diameter and about 160-170 μm long. Single central stylet was damaged, but well-formed reserve stylets measuring 50 μm long and 15 μm in diameter at their base; stylet to basis ratio thus approximately 1:3.3.

Posterior chamber comprising glandular epithelium 30–35 μm in maximum height, longitudinal muscle layer 15–20 μm thick and inner lining. Neither proboscis nerves nor circular-muscle layer distinguishable in posterior region of proboscis.

Alimentary canal: Oesophagus (Fig. 39) opening from rhynchodaeum close in front of its circular muscle sphincter, forming a long, dorsoventrally compressed tubular canal up to about 50–55 μm wide; its epithelium at most about 5 μm thick, neither ciliated nor glandular. Behind brain oesophagus gradually widening posteriorly to about 120–130 μm where merging with stomach. At junction between oesophagus and stomach, marked by appearance of basophilic glands in densely ciliated stomach epithelium, ventral stomach epithelium extending more anteriorly than dorsal, hence oesophagus appearing as open canal running along upper margin of stomach for short distance.

Two histologically distinct regions recognisable in stomach; smaller, anterior, region essentially forming rather compressed tubular channel (Fig. 38), up to about 350 μm wide and 120 μm high, in which epithelium, 20–40 μm thick, very little folded and composed predominantly of basophilic gland cells. Farther back, however, stomach wall becoming increasingly folded posteriorly, with acidophilic glands simultaneously appearing between basophils. Towards rear of stomach, approaching the pyloric portion of foregut, epithelial folding becoming increasingly less pronounced, epithelial height reduced to 15 μm or less, and gland-cell density reduced. Stomach and pyloric region merging imperceptibly as gland cells in epithelium gradually disappear and foregut forms a dorsoventrally compressed tubular canal extending beneath rhynchocoel. Pyloric portion of the foregut gradually narrowing to a dorsoventrally compressed tube only 60–70 μm wide and extending back for about 1.6 mm, comprising longest part of anterior gut region; entire foregut accounts for only about 12% (approximately 2.7–3 mm) of total body length, of which more than half is accounted for by pylorus.

Narrow intestinal caecum extending anteriorly for some 1.4–1.5 mm below pyloric portion of foregut but not reaching the stomach. Caecum lacking lateral diverticula along its length, but just behind its anterior limit a single lateral pouch emerging on each side and bending forward to extend anteriorly on either side of rhynchocoel; these pouches not reaching rear of brain, ending just behind anterior portion of stomach. Intestine is first dorsolaterally compressed but farther back forming a more or less tubular ventral canal, its sparsely ciliated epithelium 30 μm or more thick. Throughout intestine length paired and distally lobed lateral diverticula reaching outwards on either side, inserting between dorsal and ventral 'layers' of testes (Fig. 41). In contrast to gastrodermis lining main intestinal channel with few gland cells and either no food vacuoles or accumulations of intralumen acidophilic globules, epithelium of each diverticulum is densely packed with
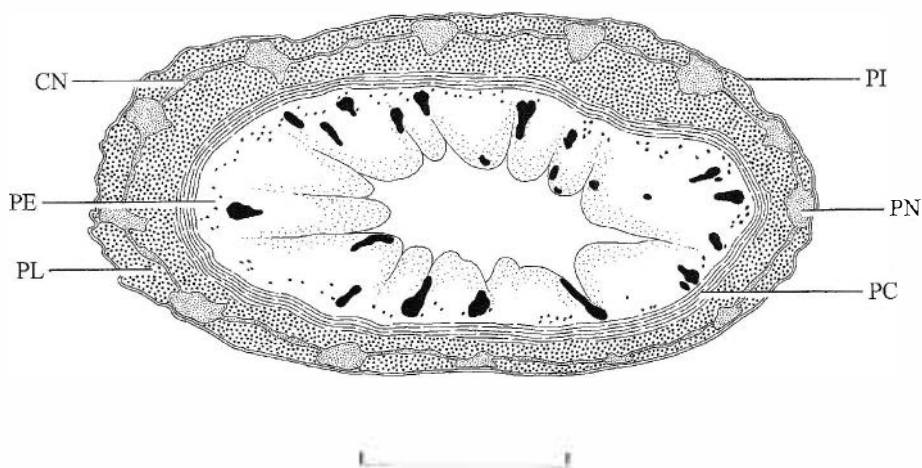

Fig. 40. *Amphiporus mortonmilleri* sp. nov. Camera lucida drawing through the anterior region of the proboscis. Scale bar = 100 μm.

large numbers of acidophilic food vacuoles 2–3 μm in diameter. Towards posterior end of intestine its diverticula contain few food vacuoles, and gastrodermal lining of both main channel and diverticula are similar in appearance.

Blood system: A pair of slender cephalic vessels in head meet close to proboscis pore by a suprarhynchodaeal connective and extend back in a lateral position, but run deeper near cerebral sensory organs to continue posteriorly close to their inner margins; as these vessels approach brain they expand to form distinct vascular chambers, 40 μm or more across, that run next to rhynchocoel wall between anterior limits of dorsal and ventral brain lobes on each side, then narrow as sandwiched between brain lobes and ventrolateral rhynchocoel margins, continuing in this position until, towards rear of ventral cerebral commissure, they turn inwards and meet below rhynchocoel to form origin of middorsal vessel. This vessel runs for a short distance in ventral rhynchocoel wall before emerging to continue back below rhynchocoel; throughout much of foregut and anterior intestinal regions it is compressed between gut and rhynchocoel and often indistinguishable.

Whether or not middorsal vessel forms a vascular plug where it runs in rhynchocoel wall not certainly determined but a small protrusion, only about 15 μm in diameter, may represent a plug compressed when proboscis fully retracted. Soon after it emerges from rhynchocoel wall, middorsal vessel branches on each side, originating lateral blood vessels. These continue posteriorly close to the lateral nerve cords (Figs 38, 41), meeting just anterior to anus by a supraintestinal connective. Pseudometameric transverse connectives lacking between middorsal and lateral vessels in intestinal regions of body.

Nervous system: No unusual features of the nervous system distinguishable. Cerebral ganglia are enclosed by a thin but distinct outer neurilemma, but an inner neurilemma separating neuroganglionic and fibrillar brain components lacking. Dorsal and ventral ganglia of similar size, but dorsal lobes set wider apart than and dorsolateral to ventral. Dorsal and ventral cerebral commissures, respectively ~ 15 μm and 45 μm thick, dorsal with more anterior origin, curving backwards to loop over rhynchocoel. In dorsal tissues of each ventral lobe a single giant cell, 15–20 μm in diameter with a spherical nucleus 8–10 μm across and single acidophilic nucleolus 2–3 μm diameter. Towards posterior brain region, dorsal and ventral lobes separated by outer neurilemma but otherwise remaining in contact, the posterior end of each dorsal lobe extending back above anterior portion of each lateral nerve cord; lateral nerve cords extending almost to posterior end of body, there joined by a supraintestinal commissure. Lateral nerve cords throughout their length with only a single neuropil.

Apical organ and cephalic glands: Typical lobular cephalic glands anteriorly medially concentrated where extended in front of proboscis pore, opening just behind tip of head on ventral surface, the apical (frontal) organ appearing as a simple ciliated pore at anterior end of ventral epidermal median furrow; cephalic glands apparently not discharging via improvised pores as in several terrestrial hoplonemerteans. Farther back glands continuing medially above rhynchodaeum, but laterally separating to form isolated, scattered lobules (Fig. 42).

Sense organs: Four groups of eyes comprising an anterior row of 4–6 ocelli close to each anterolateral margin, with 2 groups of about 8 ocelli lying dorsolaterally about midway between 2 pairs of cephalic furrows (Fig. 37B). Eyes are mostly small, about 20–25 μm in diameter.

Cerebral sensory organs (Fig. 42) complex, very large, well developed, opening ventrolaterally from anterior pair of cephalic furrows close below lateral head margins. Ciliated cerebral canals initially about 20–25 μm in diameter, lined by columnar epithelium some 15 μm tall, but after penetrating epidermal basement membrane, expanding to form a large ciliated chamber, 60 μm wide and 15 μm dorsoventrally, mostly surrounded by epithelium 20–25 μm tall. Acidophilic glands appearing on inner lateral margin of each chamber soon after ciliated canal has passed through epidermal basement membrane; chambers extending back, passing circular muscle sphincter enclosing rhynchodaeum, then forking to form outer lateral pouch and main cerebral canal; pouch up to
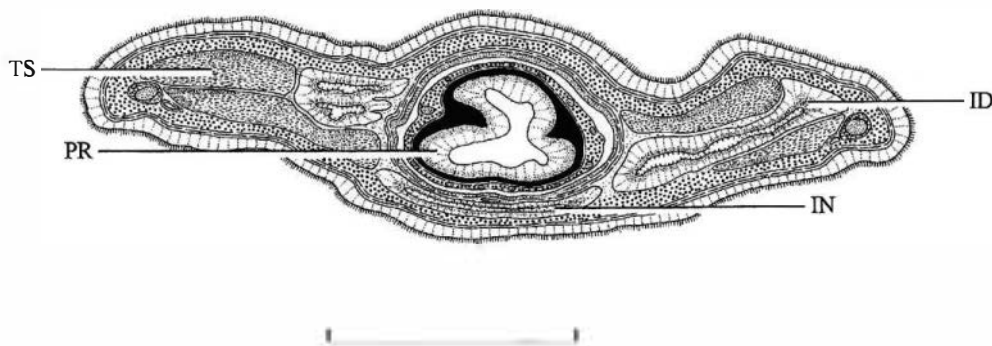

Fig. 41. *Amphiporus mortonmilleri* sp. nov. Camera lucida drawing through the posterior body region to show the testes and lateral intestinal diverticula. Scale bar = 500 μm.

about 90 μm wide and 45–50 μm tall, continuing back for short distance then ending blindly. Main ciliated canal continues directly backwards as a densely ciliated tubule, some 45 μm in overall diameter, in which major and minor canals similar to those described by Ferraris (1979) are distinguishable. Epithelium lining main cerebral canal with a densely striated appearance, contrasting markedly with near-vacuolate appearance of epithelium lining lateral pouch. Behind posterior limit of lateral pouch cerebral organs essentially consisting of a median dorsal ciliated canal bounded ventrally by neuroganglionic tissue and on both sides by various types of glandular tissues, though in one cerebral organ outer lateral glandular region extends dorsally above ciliated canal, the whole organ appearing almost to have rotated through 90°. Ciliated canal ends blindly in a neuroganglionic mass, from which the thick (25–30 μm) cerebral organ nerve continues directly posteriorly to join with ventral brain lobes towards rear of ventral cerebral commissure. Glandular components of cerebral organs extend back either below or alongside the brain to a level just behind ventral commissure. In transverse section the glands have a broadly oval shape, up to about 180 μm in overall width, 75–90 μm in dorsoventral height, extending throughout about 400 μm longitudinally.

No other sensory organs distinguishable in the specimen.

Excretory system: Excretory system extending from close behind rear of brain back to about mid-stomach region, comprising 2 or 3 thick-walled collecting tubules on each side of body running near lateral nerve cords (Figs 38, 39). Tubules have maximum diameter of 15–20 μm. A single, slender efferent duct on each side opening on ventrolateral body surface about two-thirds along length of excretory system.

Reproductive system: Single known specimen is a mature male: testes first appear in pyloric region of foregut, located singly on either side of rhynchocoel, their number increasing posteriorly and throughout much of intestinal region dorso- and ventrolateral rows of testes more or less packing each side of body. Lobes of intestinal diverticula located medially between the rows on either side, but between diverticula dorsal and

ventral testes abut directly against each other (Fig. 41). Testes large, very irregular in shape, packed with ripe spermatozoa; testicular walls with large numbers of both spermatogonia and primary spermatocytes. Testes occur almost to posterior tip of body, although in posteriormost region their 'two-tiered' arrangement lost, occurring singly on either side of gut. In rectal region of intestine small accumulations of ripe spermatozoa distinguishable in intestinal lumen, an artefact induced during collection. A duct system comparable to Takakura's duct of mature male *Carcino-nemertes* species (Humes 1941) not found. No open gonoducts found, but in several places sperm-filled extensions of testes extending laterally or dorsolaterally above longitudinal nerve cords almost to body surface.

DISCUSSION: The morphology of the present specimen broadly conforms with previous accounts given for the genus *Amphiporus*, although this taxon still lacks a definitive diagnosis (Gibson 1985; Norenburg 1986; Gibson & Crandall 1989) and several of the species at present retained within the genus will almost certainly be taxonomically relocated in the future. One heterogeneous group of species, originally separated from *Amphiporus sensu stricto* (*A. bioculatus* McIntosh, 1873–74; *A. hastatus* McIntosh, 1873–74; *A. korschelti* Friedrich, 1940; *A. nebulosus* Coe, 1901) and collectively known as the "*Amphiporus hastatus* group", is at present retained within *Amphiporus* only because they are too poorly described to be reliably reassigned to other genera (Kirsteuer 1974). One anatomical feature shared by each member of the "*hastatus* group" is an anteriorly divided body-wall longitudinal musculature, but this character is also found in some other monostiliferous hoplonemertean taxa (Table 3). The longitudinal musculature of the present specimen is also anteriorly divided, but by connective-tissue membranes rather than distinct parenchymatous wedges. Of the taxa known to possess a divided longitudinal muscle layer, the genus *Cryptonemertes* and three of the four species comprising the "*hastatus* group" differ from the present specimen in possessing extracerebral blood vessels which may or may not form a lacunar complex depending upon the species, whilst in *Crypto-*
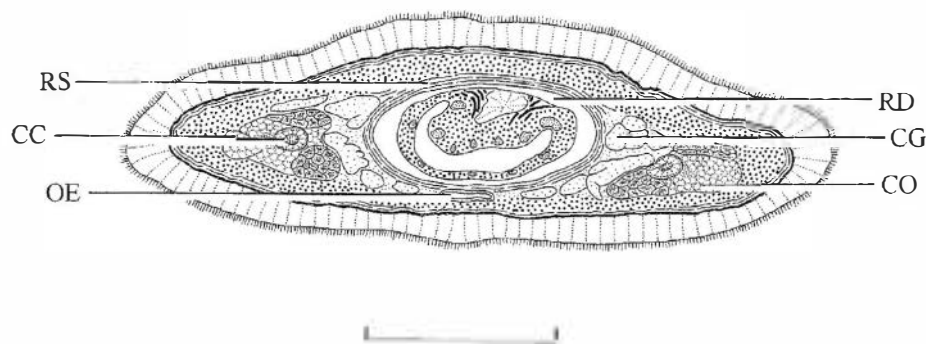

Fig. 42. *Amphiporus morton-milleri* sp. nov. Camera lucida drawing through the head at the beginning of the rhynchodaeal circular muscle sphincter to show the cerebral sensory organs and cephalic glands. Scale bar = 250 μm.

nemertes, Eonemertes, Tetranemertes, and most species of *Paranemertes* the rhynchocoel is less than half the body length and often significantly much less. *Amphiporus korschelti* and *Pantinonemertes* species differ from the present form in possessing a diagonal muscle layer in their body wall, members of the latter taxon also possessing a very much more complex excretory system which includes large numbers of binucleate flame cells (Moore & Gibson 1981). *Prosadenoporus* and *Prosorhochmus* differ from the New Zealand specimen in possessing simple, unbranched cerebral canals and a split precerebral septum (Moore & Gibson 1988a), whilst *Paramphiporus* has a closed precerebral septum and the cephalic retractor muscles are derived from both inner and outer portions of the body-wall longitudinal musculature in *Correanemertes*. On just the features listed in Table 3, however, the present form cannot be separated from *Amphiporus bioculatus*, *Heilogonemertes*, certain species of *Paranemertes*, or *Poseidonemertes*. *Heilogonemertes* differs from the present specimen in possessing a rhynchocoel only about three-quarters of body length, no inner circular-muscle layer in body wall, no apical organ, lateral nerve cords with short accessory nerves and a long intestinal caecum which possesses neither anterior pouches not lateral diverticula, whilst in *Poseidonemertes* there is a split precerebral septum. Most species of *Paranemertes* differ from the present form in possessing a short rhynchocoel, but in three forms (*P. biocellatus*, *P. incola* and some records of *P. peregrina*) the rhynchocoel is reported as extending well beyond the middle region of the body. *Paranemertes biocellatus*, however, has extracerebral blood vessels in its head, in *P. incola* the body-wall longitudinal musculature is not divided, and descriptions of *P. peregrina* differ such that probably at least two species have been recorded under this name. *Amphiporus bioculatus*, with only two eyes, is not a well-described species and, indeed, was identified as a *nomen dubium* by Gibson and Crandall (1989). Kirsteuer (1967) in fact separated Brazilian records of the species into a new genus, *Correanemertes*, pointing out that, because of differences in the cephalic blood system the European form should be excluded from the "hastatus group" and both North American and European examples of *A. bioculatus* may belong in the genus *Paramphiporus*. The present New Zealand nemertean cannot, therefore, be identified with either any of the known species of *Amphiporus* which are known to possess a divided longitudinal musculature, or with any of the other genera in which the same character is present. Though showing certain anatomical differences from most species of *Amphiporus* for which descriptions have been given, the separation of the present form into a distinct genus cannot at present be justified, and the New Zealand form is therefore placed in this group as a new species, *Amphiporus mortonmilleri* sp. nov.

Amphiporus novaezelandiae (Quoy & Gaimard, 1833)
(Figs 43–44)

ORIGINAL DESCRIPTION: Quoy & Gaimard, 1833: 290–291, pl. 24, figs 15–19 (as *Borlasia novae-zelandiae*).

ADDITIONAL LITERATURE RELATING TO NEW ZEALAND RECORDS: Hutton 1880 (as *Borlasia novae-zealandiae*), 1904 (uncertainly as either *Amphiporus novae-zealandiae* or *Drepanophorus novae-zealandiae*); as *Amphiporus novaezelandiae* (Bürger 1904; Gibson & Crandall 1989; Gibson 1995, in press; Gibson *et al.* in press); for other synonyms see Gibson 1995.

DESCRIPTION: *External features:* About 7–8 cm long, the dorsoventrally flattened body ending in a sharply pointed tail. Head heart-shaped, distinctly marked off from body by an obvious constriction from rear of which extend several short intensely reddish-brown streaks. Overall colour reddish-brown dorsally, somewhat darker in midline (Fig. 43A), yellowish ventrally. Paired lateral blood vessels and intestinal diverticula visible through ventral body surface (Fig. 43B).
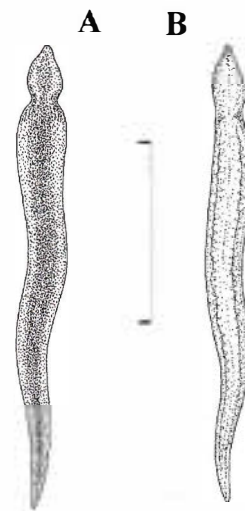

Fig. 43. *Amphiporus novaezelandiae.* The external features of a complete specimen, viewed from dorsal (A) and ventral (B) aspects. Redrawn from Quoy & Gaimard (1833). Scale bar = 30 mm.

Internal anatomy: Nothing is known about the internal anatomy of this species, Quoy and Gaimard (1833) established the taxon entirely on external features. Diesing (1850), with neither justification nor further details, renamed the species *Chlamydocephalus gaimardi*, and Hutton (1904) commented that it may belong in either the genus *Amphiporus* or *Drepanophorus*. Gibson and Crandall (1989) cited the species as a *nomen dubium*. Whether or not this species is even a hoplonemertean is uncertain, since Quoy and Gaimard (1833: 290) noted that "La bouche est une longue fente très-déliée", which suggests that it may be some form of heteronemertean.

OCCURRENCE: Quoy and Gaimard (1833) found the species in the Bay of Islands, North Island (Fig. 44), but provided no details about its habitat.

Table 3

Some of the major morphological features which can be used to distinguish between monostiliferous hoplonemertean taxa in which the body-wall longitudinal muscle layer is anteriorly divided, completely or incompletely, into inner and outer zones. Data taken from McIntosh (1873–74), Oudemans (1885), Joubin (1890), Bürger (1895), Coe (1901, 1905), Bergendal (1903), Friedrich (1940), Kirsteuer (1965, 1967, 1974), Sánchez and Cancino (1980), Moore and Gibson (1981, 1988a), Stricker (1982), Gibson (1982, 1990a, b), Gibson et al. (1982, 1990), Roe and Wickham (1984), Gibson and Moore (1985), Riser (1988a), Gibson and Crandall (1989), Kajihara et al. (2001).

Taxon	1	2	3	4	5	6
Alaxinus	O	O	O	O	I	+
"*Amphiporus hastatus* group"[a]						
A. bioculatus McIntosh, 1873-74[b]	O	O	?	?	+	?
A. hastatus McIntosh, 1873-74[b]	E+	O	?	?	+	?
A. korschelti Friedrich, 1940[c]	E	+	O	?	+	O?
A. nebulosus Coe, 1901[c]	E	O	?	?	+	O?
Correanemertes	O	O	O	O+I	+	O?
Cryptonemertes[d]	E+	O	O	O	O	O
Dananemertes	O	+	C	?	+	?
Diopsonemertes	O	+	O	I	+	O
Eonemertes	O	O	O	O	O	O
Fasciculonemertes	O	+	O	I	+	+
Notogaeanemertes[d]	E	O?	O	?	+	+?
Pantinonemertes	O[e]	+	O	O	+	O
Paramphiporus[d]	O	O	C	O	+	O?
Paranemertes[f]	O[g]	O	?[h]	?[h]	O[I]	O?
Paranemertopsis[d]	O	+	C/O[j]	O	O	O
Poseidonemertes	O[k]	O	S	I	+	O[l]
Prosadenoporus[d]	O	+	S	I	+	+
Prosorhochmus	O	+	S	I	+	O[m]
Tetranemertes	O	O	O	O	O	O
Heilogonemertes gen. nov.	O	O	O	O+I	+	O
Noteonemertes gen. nov.	O	+	O	O+I	+	O

1   Cephalic blood system a simple vascular loop (O), with extracerebral vessels (E) or forming a lacunar complex (+).
2   Body-wall musculature with (+) or without (O) a diagonal layer between circular and longitudinal muscles.
3   Precerebral septum absent (O), split (S), or closed (C) (see Kirsteuer (1974), for explanation of terminology).
4   Cephalic retractor muscles derived from inner (I) or outer (O) portions of body-wall longitudinal musculature.
5   Rhynchocoel more than half length of body (+) or confined to anterior half (O), mostly less than one-third of body length.
6   Neurochord cells present (+) or absent (O) in central nervous system.
[a]   The "*Amphiporus hastatus* group" is a heterogeneous assemblage of species, originally separated from *Amphiporus sensu stricto* by Friedrich (1955), at present retained within the genus because they are too poorly described to be reliably assigned to other genera (Kirsteuer 1974; Gibson & Crandall 1989; Gibson 1995).
[h]   Identified as *nomina dubia* by Gibson and Crandall (1989) but retained as valid species by Gibson (1995).
[c]   These taxa were regarded as *species inquirendae* by Gibson and Crandall (1989) but retained as valid by Gibson (1995).
[d]   The body-wall longitudinal-muscle layers in these genera are incompletely divided, though not in the same way in each genus (Kirsteuer 1965; Gibson 1986b, 1990a; Moore & Gibson 1988a; Riser 1988a).
[e]   Except in *P. californiensis* Gibson, Moore & Crandall, 1982, where the cephalic blood supply forms a capillary network of small vessels (Gibson et al. 1982).
[f]   In two members of this genus, *P. incola* Iwata, 1952, and *P. plana* Iwata, 1957, the longitudinal musculature is not apparently anteriorly divided (Iwata 1952, 1957).
[g]   Except in *P. biocellatus* Coe, 1944, where the blood system in the head includes extracerebral vessels (Kirsteuer 1974).
[h]   With the exception of *P. biocellatus* and *P. brattstroemi* Friedrich, 1970; in the former there is no precerebral septum and the cephalic retractor muscles are formed from the inner longitudinal muscle layer, in the latter no precerebral septum has been noted but the cephalic retractors are derived from the outer longitudinal-muscle layer (Kirsteuer 1974); in *P. sanjuanensis* Stricker, 1982, the same condition as in *P. biocellatus* prevails (Stricker 1982).
[i]   Except in *P. biocellatus*, *P. incola* and some records of *P. peregrina* Coe, 1901, where the rhynchocoel is recorded as extending well behind the middle region of the body (Coe 1944; Iwata 1952; Kirsteuer 1974).

[j] The precerebral septum in this genus is described as intermediate in organisation between the closed type and no septum (Gibson 1990a).

