A new genus and species of freshwater monostiliferous hoplonemertean (Nemertea, Enopla) from the People's Republic of China

Ray Gibson[1] & Hongzhu Wang[2]

[1] *School of Biological and Earth Sciences, Liverpool John Moores University, Byrom Street,*
Liverpool L3 3AF, U.K.
E-mail: r.gibson@livjm.ac.uk
[2] *State Key Laboratory of Freshwater Ecology and Biotechnology, Institute of Hydrobiology,*
Chinese Academy of Sciences, Wuhan, Hubei 430072, People's Republic of China

Abstract

A new genus and species of freshwater monostiliferous hoplonemertean, *Limnemertes poyangensis* gen. et sp. nov., from Poyang Lake, People's Republic of China, is described and illustrated. The taxon is compared and contrasted with previously described freshwater hoplonemerteans. This is the fourth species of freshwater nemertean to be described from China and the first recorded from Poyang Lake.

Introduction

The phylum Nemertea, with more than 1100 species known worldwide (Gibson, 1995), is predominantly composed of marine taxa. Twenty-one species, however, have been reported from freshwater habitats (Gibson, in press). Of these, five monospecific genera are contained within the anoplan subclass Heteronemertea and the remaining 16 belong in the hoplonemertean superorder Monostilifera. Except for the genera *Potamonemertes* and *Otonemertes*, both of which contain two described species (one of the two *Otonemertes* species is marine, the other freshwater), the only monostiliferous genus at present with more than a single species is *Prostoma*, with 11.

Three species of freshwater nemerteans have previously been reported from the People's Republic of China. These are the heteronemerteans *Amniclineus zhujiangiensis* Gibson & Qi, 1991, found in the lower part of the Zhujiang (Pearl) River, and *Yinia pratensis* Sun & Lu, 1998, from the Changjiang (Yangtze) River,

and the monostiliferous hoplonemertean *Prostoma eilhardi macradenum* Sun & Yin, 1995, from Qingdao, which Chernyshev et al. (1998) elevated to specific status as *Prostoma macradenum*. There are no previous records of freshwater nemerteans from Poyang Lake.

Materials and methods

The nemerteans were found during a survey of Poyang Lake carried out during 1998 (see Wang et al., 1999; Wang & Liang, 2001). Specimens were preserved in formalin, embedded in 56 °C m.p. paraffin wax, sectioned at 6 μm and stained with Crandall's modified Mallory trichrome method. Type specimens are deposited with the Institute of Hydrobiology, Chinese Academy of Sciences, Wuhan Hubei (IHBCAS) and the British Museum (Natural History) (BMNH), London.

Description

Family: Tetrastemmatidae

Genus: *Limnemertes* **gen. nov.**

Type species

Limnemertes poyangensis *sp. nov.*

Etymology

The generic name, which is masculine, is derived by prefixing the name *nemertes* with a condensation of the Greek word *limne* (a pond or lake) and indicates the type of freshwater habitat in which the taxon was first found. The specific epithet is derived by adding the Latin adjectival suffix *–ensis* (belonging to) to the lake's name, Poyang, to indicate the type locality.

Diagnosis

Monostiliferous freshwater hoplonemerteans; rhynchocoel short, less than half body length, with wall containing separate circular and longitudinal muscle layers; proboscis slender; dermis thin; body wall musculature moderately well developed, without diagonal layer, longitudinal layer anteriorly divided; no pre-cerebral septum; apical organ present, small; cephalic glands well developed, posteriorly reaching anterior margin of brain lobes, discharging via apical organ; cerebral sensory organs large, extending throughout much of cephalic region and ending below ventral cerebral commissure, opening laterally into shallow oblique anterior ciliated furrows; brain moderately well developed, with neither inner nor outer neurilemma, without neurochord cells; lateral nerve cords without accessory nerve; foregut with distinct oesophagus and stomach but no pyloric region, stomach opening directly into intestine; intestine without caecum but with pair of long anterior pouches that reach brain; blood system comprising a simple vascular loop, post-cerebral supply with paired lateral and single mid-dorsal vessels which meet posteriorly by supra-alimentary loop but without pseudometameric transverse connectives, mid-dorsal vessel with single vascular plug; excretory system well developed, extending from cephalic to anterior intestinal region of body, opening via several nephridiopores; six eyes; sexes separate.

Table 1. Summary of the physico-chemical parameters of the location in Poyang Lake, People's Republic of China, where the specimens of *Limnemertes poyangensis* gen. et sp. nov. were obtained (data from Liu, unpublished)

Parameter	Value
Water flow rate:	$0.1 \ m/s^{-2}$
Temperature:	$24\,°C$
Secchi disc transparency (cm):	110
pH:	7.38
Conductivity (μS/cm):	104
Hardness:	3.22
Alkalinity ($CaCO_3$, mg/l):	40.04
SiO_2 (mg/l):	4.694
Ca^{2+} (mg/l):	18.04
Mg^{2+} (mg/l):	3.04
PO_4-P (mg/l):	0.016
TP (mg/l):	0.084
NO_2-N (mg/l):	0.0007
NO_3-N (mg/l):	0.178
NH_4-N (mg/l):	0.196
TN (mg/l):	0.67
Submerged macrophytes:	None
Chlorophyll *a*:	$1.3 \pm 1.1 \ \mu g/l$

Limnemertes poyangensis *gen. et sp. nov. (Figs 1–21)*

Type specimens

Holotype mature male, transverse sections through anterior body, oblique and longitudinal sections through posterior regions, complete animal excluding proboscis, 101 slides, IHBCAS JX 1998015a001–1998015a101; paratype female, complete specimen in mixed oblique and transverse sections, 22 slides, IHBCAS JX 1998015b001–1998015b022; paratype female, complete specimen in mixed transverse and oblique sections, 33 slides, BMNH 2001.6817.

