A NEW SPECIES FROM TASMANIA OF THE FRESHWATER HOPLONEMERTEAN, POTAMONEMERTES

by J.L. Hickman and J.Moore

(with two tables and five plates)

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ISSN 0080-4703. Department of Zoology, University of Tasmania, GPO Box 252C, Hobart, Tasmania, Australia 7001 (JLH); and Department of Zoology, Downing Street, Cambridge CB2 3EJ, England (JM).

A new species of freshwater hoplonemertean, *Potamonemertes gibsoni*, is described from lakes in Tasmania and its relationship to the type species from New Zealand and to the terrestrial nemerteans of the region is discussed. **Key Words:** freshwater, nemerteans, *Potamonemertes*, Tasmania.

INTRODUCTION

All known freshwater hoplonemerteans belong either to the genus *Prostoma* Dugès 1828 (family Tetrastemmidae) or to the monotypic genera more recently described from New Zealand, Potamonemertes Moore & Gibson 1973 and Campbellonemertes Moore & Gibson 1972. These New Zealand genera are very different from *Prostoma* and have been placed in the same family as the terrestrial nemerteans of New Zealand and Australia, which they closely resemble (Gibson & Moore 1976). Fulton (1983) reported the finding of a nemertean in Great Lake, Arthurs Lake and Lake Sorell, in central Tasmania. The present paper identifies this form as a new species of Potamonemertes to be named P. gibsoni in tribute to Professor Ray Gibson, Liverpool Polytechnic, England. Since the genus *Potamonemertes* was previously known only from the New Zealand type species, P. percivali Moore & Gibson 1973, it is particularly interesting that another species has been found in Tasmania. This paper describes the new species and also considers the distribution of the genus and its relationship to the terrestrial nemerteans of the region.

MATERIALS AND METHODS

Samples were collected between 1975 and 1978 from the floor of Great Lake (11 to 17.5 m) and Arthurs Lake (6.5 to 14 m) on the Central Plateau, using an Ekman grab of 232 cm² gape (Fulton 1983). The samples were then sieved (0.7 mm mesh size) and the animals retained by the sieve were preserved

in 70% ethanol: some were fixed in Clarke's fixative prior to preservation. The samples were subsequently found to include nemerteans, which were presented to JLH for identification. In total 19 preserved specimens were received and also 11 live nemerteans: these were fixed in hot Susa's fixative, rinsed in iodised 70% ethanol and preserved in 90% ethanol. Twenty-five of the specimens were sectioned at 10 mm and stained in Ehrlich's haematoxylin and eosin. Three specimens were stained in Mallory's triple stain by JM, to facilitate comparison with similarly stained sections of Potamonemertes percivali, Fulton (1983) also records the finding of the nemertean in Lake Sorell. Central Plateau, in 1981, and in 1987 further specimens were obtained (using a surber sampler. 500 mm mesh) from the sandy gravel of the Giblin River on the southwestern coast of Tasmania and from Giblin Bay in Lake Pedder — both sites being within the Tasmanian Wilderness World Heritage Area. These were given to JM, sectioned and stained in Mallory's triple stain, and added to the Pantin Collection.

POTAMONEMERTES GIBSONI SP.NOV.

Type Material (letters in parentheses refer to slide series)

Holotype

Arthurs Lake (West Lake north), 23/7/77, W. Fulton, T.S., 20 slides (S). Tasmanian Museum, Hobart Reg. No. K1135.

Paratypes

Arthurs Lake, 4.iv.77, T.S. 10 slides (H). Pantin collection, British Museum (Nat. Hist.), London (at present in the care of JM at the Zoology Department, Cambridge). Great Lake (Cramps Bay), 4.xii.75, T.S. 19 slides (E); Arthurs Lake (East Lake south), 10.x.77, L.S. 10 slides (0); Arthurs Lake (East Lake north), 24.i.77, H.S., 3 slides (W); Great Lake (Brandurn Bay), 2.vi.75, H.S. 5 slides (BB); Arthurs Lake (Tea-tree Bay), 28.xi.77, H.S. 9 slides (EE).

