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To cite this article: Nathan W. Riser (1998) New Zealand nemertines from kelp holdfasts: Hoplonemertinea 1. *Nipponnemertes sanguinea* sp. n., *New Zealand Journal of Zoology*, 25:3, 287-294, DOI: [10.1080/03014223.1998.9518157](https://doi.org/10.1080/03014223.1998.9518157)

To link to this article: <http://dx.doi.org/10.1080/03014223.1998.9518157>



Published online: 30 Mar 2010.



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New Zealand nemertines from kelp holdfasts: Hoplonemertinea 1. *Nipponnemertes sanguinea* sp. n.

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Abstract A new hoplonemertean species belonging to the genus *Nipponnemertes* is described from kelp holdfasts washed up on two New Zealand beaches following a major tropical storm. The new species is characterised by the presence of circulating erythrocytes and the presence of distinctive “nuage-like” material in oocytes.

Keywords *Nipponnemertes sanguinea* sp. n.; morphology; erythrocytes; nuage; New Zealand; Nemertinea

INTRODUCTION

Large numbers of holdfasts of *Lessonia variegata* that washed up on the beach at Kaikoura, New Zealand, following storms from mid February to mid March of 1986, were collected to obtain cryptic inhabitants for meiofaunal studies. The holdfasts were sashed up and down in buckets of clean sea water upon being returned to the Edward Percival Field Station in order to remove sand and other debris. The buckets containing the holdfasts were then filled with sea water and placed on the laboratory floor to stagnate, forcing motile organisms to creep out and aggregate along the wall of the bucket near the meniscus. In addition to the meiofaunal animals, a surprisingly large number of nemertine individuals and species accumulated along this surface. One of the nemertine species swam actively with a flexing motion much like that of the juvenile ophelinin

polychaetes which were also present in the samples. When living specimens were examined under a coverslip on a slide, slugs of red blood cells surging in the blood vessels immediately attracted attention, as did a proboscis-stylet apparatus which was strikingly different from that of other hoplonemertines that were collected from the same area at the same time. The slender stylet seemed to be abnormally long and attached to a rather small basis. The habitus was similar to that of *Nipponnemertes pulchra* (Johnston, 1837) which I had obtained from ectoproct turf collected subtidally in the Gulf of Maine, USA. However, all of the individuals obtained from the *Lessonia* holdfasts were smaller than 22×2 mm fully extended while gliding. My frequent finding of these relatively small worms, some with developing gonads, indicated that they were living in the holdfasts as a refuge during early life. However, I encountered larger individuals with fully developed gonads, as well as similar juveniles in *Ecklonia* holdfasts stranded on Goat Island Beach at Leigh, New Zealand, a few weeks after the collections had been made at Kaikoura. At the light microscope level, oocytes were found to contain “nuage-like” concretions, which will be referred to as “nuage” in the description.

MATERIALS AND METHODS

Collection, preservation, and preparation of slides of serial sections were described in Riser (1988). Anaesthetised individuals were stretched on a glass plate, and the fixative was applied with a pipette along the length, ensuring that specimens selected for sectioning were fully extended. More than 32 individuals, most of which were sacrificed for proboscis stylet measurement and to determine possible directiveness of blood flow, were obtained from *Lessonia* holdfasts washed up on the beach at Kaikoura, and five specimens were isolated from *Ecklonia* holdfasts collected from the beach at Leigh. Specimens for histological studies were anaesthetised with 7.5% $MgCl_2$; fixed in Hollande's

Z97037

Received 21 October 1997; accepted 26 February 1998

cupri-picri-formal-acetic; embedded in polyester wax; sectioned at 8 μm ; stained with Heidenhain's Azan or Bensley & Bensley (1938) copper chrome haematoxylin counterstained with mucicarmine. Serial transverse sections were made from three specimens, and one was sectioned longitudinally.

SYSTEMATICS

Family CRATENEMERTIDAE Friedrich 1968

Genus *Nipponnemertes* Friedrich, 1968, emended

Cratenemertidae with frontal organ and frontal glands. Cerebral organs large, extend behind brain. Longitudinal muscle fibres between ganglion layer and fibrous core of lateral nerve cords. Rhynchodaeum and oesophagus open together at mouth. Rhynchocoel to posterior end of body. Oesophagus extends from mouth back to brain. Subepithelial oesophageal longitudinal muscles present. Excretory system between brain and entrance of pylorus into intestine. Excretory pores ventrolateral.

