On four monostiliferous hoplonemerteans, including three new genera and species from Washington state and British Columbia

FUMIO IWATA

Zoological Institute, Faculty of Science, Hokkaido University, Sapporo 060-0810, Japan, and Friday Harbor Laboratories, University of Washington, Friday Harbor, Washington 98250, USA

(Accepted 31 December 2005)

Abstract

Frontonemertes serpentina, Satellitenemertes satellitensis and Sanjuannemertes willowsi new genera and species are described as three members of the order Hoplonemertea, suborder Monostilifera. In general morphology, F. serpentina is most similar to Nemertes rubrolineata in having the two layers of the body wall longitudinal musculature, no pre-cerebral septum and retractor muscles originating in the outer longitudinal muscle layer in the cephalic region {Chernyshev (1992) proposed a new genus, Tetranemertes, for Nemertes [type species, N. antonina Quatrefages, 1846]}. Satellitenemertes satellitensis appears to be most closely related to members of the genus Amphiporus. Sanjuannemertes willowsi has a common atrium for the proboscis pore and mouth, as in some polystiliferous hoplonemerteans. The original description of Nipponnemertes bimaculata (Coe 1901) is supplemented on the basis of re-observation of its features. The significant characters are explained and discussed.

Keywords: Monostiliferous hoplonemerteans, Frontonemertes serpentina, Satellitenemertes satellitensis, Sanjuannemertes willowsi, Nipponnemertes bimaculata

Introduction

Of monostiliferous hoplonemerteans collected in the San Juan Archipelago, Washington and on the east side of Vancouver Island, British Columbia in 1964, are here described as three new genera and species. These nemerteans possess characters that separate them from any of the previously described genera and species belonging to the order Hoplonemertea and the suborder Monostilifera. New information concerning Nipponnemertes bimaculata, described by Coe (1901) as Amphiporus bimaculatus, is also presented.
Materials and methods

All specimens were collected by dredging and fixed in Bouin’s solution. They were sectioned at 8 µm and stained with Delafield’s hematoxylin and eosin. A Sony video camera with Symphonic monitor television and Sony or Hitachi color video printers, in addition to Olympus BH-2 and FH microscopes, were used for observation of the material. The specimens are deposited in the US National Museum of Natural History.

Taxonomy

Genus Frontonemertes gen. nov.

Type species

Frontonemertes serpentina gen., sp. nov.

Etymology

The generic name is a composite of the Latin prefix fronto (forehead) name nemertes, and refers to the well-developed apical organ of the specimen. The species name alludes to the snake-like form of the worm.

Diagnosis

Monostiliferous marine hoplonemerteans with non-threadlike appearance; with color pattern; cephalic grooves weakly developed on ventral surface of body; ocelli numerous, forming four groups; rhynchocoe, confined to anterior one-third of body length, with wall of two muscle layers; body wall musculature with very sparse lattice-type diagonal layer, longitudinal muscle layer anteriorly divided in parenchyma, its inner portion surrounding brain lobes and rhynchodeum wall, its outer portion reaching together with circular muscle layer into tip of head; cephalic retractor muscles from outer portion of longitudinal musculature well developed; parenchyma well developed; pre-cerebral septum lacking; proboscis insertion formed by fibres from inner portion of longitudinal musculature and by rhynchodeum wall turning internally; rhynchodeum provided with a longitudinal muscle coat derived from inner portion of longitudinal musculature and a weakly-developed sphincter of circular muscles; proboscis armature consisting of a single central stylet and three accessory stylet pouches; stylet bulb without plate-like connective tissue or thick layer of glandular cells; foregut divisible into oesophagus, stomach, pylorus, intestine and hindgut; oesophagus opening into rhynchodeum near anterior end of head; stomach without a small diverticula or caecal folds; intestinal caecum present, without anterior diverticula but with lateral diverticula; main intestinal canal without deep lateral diverticula; blood vascular system with three longitudinal vessels, with simple vascular loop in head, mid-dorsal vessel with single vascular plug; nervous system with neither neurochord cells nor inner neurilemma; lateral nerve cords with one fibrous core with peripheral nerves well developed and without accessory lateral nerves and myofibrillae; single apical organ, frontal glands and cephalic glands present in anterior cephalic region, sub-muscular glands small and few in number; cerebral sensory organ small and anterior to brain; excretory system present, weakly developed in foregut region; sexes separate.
Type species

*Frontonemertes serpentina*

Body whitish with two lateral orange bands; ventral surface of head with slender cephalic groove and two cephalic V-shaped grooves; dermis thin; anterior chamber of proboscis with two muscle layers (outer circular and inner longitudinal); proboscis with 12 nerves; brain with fibrous connective tissue and without large ganglion cells; mid-dorsal nerve not extending anteriorly beyond the brain; dorsal ganglia not distinctly separated from the ventral ganglia except posteriorly; dorsal ganglia without bifurcated fibre core; paired foregut and rynchodeum nerves originating from the ventral brain; cerebral sensory organ with fibrous connective tissue; cerebral organ canal, located at anterior end of the cerebral sensory organ; without U-shaped ciliated sensory portion, opening at ventrolateral side of anterior cephalic groove of head; excretory pores ventral to nerve cords and situated in posterior portion of the nephridial region.

*Frontonemertes serpentina* gen., sp. nov.

Type specimen

Holotype: USNM 1072177; 28 slides of stained serial section of one specimen, including transverse sections of the anterior portion of the body (17) and midgut (11). Paratype: USNM 1072178; 17 slides of stained serial section of head region (8) and tail (9). Three pieces of the holotype and long piece of the paratype were not sectioned.

Type locality

Satellite Channel, Vancouver Island, British Columbia, Canada (Lat. 48°41.9’ N, Long. 123°28’ W), depth 15–22 fathoms, September 9, 1964.

Description

External features

Holotype 13 cm long and 2 mm wide when moving, narrowing gradually towards posterior end (Figure 1.1). Body, however, can stretch to 30 cm and width of 3 mm in foregut region. Paratype 17 cm long and 2 mm wide.

Body soft, contractile, and semitransparent, becoming very slender in the posterior portion when elongated. The animal could attach itself to glass and could raise its anterior portion like a snake’s head. Many folds extended transversely across the dorsal surface. The color was whitish, with two wide lateral orange bands. Along the midline, between the orange bands, there was a slender whitish line. The head, not demarcated from the rest of the body by a constriction, had a pair of orange bars on the dorsal surface (Figure 2a, c, d–f). On the ventral surface, a slender cephalic groove ran transversely across the anterior portion of the head (Figure 2b, c). Two cephalic grooves situated farther posteriorly (Figure 2b, c) a nearly V-shaped configuration, but the grooves did not quite meet.

There were four groups of ocelli. The number of ocelli in each anterior group was about 30 and in each posterior group there were about 10. The ocelli in the anterior group could be seen from the dorsal- and ventral side of the head (Figure 2b). The brain, reddish in color, was observed in the space between the orange-coloured bars on the head and the
Figure 1. (1) Dorsal view, sketch of living holotype specimen of *Frontonemertes serpentina*, new genus and species; (2) dorsal view, sketch of living holotype specimen of *Satellitenemertes satellitensis*, new genus and species; (3) dorsal view, sketch of living specimen of *Nipponnemertes bimaculata* (Coe) from Satellite Channel; (4) dorsal view, sketch of living holotype specimen of *Sanjuaninemertes willowsi*, new genus and species.
anterior ends of the wide orange lateral bands (Figure 2a). At the anterior tip of the head there were two small pores; one was the proboscis pore, the other was the opening of the apical organ (Figure 2b). When the head was raised (Figure 2d–f), the proboscis pore and the opening of the apical organ, the two orange bars, the ocelli and the anterior ends of the two orange bands were visible. The raising of the head seems to be effected by numerous bundles of retractor muscles (Figure 3g, h).

Body wall, musculature, and parenchyma

The epidermis is of uniform thickness both in the cephalic region (average 70 µm) and in the midgut region (average 50 µm) (Figure 3a). Large unicellular glands are distributed
Figure 3. *Frontonemertes serpentina*, new genus and species, holotype. (a) Transverse sections between 22 and 194 from anterior end of body, showing body wall and mid-dorsal nerve; (b) mid-ventral furrow and a pair of lateral grooves, frontal glands and cephalic glands; (c) anterior dorsal wall of proboscis pore, frontal glands and cephalic glands enlarged from (b); (d) mid-ventral furrow and pair of lateral grooves, rhynchodeum and frontal glands; (e) opening of oesophagus into rhynchodeum and circular musculature surrounding rhynchodeum; (f) rhynchodeum near anterior end of the head, with row of longitudinal muscles surrounding it; (g) rhynchodeal wall and its longitudinal muscular coat derived from inner longitudinal muscle layer; (h) proboscis insertion developing from the posterior end of the rhynchodeal wall, inner longitudinal muscle of rhynchodeal wall derived from the body wall longitudinal muscle layer, retractor muscles, cephalic blood vessel extending toward rhynchodeal wall and oesophagus. Scale 100μm (a, c, e–h), and 200μm (b, d). Abbreviations: bc, body wall circular muscle layer; bl, body wall longitudinal muscle layer; cb, cephalic blood vessel; cg, cephalic glands; cm, circular muscles of rhynchodeum; df, dorso-lateral deep furrow; dp, dorsal wall of proboscis pore; dr, dermis; es, oesophagus; fg, frontal glands; hr, head retractor muscles; ic, inner, cytoplasmic portion of rhynchodeal epithelium; lf, longitudinal muscle fibres of rhynchodeum; lm, inner longitudinal muscle coat of rhynchodeum; lp, longitudinal muscle layer of proboscis; mc, muscular coat of longitudinal muscle fibres of rhynchodeum; md, middorsal nerve; mf, median dorso-ventral furrow; oc, ocellus; oe, opening of oesophagus into rhynchodeum; ol, body wall outer longitudinal muscle layer; on, outer, nucleated portion of rhynchodeal epithelium; rd, rhynchodeum; rn, rhynchodeum nerve; wr, wall of rhynchodeum.
over the entire body and are especially well developed in the midgut region. Small columnar cyanophilic glands are embedded between the large glands.

In the anterior half of the head, between its tip and the brain, a median dorsoventral furrow, measuring 70 μm wide at the bottom, 200 μm deep and 400 μm long can be seen in transverse section on the ventral side of the head (Figure 3b, c). On the dorsal side of the head, the epidermis sinks inward in the dorsolateral portions and forms a pair of deep furrows; these become shallower posteriorly and disappear behind the brain (Figure 3b, d). The dermis, 5–20 μm thick, is one-third to one-fifth as thick as the epidermis (Figure 3a). It has transverse fibrils and contains no cellular bodies or small nerves. Sub-epithelial glands found in the members of Paranemertes are lacking.

The body wall musculature consists of a very thin outer circular coat, 20 μm thick in the brain region and an inner longitudinal layer 70 μm wide (Figure 3a). There is a very sparse lattice-type diagonal muscle layer and dorsoventral muscles are absent. Parenchyma is extremely well-developed in the holotype and especially in the paratype.

