

A new species of *Tetrastemma* (Nemertea: Enopla: Monostiliferoidea) from Ría de Foz, north-western Spain, found living in the mantle cavity of the bivalve mollusc *Scrobicularia plana*

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A new species of monostiliferoidean nemertean, *Tetrastemma fozensis*, from the mantle cavity of the bivalve mollusc *Scrobicularia plana*, in the Ría de Foz, north-western Spain, is described and illustrated. Other nemerteans from the mantle cavity of *Scrobicularia* collected in Poole Harbour, southern England, are provisionally identified as conspecific with the Ría de Foz material, but show certain anatomical differences whose taxonomic significance cannot at present be assessed.

KEY WORDS:—Nemertea – Monostiliferoidea – taxonomy – *Tetrastemma fozensis* sp. nov. – *Scrobicularia plana*.

CONTENTS

Introduction	225
Material and methods	226
Family Tetrastemmidae Hubrecht, 1879	226
Genus <i>Tetrastemma</i> Ehrenberg, 1831	226
<i>Tetrastemma fozensis</i> sp. nov.	227
The Poole Harbour nemerteans	238
Acknowledgements	239
References	239
Abbreviations used in the figures	240

INTRODUCTION

There are many records in the literature of nemerteans found in commensal or parasitic association with invertebrates, although in many instances a definite nemertean–host relationship has not been demonstrated. Most reports (e.g. Marion, 1874; Bürger, 1897–1907, 1904; Coe, 1905; Kato, 1939; Corrêa, 1966; Gibson, 1972, 1982a, 1990) list cirripede or decapod crustaceans, actiniarian cnidarians or ascidian tunicates as hosts, and few nemertean taxa have been identified from bivalve molluscs. Indeed, virtually all reports of nemerteans from bivalves refer to species of the entocommensal bdellonemertoidean genus

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Malacobdella, whose members are dorsoventrally compressed and leech-like in shape, with a doliiform foregut, sinuous intestine and single posterior ventral sucker (Gibson, 1982a), although Iwata (1967) described a heteronemertean, *Uchidana parasita* Iwata, as a gill-feeding parasite of *Mactra sulcataria* Reeve from Japanese waters.

During an investigation of the intertidal macrofauna in the Ría de Foz, north-western Spain (Junoy, 1988), many specimens of the bivalve *Scrobicularia plana* (da Costa) were found to harbour monostiliferoidean nemerteans in their mantle cavities. Recently we have also been sent nemerteans from Poole Harbour, southern England, found in the mantle cavity of the same bivalve species. *Scrobicularia* has not previously been recorded as a host to nemertean worms.

Histological studies of specimens from both localities reveal that the nemerteans belong in the genus *Tetrastemma*. Those from Ría de Foz represent a previously unknown taxon and are named *T. fozensis* sp. nov., but the identity of the Poole Harbour material cannot be resolved with certainty; they are provisionally identified as *T. fozensis* sp. nov. but exhibit certain morphological differences whose taxonomic significance cannot at present be assessed.

MATERIAL AND METHODS

Specimens of *Scrobicularia plana* were collected from intertidal mud-flats at Ría de Foz (43°34'N, 7°14'W), north-western Spain, during July 1989 and January 1990. Several nemerteans were removed from the mantle cavities of bivalves which had their shells opened, but larger numbers of worms were obtained by standing the *Scrobicularia* in clean seawater, without aeration, for 24–48 hours; under these conditions the nemerteans left their hosts and congregated around the edges of the tray.

The nemerteans were examined alive both before and after anaesthetization in 7.5% MgCl₂. Specimens were then fixed in either Susa's or Bouin's fluids, embedded in 56°C m.p. paraffin wax, sectioned at 6 µm and stained with the Mallory triple method (Pantin, 1960). A total of 26 specimens has been examined histologically.

Live samples of the Poole Harbour nemerteans, previously removed from *Scrobicularia*, were sent to us by Dr W. J. Langston of the Plymouth Marine Laboratory. These nemerteans were subjected to the same procedures as the Foz material, six individuals being sectioned for histological study.

Type specimens of the Ría de Foz species are deposited with the Natural History Museum, London, the United States National Museum, Smithsonian Institution, Washington and the Museo de Ciencias Naturales, Madrid.

FAMILY TETRASTEMMIDAE HUBRECHT, 1879

Genus Tetrastemma Ehrenberg, 1831

Gibson (1985: 6) pointed out that "Many of the older established genera [including *Tetrastemma*] . . . still lack sound diagnoses". The following diagnosis of the genus is based on that given by Gibson (1982b).

Diagnosis. Generally small slender monostiliferoidean nemerteans in which the body wall musculature is not strongly developed; eyes usually distinct, typically

four arranged at the corners of a square or rectangle, occasionally fragmented; rhynchocoel extending to (or almost to) posterior end of body, with wall containing two distinct muscle layers; proboscis not strongly developed; frontal organ probably present; cephalic glands mostly well developed but rarely extending behind brain; cerebral sensory organs small, situated close to anterior margins of brain; nervous system with neither neurochords nor neurochord cells, without accessory lateral nerves; blood vascular system with three post-cerebral longitudinal vessels, mid-dorsal vessel with or without single vascular plug; excretory system confined to foregut region, with two or only a few nephridiopores; intestinal caecum present, with anterior diverticula; sexes separate; marine or estuarine.