Tasmanian Museum, Hobart Reg. Nos. K1136 (T.S. 19 slides); K1137 (L.S. 10 slides); K1138 (H.S. 3 slides); K1139 (H.S. 5 slides); K1140 (H.S. 9 slides)

Distribution

The species has been recorded only from Tasmania. It has been found on the Central Plateau at Arthurs Lake, Great Lake and Lake Sorell; and in the Tasmanian Wilderness World Heritage Area at



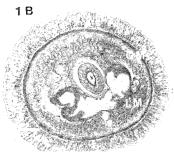


PLATE 1

Potamonemertes gibsoni sp.nov. (A) LS anterior region; (B) TS brain region. Showing the relative thickness of circular muscle (CM) and longitudinal muscle (LM), the ventral cerebral commisure (VC) and the posterior extent of the cephalic gland (CG). Scale bar=500 µm for both.

Giblin River on the southwestern coast and Giblin Bay in Lake Pedder.

Appearance in Life and Behaviour

The specimens were pale red to white in colour and small, attaining a maximum length of 20 mm. Spontaneous fragmentation was pronounced. This phenomenon has been observed in certain terrestrial nemerteans when in poor condition, and recorded from the Australian terrestrial nemertean Argonemertes stocki which shows controlled fragmentation of the posterior end into millimetre cubes (Moore 1975), but has not been recorded from any freshwater nemertean other than Potamonemertes percivali. Percival in 1943 recorded that "The animals were difficult to take whole, as they fragmented quickly and easily" (pers. comm. to Dr C.F.A. Pantin). This also was the experience of JM on revisiting Percival's type locality in January 1988 to observe P. percivali.

Anatomy

The general morphology of the present specimens is similar to that described by Moore & Gibson (1973) for *Potamonemertes percivali*. A full anatomical description is thus unnecessary. In the following brief account emphasis is given to characters significant in the taxonomy of related genera and to points of comparison with *P. percivali*.

Measurements made on the histological preparations are recorded where relative values may be interesting. However, living specimens were up to 20 mm in length while preserved mature specimens ranged from 2.5 to 8 mm. Such shrinkage is usual in nemerteans which have not been narcotised before preservation, and may occur unevenly.

Body Wall

The body is covered by a thick (35–80 mm) ciliated epidermis including gland cells. The underlying dermis, composed of connective tissue, is relatively thick (5–13 mm). The musculature is (as in *P. percivali*) particularly well developed for a small nemertean, most especially in the anterior part of the body. Whereas in *P. percivali* the two muscle layers are approximately equal in thickness, in the present specimens the longitudinal muscle layer of the anterior region (12.5–137 mm) is considerably thicker than the circular muscle (5–25 mm) (pl. 1A,B).

Parenchyma

Parenchyma is fairly extensive in most parts of the body posterior to the pyloric region.

Rhynchocoel

This is "full body length", i.e. extends to within 100 to 500 mm of the posterior tip of the body. Its muscular wall can be described as a single layer composed of circular, longitudinal and oblique fibres: it is constructed as a wickerwork of circular and longitudinal muscle fibres as is characteristic also of the Australian and New Zealand land nemerteans and other related forms. According to Gibson (1988) this character state defines a major subdivision of the hoplonemerteans, the Paramonostilifera (pls 2A, 5A).

Proboscis

This is very large, being approximately 1/2 to 3/4 the length and 1/5 to 1/3 the diameter of the worm. Everted, it measures 3/4 to 1 1/3 the length and 1/3 to 2/3 the diameter of the worm. The anterior proboscis consists of the usual layers, without muscle crosses and without enclosure of circular muscles in the dermis. There are 12–18 proboscis nerves. The stylet region includes 2–4 accessory stylet sacs each containing 3–7 stylets which measure 60–87mm in length and 15–20 mm in diameter at their base. Unlike *P. percivali* each accessory sac has a duct which opens near the base of the main stylet (pl. 2B). The main stylet measures 43–70 mm in length and 13–20 µm in diameter at its base. The basis is urn shaped 65×42.5–126×78 mm.

Gut

The gut is typical: the oesophagus is a short unciliated tube leading from the rhynchodeum into the large glandular stomach (approximately 1/10 the length of the worm) which extends posteriorly as a wide dorsoventrally flattened pyloric tube (1/6 to 1/17 the length of the worm) leading to the intestine. From the point where the pylorus joins the intestine a ventral caecum extends anteriorly, ventral to the pylorus, and bifurcates into blind diverticula 100–350 mm long, which extend forwards to the brain.