**Rhynchodeum, rhynchocoel and proboscis**

The proboscis pore, 130 μm long and 100 μm wide, opens on the dorsal side of the deep cephalic furrow (Figure 3b, c). Its wall is 20 μm thick and has crowded long cilia but no glands. The rhynchodeum behind the proboscis pore is flattened dorsoventrally and protrudes dorsally owing to the cephalic furrow (Figure 3d). Behind the level at which the oesophagus opens into it, the rhynchodeum is covered by a weakly-developed sphincter of circular muscles (Figure 3e, f). Above the oesophagus, the rhynchodeum becomes cylindrical for a length of 570 μm. About 500 μm from the opening of oesophagus, a row of longitudinal muscle fibres covers the rhynchodeum (Figure 3f). This muscular coat becomes thicker posteriorly for 70 μm and then its thickness gradually increases to 30 μm at the posterior end of the rhynchodeum (Figure 3g). The rhynchodeum wall, 30 μm thick, consists of a row of columnar cells with dense cilia in anterior portion (Figure 3e–g). At its posterior end, where the proboscis insertion occurs (Figure 3h), it becomes somewhat laminated into outer nucleated and inner cytoplasmic portions. The longitudinal muscle coat is derived from the inner portion of the body wall longitudinal layer.

Close behind the brain, the body wall longitudinal muscle is divided into inner and outer portions, separated by parenchyma (Figure 4a), instead of forming a single layer. The outer layer continues into the tip of the head without contributing to the proboscis insertion; a pre-cerebral septum is lacking. The inner layer consists of both large and small bundles, with surrounding membrane, and anteriorly it forms a closed cylinder covering the brain (Figure 4b–e). The muscle fibres run transversely, covering the anterior end of the cerebral ganglia; together with the rhynchodeal wall, they contribute to the proboscis insertion (Figures 3h and 4e).

At the proboscis insertion, the rhynchodeal wall and inner longitudinal fibres are transformed into the layers of the proboscis: proboscis epithelium, circular and longitudinal muscle layers containing 12 proboscis nerves, rhynchocoel and proboscis sheath consisting of longitudinal and circular muscle layers (Figures 3g, h and 4d, e). The transformation occurs in front of the brain and 120 μm in length.

The head retractor muscles, forming a number of bundles with surrounding membranes, are derived from the outer portion of the longitudinal muscle layer of the body wall (Figure 3f–h).
Figure 4. *Frontonemertes serpentina*, new genus and species, holotype. (a) Transverse sections between 115 and 552 from anterior end of body, showing indistinct inner longitudinal fibres separated from the longitudinal muscle layer of the body wall in parenchyma above the brain lobes and circular muscle layer around rhynchocoel; (b) dorsal and ventral fibre cores of brain, nerve of cerebral sensory organ from right dorsal brain lobe and inner longitudinal muscle fibres surrounding brain; (c) brain with dorsal and ventral commissures at same transverse level and inner longitudinal muscle coat surrounding brain; (d) a pair of trunks of proboscis nerve from the ventral commissure of brain, a pair of cephalic blood vessels, and proboscis sheath and proboscis; (e) proboscis insertion in front of brain lobes and cephalic blood vessels inside brain ring; (f) central stylet on its basis; (g) accessory stylets in accessory stylet pouch; (h) stylet bulb surrounded thick circular muscle layer, pylorus, and intestinal caecum with lateral diverticula. Scale 50 μm (f, g), 100 μm (a, d, e), and 200 μm (b, c, h). Abbreviations: as, accessory stylet; bp, beginning of nerve to cerebral sensory organ; cb, cephalic blood vessel; cp, circular muscle layer of proboscis sheath; cs, central stylet; cu, intestinal caecum; dc, dorsal commissure of brain; dg, dorsal ganglion; ep, epithelium of proboscis; es, oesophagus; il, inner longitudinal muscular bundles; im, inner longitudinal muscular coat covering brain lobes; ld, lateral diverticula of intestinal caecum; lm, inner longitudinal muscle coat of rhynchodeum; ln, lateral nerve; lp, longitudinal muscle layer of proboscis; ol, body wall outer longitudinal muscle layer; pa, pouch of accessory stylets; pn, proboscis nerve; pr, proboscis; pt, proboscis nerve trunk; rc, rhynchocoel; rn, rhynchodeum nerve; sb, stylet bulb; vc, ventral commissure of brain; vg, ventral ganglion.
The rhynchocoel is short, being less than one-third the body length. The proboscis apparatus is found in the pyloric region and is about 1 mm long (Figure 4h). In its anterior portion, the proboscis is provided with outer circular and inner longitudinal muscle layers, but posteriorly the outer circular layer is not recognizable. Proboscis armature consists of a single central stylet and three accessory stylet pouches. The basis of the central stylet is conical in form and surrounded by thick radial muscles. The central stylet is 30 μm long (Figure 4f). There are three accessory stylet pouches, two arranged as a pair and the other situated posterior to the pair. There are three, four and five accessory stylets. Each has a posterior cyanophilic protrusion and an umbrella-like edge at its posterior end (Figure 4g). The ductus ejaculatorius is joined to the stylet bulb by a narrow canal. The stylet bulb is surrounded by a thick circular muscle layer (Figure 4h).

**Alimentary canal**

The alimentary canal has five major divisions: oesophagus, stomach, pylorus, midgut (with anteriorly directed caecum and lateral diverticula) and hindgut. The oesophagus opens into the rhynchodeum (Figure 3e) 220 μm behind the proboscis pore. The oesophagus and stomach lack a longitudinal and circular musculature.

The oesophagus, compressed between the rhynchodeum and the longitudinal muscle layer of the body wall, is flattened dorsoventrally (Figure 3h). It extends far posterior to the brain (Figure 5b, c); the distance between the oesophageal–rhynchodeal junction and the posterior end of the brain is about 0.9 mm and that between the end of the brain and posterior end of the oesophagus is 320 μm. The transition of the oesophagus into the stomach is long, about 420 μm (Figure 5c). In this area, the oesophagus becomes about three times as wide as the oesophageal–rhynchodeal junction.

The stomach, 420 μm long, and has more than 10 folds in transverse section (Figure 5d). Measured from the antero-posterior limits of the gastric length, the stomach is about two and a half times as long as the brain.

The pylorus, which succeeds the stomach, is about 1.7 mm long and about four times as long as the stomach. It is wide and flattened dorsoventrally in transverse sections, being 1.4 mm wide at its junction with the stomach. At the point where it opens into the midgut, it narrows to 0.2 mm (Figure 5e). The ciliated epithelium of the pylorus contains cyanophilic glands similar to those of the stomach (Figure 4h).

The intestinal caecum lacks anterior tubular branches and its anterior end is situated 2 mm from the posterior end of the brain. The caecum has five pairs of lateral diverticula. The intestine is flattened dorsoventrally has only short lateral diverticula.

In the series of sections of the holotype, the posterior end of the body was missing. In the paratype, there is a long and deep furrow, measuring 240 μm long and 130 μm deep on the ventral side of the body. The anus and rectum were not observed.

**Blood vascular system**

The blood vascular system has three longitudinal vessels. The two cephalic blood vessels lateral to the rhynchodeum anastomose above the rhynchodeum near the tip of the head to form the cephalic loop, 100 μm wide, 20 μm high and 30 μm in length. Farther posteriorly, however, the cephalic vessels turn medially in front of the proboscis insertion (Figure 3h). At the level of the anterior end of the brain, they enter the brain ring without giving off cerebral vessels, and then run posteriorly alongside the ventro-lateral portions of the
Figure 5. *Frontonemertes serpentina*, new genus and species, holotype. (a) Transverse sections between 11 and 839 from anterior end of body, showing dorsal blood vessel branched from right cephalic vessel and two nerves derived from right brain lobes; (b) single median vascular plug with a communication to rhynchocoel, a pair of foregut nerves and oesophagus; (c) dorsal blood vessel, transitional wall of stomach in oesophagus and body wall longitudinal muscle layer with muscular bundles for inner longitudinal fibres in cephalic region; (d) stomach with 10 folds and anterior portion of proboscis in rhynchocoel; (e) opening of pylorus into intestine; (f) peripheral nerve of lateral nerve cord in stomach region; (g) ocellus composed of outer cellular portion and central cytoplasmic area, and a nerve from its anterior end; (h) pore of apical organ, its minute glands and cephalic glands. Scale 50 µm (g), 100 µm (a–c, e, f, h) and 200 µm (d). Abbreviations: cg, cephalic glands; cp, circular muscle layer of proboscis sheath; db, dorsal blood vessel; dg, dorsal ganglion; dv, dorsal blood vessel separated from right cephalic blood vessel; es, oesophagus; fd, fold of stomach; fn, foregut nerve; ga, glands of apical organ; hr, head retractor muscle; il, inner longitudinal muscular bundles; in, intestine; lb, lateral blood vessel; ln, lateral nerve; lv, left cephalic blood vessel; mf, median dorso-ventral furrow; nb, nerves originated from brain; oc, ocellus; op, opening of pylorus; pa, pore of apical organ; ph, peripheral nerve; pr, proboscis; rc, rhynchocoel; rv, right cephalic blood vessel; st, stomach; ts, transitional wall of stomach in oesophagus; vg, ventral ganglion; vp, vascular plug inside proboscis sheath.
rhynchocoel (Figure 4d, e). Near the posterior end of the brain, the right vessel communicates with the dorsal vessel, which then enters the proboscis sheath behind the brain as a single median vascular plug. This plug, about 200 \( \mu \)m long, extends medioventrally in the sheath as far as the posterior end of the oesophagus (Figure 5a, b). This portion of the vascular plug seems to form a specialized communication with the rhynchocoel (Figure 5b). The dorsal vessel then continues posteriorly under the proboscis sheath between the rhynchocoel and the alimentary canal (Figure 5c). The three post-cerebral vessels are not transversely linked by pseudometameric transverse connectives.

Behind the brain, the lateral vessels enter the nephridial region, which extends from the level far posterior of the brain to that of the transitional area of the oesophagus into the stomach. The lateral vessels are situated inside the lateral nerves and exhibit no branches that contact the nephridia. There are no transverse anastomoses of the lateral vessels in the intestinal region.

In the paratype, which lacks the cephalic region of the body, the dorsal and lateral vessels anastomose at about 3 mm anterior to the posterior end of the body.

**Nervous system**

The cerebral ganglia are large and have neither neurochord cells nor an inner neurilemma. The ventral ganglia are not distinctly separated from the dorsal ganglia except posteriorly (Figure 5a). They become completely separated for a distance of 30 \( \mu \)m.

The dorsal and ventral fibre cores are not divided anterior to the middle portion of the brain; the dorsal cores are more voluminous than the ventral cores (Figure 4b). Behind the posterior end of the dorsal ganglia, the ventral ganglia soon extend laterally, forming the lateral nerve cords (Figures 4b and 5a, b). Posteriorly, the dorsal ganglia do not branch into dorsal and ventral lobes.