***Tetrastemma fozensis* sp. nov.**

(Figs 1–4)

Etymology. The specific epithet refers to the type locality of the nemerteans.

Type specimens. A list of the type and voucher specimens deposited in the Natural History Museum, London, United States National Museum and the Museo de Ciencias Naturales is provided in Table 1.

Type locality. Ría de Foz, Lugo, north-western Spain, in mantle cavity of the scrobiculariid eulamellibranch bivalve, *Scrobicularia plana*, dug from intertidal mud-flats.

External features

Most of the nemerteans examined alive, before or after anaesthetization, were 1–4 mm long and 0.2–0.5 mm wide; the largest specimen seen was about 10 mm long and 0.6 mm in maximum width. The body possesses a more or less uniform width throughout its length (Fig. 1A), tapering only near the tail to end in a blunt tip. Anteriorly the rounded head, not demarcated from the body, bears two pairs of shallow oblique furrows (Fig. 1A–E). The anterior furrows, which do not meet dorsally, extend ventrally forwards between the two pairs of eyes, whereas the posterior furrows meet medially on the dorsal surface to form a

TABLE 1. Type and voucher specimens of *Tetrastemma fozensis* sp. nov. deposited in the Natural History Museum, London (NHM), the United States National Museum, Washington (USNM) and the Museo de Ciencias Naturales, Madrid (MCN). The plane of sectioning of the specimens is indicated by T.S. or L.S. for transverse and longitudinal respectively

Depository	Material	Registration number
NHM	Holotype, immature, T.S.	1990.6.5
NHM	Paratype, immature, L.S.	1990.6.6
NHM	Paratype, female, T.S.	1990.6.7
NHM	Voucher, unsectioned	1990.6.8–12
USNM	Paratype, immature, T.S.	136601
USNM	Paratype, female, T.S.	136602
MCN	Paratypes, one immature, one female, both T.S.	05.02/1

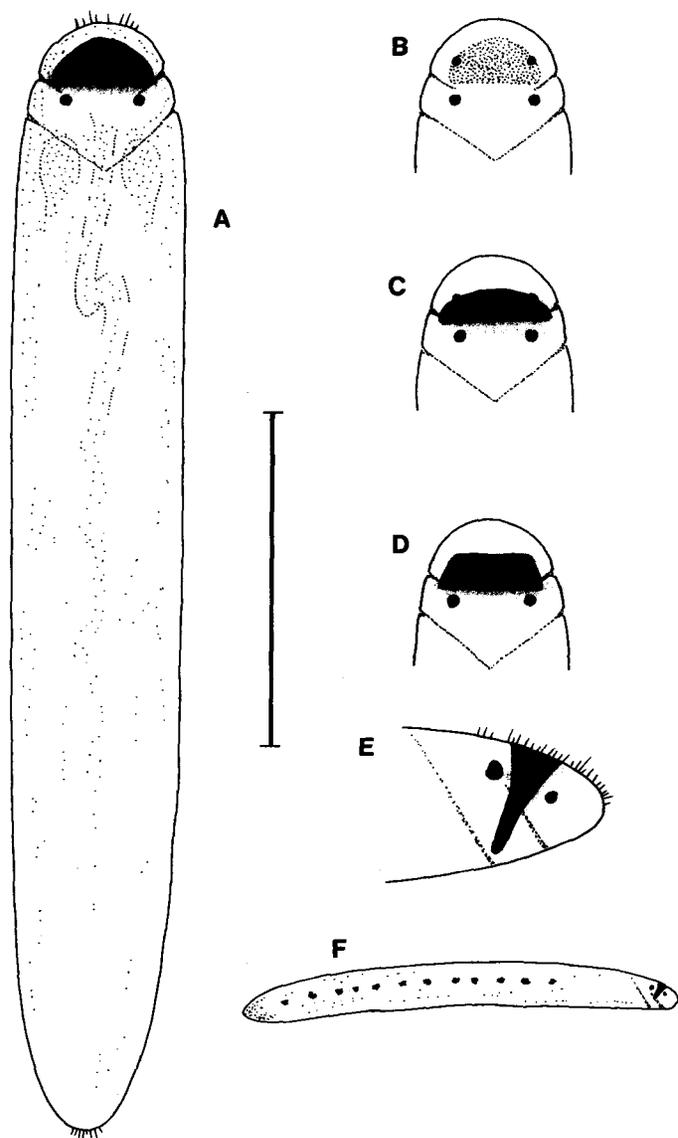


Figure 1. *Tetrastemma fozensis* sp. nov. A, Drawing of immature specimen, in dorsal view, to show the general appearance of a living individual. Note the two pairs of cephalic furrows, anterior and posterior epidermal sensory cirri and the patch of pigment on the head. B, Dorsal view of the head to show the relative positions of the pigment patch (stippled) and the eyes. C, D, Drawings of the heads of two specimens, in dorsal aspect, to show variations in the shape of the cephalic pigmentation. E, Lateral view of the head of an individual in which the cephalic pigment extends ventrally; note the row of epidermal sensory cirri. F, Lateral view of an individual possessing pigment spots distributed along the sides of the body. Scale bar (refers to A only) = 1 mm.

backward pointing V-shape located behind the rear eyes. On the upper surface of the head two longitudinal rows of 20–30 sensory cirri extend from above the cerebral region forwards to the tip of the snout. Another cluster of cirri is located on the posterior tip of the body (Fig. 1A).