Eyes

Eyes are absent. This character state is shared by *P. percivali, Campbellonemertes*, one species of

Prostoma and all known freshwater heteronemerteans. Most marine and all known terrestrial nemerteans possess eyes.

Cerebral Organs

As in *P. percivali* these open laterally from short longitudinal epidermal furrows. However, they are much larger and have a different shape. The cerebral canal passes posteroventrally from the furrow for 100–125 mm to enter the ganglionic mass which is ovoid (60×62–100×125 mm) and situated anterolateral to the ventral cerebral ganglion. Within the mass the canal passes round to the ventral and inner posterior region where it ends blindly among the cerebral gland cells. Although the canal does not fork, in some sections a very small dorsal diverticulum appears to be present where the canal enters the ganglionic mass. The cerebral gland cells extend backwards for 110–200 mm along the ventro-lateral aspect of the dorsal cerebral ganglion to nearly level



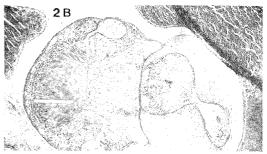


PLATE 2

Potamonemertes gibsoni sp. nov. (A) LS to show the cerebral organ: the cerebral canal opening (O) and the ganglionic region (G) beside the ventral cerebral ganglion (VG) are evident; the wickerwork structure of the rhynchocoel wall musculature (RM) is also shown. (B) Stylet region of proboscis to show an accessory stylet sac (ASS) with duct. Scale bar = 100 µm for both.

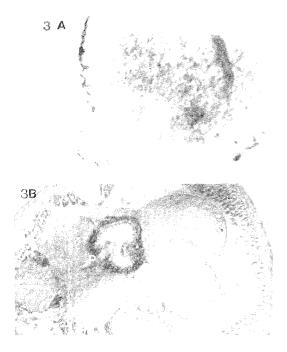


PLATE 3

Potamonemertes gibsoni sp. nov. (A) LS anterior end to show the discharge of the cephalic glands (CG) into the frontal organ (FO); scale bar = $50 \mu m$. (B) TS brain region to show the two vascular plugs (P) and the posterior extent of the cephalic gland (CG); scale bar = $200 \mu m$.

with the posterior margin. The cerebral gland has a maximum diameter (40–75 mm) where it adjoins the ganglionic mass (pl. 2A).

Frontal Organ

There is a small but distinct frontal organ, 50–80 mm in diameter, through which the cephalic glands discharge (pl. 3A). The organ opens into a cavity approximately 15 mm in diameter and 30 mm in depth. In *P. percivali* the frontal organ and cephalic glands are described as having separate openings.

Cephalic Gland

This is considerably larger than in *P. percivali* where it is restricted to a small anterior dorsal cap. In the new species, the gland (consisting solely of basophilic lobules) extends back, 212–464 mm, as far as the posterior surface of the dorsal cerebral ganglion (pls 1B, 3B).

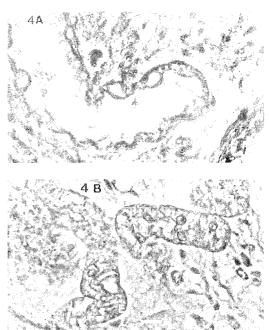


PLATE 4

Potamonemertes gibsoni sp. nov. (A) Lateral blood vessel (BV) to show valves in the wall. (B)Excretory ducts (E) and flame cells (F). Scale bar = 30 μ m for both.

Nervous System

The nervous system is typical of hoplonemerteans but lacks the posterior protuberances on the ventral cerebral commissure which constitute a unique feature of *P. percivali*: this must therefore be seen as a specific rather than a generic specialisation. The present specimens resemble *P. percivali* in having no neurochord cells, no accessory lateral nerve and no dorsal contribution to the lateral nerve from the dorsal cerebral ganglion.

Vascular System

As in *P. percivali* and all other known freshwater nemerteans, the only cross-connections present between the dorsal and lateral blood vessels are the cephalic loop, which passes through the cephalic gland, and the supra-anal commissure. Accordingly the two vascular plugs are borne on the lateral vessels, anterior to the origin (from one lateral

vessel) of the mid-dorsal vessel. The plugs (about 70 mm in diameter) project into the rhynchocoel in the cerebral region (pl. 3B). The lateral vessels, as in *P. percivali*, are lacunar but smaller, and valves (rare in *P. percivali*) are evident in the blood vessels of the present specimens (pl. 4A).