Type locality

Poyang Lake, People's Republic of China, in the northern Jiangxi Province at the junction between the middle and lower reaches of Changjiang (Yangtze) River, 28° 25′–29° 45′ N, 115° 48′–116° 44′ E. Collected 15 April 1998. The single location (Station 15) within the lake where the nemerteans were found was at 29° 11.8′ N, 116° 16.08′ E. The specimens came from a depth of 1.9 m on clay; physico-chemical para-

Figure 1. Limnemertes poyangensis gen. et sp. nov. Photograph of the holotype, in dorsal aspect, after preservation; the head is to the right. Note the testes visible through the epidermal surface.
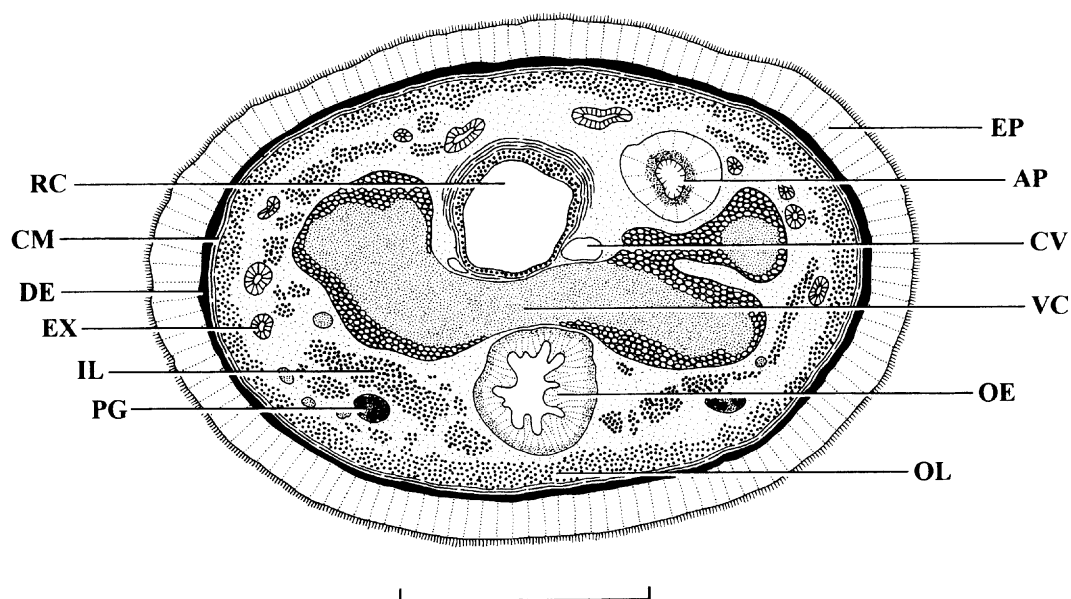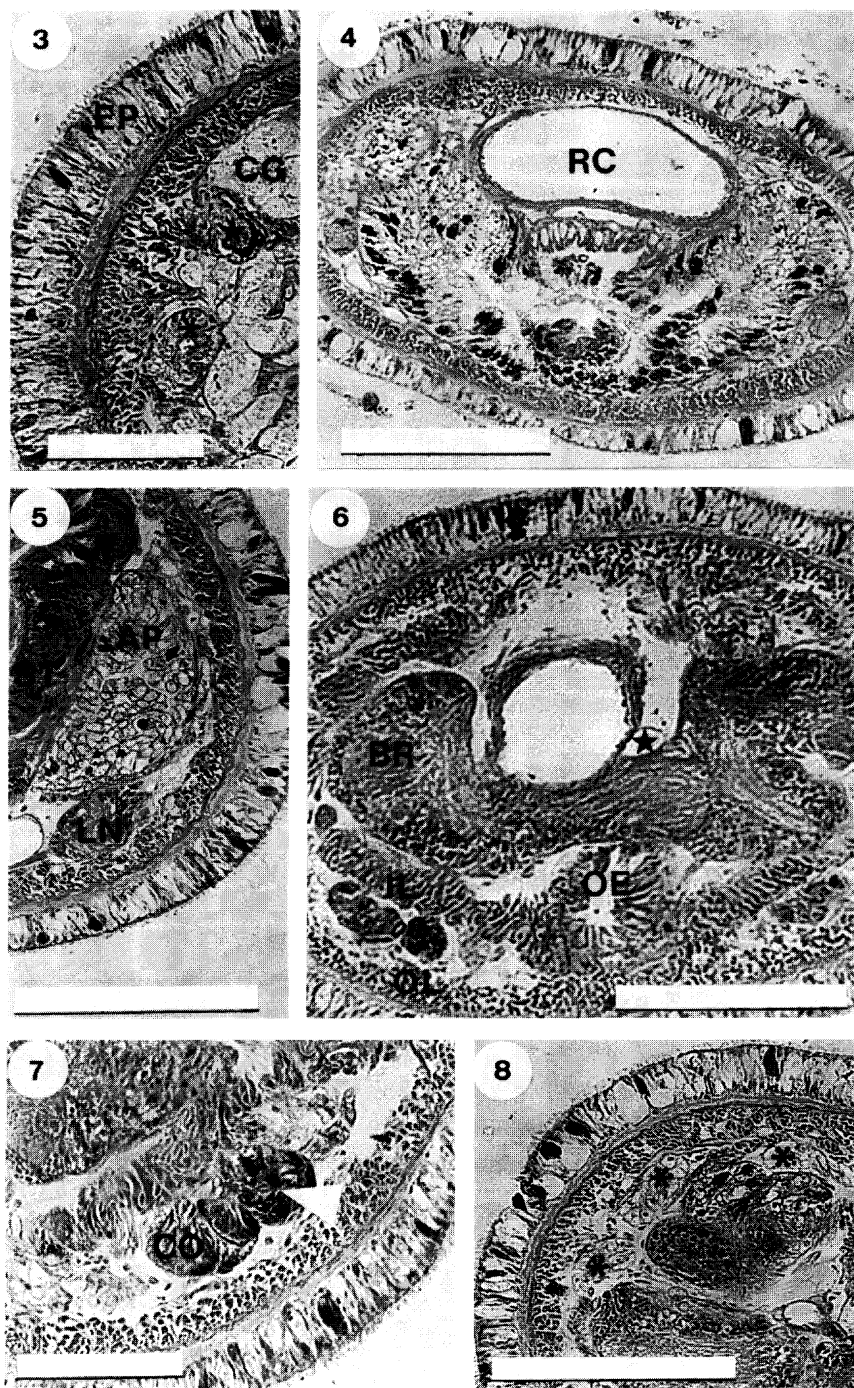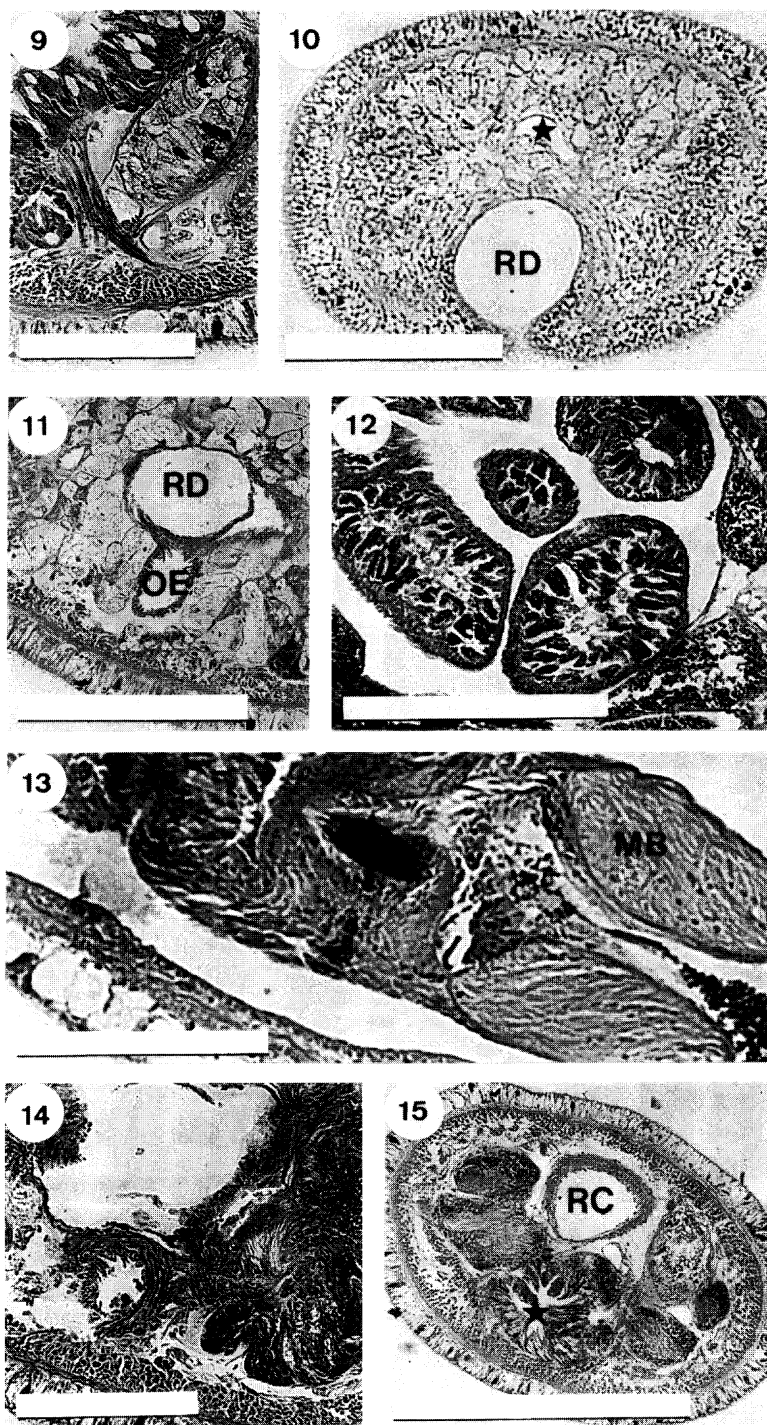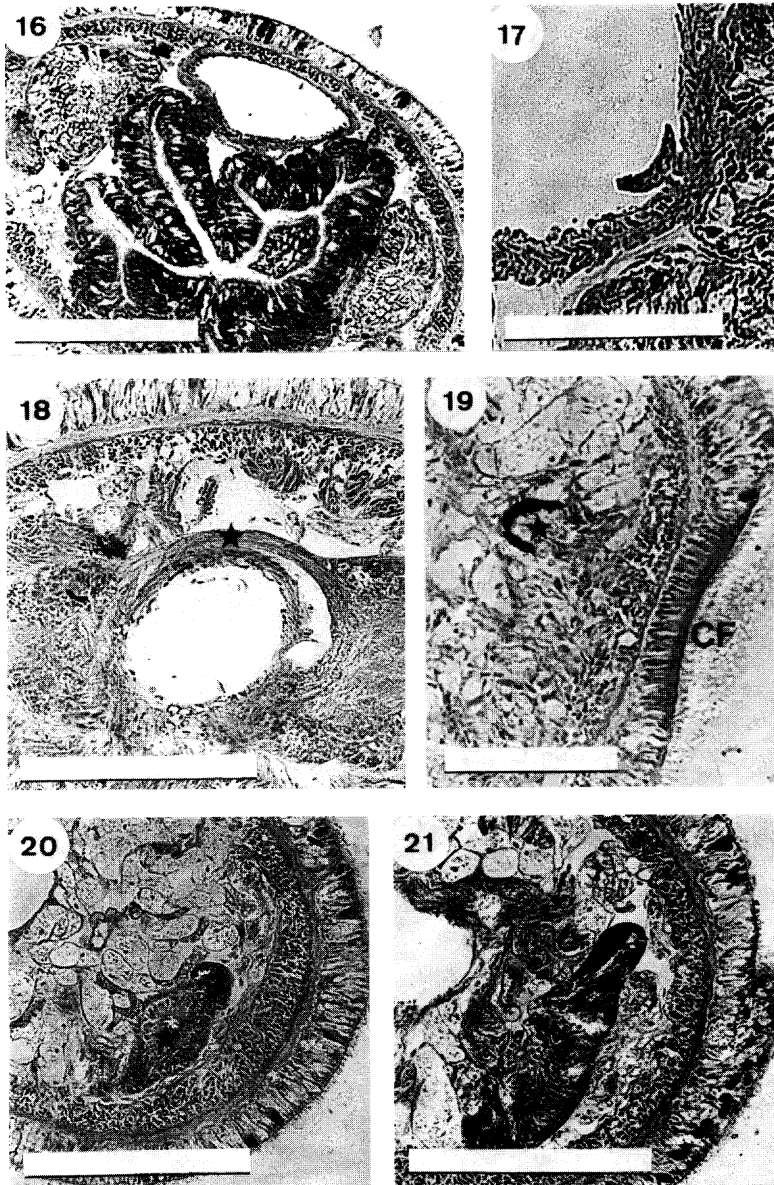