The four dark eyes are arranged at the corners of a rectangle whose longest axis is transverse (Fig. 1B). Typically the anterior eyes are partially or completely masked by the cephalic pigmentation.

The body is generally a pale yellow to light pink colour. On the head a semicircular to trapezoid patch of dark brown pigment extends from the anterior pair of eyes back to just in front of the posterior eyes (Fig. 1A–D). Immediately behind this brown pigment is a distinctly white area in which the rear eyes are situated. In most individuals the cephalic pigment extends ventrally on either side of the head to form slender dorsoventral bands (Fig. 1E); frequently these bands meet ventrally and form a continuous ring of pigment encircling the head. In 17 of the 63 specimens examined (27%) spots of regularly distributed dark brown pigment extend along the lateral margins of the body (Fig. 1F). Animals with these spots usually have a significantly darker general body colour with a distinctly pink posterior tip.

When mechanically irritated the nemerteans neither contract strongly nor show waves of muscular activity passing along their bodies.

Body wall, musculature and parenchyma

The epidermis (Fig. 2A), mostly 20–30 μm thick, possesses a typical construction and is generally similar to that described by Norenburg (1985) for other enoplan taxa. The epithelial lining of the cephalic furrows is distinguishable from the remaining epidermis by its lack of gland cells. Internally the epidermis is bordered by a thin but distinct connective tissue dermis (Fig. 2A).

The body wall muscles comprise outer circular and inner longitudinal layers (Fig. 2A), respectively 3–5 μm and 10–25 μm thick; there is no diagonal muscle layer between them, and the longitudinal muscles are not, as in some genera (Gibson, 1982c), anteriorly divided. Both muscle layers are reduced in thickness posteriorly. The circular muscle layer extends to the tip of the head, but in front of the brain the longitudinal layer is less well defined and many of its fibres are dispersed between the lobules of the cephalic glands. Just in front of the cerebral ganglia isolated bundles of fibres lead inwards from the longitudinal muscle layer to the proboscis insertion; these comprise the pre-cerebral septum, which is thus of the dissolved type as defined by Kirsteuer (1963).

A delicate layer of circular somatic muscles surrounds the stomach portion of the foregut, but is not distinguishable around either the oesophagus or the pylorus. Throughout the intestinal region weakly developed dorsoventral muscles cross the body between the lateral gut diverticula.

Parenchymatous connective tissues are poorly developed and mainly occur between the foregut and rhynchocoel.

In sections of animals which possess the lateral rows of dark brown spots, dense accumulations of pigment granules are located between the body wall longitudinal muscle layer and the intestinal epithelium, immediately above the lateral nerve cords, on either side of the body (Fig. 2B).

Proboscis apparatus

The proboscis pore is situated anteroventrally near the tip of the head. It opens into a thin-walled rhynchodaeum whose epithelium is neither ciliated nor glandular.

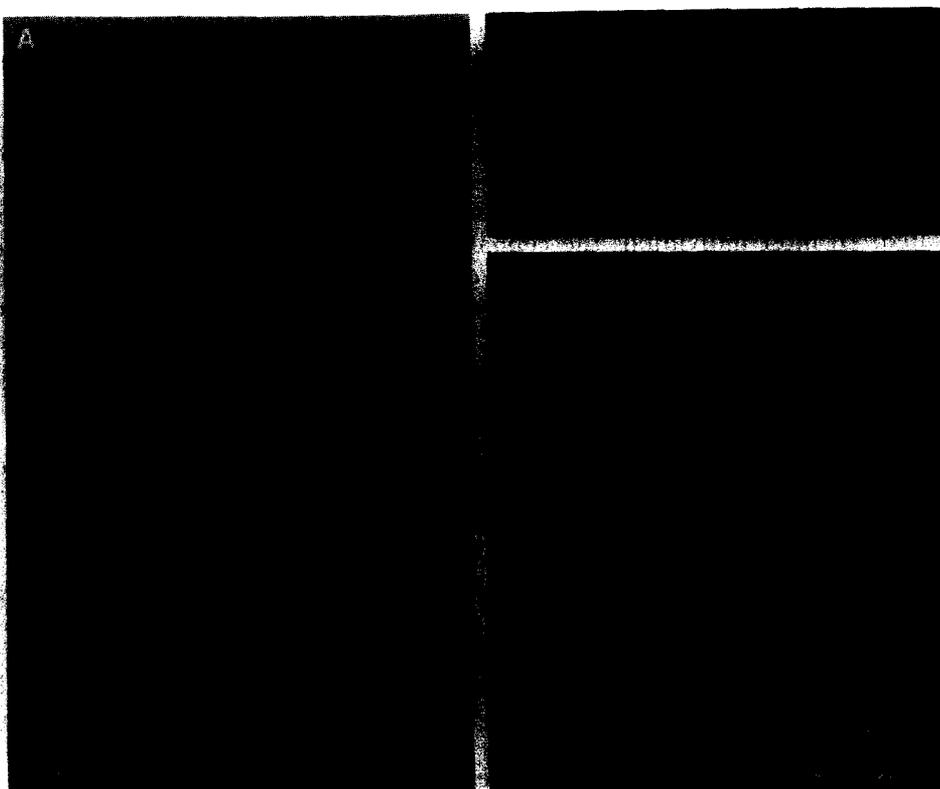


Figure 2. *Tetrastemma fozensis* sp. nov. A, Transverse section to show the organization of the body in the posterior foregut region. B, Transverse section to show an accumulation of pigment granules (arrowhead) situated close to a lateral nerve cord in the intestinal region of the body. C, Transverse section to show the organization of the anterior portion of the proboscis. Large arrowheads point to the two circular muscle layers, small arrowheads indicate four of the proboscis nerves. All photomicrographs of sections stained by the Mallory triple method. Scale bars: A, B = 100 μ m, C = 50 μ m.