Excretory System

The excretory system does not differ from that of *P. percivali*: it is very well developed and extends throughout the animal. Simple paired mononucleate flame cells lead into excretory ducts which open by a very large number of small pores. The excretory ducts are thick walled with the specialised structure unique to Australian and New Zealand terrestrial nemerteans and *Potamonemertes* (pls 4B, 5A).

Gonads

The animals are simultaneously hermaphroditic and probably also variably protandrous. As in *P. percivali*, the testes generally extend further forward than the ovaries, however, there is no sharp separation of the testicular from the ovarian field. Testes may occasionally occur as far forward as the brain but more commonly extend posteriorly from the region of the pyloric tube, being dorsal, lateral and ventral in position (pl. 5B). The maximum dimension of mature testes varies from 125–192 mm and that of mature ovaries from 230–272 mm. Ripe ova measure 224–272 mm and have nuclei 56–64 mm in diameter.

GENERIC DIAGNOSIS AND SPECIFIC DIFFERENCES

Now that a second species of *Potamonemertes* has been described, a generic diagnosis can be given and the specific differences between the type species from New Zealand, *P. percivali*, and the present Tasmanian species, *P. gibsoni*, can be tabulated.

Potamonemertes Moore & Gibson 1973

Diagnosis

Freshwater Paramonostilifera with body wall musculature particularly well developed in anterior portion of body; epidermis typical, dermis thick, parenchyma extensive in most of body; rhynchocoel full body length with wall composed of wickerwork of interwoven circular, oblique and longitudinal

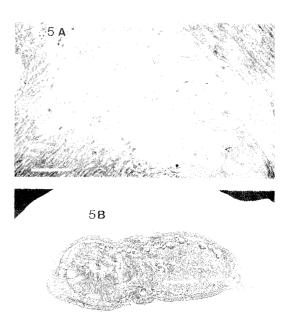


PLATE 5
Potamonemertes gibsoni sp. nov. (A) Excretory ducts (E), flame cells (F) and rhynchocoel musculature (RM); scale bar = 100 µm. (B) LS to show the position of the gonads; ovaries(O), testes

(T); scale bar = $1000 \mu m$.

muscle fibres; proboscis massive and at least as long as the body; alimentary canal with mid-ventral caecum bearing anterior diverticula; eyes absent; cerebral organs anterior, with canal unforked and no anterior sac, opening into a pair of lateral longitudinal cephalic furrows; frontal organ present, cephalic gland opening to the exterior through a single pore which is either the frontal organ or a small median pore dorsal to it; nervous system with no neurochord cells, no accessory lateral nerve and no contribution from the dorsal cerebral ganglion to the lateral nerve; blood vascular system with lacunar lateral vessels and mid-dorsal vessel arising from one of them post-cerebrally, these vessels having no commissural connection other than the cephalic vascular loop and the supra-anal commissure; two vascular plugs, borne on the two lateral vessels, projecting into the rhynchocoel in the cerebral region; excretory system extending throughout body consisting of simple paired mononucleate flame cells and excretory ducts opening by numerous pores, these ducts being thick walled specialised structures; hermaphrodite, simultaneous, and

probably variably protandrous, gonads either sharply regionalised or overlapping with testes at least extending further forward than ovaries; readily fragments.

FAMILIAL PLACING OF POTAMONEMERTES

Potamonemertes and Campbellonemertes were originally placed in the family Prosorhochmidae, with the undivided genus Geonemertes (Moore & Gibson 1972, 1973). Further information about the convergent origin of terrestrial nemerteans led to the splitting of the genus Geonemertes (Moore & Gibson 1981) and the recognition of two distinct groups of land nemerteans. Redescription of the genus Prosorhochmus (Gibson & Moore 1985) established that only the first group of land nemerteans (the redefined genus Geonemertes, and Pantinonemertes) should remain in Prosorhochmidae. Potamonemertes and Campbellonemertes belong with the Australian terrestrial genus Argonemertes, the New Zealand terrestrial genus Antiponemertes, and Acteonemertes in the newly erected family Plectonemertidae (Moore & Gibson 1988) which includes forms with wickerwork rhynchocoel musculature, two vascular plugs and other uniting characters (see table 1).