[k] Roe and Wickham (1984) noted that in some specimens of *P. collaris* Roe & Wickham, 1984, a thin diagonal-muscle layer could be distinguished.

[l] Most accounts of *Poseidonemertes* species make no reference to neurochord cells, but Roe and Wickham (1984) record them as absent from *P. collaris*.

[m] Bürger (1895) commented that in the type species of this genus, *P. claparedii* Keferstein, 1862, there were neither neurochord cells nor neurochords, but Gibson and Moore (1985: 153) noted for other members of the genus that "Occasional cells [larger than most of the brain cells] ... appear to represent neurochord cells."

Fig. 44. *Amphiporus novaezelandiae*. Recorded distribution in New Zealand.

Correanemertes Kirsteuer, 1967

TYPE SPECIES: *Correanemertes bioculatus* (Corrêa, 1958)

DIAGNOSIS: Monostiliferous marine nemerteans; rhynchocoel extending into posterior half of body, with wall containing 2 distinct muscle layers; anterior region of proboscis with 2 muscle layers (outer circular, inner longitudinal), proboscis armature consisting of single central stylet and 2 accessory stylet pouches. Body-wall musculature with neither diagonal nor inner circular layers, longitudinal muscles anteriorly divided into inner and outer regions; no precerebral septum; apical organ present, cephalic glands extensive, posteriorly reaching behind brain; cerebral sensory organs situated in front of brain; cerebral ganglia with neither neurochord cells nor inner neuri-lemma; lateral nerve cords without accessory nerves. Foregut opening into rhynchodaeum, divisible into oesophagus, stomach and pyloric regions, intestinal caecum short with pair of very long anterior pouches, lateral diverticula confined to main intestinal canal; blood system simple, with cephalic loop, single middorsal and paired lateral vessels, dorsal vessel forming vascular plug, longitudinal vessels not transversely linked by pseudometameric transverse connectives; parenchyma not extensive; excretory system confined to foregut region; eyes 2; sexes probably separate (based on Corrêa 1958 and Kirsteuer 1974).

Correanemertes gordoni sp. nov.   (Figs 45–50)

TYPE SPECIMEN: Holotype ripe female, complete set of transverse sections, 83 slides, H-720 deposited in NIWA/NZOI collection in Wellington.

TYPE LOCALITY: Waitara Beach (Fig. 45), lower shore under boulder embedded in coarse black volcanic sand, collected 30 August 1992, one specimen.

ETYMOLOGY: The species is named after Dr Dennis P. Gordon as a tribute to his work on the marine fauna of New Zealand.

DESCRIPTION: *External features:* Unique specimen was about 18 mm long and 1 mm or less wide in life. Anterior third of body pale brown above, whitish-brown below, but throughout most of intestinal region large numbers of white gonads were evident on all sides of body (Fig. 46A). Head bluntly pointed, with a single pair of oblique cephalic slits meeting neither dorsally nor ventrally; in lateral aspect the furrows giving head a somewhat shark-like appearance (Fig. 46B). On upper surface of head a distinct median longitudinal ridge (Fig. 46C). Tail bluntly pointed with no trace of caudal cirrus. Body widest in intestinal regions and more or less dorsoventrally flattened. Four distinct eyes.

Body wall, musculature and parenchyma: Glandular epidermis anteriorly 15–30 μm in height, reduced to 10-15 μm in posterior half of body. Connectivie-tissue

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Fig. 45. *Correanemertes gordoni* sp. nov. Recorded distribution in New Zealand.

dermis distinct but nowhere more than about 3–4 μm thick. Body-wall musculature comprising outer circular and inner longitudinal layers; no evidence of a diagonal layer distinguished and no inner circular muscles. In stomach region (Fig. 47) circular and longitudinal muscle layers respectively 7–8 μm and 15–25 μm thick, both reduced to about half these values in posterior half of body. Longitudinal musculature anteriorly divided. Close behind brain postcerebral extensions of cephalic gland lobules intruding into longitudinal-muscle layer, at first isolating discrete bundles of fibres that continue forwards towards brain; passing brain, however, they coalesce to form a distinct inner layer up to 6–7 μm thick, running adjacent to outer neurilemma of cerebral ganglia (Fig. 48). This inner longitudinal muscle layer less obvious above rhynchocoel, but distinct on lateral, ventrolateral, and
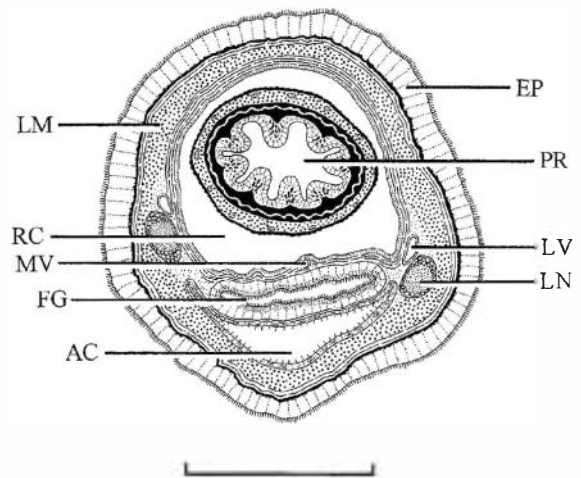
Fig. 47. *Correanemertes gordoni* sp. nov. Camera lucida drawing through the posterior foregut region to show the arrangement of the various body structures. Scale bar = 200 μm.
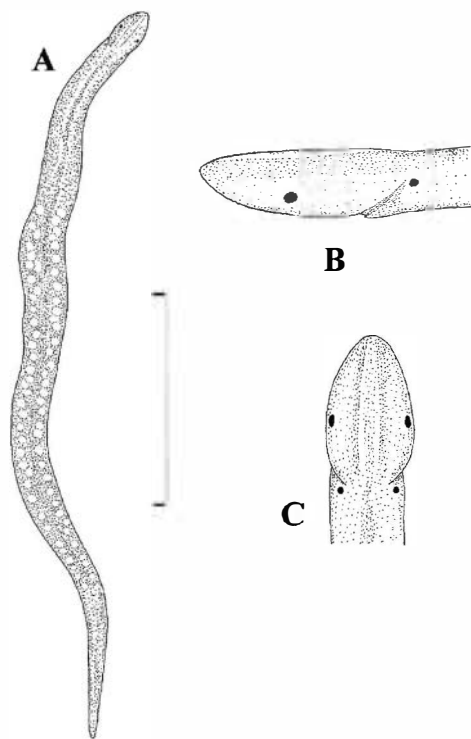

Fig. 46. *Correanemertes gordoni* sp. nov. Drawings made from life to show: **A**, the general features of the complete specimen; **B**, the shark-like appearance of the head in lateral view; **C**, the head in dorsal aspect (C). Scale bar = 5 mm (refers to A only).

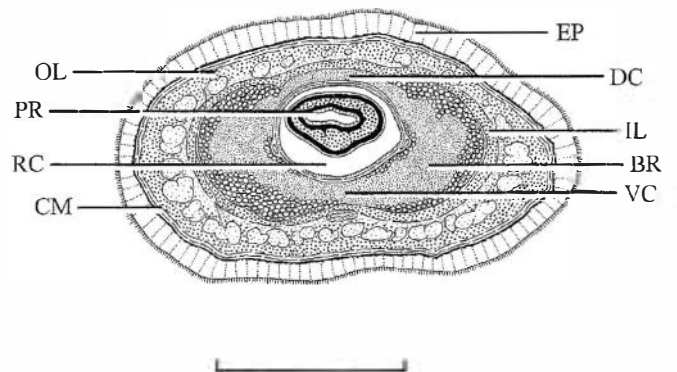**Fig. 48.** *Correanemertes gordoni* sp. nov. Camera lucida drawing through the cerebral region to show how the body wall longitudinal muscle layer is anteriorly divided by posterior extensions of the cephalic glands. Scale bar = 200μm.

ventral cerebral margins. In front of brain proboscis insertion formed only from muscle fibres of inner body-wall longitudinal layer, hence no precerebral septum, as defined and illustrated by Kirsteuer (1974: fig. 36). Outer portion of longitudinal musculature and circular muscle layer, together continue forwards into the head.

Parenchymatous connective tissues sparingly developed throughout body.

Proboscis apparatus: Proboscis pore opening close to anterior tip of body into an elongate rhynchodaeum that is dorsoventrally compressed by well-developed cephalic glands. For most of its length rhynchodaeal wall thin, but near proboscis insertion epithelium up to about 6–8 μm thick, more distinct, and layer of circular muscles 10–12 μm across surrounding chamber. Rhynchodaeum not ciliated or glandular.

Rhynchocoel extending for about 60% of body length; its wall with 2 separate muscle layers (Fig. 47) — inner longitudinal fibres compact, only 2–4 μm thick, outer circular fibres are more loosely disposed, forming a layer 12–15 μm across.

Proboscis just less than half body length, but well developed. Its anterior chamber not uniformly constructed; leading back from proboscis insertion, first

portion of anterior chamber (Fig. 49A) some 70–80 μm in overall diameter, consisting of low outer epithelium lacking gland cells, a thick outer connective-tissue layer, a longitudinal-muscle coat about 15 μm deep, a distinct inner connective-tissue zone and a delicate inner lining. The 12 proboscis nerves in this region small and indistinct, lying in proximal portion of longitudinal muscle layer. Towards rear of brain proboscis beginning to increase diameter to 90–100 μm, its epithelium also becoming thicker and beginning to develop isolated acidophilic gland cells. By stomach region of body, anterior chamber of proboscis 150–180 μm in overall diameter, the epithelium distinctly papillate, richly provided with acidophilic glands and first traces of outer circular-muscle layer beginning to appear in outer connective-tissue zone. This circular musculature at first appearing as a slender (1–2 μm across) continuous strand of muscle zigzagging its way through outer connective-tissue zone (Fig. 49B) for most of remaining length of anterior chamber, but gradually thickening posteriorly to reach maximum of about 7–8 μm. In portion immediately preceding stylet-bulb region of proboscis, circular-muscle layer nearly lacking zigzag appearance, mostly lying adjacent to longitudinal-
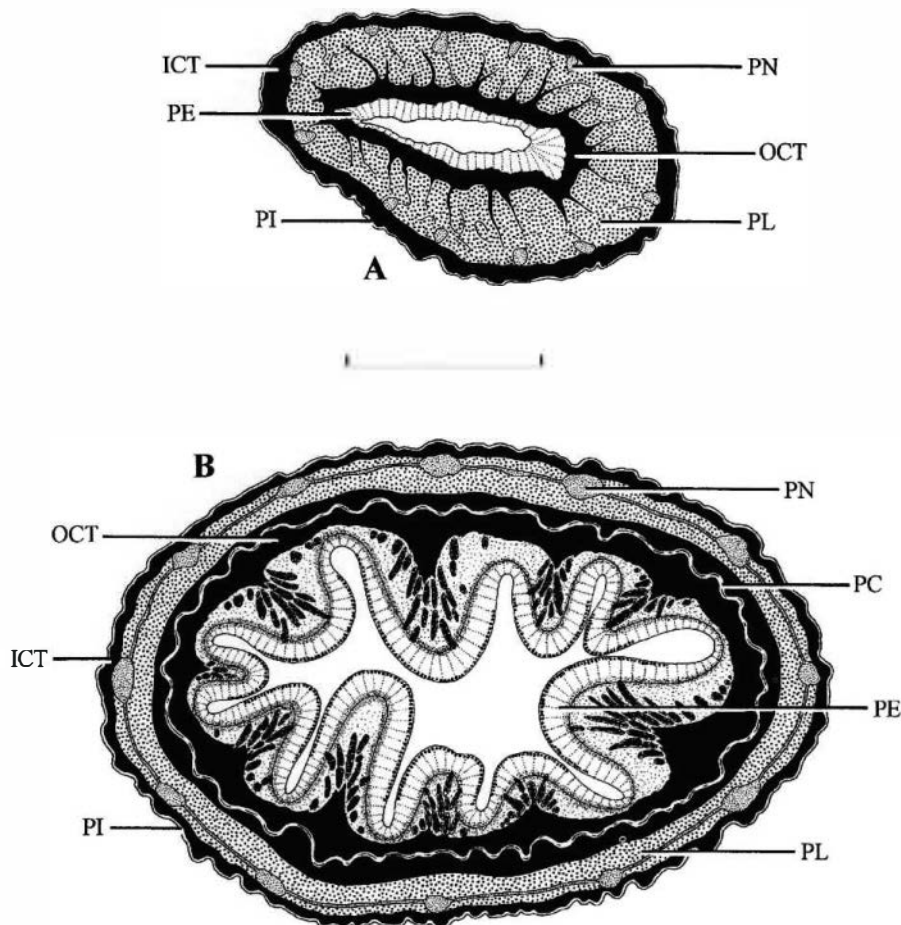

Fig. 49. *Correanemertes gordoni* sp. nov. Camera lucida drawings to show: **A**, the structure of the extreme anterior; **B**, main regions of the proboscis anterior chamber. Scale bar = 45 μm.

muscle coat but in places separated from it by distinct 'wedges' of connective tissue. Here epithelial papillae up to 45 μm or more tall, with 12 distinct proboscis nerves in proximal (inner) half of longitudinal muscle layer; these nerves circumferentially linked by nerve ring dividing muscle layer into 2 almost equal concentric zones.

Stylet-bulb region about 200 μm in diameter, typically monostiliferous in form, housing a single central stylet about 55 μm long and 14–15 μm wide at its base, borne on a cylindrical basis 130 μm long and 45 μm in maximum diameter; stylet : basis ratio thus about 1:2.4. Two spacious accessory stylet pouches each with 3–5 accessory stylets in various stages of development.

Posterior region of proboscis 110–120 μm in diameter, with much simpler construction, having low epithelium, longitudinal-muscle layer and flattened inner lining. No nerves seen in this region. Longitudinal muscle fibres posteriorly merging with proboscis retractor muscle.

Alimentary canal: Oesophagus opening from rhynchodaeum close in front of proboscis insertion, forming elongate tubular canal, the epithelium not ciliated or glandular. Oesophagus merging into stomach about 0.18–0.20 mm behind posterior limit of dorsal cerebral lobes, stomach epithelium distinguished by appearance of cilia and gland cells; short anterior portion of stomach dominated by acidophilic glands but farther back typical large basophilic glands appearing in the epithelium and longer posterior part of stomach dominated by these. Wall of stomach not deeply folded, up to 45 μm or more thick. Towards its rear, stomach gradually becoming narrower and more dorsoventrally compressed, leading imperceptibly into long pyloric portion of foregut. Pyloric epithelium at most about 15–20 μm thick, thinning posteriorly with fewer gland cells than stomach wall. Pylorus opening into dorsal wall of intestine, a remarkably long (2.4 mm) intestinal caecum (Fig. 47) extending anteriorly below pylorus and posterior stomach. Caecum lacking diverticula, its epithelium thin (3–5 μm) and mostly without gland cells. For a short distance in front of pyloric-intestinal junction, caecum walls extending dorsolaterally on either side of pylorus, with typical gastrodermal acidophilic glands appearing in epithelium.

Intestine initially forming wide, dorsoventrally compressed canal arching below rhynchocoel, lacking lateral diverticula but gastrodermal lining of lateral margins generally somewhat thicker (up to about 20–25 μm at most) than in median portion which is often only 10–12 μm tall. Farther back, as gonads appear, intestine losing its dorsoventrally compressed form, and its walls increasingly squeezed between densely packed gonads into irregularly shaped and distributed pouches (Fig. 50). Anus opening at posterior tip of body.
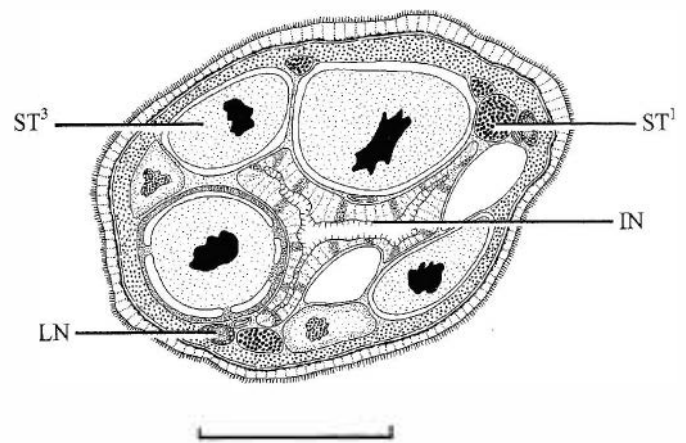

Fig. 50. *Correanemertes gordoni* sp. nov. Camera lucida drawing through the posterior body region to show the ovaries and intestine. Scale bar = 200 μm.

Blood system: Comprising a simple cephalic loop and 3 post-cerebral vessels (Fig. 47) not linked by pseudometameric transverse connectives. Immediately behind ventral cerebral commissure a slender connective, arching below rhynchocoel, links 2 slender cephalic vessels running through cerebral ring; mid-dorsal blood vessel has its origin in this connective. This vessel soon bulging slightly into ventral rhynchocoel wall, but vascular plug could not be distinguished. Post-cerebral regions of body lateral vessels running close to dorsal surface of nerve cords.

Nervous system: Brain lobes well developed, enclosed by thin, distinct outer neurilemma; no inner neurilemma or neurochord cells. Dorsal lobes extending slightly anterior to ventral and are more widely-set to accommodate rhynchocoel. Dorsal cerebral commissure (Fig. 48), 17–18 μm thick, located above anterior limits of thicker (30 μm) ventral commissure.

Lateral nerve cords containing only a single neuropil throughout their length.

Peripheral nerve supply well developed and several distinct nerves traceable. Among these, one emerges from outer dorsolateral margin of each ventral lobe just in front of where dorsal and ventral lobes separate posteriorly, turns forward and runs along the ventro-lateral borders of brain immediately outside the outer neurilemma. Level with ventral commissure, the nerve on each side divides, its branches leading peripherally towards lateral body margins. From front of brain lobes several thick cephalic nerves lead forward to supply various structures of head; one pair of these form a slender neural ring surrounding proboscis insertion and appear to constitute origin of proboscis nerve supply. Others lead towards eyes and cerebral sensory organs, whilst yet others divide and lead peripherally towards body surface.

Apical organ and cephalic glands: Extreme anterior

tip of body was lost during sectioning; an apical organ not therefore determinable.

Cephalic glands extremely well developed, near tip of head forming a small median block of typical irregularly shaped lightly basophilic lobules extending back immediately above rhynchodaeum; where anterior pair of eyes is reached, glands dispersed to almost completely fill available cephalic space, with acidophilic submuscular glands, cephalic retractor muscles, and other tissues distributed between them. On all sides of head glands extending back to anterior borders of cerebral lobes, but then becoming increasingly confined to lateral and ventral margins, intruding into body-wall longitudinal-muscle layer dividing it into inner and outer zones. Behind brain, cephalic gland lobules extending dorsolaterally (Fig. 48), but farther back where excretory tubules appear, the glands becoming confined to 2 ventrolateral blocks of tissue, one below each lateral nerve cord, here extending back just beyond anterior tip of intestinal caecum. Throughout their length, glands opening to body surface via numerous, irregularly disposed tracts of secretion.

Sense organs: Four well-developed pigment cup ocelli, each about 45 μm in diameter; anterior pair situated laterally about half way along head (Fig. 46), posterior pair dorsolaterally level with proboscis insertion.

Cerebral sensory organs comparatively large, about 190–200 μm long and 55-60 μm or more in maximum diameter. Ciliated cerebral canals opening ventrolaterally a short distance behind the anterior pair of eyes by simple pores about 15 μm in diameter. Epidermis surrounding the pores not differing histologically from that of other parts of the body, and wall of cephalic furrows resembles remaining epidermis. Ciliated canals turn posteriorly to run for about 50 μm before entering anterior borders of cerebral organs; canals initially surrounded only by neuroganglionic tissue, but farther back predominantly acidophilic glands appearing on outer lateral margin of each organ. Glandular tissues mainly posterior, forming a large glandular cap in which ciliated canals terminate near rear.

Excretory system: Extending from just behind anterior end of intestinal caecum forwards to region where oesophagus merges into anterior stomach; for most of its length consisting of a single, dorsolateral, thick-walled collecting tubule about 15 μm in maximum diameter, extending close above lateral blood vessel on each side of body; in some sections 2 tubules distinguishable on either side. Near anterior limits, tubule on each side turning ventrally, passing around outer margin of lateral nerve cord and leading to slender efferent duct opening via a small, ventrolateral nephridiopore.

Reproductive system: Unique specimen a gravid female: ovaries first appear some distance behind pyloric region of foregut, far back in intestinal region on ventrolateral body margins, virtually packing body around intestine behind end of rhynchocoel (Fig. 50). Thiel and Dernedde (1996) devised a histological classification for gonad development in the hoplonemertean *Amphiporus lactifloreus* (Johnston, 1828), recognising 5 distinct stages, from Stage 0 when no gonads are visible in sections, to post-reproductive Stage 4, with open gonopores and empty gonads. In present specimen, gonads from Stages 1–3 are present (Fig. 50). Stage 1 gonads, located close to body wall, about 20–25 μm in maximum dimension, mostly filled with strongly acidophilic globules; Stage 2 recognisable by their pale and ill-defined nuclear region; Stage 3 ovaries contain oval eggs, 170–180 μm in maximum diameter, with uniformly and densely stained stellate nucleus 45 μm or more in diameter. Ova of this form show several cytoplasmic stalks joining them with their ovarian walls. Ovaries in intermediate stage of development contain distinct eggs in which nuclei, 20–25 μm in diameter, are bounded by a thin but distinct nuclear membrane and contain darkly staining globules of varying size.

DISCUSSION: Comparatively few monostiliferous hoplonemertean genera are known in which the body-wall longitudinal-muscle layer is anteriorly divided, as in the present specimen; for those that do possess this character other features can be used to distinguish between them (Table 3). The present specimen is also characterised by a proboscis insertion, derived only from the inner portion of the body-wall longitudinal musculature, no precerebral septum, a rhynchocoel which is more than half the length of the body, and a cephalic blood supply consisting of a simple vascular loop. This combination of characters enables the form to be distinguished from all the taxa listed in Table 3 except *Amphiporus bioculatus, Correanemertes,* and *Pantinonemertes. Pantinonemertes* species, however, possess a diagonal muscle layer in their body wall, which is not found in the present New Zealand species, although other anatomical characteristics, such as the degree of organisation of the excretory system, exclude the present taxon from this genus. The genus *Correanemertes* was established for a species from Brazil which Corrêa (1958) had originally identified as *Amphiporus bioculatus.* Kirsteuer (1974: 159) commented that "*Amphiporus bioculatus,* having a normal blood-vascular system [i.e., no extra-cerebral vessels], should be removed from the 'hastatus group', yet not all the animals reported hitherto as *A. bioculatus* seem to be conspecific ... Only for *A. bioculatus* sensu Corrêa (1958) ... the available information on anatomical features appeared adequate for generic delineation

and, therefore, the genus *Correanemertes* was established for this taxon [Kirsteuer 1967]." Comparison between the diagnosis of the genus *Correanemertes* given by Kirsteuer (1974) and the morphology of the New Zealand individual thus enables the latter to be placed in this previously monotypic taxon.

The New Zealand specimen can be distinguished from the Brazilian form, however, in several ways, summarised in Table 4, and it is accordingly identified as a new species for which the name *Correanemertes gordoni* is proposed.

Table 4

Comparison between some of the morphological features of *Correanemertes bioculatus* (Corrêa, 1958) from Brazil and the present specimen from New Zealand.

Character	*Correanemertes bioculatus*	*Correanemertes gordoni* sp. nov.
Cephalic furrows meet mid-dorsally to form backward-pointing V-shape (+) or do not meet mid-dorsally (0)	+	0
Number of eyes	2	4
General body colour	uniformly reddish-purple	anterior third pale brown, otherwise whitish-brown
Number of proboscis nerves	10	12

Ischyronemertes Gibson, 1990

TYPE SPECIES: *Ischyronemertes albanyensis* Gibson, 1990

DIAGNOSIS: Monostiliferous marine nemerteans; rhynchocoel short, between one-third and one-half body length, with wall containing 2 distinct muscle layers; anterior region of proboscis with 3 muscle layers (outer circular, middle longitudinal, inner circular), proboscis armature consisting of single central stylet and 2 accessory stylet pouches; body-wall musculature extremely well developed, diagonal layer, with inner circular layer extending throughout most of body length, and longitudinal muscles not divided anteriorly. Precerebral septum closed; apical organ present, cephalic glands moderately extensive, posteriorly reaching just behind brain, submuscular glands restricted to cephalic region; cerebral sensory organs situated close in front of precerebral septum but opening further forwards by lateral or ventrolateral pores; cerebral ganglia with neither neurochords nor inner neurilemma; lateral nerve cords with myofibrillae and short accessory nerves. Foregut opening into rhynchodaeum, divisible into oesophagus, stomach, and pyloric regions; intestinal caecum short with pair of very long anterior pouches, lateral diverticula confined to main intestinal canal; blood system simple, with cephalic loop, single middorsal and paired lateral vessels, dorsal vessel not forming vascular plug and longitudinal vessels without pseudometameric transverse connectives; parenchyma not extensive; excretory system confined to foregut region; eyes 4 or 4 groups; sexes probably separate. (Gibson 1990a: 153–154) .