The rhynchocoel extends almost to the posterior tip of the body. Its wall contains separate circular and longitudinal muscle layers, neither of which is strongly developed.

The proboscis is slender, with a maximum retracted diameter of about 80–90 μ m. Its anterior portion (Fig. 2C) comprises a glandular epithelium arranged into simple conical papillae 15–20 μ m tall, a thin but distinct connective tissue layer, and delicate outer and inner circular muscle layers enclosing a zone of longitudinal muscle fibres between which the ten proboscis nerves are situated; the three muscle layers together are at most about 10–12 μ m across. The lining endothelium is delicate and indistinct. Kirsteuer (1963: 607), in a study of the anatomy of 13 species of *Tetrastemma* from the Adriatic Sea, found that in some species, including *T. melanocephalum* (Johnston), the “proximalen Rüsselzylinder ... [has] ... eine Ring- und eine Längsfibrillenschicht”, whereas in others, like the present nemerteans, there is “eine innere, etwas schwächer realisierte Ringfaserlage hinzukommt”. Gibson & Tait (1984) also describe three muscle layers from the anterior proboscis wall of *T. unilineatum* Joubin.

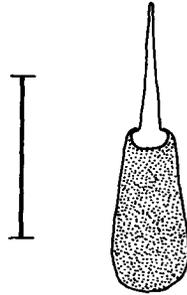


Figure 3. *Tetrastemma fozensis* sp. nov. Drawing of a typical central stylet and basis. Scale bar = 50 μm .

The proboscis armature is generally similar to that described for many other tetrastemmid species, and consists of a single central stylet borne on a cylindrical basis (Fig. 3), with two accessory stylet pouches each containing two to four reserve stylets in various stages of formation. Measurements made on the stylet apparatus of eight specimens are shown in Table 2.

The short, posterior portion of the proboscis is much simpler in construction, its wall comprising a predominantly acidophilic epithelium 15 μm thick which is not arranged in papillae, delicate outer longitudinal and inner circular muscle layers, each only one or two fibres thick, and a thin endothelium.

The proboscis retractor muscle is attached to the dorsal wall of the rhynchocoel near its posterior end.

Alimentary canal

A short oesophagus, whose thin epithelium is neither ciliated nor glandular, emerges from the rhynchodaeum just in front of the pre-cerebral septum and opens into the stomach close behind the ventral cerebral commissure.

The transitional anterior portion of the stomach is tubular and possesses a densely ciliated epithelium in which only acidophilic gland cells can be distinguished (Fig. 4A). In contrast, the main stomach region is marked by a single infolding and an epithelium, 25–30 μm thick, in which acidophilic and basophilic gland cells are present in approximately equal numbers (Fig. 4B). At its rear the stomach merges directly into the pyloric portion of the foregut without forming caecal pouches as described, for example, in *T. fulvum* Kirsteuer and *T. vastum* Bürger by Kirsteuer (1963).

TABLE 2. Measurements recorded for the stylet apparatus of eight specimens of *Tetrastemma fozensis* sp. nov

	Range	Average
Length of central stylet (μm)	33–65	47.5
Length of basis (μm)	52–78	59.6
Maximum width of basis (μm)	18–31	24.1
Ratio of basis length to central stylet length	1.1–1.5	1.25
Ratio of basis length to basis width	2.0–2.8	2.4
Number of accessory stylet pouches	2	2
Number of reserve stylets per pouch	2–4	3