Nipponnemertes sanguinea sp.n.

SPECIES DIAGNOSIS: Buff, yellowish, or orange members of the genus with as many as 20 eyes extending in 2 irregular rows from apex of head to region of brain on each side; posteriormost pair usually with hyalin cups. Length to at least 56 mm and width 2.5 mm. Longitudinal ridges on head not evident. Central stylet long, thin; basis barrel-shaped with rounded bottom. Subepidermal glands precerebral, not present behind cerebral organs. Longitudinal muscles of body wall divided anteriorly; some inner longitudinal muscles form proboscis insertion, others continue anteriorly as apex retractors. Each oocyte develops nucleolar satellites which pass into the cytoplasm and enlarge to form discrete elliptical nuage concretions attaining a length of 25 μm . With red blood corpuscles.

DESCRIPTION: External features. The largest specimen was female, 56 mm long by 2.4 mm maximum breadth while gliding. Individuals 12–14 mm long by c. 1 mm diameter when fully extended were round in cross-section and contained developing gonads. Anterior and posterior ends of living individuals are bluntly rounded, posterior end of animals at rest usually broader than anterior; intestinal region of swimming individuals dorsoventrally flattened. Colour varied from buffy white to pale yellow to orange, with reddish lines where groups of red blood

corpuscles aggregated in the blood vessels; ventral surface paler than dorsal; brain lobes pink. The notch at the openings of the cerebral organ canals is distinct in living individuals, and the anterior cephalic grooves extend from there onto the dorsal surface. Posterior cephalic grooves were not observed.

Body wall. The epidermis is very high with bacillary cells so numerous in sectioned material that they appear more abundant than serous and mucous cells combined. Subepidermal (cephalic glands, *auctorem*) glands are intermingled with the longitudinal muscles anterior to the brain. Some of these form a layer of relatively uniform height beneath the cutis. A few basophilic (serous) subepidermal glands occur, primarily anterior to the openings of the cerebral canals. The cutis contains occasional neurons associated with the outer nerve plexus, and widely scattered cell bodies of fibrocytes. It is thick anteriorly, and in histological preparations shows the effects of contraction of various tissue elements (see Fig. 6) so that, where highly compressed, the amorphous intercellular substance is not evident, and the tissue appears totally fibrous. The layer is very thin and is dominated by fibrillar elements in the intestinal region. The muscle fibers forming the circular layer of the body wall are not bound together in bundles and appear to be isolated in the amorphous intercellular substance as recorded for *N. pulchra* by Pedersen (1968). The layer is very thick in the rectal region of the body, and forms a sphincter between the rectum and anus. Non-fasciated "diagonal" muscle fibres are apparent on occasion on the inner surface of the circular muscle layer; some of these are derived from the dendritic processes of the radial muscles, and others are isolated fibres from the inner surface of the circular layer displaced by contraction as the result of fixation. Rare, isolated, diagonal fibres have been observed in surficial sections, but never forming a distinct cross-hatched layer. Retraction of the apex of the head to form a ventral furrow deepens the atrium behind the mouth, and results in the frontal glands being pressed between the atrial epithelium and the circular muscles ascending to the rhynchodaeum. The longitudinal muscles of the body wall divide into inner and outer bundles of fibres near the juncture of the stomach and oesophagus. The outer bundles form a layer of uniform thickness (Fig. 2), interdigitated with the subepidermal glands abutting the cutis. Most of the inner bundles form the proboscis insertion, and others continue to the apex, concentrating around the rhynchodaeum and oesophagus; some intermingle