Ischyronemertes heterophthalma (Schmarda, 1859)
(Frontis., fig. B; Figs 51–52)

ORIGINAL DESCRIPTION: Schmarda, 1859: 41, pl. 10, figs 90–90b (as *Ommatoplea heterophthalma*).

ADDITIONAL LITERATURE RELATING TO NEW ZEALAND RECORDS: As *Ommatoplea heterophthalma* (Hutton, 1879); as *Amphiporus heterophthalma* (Hutton, 1904); as *Amphiporus heterophthalmus* (Bürger, 1904; Gibson 1995; Gibson *et al.* in press); as *Ischyronemertes heterophthalma* (Senz, 1997; Gibson in press): for other synonyms see Gibson (1995).

DESCRIPTION: *External features:* Strikingly marked, body flattened and rather strap-like, about 60 mm long and 4 mm wide (Fig. 51). Dorsal colour red with a median longitudinal white stripe extending full length of body, ventral surface is pale red. Head pointed with pair of eyes near tip and then on each side, farther back, 7 ocelli arranged in longitudinal line followed by 3 eyes arranged as triangle.

Internal anatomy: Internal anatomy was unknown until Senz (1997) studied syntypic species. Some differences occur between generic diagnosis above and
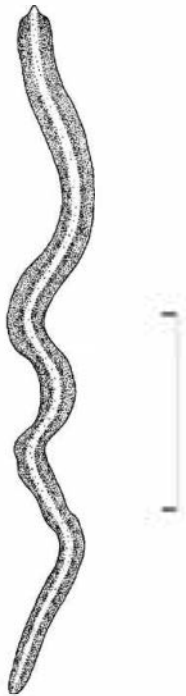
Fig. 51. *Ischyronemertes hetero-phthalma.* Drawing to show the general appearance of a complete specimen viewed from the dorsal aspect. Redrawn from Schmarda (1859). Scale bar = 20 mm.

features of New Zealand species, such as rhynchocoel reaching into posterior half of body, arrangement of eyes and circular muscle layer of rhynchocoel wall being intermingled with several longitudinal muscle fibres, but Senz (1997) concluded that it should be transferred to *Ischyronemertes*.

OCCURRENCE: So far known only from under stones near Auckland, North Island (Fig. 52).

Fig. 52. *Ischyronemertes heterophthalma.* Recorded distribution in New Zealand.

Noteonemertes gen. nov.

TYPE SPECIES: *Noteonemertes novaezealandiae* sp. nov.

ETYMOLOGY: The generic name, derived by prefixing *nemertes* with the Greek *noteo* (= southern), is indicative of its southern hemisphere origin; the specific epithet is self-explanatory.

DIAGNOSIS: Monostiliferous marine nemerteans; rhynchocoel extending almost to posterior end of body, with wall containing 2 distinct muscle layers; anterior region of proboscis with 2 muscle layers (outer circular, inner longitudinal), proboscis armature consisting of single central stylet and 2 accessory stylet pouches; body-wall musculature strongly developed, with diagonal layer, longitudinal muscles anteriorly divided into inner and outer zones by post-cerebral extensions of the cephalic glands; inner longitudinal muscle bundles only contributing to proboscis insertion. Precerebral septum absent; apical organ present, cephalic glands extensive, posteriorly reaching behind brain to stomach region; cerebral sensory organs situated close in front of brain, opening from short horizontal ventro-lateral cephalic furrows; cerebral canals forked; cerebral ganglia with neither neurochord cells nor inner neurilemma; lateral nerve cords with accessory nerves. Foregut opening into rhynchodaeum, divisible into oesophagus, stomach, and pyloric regions; intestinal caecum long, anterior extremity with neither lateral diverticula nor anterior puches; blood system with cephalic loop, single middorsal and paired lateral vessels, but lateral vessels in posterior foregut region developed in complex capillary network, dorsal vessel not forming vascular plug, longitudinal vessels in intestinal region without pseudometameric transverse connectives; parenchyma extensive; excretory system extensively branched, confined to foregut region, with mononucleate flame cells; eyes in 4 groups; sexes separate, gonads numerous.

Noteonemertes novaezealandiae sp. nov.
(Cover, Frontis., fig. E; Figs 53–58)

TYPE SPECIMENS: Holotype, mature female, complete set of mixed transverse (anterior regions) with oblique/longitudinal (posterior region) sections, 237 slides, H-791; paratype, mature male, set of transverse sections almost to posterior tip of body, 175 slides, P-1251, in NZOI collection at NIWA in Wellington.

TYPE LOCALITY: Matheson Bay (Fig. 53), lower shore under rocks with *Evechinus,* starfish, prawns and other invertebrates on clean, hard surface, 2 specimens, collected 24 August 1992.

ADDITIONAL MATERIAL: Whangamumu Bay, lower shore and shallow subtidal, under rocks on clean, hard surfaces, 8 specimens, collected 25 August 1992; Pukerua Bay, under stones and boulders or in rock pools, 14 specimens, collected 30 August 1992 (Fig. 53).
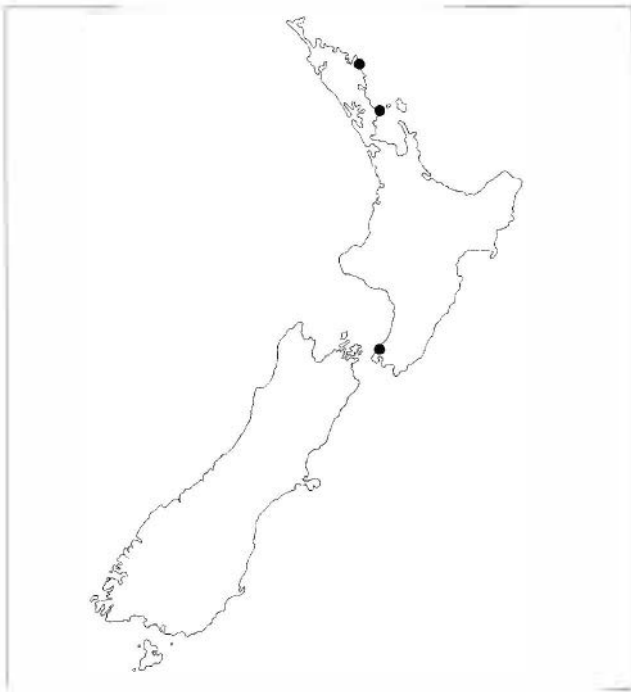

Fig. 53. *Noteonemertes novaezealandiae* gen. et sp. nov. Recorded distribution in New Zealand.

DESCRIPTION: *External features:* In life closely resembling Morton and Miller's (1968: Pl. 9, fig. 1) (Figs 54A, B) coloured illustration of an unnamed nemertean found under stones and rocks in the sublittoral fringe of Goat Island Bay, Leigh, differing only in that the colour of the present specimens was more of a brownish-purple hue, pale grey ventrally, with dorsal coloration fading to that of ventral surface along lateral margins, without the clear-cut distinction shown in their illustration; viewed from above, lateral margins appear translucent (Fig. 54C). On dorsal surface usually a slender, darker 'stripe' or streak extending medially along body. Extreme, bluntly pointed, tip of head white, with short oblique cephalic furrows on head continuing ventrad to end just behind distinct median longitudinal furrow extending forwards almost to proboscis pore (Fig. 54D). Gonads visible through body wall as pale, more or less rounded patches. Tail bluntly rounded with no caudal cirrus. Anterolateral margins of head acute, remarkably straight, giving head an almost equilateral triangular shape when viewed dorsally (see Morton & Miller, *ibid.*, and Fig. 54E), although width at the 'base' slightly more than length of 'sides'. Largest specimen

found was about 60 mm long, and 3–3.5 mm in maximum width; Morton and Miller's illustration is of a specimen 110 mm long. Living specimens have rounded triangular shape in cross section, with flat or slightly concave ventral surface. Four groups of 6–10 or more eyes on head (Fig. 54E). Specimens from Pukerua Bay had a distinct median longitudinal ridge on head, more beaked in shape from above, and cephalic pigmentation markedly darker than on rest of body. Proboscis large, white, readily everted and retracted when animals are disturbed. Ova are white.

Body wall, musculature and parenchyma: Epidermis, dermis, and body-wall muscle layers throughout most of the body very variable in thickness, depending upon degree of local folding. Near tip of head, epidermis mostly about 30–45 μm tall but behind the brain varying from 35-40 μm to 80–85 μm or more, whereas dermis generally only 4–7 μm across but in places appearing very much thicker (Fig. 55). In sections, accumulations of small, dark pigment granules, evidently responsible for dorsal colouration in life, mainly situated in epidermis, forming a loosely arranged proximal zone some 15–30 μm deep, but other granules scattered between outer portion of body-wall longitudinal-muscle fibre bundles and among cephalic gland lobules; granules missing from ventral and ventrolateral portions of epidermis.

Main body-wall muscle layers strongly developed (Fig. 55), the outer circular and inner longitudinal layers in foregut regions respectively some 15-20 μm and 75-80 μm in thickness, although along lateral body margins or below epidermal folds both may appear much thicker (Fig. 55). Body-wall circular muscle layer extremely thin in anterior cephalic regions and is distinguishable in all parts of head. Also a delicate diagonal muscle layer between circular and longitudinal musculature. As it approaches rear of brain, body-wall longitudinal-muscle layer is anteriorly divided into inner and outer layers by post-cerebral extensions of cephalic glands (Fig. 56); outer portion remaining as distinct layer but inner longitudinal fibres instead forming a number of discrete longitudinal fibre tracts separated from each other by cephalic gland lobules (Fig. 56) extending anteriorly adjacent to brain and on either side of anterior stomach. Cephalic retractor muscles (Fig. 57) apparently derived from both inner and outer components of longitudinal musculature, but only bundles of inner fibres contribute to proboscis insertion, i.e., a precerebral septum lacking.

Parenchymatous connective tissues fairly extensive, particularly in foregut region of body (Fig. 55) and between intestine and gonads.

Proboscis apparatus: Proboscis pore ventral and subterminal, leading into thin-walled rhynchodaeum with epithelium lacking gland cells.

ADDITIONAL MATERIAL: **Whangamumu Bay**, lower shore and shallow subtidal, under rocks on clean, hard surfaces, 8 specimens, collected 25 August 1992; Pukerua Bay, under stones and boulders or in rock pools, 14 specimens, collected 30 August 1992 (Fig. 53).

Fig. 53. *Noteonemertes novaezealandiae* gen. et sp. nov. Recorded distribution in New Zealand.

DESCRIPTION: *External features:* In life closely resembling Morton and Miller's (1968: Pl. 9, fig. 1) (Figs 54A, B) coloured illustration of an unnamed nemertean found under stones and rocks in the sublittoral fringe of Goat Island Bay, Leigh, differing only in that the colour of the present specimens was more of a brownish-purple hue, pale grey ventrally, with dorsal coloration fading to that of ventral surface along lateral margins, without the clear-cut distinction shown in their illustration; viewed from above, lateral margins appear translucent (Fig. 54C). On dorsal surface usually a slender, darker 'stripe' or streak extending medially along body. Extreme, bluntly pointed, tip of head white, with short oblique cephalic furrows on head continuing ventrad to end just behind distinct median longitudinal furrow extending forwards almost to proboscis pore (Fig. 54D). Gonads visible through body wall as pale, more or less rounded patches. Tail bluntly rounded with no caudal cirrus. Anterolateral margins of head acute, remarkably straight, giving head an almost equilateral triangular shape when viewed dorsally (see Morton & Miller, *ibid.*, and Fig. 54E), although width at the 'base' slightly more than length of 'sides'. Largest specimen

found was about 60 mm long, and 3–3.5 mm in maximum width; Morton and Miller's illustration is of a specimen 110 mm long. Living specimens have rounded triangular shape in cross section, with flat or slightly concave ventral surface. Four groups of 6–10 or more eyes on head (Fig. 54E). Specimens from Pukerua Bay had a distinct median longitudinal ridge on head, more beaked in shape from above, and cephalic pigmentation markedly darker than on rest of body. Proboscis large, white, readily everted and retracted when animals are disturbed. Ova are white.

Body wall, musculature and parenchyma: Epidermis, dermis, and body-wall muscle layers throughout most of the body very variable in thickness, depending upon degree of local folding. Near tip of head, epidermis mostly about 30–45 μm tall but behind the brain varying from 35-40 μm to 80-85 μm or more, whereas dermis generally only 4–7 μm across but in places appearing very much thicker (Fig. 55). In sections, accumulations of small, dark pigment granules, evidently responsible for dorsal colouration in life, mainly situated in epidermis, forming a loosely arranged proximal zone some 15–30 μm deep, but other granules scattered between outer portion of body-wall longitudinal-muscle fibre bundles and among cephalic gland lobules; granules missing from ventral and ventrolateral portions of epidermis.

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Parenchymatous connective tissues fairly extensive, particularly in foregut region of body (Fig. 55) and between intestine and gonads.

Proboscis apparatus: Proboscis pore ventral and subterminal, leading into thin-walled rhynchodaeum with epithelium lacking gland cells.
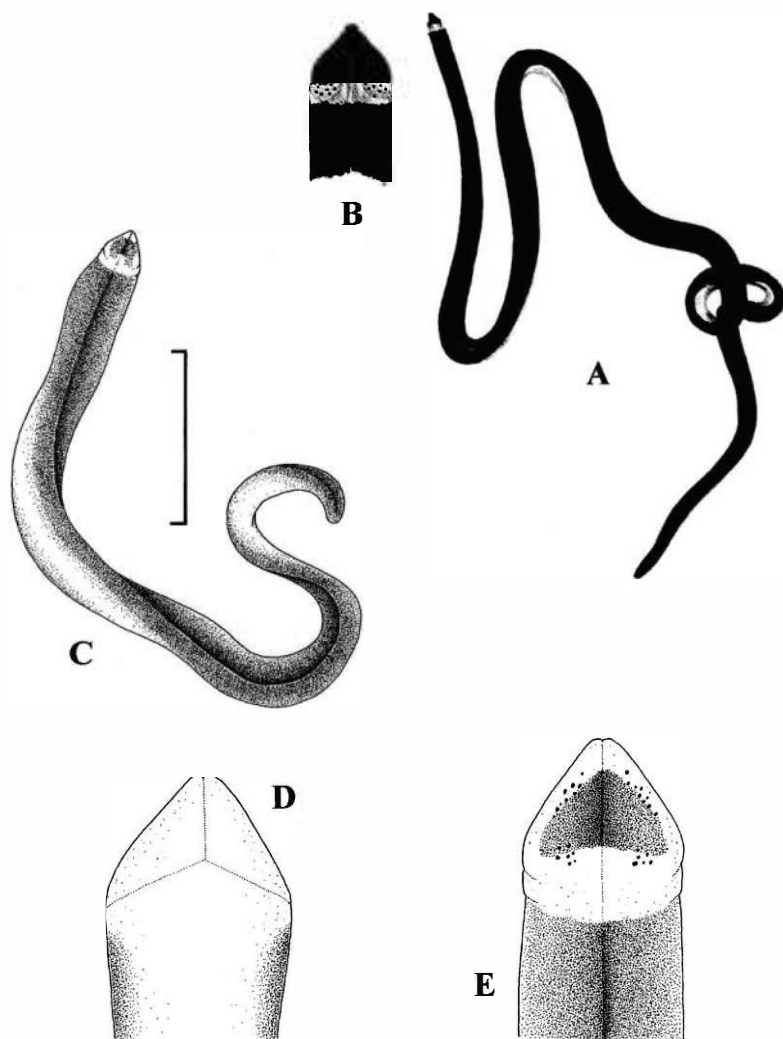
Fig. 54. *Noteonemertes novae-zealandiae* gen. et sp. nov. Colour paintings of: A, a complete specimen, and B, enlargement of the head viewed dorsally, of an unnamed species of nemertean found beneath stones and rocks at Goat Island, Leigh [reproduced from Morton & Miller (1968: pl. 9, fig. 1), with permission of John Morton]. C–E, drawings of specimens found during 1992, all based on sketches made from life: **C**, appearance of a complete individual; **D**, enlargement of the head viewed from the ventral surface; **E**, enlargement of the head in dorsal view to show its distinct triangular shape and the distribution of the eyes. Scale bar = 10 mm (refers to C only).
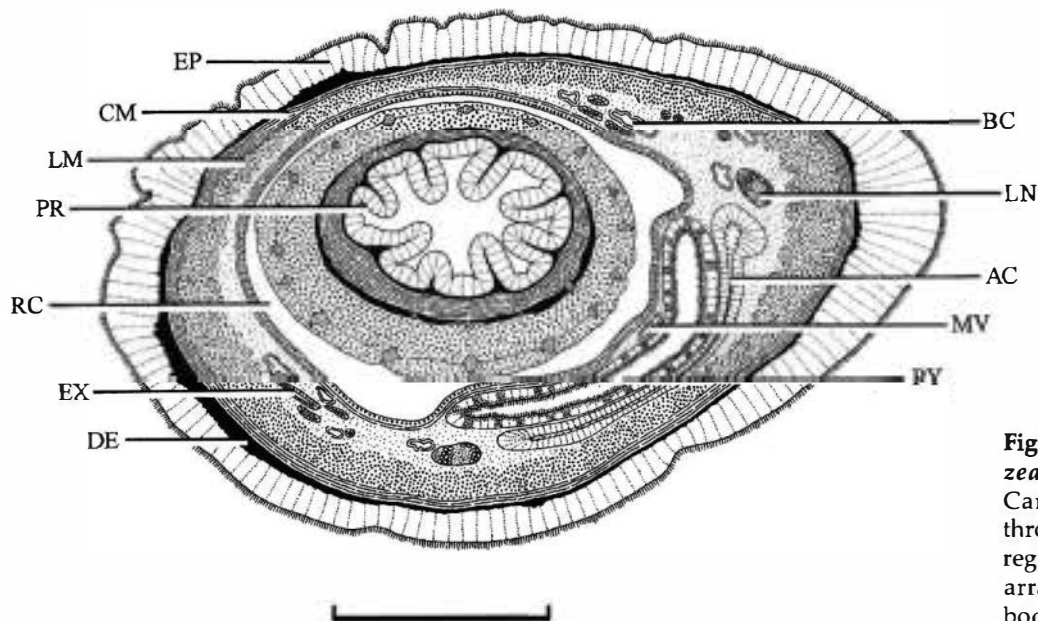

Fig. 55. *Noteonemertes novae-zealandiae* gen. et sp. nov. Camera lucida drawing through the posterior foregut region of the body to show the arrangement of the various body structures. Scale bar = 500 μm.

Rhynchocoel extending almost to posterior end of body, its wall possessing separate circular and longitudinal muscle layers (Figs 55, 56).

Relative to size of body, proboscis is large and well developed. Anterior region (Figs 55–57) up to about 570–600 μm in overall diameter (i.e., approximately 70% of the body diameter), lined by glandular but predominantly basophilic epithelium 15–20 μm thick, this developed into broadly conical papillae 60–80 μm or more tall with connective-tissue core. Beneath epithelium, a thin but distinct outer connective-tissue layer, outer circular-muscle layer 5–7 mm across, a
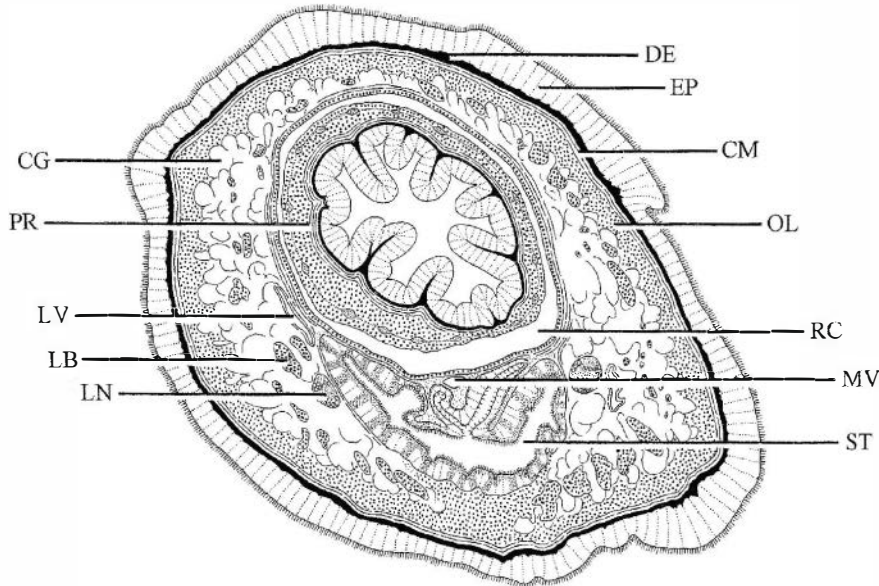

Fig. 56. *Noteonemertes novae-zealandiae* gen. et sp. nov. Camera lucida drawing to show the organisation of the various body structures a short distance behind the brain. Note the posterior extent of the cephalic glands and the bundles of longitudinal muscle fibres which comprise the inner region of the anteriorly divided body-wall longitudinal musculature.
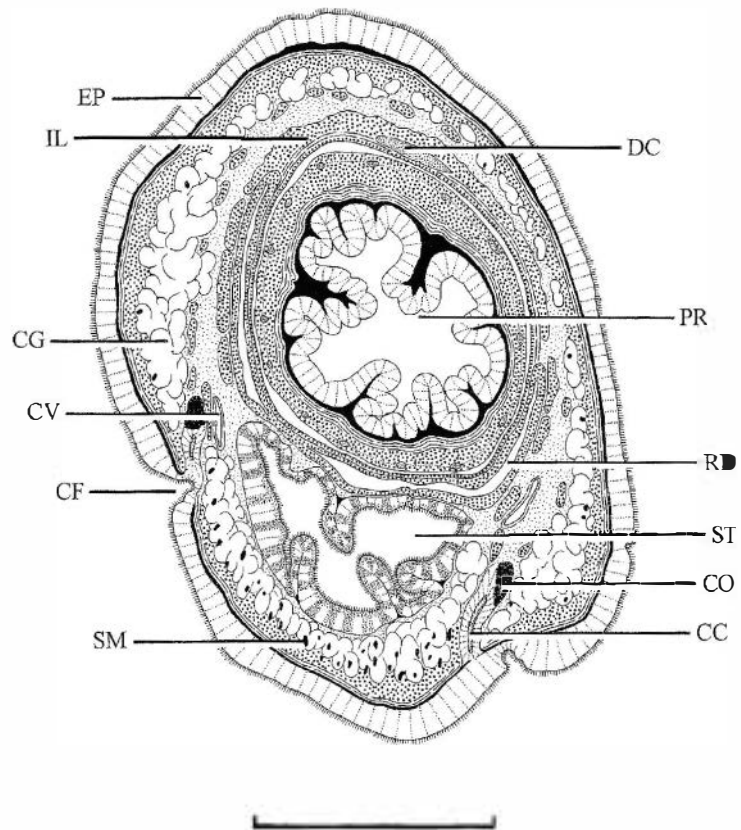Scale bar = 500 μm.

Fig. 57. *Noteonemertes novaezealandiae* gen. et sp. nov. Camera lucida drawing through the ciliated cerebral canals and anterior portion of the cerebral sensory organs. Scale bar = 500 μm.

distinct middle connective-tissue coat, inner longitudinal muscle layer 45–75 μm wide divided into thicker outer and thinner inner zones by proboscis neural supply, thin inner connective-tissue layer, and delicate innermost lining layer. Proboscis neural supply well developed, but number of distinguishable nerves in anterior chamber varying from 14 to 17 in different parts of same organ.

Stylet region with maximum diameter about 300 μm and bulb chamber with deeply folded and strongly acidophilic epithelium. A slender canal leads back from this chamber through muscle bulb portion to posterior proboscis lumen. Cylindrical basis 45–50 μm in diameter, about 90–100 μm long, with single central stylet. Two accessory stylet pouches, each housing several reserve stylets in various stages of formation.