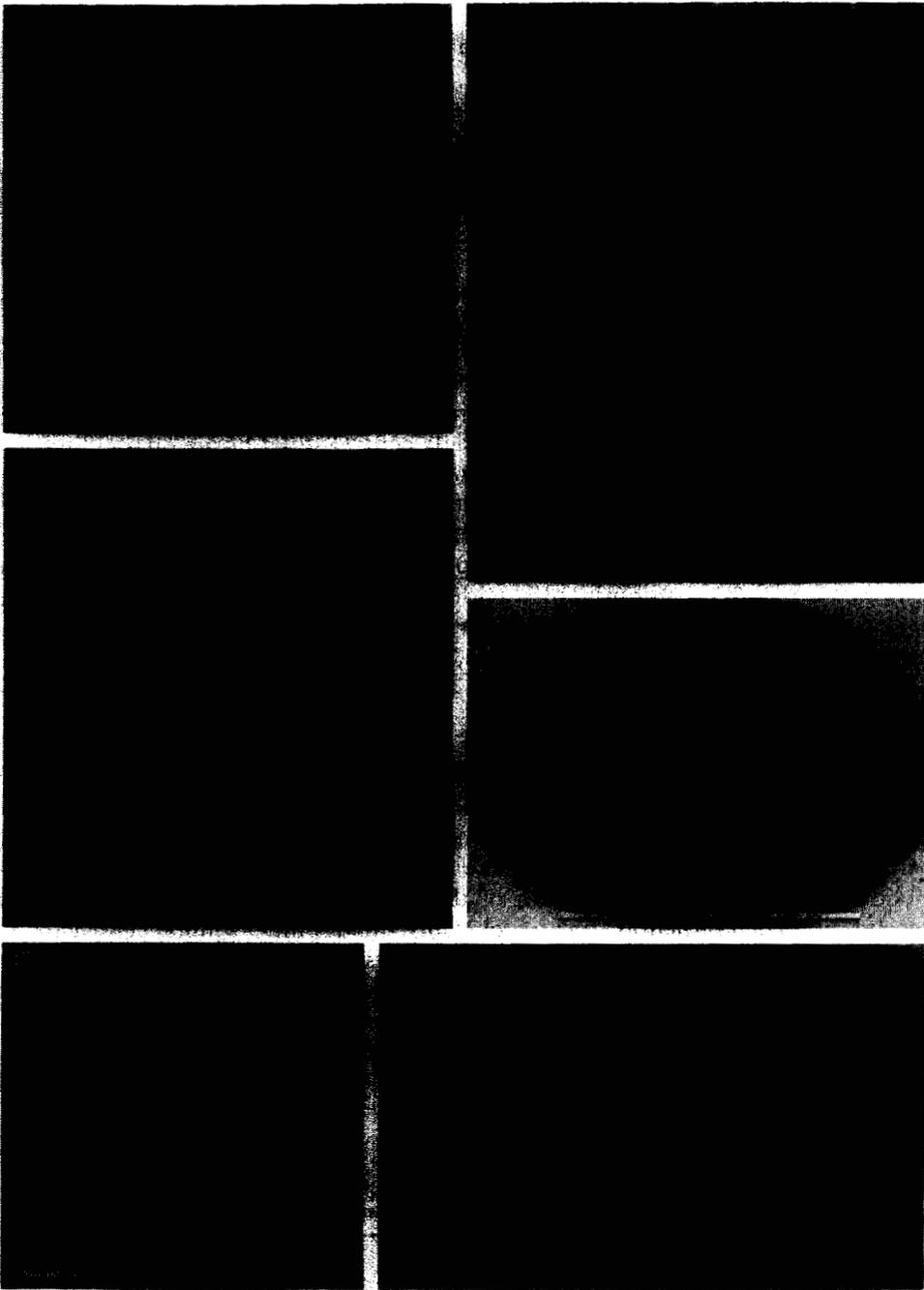


Figure 4. *Tetrastemma foxensis* sp. nov. A, Transverse section through the cerebral region to show the appearance of the anterior portion of the stomach. The arrowhead indicates the outer neurilemma investing the brain lobes, and the single vascular plug is clearly visible protruding into the rhynchocoel. B, Transverse section through the posterior stomach region; note the lateral blood vessels (arrowheads) and the anterior pouches of the intestinal caecum. C, Transverse section through the stomach region to show two of the excretory collecting tubules (arrowheads) and the single neuropil in a lateral nerve cord. D, Transverse section through the head to show basophilic cephalic glands (large arrowheads) extending above the brain, and some of the ventral acidophilic

The pylorus forms a wide but dorsoventrally compressed and unfolded canal (Fig. 2A), approximately as long as the stomach and oesophagus together. Gland cell density in the pyloric epithelium decreases posteriorly. Towards its rear the pylorus narrows rather abruptly before opening into the dorsal wall of the intestine.

The intestine has a normal enoplan appearance and, except for a short rectal region, bears lobed lateral diverticula throughout its length. The intestinal caecum, which also possesses lateral diverticula, ends near the rear of the stomach; a single pair of tubular anterior pouches continues forwards dorsolaterally (Fig. 4B) to terminate close behind the dorsal cerebral lobes.

Blood system

The organization of the blood system is typically tetrastemmid (Kirsteuer, 1963) and consists of paired lateral and single mid-dorsal vessels which are transversely joined only by cephalic and caudal loops; there are no pseudometameric transverse connectives in the intestinal region, as occur in several enoplan taxa (Gibson, 1972). The mid-dorsal blood vessel emerges as a branch of one of the lateral vessels, most often the left, in the cerebral region. It immediately enters the rhynchocoel floor to form a single vascular plug, 15 μm in diameter (Fig. 4A), and then runs for the remaining body length close above the gut. Throughout the body the blood vessels are thin-walled and possess few valves.

Nervous system

The brain is well developed, the dorsal and ventral lobes being of approximately the same size. A thin outer neurilemma encloses the brain as a whole (Fig. 4A), but no inner neurilemma separating the fibrous and ganglionic cerebral components could be distinguished. The dorsal cerebral commissure, 7–15 μm thick, is positioned a little way forward of the thicker (25–45 μm) ventral commissure.

The lateral nerve cords throughout their length contain only a single neuropil (Fig. 4C), and there are no accessory lateral nerves. One or two myofibrils run along the inner dorsolateral margins of each neuropil. The nerves meet posteriorly via a sub-intestinal commissure.

There are neither neurochords nor neurochord cells in the nervous system.

Several cephalic nerves lead forwards from the anterior borders of the brain lobes. One pair of these enters the proboscis insertion dorsolaterally to provide the proboscis neural supply, but the ultimate fate of the remaining nerves was not traced.