The right and left ganglia are connected by a short, thin dorsal commissure, 40 \( \mu \)m thick, and a short, much thicker ventral commissure, 90 \( \mu \)m thick, at about the same transverse level (Figure 4c).

The lateral nerve cords, situated ventrolaterally, lie in the parenchyma above the longitudinal musculature of the body wall. They give off dorsal or dorsoventral peripheral nerves that extend toward the dorsal and ventral sides of the body (Figure 5f).

Several slender but conspicuous nerves originate from the brain. They branch out pre- and post-cerebrally to supply various structures. A proboscis nerve trunk arises from the dorsal surface of the brain at the root of the ventral commissure and extends dorsally into the proboscis sheath where the proboscis is inserted (Figure 4d). Both trunks of the proboscis nerves soon branch into 12 nerves that lie in the proboscis sheath (Figure 4e). A small nerve, 320 \( \mu \)m long, extends from the lateral side of each dorsal ganglion to the posterior end of each cerebral sensory organ (Figure 4b). The rhynchodeum nerves emanate from the ventral surface of the ventral commissure and extend anteriorly along the dorsal side of the oesophagus (Figures 3h and 4d). The foregut nerves, which are paired, originate internally from the posterior ends of the ventral ganglia and run posteriorly in the parenchyma above the oesophagus (Figure 5a, b). A conspicuous nerve originates from the lateral surface of each dorsal and ventral ganglion (Figure 5a). The mid-dorsal nerve lies in the dermis just above the circular muscle layer of the body wall (Figure 3a).

The lateral nerve cords have one fibrous core which lacks myofibrillae and accessory nerves. The commissure on the dorsal side of the rectum was not observed in the paratype specimen.
Special sensory organs and apical organ

The ocelli are distributed in four groups and 68 could be counted in transverse sections. They are large and confined to an area, 550 µm long, between the anterior end of the rhynchodeum and the posterior end of the cerebral sensory organs, which are far anterior to the brain. There are 35 ocelli on the right side of the head and 33 on the left. Two groups are recognizable on each side; 26 and nine on the right side and 23 and 10 on the left. The ocelli are of the inverted pigment-cup type and have dimensions of up to 50 µm wide and 60 µm height (Figure 5g).

The apical organ consists of a pore and cluster of minute glands in the mid-dorsal portion of the worm, above the anterior end of the proboscis pore (Figures 5h and 6a).

The mass of frontal glands, in the dorsal side of the head, extends posteriorly for a distance of 320 µm; the posterior end of the mass is separated by a distance of about 400 µm from the cerebral sensory organs (Figure 3b–d). The opening of the frontal gland mass is found at the anterior tip of the mid-dorsal furrow of the head below the minute glands forming the apical organ (Figure 6a).

The cephalic glands, confined to the lateral sides of the head, are separate from the frontal glands (Figures 3b, c and 6a). They occupy an area 260 µm long.

The frontal and cephalic glands end a short distance anterior to the opening of the oesophagus (Figure 3e). The distance between the posterior end of the cephalic glands and the brain is considerable, about 600 µm. Sub-muscular glands are very small and few in number and located only on the ventral side of the head.

The cerebral sensory organs are very small (120 µm) and lie 140 µm in front of the brain. The cerebral organs are nearly circular in transverse section, 65 × 55 µm in their posterior portions (Figure 6b).

The cerebral organ canal is ciliated and measures 50 µm in length. It begins at the ventrolateral side of the anterior oblique cephalic groove of the head and extends posteriorly inside the longitudinal musculature of the body wall (Figure 6c, d). Its epithelium is 10 µm thick. The canal widens just before entering the cerebral organ, but does not have a U-shaped ciliated sensory portion. At the entrance of the cerebral organ, there is a pair of thickenings of the ganglion cells (Figure 6e). The sensory canal (40 × 30 µm in dimension) is situated medially in the cerebral organ (Figure 6b). The canal soon disappears. Its glandular cells form a mass (Figure 6b). A slender nerve, 320 µm long, runs from the lateroventral corner of the dorsal ganglion to the posterior end of the cerebral organ (Figure 4b).

Excretory and reproductive systems

The excretory system is weakly developed in the foregut region. Excretory tubules winding around and along the lateral blood vessels were not observed. The efferent duct is not conspicuous and extends laterally to the lateral nerve cord, reaching the excretory pore on the lateroventral side of the body (Figure 6f). The pore is ventral to the lateral nerve cord and is at the level of the posterior portion of the oesophageal region. An efferent duct on the left side of the body was not found.

Sexes are separate and fully mature eggs are independently arranged between the body wall and the intestine; there are no distinct gonad sacs (Figure 6g, h). No eggs were found in the foregut region.
Figure 6. *Frontonemertes serpentina*, new genus and species, holotype. (a) Transverse sections between 14 and 234 from anterior end of body and 206 from middle portion of body showing minute glands of apical organ, opening of frontal glands and cephalic glands; (b) posterior portion of cerebral sensory organ showing sensory canal, ganglionic mass and eosinophilic glands; (c) opening of cerebral organ canal and cephalic groove; (d) posterior end of cerebral organ canal; (e) anterior portion of cerebral sensory organ with sensory canal and ganglionic masses; (f) right efferent duct and its opening, peripheral nerve of lateral nerve cord and lateral blood vessel in stomach region; (g) intestine and row of eggs; (h) enlargement of egg in (g). Scale 50 μm (b, d, e), 100 μm (a, c, f, h) and 200 μm (g). Abbreviations: bl, body wall longitudinal muscle layer; cg, cephalic glands; cn, cerebral organ canal; cs, cerebral sensory organ; dr, dermis; ed, efferent duct; eo, eosinophilic glandular mass; gc, ganglionic mass; ga, glands of apical organ; hr, head retractor muscles; in, intestine; lb, lateral blood vessel; le, egg enlarged; ln, lateral nerve; mf, median dorso-ventral furrow; ne, nephridia; of, opening of frontal glands; oo, opening of cerebral organ canal; ph, peripheral nerve; rg, right cephalic groove; sa, sensory canal of cerebral sensory organ; st, stomach.
Systematic discussion

Frontonemertes serpentina, here established as a new genus and species, is in the family Emplectonematidae; the body is long and slender, the rhynchocoel does not extend to the middle of the body, the cerebral sensory organs are small and situated in the anterior portion of the head, and the wall of the rhynchocoel consists of two distinct muscle layers. However, the most important characteristics of this new genus are the inner longitudinal muscle layer derived from the outer longitudinal muscle layer; the retractor muscle bundles are also derived from the outer layer. With respect to these characteristics, Nemertes rubrolineata Kirsteuer (1965) is most closely related to this species, but differs in that the inner longitudinal musculature of the former extends inside the wall; whereas in the latter, the rhynchodeal wall has a thick inner longitudinal muscular coat (Kirsteuer 1974). Kirsteuer (1974) wrote that “The closed cylinder of inner longitudinal fibres (loc. cit., Figure 16) forms the proboscis insertion anterior to the brain and also sends fibres into the wall of the rhynchodeaeum where they can be traced to about the junction with the oesophagus (cf. Figure 37)". In the generic diagnosis of this species, he also wrote “body wall musculature without diagonal fibre layer, longitudinal muscle layer divided in anterior region of body, outer portion reaches together with circular muscle layer into tip of head; precerebral septum lacking, proboscis insertion formed by fibres from inner portion of longitudinal musculature; head retractor muscles related to outer portion of longitudinal musculature”.

Kirsteuer (1974) cited 12 features of the genus Nemertes Johnston, 1837. Gibson and Sundberg (2001) used five of these, divided into six characters and an additional character for the comparative study of 18 monostiliferous hoplonemertean genera that have a longitudinal body wall muscle layer that is divided anteriorly. Five characters used by Gibson and Sundberg (2001) were: (1) body wall musculature without diagonal fibre layer, longitudinal muscle layer divided in anterior region of body, outer portion reaches together with circular muscle layer into tip of head; (2) precerebral septum lacking, proboscis insertion formed by fibres from inner portion of longitudinal musculature; (3) head retractor muscles related to outer portion of longitudinal musculature; (4) musculature of proboscis sheath in separate layers, rhynchocoel without diverticula and confined to anterior half of body; and (5) blood vascular system without cephalic lacunae and extra cerebral vessels. They included an additional feature on neurochord cells. However, in some species originally thought to lack a diagonal muscle layer, a very thin lattice of widely spaced fibres has since been demonstrated (Crandall 1993).

Thus, seven features of Kirsteuer’s generic diagnosis were not used: (1) body of threadlike appearance, (2) cerebral organs anterior to the brain, (3) lateral nerve cords with one fibrous core, (4) foregut opening into rhynchodeum, (5) intestinal caecum present, (6) excretory system present, and (7) sexes separate.

As taxonomically significant features in the present nemerteans, 11 features were included: (1) divided body wall longitudinal musculature present, (2) cephalic retractor muscles derived only from the outer longitudinal muscle layer, (3) a short rhynchocoel, (4) pre-cerebral septum lacking, (5) body wall diagonal muscles very sparse and of lattice type, (6) cephalic lacunae or extra-cerebral vessels lacking, (7) neurochord cells lacking, (8) presence of longitudinal musculature in rhynchodeum wall, (9) single vascular plug in middorsal vessel, (10) peripheral nerves arising from lateral nerves, and (11) single apical organ, frontal glands and cephalic glands.

Among 18 genera of monostiliferous hoplonemertean taxa with an anteriorly divided body wall longitudinal muscle layer, Tetranemertes Chernyshev, 1992 (type species Nemertes antonina Quatrefages, 1846) is similar to the species described in this paper in that the
rhynchocoel is confined to anterior one-third of body length; the longitudinal muscle layer is divided; cephalic retractor muscles are derived from the outer portion of the longitudinal musculature; a pre-cerebral septum is lacking; the blood vascular system has simple vascular loop in head; neurochord cells are lacking.

In *Frontonemertes serpentina*, however, the longitudinal fibres form a longitudinal muscle coat running outside the wall of rhynchodeum, but not inside as in the species of *Nemertes*. The other features that were not used by Gibson and Sundberg (2001) were: blood system with a single vascular plug in the mid-dorsal vessel; lateral nerve cords with peripheral nerves well-developed; and an apical organ, frontal glands, and cephalic glands in the anterior region of the head.

The structural features of body cited above were not reported in four members of the genus *Nemertes* (*N. antonina* Quatrefages, 1840, *N. ophiocephala* (Schmada), 1859, *N. rubrolinea* Kirsteuer, 1965, and *N. hermaphroditicus* Gibson, 1982).

The absence of these characters confirms that the present American specimens should not be included in the genus *Nemertes* Johnston, 1837 or *Tetranemertes* Chernyshev, 1992. Owing to this, a new genus is proposed to accommodate it.

Genus *Satellitenemertes* gen. nov.