Figure 2. Limnemertes poyangensis gen. et sp. nov. Diagrammatic camera lucida drawing through the brain region to show the arrangement of the various body structures. AP – anterior pouch of intestine; CM – body wall circular muscle layer; CV – cephalic blood vessel; DE – dermis; EP – epidermis; EX – excretory tubule; IL – inner portion of body wall longitudinal muscle layer; OE – oesophagus; OL – outer portion of body wall longitudinal muscle layer; PG – posterior gland of cerebral sensory organ; RC – rhynchocoel; VC – ventral cerebral commissure. Scale bar = 250 μm.

Figures 3–8. Limnemertes poyangensis gen. et sp. nov. 3. Transverse section through the head to show the appearance of the epidermis (EP). CG, cephalic gland. A ciliated cerebral canal is indicated by the asterisk, an eye by the star. 4. Transverse section to show the appearance of the epidermal vacuolate glands and the junction between stomach and intestine. RC – rhynchocoel. 5. Transverse section through the foregut region to show the arrangement of the body wall muscle layers. AP – anterior pouch of intestine; LN – lateral nerve cord; ST – stomach. 6. Transverse section through the brain region to show the body wall longitudinal musculature divided into inner (IL) and outer (OL) layers. BR – brain; OE – oesophagus. The star indicates one of the cephalic blood vessels. 7. Transverse section to show the posterior portions of a cerebral sensory organ (CO) extending between the inner and outer layers of the longitudinal musculature. Arrowhead, posterior gland of cerebral sensory organ. 8. Transverse section to show excretory tubules, indicated by asterisks, lying just inside the outer portion of the body wall longitudinal musculature. All photomicrographs are of the holotype. Scale bars: 3, 7 = 100 μm; 4 = 250 μm; 5, 6, 8 = 200 μm.

Figures 9–15. Limnemertes poyangensis gen. et sp. nov. 9. Transverse section through part of the stomach region to show muscle fibres radiating inwards towards the stomach wall. 10. Transverse section near the tip of the head through the proboscis pore and anterior portion of the rhynchodaeum (RD). The cephalic vascular loop is indicated by a star. 11. Transverse section just behind the origin of the oesophagus (OE) from the rhynchodaeum. 12. Transverse section through part of the anterior proboscis region. 13. Longitudinal section through the central stylet basis. MB – muscle bulb of stylet region. 14. Transverse section through the proboscis insertion to show the circular muscle sphincter encircling the oesophagus. 15. Transverse section to show the appearance of the extreme anterior portion of the stomach, indicated by a star. RC – rhynchocoel. Figures 12 and 13 are of one of the paratypes, the remaining photomicrographs of the holotype. Scale bars: 9, 12, 14 = 150 μm; 10 = 200 μm; 11 = 250 μm; 13 = 100 μm; 15 = 500 μm.