Excretory system

The excretory system is well developed but confined to the foregut region of the body. It consists of two pairs of thick-walled longitudinal collecting tubules,

glands (small arrowheads). The opening of a ciliated cerebral canal is visible on the right ventrolateral body surface. E, Transverse section to show the appearance of a cerebral sensory organ. The ciliated cerebral canal is indicated by an arrowhead. F, Longitudinal section through an ovary to show one of the stalk-like connections (arrowhead) between an egg and the ovarian wall. All photomicrographs of sections stained by the Mallory triple method. Scale bars: A, B, E, F = 100 μm , C = 50 μm , D = 200 μm .

running close to the lateral nerve cords (Fig. 4C). Near the rear of the brain the two tubules on each side of the body fuse into a single duct, which in turn leads to a short efferent canal which opens by a single lateral nephridiopore located just behind the cerebral ganglia. No evidence of flame cells could be found.

Frontal organ and cephalic glands

A small single frontal organ opens ventroterminally just in front of the proboscis pore; it has a maximum diameter of about 20–25 μm .

Two types of cephalic glands can be distinguished. Typical basophilic lobules form the most abundant type and occupy much of the cephalic space. Posteriorly they just reach over the anterior portion of the cerebral ganglia (Fig. 4D), but ventrally are largely replaced by acidophilic glands in the vicinity of the proboscis insertion. The acidophilic glands, containing coarsely granular cytoplasm, are irregularly distributed between the basophilic lobules in the anterodorsal part of the head, but further back are increasingly confined to the ventral half of the cephalic region and form a distinct ventral wedge of cells extending back below the brain (Fig. 4D) to the stomach region. The cephalic glands appear to discharge to the exterior through the frontal organ.

Sensory structures

There are four eyes, arranged at the corners of a rectangle (Fig. 1). In an average-sized specimen the anterior pair of eyes is located about 70 μm back from the tip of the head, the posterior eyes some 80 μm behind these. The transverse distance between eyespots of each pair is some 145 μm . Eyes are of a typical pigment cup ocellus type, 20–30 μm in diameter, and are situated 10–80 μm beneath the epidermal basement layer.

The cerebral sensory organs (Fig. 4E) are moderately large relative to the size of the nemerteans and are *c.* 65–70 μm long and 75 μm wide. They open ventrolaterally from the anterior pair of oblique cephalic furrows, a short distance in front of the brain, via thick-walled ciliated canals 20–25 μm in diameter. The canals lead directly inwards, meet the anterior ganglionic components of the cerebral organs and then turn posteriorly for a short distance before terminating. Glandular components of the organs, predominantly acidophilic in nature, comprise a distinct posterior cap but extend a short distance along the inner lateral margins of the ganglionic tissues. The cerebral organs are located entirely behind the pre-cerebral septum and reach posteriorly below the ventral cerebral commissure to the end of the oesophageal region.

Reproductive system

Specimens of *Tetrastemma fozensis* sp. nov. collected during January 1990 all proved to be sexually immature, whereas 10 of the 13 individuals sectioned from the July 1989 collection contained developing ovaries; no males have been found.

The ovaries extend from the stomach region backwards, lying dorsolaterally between the diverticula of the intestine and its caecum. Each ovary typically contains a single oocyte, 100–130 μm in diameter, in which the nucleus is 35–55 μm across. In longitudinal sections stalk-like connections between the ova and the ovarian walls (Fig. 4F), similar to those described for *Pheroneonemertes*

(Gibson, 1991), can be distinguished. None of the individuals examined possessed evidence of gonoducts.

Habitat

Tetrastemma fozensis sp. nov. lives in the mantle cavity of the bivalve mollusc, *Scrobicularia plana*. Of 61 *Scrobicularia* examined during January 1990, 44 specimens (72%) yielded a total of 102 nemerteans, with up to six worms occurring in any one host (Table 3). Multiple infestations occurred in 44% of the molluscs examined, but there is no evidence to suggest that either the overall infection incidence nor the number of multiple infestations increases with the size of the bivalves. This contrasts markedly with the situation occurring in instances of *Malacobdella grossa* (Müller) infesting the bivalve *Zirfaea* (Gibson, 1967), in which there is a definite correlation between host size and number of nemerteans.

The sediment from which the *Scrobicularia* were obtained contained both a high silt-clay fraction (about 60%) and significant levels of organic matter. Salinity levels in the region rarely fall below 24‰ (Junoy, 1988). The benthic community of the inner part of Ría de Foz is characterized by a complex of estuarine species, corresponding to the "*Cardium edule*—*Scrobicularia* variety" of the "*Macoma balthica* community" as defined by Thorson (1957). In addition to *Scrobicularia*, dominant species of this assemblage in the Ría de Foz are the gastropod mollusc *Peringia* (= *Hydrobia*) *ulvae* (Pennant), the bivalve *Cerastoderma edule* (L.), the polychaetes *Capitella capitata* (Fabricius), *Heteromastus filiformis* (Claparède), *Pygospio elegans* Claparède, *Spio* cf. *martinensis* Mesnil and *Streblospio benedicti* Webster, and unidentified oligochaete species. Other common, though not dominant, fauna include the polychaetes *Eteone* cf. *longa* (Fabricius) and *Hediste* (= *Nereis*) *diversicolor* (Müller), and the decapod crustacean *Carcinus maenas* (L.) (Junoy, 1988).

Other bivalve species from the same area (*Cerastoderma edule* and *Venerupis decussata* [L.]) were also examined but none contained nemerteans.