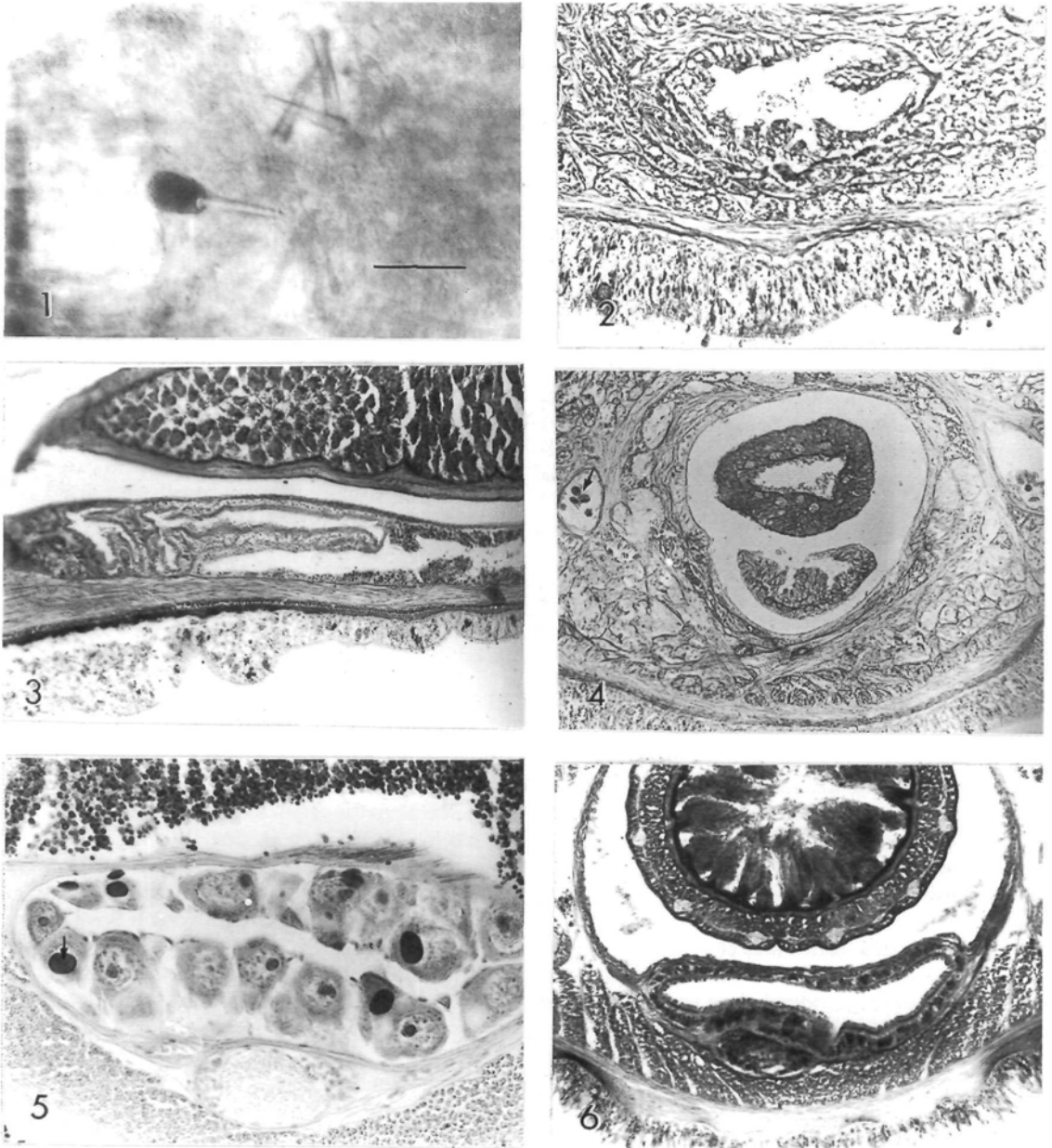


Fig. 1-6 *Nipponnemertes sanguinea*. 1, Stylet apparatus *in situ*; central stylet slightly tilted (bar = 0.08 mm). 2, Cross-section through oesophagus. 3, Longitudinal section through pylorus; stomach retracted against pylorus. 4, Cross-section slightly behind mouth; proboscis and floor of oesophagus everted into atrium. Erythrocytes indicated by arrow. 5, Cross-section through an ovary. Nuage concretion indicated by arrow. 6, Cross-section through pylorus above anterior end of intestinal caecum, folds in cutis to either side.