Posterior region of proboscis about 350–370 μm in diameter, comprising acidophilic and richly glandular epithelium, outer longitudinal and inner circular muscle layers together about 15-25 μm across, and thin inner lining.

Alimentary canal: In holotype, stomach is pushed forwards in front of brain (Fig. 57), so oesophagus, which opens from rhynchodaeum in front of cerebral organs, consequently appearing both spacious and dorsally extending farther back into the stomach than it does ventrally. Oesophageal epithelium unciliated, 10–12 μm or more thick, with moderately large numbers of coarsely granular basophilic gland cells.

Occurrence of cilia on stomach epithelium and epithelial folding marks junction between oesophagus and stomach; stomach divisible into two regions histologically. In shorter, anterior, portion, 30–35 μm thick epithelium is dominated by pale blue basophilic glands with finely granular cytoplasm, interspersed with strongly basophilic pyriform glands and occasional, slender acidophils. Epithelium of anterior stomach extending a short distance back on dorsal margins of main stomach, where it has appearance of a median pouch (Fig. 56). Main stomach region, up to about 750 μm or more in maximum width, comprising a folded epithelium 30-45 μm thick dominated by pale blue basophilic glands interspersed with acidophilic glands. Strongly basophilic, dark-blue staining, glands of anterior stomach wall lacking from posterior portion. A slender layer of circular somatic muscles, derived from rhynchocoel wall circular musculature, surrounds stomach.

Towards its rear, stomach wall gradually becoming less folded and narrower, leading into an exceptionally long pyloric region of foregut. In holotype, pylorus more than 8 mm long, throughout its length imperceptibly narrowing to a tubular canal lined by an epithelium only about 20 μm or less thick which, for much of its length, completely lacks gland cells. Pylorus opening into dorsal wall of intestine. From this junction a long (approximately 7.1 mm) intestinal caecum extends anteriorly below pylorus and posterior stomach (Fig. 55). Anterior 1.7 mm of caecum lacking lateral diverticula, terminating without anterior pouches found in some hoplonemerteans. For remainder of its length, caecum bears lateral diverticula that become progressively deeper and more lobed towards pyloric-intestinal junction.

Behind caecum, the intestine throughout its length with deep, spacious lobed lateral diverticula; its branches extending dorsolaterally between gonads (Fig. 58). Gastrodermis, 30 μm or more thick, with a typical hoplonemertean appearance.

Blood system: Close to tip of head a simple transverse vascular loop extends above proboscis pore. The 2 cephalic vessels extend back to brain, passing close to cerebral sensory organs (Fig. 57) before entering cerebral ring. Behind brain, where post-cerebral extensions of cephalic glands extend back to divide the body-wall longitudinal-muscle layer, the basic hoplonemertean arrangement of single middorsal and paired lateral blood vessels is retained (Fig. 56). Throughout remaining foregut (Fig. 55) and into the intestinal regions, however, lateral vessels are developed to form complex, extensive capillary network.

Close behind ventral cerebral commissure, a slender connective links 2 cephalic vessels below rhynchocoel; from this connective middorsal blood vessel extends posteriorly. Unlike in most hoplonemerteans, vascular plug of middorsal vessel not evident.

Nervous system: Compared to size of body, brain is comparatively small; the dorsal ganglionic lobes smaller than ventral lobes reaching some distance in front of them and wider set. Brain lobes enclosed by thin but distinct outer neurilemma, but no inner neurilemma separating the fibrous and ganglionic tissues or neurochord cells distinguished. Ventral cerebral commissure, possibly because the large proboscis is partially everted, is unusually long and slender, only about 20–25 μm across. Dorsal commissure, about 15 μm in maximum diameter, looping anteriorly some distance in front of ventral commissure, reaching level of cerebral sensory organs.

Both lateral nerve cords anteriorly have large, well developed accessory nerve (Figs 55, 56); these extending back into posterior stomach region then merging with main neuropil. Peripheral nervous system, evidently showing no unusual hoplonemertean features in its arrangement.

Apical organ and cephalic glands: A simple apical organ, about 20 μm in diameter, opening just subterminally and ventrally in front of proboscis pore.

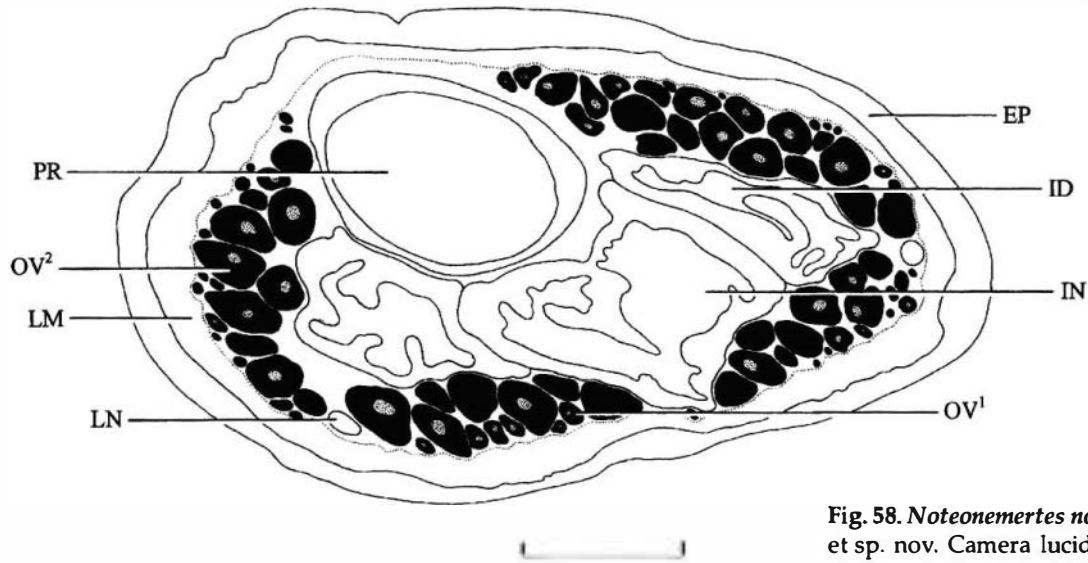Cephalic glands typically staining pale blue, with a

Fig. 58. *Noteonemertes novaezealandiae* gen. et sp. nov. Camera lucida drawing through the anterior intestinal region of the holotype, drawn to emphasise the distribution and number of ova. Note the immature ova mainly situated adjacent to the inner margin of the body-wall longitudinal-muscle layer. Scale bar = 500 μm.

lobular appearance, very well developed; occurring on all body margins precerebrally, situated just below longitudinal muscle layer (Fig. 57), posteriorly extending back behind brain into posterior stomach region (Fig. 56); post-cerebrally mainly distributed along lateral body margins. The glands appear to open both via a median channel discharging through apical organ, and also via independent ducts radiating out through epidermis — tracts of secretion can be seen running from individual glandular lobules through dermis and into proximal portion of epidermis throughout the cephalic region.

Ventrolateral acidophilic submuscular gland cells also present in posterior head region, extending to near rear of brain lobes, but also scattered between other cephalic structures towards tip of head.

Sense organs: Four groups of 6–10 eyes occurring on head (Fig. 54E), each eye of pigment-cup ocellus type; eyes oval to spherical in transverse sections, varying in size from 40 to 45 μm up to 90–100 μm.

Cerebral sensory organs small, situated close in front of brain, their ciliated cerebral canals, 30-40 μm in width, opening ventrolaterally from a pair of short, horizontal cephalic furrows not evident in life. These continuing posteriorly some distance behind origin of ciliated canals. Each cerebral canal extending dorsally for about 180 μm, its deeper, upper, portion meeting an acidophilic glandular region initially restricted to outer margin of canal (Fig. 57). Soon after ciliated canal forks, the lower branch forms an elliptical ciliated chamber, some 45 μm wide and 90 μm tall, extending posteriorly below cerebral organ for about 60 μm before ending blindly. The epithelium of this chamber lacks glandular components. The upper branch, which becomes separated from lower by neural tissues,

turns through 90° to continue posteriorly along median upper portion of cerebral organ. Acidophilic glands extend to inner margin of cerebral organ, whilst on their outer border acidophils become progressively replaced by basophilic glands that form a posterior mass on each organ. Cerebral organs about 265 μm long, 150 μm in dorsoventral extent, 75-80 μm wide, ending just below anterior limits of dorsal brain lobes, their cerebral organ nerves leading from rear of each organ back to ventral brain lobes.

Excretory system: Situated in parenchyma of fore-gut body region, consisting of thin-walled tubules about 15μm in diameter, profusely branched, often running close to branches of the blood capillary net-work (Fig. 55). Isolated mononucleate flame cells, 30-35 μm long and 6-7 μm wide, scattered alongside excretory tubules and often connecting with them. Flame cells lacking transverse and longitudinal support bars.

Reproductive system: Sexes separate. In female holo-type, immature ova located immediately below body-wall longitudinal-muscle layer, or slightly deeper in the parenchyma, as far forwards as the posterior stomach region. Throughout intestinal region ovaries very numerous, occurring on all margins of body except for a narrow middorsal longitudinal band above rhyncho-coel (Fig. 58). Ova in several stages of development can be found within same section, with up to 50 or more ova occurring on either side of body in any one section.

DISCUSSION: The anteriorly divided body-wall longi-

tudinal-muscle layer of the present taxon is a feature possessed by comparatively few of the known monostiliferous hoplonemertean genera (Table 3). Other anatomical characters found in the present form include the presence of a body-wall diagonal muscle layer, no precerebral septum or neurochords, cephalic retractor muscles derived from both inner and outer portions of body-wall longitudinal musculature, and a rhynchocoel which extends almost to the posterior end of the body, a combination of features not found in any of the genera listed in Table 3. The New Zealand taxon cannot therefore be placed in any of the existing monostiliferous genera and the name *Noteonemertes* gen. nov. is accordingly proposed for it.

Parischyronemertes gen. nov.

TYPE SPECIES: *Parischyronemertes mathesonensis* sp. nov.

DIAGNOSIS: Monostiliferous marine nemerteans; rhynchocoel extending into posterior half of body but not reaching posterior end, with wall containing 2 distinct muscle layers; anterior region of proboscis with 2 muscle layers (outer circular, inner longitudinal), proboscis armature consisting of single central stylet and 2 accessory stylet pouches; body-wall musculature extremely well developed, with diagonal layer, inner circular layer extending throughout most of body length, longitudinal muscles not divided anteriorly. Precerebral septum closed; apical organ present, cephalic glands moderately extensive, posteriorly reaching just behind brain, submuscular glands restricted to cephalic region; cerebral sensory organs situated close in front of precerebral septum but opening further forwards by lateral or ventrolateral pores; cerebral ganglia with neither neurochord cells nor inner neurilemma; lateral nerve cords with myofibrillae and short accessory nerves. Foregut opening into rhynchodaeum, divisible into oesophagus, stomach and pyloric regions, intestinal caecum short with pair of very long anterior pouches, lateral diverticula confined to main intestinal canal; blood system simple, with cephalic loop, single middorsal and paired lateral vessels, dorsal vessel not forming vascular plug, longitudinal vessels without pseudometameric transverse connectives; parenchyma not extensive; excretory system confined to foregut region; eyes in 4 groups; sexes probably separate.

ETYMOLOGY: The generic name, using the Greek prefix *para* (= near or close), indicates the similarities between the new taxon and the existing genus *Ischyronemertes*. The specific epithet is based on the name of the type locality, Matheson Bay.

Parischyronemertes mathesonensis sp. nov.
(Figs 59-64)

TYPE SPECIMENS: Holotype, a post-reproductive male, complete set of transverse sections, 104 slides, H-792; paratype immature, complete set of mixed transverse and oblique sections, 121 slides, P-1254. Three complete voucher specimens under registration number P-1255, all deposited in the NZOI collection at NIWA in Wellington.

TYPE LOCALITY: Matheson Bay (Fig. 59), lower shore on underside of flat, clean rock, collected 24 August 1992, one specimen.

ADDITIONAL MATERIAL: One specimen under boulder in silty sand, Lyall Bay, 29 August 1992; 7 specimens in crevices in metamorphosed sandstone ('greywacke'), lower shore, Pukerua Bay, 30 August 1992 (Fig. 59).
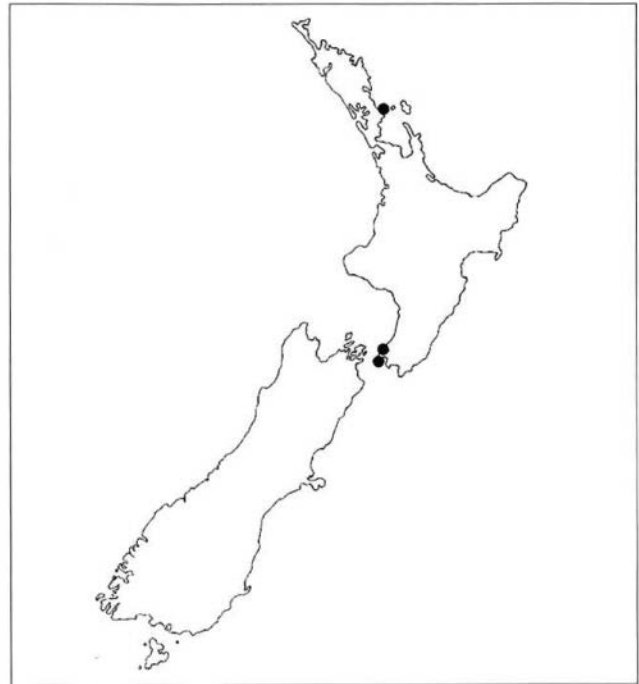

Fig. 59. *Parischyronemertes mathesonensis* gen. et sp. nov. Recorded distribution in New Zealand.

DESCRIPTION: *External features:* Anaesthetised specimens varied in length from 25 to 50 mm, with a maximum width of 1–1.5 mm. During normal movement, head is rounded, wider than adjacent body regions with about 16–20 dark eyes arranged in 4 groups (Fig. 60). No evidence of cephalic furrows seen in life. Behind head body more or less uniform width throughout, terminating in bluntly rounded tail.

General colour translucent whitish to very pale orange, with distinct pale blue-grey hue on dorsal
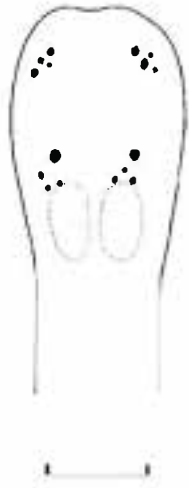
Fig. 60. *Parischyronemertes mathesonensis* gen. et sp. nov. Drawing of the anterior body, viewed dorsally, to show the distribution of the eyes, typical head shape and position of the brain lobes; drawing based on sketches made in life. Scale bar = 1 mm.

cephalic surface and on either side of gut throughout anterior half of body. Intestine and its shallow lateral diverticula are orange, brain lobes orange to pink.

Body wall, musculature and parenchyma: Structure of epidermis, 24–46 μm thick in foregut and anterior intestinal regions, corresponding with that described by Norenburg (1985) and dominated by acidophilic serous glands. Epidermal thickness decreasing precerebrally and in posterior body regions. Below epidermis, the distinct dermis, 4–6 μm deep, distally developed into a basal-cup zone, typical of many hoplonemerteans (Norenburg 1985).

Body-wall muscle layers strongly developed; in addition to typical hoplonemertean outer circular and inner longitudinal layers, respectively 4–8 μm and 25–65 μm thick, there are also diagonal and inner circular layers (Figs 61, 62). Diagonal coat about 7–8 μm in maximum thickness, situated between outer circular and longitudinal layers in precerebral and foregut portions of body but distinguished in intestinal region. Inner circular muscles forming irregularly interconnected bundles of fibres rather than discrete layer, appearing in posterior cerebral region but strongest in foregut region where they are up to 8–10 μm or more thick, extending throughout length of body. Fibres extending on all sides of gut, on either side dividing to enclose lateral nerve cords and, farther back, ventrolateral gonads. Along lateral body margins many muscle fibres giving off branches that pass between bundles of longitudinal muscles and lead towards proximal region of dermis. Precerebrally, fibres of inner circular musculature contribute to proboscis insertion, predominantly formed by radially orientated muscles leading from longitudinal musculature.

Longitudinal musculature not anteriorly divided, as in several hoplonemertean genera; both it and outer circular muscles extending to tip of head.

Adjacent to ventral and lateral foregut margins small, isolated bundles of longitudinal muscle fibres distinguishable, but these not forming distinct somatic layer found in several other nemerteans.

Parenchymatous connective tissues, nowhere especially extensive, most abundant around foregut.

Proboscis apparatus: Proboscis pore opening ventrally from short, longitudinal furrow situated about 150 μm behind the tip of head, leading into rhynchodaeum which, for most of its length, is thin-walled, its epithelium not ciliated or glandular. Rhynchodaeum appears as dorsoventrally compressed tube about 75 μm maximum width; towards proboscis insertion rhynchodaeal chamber becoming slightly enlarged and epithelium thickening to 8–15 μm or more and becoming distinctly acidophilic though still without obvious gland cells. Canal of proboscis insertion narrow, oval in section, no more than 45 μm in diameter, lined by slender epithelium overlying thin but distinct connective-tissue layer surrounded by radial muscle fibres leading inwards from body-wall longitudinal musculature.

Rhynchocoel extending almost to posterior end of the body, its wall containing separate circular and longitudinal muscle layers (Figs 61, 62).

Proboscis large relative to size of body; anterior portion (Fig. 63) 250–300 μm or more in overall diameter, composed of a distinctly papillate and richly glandular epithelium, a connective-tissue layer 6–15 μm thick that extends into epithelial papillae as a basal 'core', an outer circular-muscle layer 2–4 μm across, an inner connective-tissue zone up to about 2 μm deep but mostly thinner, an inner longitudinal muscle coat 15–20 μm thick, and a delicate inner lining layer. The 16 proboscis nerves distinct, located in proximal half of longitudinal muscle layer. Towards stylet bulb region, anterior proboscis gradually reducing in diameter, its epithelial papillae no longer distinguishable and outer connective-tissue zone remaining only as a delicate layer.

Stylet bulb region about 200 μm in diameter, typically monostiliferous in form, housing a single central stylet, about 45–50 μm long, borne on a tapering cylindrical basis about 90 μm long and 30 μm in maximum diameter; stylet : basis ratio is thus about 1 : 1.8. The 2 accessory stylet pouches spacious, each containing several accessory stylets in various stages of development.

Posterior region of proboscis, about 150 μm in diameter, with simpler construction, consisting of low glandular epithelium 15–20 μm deep, a longitudinal muscle layer 7–8 μm across, and a delicate inner lining. No evidence of nerves in this region.

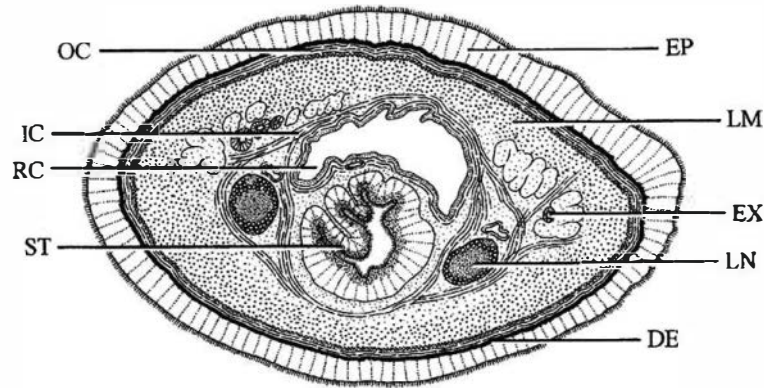*Alimentary canal:* Slender, tubular oesophagus open-

Fig. 61. *Parischyronemertes mathesonensis* gen. et sp. nov. Camera lucida drawing through the anterior stomach region to show the organisation of the various body structures and post-cerebral extensions of the cephalic glands. Scale bar = 250 μm.
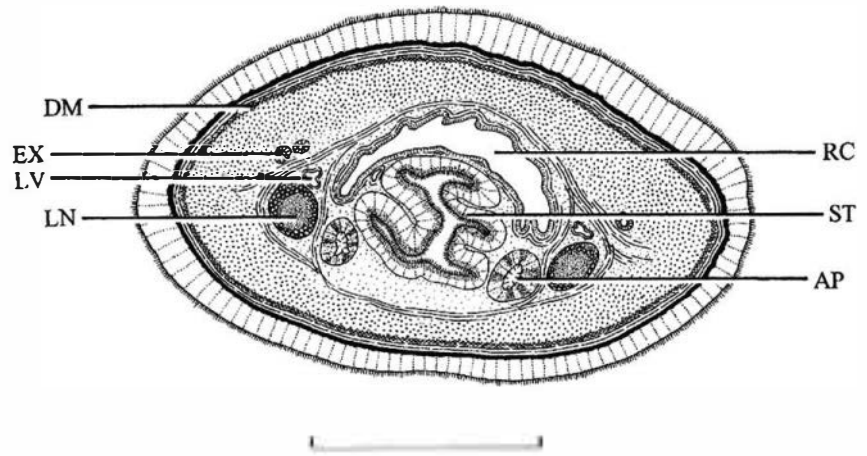

Fig. 62. *Parischyronemertes mathesonensis* gen. et sp. nov. Camera lucida drawing through the stomach region farther back than in Fig. 61 to show the tubular anterior pouches of the intestinal caecum. Scale bar = 250 μm.
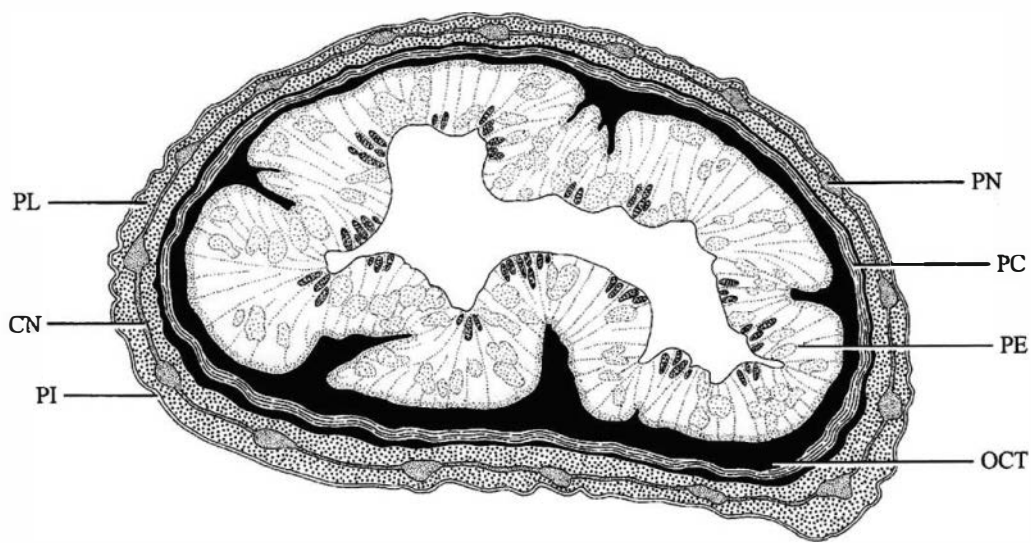

Fig. 63. *Parischyronemertes mathesonensis* gen. et sp. nov. Camera lucida drawing to show the structure of the anterior proboscis region. Scale bar = 100 μm.

ing from ventral wall of rhynchodaeum shortly in front of proboscis insertion, about 45 μm in diameter, with unciliated epithelium 12-15 μm thick. Anteriorly oesophagus completely lacking gland cells, but subjacent to cerebral ganglia (Fig. 64) isolated acidophilic glands appearing in its wall, their density gradually increasing farther back. Behind brain, oesophageal diameter increases until 60-65 μm across, where it joins stomach. Overall length of oesophagus in holotype 0.8 mm.

Junction between oesophagus and stomach marked by appearance of cilia on stomach epithelium. Histologically stomach is divisible into 2 distinct regions; shorter anterior portion, with epithelium to about 30 μm thick, with 3 types of gland cells: the dominant type comprises purple-staining glands with coarsely globular contents, between which are irregularly scattered small numbers of flask-shaped acidophilic glands filled with coarsely granular secretory globules, and oval to irregularly shaped basophilic glands containing finely fibrillar to homogeneous cytoplasm. Epithelium of this region little folded. Farther back, however, the purple-staining glands becoming increasingly restricted to dorsal half of stomach, eventually disappearing entirely, and the epithelium dominated by pale-blue-staining basophils interspersed with acidophilic glands. This major portion of stomach (Figs 61, 62) up to 170-200 μm in overall diameter, its epithelium deeply folded, about 45 μm in maximum thickness. Small, isolated bundles of longitudinal muscle fibres running close to ventral and ventrolateral stomach wall, these not forming a distinct gut muscle layer.