**Type species**

*Satellitenemertes satellitensis* gen., sp. nov.

**Etymology**

The generic and specific name refers to the place where the collection was made.

**Diagnosis**

Monostiliferous marine hoplonemerteans without cephalic grooves; body wall musculature with very thin and sparse lattice-type diagonal layer, longitudinal muscles not divided anteriorly; foregut opening into rhynchodeum near anterior end of brain and divisible into oesophagus, stomach and pylorus, and intestinal caecum with anterior and lateral diverticula; pre-cerebral septum of closed type, composed of radial bundles of longitudinal muscles; cephalic retractor muscles absent; rhynchodeum with thick circular muscle layer in posterior region; rhynchocoel extending more than half the body length, with wall containing two distinct layers; proboscis armature consisting of a single central stylet and two accessory stylet pouches; stylet bulb with plate-like connective tissue and thick layer of glandular cells; cerebral sensory organs large, reaching below anterior end of brain lobes; cerebral ganglia large, with neither neurochord cells nor inner neurilemma; lateral nerve cords without accessory nerves, myofibrillae, and peripheral nervous system; blood vascular system consisting of a simple vascular loop in head, dorsal vessel with a single vascular plug, and three post-cerebral vessels not transversely linked by pseudometameric connectives; frontal organ present, the frontal glands arranged as paired, well developed ventrolateral masses, and reaching the cerebral ganglia; cephalic glands present; sub-muscular glands absent; dorsoventral muscles and parenchyma absent; excretory system weakly developed and confined to foregut region of body; sexes separated.
Type species

*Satellitenemertes satellitensis*

Body color without pattern; ocelli forming two pairs of groups arranged parallel to the lateral sides of head; dermis thin; 11 proboscis nerves; intestinal diverticula not branched; a pair of excretory pores situated behind brain.

*Satellitenemertes satellitensis* gen., sp. nov.

Type specimen

Holotype: USNM 1072179; 15 slides of stained serial section, including transverse sections of the anterior portion of the body (8) and proboscis (5) and horizontal sections of the proboscis (2). Two short pieces were not sectioned.

Type locality

Satellite Channel, Vancouver Island, British Columbia, Canada (Lat 48°41.9′ N, Long. 123°28′ W), depth 15–22 fathoms, September 9, 1964.

Description

External features

The worm was small and nearly cylindrical, 2 cm long and 0.8 mm wide, and moved slowly (Figure 1.2). The anterior end of the head was rounded when viewed from above (Figure 7a). Neither cephalic grooves nor the proboscis pore were observed. The general color of the body was orange, but the lengthwise ventrolateral ridges of the body wall were more brightly coloured (Figure 7b). There were four groups of ocelli. Each of the two more anterior-most groups consisted of about ten ocelli arranged in a nearly semicircular pattern; behind these were two groups consisting of five or six ocelli. The proboscis sheath was visible through the body wall as a slender duct in the anterior portion of the body (Figure 7a). Two days after the worm was captured, the proboscis was protruded. It was long, stout and reddish orange in color; three portions (anterior and posterior chambers, proboscis diaphragm and stylet bulb) were easily recognized (Figure 7c).

Body wall, musculature and parenchyma

The epidermis of the dorsal side was damaged during fixation (Figure 8a). It contains unicellular elliptical glands sparsely arranged in a row, and there are no cyanophilic glands between them (Figure 8b). The dermis is thin, averaging 7–15 µm in thickness (Figure 8a, b). The body wall musculature is weakly developed and has a thin and sparse layer of lattice-type diagonal muscles between the outer circular and inner longitudinal muscle layers (Figure 8b). The outer circular muscle layer, 10 µm in thickness, is thin, while the inner longitudinal muscle layer is 90 µm thick. The longitudinal muscle layer is not divided anteriorly by connective tissue and cephalic retractor muscles are absent. Dorsoventral muscles and parenchyma are also absent (Figure 8c).
Rhynchodeum, rhynchocoel and proboscis

The pre-cerebral region lacks a short snout or a mid-ventral epidermal furrow. The proboscis pore is a short median ventral groove (30 μm long), 50 μm behind the opening of the frontal organ (Figure 8d, e). The rhynchodeum rises upward behind the transverse anastomoses of the cephalic blood vessels, is bordered by a pair of large frontal glands, and then extends to the dorsal side of these (Figures 8f–h and 9a). It is covered by a thick layer of circular muscles (20–40 μm) and opens ventrally into the oesophagus (Figure 9b, c). The rhynchodeum is provided with a thick epithelium folded internally (Figure 9d). The pre-cerebral septum of the proboscis apparatus is of the closed type, and composed of radial bundles of muscles from the longitudinal muscle layer of the body wall (Figure 9e).
Figure 8. *Satellitenemertes satellitensis*, new genus and species, holotype. (a) Transverse sections between 5 and 299 from anterior end of body, showing body wall and proboscis sheath; (b) body wall in lateral side of body, lateral nerve, nephridia and lateral blood vessel; (c) opening of pylorus and lateral diverticula of intestine; (d) pore of frontal organ; (e) frontal glands and proboscis pore; (f) rhynchodeum; (g) anastomose of cephalic blood vessel; (h) rhynchodeum bordered by frontal glands. Scale 100 μm (a–h). Abbreviations: ac, anastomose of cephalic blood vessels; bc, body wall circular muscle layer; bl, body wall longitudinal muscle layer; bw, body wall longitudinal muscle layer deformed; cg, cephalic glands; cp, circular muscle layer of proboscis sheath; db, dorsal blood vessel; dr, dermis; ed, efferent duct; fg, frontal glands; in, intestine; la, lateral diverticula of intestine; lb, lateral blood vessel; ln, lateral nerve; ls, longitudinal muscle layer of proboscis sheath; ne, nephridia; op, opening of pylorus; pf, pore of frontal organ; pp, proboscis pore; ps, proboscis sheath; rc, rhynchocoel; rd, rhynchodeum; st, stomach.
Figure 9. _Satellitenemertes satellitensis_, new genus and species, holotype. (a) Transverse sections between 37 and 52 from anterior end of body, showing rhynchodeum covered on its ventro-lateral sides by frontal glands; (b) circular muscles covering dorsal side of rhynchodeum; (c) opening of oesophagus into rhynchodeum with a thick layer of circular muscles; (d) rhynchodeum provided with thick epithelium and circular muscle layer; (e) radial longitudinal muscles from body wall longitudinal muscle layer; (f) basis of central stylet, bolster and pouches of accessory stylets; (g) plate-like muscular wall and dense layer of glandular cells in anterior wall of stylet bulb; (h) central stylet. Scale 50 μm (h) and 100 μm (a–g). Abbreviations: as, accessory stylet; bs, bolster; cb, cephalic blood vessel; ce, central stylet; cm, circular muscles of rhynchodeum; cr, circular muscle layer of rhynchodeum; cs, cerebral sensory organ; ct, basis of central stylet; es, oesophagus; fg, foregut; is, inner lumen of stylet bulb; oe, opening of oesophagus into rhynchodeum; pa, pouch of accessory stylet; pm, plate-like muscular wall; rd, rhynchodeum; rl, radial longitudinal muscles from body wall longitudinal muscle layer; sb, stylet bulb; sp, sheath of pear-shaped basis; tg, dense layer of glandular cells; wr, wall of rhynchodeum.
The rhynchocoel has two distinct muscle layers and reaches posteriorly more than half the body length (Figure 8a). The anterior region of the proboscis is provided with outer circular and inner longitudinal muscle layers. The proboscis insertion could not be observed because the proboscis had been protruded.

The proboscis diaphragm has a central stylet apparatus consisting of a pear-shaped basis 90 \(\mu\)m long and 60 \(\mu\)m wide; the anterior half of the basis is enclosed by a sheath (Figure 9f, g). The central stylet is 39 \(\mu\)m long (Figure 9h). The basis has no posteriorly inserted accessory stylet. It rests on a large bolster, 150 \(\mu\)m wide and 30 \(\mu\)m thick, consisting of interwoven circular and longitudinal muscle (Figure 9f, g). The stylet bulb, 110 \(\mu\)m wide and 30 \(\mu\)m high, consists of plate-like connective tissue and has a thick layer of glandular cells in anterior portion of its wall (Figure 9g). The remainder of the wall has a layer of connective tissue and a narrow canal into the posterior chamber of the proboscis. There are two accessory stylet pouches, each containing two stylets (Figure 9f). The proboscis has 11 nerves.

**Alimentary canal**

The foregut opens into the rhynchodeum near the anterior end of the brain (Figure 9c). The anterior part of the oesophagus is bordered on both sides by large masses of frontal glands (Figures 9a–e and 10a), and posteriorly it is surrounded by longitudinal muscles (Figure 10b). It has a length of 140 \(\mu\)m, measured from the opening of the oesophagus to the anterior end of the brain, and then extends for 50 \(\mu\)m under the ventral commissure of the brain (Figure 10c). The transition of the oesophagus into the stomach, measuring 90 \(\mu\)m long, is found between the brain lobes (Figure 10d–f).

The stomach (330 \(\mu\)m long) has four deep folds, is longer than the brain (250 \(\mu\)m) and lacks a diverticulum (Figure 10g, h). The pylorus is four times as long as the stomach, and its posterior end opens into the intestine (Figures 8c and 11a, b). The intestinal caecum has a pair of anterior diverticula, 460 \(\mu\)m long, and two pairs of lateral diverticula, which begin at the level of the posterior portion of the brain (Figures 10f–h and 11a, b). The intestinal canal has deep lateral diverticula (Figure 8c).

**Blood vascular system**

The blood vascular system has three longitudinal vessels. The two cephalic blood vessels anastomose above the rhynchodeum near the tip of the head to form a simple vascular loop (Figure 8g). Farther posteriorly, the cephalic vessels do not become large lacunae, but enter the brain ring without giving off cerebral vessels and run alongside the rhynchocoel (Figure 10e). The dorsal vessel originates from the left cephalic vessel and enters the rhynchocoel wall where it forms a median vascular plug (Figure 10f, g). It extends about 120 \(\mu\)m mid-ventrally in the sheath to anterior stomach region. After passing ventrally out of the rhynchocoel, the dorsal vessel continues posteriorly under the proboscis sheath between the rhynchocoel and the alimentary canal. The three post-cerebral vessels are not transversely linked by pseudometameric connectives. In the posterior portion of the brain, the lateral vessels enter the nephridial region but have no loops in contact with the nephridial tubes (Figure 10h).