with the frontal glands, and a few form a distinct band beneath the dorsal glands posteriorly, and enclose the combined necks of the 3 glands prior to insertion around the frontal organ. Radial muscles

are abundant; their fibres ramify in the circular muscle layer and insert in the myoseptum. They frequently accompany nerves from the lateral nerve cords to the nerve plexus internal to the circular

muscle layer. Some dorsoventral fibres cross beneath the rhynchocoel to pass around and cross beneath the foregut. Dorsoventral and radial fibres enclose the lateral nerve cords and the intestine. These fibres form a thick layer around the rectum producing a sphincter that is separated from the body wall circular muscles by a thin layer of longitudinal muscles. The nerve plexus internal to the circular muscle layer is much more obvious than the one associated with the plexus on the outer side of these muscles. Surficial sections show the cell bodies of the internal plexus to be arranged in rows between longitudinal muscle bundles. Dendritic processes from these neurons connect the two plexi at intervals. The tissue between the longitudinal muscles and internal organs is a collenchyme consisting primarily of amorphous intercellular substance with few cell bodies, and rare connective tissue fibres. This tissue does not condense, as does the more fibrous cutis, and occupies a large area between the longitudinal muscles and gut in the preintestinal region.

Digestive system. The mouth is subapical, opening a very short distance behind the frontal organ. It opens into a chamber from which the rhynchodaeum and oesophagus immediately diverge. The oesophagus is short, extending from the mouth to the brain. The epithelium of the ventral wall meets the epidermis without intergradation. A few cells in the epithelium contain granules, otherwise they are empty with no indication of glandular secretion. Small bundles of subepithelial longitudinal muscles enclose the oesophagus (Fig. 2). The stomach is short, with rugae of various heights allowing for expansion and elongation (Fig. 3). Its epithelium is dominated by large mucous cells, and is densely ciliated. The pylorus (Fig. 3, 6) occupies about half the length of the foregut and, although ridged, does not have marked rugae. The epithelium contains some mucous cells, but they stain much more weakly than do those of the stomach. The intestinal caecum extends anteriorly beneath the pylorus (Fig. 3, 6). The first pair of intestinal diverticula extend forward to either side of the pylorus. They are long, and contraction of the preintestinal region may carry them forward beyond the bases of the cerebral organs. Dorsoventral and radial muscles pass between the intestinal caeca. The intestine continues as a straight tube behind the last caeca and is enclosed by radial fibres. The epithelium of this region shows reduced activity. The junction of the intestine and rectum is beneath the transverse commissure of the nerve cords. The rectal lumen is small, and the tall ciliated pseudostratified epithelium is not folded. The

vacuolated cells of the epithelium indicate a mucoid activity, and while basophilic secretions have not been observed in the cells, some have always been present in the lumen at the apices of the cells.

Proboscis apparatus. The rhynchodaeum is enclosed by circular muscles throughout its entire length. The rhynchodaeal epithelium extends to the dorsal lip of the mouth and is cuboidal in the empty organ, but when the proboscis projects into it, the cells form a flattened pavement layer. The proboscis insertion arises immediately in front of the brain commissures and is derived from an inner layer of longitudinal muscle bundles. Twelve longitudinal nerves are present in the proboscideal nerve plexus. The 2 accessory stylet pouches each contain 4–7 accessory stylets measuring 55–80 μm in length. The central stylet is thin and is attached to an ovate basis which is slightly broader basally, up to 30 μm diameter, than apically. A st/so ratio of 1.1–1.8 ($n = 23$) reflects the difficulty of orienting the stylet in one plane. The shape of the basis of the central stylet results in tilting (Fig. 1), so that accurate measurements can not be guaranteed. The proboscis is attached anterior to the middle of the rhynchocoel.