Towards its rear, stomach gradually becoming less folded and smaller, leading imperceptibly into long, gradually narrowing, pyloric portion of foregut; its most posterior portion completely lacking gland cells. Total length of the stomach and pyloric regions of foregut in holotype is 4.06 mm. Pylorus opens into dorsal wall of intestine, a short (160 μm) intestinal caecum projecting in front of junction. At its front, caecum divides forming a pair of long, tubular anterior diverticula (Fig. 62) which extend, one on either side, ventrolateral to foregut for about 82% of stomach/pyloric length; these diverticula lacking lateral pouches, and only about 45-50 μm in diameter for much of their length.

Intestine essentially forming a long, somewhat dorsoventrally compressed tubular canal, mostly about 230-250 μm wide, with occasional small lobular, unbranched lateral diverticula extending for much of its length. Gastrodermis with a typical hoplonemertean appearance, 15-30 μm thick. Anus opening at posterior tip of body.

Blood system: This follows a basic hoplonemertean plan; in head cephalic loop passing over anterior portion of rhynchodaeum close behind proboscis pore. Two cephalic vessels extending backwards, passing close to cerebral sensory organs, then narrowing to enter cerebral ring. Behind brain, the 3 longitudinal vessels, paired lateral and single middorsal, extending to hind end of body (Figs 61, 62). Middorsal vessel not, as in most hoplonemerteans, forming a vascular plug, and transverse connectives linking the 3 longitudinal vessels intestinal region not found.

Nervous system: Cerebral ganglia large, well developed (Fig. 64), enclosed by thin, distinct outer neurilemma, with no inner neurilemma or neurochord cells. Dorsal cerebral commissure 30 μm thick, looping anteriorly in front of brain some distance anterior to the thicker (55-60 μm) ventral commissure.

Dorsal and ventral cerebral lobes posteriorly separated. Close to posterior end of each dorsal lobe is a small nerve ca. 10-12 μm in diameter leading from its ventral surface and extending backwards for a short distance to enter dorsal wall of lateral nerve cord together forming accessory lateral nerve. This extending throughout most of foregut body region along
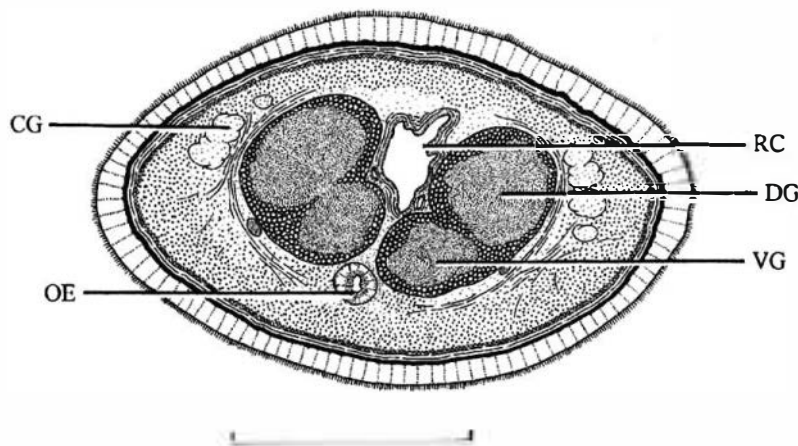

Fig. 64. *Parischyronemertes mathesonensis* gen. et sp. nov. Camera lucida drawing through the anterior brain region to show the organisation of the various body structures. Scale bar = 250 μm.

upper surface of lateral nerve, and traceable back almost to level of intestinal caecum. Main neuropil of lateral nerves is 40-45 μm in diameter, these nerves continuing to hind end of the body and joined by a sub-intestinal transverse commissure.

Peripheral nervous system well developed but typically hoplonemertean in its arrangement; several large, distinct cephalic nerves leading forwards from front of brain lobes and small nerves emerging from lateral nerve cords throughout their length to lead towards body-wall muscle layers. The ultimate fate of these peripheral nerves was not traced.

Apical organ and cephalic glands: The frontal, or apical, organ comprises a single ciliated chamber, 30-35 μm in diameter, opening on ventral cephalic surface just behind tip of head.

Cephalic glands consisting of typical, irregularly shaped, pale-staining lobules, mainly confined to dorsal half of head where they are loosely distributed above rhynchodaeum; towards rear of rhynchodaeum the glands becoming concentrated into dorsolateral accumulations that reach past brain into anterior stomach region of body (Fig. 61).

Loosely distributed acidophilic submuscular glands in the head mainly situated ventrally.

Sense organs: Eyes arranged in 4 groups on head, the 2 posterior groups located close to anterior borders of brain, the anterior groups a short distance behind tip of head (Fig. 60). Each group consists of 4 or 5 pigment-cup ocelli, individual ocelli varying in size from about 30-60 μm in diameter.

No cephalic furrows distinguishable, but, commencing about 300 μm behind tip of head, a modified 'tract' of epidermal tissue angles obliquely backwards from ventrolateral to lateral cephalic margins. This 'tract' differs from its adjacent epidermis in lacking gland cells and in its cilia being longer. Ciliated cerebral canals opening towards rear of this 'tract' just below lateral level. The canals, 20-25 μm wide, lead obliquely inwards then turn posteriorly to form elongate chambers some 30-35 μm in diameter which lead to acidophilic glandular masses. The ciliated canals extend almost to rear of cerebral organs, narrowing as they do so to a maximum diameter of 12-15 μm, ending in posterior neuroganglionic tissues that are innervated by thick nerves entering cerebral organs from their dorsoposterior margins. Glandular tissues of cerebral organs mainly arranged bilaterally but have a small ventral component; cerebral organs about 250 μm long, including their ciliated canals, and about 45-50 μm in diameter ending just in front of proboscis insertion.

Excretory system: Well developed, extending from posterior oesophageal part of body back to anterior intestinal region. The system consists of 2 or 3 thick-walled collecting tubules on each side of body, running dorsolaterally between the inner circular-muscle fibres and the body-wall longitudinal musculature (Figs 61, 62). The tubules mostly 10-15 μm in diameter but in places twice as wide. Towards their posterior limit, occasional tubules pass through inner circular muscles, for a short distance running close to lateral blood vessels. At anterior end of excretory system only a single collecting tubule on each side; this turning outwards to form a slender efferent canal about 10 μm wide leading to a lateral nephridiopore.

Reproductive system: Gonads distributed along both dorsolateral and ventrolateral margins of body throughout intestinal region. In holotype, most gonads are empty, but gonoducts open to body surface indicating that specimen is just post-reproductive. Towards more posterior portions of body, however, some gonads are found which remain largely packed with ripe spermatozoa; spermatozoa also distinguishable both in gonoducts and on adjacent epidermal surface.

DISCUSSION: The general morphology of the present species, particularly its diagonal and inner body-wall muscle layers, and the organisation of its blood system, nervous system, and alimentary canal, closely resembles that of the genus *Ischyronemertes* Gibson (1990a) (Table 5). Two apparently significant features of the New Zealand nemerteans, however, are at variance with the generic diagnosis of *Ischyronemertes*, namely the length of the rhynchocoel and the number of muscle layers in the anterior region of the proboscis. Gibson (1990a: 153) stated of these "rhynchocoel short, between one-third and one-half of body length ... anterior region of proboscis with three muscle layers"; in the present specimens the rhynchocoel extends almost to the posterior tip of the body and there are only two muscle layers in the anterior portion of the proboscis. In his redescription of *Amphiporus heterophthalmus* (Schmarda, 1859), Senz (1997) transferred this species to *Ischyronemertes*; he noted that in this taxon the rhynchocoel extended into the posterior half of the body but did not get close to the posterior end, though the anterior proboscis wall contained three muscle layers. Other hoplonemertean genera are known, such as *Paranemertes*, in which the length of the rhynchocoel differs interspecifically, but in these taxa their contained species all have the same number of proboscis-muscle layers. Although many morphological features are shared by the present forms and species of *Ischyronemertes*, particularly the presence of a well-developed inner circular musculature, which is not a common character in monostiliferous hoplonemerteans, it is concluded that the significantly longer rhynchocoel length and different number of proboscis-muscle layers in the present species exclude it from the genus *Ischyronemertes*. Accordingly, the new

Table 5

Major anatomical features of the genus *Ischyronemertes* compared with those of the new genus, *Parischyronemertes*. Data taken from Gibson (1990a), Senz (1997) and the present paper.

	Ischyronemertes	*Parischyronemertes*
A. Features common to both taxa		
Body-wall musculature with additional diagonal and inner circular layers, longitudinal muscles not anteriorly divided	+	+
Precerebral septum closed	+	+
Apical organ present	+	+
Basophilic cephalic gland lobules extending post-cerebrally	+	+
Cerebral sensory organs situated close in front of precerebral septum, opening anteriorly	+	+
Brain with neither neurochord cells nor inner neurilemma, lateral nerve cords with short accessory nerves	+	+
Short intestinal caecum present, with anterior but no lateral diverticula	+	+
Blood system with three longitudinal post-cerebral vessels, middorsal vessel not penetrating rhynchocoel floor to form vascular plug	+	+
B. Distinguishing features between the two taxa		
Rhynchocoel extending almost to posterior end of body (+) or is only between one-third and one-half of body length (0)	0[1]	+
Anterior portion of proboscis with two (outer circular, inner longitudinal) (2) or three (outer circular, middle longitudinal, inner circular) (3) muscle layers	3	2
Nephridiopores dorso- or ventrolateral (DV) or lateral (L)	DV	L

[1] Except in *Ischyronemertes heterophthalma* (Schmarda, 1859), where the rhynchocoel extends into the posterior half of the body but does not reach anywhere near the posterior tip (Senz 1997).

genus *Parischyronemertes* is established for them, with *Parischyronemertes mathesonensis* sp. nov. forming the type species.

Family **CRATENEMERTIDAE** Friedrich, 1968

Nipponnemertes Friedrich, 1968

TYPE SPECIES: *Nipponnemertes pulchra* (Johnston, 1837)

DIAGNOSIS: "Monostiliferous hoplonemerteans with a proboscidial sheath reaching to posterior tip of body; muscle layers of sheath interwoven. Cerebral sense organs large and extending behind cerebral ganglia" (Berg 1985b: 239). Riser (1998a) added the following features: apical organ and frontal glands present; longitudinal muscle fibres between ganglion layer and fibrous core of lateral nerve cords; rhynchodaeum and oesophagus opening together at mouth; subepithelial oesophageal longitudinal muscles present; excretory system situated between brain and opening of pylorus into intestine; excretory pores ventrolateral.

Nipponnemertes sanguinea Riser, 1998

(Figs 65-66)

ORIGINAL DESCRIPTION: Riser, 1998a: 288–291, figs 1-6.

ADDITIONAL LITERATURE RELATING TO NEW ZEALAND RECORDS: As *Nipponnemertes* sp. (Gibson *et al.* in press); as *Nipponnemertes sanguinea* (Gibson in press).

DESCRIPTION: *External features:* Body shape very variable depending upon degree of contraction or elongation, ranging from short, fat, and wide to slender, more elongate, and dorsoventrally flattened (Fig. 65A); Riser (1998a: 291) noted that "Swimming *N. sanguinea* are oar shaped, whereas contracted animals range from sausage shaped to isosceles triangular with a broad base". Most examples are 15–20 mm long and about 2 mm wide, but larger specimens up to 56 mm long and 2.5 mm wide have been found. In strongly contracted individuals epidermal surface is distinctly wrinkled. Colour varies from vivid orange overall to pale yellowish, dorsal surface usually being rather darker than ventral; one individual was dorsally

marked with brown speckles. Intestine may have a brownish-grey tinge, with brain lobes behind the eyes visible as pinkish patches. Head with a small tuft of bristles at its tip; no cephalic slits but on each side there are about 20 eyes arranged into 1 or 2 more or less irregular rows (Fig. 65B). Bright red blood cells normally seen moving through lateral blood vessels in the intestinal regions of the body, making vascular system, especially on ventral surface, conspicuous (Fig. 65A).

Internal anatomy: Generally very similar to *Nipponnemertes pulchra* redescribed by Berg (1972), the New Zealand species differs in the shape of its stylet basis, the absence of an accessory stylet from the basis, nuage development (coalescence of nucleolar satellites) in oocytes, and in the bright red blood corpuscles.

OCCURRENCE: Originally found in holdfasts of the kelp *Lessonia variegata* washed ashore at Kaikoura, South Island, later found in stranded holdfasts of *Ecklonia* on Goat Island Beach, Leigh, North Island (Fig. 66). Subsequent collections have found specimens under stones lying on more or less hard rocky surfaces, or in coralline turf, on the lower shores at Matheson Bay, Leigh, Pukerua Bay, and Whangaparaoa, where it is sometimes locally common. Starfish, prawns and the echinoderm *Evechinus* are common associated faunal types.
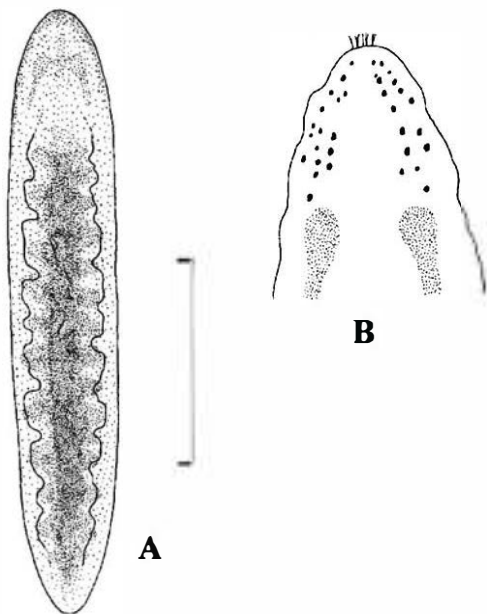

Fig. 66. *Nipponnemertes sanguinea.* Recorded distribution in New Zealand.

VOUCHER SPECIMENS: Voucher specimens are two complete series of transverse sections, both mature females, and complete specimens (all unregistered) deposited in the type room at NIWA, Wellington.

Fig. 65. *Nipponnemertes sanguinea.* **A.** Drawing made from life to show the general appearance of a moderately contracted specimen viewed from the ventral aspect; note how the blood vessels are distinct, their loops approximately corresponding with the lateral diverticula of the intestine. **B.** Enlargement of the head, viewed from the dorsal aspect, drawn to emphasise the distribution of the eyes; note the small tuft of cirri at the tip of the head and the position of the cerebral ganglia (stippled). Scale bar = 5 mm (refers to A only).
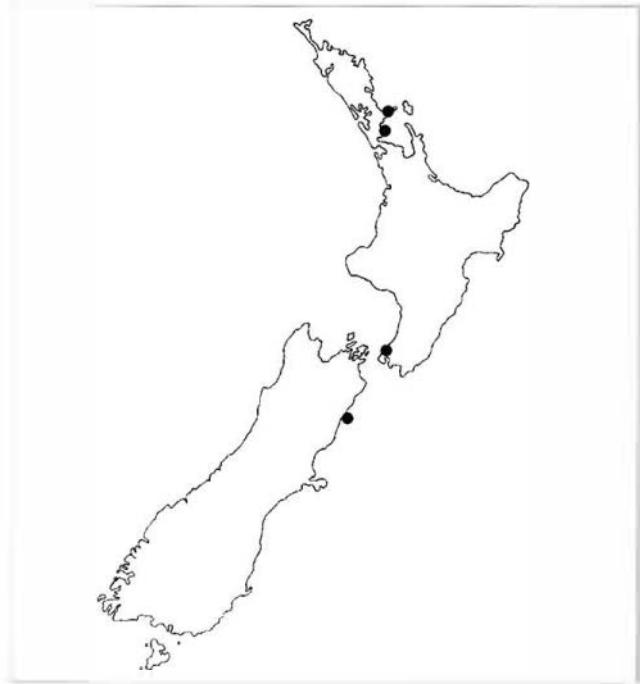
Family **PLECTONEMERTIDAE** Gibson, 1990

Acteonemertes Pantin, 1961

TYPE SPECIES: *Acteonemertes bathamae* Pantin, 1961

DIAGNOSIS: Upper littoral to fully terrestrial monostiliferous hoplonemerteans; rhynchocoel extending full body length, with wall composed of wickerwork of interwoven longitudinal- and circular-muscle fibres. Proboscis small, less than half body diameter, used in locomotion; body-wall musculature strongly developed; dermis thin; parenchyma extensive. Apical organ absent; cephalic glands extensive, basophilic, opening via improvised pores; cerebral sensory organs small, simple, with posterior glandular region, opening ventrally from transverse cephalic furrow; lateral nerve cords without accessory lateral nerve but with fibres contributed by dorsal brain lobes; blood system in cephalic region developed as an extensively branched submuscular capillary network; middorsal blood vessel with 2 vascular plugs. Excretory system well developed, branching throughout the body and opening via

large number of pores, with scattered mononucleate flame cells which lack cuticular support bars, excretory tubules without thick-walled terminal region; 4 (occasionally 6) eyes; sexes separate, oviparous (Moore & Gibson 1981).

Acteonemertes bathamae Pantin, 1961 (Figs 67–68)

ORIGINAL DESCRIPTION: Pantin, 1961a: 154–155, pl. 1, figs 1–4.

ADDITIONAL LITERATURE RELATING TO NEW ZEALAND RECORDS: Pantin (1969), Moore (1973, 1985, 1989), Dawson (1975, 1993), Moore & Gibson (1981, 1985, 1993), Jespersen (1987), Duffy & Ackley (1988), Jespersen & Lützen (1988a, b), Riser (1988a), Gibson (1995, in press), Gibson *et al.* (in press) (all as *Acteonemertes bathamae*).

DESCRIPTION: *External features:* Typically 30–80 mm long, 2–3 mm in diameter, with dorsal surface marked by 2 very broad dark chocolate-brown longitudinal stripes, commencing behind the head, separated by a narrow cream median line (Fig. 67A). Ventral surface cream without markings, the head also pale but may be somewhat darker anterodorsally. On head usually 4 small eyes, the posterior pair smaller, sometimes doubled (Fig. 67B). Individuals living in fully terrestrial conditions tend to be uniformly light grey, without the 2 longitudinal stripes.

Internal anatomy: Pantin's (1961a, b) accounts of the anatomy of this species have been supplemented by additional information given by Pantin (1969), Moore (1973), and Moore and Gibson (1981, 1988b), among others. Ultrastructural investigations have also been made on the protonephridia (Jespersen 1987), eyes
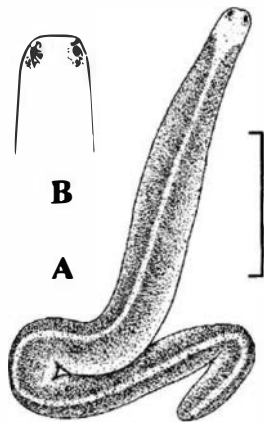
(Jespersen & Lützen 1988a) and blood system (Jespersen & Lützen 1988b). The genus *Acteonemertes* is monospecific; the main anatomical characteristics of the species are thus the same as given in the generic diagnosis.

OCCURRENCE: Originally found under large stones in the splash zone between high spring and neap tide levels in sheltered bays on the Portobello Peninsula, South Island. The type locality is Crib Beach (Pantin 1961a) (Fig. 68). Moore (1973, 1989) recorded subsequent discoveries of the species supralittorally on Auckland, Ocean and Stewart Islands, and Riser (1988a: 132) found examples at Rhino Horns near the Kaikoura Marine Laboratory, South Island, where it occurred in limestone and mudstone rubble beneath rotting kelp on the upper shore, the "storm wrack [teeming] with amphipods and dipteran larvae ... the rubble beneath [being] coated with a mucoid mixture of algal exudate, rotted algae, and faeces of amphipods and dipteran larvae." On Auckland and Ocean Islands it has also been found under small logs at the margins of scrub remnant at an altitude of about 33 m above sea level (Moore 1973).
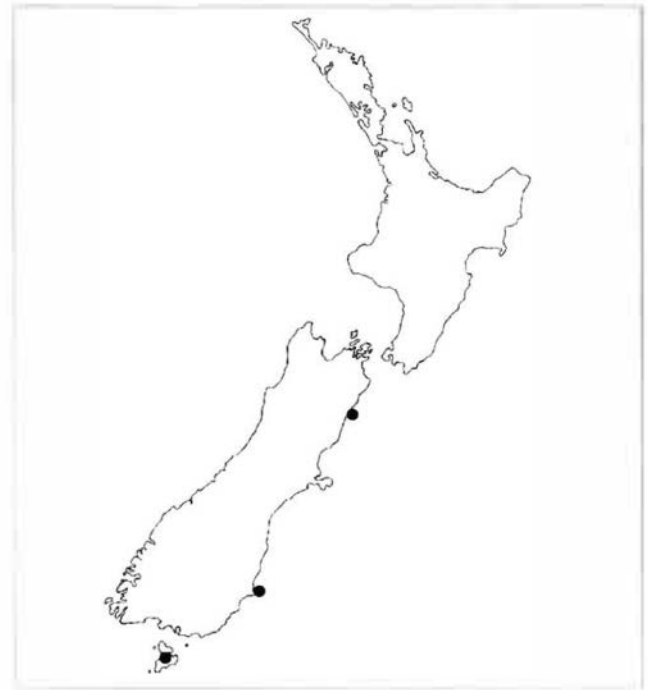

Fig. 68. *Acteonemertes bathamae.* Recorded distribution in New Zealand.

Antiponemertes Moore & Gibson, 1981

TYPE SPECIES: *Antiponemertes novaezelandiae* Dendy, 1895

Fig. 67. *Acteonemertes bathamae.* Drawing of: A, complete individual; B, enlargement of the head to show the eye pattern. Both based upon photographs in Pantin (1961a). Scale bar = 5 mm (refers to A only).

DIAGNOSIS: Terrestrial monostiliferous hoplonemer-
teans; rhynchocoel extending full body length, with wall
composed of wickerwork of interwoven longitudinal-
and circular-muscle fibres; proboscis large, used in loco-
motion; body-wall musculature strongly developed;
dermis thin; parenchyma poorly developed. Apical
organ absent; cephalic glands extensive, basophilic,
opening via numerous improvised pores; cerebral
sensory organs large, with anterior sac, forked ciliated
cerebral canal and posterior glandular region, opening
ventrally from transverse cephalic furrow; lateral
nerve cords with or without accessory lateral nerve;
blood system in cephalic region either developed as an
extensively branched submuscular capillary network
or, in one small species, with simple vascular loop
replacing capillary network; middorsal blood vessel
with 2 vascular plugs. Excretory system extensive,
branching throughout the body and opening via large
number of pores, with scattered mononucleate flame
cells which lack cuticular support bars, excretory
tubules with thick-walled terminal region; 2-4 eyes;
sexes separate, oviparous (Moore & Gibson 1981).

Antiponemertes allisonae (Moore, 1973)

(Figs 69–70)

ORIGINAL DESCRIPTION: Moore, 1973: 301–305, table 1, figs 1,
5–11 (as *Geonemertes allisonae*).

ADDITIONAL LITERATURE RELATING TO NEW ZEALAND RECORDS: As
Geonemertes allisonae (Dawson 1975); as *Antiponemertes
allisonae* (Dawson 1993; Moore & Gibson 1981, 1985, 1993;
Wells *et al.* 1983; Moore 1985, 1989; Gibson 1995, in press).

DESCRIPTION: *External features:* A small species; mature
females up to about 10 mm long, 0.5–1 mm wide, with
2 relatively large and distinct eyes on head (Fig. 69A);
males of this species have not yet been found. Dorsal
body surface behind head mottled with brown, with a
clear middorsal longitudinal stripe above the
rhynchocoel (Fig. 69B).

Internal anatomy: Apart from its size at maturity,
colour pattern and the presence of only 2 eyes, distinc-
tive features of the species include a cephalic blood
supply consisting of a simple vascular loop rather than
a capillary network, and the presence of accessory
lateral nerves in each longitudinal nerve cord. *Antipo-
nemertes pantini* also possesses accessory lateral nerves
but *Antiponemertes novaezealandiae* does not.