**Nervous system**

The brain and lateral nerves are covered by a thin layer of fibrous connective tissue. (Figures 8b and 10c–h). The cerebral ganglia are large, but contain no neurochord cells and
Figure 10. *Satellitenemertes satellitensis*, new genus and species, holotype. (a) Transverse sections between 55 and 89 from anterior end of body, showing trunk of proboscis nerves and beginning of proboscis insertion; (b) trunk of proboscis nerve from dorsal side of ventral commissure and oesophagus surrounded by longitudinal muscles; (c) ventral commissure of brain; (d) dorsal commissure of brain; (e) cephalic blood vessels inside brain lobes and transitional portion of stomach; (f) anterior diverticulum of intestinal caecum on brain lobe and dorsal blood vessel branched from left cephalic blood vessel; (g) vascular plug of dorsal blood vessel, anterior diverticula of intestinal caecum, and stomach; (h) dorsal and ventral ganglia separated posteriorly, stomach with four folds, and nephridia. Scale 100 μm (a–h). Abbreviations: ab, anterior end of brain; ai, anterior diverticulum of intestinal caecum; bn, beginning of lateral nerve; cb, cephalic blood vessel; cs, cerebral sensory organ; dc, dorsal commissure of brain; dg, dorsal ganglion; dl, dorsal blood vessel separated from left cephalic blood vessel; es, oesophagus; fg, frontal glands; lb, lateral blood vessel; ln, lateral nerve; nc, nerve from cerebral sensory organ; ne, nephridia; ot, trunks of proboscis nerve from ventral commissure; rc, rhynchocoel; rd, rhynchodeum; st, stomach; tp, U-shaped trunk of proboscis nerve; vc, ventral commissure of brain; vg, ventral ganglion; vp, median vascular plug of dorsal blood vessel.
Figure 11. *Satellitenemertes satellitensis*, new genus and species, holotype. (a) Transverse sections between 8 and 151 from anterior end of body, showing transitional part of stomach into pylorus and anterior diverticula of intestinal caecum; (b) pylorus and lateral diverticula of intestinal caecum; (c) ocelli and frontal organ; (d) opening of cerebral organ canal, rhynchodeum and frontal and cephalic glands; (e) cerebral organ canal and rhynchodeum bordered by a pair of masses of frontal glands; (f) posterior end of cerebral organ canal; (g) cerebral sensory organ, frontal glands and oesophagus; (h) cerebral sensory organ. Scale 100 μm (a–h). Abbreviations: ai, anterior diverticula of intestinal caecum; cb, cephalic blood vessel; cg, cephalic glands; cn, cerebral organ canal; cs, cerebral sensory organ; db, dorsal blood vessel; eo, eosinophilic glandular mass; es, oesophagus; fo, frontal organ; gc, ganglionic mass; in, intestinal caecum; lb, lateral blood vessel; ld, lateral diverticula of intestinal caecum; ln, lateral nerve; ne, nephridia; oc, ocellus; oe, opening of oesophagus into rhynchodeum; oo, opening of cerebral organ canal; ps, proboscis sheath; py, pylorus; rc, rhynchocoel; rd, rhynchodeum; sa, sensory canal of cerebral sensory organ; st, stomach; wr, wall of rhynchodeum.
lack an inner neurilemma. The dorsal ganglia do not have bifurcated fibre cores (Figure 10h). The right and left ganglia are connected by a short dorsal commissure 20 μm thick and a short ventral commissure 60 μm thick, the latter a little more anterior than the former (Figure 10b–d). The ventral ganglia are separated from the dorsal ganglia posteriorly (Figure 10g, h). The lateral nerve cords are without accessory nerves, myofibrillae, or peripheral nerves (Figures 8b and 10h). The root of the proboscis nerves originating from the right and left dorsal sides of the ventral commissure, becomes a U-shaped trunk, from which the proboscis nerves extend toward the rynchocoel (Figures 10a, b and 12e–g). There is no mid-dorsal nerve. A pair of the foregut nerves originates from the ventral ganglia immediately behind the ventral commissure and a transverse connective.

Special sensory organs and frontal organ

The ocelli in cross-section are found as spherical masses of large ocular cells, the inner surfaces of which form small pores (Figure 11c). Four ocelli are clearly arranged in the right side of the tip of the head and the other ocelli are not detectable among the cephalic glands. The frontal organ opens on the ventral side of the anterior end of the head (Figure 8d). The frontal glands extend posteriorly as a pair of large ventrolateral masses that reach the anterior end of the cerebral ganglia (Figure 10a–c). The largest portion of the mass is 200 μm high and 80 μm wide at the mouth region, which is 350 μm from the tip of the head. The cephalic glands are well-developed on the lateral sides of the head and extend posteriorly. The bases of these cells are situated in the following body regions: close to the opening of the oesophagus, 150μm from the proboscis pore or 130 μm anterior to the brain (Figure 9c). Sub-muscular glands are absent. There are no cephalic grooves (Figure 11d).

The cerebral sensory organs are large 310 μm long and reach below the brain lobes, but do not extend behind them as they do in the members of Nipponnemertes (Figure 10e–g). The cerebral organ canal (110 μm long) is found on the lateral side of the head, near the anterior tip, and the lateral sac is not divided at its posterior end (Figure 11e, f). The sensory canal of the cerebral sensory organ, 180 μm long by 90 μm wide at its largest portion, is located medially. The cerebral organ is provided with large eosinophilic glands and ganglionic masses on both the dorsal and ventral sides (Figure 11g, h). Behind the sensory canal, a mass of cyanophilic glands run underneath the brain until its posterior portion (Figures 10b–f and 12a–d). A thick nerve (100 μm long) derived from the dorsal ganglion enters the posterior portion of the cerebral sensory organ (Figures 10c–e and 12b–d).

Excretory and reproductive systems

The excretory tubules are weakly developed and extend from the level of the posterior portion of the brain or of the posterior end of the cerebral sensory organ to the end of the pylorus. The two efferent ducts, originating in the anterior portion of the nephridial region, are short; they are lateral to the nerve cords and open on the lateral side of the body (Figure 8b). Sexes are separate. The eggs are arranged individually in a row between the body wall musculature and the intestine (Figure 12h).

Systematic discussion

The new genus Satellitenemertes has some characteristics comparable to those of Amphiporus, notably the organization of the foregut, type of pre-cerebral septum, and configuration of the proboscis apparatus and cephalic blood vessels. It differs, however, in
Figure 12. *Satellitenemertes satellitensis*, new genus and species, holotype. (a) Transverse sections between 53 and 351 from anterior end of body, showing cerebral sensory organ, oesophagus, anterior end of brain; (b) cerebral sensory organ and thick nerve from dorsal ganglion; (c) cerebral sensory organ under ventral brain lobe, thick nerve from dorsal ganglion and oesophagus with stomach wall; (d) cerebral sensory organ under ventral brain lobe and anterior end of stomach; (e) beginnings of proboscis nerves derived from the root; (f) U-shaped root of proboscis nerves and proboscis insertion; (g) roots of proboscis nerves from ventral commissure; (h) eggs arranged in a row between body wall and intestine. Scale 100 μm (a–h). Abbreviations: ab, anterior end of brain; bc, body wall circular muscle layer; bl, body wall longitudinal muscle layer; br, brain lobe; cb, cephalic blood vessel; cs, cerebral sensory organ; cy, cyanophilic glandular mass; dg, dorsal ganglion; dr, dermis; eg, eggs; eo, eosinophilic glandular mass; es, oesophagus; fg, frontal glands; id, intestinal diverticula; li, longitudinal muscles of proboscis insertion; nc, nerve from cerebral sensory organ; ot, trunks of proboscis nerve from ventral commissure; rc, rhynchocoel; rd, rhynchodeum; rl, radial longitudinal muscles from body wall longitudinal muscle layer; rp, rudiment of proboscis nerves; sa, sensory canal of cerebral sensory organ; tp, U-shaped trunk of proboscis nerve; vc, ventral commissure of brain; vg, ventral ganglion; wr, wall of rhynchodeum.
that the foregut opening is near the anterior end of the brain, the cerebral sensory organs
are large and extend beneath the ventral brain lobes as far as the ventral brain commissure,
the rhynchocoel is more than half but less than full body length, and the frontal glands are
enormously well-developed as a pair of large masses extending to the brain.

**Genus Nipponnemertes Friedrich, 1968**

**Species**

*Nipponnemertes bimaculata* (Coe 1901)

**Specimen**

USNM 1072180; 10 slides of stained serial section, including transverse sections of the
anterior portion of the body (4) and tail (4) and longitudinal sections of the midgut (2).
Another specimen was not sectioned (it dried out after it was preserved).

**Locality**

Obstruction Pass, between Obstruction Island and Orcas Island, Washington (Lat. 48°36’
W, Long 122° 49’ W), and Satellite Channel, Vancouver Island, British Columbia,
Canada, August 22, 1964.

**Description**

*External features*

The specimen collected in Obstruction Pass was only 8 mm long and 0.5 mm wide, but the
one from Satellite Channel was 18 cm long and 6 mm wide (Figure 1.3). When contracted,
it was 10 cm long and 1 mm wide.

The body of the first specimen was slender and cylindrical in the posterior portion
(Figure 13a). The head was somewhat triangular in shape and had two dark brown
markings on an otherwise whitish background (Figure 13a). The rest of the body was
brown on both the dorsal and the ventral sides, except at the posterior end, where it was
whitish (Figure 13b). Behind the dorsal markings of the head were two oblique cephalic
grooves. A longitudinal cephalic groove was visible as a long line running in the colourless
midline of the anterior region of the body and continuing into the post-cephalic region. Five
right and three left ocelli were arranged close to the lateral margins of the head and continuing
into the post-cephalic region. Five right and three left ocelli were arranged on the lateral margins of the head. Two groups of 13 ocelli were arranged close to the lateral margins of the head and two groups of eight were
arranged near the posterior edges of the brown markings (Figure 13c). Two pairs of large
ocelli were located behind the oblique cephalic grooves. There was a longitudinal cephalic
groove in the midline of the anterior portion of the body. The ventral portions of the
oblique cephalic grooves ran forward along the lateral margin of the head and met at the anterior tip of the head, where the proboscis pore was visible as a short line (Figure 13e).

**Body wall, musculature and parenchyma**

The epidermis contains elliptical unicellular glands sparsely arranged in a row (Figure 14a). The thickness of the dermis averages 40 μm. The body wall musculature is well-developed and has a layer of fasciated diagonal muscles between the outer circular and inner longitudinal layers (Figure 14a). The outer circular muscle layer is only 7 μm thick, while
Figure 14. *Nipponemertes bimaculata* (Coe). (a) Transverse sections between 8 and 143 from anterior end of body, transverse section 20 from posterior end of body and frontal sections between 56 and 62 of proboscis apparatus, showing proboscis sheath, consisting of interwoven circular and longitudinal muscles; (b) opening of frontal organ; (c) proboscis pore; (d) end of rhynchocoel, dorsal and lateral blood vessels, and hindgut; (e) circular muscle layer of rhynchodeum, oesophagus and right cephalic blood vessel; (f) precerebral septum of proboscis apparatus, proboscis nerves entering longitudinal muscle layer of proboscis and right cephalic blood vessel; (g) basis of central stylet; (h) structure of stylet bulb. Scale 50 μm (b–h) and 100 μm (a). Abbreviations: bc, body wall circular muscle layer; bl, body wall longitudinal muscle layer; bs, bolster; cb, cephalic blood vessel; cg, cephalic glands; cm, circular muscle layer of rhynchodeum; cn, cerebral organ canal; dr, dermis; dv, dorsal blood vessel; er, end of rhynchocoel; es, oesophagus; fg, frontal glands; is, inner lumen of stylet bulb; lp, lumen of proboscis canal directed upward from basis; lv, lateral blood vessel; md, middorsal nerve; np, narrow canal of stylet bulb into posterior chamber of proboscis; oc, ocellus; of, opening of frontal organ; pa, pouch of accessory stylet; pc, precerebral septum of proboscis; pm, plate-like muscular wall of stylet bulb; pn, proboscis nerve; pp, proboscis pore; pw, proboscis sheath, consisting of interwoven circular and longitudinal muscles; rc, rhynchocoel; rd, rhynchodeum; rp, rudiment of proboscis nerves; tb, central stylet basis, its content discharged outside in section; tg, dense layer of glandular cells; vt, connective tissue of stylet bulb.
the inner longitudinal muscle layer is three or four times this thickness, averaging 23 μm. The longitudinal layer is not divided anteriorly by connective tissue and there are no cephalic retractor muscles. Dorsoventral muscles are well-developed and parenchyma is moderate in extent.