DISCUSSION

We now have further knowledge of the distribution of Potamonemertes and a better basis for distinguishing the generic from the specific characters. Do we, however, have further clues to its evolutionary history? That species of the same freshwater genus should occur both in New Zealand and in Tasmania is not unusual, being known to occur, for example, in the following genera, Coleoptera: Hydraena, Meropathus; Crustacea: Boeckella; Mollusca: Gyraulus, Physastra, Sphaerium; Platyhelminthes: Temnocephala, Cura. While Potamonemertes is known only from New Zealand and Tasmania, and Campbellonemertes only from one species on Campbell Island, the other freshwater hoplonemertean genus, Prostoma, is worldwide in distribution. In many countries details of its occurrence are unknown: in Tasmania it appears only to occur in areas which have been settled at one time or another by Europeans, suggesting that it may have been introduced. Both Potamonemertes and Campbellonemertes resemble the terrestrial nemertines of New Zealand (the genus

Antiponemertes, and the upper littoral/terrestrial genus Acteonemertes) and Australia (the genus Argonemertes) in morphology as well as geographical distribution (see table 1). Potamonemertes and Campbellonemertes are unlike terrestrial nemerteans and resemble each other in the rather mysterious "freshwater features" concerning absence of eyes, absence of cross connections between the longitudinal blood vessels and being hermaphroditic (but Argonemertes dendyi is one terrestrial nemertean which also is hermaphroditic). Absence of eyes in freshwater forms may be indicative of the animals living within the organic debris and silt in the bed of the stream, pond or lake. Similarly among the terrestrial turbellarians, eves are extremely well developed along the lateral margin of the rather flat body of those species which feed on the surface inhabiting fauna. During the day they can be found in crevices in logs or under logs, stones and litter. They probably use their eyes to detect (among other things) the light intensity gradient within which they can safely move and feed. A few species are blind and during the day are found in cavities under stones and logs. These may well feed on fauna below the surface, in cavities such as burrows or tunnels in the ground or in logs. Apart from the "freshwater features" Potamonemertes and Campbellonemertes do not seem to be particularly closely related within the family: Campbellonemertes is quite different in size and shape and has a great many specialisations. It is Potamonemertes which more closely resembles terrestrial nemerteans, in particular in having a very large proboscis and the specialisation of the excretory ducts which is otherwise unique to Argonemertes and Antiponemertes.

Moore & Gibson (1973) built on this resemblance to postulate an evolutionary sequence: they suggested that Potamonemertes may have colonised freshwater by way of the land. The points of resemblance are functionally appropriate for terrestrial nemerteans, for example a greatly enlarged proboscis which is used for quick escape movements is almost universal among terrestrial nemerteans of both families (Prosorhochmidae and Plectonemertidae). Further, in contrast to *Prostoma*, Potamonemertes and Campbellonemertes belong to a family with no known estuarine species. However, this hypothesis is not supported by cladistic analysis (Sundberg 1989) and must remain in doubt. Some marine features which Potamonemertes has retained which conceivably would have been modified had its progenitors been terrestrial are: (a) the lateral longitudinal furrows into which the cerebral organs open; (b) the presence of a frontal organ; (c) the

TABLE 1 Comparison of *Potamonemertes* with Australian Land and Freshwater Genera and with *Prostoma*

	Acteo- nemertes	Antipo- nemertes	Argo- nemertes	Potamo- nemertes	Campbello- nemertes	Prostoma
Rhynchocoel musculature:						
wickerwork (+), separate layers (0)	+	+	+	+	+	0
Rhynchocoel full body						
length (+), much shorter (0)	+	+	+	+	+	0
Number of vascular plugs	2	2	2	2	2	i
Body musculature well developed						
with thick dermis (+), not so (0)	+	+	+0	+	+	0
Parenchyma extensive (+),						
sparse (0)	+	+	+	+	+	0
Proboscis large, active in loco-						
motion (+), not so (0)	+	+	+	+?	0	0
Gut with pyloric tube and ventral						
caecum (+), without (0)	+	+	+	+	+	0
Anterior caecal diverticula						
long (++), short, variable (+)	++	+	++	+	+	++
Frontal organ present (+), absent (0)	0	0	0	+	0	+
Cephalic gland opens into frontal organ or nearby duct (+) or into						
improvised openings (0)	0	0	0	+	0	+
Cephalic gland very extensive (++)						
fairly extensive(+), restricted (0)	++	++	++	+0	++	+0
Cerebral organ large with forked canal (++) unique specialization(+),						
smaller and simple (0)	0	++	++	0	+	0
Multiplication of excretory ducts						
and pores very great (++),						
slight (+)	++	++	++	++	++	+
Excretory ducts with specialised						
region (+), uniform (0)	0	+	+	+	0	0
Habitat:Upper littoral (UL),						
Terrestrial (T), Freshwater(FW)	UL	T	T	FW	FW	FW
Number of eyes	46	2–4	20 - 180	0	0	0-6
Cerebral organ opens into lateral long- itudinal furrows (0), single						
ventral transverse furrow (+)	+	+	+	0	0	O
Blood vessels with capillary net						
work extensive (+), without						
cross links between cephalic &						
anal region (0)	+	+	+	0	0	0
Gonads: hermaph.(+), single sex (0)	0	0	0+	+	+	+