Blood vascular system. The 2 lateral blood vessels lie between the brain and rhynchocoel in the highly compressible amorphous intercellular substance. The dorsal blood vessel arose from the right lateral vessel posterior to the cerebral organs in all living specimens in which it was possible to determine orientation, and also in the specimens which were sectioned, and it exited the rhynchocoel posterior to the cerebral organs. The lateral vessels have valves which are not apparent in the dorsal vessel nor in the anterior cephalic loop connecting the 2 sides. This is similar to the vessel morphology of *N. pulchra*. The lateral vessels lack intrinsic muscles, but the walls are in intimate contact with dorsoventral muscles. Segmental vessels connecting the dorsal vessel with the lateral vessels are few in number and are widely spaced. Observation of blood flow in living animals was facilitated by the presence of the clumps of erythrocytes. It basically follows the description of circulation in enoplans by McIntosh (1873). The dorsal blood vessel contracts independent of body movement, forcing the blood forward into the rhynchocoelic vessel and out through the transverse vessels into the lateral vessels. Back flow of erythrocytes in the lateral vessels is controlled by the valves. Erythrocytes are nucleated, more round than elliptical, 6–11 μm in diameter, but after histological fixation they are variable in shape, as well as

crenulate. Erythrocytes packed with stainable material shrink less than those containing small amounts.

Excretory system. The nephric tissue extends dorsal and internal to the lateral nerves, from beneath the posterior ends of the cerebral organs to the region of the origin of the pylorus. Some of the termini of the capillaries are scattered in the collenchyme in addition to those intimately associated with the lateral blood vessels. A single efferent duct extends ventrolaterally from near the posterior end of the system on each side, but, in sections, a few capillary termini are usually present for a short distance behind the ducts.

Frontal organ / frontal glands. The frontal organ occupies the apex of the head and, in actively moving individuals, has the appearance of a large ciliated doughnut. The circular muscles of the body wall diverge around its base to wrap around the necks of the 3 frontal glands. These glands are large and about equal in size, occupying much of the precerebral medulla. Their necks pass beneath the cerebral vascular loop between radial muscles that cross beneath the loop and the rhynchodaeal circular muscles. The 2 lateral glands sometimes extend back alongside the dorsal ganglia in sections, as the result of differential contraction following fixation.

Cerebral organs. The cerebral organs are elongate and somewhat gourd shaped, slightly expanded posteriorly. They extend behind the brain, and the cerebral nerve enters near the middle of the organ of fully extended individuals. The duct is not branched, and the ampulla is large.

Reproductive organs. All specimens were collected in February or March, and the female gonads contained only gonial cells and young oocytes. The anterior ends of these immature gonads were dorsal to the lateral nerve cords, and expanded posteriorly between the nerve cords and the intestine. The first pair of gonads is situated behind the opening of the pylorus into the intestine. One to three nuage concretions (paranuclei of Hubrecht 1887), in various stages of development, were present in each oocyte. Preformed gonopores were not present.

TYPE DATA: **Holotype.** Te Papa Museum of New Zealand ZW1456. 15 slides; transverse sections of anterior half of female 23 mm long.

Paratype. National Museum of Natural History, Smithsonian Institution USNM178247; 8 slides transverse sections.

ETYMOLOGY: L.; sanguineus, a, um, of blood, bloody.

TYPE LOCALITY. Kaikoura, New Zealand, from holdfast of *Lessonia variegata* washed up on beach. 19 February 1986.

DISCUSSION

Morphology

In delineating the morphological characters that could be of use in taxonomic treatment of generic and higher units of the Enopla, Crandall (1993) noted the consistent presence of myofibrillae in the longitudinal nerve cords of the Cratenemertidae. This feature should be added to the family definition. Berg (1972) described in detail the histology and organology of *Nipponnemertes pulchra*, noting various artifacts which previous authors had considered to be of systematic value. At the present time, it appears that many of the morphological characters defining the genus *Nipponnemertes* are autapomorphies of the family Cratenemertidae, and some of those included in the diagnosis of species are autapomorphies of the genus.

Gliding immature individuals of *N. pulchra* and *N. sanguinea* are of rather uniform diameter, and the preanterior groove region of the head is long. In most published figures of the head of *N. pulchra*, the region anterior to the anterior cephalic groove is contracted, which may account for the presence of the parallel longitudinal ridges.

Swimming *N. sanguinea* are oar shaped, whereas contracted animals range from sausage shaped to isosceles triangular with a broad base.