**Rhynchodeum, rhynchocoel and proboscis**

The proboscis pore is situated at the anterior end of the head immediately behind the opening of the frontal organ (Figure 14b, c). The proboscis sheath reaches nearly to the posterior end of the body (Figure 14d). The rhynchocoel has a wickerwork of interwoven circular and longitudinal muscles (Figure 14a). The rhynchodeum has a circular muscle sphincter (Figure 14e). The pre-cerebral septum is of the closed type and is composed of radial muscles derived from the longitudinal muscle layer of the body wall (Figure 14f).

The proboscis diaphragm has the central stylet apparatus consisting of a conical basis about 40 μm wide; the content of this, in the section, was extruded (Figure 14g). The basis rests on a large bolster consisting of interwoven circular and longitudinal muscles (Figure 14g). Posterior to the bolster, the stylet bulb consists of a plate-like muscular wall, a thick layer of glandular cells in its anterior wall, thick connective tissue, and interlacing circular muscles similar to those of *Nipponnemertes fernaldi* (Iwata 2001) and *Satellitenemertes satellitensis* of the present report (Figure 14h). There are two accessory stylet pouches, each containing eight stylets. The proboscis has 16 nerves.

**Alimentary canal**

Near the anterior end of the head, the oesophagus opens into the rhynchodeum (Figure 15a). The oesophagus does not have a caecum; according to Coe (1905); however, a rather extensive oesophageal caecum extends beneath the stomach of this species. The oesophagus and the stomach have no circular muscles. The stomach has two deep folds and is about the length of the brain. The pylorus is long and two times the length of the stomach. The intestinal caecum has a pair of anterior pouches and three pairs of lateral diverticula. The anterior pouches are short and have a length of about 110 μm. They are situated a long distance behind the posterior end of the brain, and are about as long as the brain. The intestinal diverticula are unbranched.

The anus opens on the ventral side of the posterior end of the body (Figure 15b). The rectum, 80 μm long, has a sphincter of circular muscle fibres (Figure 15c). The lateral nerves are connected to each other by a commissure on the dorsal side of the rectum (Figure 15d). A short distance (20 μm) anterior to the commissure, the blood vessels anastomose into a slender vessel (Figure 15e). The rhynchocoel ends a little anterior to this anastomosis (Figure 14d).

**Blood vascular system**

The blood vascular system has three longitudinal vessels. The dorsal vessel, originating from the right cephalic vessel, enters the rhynchocoel wall and forms a median vascular plug (Figure 15f). The lateral vessel makes a large lacuna-like enlargement immediately behind the cerebral sensory organ (Figure 15g). The cephalic vessels enter the brain ring without giving off cerebral vessels. There are no pseudometameric anastomoses of blood vessels.
Figure 15. Nipponnemertes bimaculata (Coe). (a) Transverse sections between 18 and 103 from anterior end of body and 2 and 17 from posterior end of body showing opening of oesophagus into rhynchodeum; (b) anus; (c) rectum; (d) commissure of lateral nerve; (e) anastomoses of dorsal and lateral blood vessels and hind gut; (f) right cephalic blood vessel entering into single median vascular plug of dorsal blood vessel; (g) myofibrillae of lateral nerve cord; (h) ocellus and cerebral organ canal composed of inner wall of sensory canal and outer wall of sac of cerebral sensory organ. Scale 50 µm (a–h). Abbreviations: an, anus; av, anastomose of dorsal and lateral blood vessels; br, brain; cb, cephalic blood vessel; cg, cephalic glands; cn, cerebral organ canal; co, commissure of lateral nerves; dv, dorsal blood vessel; es, oesophagus; fg, frontal glands; hg, hindgut; ln, lateral nerve; lv, lateral blood vessel; mf, myofibrillae; oc, ocellus; oe, opening of oesophagus into rhynchodeum; pn, proboscis nerve; pr, proboscis; rc, rhynchocoel; rd, rhynchodeum; rm, rectum; st, stomach.
Nervous system

The brain and lateral nerves are covered by a thin layer of fibrous connective tissue. The nervous system has no neurochord cells or accessory lateral nerves. The mid-dorsal nerve extends anteriorly beyond the brain (Figure 14a). The lateral nerve cords have myofibrillae in a connective tissue band on the medial side of the fibre core and peripheral nerves (Figure 15g).

The ventral ganglia are separated from the dorsal ganglia posteriorly. The dorsal ganglia have no bifurcated fibre core. There is a pair of foregut (splanchnic) nerves originating from the ventral ganglia immediately behind the ventral commissure.

Special sensory organs and frontal organ

The cephalic grooves have secondary transverse grooves. There is a lengthwise row of six ocelli on the left side of the anterior portion of the head, a row of four ocelli on the right side and two ocelli on each side behind the cephalic grooves. The ocelli behind the cephalic grooves are remarkably large, being 55 µm in diameter (Figures 15h and 16a). The frontal organ and frontal glands are well-developed: the former forms a short duct, opening at the anterior end of the head (Figure 14b); the latter reaches posteriorly to the anterior end of the brain. The cephalic glands are moderately developed along the lateral sides of the head and reach posteriorly to the anterior end of the brain. Sub-muscular glands are small and situated in the ventral side of the head.

The cerebral organ is large, extends behind the cerebral ganglia (Figure 16b, c), and is covered by a neurilemma. The cerebral organ canal branches into a medial sensory canal and a lateral sac (Figure 16d–f); the former has a cyanophilic glandular mass and the latter an eosinophilic glandular mass (Figure 16c, g). The cerebral organ opens laterally into a cephalic groove of the head (Figure 16h). The sensory canal is evident as a small number of cells surrounding the inner lumen of the cerebral organ canal (Figures 15h and 16a).

Excretory and reproductive systems

The excretory tubules extend from the level immediately behind the cerebral organ to the level of the posterior portion of the pylorus. The two efferent ducts, originating in the posterior portion of the nephridial region, are short and run lateral to the lateral nerve cords, opening on the ventral side of the body. The male gonads are immature.

Systematic discussion

The oesophagus of this specimen has no oesophageal diverticulum. This disagrees with Coe’s statement (1905) that “a rather extensive oesophageal caecum extends beneath the stomach. It branches off from the oesophagus proper shortly behind the brain as a small canal which enlarges posteriorly until it is as large as the stomach beneath which it lies. It terminates blindly posteriorly somewhat behind the anterior ends of the intestinal caeca, as is the case also with A. occidentalis”. In Nipponnemertes fernaldi, the oesophagus also lacks an oesophageal diverticulum (Iwata 2001). It should be noted that the present specimen has diagonal muscles between the outer circular and inner longitudinal layers but they are difficult to see because they lie immediately against the circular layer; whereas in
Figure 16. *Nipponemertes bimaculata* (Coe). (a) Transverse sections between 47 and 94 from anterior end of body, showing cerebral organ canal, its wall composed of sensory canal and sac of cerebral sensory organ; (b) thick nerve from posterior portion of dorsal ganglion; (c) cyanophilic glandular mass in posterior portion of cerebral sensory organ; (d) cerebral sensory organ with shallow ventral groove in sac; (e) sensory canal and sac of cerebral sensory organ; (f) sensory canal and ganglionic mass of cerebral sensory organ; (g) eosinophilic glandular mass behind sac of cerebral sensory organ; (h) opening of cerebral organ canal and proboscis insertion. Scale 50 μm (a–h). Abbreviations: br, brain; cb, cephalic blood vessel; cg, cephalic groove; cn, cerebral organ canal; cs, cerebral sensory organ; cy, cyanophilic glandular mass; db, dorsal blood vessel; dc, dorsal commissure of brain; dg, dorsal ganglion; eg, eosinophilic glandular mass; es, oesophagus; gm, ganglionic mass; lm, lateral nerve; lv, lateral blood vessel; nd, nerve from dorsal ganglion to cerebral sensory organ; rc, rhynchocoel; rd, rhynchodeum; rg, right cephalic groove; sa, sensory canal of cerebral sensory organ; se, sac of cerebral sensory organ; st, stomach; vg, ventral ganglion; ws, wall of sensory canal of cerebral sensory organ.
Nipponnemertes punctatula they were fairly easy to see because they were separated from the circular layer by a thin sheet of connective tissue (Coe 1905; Crandall 1993).

**Genus Sanjuannemertes gen. nov.**

**Type species**

Sanjuannemertes willowsi gen., sp. nov.

**Etymology**

The genus name refers to the area in which the type specimen was collected. The species name is dedicated to Professor A. O. Dennis Willows for his support of my work on nemertean taxonomy.

**Diagnosis**

Monostiliferous marine hoplonemertean with two oblique cephalic grooves and four large ocelli arranged in form of a trapezoid; proboscis pore and mouth opening ventrally into common atrium on anterior tip of head; body wall musculature with a lattice-type diagonal layer, longitudinal muscles not divided anteriorly; rhynchocoel nearly equal to body length, with wall containing two distinct muscle layers; proboscis long and stout, with distinct outer circular and inner longitudinal muscle layer; proboscis armature consisting of single central stylet and two accessory stylet pouches; pre-cerebral septum and proboscis insertion ventrally incomplete; cephalic retractor muscles absent; longitudinal musculature in anterior region of head well-developed; foregut divisible into stomach, pylorus, intestinal caecum with lateral diverticula, main intestinal canal without deep lateral diverticula, and hind gut; cerebral sensory organ large and extending to lateral sides of brain lobes; cerebral ganglia small, with neither neurochord cells nor inner neurilemma; dorsal ganglia not separated from ventral ganglia; dorsal ganglia without bifurcated lobes; lateral nerve cords without accessory nerves or myofibrillae, and with peripheral nerves; blood vascular system with simple vascular loop in head, not entering brain ring; dorsal vessel without single vascular plug and three post-cerebral vessels not linked by pseudometameric transverse connectives; dorso-ventral muscle fibres and parenchyma absent; frontal organ composed of pore and small number of frontal glands; excretory system confined to foregut region of body, lacking efferent ducts; sexes probably separate.