cephalic gland opening confluent with the frontal organ and (d) the rather limited development of the cephalic gland. Other features, however, are suggestive of a prior terrestrial existence, for example, (a) the multiplication of excretory ducts; (b) the regional specialisation of the excretory ducts; (c) the small size of the frontal organ and (d) the relatively large proboscis. Whatever the evolutionary sequence, there is no doubt that *Potamonemertes* and *Campbellonemertes* are closely related to the land nemerteans of Australia and New Zealand and are far removed from *Prostoma* which originated elsewhere.

Comparison of the two species of *Potamonemertes* (table 2) shows that in every point of difference it is the Tasmanian species, *P. gibsoni*, which is less specialised. The ventral cerebral commissure is normal in form, as are the body wall muscle, oesophagus, blood vessels and stylet region. The unusual regional division of the gonads is less marked in *P. gibsoni*. Possession of a frontal organ (by both species) is a common feature of marine nemerteans but is in strong contrast to the less restricted outlet for the mucus secretion found in

terrestrial forms in the Plectonemertidae (presumably reflecting the greater demand for copious mucus secretion in the terrestrial forms). The amount of cephalic gland present in P. gibsoni is nearer to that of the terrestrial genera. Of the two species, then, it is the Tasmanian one which more closely resembles both the terrestrial nemertines and their marine relatives. Whether the ancestors of Potamonemertes colonised freshwater directly (up rivers) or by an overland route (thus requiring them to first become completely terrestrial) or via lagoons and swamps (the conditions of which fluctuated in such a way as to favour the emergence of some terrestrial preadaptation but also an adaptation to freshwater), it is tempting to suppose that this might have happened in Australia rather than New Zealand. It is hard to decide whether Potamonemertes is closer to Argonemertes or Antiponemertes: these two genera differ primarily in the number of eyes, and *Potamonemertes* has none. between Argonemertes Differences Antiponemertes concerning the size of the posterior gland of the cerebral organ, the mobility of the stomach and the relative length of the anterior caecal

TABLE 2
Differences Between the Two Known Species of *Potamonemertes*

	P. percivali	P. gibsoni
Sites of occurrence	New Zealand:	Tasmania:
	Coe's Ford, Selwyn	Great Lake, Arthurs Lake,
	River, Canterbury	Lake Sorell, Lake Pedder, Giblin River
Ventral cerebral commissure	With posterior protuberances	Normal, i.e without posterior protuberances
Cephalic gland	Small dorsal/anterior cap only. Opens by separate pore dorsal to frontal organ	Extends from anterior to brain region. Opens through frontal organ
Cerebral organ	Ganglionic mass elongate and small, less than one third of the size of the ventral cerebral ganglion; gland short	Ganglionic mass compact nearly spherical and nearly as large as ventral cerebral ganglion; gland elongated
Oesophagus	Ciliated	Unciliated
Body wall muscle	Longitudinal and circular layers equally well developed	Longitudinal muscle layer much thicker than circular in anterior part of body
Blood vessels	Very large lacunae	Moderate sized lacunae
	Valves rare	Valves common
Stylet region	No canals between accessory sacs and main stylet	Canals present
Gonad distribution	Sharply regionalised	Testes and ovaries extensively overlap

diverticula are not sufficiently marked for any hypothesis. The two terrestrial genera are distinctly different in behaviour (Moore 1989) but this is no help. All that can be said is that the New Zealand species of *Potamonemertes* has more secondary specialisations than the Tasmanian one.

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