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Figures 16–21. Limnemertes poyangensis gen. et sp. nov. 16. Transverse section to show the appearance of the main anterior portion of the stomach with a deeply folded epithelium. 17. Transverse section through a vascular plug. 18. Transverse section through the dorsal cerebral commissure, indicated by a star. 19. Part of the head in transverse section to show a cephalic furrow (CF) and one of the eyes (indicated by a star). 20.Transverse section through the thick-walled chamber region of a ciliated cerebral canal, indicated by a star. 21. Transverse section through a cerebral sensory organ, flanked dorsally and ventrally by acidophilic glandular masses. All photomicrographs are of the holotype. Scale bars: $16 = 250 \mu$m; $17, 19 = 100 \mu$m; $18, 20, 21 = 200 \mu$m.

meters measured for the location are summarised in Table 1.

Poyang Lake covers an area of 3283 km² at a water level of 21.71 m above mean sea level. The maximum length of the lake is 173 km, the maximum width 73 km. The nemerteans had a density of 48 specimens per m² and a wet biomass of 0.4 g per m². As-

sociated fauna included haplotaxid (*Haplotaxis* sp.), naid (*Pristina longiseta*) and tubificid (*Spirosperma* sp.) oligochaetes, Hirudinea (*Glossiphonia* sp.), gastropod molluscs (*Bellamya* sp., *Parafossarulus* sp. and *Hippeutis* sp.), bivalve molluscs(*Corbicula fluminea*), and among the insects Zygoptera and *Lype* sp. (Odonata) and the chironomids *Cryptochironomus* sp.,

Parachironomus sp., *Polypedium* sp. and *Zavrelia* sp. (Diptera). The biology of the lake is discussed in Wang et al. (1999).

External features

No observations were made on living specimens. After preservation in formalin the worms had an overall dull greenish colour. The largest specimen examined was about 16 mm long and 0.96 mm in maximum width (Fig. 1). The bluntly rounded head showed no evidence of cephalic furrows, and no eyes were visible. The body of the holotype was rather dorsoventrally flattened and a more or less uniform width throughout its length, the two paratypes were more rounded in cross section. Gonads, more or less regularly distributed throughout the posterior 75–80% or more of the body length, were visible through the epidermal surface as whitish oval patches about 0.3 mm in maximum diameter. There was no evidence of a caudal cirrus at the posterior tip of the body.

After clearing in xylene six black eyes were distinguishable, arranged as a row of three on each side of the head, and it could be seen that the rhynchocoel extended for less than half the body length.

Body wall, musculature and parenchyma

Throughout most of body length the epidermis (Fig. 2) is 30–45 μm thick, rather less in the cephalic and more posterior regions. In the cephalic region it is composed mainly of columnar ciliated cells with scattered acidophilic and basophilic glands containing homogeneous contents irregularly distributed between them (Fig. 3), whereas from the brain region backwards the epidermis becomes increasingly dominated by large, ovoid, vacuolate cells which extend the full epidermal height (Fig. 4). Similar to those described by Norenburg (1985), the ciliated cells are broader distally, their nuclei being mainly located close to their basal margin. The vacuolate gland cells, which are almost without exception spherical and appearing either empty or filled with a faintly basophilic and 'stringy' cytoplasm, appear to correspond with the mucous cell types which tend to dominate the hoplonemertean epidermis (Norenburg, 1985), no evidence of bacillary cells being distinguished. The acidophilic and basophilic glands containing homogeneous cytoplasm vary in shape from ellipsoidal to pyriform; according to Norenburg's (1985) definition these glands constitute a serous cell type.

The dermis (Fig. 2) is generally about 6–7 μm thick, somewhat thinner in the posterior half of the body. Traces of the epidermal basal lamina extending peripherally between the mucous glands in the postcerebral body regions give the dermis a cup-like distal margin similar to that reported from several other hoplonemerteans.

The body wall musculature comprises outer circular and inner longitudinal layers (Figs 2 and 5). No evidence of a diagonal muscle layer could be found in any part of the body. The circular muscles are mostly thin, reaching a maximum depth of some 5–6 μm, and extend to the tip of the head, whereas the longitudinal musculature is somewhat better developed and has a maximum thickness of about 30 μm in the foregut region of the body. The longitudinal muscle layer is anteriorly divided (Figs 2 and 6). Close behind the brain isolated bundles of longitudinal muscle fibres separate off from the main layer, running progressively deeper into the parenchyma as they approach the rear of the brain lobes. By about mid-brain level, the inner portion of the longitudinal musculature is mostly separated from the main outer region by parenchymatous connective tissue, but on the ventrolateral margins posterior extensions of the cerebral sensory organ glands intrude between the two muscle zones (Figs 2 and 7), and on the dorsolateral margins the two longitudinal layers are separated by groups of excretory tubules (Figs 2 and 8). Only the inner longitudinal muscle layer contributes to the proboscis insertion, so by Kirsteuer's (1974) definition there is no precerebral septum. The main outer longitudinal muscle layer extends to the tip of the head, circular and longitudinal layers together being only some 5–6 μm across in the anterior cephalic region. In the stomach region occasional, isolated, bundles of muscle fibres radiate inwards from the main body wall longitudinal muscle layer, passing below the lateral nerve cords and blood vessels to reach the stomach wall (Fig. 9). Other, more weakly developed, dorsoventral muscle bundles pass across the body on either side of the foregut, partially enclosing the anterior pouches of the intestinal caecum. In the head isolated muscle fibres radiate inwards between the cephalic glands from the longitudinal layer, other fibres crossing the head to pass close above the rhynchodaeum.