**Type species**

Sanjuannemertes willowsi

Body color without pattern; two cephalic grooves present, with opening of cerebral organ at lateral side of anterior groove; epidermis thick, with columnar glands confined to upper portion; proboscis with 10 nerves; proboscis anterior chamber with two muscle layers (outer circular and inner longitudinal); brain with a thin neurilemma; mid-dorsal nerve lacking; dorsal ganglia not separated from ventral ganglia, without bifurcated fibre core; paired foregut nerves originating from ventral ganglia; cerebral sensory organ with thin neurilemma; cerebral organ canal, beginning at mid-lateral side of anterior cephalic groove with a widened sac; excretory tubules lacking.
Sanjuannemertes willowsi gen., sp. nov.

**Type specimen**

Holotype: USNM 1072181; 22 slides of stained serial section, including transverse sections of the anterior portion of the body (9) and tail (5) and horizontal sections of the midgut (8).

**Type locality**

San Juan Channel, Washington, USA (48°34.3’ N, 123°1.7’ W), depth 62 fathoms, October 21, 1964.

**Description**

**External features**

The body was small and cylindrical, 15 mm long and 1.5 mm wide (Figure 1.4). When contracted, it was 10 mm long and 2 mm wide. The anterior edge of the head was rounded (Figure 17a, c) or slightly indented (Figure 17b). The posterior end of the body had a papilla-like protrusion (Figure 17e). There were two oblique cephalic grooves on both the dorsal and the ventral sides of the head (Figure 17a–d). On the ventral side, the mouth and proboscis pore are in a slit-like depression that crosses the anterior cephalic groove (Figure 17b). The color of the body was orange or light vermilion. On both the dorsal and the ventral surfaces of the anterior portion of the body there were numerous narrow, pale orange or whitish transverse lines. The whitish proboscis apparatus could be seen through the body wall; the basis of the central stylet was evident as a milky white patch. The four ocelli, visible on the dorsal side, were arranged in the form of a trapezoid. The two anterior ocelli were closer than those of the posterior pair and were situated just in front of the anterior cephalic groove, whereas the other pair was situated underneath the posterior one (Figure 17a, c, d).

**Body wall, musculature and parenchyma**

The body in transverse section is circular in both the cephalic and midgut regions (Figure 18a). The epidermis is of uniform thickness (about 60 µm). Large unicellular glands are distributed over the entire body and are especially well developed in the midgut region. Cyanophilic glands are not present between them. In the cephalic region, the epidermis and longitudinal muscle layer of the body wall are nearly the same in thickness, and glandular cells are confined to the upper portion. The dermis, 5–10 µm thick, one-fourth to one-tenth the thickness of the epidermis (Figure 18b). The body wall musculature consists of a thin outer circular layer (10 µm thick) and an inner longitudinal layer (60 µm thick). There is sparse lattice-type diagonal muscle layer between them. The longitudinal layer is not divided into inner and outer portions anteriorly. There are no head retractor muscles related to the longitudinal muscle layer. Dorsoventral and radial muscle fibres, as well as parenchyma, are absent.

**Rhynchodeum, rhynchocoel and proboscis**

The proboscis pore, 60 µm long and 110 µm wide, is a mid-ventral furrow. With the mouth it forms a common atrium (Figures 17b, 18c and 19d). Its wall is 15 µm thick and lacks cilia
and glands. The rhynchodeum is circular in transverse section owing to the proboscis protruded into it and is covered by a thick layer (20–60 μm) of circular muscles (Figure 18d). The rhynchodeum measures 260 μm long and is at first cylindrical, but then broadens to a width of 300–450 μm (Figure 18d–h). At the posterior end of the rhynchodeum, where its circular muscle sphincter disappears, the pre-cerebral septum is formed by radial longitudinal muscles derived from the longitudinal muscle layer in the dorsal side of the body; the proboscis insertion also becomes evident (Figure 18g). The lateral and ventral sides of the body contain no radial longitudinal muscles in the pre-cerebral septum (Figure 18h).

The proboscis diaphragm has a central stylet and a vase-shaped basis 400 μm long, 70 μm wide at its top and 60 μm wide at its middle portion (Figure 19a, b). In sections, the basis shows a strong affinity for eosin and its content is not extruded. The central stylet measures 40 μm long (Figure 19a). The basis of the central stylet rests on a small bolster, is
Figure 18. *Sanjuannemertes willowisi*, new genus and species, holotype. (a) Transverse sections between 19 and 104 from anterior end of body, showing body circular in transverse section; (b) stomach region; (c) proboscis pore and mouth separated; (d) circular muscle layer of rhynchodeum and proboscis; (e) end of the mouth and stomach wall (oesophagus lacking); (f) stomach; (g) radial longitudinal muscles from body wall longitudinal muscle layer in the dorsal side of the head; (h) proboscis insertion in the lateral side of the head. Scale 100 μm (b–h) and 200 μm (a).

Abbreviations: ad, anterior cephalic groove formed by dorsal and ventral grooves united at mid-lateral portion of head; ag, anterior ventral cephalic groove; bc, body wall circular muscle layer; bl, body wall longitudinal muscle layer; br, brain; cb, cephalic blood vessel; cn, cerebral organ canal; cr, circular muscle layer of rhynchodeum; cs, cerebral sensory organ; cv, cephalic nerves; dg, dorsal ganglion; dr, dermis; mo, mouth; oc, ocellus; pn, proboscis nerve; pr, proboscis; ps, proboscis sheath; rc, rhynchocoel; rd, rhynchodeum; rl, radial longitudinal muscles from body wall longitudinal muscle layer; st, stomach; vg, ventral ganglion; wt, wall of stomach.
Figure 19. *Sanjuanemertes willowsi*, new genus and species, holotype. (a) Longitudinal sections between 57 and 63 in proboscis diaphragum and transverse sections between 16 and 209 from anterior end of body, showing central stylet and anterior portion of basis; (b) posterior portion of basis and its bolster; (c) accessory stylet pouch; (d) proboscis pore, mouth and lips of mouth; (e) posterior portion of mouth and transitional part of stomach without showing oesophagus; (f) transitional area of stomach into pylorus and anterior diverticula of intestinal caecum; (g) deep lateral diverticula of intestine; (h) anastomose of cephalic blood vessels. Scale 50 μm (a), 100 μm (b–f, h) and 200 μm (g). Abbreviations: ac, anastomose of cephalic blood vessel; ag, anterior ventral cephalic groove; ai, anterior diverticula of intestinal caecum; as, accessory stylet; bs, bolster; ce, central stylet; cp, circular muscle layer of proboscis sheath; ct, central stylet; db, dorsal blood vessel; in, intestine; la, lateral diverticula of intestine; ls, longitudinal muscle layer of proboscis sheath; mo, mouth; oc, ocellus; pa, pouch of accessory stylet; pn, proboscis nerve; pr, proboscis; ps, proboscis sheath; py, pylorus; rc, rhynchocoel; wt, wall of stomach.
surrounded by a thick layer of circular muscles (Figure 19b) and, in sections, shows no posteriorly inserted accessory stylet. The stylet bulb consists of a thick wall of circular muscles, 300µm wide. There are two accessory stylet pouches, each containing two stylets (Figure 19c). The proboscis has 10 nerves.

**Alimentary canal**

The alimentary canal has four major divisions; stomach, pylorus, midgut (with anteriorly directed caecum and lateral diverticula) and hind gut. The mouth and the proboscis pore open into a common atrium on the ventral side of the head; they are not joined together (Figures 17b, 18c, e and 19d, e). There is no oesophagus; the mouth leads directly to the stomach (500µm long). The stomach has a deep lengthwise fold for its entire length and is far longer (160µm) than the brain (Figure 18e, f). The stomach has no diverticulum.

The pylorus is long, measuring one and one-sixth times the length of the stomach. The intestinal caecum has a pair of short anterior pouches 40µm long (Figure 19f) and three pairs of lateral diverticula, beginning immediately behind the posterior end of the brain. The intestinal canal has long lateral diverticula (Figure 19g). The hindgut is 100µm long and ends at the anus.

**Blood vascular system**

The blood vascular system has three longitudinal vessels. The two cephalic vessels lateral to the rhynchodeum anastomose above the rhynchodeum near the tip of head to form a simple vascular loop 200µm wide, 10µm high and 20µm long. The vascular loop is not a continuous space (Figure 19h). Farther posteriorly, the cephalic vessels do not form large lacunae and do not give off cerebral vessels. They are slender, at first running alongside the rhynchocoel or near the dorsolateral side of the cerebral organ canal, and then above the cerebral organs, but do not enter the brain ring (Figures 18d, h and 20b–d, f, h). Near the posterior end of the cerebral organ, the cephalic vessels extend down between the brain lobes and the rhynchocoel, and fuse into a dorsal vessel; this does not form a median vascular plug inside the proboscis sheath. A lateral vessel from the cephalic vessels, on the other hand, comes down outside the cerebral ganglia (Figure 20a). There are no pseudometameric anastomoses of blood vessels. The dorsal and lateral vessels anastomose at a level, 40µm from the posterior end of the body.

**Nervous system**

The brain and lateral nerves are covered by a thin layer of fibrous connective tissue. The cerebral ganglia are small; they lie immediately outside the large rhynchocoel and have neither neurochord cells nor an inner neurilemma. The nervous system has no accessory lateral nerves. The dorsal and ventral ganglia are not demarcated externally. The ventral ganglia are not distinctly separated from the dorsal ganglia except posteriorly (Figures 18a and 20a, g).

The dorsal and ventral fibre cores, measuring 140µm in length, are not divided anterior to the middle portion of the brain; the dorsal cores (30µm long), are less voluminous than the ventral cores (Figure 18a). The ventral ganglia behind the posterior end of the dorsal ganglia do not immediately extend laterally to form the lateral nerve cords (Figure 20a). The dorsal ganglia do not have bifurcated fibre cores.
Figure 20. *Sanjuanemertes willowsi*, new genus and species, holotype. (a) Transverse sections between 12 and 97 from anterior end of body, showing posterior portion of right dorsal ganglion, dorsal and lateral blood vessel; (b) cephalic furrow united from dorsal and ventral transverse grooves; (c) short canal of cephalic groove above the dermis; (d) posterior ocelli on cerebral sensory organ; (e) ocelli in the right side of the head and frontal glands; (f) cerebral sensory organ in the right side of the head; (g) cerebral sensory organ in the left side of the head and brain lobes; (h) posterior end of cerebral organ canal widened in its outer portion. Scale 100 μm (a–h). Abbreviations: ad, anterior cephalic groove formed by dorsal and ventral grooves united at mid-lateral portion of head; ao, anterior ocellus; br, brain; cb, cephalic blood vessel; cn, cerebral organ canal; cp, canal of cephalic groove in epidermis; cr, circular muscle layer of rhynchodeum; cv, cephalic nerves; cw, cerebral organ canal widened outward; dg, dorsal ganglion; dr, dermis; dv, dorsal blood vessel; eo, eosinophilic glandular mass; fg, frontal glands; gc, ganglionic mass; lv, lateral blood vessel; ne, nephridia; pn, proboscis nerve; po, posterior ocellus; ps, proboscis sheath; rc, rhynchocoel; rd, rhynchodeum; sa, sensory canal of cerebral sensory organ; st, stomach; vg, ventral ganglion; wa, wall of sensory canal of cerebral sensory organ.
The dorsal commissure, curving dorsally for 650 μm, is 20 μm in dorsoventral thickness and 30 μm in longitudinal thickness. The ventral commissure is straight and shorter, measuring 300 μm long and 50 μm in dorsoventral thickness and 60 μm in longitudinal thickness; it is situated much farther posteriorly than the dorsal commissure, there being 160 μm between the transverse levels at which they lie.