OCCURRENCE: So far known only from under fallen logs
in a valley at the margin of bush at Menzies Bay, Banks
Peninsula, South Island (43°39′ S, 172°57′ E) (Fig. 70).
Wells *et al.* (1983) include *Antiponemertes allisonae* as
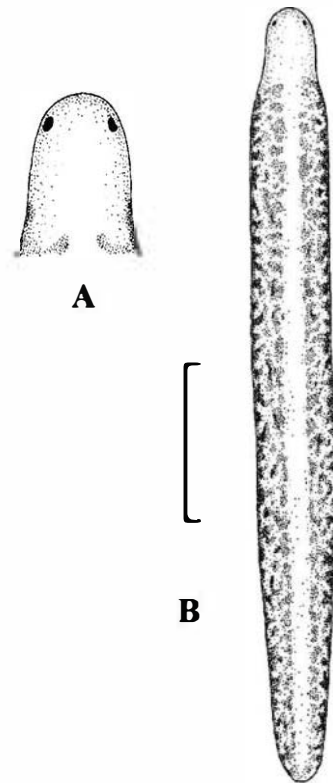an endangered species. Moore (1989: 82) commented

Fig. 69. *Antiponemertes allisonae.* Drawings (enlarged) to
show: **A**, the distribution of the eyes on the head; **B**, com-
plete specimen viewed from the dorsal aspect. Both based
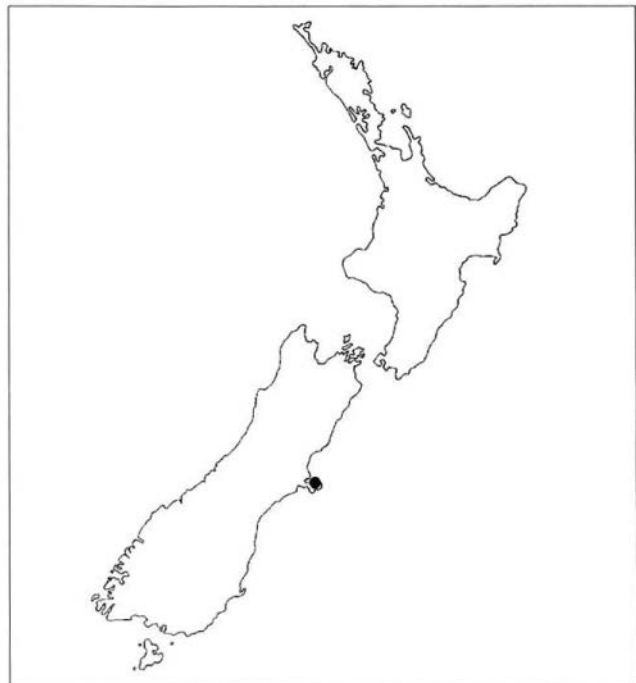on Moore (1973: fig. 5). Scale bar = 2 mm (refers to B only).

Fig. 70. *Antiponemertes allisonae.* Recorded distribution in
New Zealand.

that because almost all of the natural habitat at Menzies Bay on Banks Peninsula occupied by *Antiponemertes allisonae* has been destroyed through intensive grazing by sheep and deer, "It is feared that it may be extinct."

Antiponemertes novaezealandiae (Dendy, 1895)
(Figs 71–72)

ORIGINAL DESCRIPTION: Dendy, 1895a: 192-194 (as *Geonemertes novae-zealandiae*).

ADDITIONAL LITERATURE RELATING TO NEW ZEALAND RECORDS: As *Geonemertes novae-zealandiae* (Dendy 1894 [without description], 1895b; Darbishire 1909; Pantin 1961b); as *Geonemertes novaezealandiae* (Bürger 1897–1907, 1904; Pantin 1969; Moore 1973; Dawson 1975); as *Geonemertes novae-zelandiae* (Darbishire 1909; Pantin 1961b); as *Geonemertes novo-zelandiae* (Hett 1927); as *Antiponemertes novaezealandiae* (Moore 1989; Dawson 1993; Moore & Gibson 1981, 1985, 1993; Gibson 1995, in press; Gibson *et al*. in press); as *Antipodonemertes novae-zealandiae* (Dawson 1993).

DESCRIPTION: *External features:* Larger individuals up to about 80 mm long and 1.5–3.0 mm wide when extended. Dorsal body surface with 4 dark purplish-brown longitudinal stripes on pale cream, pale pink, or dull yellowish background, the inner, more dorsal stripes wider than the outer (Fig. 71); all stripes ending abruptly a short distance behind eyes; colour of stripes resulting from a porphyrin or porphyrin-like pigment (Pantin 1969). Ventral body surface nearly white, the head a pale brownish-yellow. Four eyes on rounded head, the anterior pair larger than the posterior. Both this species and *Antiponemertes pantini*, when moving by their characteristic form of ciliary gliding on secreted mucus, exhibit a pronounced side-to-side motion of the head which is accompanied by a slight rotation about their longitudinal axis (Moore 1989).

Internal anatomy: Details of the anatomy of this species given by Dendy (1895a) have since been supplemented by several authors, particularly Pantin (1969) and Moore (1973). The species differs anatomically from both *Antiponemertes allisonae* and *Antiponemertes pantini* in having no accessory lateral nerves, and from *Antiponemertes allisonae* in its cephalic blood supply consisting of a capillary network rather than a simple loop.

OCCURRENCE: *Antiponemertes novaezealandiae* has a wide distribution throughout New Zealand (Fig. 72) and has also been found on Ocean Island, off Auckland Island. In North Island it has been found near Auckland, Mount Egmont, Lake Waikaremoana, Mount Ruapehu, and Wellington, and in the Napier area, whilst in South Island specimens have been obtained from Toi Toi, Fortrose (Dendy 1894), near Invercargill (the type
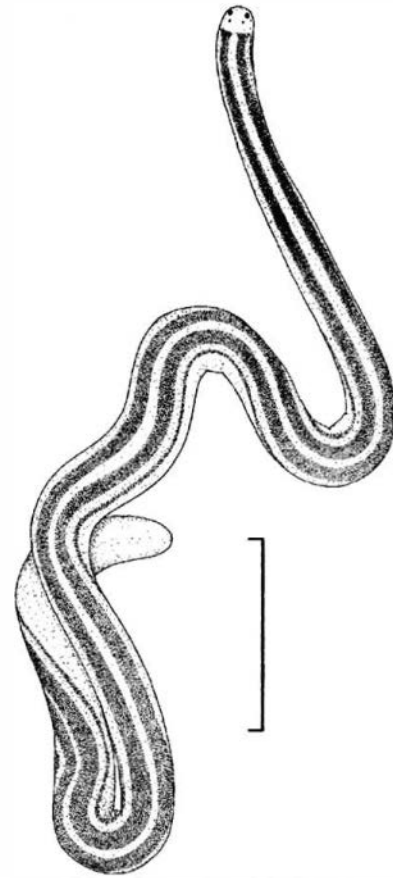

Fig. 71. *Antiponemertes novaezealandiae*. Drawing of a complete individual to show the typical arrangement of the four longitudinal stripes. Based on photographs in Pantin (1961b, 1969). Scale bar = 10 mm.
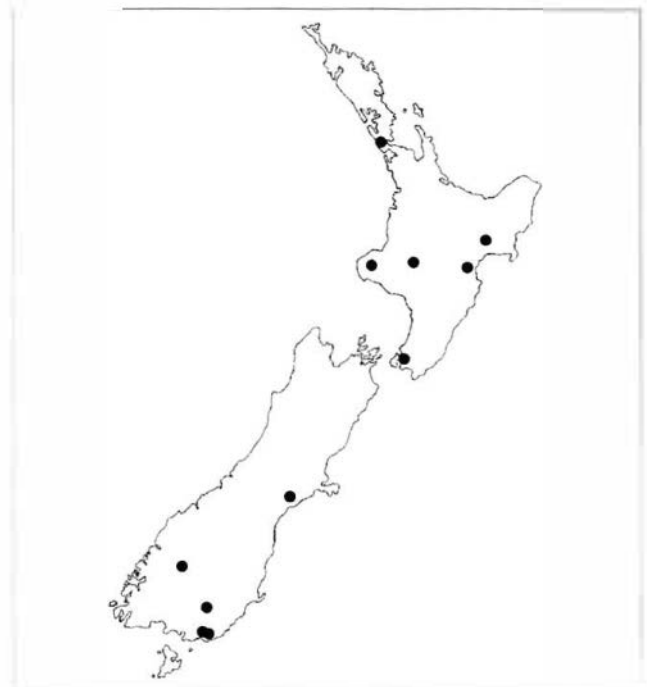

Fig. 72. *Antiponemertes novaezealandiae*. Recorded distribution in New Zealand.

locality), near Tokanui, west of Queenstown and in the Southland Scenic Reserve of Edendale (Table 6). The species occurs under fallen logs and in crevices and hollows in rotten tree fern trunks, under rotten logs in wet conditions, and in *Nothofagus* and mixed broadleaf forests under logs. Nemerteans obtained from bush or under a burnt log at Greville Harbour, D'Urville Island, "probably belong to this species but certain identification is not possible" (Moore 1973: 295).

Table 6

The recorded distribution of *Antiponemertes novaezealandiae*. Based on data given in Moore (1973, 1989).

Location	Latitude and Longitude
North Island	
Stokes Valley, near Wellington	41°10' S, 174°59' E
Napier area, near the coast at Waipatiki	39°17' S, 176°58' E
Erua, near Mount Ruapehu by Cuffs Road	39°15' S, 175°21' E
Near Lake Waikaremoana	38°45' S, 177°10' E
Piha Gorge, Auckland	36°57' S, 174°28' E
Near Mount Egmont	39°19' S, 174°06' E
South Island	
Toi Toi, Fortrose, near Invercargill, Southland	46°32' S, 168°49' E
Deserted farmhouse 3 miles south of Waimahaka on road to Fortrose	46°32' S, 168°49' E
Tokanui, in a wood 1.5 miles SE of township	46°34' S, 168°57' E
Mount Somers, near Ashburton, Canterbury, at edge of Alford Forest near Springburn	43°42' S, 171°29' E
Edendale Scenic Reserve, Southland	46°19' S, 168°52' E
Bob's Cove, 15 km west of Queenstown	45°03' S, 168°34' E
Ocean Island, off Auckland Islands	
In coastal rata forest	51°00' S, 166°00' E

Antiponemertes pantini (Southgate, 1954)

(Figs 73–74)

ORIGINAL DESCRIPTION: Southgate, 1954: 157–160, figs 1-4 (as *Geonemertes pantini*).

ADDITIONAL LITERATURE RELATING TO NEW ZEALAND RECORDS: As *Geonemertes pantini* (Pantin 1969; Moore 1973; Dawson 1975); as *Antiponemertes pantini* (Moore & Gibson 1981, 1985; Moore 1989; Dawson 1993; Gibson 1995, in press); as *Antipodonemertes* [sic] *pantini* (Dawson, 1993).

DESCRIPTION: *External features:* Up to about 75 mm long and 5 mm in maximum width; dorsal colour pattern somewhat variable, most individuals with 2 brown dorsolateral stripes (Fig. 73A) (their pigment probably a melanin [Pantin 1969]) but occasional examples with 3 or 4 dorsal longitudinal brown stripes; in some specimens essentially 2 stripes but each with a pale centre more or less dividing it longitudinally (Fig. 73B), cf. examples from the Isles of Scilly with 2 broad and more or less regularly mottled dorsolateral longitudinal bands (Fig. 73C). Background colour is light orange, pinkish or cream. Four eyes on head, anterior 2 distinctly larger and more widely spaced than the smaller, more dorsal, posterior pair. Southgate (1954: 159) noted that the species possesses a pair of "vertical cephalic slits which define the posterolateral margins of the 'head'."

Internal anatomy: Southgate's (1954) brief description of the anatomy of this species has been supplemented by Pantin (1969) and Moore (1973). Generally very similar to *Antiponemertes novaezealandiae*, the most striking difference between the two is that *Antiponemertes pantini* possesses accessory lateral nerves which are both variable in size and may be detached from the main longitudinal nerve cords. It differs from *Antiponemertes allisonae* in possessing a capillary blood network in its cephalic region.

OCCURRENCE: This species, like the one above, has a wide distribution throughout New Zealand (Fig. 74). In North Island it has been found only at Coroglen, Mount Kaku and Mangawhoio, but on South Island is much more widespread, occurring at Signal Hill near Dunedin (the type locality), Mataura, Cass, Kaikoura, Westport and in Lewis Pass, Minchin Pass, Trotter's Creek and on Banks Peninsula (Table 7). *Antiponemertes pantini* has been found in deep leaf mould on porous rock with no ground water, in *Nothofagus* forest, in podocarp and mixed broadleaf woodland which was dry to very dry during the summer months that the specimens were discovered, and in South Island at altitudes up to 1600 m in subalpine conditions. It has also been found on Stewart Island (Easy Cove) and in primary forest on Ulva Island in Paterson Inlet. A recent finding of specimens under stones in the Isles of Scilly, U.K., is the first record of any *Antiponemertes* species outside New Zealand (Moore *et al.* 2001).

Argonemertes Moore & Gibson, 1981

TYPE SPECIES: *Argonemertes australiensis* (Dendy, 1892)

DIAGNOSIS: Terrestrial monostiliferous hoplonemerteans; rhynchocoel extending the body length, with wall composed of wickerwork of interwoven longitudinal- and circular-muscle fibres; proboscis massive
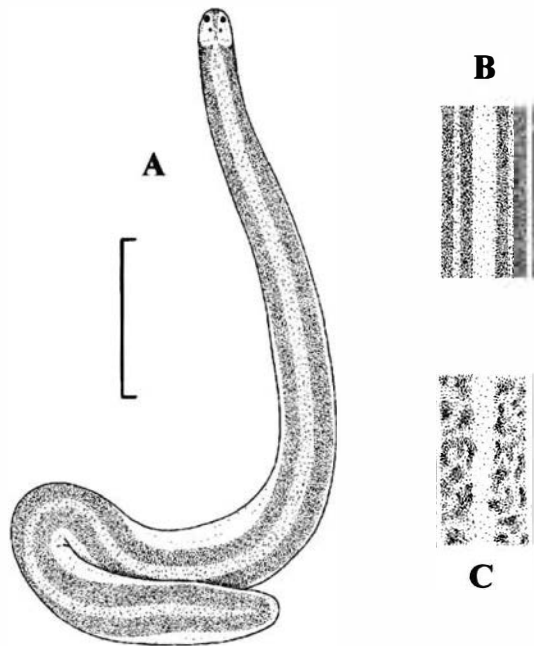
Fig. 73. *Antiponemertes pantini*. A. Drawing of a complete individual to show the most commonly recorded colour pattern, comprising two broad dorsolateral stripes; based on drawings in Southgate (1954) and a photograph by E.J. Batham *in* Pantin (1969). B, C. Schematic representations of two of the other colour pattern variations recorded for this species. Scale bar = 10 mm (refers to A only).
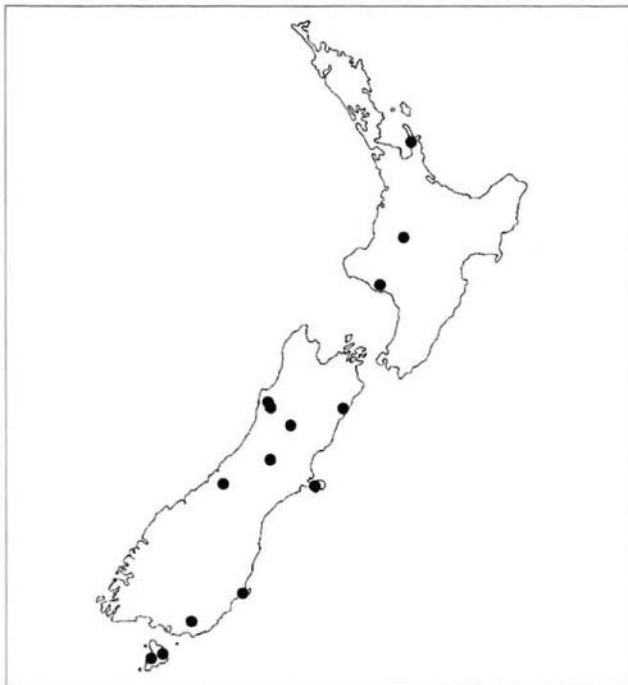

Fig. 74. *Antiponemertes pantini*. Recorded distribution in New Zealand.

Table 7

The recorded distribution of *Antiponemertes pantini*. Based on data given in Moore (1973, 1989).

Location	Latitude and Longitude
North Island	
Mangawhoio, near Waitotara, near Wanganui	39°47′ S, 174°44′ E
Mount Kaku, Hauhangaroa Range, near Lake Taupo	38°47′ S, 175°35′ E
Coroglen, Coromandel	36°55′ S, 175°41′ E
South Island	
Signal Hill, Dunedin, near the Centennial Memorial	45°49′ S, 170°30′ E
Leith Valley, Dunedin	45°50′ S, 170°30′ E
Thornhill Farm, 7 miles SE of Mataura	46°13′ S, 168°52′ E
Cass, Canterbury, *Nothofagus* forest by stream near University Field Station	43°02′ S, 171°46′E
Hapuku near Kaikoura; coastal *Ngaio* forest	42°19′ S, 173°44′ E
Lewis Pass; subalpine	42°24′ S, 172°24′ E
Minchin Pass, Arthur's Pass National Park; subalpine	42°06′ S, 171°36′ E
Paparoa Range near Westport	42°08′ S, 171°24′ E
Trotter's Creek, Moeraki, S. Westland	43°41′ S, 169°14′ E
Banks Peninsula, Cooper's Knob	43°40′ S, 172°40′ E
Stewart Island	
Easy Cove (Easy Harbour)	47°09′ S, 167°34′ E
Ulva Island in Paterson Inlet	46°56′ S, 168°08′ E

and powerful, used in locomotion, body-wall musculature and dermis variably developed; apical organ absent. Cephalic glands extensive, mostly basophilic, opening via improvised pores; cerebral sensory organs large, with anterior sac, forked ciliated cerebral canal and elongate posterior glandular region, opening ventrally from transverse cephalic furrow; lateral nerve cords with accessory lateral nerve; blood system developed as an extensively branched submuscular capillary network, one species with both a vascular loop and capillary network in the head. Middorsal blood vessel with 2 vascular plugs. Excretory system extensive, branching throughout the body and opening via large number of pores, with scattered mononucleate flame cells which lack cuticular support bars, excretory tubules with thick-walled terminal region; 20–180 eyes, eye number increasing with age and size; sexes separate or hermaphroditic, oviparous (Moore & Gibson 1981).

Argonemertes dendyi (Dakin, 1915)   (Figs 75–76)

ORIGINAL DESCRIPTION: Dakin, 1915: 567–570, fig. 1 (as *Geonemertes dendyi*).

ADDITIONAL LITERATURE RELATING TO NEW ZEALAND RECORDS: Gibson (1995, in press), Moore *et al.* (2001) (all as *Argonemertes dendyi*).

DESCRIPTION: *External features:* Up to about 25 mm long, 1.0-1.5 mm in diameter; protandrous, hermaphrodites, males usually smaller than females. Background colour pale yellowish, orange, dark brown, purplish-pink or cream, marked by a pair of dark brown dorsolateral longitudinal stripes extending from behind the eyes to the tail (Fig. 75A). Ventral surface more uniformly coloured and lacking stripes. Older specimens often darker in their more posterior regions, in some examples the dorsolateral stripes so broad that they are medially separated only by a slender pale longitudinal line. Eyes on head arranged in 4 groups, generally with 3-8 or more ocelli in each group (Fig. 75B).

   Internal anatomy: Cephalic blood supply comprising a capillary network with no vascular loop. Though superficially resembling the commonest colour variant of *Antiponemertes pantini*, *Argonemertes dendyi* can easily be distinguished by its eye multiplication (cf. Figs 73A and 75A).
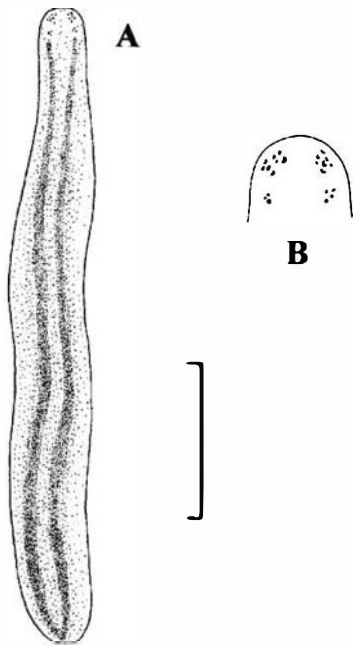

Fig. 76. *Argonemertes dendyi.* Recorded distribution in New Zealand.

OCCURRENCE: *Argonemertes dendyi* is a native of south-western Australia but has previously been found as an immigrant in the British Isles, Azores, Canary Islands, Hawaii, the United States of America, and in European greenhouses. It has also been introduced into North Island, New Zealand, where it has been found beneath logs at Papatea Bay, East Cape (Fig. 76).

Campbellonemertes Moore & Gibson, 1972

TYPE SPECIES: *Campbellonemertes johnsi* Moore & Gibson, 1972

DIAGNOSIS: Freshwater monostiliferous hoplonemerteans; rhynchocoel extending full body length, with wall composed of wickerwork of interwoven longitudinal- and circular-muscle fibres; proboscis small in comparison with body size, not apparently used in locomotion; body-wall musculature well developed; dermis thin. Apical organ absent; cephalic glands extensive, posteriorly reaching behind rear of brain and opening via numerous improvised pores; cerebral sensory organs well developed, but with neither anterior sac nor forked ciliated cerebral canal, opening laterally from the posterior of 2 pairs of short horizontal cephalic furrows arranged *in tandem*; lateral nerve cords without accessory lateral nerves; blood system comprising paired longitudinal lateral vessels, joined by cephalic and anal loops, posterior part of cephalic

Fig. 75.   *Argonemertes dendyi.* Drawings to show: **A**, the general appearance a complete individual; **B**, an enlargement of the head to show the four groups of eyes. Based on illustrations in Dakin (1915) and Pantin (1961b). Scale bar = 2 mm (refers to A only).

66

loop in brain region developed into 2 vascular plugs, and single middorsal vessel. Excretory system extensive, branching throughout post-cerebral regions of the body and opening via large number of pores, with scattered mononucleate flame cells which lack cuticular support bars, excretory ducts without specialised end regions; without eyes. Sexes hermaphroditic, separate ovaries and testes distributed throughout body posterior to intestinal caecum, ovaries lateral, testes ventral or ventrolateral, oviparous (Moore & Gibson 1972).

Campbellonemertes johnsi Moore & Gibson, 1972
(Fig. 77)

ORIGINAL DESCRIPTION: Moore & Gibson, 1972: 187–202, tables 1, 2, figs 1–17.

ADDITIONAL LITERATURE RELATING TO NEW ZEALAND RECORDS: Gibson & Moore (1976), Friedrich (1979), Moore & Gibson (1985, 1988b), Gray (1988), Dawson (1993), Gibson 1995, in press (all as *Campbellonemertes johnsi*).

DESCRIPTION: *External features:* Body extremely slender (0.5 mm or less) but attaining a length of about 100 mm. Overall colour grey, with a single longitudinal middorsal white stripe extending full length of body (Fig. 77).
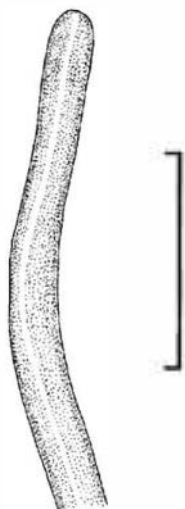

Fig. 77. *Campbellonemertes johnsi.* Drawing of the anterior end, viewed dorsally, to show the colour pattern characteristic of the species. Based on the descriptions given by Moore and Gibson (1972, 1985). Scale bar = 2 mm.

Internal anatomy: The genus is monospecific, the major internal anatomical features of the species being summarised in the generic diagnosis above. The familial position of *Campbellonemertes johnsi* was discussed by Moore and Gibson (1988b).

OCCURRENCE: So far known only from a pond near Tucker Cove, Perseverance Harbour, Campbell Island.

Potamonemertes Moore & Gibson, 1973

TYPE SPECIES: *Potamonemertes percivali* Moore & Gibson, 1973

DIAGNOSIS: Freshwater monostiliferous hoplonemerteans; rhynchocoel extending full body length, with wall composed of wickerwork of interwoven oblique, longitudinal- and circular-muscle fibres; proboscis massive, used in locomotion; body-wall musculature well-developed, particularly in anterior regions; dermis thick; parenchyma extensive. Apical organ present; cephalic glands present but not extensive, posteriorly not reaching brain, opening either through apical organ or by a separate median anterior pore just above apical organ; cerebral sensory organs small, with neither anterior sac nor forked ciliated cerebral canal, opening laterally from horizontal cephalic furrows; lateral nerve cords without accessory lateral nerve; blood system comprising paired longitudinal lateral vessels joined by cephalic and anal loops, cephalic loop in brain region forming 2 vascular plugs, and single middorsal vessel. Excretory system extensive, branching throughout body and opening via large number of pores, with scattered mononucleate flame cells that lack cuticular support bars, excretory ducts with thick walled and glandular end regions. Without eyes; sexes hermaphroditic, simultaneous and probably variably protandrous, gonads either sharply regionalised or overlapping but with testes extending more anteriorly than ovaries.