Parenchymatous connective tissues are most evident in the cerebral and foregut regions of the body, where they form an extensive packing tissue between the various body organs. Elsewhere in the body parenchyma is sparsely developed.

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Proboscis apparatus

The rhynchodaeum opens just subterminally on the ventral surface of the head (Fig. 10). Its lining epithelium is thin and possesses neither gland cells nor cilia. Isolated longitudinal muscle fibres, which appear to originate from the body wall muscle layer, run close below the rhynchodaeal wall, but there is no specific rhynchodaeal musculature. The oesophagus (Fig. 11) emerges from the ventral wall of the rhynchodaeum just in front of the proboscis insertion , the rhynchodaeal wall behind the oesophageal opening becoming slightly thicker than it is for its remaining length. There is no circular muscle layer associated with the posterior portion of the rhynchodaeum, although in many hoplonemerteans a distinct circular muscle sphincter is developed immediately in front of the proboscis insertion.

The rhynchocoel is at most less than half the body length. Its wall contains separate circular and longitudinal muscle layers (Fig. 2). In the stomach region of the holotype, which has lost its proboscis, the rhynchocoel is about 25% of the body diameter.

The proboscis is slender, its anterior region being at most only about 125 μm in overall diameter in the retracted position. The anterior region (Fig. 12) is externally covered by a papillate epithelium, 30–35 μm tall, containing both acidophilic and basophilic gland cells. Below the epithelium the outer circular and inner longitudinal muscle layers are respectively about 3–4 μm and 12–15 μm thick.

The inner lining is thin but distinct. The proboscis nerves are extremely small and indistinct; so far as could be determined there are either 9 or 10 nerves.

In only one of the three specimens sectioned, one of the paratypes, could the proboscis armature be clearly distinguished. The cylindrical stylet basis (Fig. 13) is about 40 μm long and 18 μm in maximum diameter, with a bluntly rounded proximal end. The single central stylet is approximately 30 μm long, i.e., the stylet: basis ratio is about 0.75:1. The muscle bulb of the stylet region (Fig. 13) has a typical monostiliferous construction. There are two accessory stylet pouches, each containing 2–3 reserve stylets.

The epithelium of the posterior proboscis region, which is not developed into papillae, is dominated by basophilic glands. The musculature of this region is thin and indistinct and its arrangement could not be certainly determined.

Alimentary canal

The oesophagus (Fig. 11) opens from the ventral wall of the rhynchodaeum just in front of the proboscis insertion. The oesophageal epithelium, which possesses neither gland cells nor cilia, is at first about 10 μm in maximum thickness, the oesophagus as a whole having an overall diameter of some 80–90 μm. As it passes through the proboscis insertion the oesophagus is reduced to a diameter of only 45–50 μm, its epithelium increases in thickness to about 15 μm and it is surrounded by a circular muscle sphincter 15 μm or more thick (Fig. 14). Behind this sphincter the epithelium gradually becomes thicker and folded, merging with the anterior region of the stomach below the ventral cerebral commissure. The junction between oesophagus and stomach is marked by the appearance of the cilia and gland cells which are typical of a monostiliferous hoplonemertean stomach.

Behind the ventral cerebral commissure the stomach expands rapidly. A very short anterior region (Fig. 15) leading from the oesophagus is characterised by the absence of acidophilic gland cells, the epithelium, 30 μm thick, consisting mainly of ciliated columnar cells but with a few, coarsely granular basophilic glands situated proximally. The stomach is about 750 μm long, and divided into two histologically distinguishable regions. In the anterior half the epithelium, 30–45 μm thick, is deeply folded and contains homogeneous acidophilic glands, vacuolate glands and homogeneous basophilic glands in more or less equal proportions (Fig. 16). This region is some 50–55% of the body diameter. In the posterior half, however, the epithelium is progressively less folded and becomes dominated by vacuolate glands, at the same time the stomach gradually narrowing to a diameter of about 150–160 μm where it leads into the intestine. Unlike the situation in most monostiliferous hoplonemerteans, there is neither a pyloric canal nor an intestinal caecum, the foregut merging directly into the intestine.

From the junction between foregut and intestine a pair of long anterior pouches extend forwards to reach alongside the dorsal cerebral lobes (Figs 2, 6 and 15). The intestine itself is histologically unusual in that its ventral epithelium throughout most of its length contains pyriform gland cells filled with strongly basophilic globules 1–2 μm in diameter, whereas the glands of the anterior pouches, lateral diverticula and the dorsal epithelium are similar in size and shape but filled with strongly acidophilic globules. Basophilic

intestinal glands have not previously been reported from hoplonemerteans and their ventral distribution and presence in all three specimens sectioned suggests that they do not merely represent the normal type of gastrodermal gland in a different physiological state. Both the anterior pouches and main intestine bear deeply branched lateral diverticula.

Gut contents in one of the paratypes, although not positively identifiable, show no evidence of either annelid or mollusc structures and may possibly be insect remains.