A proboscis nerve trunk arises from the anterior surface of the brain at the root of the dorsal commissure and extends upward, soon branching into 10 nerves. The pair of foregut nerves originate from the ventral ganglia and run anteriorly along the lateral side of the stomach. There are no transverse connectives.

**Special sensory organ and frontal organ**

Of the two oblique cephalic grooves, the anterior one is narrow and has a ridge bearing long cilia (Figure 18e). The anterior grooves on both the dorsal and ventral sides of the head are united laterally and, at the point of union, form a short canal that extends nearly to the dermis (Figure 20b, c).

The anterior two ocelli are buried in the middle portion of the head, where the longitudinal musculature is dominant (Figure 20e), but the posterior ones are situated above the posterior portion of the cerebral sensory organs (Figure 20d). All four ocelli are the same size, measuring 60 μm wide, 90 μm high and 60 μm long (Figure 20d, e). Each ocellus consists of an outer layer of ocular cells and an internal cytoplasmic portion.

The frontal organ and frontal glands are not well-developed; the former opens on the ventral side of the anterior end of the head, while the latter forms a small mass of glands, 20 μm long (Figure 20e). Cephalic glands and sub-muscular glands are absent.

The cerebral sensory organs are large and reach the lateral sides of the brain lobes. The one on the right side of the head is crescentic in section, 230 × 90 μm in diameter in its anterior portion (Figure 20f); whereas on the left side is flattened between the body wall and the brain, being 70 μm wide, 420 μm high and 110 μm long in the middle portion (Figure 20g). It has a sensory canal that is 50 × 70 μm in diameter and possesses well-developed eosinophilic glands on both the dorsal and ventral sides (Figure 20f, g). The ganglionic mass is found lateral to the sensory canal (Figure 20f, g).

The cerebral organ canal, ciliated and 120 μm long, begins at the mid-lateral side of the anterior cephalic groove of the head, and extends posteriorly inside the longitudinal muscle layer of the body wall (Figures 17d and 20h). The canal consists of a medial part with a sensory function and a ciliated outer wall that is widened outward forming a sac (Figure 20h). A slender nerve from the lateroventral corner of the dorsal ganglion enters the posterior end of the cerebral organ.

**Excretory and reproductive system**

The excretory system is weakly developed and quite short in the foregut region. No excretory tubules winding around and along the lateral blood vessels have been observed. The single efferent ducts on each side opens dorsolaterally. The gonads are immature.

**Systematic discussion**

*Sanjuanemertes willowsi*, here described as new genus and species, has characters different from those of all other genera of the monostiliferan Hoplonemertea in that the mouth and
proboscis pore are completely separated but open into a common atrium. There are a number of species where the foregut and rhynchodaeum open together or almost together at the body surface. This does not necessarily indicate an atrium. Stiasny-Wijnhoff (1936) showed that even some Reptantia with slightly separated mouth and proboscis pore on a flat body surface had them opening into an area of differentiated epithelium of the type that is usually seen lining an atrium. The differentiated epithelium is really the hallmark of an atrium. In the present specimen, there does appear to be a differentiated epithelium with a number of prominent strongly acidophilic gland cells surrounding this area. However, both the partially everted proboscis and an everted foregut greatly complicate the true picture of what the animal would be like in a normal relaxed state. Given the number of other species with somewhat similar atrium-like conditions, it may be a bit risky to stake a new genus on a single specimen in a somewhat contorted condition, just as in some polystiliferan hoplonemerteans such as Kameginemertes parmiornatus (Iwata 1998). Crandall (1993) wrote that “Relationships between mouth and proboscis openings and the corresponding association between oesophagus and rhynchodaeum have been long used at generic and higher levels. In most of the monostiliferous forms the oesophagus opens into the rhynchodaeum internally whereas Malacobdella is sharply distinguished by the rhynchodaeum opening into an oesophagus of unique histological structure”. The recent molecular study of Thollesson and Norenburg (2003) shows that Malacobdella fits quite comfortably in the middle of the Monostilifera. So Crandall’s morphological observation may just indicate a major adaptation rather than a large phylogenetic divergence. This is a main reason why a new genus Sanjuannemertes has been established. Furthermore, configuration of the vascular system and the cerebral organs of the new genus are different from those of the genera Tétarstemma, Oerstedia and Prosorhocmus.

In Atrionemertes greenlandica, Senz (1993) reported that “Anteriorly the foregut opens into the posterior end of the atrium” and that “the rhynchodaeum is comparatively narrow (Figure 1.5) and opens into the posterior end of the atrium”. In discussion of the same species, he also stated that “in a small number of species both organs (oesophagus and rhynchodeum) open either independently from each other to the exterior, or via a common atrium. The last one is true in the present material”. In his Figure 1.5, it seemed likely that the openings of the rhynchodeum and foregut are much narrow to perform their functions. In the members of Communoporus (Friedrich 1955), both organs open separately.

Kajihara et al. (2003), however, placed Senz’s genus Atrionemertes among six monostiliferous hoplonemerteian genera with a bilayered rhynchocoel wall and an oesophagus emerging from the rhynchodeum close behind the proboscis pore. These six genera are Arctonemertes Friedrich, 1957; Atrionemertes Senz, 1993; Communoporus Friedrich, 1955; Divanella Gibson, 1973; Koinoporus Sánchez and Moretto, 1988; and Potamostoma Kajihara et al. 2003.

Acknowledgements

I thank A. O. Dennis Willows, Director of Friday Harbor Laboratories, University of Washington, for his constructive comments and for providing facilities for research. Eugene Kozloff, also of Friday Harbor Laboratories, helped by reviewing the manuscript. This study was supported in part by a NSF Grant, USA in 1964.
References

Chernyshev AV. 1992. O nazvaniyakh nekotoruikh nemertin. Zoologicheskij Zhurnal 71:134–136.
Coe WR. 1901. Papers from the Harriman Alaska Expedition. XX. The nemerteans. Proceedings of the Washington Academy of Sciences 3:1–110.
Coe WR. 1905. Nemerteans of the west and north-west coasts of America. Bulletin of the Museum of Comparative Zoology at Harvard College 47:1–318.
Crandall FB. 1993. Major characters and enoplan systematics. Hydrobiologia 266:115–140.
Friedrich H. 1955. Beiträge zu einer Synopsis der Gattungen der Nemertini monostilifera nebst Bestimmungsschlüssel. Zeitschrift für wissenschaftliche Zoologie 158:133–192.
Friedrich H. 1957. Beiträge zur kenntnis der Arktischen Hoplonemertinen. Videnskabelige Meddelelser fra Dansk Naturhistorisk Forening Vidensk 119:129–154.
Friedrich H. 1968. Sagaminemertes, eine bemerkenswerte neue Gattung der Hoplonemertinen und ihre systematische Stellung. Zoologischer Anzeiger 180:33–36.
Gibson R. 1973. A new littoral hoplonemertean (Divanella evelinae gen. et sp. nov.) from the coast of Brazil. Bulletin of Marine Sciences 23:793–810.
Gibson R. 1982. Nemerteans of the Great Barrier Reef. 5. Enopla Hoplonemertea (Monostilifera). Zoological Journal of the Linnean Society 75:269–296.
Gibson R, Sundberg P. 2001. Some nemerteans (Nemertea) from Queensland and the Great Barrier Reef, Australia. Zoologica Science 18:1259–1273.
Iwata F. 1954. The fauna of Akkishi Bay. XX. Nemertini in Hokkaido. Journal of the Faculty of Sciences, Hokkaido University, Series 6, Zoology 12:1–39.
Iwata F. 1998. On the hoplonemertean, Kameginemertes parmiornatus (Iwata, 1957) gen. n., comb. n. from Sagami Bay, Japan. Hydrobiologia 365:199–213.
Iwata F. 2001. Nipponnemertes fernaldi, a new species of swimming monostiliferous hoplonemertean from the San Juan Archipelago, Washington, USA. Proceedings of the Biological Society of Washington 114:833–857.
Johnston G. 1837. Miscellanea Zoologica. II. A description of some planarian worms. Magazine of Zoology and Botany 1:529–538.
Kajihara H, Gibson R, Mawatari SF. 2003. Potamostoma shizunaiense gen. et sp. nov. (Nemertea: Hoplonemertea: Monostilifera): a new brackish-water nemertean from Japan. Zoological Sciences 20:491–500.
Kirsteuer E. 1965. Über das Vorkommen von Nemertinen in einem tropischen Korallenriff. 4. Hoplonemertini monostilifera. Ergebnisse der Österreichischen Indo-Westpazifik-Expedition 1959/60 Teil VII. Zoologische Jahrbücher, Abteilung Systematik, Ökologie und Geographie der Tiere 92:289–326.
Kirsteuer E. 1974. Description of Poseidonemertes caribensis sp. n., and discussion of other taxa of Hoplonemertini Monostilifera with divided longitudinal musculature in the body wall. Zoologica Scripta 3:153–166.
de Quatrefages A. 1846. Études sur les types inférieurs de l’embranchement des annélés. Mémoire sur la famille des Nemertiens (Nemertea). Annales de Sciences Naturelle, Zoologie, Series 3 6:173–303.
Sánchez M, Moretto HJA. 1988. A new genus of freshwater hoplonemerteans from Chile. Zoological Journal of the Linnean Society 92:193–207.
Schmarda LK. 1859. Neue Turbellarien, Rotatorien und Anneliden beobachtet und gesammelt auf einer Reise um die Erde 1853 bis 1857. Leipzig: W. Engelmann, Volume 1. p 1–66.
Senz W. 1993. Arrionemertes greenlandica gen. et spec. nov. (Nemertini: Hoplonemertini). Zoologischer Anzeiger 231:99–110.
Stiasny-Wijnhoff G. 1936. Die Polystilifera der Siboga-Expedition. Siboga Expedition 22:1–214.
Thollesson M, Norenburg JL. 2003. Ribbon worm relationships – A phylogeny of the phylum Nemertea. Proceedings of the Royal Society of London B 270:407–415.