TABLE 3. The incidence of *Tetrastemma fozensis* sp. nov. in 61 specimens of *Scrobicularia plana* collected from the Ría de Foz, north-western Spain, during January 1990

Number of nemerteans per host	Number of hosts	<i>Scrobicularia plana</i>			
		%	Valve length range in mm	Average	
0	17	27.8	30–39	35.06	
1	17	27.8	32–39	35.29	
2	9	14.8	27–37	34.00	
3	10	16.4	31–40	35.22*	
4	4	6.6	34–38	35.75	
5	3	4.9	31–36	33.67	
6	1	1.6	33	33	
	61	99.9			

*One *Scrobicularia* with three nemerteans in its mantle cavity had broken shells and is not included.

Systematic discussion

The single central stylet of the proboscis and bilayered rhynchocoel wall musculature identify the Ría de Foz nemerteans as members of the enoplan order Distromatorhynchocoela, suborder Monostiliferoidea, as defined by Gibson (1988) to contain six families (Amphiporidae, Carcinonemertidae, Emplectonematidae, Ototyphlonemertidae, Prosorhochmidae and Tetrastemmidae). Seven terrestrial and freshwater genera (Moore & Gibson, 1981, 1985), previously included in the Prosorhochmidae, have recently been transferred to the urichorhynchocoel family Plectonemertidae (Moore & Gibson, 1988); the Monostiliferoidea thus at present comprises 66 genera (see Sánchez & Cancino, 1980; Gibson, 1982a, 1986a, b, 1989, 1990, 1991; Norenburg, 1986; Riser, 1988; Sánchez & Moretto, 1988; Gibson, Wickham & Kuris, 1990).

Several anatomical features have been used to distinguish between these genera (e.g. see Friedrich, 1955; Gibson, 1982a, b), but differences of major systematic significance are evident in the organization of the body wall musculature, pre-cerebral septum, gut, proboscis apparatus, blood and nervous systems, and cerebral sensory organs. The present nemerteans have body wall muscles in which there is no diagonal layer and the longitudinal layer is not anteriorly divided, a dissolved pre-cerebral septum, a stomach with no caecal pouches, no well-developed circular muscle layer around the axial portion of the intestine, an intestinal caecum bearing both anterior pouches and lateral diverticula, a long rhynchocoel housing a slender proboscis in which the anterior portion contains three muscle layers, a simple blood system, a nervous system with neither neurochord cells nor accessory lateral nerves, and moderately large cerebral sensory organs located immediately in front of and extending below the brain. On the basis of these characters the nemerteans can be excluded from all the known monostiliferoidean genera except *Amphiporus* and *Tetrastemma*.

Neither of these two genera, both of which contain large numbers of species and share many features in common, can at present be adequately defined (Gibson, 1988) and, as Norenburg (1986; 290) commented, “[they] include many inadequately described species on the basis of a few characters”. Gibson & Crandall (1989) pointed out that because the type species of *Amphiporus*, *A. albicans* Ehrenberg, must be declared a *nomen dubium*, the status of the genus itself is uncertain. Friedrich (1955) distinguished between *Amphiporus* and *Tetrastemma* only at the penultimate couplet in his key, defining *Tetrastemma* as small slender forms, generally with four eyes, in which the lateral intestinal diverticula are shallow and typically not branched, whereas *Amphiporus* characteristically comprises larger stout nemerteans, normally with numerous eyes and deep, branched lateral intestinal diverticula. The present nemerteans, with four eyes and unbranched intestinal diverticula, are thus placed in the genus *Tetrastemma*.

Twelve species of *Tetrastemma* have been described which have a pale general body colour but are marked with a dark patch of pigment on the dorsal surface of the head. Six of these, *T. coronatum* (Quatrefages), *T. diadema* Hubrecht, *T. longissimum* Bürger, *T. melanocephalum* (Johnston), *T. nibatatum* Bürger and *T. peltatum* Bürger, have been recorded from European waters. For most of these taxa there are few data on their internal morphology and their separation has principally been achieved on the basis of variations in the shape of the cephalic pigment patch and the general colouration.

Kirsteuer (1963), in a study of the systematics and anatomy of 13 species of Adriatic tetrastemmids, including five of the taxa listed above, concluded that their specific separation could be justified by differences in their internal morphology. *Tetrastemma nimbatum* he subsequently also referred to (Kirsteuer, 1965) as a valid taxon. Amongst the features described, Kirsteuer distinguished between taxa in which the anterior region of the proboscis contained only two muscle layers in its wall (including *T. diadema*, *T. longissimum*, *T. melanocephalum* and *T. peltatum*) and those which, like the Ría de Foz nemerteans, have three layers (including *T. coronatum*). Other anatomical features used by Kirsteuer (1963) to distinguish between the various species included the origin of the mid-dorsal blood vessel and whether or not it formed a vascular plug connection with the rhynchocoel, whether the lateral nerve cords emerged from the brain directly or in an arched fashion, and whether the junction between stomach and pyloric

TABLE 4. Comparison between certain anatomical features of five species of European *Tetrastemma* possessing a dorsal cephalic colour pattern and the nemerteans obtained from the mantle cavity of *Scrobicularia plana* in Ría de Foz, north-western Spain, and Poole Harbour, southern England; data from Kirsteuer (1963) and the present studies