Blood system

The blood system represents a simple monostiliferous hoplonemertean pattern (Gibson, 1972). The two cephalic vessels meet by a supra-rhynchodaeal loop above the proboscis pore. The vessels are thin-walled but possess semi-lunar flaps or pouches similar to those described for several other monostiliferous taxa. The vessels do not meet as they pass through the cerebral ring, but behind the brain the right cephalic vessel branches to give rise to the mid-dorsal vessel. This almost immediately enters the ventral rhynchocoel wall to form a single vascular plug (Fig. 17), some 30 μm in diameter, located a short distance behind the brain lobes. Behind the vascular plug the mid-dorsal vessel continues posteriorly immediately below the rhynchocoel.

The three post-cerebral blood vessels are also thin-walled with semi-lunar flaps. They meet posteriorly by a supra-alimentary loop, and there are no pseudo-metameric transverse connectives, as found in the intestinal region of many hoplonemerteans. A similar arrangement is found in all freshwater hoplonemerteans whose blood systems have been examined.

Nervous system

The brain (Figs 2 and 6) is moderately well developed, the dorsal lobes being slightly smaller and set wider apart than the ventral. No trace of either an outer or inner neurilemma, nor of neurochord cells, could be discerned. The ventral cerebral commissure (Fig. 2) is 45–50 μm in diameter, the longer dorsal commissure, about 15 μm in diameter, curving anteriorly close above the dorsal rhynchocoel wall (Fig. 18).

Throughout their length the lateral nerve cords contain only a single neuropil, i.e., there are no accessory lateral nerves. The cords meet posteriorly via a sub-intestinal commissure.

The peripheral nervous system includes a single well-developed nerve emerging from about mid-brain level on either side, which extends anteriorly for a short distance before turning ventrolaterally to enter the cerebral sensory organs.

Additonal nerve tracts seen but not traced comprised several small nerves extending from the front of the brain to lead anteriorly between the cephalic gland lobules of the head.

The proboscis nerve supply was too indistinct to be accurately assessed; the wall of the anterior chamber appears to contain either 9 or 10 minute nerves.

Excretory system

The excretory system extends from the mid-cephalic region back into the anterior intestinal portions of the body. It consists of a complex arrangement of thick-walled (up to 15 μm) tubules, with an overall diameter up to 45–50 μm, situated on the dorsolateral and lateral sides of the body. The tubule epithelium in many places has a distinctly vacuolate appearance. In the brain region the tubules are mostly located between the inner and outer body wall longitudinal muscle layers (Figs 2 and 6), with occasional tubules reaching ventrally to run close to the posterior regions of the cerebral sensory organs. Several slender efferent ducts leading to dorsolateral nephridiopores could be seen, but their number was not determined. No evidence of flame cells could be distinguished.

Sensory organs

On the head, situated close behind the level of the proboscis pore, there is a single pair of short oblique lateral cephalic furrows (Fig. 19). These furrows are directed slightly posteriorly from the ventrolateral to the dorsolateral body margins, the ciliated cerebral canals leading inward from their mid-lateral position. The cerebral canals, at first about 30 μm in diameter, lead directly inwards through the dermis and body wall muscle layers and then turn 90° posteriorly to run adjacent to the longitudinal muscles (Fig. 3). After some 50–55 μm each canal expands to form a thick-walled chamber (Fig. 20), 60 μm in diameter, whose outer lateral margin is associated with neuroganglionic cells flanked above and below by acidophilic gland cells (Fig. 21). Behind this chamber each cerebral canal, 15–20 μm wide, continues posteriorly along the inner border of the cerebral organ to end in a mass of basophilic gland cells. The canal does not

Table 2. The 16 species of monostiliferous hoplonemerteans previously recorded from freshwater habitats at various locations around the world

Genus	Species	Naming authority	Recorded distribution
Campbellonemertes	johnsi	Moore & Gibson (1972)	Campbell Island, New Zealand
Koinoporus	mapochi	Sánchez & Moretto (1988)	Chile
Otonemertes	denisi	Dawydoff (1937)	Cambodia
Potamonemertes	gibsoni	Hickman & Moore (1990)	Tasmania, Australia
	percivali	Moore & Gibson (1973)	New Zealand
Prostoma	asensoriatum	Montgomery 1896	U.S.A.
	canadiensis	Gibson & Moore (1978)	Canada, Holland
	communopore	Senz (1996)	Austria
	eilhardi	Montgomery 1894	Europe, Kenya, southern Africa, South America, Australia, New Zealand
	graecense	Böhmig 1892	Europe, Kenya, southern Africa, Australia, New Zealand, Japan, Russia, possibly South America
	hercegovinense	Tarman (1961)	Bosnia
	jenningsi	Gibson & Young (1971)	England
	kolasai	Gibson & Moore (1976)	Poland
	macradenum	Sun & Yin (1995)	People's Republic of China
	ohmiense	Chernyshev, Timoshkin & Kawakatsu (1998)	Japan
	puteale	Beauchamp (1932)	France, Switzerland

branch. The ventral and dorsal acidophilic glandular components do not communicate with each other; the ventral group extends behind the end of the cerebral canal, immediately external to the body wall inner longitudinal muscle layer, to end below the ventral cerebral commissure (Figs 2 and 6). The cerebral organs are about 240 μm long, 200 μm in dorsoventral height and 65–70 μm wide. Their dorsal and ventral acidophilic glandular components account for approximately two-thirds of the total volume.