Potamonemertes percivali Moore & Gibson, 1973
(Figs 78-79)

ORIGINAL DESCRIPTION: Moore & Gibson, 1973: 142–156, figs 1–10.

ADDITIONAL LITERATURE RELATING TO NEW ZEALAND RECORDS: Dawson (1975, 1993), Gibson & Moore (1976), Friedrich (1979), Moore & Gibson (1985, 1993), Gray (1988), Hickman & Moore (1990), Gibson (1995, in press) (all as *Potamonemertes percivali*).

DESCRIPTION: *External features:* Slender, white or colourless apart from a faint greyish tinge to gut (Fig. 78). Preserved lengths of 10-20 mm suggest a normal living extension of up to about 20–30 mm, perhaps somewhat longer; and about 750 μm in diameter. The worms are extremely difficult to collect intact as they readily fragment.

Internal anatomy: Among the features which enable the New Zealand species to be distinguished from the only other member of the genus, *Potamonemertes gibsoni* Hickman & Moore, 1990, from Tasmania, are the way its cephalic glands discharge anteriorly by a median
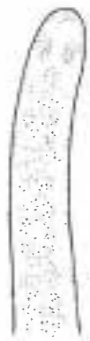
Fig. 78. *Potamonemertes percivali.* Drawing of the anterior end, viewed dorsally, based on the description given by Moore & Gibson (1973). Scale bar = 2 mm.

pore separate from the apical organ, and the sharply regionalised distribution of its testes and ovaries. Moore and Gibson's (1988b) discussion of the familial position of the genus is extended by Hickman and Moore (1990).

Gregarine parasites exhibiting *in tandem* syzygy have been found in the blood system of *Potamonemertes percivali* (Moore & Gibson 1973), but whether these are the same species as gregarines living in the gut lumen remains unknown.

OCCURRENCE: So far known only from gravel beds or among fairly solid gravel and clay in the Selwyn River, Canterbury, South Island, near Coe's Ford (Fig. 79), occurring with the turbellarians *Prorhynchus putealis* and *Prorhynchus haswelli*. When disturbed, the worms move rapidly, quickly everting and retracting their proboscis for locomotion. They readily fragment when handled.

Fig. 79. *Potamonemertes percivali.* Recorded distribution in New Zealand.

Family PROSORHOCHMIDAE Bürger, 1895

Heilogonemertes gen. nov.

TYPE SPECIES: *Heilogonemertes cooki* sp. nov.

DIAGNOSIS: Monostiliferous marine nemerteans; rhynchocoel extending for about 75% of body length, with wall containing 2 distinct muscle layers; anterior region of proboscis with 2 muscle layers (outer circular, inner longitudinal), proboscis armature consisting of single central stylet and 2 accessory stylet pouches; body- wall musculature with neither diagonal nor inner circular layers, longitudinal musculature anteriorly divided. No precerebral septum; apical organ absent, cephalic glands few, isolated, restricted to cephalic region; cerebral sensory organs situated close in front of brain lobes but separate from them, opening anteriorly by ventral pores discharging into ventral transverse cephalic furrow; lateral nerve cords with myofibrillae and short accessory nerves, without neurochord cells. Foregut opening into rhynchodaeum, stomach regionally differentiated, pyloric region of foregut extremely long, intestinal caecum long but with neither anterior nor lateral pouches. Blood system simple, with cephalic loop, single middorsal and paired lateral vessels without pseudometameric transverse connectives in intestinal region, presence of vascular plug on middorsal vessel uncertain; parenchyma poorly developed. Excretory system confined to foregut region. Eyes in 3 groups, anterior group extending across tip of head. Sexes separate, gonads numerous and tightly packed.

ETYMOLOGY: The generic name, a composite of the Greek *heilo* (to pack closely) and *gone* (progeny or seed) linked with the name *nemertes*, refers to the numerous closely packed gonads present in adults. The species is named after Steve de C. Cook, both as a tribute to his work in producing the *Coastal Marine Invertebrates of New Zealand* and in thanks for his considerable hospitality and assistance with the collection of nemerteans during the author's 1992 visit to New Zealand.

Heilogonemertes cooki sp. nov.   (Figs 80-83)

TYPE SPECIMEN: Holotype, mature male, complete set of transverse sections, 94 slides, NZOI H-721; paratypes, series of transverse sections, 146 slides, of mature male and mature female, NZOI P-1256. Ten unsectioned voucher specimens are also registered under NZOI P-1257, deposited in the NZOI collection at NIWA in Wellington.

TYPE LOCALITY: The eastern end of Devonport Beach,

Auckland, lower mid-shore under stones in silty sand, one specimen collected 18 August 1992.

ADDITIONAL MATERIAL: The species appears to be fairly common around North Island (Fig. 80), also being found on Rangitoto Island (3 specimens, 20 August 1992), at Matheson Bay (6 specimens, 24 August 1992),
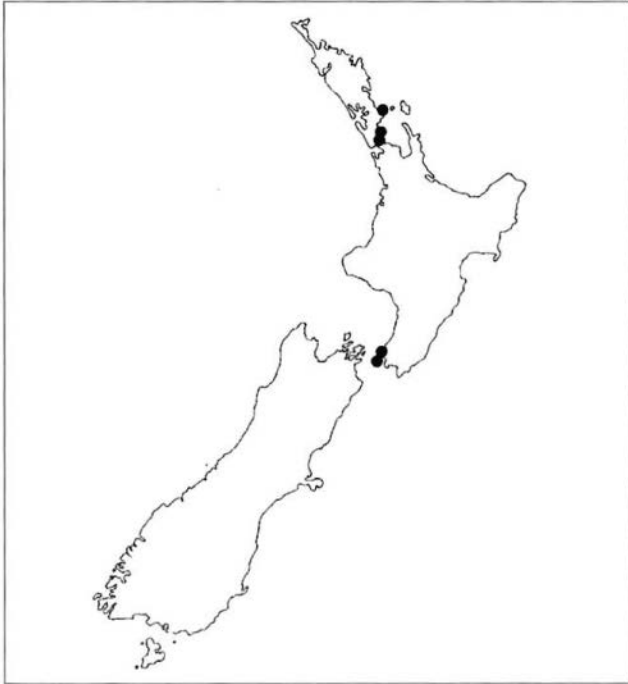

Fig. 80. *Heilogonemertes cooki* gen. et sp. nov. Recorded distribution in New Zealand.
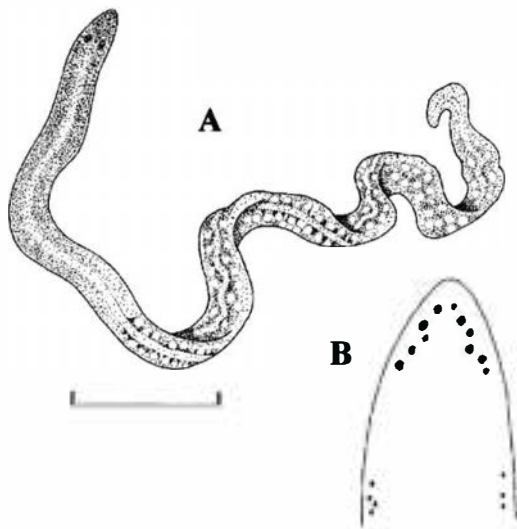

Fig. 81. *Heilogonemertes cooki* gen. et sp. nov. **A**. Drawing of the holotype to show the general appearance of a complete specimen. **B**. Enlargement of the head, drawn to emphasise the distribution of the eyes. Based on sketches made from life. Scale bar = 3 mm (refers to A only).

Lyall Bay (14 specimens, 29 August 1992), Pukerua Bay (1 specimen, 30 August 1992), and Whangaparaoa (1 1 specimens, 1 September 1992). It occurs in the mid- to lower-shore zones, under stones, rocks and boulders in medium to coarse silty sand, and in fine compacted silty-clay or in mudstone crevices.

DESCRIPTION: *External features:* Up to 70–80 mm long but mostly only about 1 mm in maximum width, the posterior two-thirds of body somewhat dorsoventrally compressed (Fig. 81A). From about half way, body gradually tapering to end in a blunt but rather narrow tail. Head roundly pointed, darker brown than remainder of anterior region, with 3 groups of dark brown or black eyes (Fig. 81B). An anteriorly directed V-shaped group of 8–10 or more eyes situated near anterior tip; farther back, above anterior margins of brain lobes on each side, a smaller group of 3 or 4 eyes; ocelli forming anterior group larger than those in posterior groups. Brain lobes just visible through body wall as pinkish patches. Cephalic furrows not distinguishable in life. Anterior third or less of dorsal surface reddish-brown, remainder of body whitish with dark-grey and irregularly arranged transverse streaks or patches between gonads. Ventral surface with a paler irregular 'stripe' running medially below greyish gut.

When disturbed, body often curling up into a tight ball enclosed by a thick layer of mucus.

Body wall, musculature and parenchyma: In cerebral and foregut regions glandular epidermis 35–45 μm tall (Fig. 82), with well-developed basal-cup zone similar to that described by Norenburg (1985), but in posterior body regions reduced to a maximum height of about 30 μm. Beneath epidermis, connective-tissue dermis up to about 7-8 μm in maximum thickness in anterior body regions, but only 2–3 μm posteriorly.

Body-wall musculature comprising 2 layers (Fig. 82). In foregut region outer circular layer up to about 15 μm thick, inner longitudinal coat 30–60 μm deep; in posterior intestinal regions these layers respectively about 4–5 μm and 7–20 μm thick. At more or less regular intervals isolated fibres radiate from circular-muscle layer, some peripherally to pass through dermis and penetrate proximal portions of epidermis, others inwardly to extend between bundles of longitudinal muscle fibres, particularly in dorso- and ventrolateral portions of body where they appear to join with dorso-ventral muscle strands derived from rhynchocoel-wall circular muscles. Longitudinal muscles in bundles enclosed by connective tissue. The longitudinal layer anteriorly divided. Close behind the brain isolated bundles of longitudinal fibres, each enclosed by a thin connective-tissue membrane, form origin of inner region; density of fibres forming inner layer distinctly greater than that of the outer layer. By rear of brain,
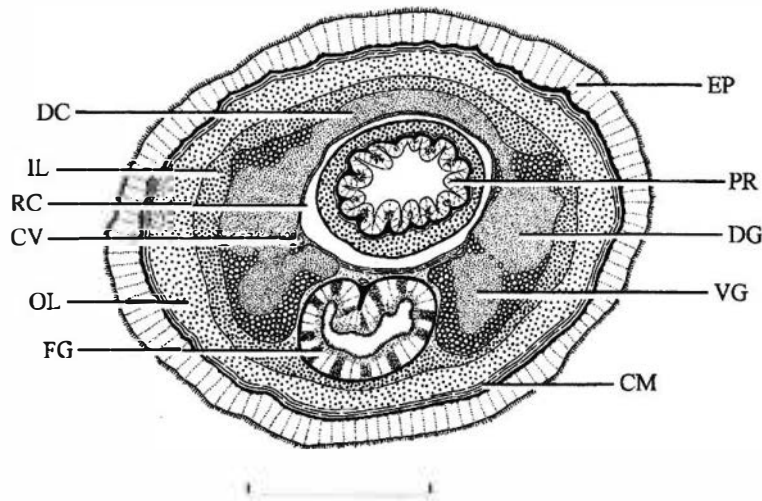
Fig. 82. *Heilogonemertes cooki* gen. et sp. nov. Camera lucida drawing of holotype to show the organisation of the various body structures in the brain region. Scale bar = 200 μm.

the inner and outer longitudinal-muscle zones more or less well established, their separation becoming increasingly clear farther forwards (Fig. 82). Inner layer, about 30 μm in maximum thickness, separated from outer region only by a thin but distinct connective-tissue membrane. Only inner longitudinal-muscle fibres contributing to proboscis insertion, so there is no precerebral septum (Kirsteuer 1974), but isolated bundles of fibres also extending anteriorly to form cephalic retractor muscles, similar to arrangement illustrated by Kirsteuer (1974: fig. 36) for *Correanemertes*.

Parenchymatous connective tissues sparsely developed, mostly confined to small amounts in lateral foregut regions.

In posterior cerebral and foregut regions of body isolated circular-muscle fibres from rhynchocoel wall extending ventrally on each side of gut to form slender dorsoventral muscle strands. Similar dorsoventral muscles not found in intestinal body regions.

Proboscis apparatus: Proboscis pore opening ventrally at tip of head into a rhynchodaeum with thin, unciliated epithelium lacking gland cells.

Proboscis insertion situated immediately in front of brain. Rhynchocoel wall containing separate circular and longitudinal-muscle layers, in the foregut region both about 12–15 μm thick, their thickness decreasing posteriorly. Rhynchocoel extending for about 75% of body length, its more posterior region narrowed and, together with intestine, entirely surrounded by densely arranged peripheral gonads.

Proboscis large, well developed, its anterior region comprising about 75–80% of total proboscis length and regionally differentiated. Anteriormost portion (Fig. 82), leading from the proboscis insertion, about 180–200 μm in maximum diameter, consisting of a folded glandular epithelium about 45 μm tall, a connective-

tissue layer, a thin outer circular-muscle layer at most 3–4 μm thick, an inner longitudinal-muscle coat 15–25 μm across, an inner connective-tissue zone and a lining layer. Proboscis nerves not clearly distinguishable in this portion of proboscis, although traces of a neural supply can be seen in longitudinal musculature. The bulk of the anterior proboscis, however, more massive, up to 65–70% of body diameter, its epithelium richly provided with both acidophilic and basophilic glands, 15–30 μm thick and, in retracted position, deeply folded into papillae some 75 μm or more tall. Beneath this the distinct connective-tissue layer in several places extended peripherally to form a core in the papillae; it also contains the outer circular-muscle layer, about 15 μm in maximum thickness, although only a thin connective-tissue zone separates circular and inner longitudinal-muscle layers. In the longitudinal layer, 35–40 μm thick, the 12 proboscis nerves distinct. Internally a further thin connective-tissue membrane divides longitudinal-muscle layer from inner proboscis lining.

Stylet bulb region of proboscis with a typical monostiliferous arrangement; conical stylet basis 85–90 μm long, its rather bulbous proximal base about 45 μm in diameter; central stylet up to about 50 μm long, so stylet : basis ratio about 1 : 1.8. Two accessory stylet pouches, each containing up to 4 or 5 accessory stylets in varying stages of development.

The smaller, posterior portion of proboscis with a much more simplified construction, consisting of a nonpapillate epithelium about 45 μm high and a reduced longitudinal musculature only 12–15 μm thick. Connective tissues evident only as delicate membranes and no trace of either proboscis nerves or a circular-muscle layer could be distinguished. Proboscis retractor muscle (Fig. 83), leading from rear of proboscis, is unusually thick and almost completely fills posterior rhynchocoel,
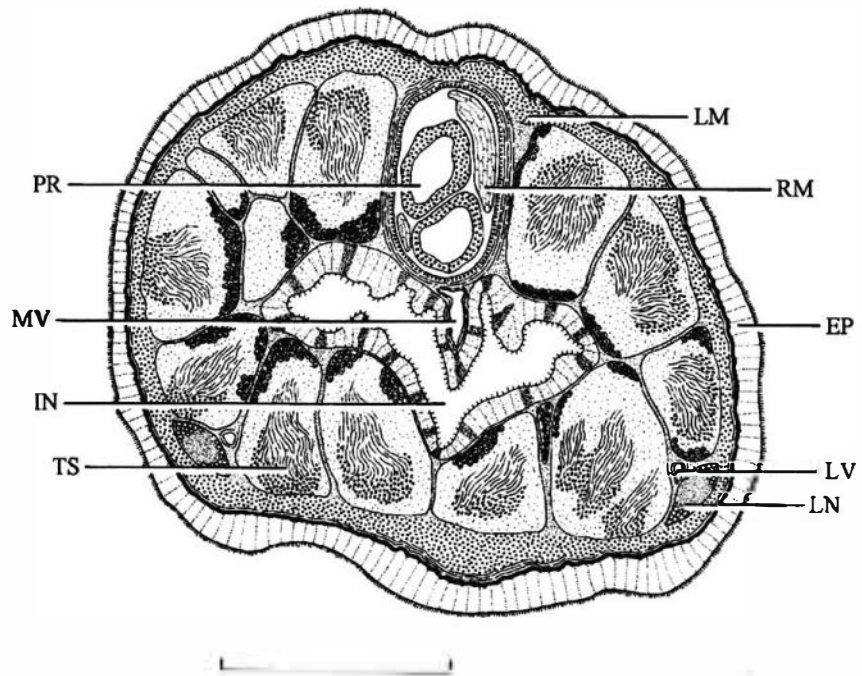
Fig. 83. *Heilogonemertes cooki* gen. et sp. nov. Camera lucida drawing through the posterior part of the body of the holotype to show the density and distribution of the testes. Scale bar = 250 μm.

probably as a consequence of being fully contracted.

Alimentary canal: In holotype foregut (Fig. 82) is pushed forwards; an oesophagus is, however, distinguishable by its unciliated and non-glandular epithelium which intervenes between anterior portion of the stomach and opening into ventral rhynchodaeal margin in cerebral organ region.

Stomach large, regionally differentiated. Its most anterior part comprises a ciliated epithelium, 25–30 μm thick, in which large vacuolate glands predominate. Where it passes underneath ventral cerebral commissure, this part of foregut is ca. 120 μm in maximum diameter, its dorsal wall deeply infolded to give an appearance resembling an annelid typhlosole. Towards rear of brain acidophilic and basophilic glands begin to increase in abundance and soon form the codominant cellular components. Behind brain, anterior stomach region gradually enlarges, its walls, particularly in dorsal half, becoming increasingly folded and acidophilic gland cells progressively reduced in number posteriorly. Main stomach region, up to about half width of the body, distinguishable by its wall being dominated by basophilic glands, with only a few, isolated acidophils scattered between them. No somatic muscles associated with foregut. Towards its rear, stomach gradually becoming less folded and spacious as it merges into pyloric canal. Pylorus forms a long, increasingly narrowing but dorsoventrally compressed tube, its epithelium posteriorly containing fewer and fewer gland cells and becoming reduced to a thickness of 10 μm or less. Where it opens into dorsal wall of intestine it is

about 150 μm wide but only 30 μm in dorsoventral height.

Midventral intestinal caecum extends forwards beneath foregut, reaching to main region of stomach. Caecum unusually long, approximately 3.2 mm (i.e., 12–13% of the body length), with neither anterior nor lateral diverticula, for most of its length is thin-walled and compressed between the pylorus and body-wall muscle layers. As it nears main intestinal canal, however, its lateral margins tend to become slightly folded and thicker. Intestine showing no unusual features, possessing shallow and rather lobed lateral diverticula but for most of its length irregularly squeezed between densely packed gonads (Fig. 83).

Blood system: In head blood system consisting of a pair of cephalic vessels meeting anteriorly by a loop passing across head in front of proboscis pore. As they extend back towards brain region, the 2 vessels run just above cerebral sensory organs before entering cerebral ring (Fig. 82). Post-cerebrally 3 longitudinal vessels, 2 lateral and single middorsal, continuing to hind end of body with no pseudometameric transverse connections. Behind ventral cerebral commissure middorsal vessel enters ventral rhynchocoel wall, but whether or not it forms a vascular plug could not be determined. Farther back, as posterior portion of rhynchocoel narrows, the middorsal vessel often very dilated and distinct (Fig. 83); anteriorly it is difficult to trace, mostly being distinguishable only as a small canal compressed between rhynchocoel and gut.

Nervous system: Cerebral ganglia (Fig. 82) enclosed

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by distinct outer neurilemma but no inner layer separating fibrous and cellular neural components. Dorsal commissure, about 30 μm thick, posterior to ventral; in holotype, ventral commissure is only 15–20 μm across, and appears stretched and thinner owing to foregut being pushed forward so as to displace the ventral cerebral lobes outwards. No evidence of neurochord cells distinguishable in cerebral tissues.

Just before the lateral nerve cords emerge from brain a stout nerve, about 15 μm in diameter, leads ventrally from each dorsal lobe to form origin of accessory lateral nerve. In anterior stomach region accessory nerves up to about 15 μm across, main neuropil about 45 μm. Accessory nerves traceable back into posterior pyloric region of foregut, becoming progressively smaller towards rear. Along inner lateral margins of main neuropil myofibrillae traceable throughout much of length of lateral nerves.

Peripheral nervous system shows no major differences from that described for many other monostiliferous hoplonemerteans.

Apical organ and cephalic glands: No evidence of an apical organ distinguishable and the few typical, pale blue-staining cephalic glands are isolated and scattered. Occasional acidophilic submuscular glands are scattered throughout much of cephalic region, particularly in ventral half of head.

Sense organs: Anterior eyes spherical, up to 45 μm or more in diameter, in contrast to posterior eyes which are at most only 30–35 μm across. Posterior eyes also more superficially positioned, close below body-wall circular-muscle layer rather than deep amongst cephalic tissues. Unlike those described for most other nemerteans, eyes have no discernible pigment-cup layer, appearing instead to be composed of radiating cells arranged around a more dense central core.

Close behind proboscis pore a pair of ventral oblique cephalic furrows lead to ciliated cerebral canals. The canals lead directly backwards, at first 30–35 μm in diameter, gradually increasing to 45 μm within a distance of 50-60 μm, then becoming almost completely surrounded by strongly acidophilic gland cells. Major (ventral) and minor (dorsal) channels distinguishable in the ciliated canals. Ciliated canals run in inner dorsolateral portion of cerebral organs, ending posteriorly close to the neural tissues. Cerebral organs ca. 150 μm long, 45 μm wide and 100–110 μm tall.

Excretory system: Collecting tubules of excretory system thick-walled, up to 25 μm or more in diameter, extending from alongside posterior regions of dorsal cerebral ganglia back into pyloric region of body, for much of their course running close to lateral blood vessels. Neither efferent ducts nor evidence of nephridiopores found.

Reproductive system: Sexes separate. Ovaries and testes extend throughout intestinal region, numerous and tightly packed. Behind posterior end of rhynchocoel they extend to almost all sides of body. In any one transverse section more than 10 ripe testes distinguishable per male (Fig. 83), up to about 16-18 ovaries per female. A single mature ovum in each ovary. Ova vary in size, the largest 140 μm or more across with a nucleus about 45–55 μm in diameter.

DISCUSSION: Among the monostiliferous hoplonemertean genera known to possess an anteriorly divided body-wall longitudinal-muscle layer, as in the present species, other features can be used to distinguish between most of them (Table 3). The present form also possesses accessory lateral nerves extending through the foregut portion of the body; only one of the other genera listed in Table 3, *Cryptonemertes*, shares this feature, the remainder having only a single neuropil in their lateral nerves. *Cryptonemertes*, however, differs from the New Zealand form in many ways, including a short rhynchocoel, extensive cephalic glands, small cerebral sensory organs located far anterior to the brain, a short intestinal caecum which bears lateral diverticula, a complex blood system forming a network of interconnected vessels throughout the length of the body (with no middorsal vessel), and the only known member of the genus, *Cryptonemertes actinophila* (Bürger, 1904), is hermaphroditic with the numerous gonads comprising ovotestes. The present species cannot, therefore, be included in any of the existing genera known to possess a divided longitudinal musculature.

Two of the features found in the present species are a rhynchocoel extending into the posterior half of the body and the occurrence of accessory nerves in the lateral nerve cords. Several hoplonemertean genera are known which possess accessory lateral nerves, although four of these (*Cryptonemertes, Gononemertes, Ischyronemertes, Parischyronemertes* gen. nov.), differ from the present form in having a rhynchocoel less than half the body length, no anterior division of the body-wall longitudinal musculature, and an inner circular-muscle layer in the body wall. Only four known monostiliferous hoplonemertean genera with accessory lateral nerves, like the New Zealand taxon, have a rhynchocoel extending into the posterior half of the body (Table 8) and the present form can be distinguished from all of these by the pattern of its eyes. It also differs from *Aegialonemertes, Antarctonemertes,* and *Oerstedia* in having a rhynchocoel that does not reach the posterior tip of the body, from *Friedrichia* in having only two muscle layers in the anterior region of its proboscis and a stomach with no caecum, from *Antarctonemertes* in having only isolated cephalic

glands that do not reach post-cerebrally, from *Aegialo-nemertes* in having a long intestinal caecum, from *Oerstedia* in lacking diverticula on its intestinal caecum, and from *Antarctonemertes*, *Friedrichia* and *Oerstedia* in its accessory lateral nerves not extending the full body length. The present species cannot therefore be placed in any of the known mono-stiliferous genera and it is accordingly identified as a new species for which the name *Heilogonemertes cooki* gen. et sp. nov. is proposed.