	<i>T. coronatum</i>	<i>T. diadema</i>	<i>T. longissimum</i>	<i>T. melanocephalum</i>	<i>T. peltatum</i>	Ría de Foz and Poole Harbour nemerteans
Number of muscle layers in wall of anterior portion of proboscis	3	2	2	2	2	3
Mid-dorsal blood vessel arising from post-cerebral loop (P) or from left (L) or right (R) lateral vessel	L	P	L	L	P	L/R
Mid-dorsal blood vessel with (+) or without (0) vascular plug	+	+	+	+	0	+
Lateral nerve cords arch laterally before continuing posteriorly (0) or lead directly back from brain (+)	0	+	0	0	+	+
Stomach-pylorus junction with (+) or without (0) caecal pouches	+	+	0	0	0	0

portions of the foregut was simple or complex. A summary of these features in the Adriatic species named above and the Ría de Foz nemerteans is provided in Table 4, and shows that the present form differs from all of these taxa. The remaining species for comparison, *T. nimbatum*, was established by Bürger (1895) purely on the basis of its external features and there are no data on its internal anatomy. The general body shape, however, is much stockier than that of the Ría de Foz nemerteans (Bürger likened it to *Amphiporus* [= *Nipponeustes*] *pulcher* [Johnston]) and its colour pattern consists of a broad black band reaching between the anterior pair of eyes, with a small blackish pigment streak running longitudinally between the front and rear eyes on either side of the head. It is concluded that the nemerteans from *Scrobicularia* in the Ría de Foz cannot be identified as conspecific with any of the known *Tetrastemma* species which possess a dorsal cephalic colour pattern, all of which are only known as free-living taxa, and the present species is thus placed in a new taxon, *Tetrastemma fozensis*.

The Poole Harbour nemerteans

Six specimens of nemerteans found living in the mantle cavity of *Scrobicularia plana* collected in Poole Harbour, on the south coast of England, during January 1990 by Dr William J. Langston, Dr Susan Spence and Mr Gary Burt, of the Plymouth Marine Laboratory, have been examined and compared with *Tetrastemma fozensis* sp. nov.

The Poole Harbour nemerteans are larger than those from Ría de Foz, with lengths of 9–20 mm and widths of 0.6–1.0 mm. Their appearance and behaviour in life is also somewhat different; in particular, the head of the Poole Harbour species is distinctly diamond-shaped and obvious, and strong waves of muscular contraction pass along the body when the worms are mechanically irritated. The cephalic pigment patch also differs slightly from that of *T. fozensis* sp. nov. in barely overlapping the anterior pair of eyes, in being rather triangular in shape with the apex pointing forwards, and in lacking the ventrolateral extensions which occur in many of the Ría de Foz specimens. In contrast to the general body colour of *T. fozensis* sp. nov., the Poole Harbour nemerteans are also a distinct pale yellowish-green hue.

A comparison between the internal morphology of the nemerteans from the two locations shows that they are in many ways very similar, especially with respect to the features listed in Table 4. Minor differences, however, can be distinguished: in the Poole Harbour specimens the cephalic glands are not as well developed as in *T. fozensis* sp. nov. and do not posteriorly extend to the brain, the pre-cerebral septum much more closely resembles the closed type, as defined by Corrêa (1955), and the thickness of the epidermis and body wall muscle layers, size of the eyes, and dimensions of the stylet armature are all larger than in the Spanish worms.

The external features of the Poole Harbour nemerteans closely correspond to those of *Tetrastemma melanocephalum* (see Gibson, 1982b), except that the cephalic pigment patch is not the quadrangular shape typical of this species; *T. melanocephalum* has a wide zoogeographic range extending from the British Isles to Scandinavia, Madeira, the Canary Islands, the Mediterranean and the coasts of the Black Sea (Gibson, 1982b) and has been recorded from northern Spain (Anadón, 1981). This species has been found in a variety of habitats but has never been recorded from the mantle cavity of bivalve molluscs. However, in their internal anatomy the Poole Harbour nemerteans differ significantly from *T. melanocephalum* in possessing an anterior proboscis wall containing three muscle layers rather than two, and in the lateral nerve cords leading directly back from the brain rather than first arching laterally (Kirsteuer, 1963; Table 4). The organization of the proboscis muscle layers, stomach-pylorus junction and lateral nerve cord origin also enable the Poole Harbour nemerteans to be distinguished from the remaining European tetrastemmids which have a cephalic pigment pattern (Table 4).

It is concluded that the morphology of the Poole Harbour specimens most closely agrees with that described for *T. fozensis* sp. nov.; such differences as are apparent between the Spanish and English nemerteans either may be a consequence of the larger size of the Poole Harbour examples or possess a taxonomic significance which cannot, with our present knowledge of intraspecific variation in nemerteans, be assessed. Accordingly, the Poole

Harbour nemerteans are provisionally identified as examples of *T. fozensis* sp. nov.

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ABBREVIATIONS USED IN THE FIGURES

AP	anterior pouch of intestinal caecum	LN	lateral nerve cord
AS	anterior portion of stomach	LV	lateral blood vessel
CO	cerebral sensory organ	PE	proboscis epithelium
DG	dorsal ganglionic lobe	PR	proboscis
EN	egg nucleus	PS	posterior portion of stomach
EP	epidermis	PY	pyloric region of foregut
IC	intestinal caecum	RC	rhynchocoel
IN	intestine	ST	stomach
LM	body wall longitudinal muscle layer	VG	ventral ganglionic lobe
		YO	egg yolk