Fixation-induced contraction of the longitudinal muscles usually carries the frontal organ posteriorly on the ventral surface so that initial transverse sections are of the dorsal surface of the head, and the rhynchodaeum arches anterior to the mouth. Similarly, contraction of the subepithelial foregut longitudinal muscles draws the stomach forward into the oesophagus, everting the ventral floor of the latter into the rhynchodaeum (Fig. 4). The ventral floor of the oesophagus and stomach is protruded through the "mouth" as a result of this contraction in Berg (1972: fig. 17). These types of "artifacts" that do not rupture the tissues duplicate conditions occurring during various activities of the living animal and are not of systematic value.

The nucleolar satellites in the oocytes of *N. sanguinea* initially appear as more deeply stained granules centrally in the nucleus. They then coalesce to form a single body almost the diameter of the nucleolus (Fig. 5). They appear to be dislodged by

the nucleolar production of a subsequent nuage, and migrate peripherally in the nucleoplasm, where they continue to elongate and increase in size. There is some increase in size after passing into the ooplasm, and a deeper staining region of granules is apparent between the concretion and the apex of the oocyte (Fig. 5). The nuage-like material in the ooplasm appears to be a solid basophilic structure which stains uniformly, and I assumed that the large ones lying free in the cavity of the ovary were dislodged during sectioning. *N. sanguinea* does not form perinuclear rosettes of nucleolar satellites associated with the production of nuage, as figured by Bürger (1897–1907) in the oocytes of species of *Drepanophorus*. *N. pulchra* spawns in northern latitudes in early summer, and each ovary produces a number of ova according to Berg (1972). The condition of the ovaries, and the apparent absence of mature sperm in the specimens of *N. sanguinea* utilised in this description, implies a similar reproductive pattern. The nature of the nuage-like material would require histochemical and TEM observations, and its fate in oogenesis or possibly embryogenesis necessitates obtaining specimens in late spring or early summer.

Systematics

Nipponnemertes sanguinea differs from *N. pulchra* in several characters: the shape of the basis of the central stylet, the absence of an accessory stylet in the basis, nuage formation in oocytes, and the presence of red blood corpuscles. Berg (1972) noted that it is difficult to observe the posterior cephalic grooves of pale individuals of *N. pulchra*. This may account for my failure to observe them on the head of *N. sanguinea*. The parallel longitudinal ridges reported to be present on the head of *N. pulchra* were not present on any of the specimens of *N. sanguinea*; however, I have never observed them on *N. pulchra* from the Gulf of Maine, and they may be temporary structures resulting from apical contraction.

Amphiporus flavens Monastero, 1930 and *A. vitae* Monastero, 1930 (both classed as *species inquirenda* by Gibson & Crandall 1989) appear to be species of *Nipponnemertes* with circulating red blood and a central stylet similar to that of *N. sanguinea*. The central stylet of the species described as *Amphiporus pulcher* (from Naples?) by Bürger (1895 pl. 9, fig. 8; 1897–1907 pl. 13, fig. 6), has a basis shaped differently from either of these or from those of *N. pulchra* and *N. sanguinea*. Bürger described and figured red blood corpuscles from "*Amphiporus pulcher*" in both of these publications. In 1895 and again in 1904, he distinguished two sub-

species based upon body and eye colour, *A. pulcher pulcher* and *A. pulcher allucens* (he referred to pl. 4, fig. 35, as *Amphiporus allucens* nov. sp.).

Wheeler (1934) recognised nucleoli in the oocytes of the species that he identified as *Amphiporus marioni* Hubrecht, 1887, and the "paranuclei" which had been recorded in the original description of the species, although F. Crandall (pers. comm.) has advised me that Wheeler's specimens are not Hubrecht's *marioni*, and that "paranuclei" also occur in *Amphiporus falklandicus* Wheeler (1934). Both species transferred to *Nipponnemertes* by Berg (1985). Wheeler (1940) commented on the size of the nucleoli in the oocytes of *Amphiporus africanus* Wheeler, 1940 (transferred to *Nipponnemertes* by Berg 1985), but made no reference to "paranuclei" which are absent in that species but are present in Wheeler's preparations of *N. lecointei* Burger, 1904 (F. Crandall pers. comm.). The species from Chile described as *Amphiporus pulcher* by Isler (1900, 1902) is a male *Nipponnemertes* with red blood corpuscles; however, the eyes are very large; basophilic subepidermal glands are present dorsally to near the entrance of the pylorus into the intestine and continue laterally and ventrally into the intestinal region in contradistinction to *N. sanguinea*. *N. moseleyi* (Hubrecht, 1887) is described as having subepidermal glands forming a lateral row, but there is no evidence of such an arrangement in Isler's specimen.