Each of the specimens possesses three pairs of well developed pigment cup ocelli, each about 30 μm wide and 45–50 μm tall. The black pigment layer mostly forms a distinct cup-like lining around the proximal half of each ocellus (Figs 3 and 19) although in some eyes the layer is rather more dispersed and extends around much of the remaining eye tissues. The anterior pair of eyes is positioned just behind the level at which the ciliated cerebral canals open, the posterior pair immediately in front of the brain lobes.

Cephalic glands and apical organ

A single, small, apical organ, 15 μm in diameter, appears as a ciliated pit on the tip of the head.

The cephalic glands are well developed, and form typical irregularly-shaped and sized, rather vacuolate basophilic lobules which fill much of the pre-cerebral region in the head (Figs 11, 19 and 20). In front of and above the anterior rhynchodaeum the glands are confined to the dorsal half of the head, but farther back extend to all sides of the head except the mid-ventral region. Behind the origin of the oesophagus the cephalic glands decline in abundance ventrolaterally but dorsally just reach the anterior margin of the brain lobes. The glands appear to discharge to the exterior via the apical organ; no evidence of independent efferent ducts, as occur in some hoplonemertean genera, could be distinguished.

Reproductive system

The sexes are separate. Both ovaries and testes are extremely numerous and extend throughout the intestinal region of the body, two or three gonads occurring on either side of the body in the interdiverticular spaces. In the male (holotype), each testis wall is lined by spermatogonia and spermatocytes, the testicular lumen being packed with developing spermatazoa which possess elongate cylindrical sperm heads some 5–6 μm long.

Table 3. Comparison between some major morphological characters of the present taxon and those of previously described freshwater monostiliferous hoplonemertean genera. Data taken from Dawydoff (1937), Moore & Gibson (1972, 1973) and Sánchez & Moretto (1988)

Feature	Plectonemertidae		Ototyphlonemertidae	Tetrastemmatidae		
	1	2	3	4	5	6
Proboscis apparatus						
Rhynchocoel full body length (+) or shorter than the body (0)	+	+	0	0	0	0
Rhynchocoel musculature comprising separate circular and longitudinal layers (2) or formed from a single layer of interwoven fibres (1)	1	1	2?	2	2	2
Proboscis massive (+) or slender (0)	0	+	0	0	0	0
Blood system						
Number of vascular plugs	2	2	?	1	1	1
Sensory organs						
Number of eyes	0	0	6^1	4–6	4–8^2	6
Reproductive system						
Hermaphroditic (H) or with separate sexes (S)	H	H	?	H	H	S
Reproduction oviparous (0) or ovoviviparous (V)	0	0	?	V	0	0
Body wall						
Longitudinal muscle layer anteriorly divided (D) or not divided (0)	0	0	0?	0	0	D

[1] Dawydoff (1937: 805) clearly stated that the freshwater species possessed "deux taches oculaires... Chacun contient trois ocelles, très nettes chez l'animal vivant", but Corrêa (1958: 449) defined the genus as possessing "um par de olhos" and illustrated only two eyes in the marine species, *Otonemertes marcusi* Corrêa, 1958; [2] Except for *Prostoma puteale*, which completely lacks eyes.

1 = *Campbellonemertes*; 2 = *Potamonemertes*; 3 = *Otonemertes*; 4 = *Koinoporus*; 5 = *Prostoma*; 6 = present taxon.

In both paratypes, each ovary contains one to several ova in a similar stage of development. Individual ova are up to about 200 μm in diameter. No evidence of open gonopores was found in any of the specimens examined.

Discussion

Sixteen species of freshwater monostiliferous hoplonemerteans, belonging to five genera, have previously been described (Table 2), and are at present distributed between three families. Moore & Gibson (1988) placed *Campbellonemertes* and *Potamonemertes* in the Plectonemertidae, Corrêa (1958) referred *Otonemertes* to the Ototyphlonemertidae, and the remaining two genera, *Koinoporus* and *Prostoma*, were united in the Tetrastemmatidae by Sánchez & Moretto (1988).

Several anatomical features can be used to distinguish between these freshwater hoplonemertean taxa.

The two plectonemertid genera are united by a rhynchocoel whose wall is composed of a single layer of interwoven circular and longitudinal muscle fibres and which extends the full length of the body; the blood system has two vascular plugs; eyes are absent. The rhynchocoel of the present form has separate circular and longitudinal muscle layers in its wall and is short; there is only a single vascular plug and there are six eyes (Table 3). It clearly does not belong in the family Plectonemertidae. It can also be excluded from the incompletely described ototyphlonemertid genus *Otonemertes* because *Otonemertes*, like all *Ototyphlonemertes* species, possesses one or two pairs of statocysts in their cerebral ganglia and none is found in the present form.

A comparison between the freshwater tetrastemmatid genera and the present nemerteans shows that whereas *Koinoporus* combines hermaphroditism with ovoviviparity, and *Prostoma* species are variably true or protandous hermaphrodites with oviparity, the

present species possesses separate sexes. A further distinguishing feature of the Chinese nemerteans is that their body wall longitudinal muscle layer is anteriorly divided, a feature not found in *Koinoporus* or *Prostoma*. It is concluded that the present specimens cannot be placed in any of the previously known hoplonemertean freshwater genera or species, and the name *Limnemertes poyangensis* gen. et sp. nov. is accordingly proposed for them.

Although no secure diagnosis is as yet available for the family Tetrastemmatidae, the similarities between *Limnemertes* gen. nov., *Koinoporus* and *Prostoma* allow the new taxon provisionally to be included in the same family.

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