Table 8

Some of the morphological features distinguishing monostiliferous hoplonemertean genera in which the rhynchocoel is long and the lateral nerve cords contain accessory nerves. Data compiled from Gibson (1990a), Chernyshev (1993), and Envall and Sundberg (1993).

	1	2	3	4[a]	5
Rhynchocoel extending full length of body (+) or only about 75–80% of body length (0)	+	+	0	+	0
Number of muscle layers in anterior region of proboscis	2	2	3	2	2
Accessory lateral nerves extending full length of body (+) or restricted to anterior regions (0)	0	+	+	0/+	0
Stomach with (+) or without (0) caecal diverticulum	0	?	+	0[b]	0
Intestinal caecum present (+) or absent (0)	0	?	+	+	+
Intestinal caecum with anterior (A) and/or lateral (L) diverticula or with neither (0)	0	?	0	A/L	0
Cephalic glands extending behind brain (+) or confined to precerebral region of head (0)	0	+	0	0	0
Eyes in 3 groups (3), four separate ocelli (4), four groups (G) or many arranged in oblique rows on either side of head (N)	N	4	G	4	3

1 *Aegialonemertes*; 2 *Antarctonemertes*; 3 *Friedrichia*; 4 *Oerstedia*; 5 *Heilogonemertes* gen. nov.

[a] Includes the previously recognised genera *Oerstediella* and *Paroerstedia*, both of which were synonymised with *Oerstedia* by Envall and Sundberg (1993).

[b] Kirsteuer (1963) described and illustrated a short, posteriorly directed diverticulum on the stomach of *Oerstediella tenuicollis* Kirsteuer, 1963, which is now *Oerstedia tenuicollis*.

Notogaeanemertes Riser, 1988

TYPE SPECIES: *Notogaeanemertes folzae* Riser, 1988.

DIAGNOSIS: Monostiliferous supralittoral nemerteans; rhynchocoel extending to posterior end of body, with wall containing 2 distinct muscle layers; anterior region of proboscis with 3 muscle layers (outer circular, middle longitudinal, inner circular), proboscis armature consisting of single central stylet and 2 accessory stylet pouches. Body-wall musculature with neither diagonal nor inner circular layers, longitudinal musculature anteriorly divided. No precerebral septum; apical organ present, cephalic glands abundant, many discharging through independent pores; cerebral sensory organs elongate, opening ventrolaterally into short longitudinal cephalic furrow; lateral nerve cords with neither myofibrillae nor accessory nerves; oesophagus short, stomach and pyloric canal about equal in length, intestinal caecum bifurcate, intestinal diverticula lobed and unbranched. Blood system with lateral vessels connected

by loop immediately in front of brain, vessels continuing anteriorly to form network of small vessels, middorsal vessel forming single vascular plug; parenchyma abundant in stomach and pyloric regions; excretory system with mononucleate flame cells, without support bars; eyes arranged into irregular anterior row and posterior clump on each side of head; sexes hermaphroditic, ovoviviparous.

Notogaeanemertes folzae Riser, 1988 (Figs 84–85)

ORIGINAL DESCRIPTION: Riser, 1988a: 126-130, figs 1-3, 5-12.

ADDITIONAL LITERATURE RELATING TO NEW ZEALAND RECORDS: Duffy and Ackley (1988), Gibson (1995, in press), Gibson *et al.* (in press) (all as *Notogaeanemertes folzae*).

DESCRIPTION: *External features:* Up to 100 mm long and 2 mm wide, overall colour creamy-white with a slight pinkish tinge and an anterior suffusion of tan which varies in intensity between different specimens.   On the rounded head, 5–9 ocelli in each anterior row, with 3–6 in each posterior clump close to the brain (Fig. 84).
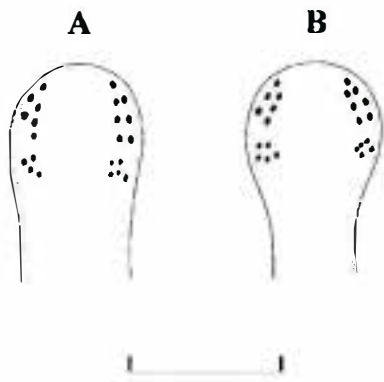

Fig. 85. *Notogaeanemertes folzae.* Recorded distribution in New Zealand.

Fig. 84. *Notogaeanemertes folzae.* Drawings of the head of a living specimen, viewed dorsally, when: **A**, at rest; **B**, during normal movement. Based on figures given in Riser (1988a). Scale bar = 2 mm.

Internal anatomy: The genus is monospecific, the major internal anatomical features of the species being summarised in the generic diagnosis above.

OCCURRENCE: Known only from beneath rotting kelp (mainly *Durvillea*) in rubble above high tide level, Rhino Horns, Kaikoura Peninsula, South Island (Fig. 85).
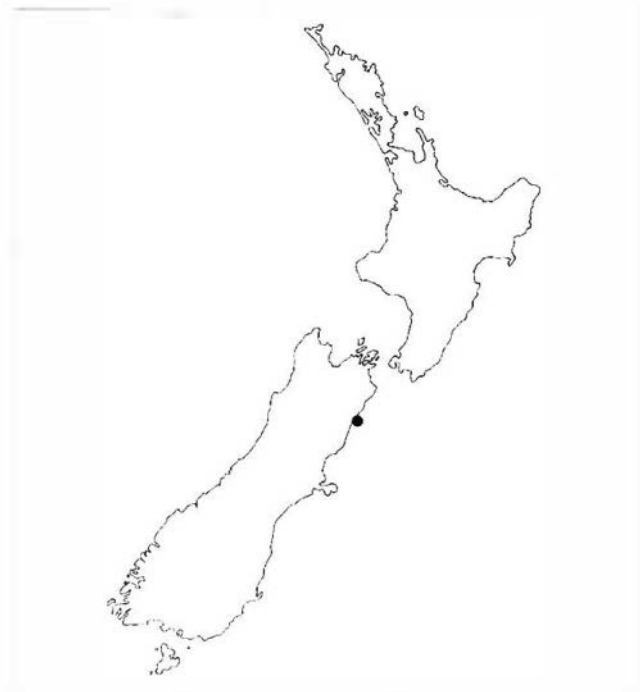
Family **TETRASTEMMATIDAE** Hubrecht, 1879

Meionemertes Gibson, 1986

TYPE SPECIES: *Meionemertes polygonimos* Gibson, 1986.

DIAGNOSIS: Monostiliferous marine nemerteans; rhynchocoel extending to posterior end of body, with wall containing 2 distinct muscle layers; main anterior region of proboscis with 2 muscle layers (outer circular, inner longitudinal), proboscis armature consisting of single central stylet and 2 accessory stylet pouches; body-wall musculature with neither diagonal nor inner circular layers; longitudinal musculature not anteriorly divided; dermis thick. Precerebral septum open; apical organ present, cephalic glands well developed but diffuse; cerebral sensory organs simple, opening ventrolaterally from shallow oblique cephalic furrows; lateral nerve cords without accessory nerves. Foregut with distinct oesophagus, stomach and pyloric regions, intestinal caecum short, intestine without lateral diverticula; blood system with paired lateral vessels anteriorly connected by cephalic loop and single middorsal vessel not forming a vascular plug;   parenchyma extensive; excretory system restricted to stomach region; eyes two; sexes probably separate, males with numerous irregularly distributed testes.

Meionemertes polygonimos Gibson, 1986

(Figs 86–87)

ORIGINAL DESCRIPTION: Gibson, 1986a: 280–287, figs 1–9.

ADDITIONAL LITERATURE RELATING TO NEW ZEALAND RECORDS: Gibson (1995, in press), Gibson *et al.* (in press) (all as *Meionemertes polygonimos*).

DESCRIPTION: *External features:* After preservation the single example was 6.5 mm long and 0.85 mm in maximum diameter, off-white to very pale brown in colour and with no evidence of a colour pattern (Fig. 86).   The appearance in life is unknown.
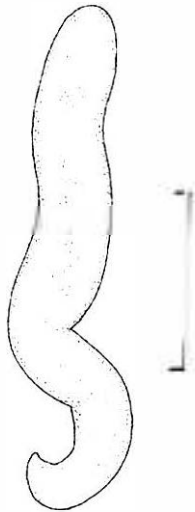

Fig. 86. *Meionemertes polygonimos.*Drawing of the complete preserved specimen, based on the description given by Gibson (1986a). Scale bar = 2 mm.

Fig. 87. *Meionemertes polygonimos*. Recorded distribution in New Zealand.

Internal anatomy: The genus is monospecific, the major internal anatomical features of the species being given in the generic diagnosis above.

OCCURRENCE: Collected sublittorally by a 10-ft Blake trawl from a depth of 95 m, approximately 140 miles east of Christchurch, South Island (43°22′ S, 175°20′ E to 43°24′ S, 175°15′ E) (Fig. 87).

Prostoma Dugès, 1828

TYPE SPECIES: *Prostoma graecensis* (Böhmig, 1892).

DIAGNOSIS: Monostiliferous freshwater nemerteans; rhynchocoel in adults not extending to posterior end of body, with wall containing 2 thin but distinct muscle layers; proboscis not strongly developed, anterior chamber with 2 muscle layers (outer circular, inner longitudinal), proboscis armature consisting of single central stylet and 2 accessory stylet pouches; body-wall musculature with neither diagonal nor inner circular layers, longitudinal musculature not anteriorly divided. Apical organ usually present, cephalic glands variably developed depending upon the species; cerebral sensory organs small, opening laterally; lateral nerve cords without accessory nerves. Foregut without pyloric region, intestinal caecum either short or absent. Blood system with paired lateral vessels anteriorly connected by cephalic loop and single middorsal vessel forming a single vascular plug. Parenchyma variable; excretory system extending the full body length and opening via numerous pores. Eyes mostly 4–8, one species eyeless. Sexes hermaphroditic, true or protandrous.

Prostoma eilhardi (Montgomery, 1894)   (Figs 88-89)

ORIGINAL DESCRIPTION: Montgomery, 1894: 19–69 (as *Stichostemma eilhardi*).

ADDITIONAL LITERATURE RELATING TO NEW ZEALAND RECORDS: Gibson and Moore (1978), Moore and Gibson (1985), Gibson, in press (as *Prostoma eilhardi*); for other synonyms see Gibson (1995).

DESCRIPTION: *External features:* In length rarely exceeding 20 mm but only 0.3–0.4 mm in diameter; typically an overall reddish-brown colour, although examples have been reported as more yellowish, greenish, brown or bright orange.   Number of eyes varying with age, younger individuals often possessing only 4 whereas adults have 6 (Fig. 88).

Internal anatomy: Montgomery's original description of this species was extensively supplemented by a subsequent paper (Montgomery 1895). *Prostoma eilhardi*

can be identified by its unciliated oesophagus, cephalic glands which only reach back to about half way between tip of head and brain lobes, and a rhynchodaeal wall lacking a well developed longitudinal muscle layer. Proboscis nerves is mostly recorded as 9.

Fig. 88. *Prostoma eilhardi* and *Prostoma graecense*. Drawing to show the general appearance of a whole individual, viewed dorsally. These two species are virtually identical in their external appearance and can only be reliably separated by histological studies. Scale bar = 5 mm.

OCCURRENCE: The zoogeographic distribution of this species closely parallels that of *Prostoma graecense*, from which it cannot be distinguished on external features alone. Gibson and Moore (1985) record the species as
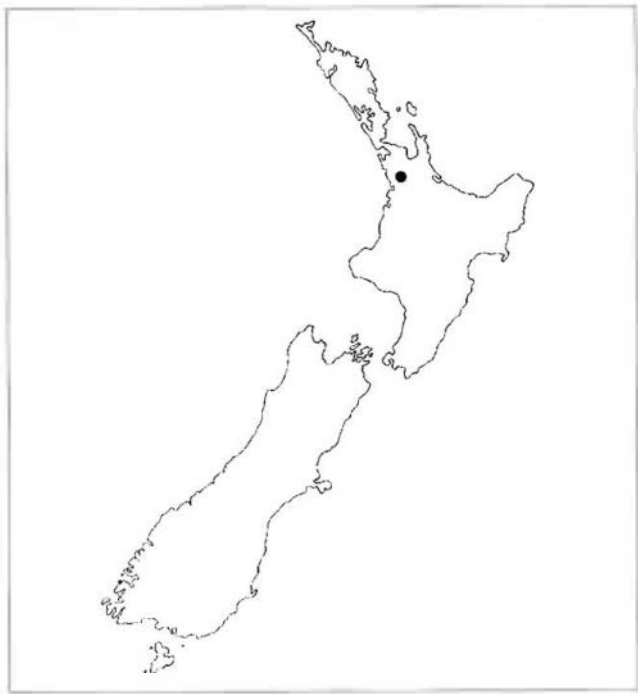

Fig. 89. *Prostoma eilhardi.* Recorded distribution in New Zealand.

occurring in decaying weeds at the edge of Lake Waahi, a small, very eutrophic lake at Huntly, North Island (Fig. 89), but Gibson (in press) commented that the identification of both these two *Prostoma* species from New Zealand is uncertain because of their remarkable similarity.

Prostoma graecense (Böhmig, 1892)   (Figs 88, 90)

ORIGINAL DESCRIPTION: Böhmig, 1892: 82–83 (as *Tetrastemma graecensis*).

ADDITIONAL LITERATURE RELATING TO NEW ZEALAND RECORDS: Gibson and Moore (1976), Gibson (1995, in press) (as *Prostoma graecense*); for other synonyms see Gibson (1995).

DESCRIPTION: *External features:* Virtually identical in external features to preceding species (Fig. 88); *Prostoma graecense* can only reliably be distinguished from *P. eilhardi* by careful histological examination of internal morphology.

Internal anatomy: Most *Prostoma* species are extremely similar in external appearance and anatomical studies are needed to distinguish between them. The main identifying features of *Prostoma graecense* are a distinct oesophagus with a ciliated epithelium, cephalic glands that reach back as far as the brain lobes, rhynchodaeal wall with a well-developed longitudinal muscle layer, and proboscis with 9–10 nerves.

OCCURRENCE: Apparently with a sporadic but worldwide distribution, *Prostoma graecense* has been found in the western basin of Lake Rotoiti, North Island (Fig. 90).

UNCERTAIN HIGHER TAXON

Arhynchonemertes Riser, 1988

TYPE SPECIES: *Arhynchonemertes axi* Riser, 1988.

DIAGNOSIS: Marine nemerteans; proboscis and rhynchocoel absent; body-wall musculature comprising outer circular and inner longitudinal layers, each only a single fibre thick. Nervous system internal to body-wall musculature; blood system a simple loop; mouth small, ventral, below brain; cerebral ganglia with single transverse commissure; cerebral sensory organs absent. Excretory system asymmetrical, unilateral; foregut not differentiated into oesophagus and stomach, intestine straight, with neither diverticula nor caeca. Hermaphroditic, testes dorsolateral, ovaries ventrolateral. With eyes.
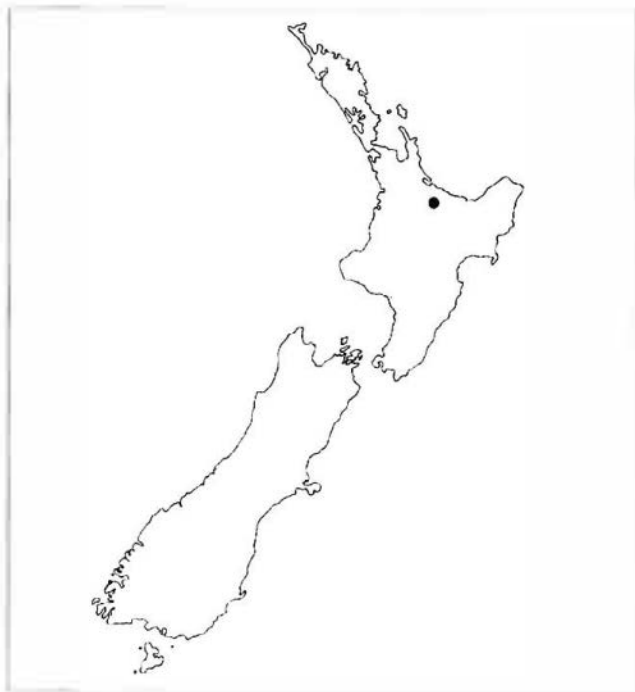
Fig. 90. *Prostoma graecense*. Recorded distribution in New Zealand

Arhynchonemertes axi Riser, 1988   (Figs 91–92)

ORIGINAL DESCRIPTION: Riser, 1988b: 367–371, figs 1–8.

ADDITIONAL LITERATURE RELATING TO NEW ZEALAND RECORDS: Gibson (1995, in press), Gibson *et al.* (in press) (all as *Arhynchonemertes axi*).

DESCRIPTION: *External features:* Up to 11 mm long, 0.6 mm in diameter, small, cigar-shaped, uniformly chalk-white in colour (Fig. 91). Head with 2–4 blackish-brown eyes arranged in tandem on each side; mouth is located ventrally below brain.

    Internal anatomy: A very atypical nemertean whose internal organisation, particularly the complete absence of a proboscis apparatus, prevents it from being placed in either of the two classes. The anatomical features of the species are summarised in the generic diagnosis above.

OCCURRENCE: Known only from specimens washed ashore in the holdfasts of the kelp *Lessonia* at Kaikoura, South Island (Fig. 92).

Fig. 91. *Arhynchonemertes axi*. Drawing to show the external appearance of a complete specimen. Redrawn from Riser (1988b). Scale bar = 1 mm.

Fig. 92. *Arhynchonemertes axi*. Recorded distribution in New Zealand.

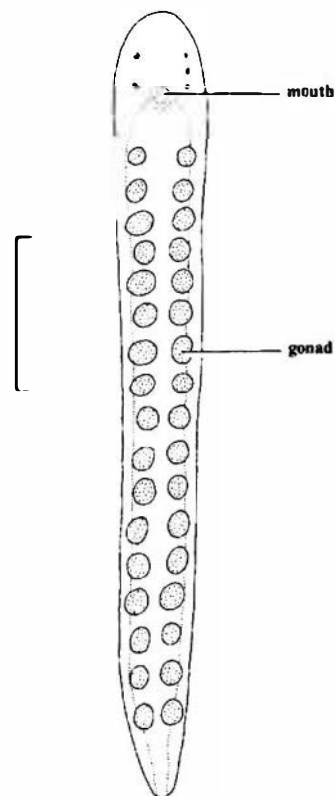# ACKNOWLEDGMENTS

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APPENDIX

Morton and Miller (1968, plate 9, fig. 9) gave coloured illustrations of a nemertean species which in the present paper is identified as *Noteonemertes novaezealandiae* gen. et sp. nov. They also illustrated in colour four other species of New Zealand nemerteans, repro-duced in the frontispiece. Three of these were attributed to particular genera: the palaeonemertean *Tubulanus* sp. (Frontis. Fig. F), the heteronemertean *Cerebratulus* sp. (Frontis. Fig. D), and the monostiliferous hoplonemertean *Amphiporus* sp. (Frontis. Fig. H), and a fourth was described as unnamed (Frontis. Fig. G). None of these forms was certainly encountered by the author during his 1992 visit to New Zealand, but this is not considered surprising as nemerteans in general are often unobtrusive in their habits and, though frequently common, are easily overlooked.

There are exceedingly few, if indeed any, species of benthic nemerteans which can be reliably placed in any genus without their internal anatomy first being investigated by means of histological methods. There are no data on the anatomy of any of the four species shown in the frontispiece, but a brief discussion on what is known about them is regarded as worthwhile in the context of the present monograph.

The *Tubulanus* species (Frontis. Fig. F) occurs under boulders in the lower regions of open shores. It is a slender but small species, with lengths of about 5 cm or more being recorded. The body has a general dark reddish-brown colour, with an obvious colour pattern consisting of an indistinctly marked median dorsal longitudinal stripe of orange and more or less regularly spaced transverse yellowish-white bands. Although the colour pattern of this form does resemble that of several other *Tubulanus* species, similar patterns are also known to occur in, for example, the palaeonemertean *Carinesta tubulanoides* Gibson, 1990 (see Gibson 1990b: plate 3A) and some species of the heteronemertean genus *Lineus*. The slightly notched shape of the head is also somewhat unusual for a *Tubulanus* species, most of which have either a rounded anterior end or a distinct cephalic lobe (e.g., see Bürger, 1895: plate 1). Whether this form possesses a ventral mouth and/or cephalic furrows is not known. The conclusion is that though Morton and Miller's (1968) species may be a *Tubulanus*, its inclusion in this genus can at best be regarded only as provisional until such time as additional individuals are found which may be investigated histologically.

The *Cerebratulus* species illustrated (Frontis. Fig. D) does show a wide and flattened intestinal region, which is typical of many members of the genus. *Cerebratulus* species, however, have a caudal cirrus which the illustration does not show, but close examination of the hind end as depicted suggests that the painting was made from a specimen which may have lost the posterior portion of its body; Morton and Miller (1968: 173) noted that "The posterior end is marked by a small indentation." In most described *Cerebratulus* species in which the intestinal region of the body is distinctly flattened, the more rounded anterior portion accounts for rather less than about 10% of the overall length rather than the almost 50% as illustrated. This species, which is found under stones on clean shores at low-water level, is described as the broadest and heaviest of the intertidal nemerteans, with a uniformly dull orange coloured body which is markedly flattened dorsoventrally, attaining extended lengths of about 23–30 cm and widths of about 15 mm. With no information on such externally visible features as a ventral mouth or lateral horizontal cephalic furrows, it is not possible to identify this form beyond it possibly being a species of *Cerebratulus*.

The *Amphiporus* species (Frontis. Fig. H) is described as the commonest of all the rocky-shore nemerteans, occurring particularly in crevices or under stones on moist silt or clay at Waitemata Harbour. Up to 15 cm or more in length when uncoiled and outstretched, the anterior body region is coral pink to reddish-brown in colour, the flattened posterior portion mauve brown with darker intestinal diverticula showing through the body surface. The somewhat flattened and spatulate head bears numerous eyes arranged into four groups. During low-tidal periods the nemerteans tend to occur in clusters of several specimens intertwined together or coiled up on themselves. One of the species found at Devonport Beach, Leigh Harbour, Pukerua Bay, Whangamumu Bay, and Whangaparaoa during 1992 superficially resembles this form, but histological studies on the 25 specimens collected have not yet been completed. Most of these individuals were anteriorly orange, tending to a brownish-orange in

an overall salmon-pink. When kept in the laboratory in clean seawater, the nemerteans tended to emerge from the water and lie just above the surface meniscus. They secreted copious volumes of a fairly viscid mucus when mechanically disturbed. On external features alone it is not possible to determine whether Morton and Miller's *Amphiporus* species should be included in this genus or in some other monostiliferous hoplonemertean taxon.

Future studies by the author will determine the identification of the specimens found during 1992 and discuss their possible conspecificity with Morton and Miller form.

The unnamed nemertean species (Frontis. Fig. **G**) was found on the west coast of North Island, living in rock pools among mussels. It is a long, slender form, reaching lengths of about 10 cm. Figure 93G, a ventral view of the head, clearly shows the mouth, indicating that this species is an anoplan nemertean. Although its long, slender shape is typical, for example, of many cephalothricid palaeonemerteans, it is not at present possible to assess its taxonomic position beyond that of class.

Morton and Miller (1968: 173) briefly referred to two other species of nemerteans. One is a large, slender species, more than 30 cm long, found either beneath stones or twined in intricate coils in kelp holdfasts. This species is apricot-coloured, with a broad white longitudinal lateral line down either side of the body. The second form is described as smaller, up to about 5 cm long and milk-white with a broad orange lateral line along either side.

Gibson (in press) concluded that the nemertean fauna of New Zealand is evidently rich and will repay detailed investigation. He also noted that, as a very rough approximation, at least 116 species of marine nemerteans should occur in New Zealand waters. Including those discussed in the Appendix, 32 species are now known from the region and only 26 (22% of the estimated minimum number) of these have been identified. That several of the latter are inadequately described and in need of taxonomic reassessment indicates that, without doubt, the New Zealand marine nemertean fauna remains poorly known and requires significant future investigation.

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