Riser (1991) noted that the distribution of the heteronemertean *Notospermus geniculatus* (Delle Chiaje, 1828) extended from the Mediterranean Sea along the west coast of Africa, to Australia, New Zealand, South Pacific islands, Japan, and the eastern Pacific coast from California to Panama. Wheeler (1934) noted the extension of the Mediterranean nemertine fauna to the Southern Hemisphere as far as South Africa, and the "complete discontinuity" with the "Falkland sector" fauna. The inadequate descriptions of species of *Nipponnemertes* from the Mediterranean Sea, as well as of the several Austral species described by Bürger (1904), Hubrecht (1887), and Wheeler (1934), make it impossible to assign the New Zealand species to any of them. *N. scoresbyi* (Wheeler, 1934) from Antarctica has red blood corpuscles (F. Crandall pers. comm.) as I have also observed in the slides of the specimen from Chile described as *Amphiporus pulcher* by Isler (loc. cit.); however, even in the absence of essential data necessary for recognising (identifying) these species, available data indicate that they are not conspecific with *N. sanguinea*.

Generic characters of nemertean are determined

from serial sections. Differences that distinguish species, however, frequently involve colour and eye pattern, which require observation of living animals. Wheeler (1934) separated his collections in the field on the basis of coloration and habitus, and included coloured figures of most of them in his publication. Many of the species he described were obtained from "kelp" holdfasts snagged from the bottom with specially devised grappling equipment. Essential information (or illustrations) on proboscis armature, however, was not included in most of the descriptions.

Berg (1972) reported a direct correlation between eye number and age (as indicated by size) for *N. pulchra*. Coe (1943) stated 20–40 eyes per side, but figured in excess of 40 on a very unusual shaped head. The figures of *Amphiporus pulchra* by Bürger (1895, 1897–1907) and *Amphiporus flavens* by Monastero (1930) show an eye pattern similar to that observed at times in *N. sanguinea*. The arrangement of the eyes in published figures of *N. pulchra* can occur in that species. However, as in *N. sanguinea*, gliding individuals of uniform diameter in which the head is not demarcated from the rest of the body have the eyes in a single irregular row on each side, except for three or more in a horizontal line along the anterior edge of the anterior cephalic groove. During movement of the precerebral region, it can be seen that there is a row of lateral eyes, and the other eyes are dorsal. The latter eyes are drawn medially, especially when the apex of the head is retracted ventrally. In most preserved specimens, this configuration prevails, and the lateral versus dorsal arrangement is distinct. In small specimens of *N. pulchra* (<30 mm long), from New England, the anteriormost pair of eyes characteristically is very large and probably represents the initial pair in development. In addition, these individuals have many cup-shaped eyes. In contrast, the posteriormost pair of eyes of *N. sanguinea* is the largest, and most other eyes are simply round, not cup-shaped.

Information on proboscis armature is essential for identification of hoplonemertean. The shape of the basis of the central stylet is constant in several genera, and the difference in the shape of this element between *N. pulchra* (elliptical tapered to either end) and *N. sanguinea* ("jug" shaped) may prove to be more than a species distinction. I have not observed the shape of the basis of the central stylet in New England material of *N. pulchra*, as in the figures by Coe (1943). The presence of red blood corpuscles and the production by oocytes of nuage concretions similar to those reported here, are apomorphic char-

acters, which may be significant in phylogenetic systematics of the family Cratenemertidae.

ACKNOWLEDGMENTS

Advice and criticism by F. B. Crandall, C. H. Ellis, K. J. Eckelbarger, and J. L. Norenburg was of significant value in the writing of this manuscript. Suggestions by the editor have improved the readability of the presentation. The loan of Isler's slides of "*A. pulcher*" by Dr G. Hartwich of the Museum für Naturkunde, Berlin was of special importance.

This is Contribution No. 226 from the Marine Science Center, Northeastern University, Nahant, MA 01908, USA.

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