

## ***Riserius pugetensis* gen. n., sp. n. (Nemertina: Anopla), a new mesopsammic species, and comments on phylogenetics of some anoplan characters**

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*Key words:* nemertine, systematics, phylogeny, meiofauna

### **Abstract**

*Riserius pugetensis* gen. n., sp. n. is described from the northwest coast of Washington, U.S.A. It is probably a heteronemertine and, as such, would be the first known mesopsammic member of that order; it lives in the interstices of medium to coarse, moderately clean sands. Its morphology presents some attributes considered characteristic of mesopsammic fauna. The effect of some of these attributes is a generalized appearance of anatomical 'simplicity' and, as with other mesopsammic metazoans, this presents difficulties in distinguishing between primitiveness and reduction. In the new species such problematic features include the lack of subepidermal glandular cells and connective tissue, reduced proboscideal musculature, simple blood-vascular system, and the presence of a 'secondary', outer circular musculature in the body wall. The general appearance of this new species is very similar to the so-called palaeonemertine *Hubrechtella* and characteristics of both suggest relationship with the baseo-discid heteronemertines. These relationships are explored in light of a modified interpretation of proboscideal musculature, a traditional cornerstone of heteronemertinean taxonomy.

### **Introduction**

*Riserius pugetensis* gen. n., sp.n. fits a basic structural definition of the Heteronemertina but resembles palaeonemertines in its simplicity. The orders Heteronemertina and Palaeonemertina are usually defined on the basis of body wall organization, arrangement of the dermis, and position of the nervous system (e.g. Hylbom, 1957; Gibson, 1982). Heteronemertina are defined as having a body wall constructed as follows: an outer zone (dermis) containing connective tissue, subepidermal glands and sometimes circular muscle fibers; an outer longitudinal musculature; the central nervous system between this longitudinal musculature and a deeper circular musculature

(Gibson, 1982). Palaeonemertina (*sensu* Iwata, 1960) are Anopla having the nervous system at the base of the epidermis and lacking outer longitudinal musculature and subepidermal gland cells. Although not explicit on the issue, Bürger (1895) effectively recognized the palaeonemertines as paraphyletic, but the heteronemertines as monophyletic. In contrast, Hylbom's (1957) phylogenetic scheme, which echoed the opinions of several other principal nemertologists, results in both orders being at least paraphyletic. A 'cutis' comprising the subepidermal cell bodies of glandular cells and often an associated zone of connective tissue, is characteristic of heteronemertines. Potential homologues of these cutis glandular cells are known from several palaeone-

mertinean genera, e.g., *Hubrechtella* Bergendal, 1902, in which submerged cell bodies form a region of pseudostratified epidermis (Gibson, 1979a; Norenburg, 1985). *Riserius pugetensis* has neither pseudostratified epidermis nor components of a cutis, a condition known among other heteronemertines only from the lineid *Colemaniella albulus* (Gibson, 1981).

Effectively, the order Heteronemertina can be separated from the order Palaeonemertina (*sensu* Iwata, 1960) only by the presence of the outer longitudinal musculature lying between the epidermis and the central nervous system; *i.e.*, this is a synapomorphy for Heteronemertina. However, less discrete longitudinal musculature may also be found in the dermis or among the epidermal cells of Palaeo- and Hoplonemertina (Friedrich, 1936, 1979). Similarly, some species of palaeo- and heteronemertines have a more or less distinct dermal or epidermal outer circular musculature, as seen in *R. pugetensis*.

*Riserius pugetensis* has been alluded to previously as a mesopsammic heteronemertine (Norenburg, 1987, 1988a, b). However, one may legitimately ask, is it in fact a heteronemertine and, if so, is it a relict species of a largely extinct clade or is its simplicity a derived function of its specialized habitat?

#### Material and methods

Six specimens of *Riserius pugetensis* gen. n., sp. n. were collected in August, 1979, from sand at 0 m (near the bottom of a moderate slope), 200 m south of an oil terminal and depot at Richmond Beach along Puget Sound, Washington (47° 40' N, 122° 25' W). Three more specimens were obtained from sand samples collected by divers in July, 1981, from Minnesota Reef near Friday Harbor, San Juan Island, Washington (48° 31' 48" N, 122° 58' 55"), at about 10 to 15 m depth. Sand samples were collected with a trowel to a depth of 5–10 cm, placed in buckets or plastic Whirl-Paks and brought back to the laboratory. Specimens were separated from the sand by swirling a subsample of sand in a bucket with seawater and quickly decanting the water through

a 63- $\mu$ m mesh sieve. The worms were examined while alive with a stereomicroscope and, while lightly squeezed under a coverslip, with a compound microscope utilizing bright-field or Nomarski optics. For preservation and histology specimens were anaesthetized briefly (5–6 min) in 7.5% MgCl<sub>2</sub>, fixed in Hollande's cupri-picri-formal-acetic fixative, and embedded in polyester wax (Steedman, 1960; Norenburg & Barrett, 1987). Transverse and longitudinal serial sections were cut at 5–7  $\mu$ m and stained with Heidenhain's azan or Heidenhain's iron hematoxylin methods.

#### Systematic account

##### *Riserius pugetensis* gen. n., sp. n.

##### Generic diagnosis

Four body-wall muscle strata, outer circular, outer longitudinal, middle circular, and inner longitudinal; cutis (subepidermal glandular cells and connective tissue) lacking. Central nervous system and plexus between outer longitudinal and middle circular musculature; dorsal ganglia not bifurcated posteriorly; without neurochord elements; middorsal nerve from dorsal commissure. Proboscis with inner longitudinal musculature; inner and outer circular musculatures reduced or lacking. Rhynchocoel short; with outer circular and inner longitudinal musculature. Cerebral organs not fused to cerebral ganglia; not projecting into vascular lacunae; open via lateral pits. Transverse cephalic furrow encircles body in front of mouth. Rhynchodaeal aperture terminal; mouth ventral, posterior to cerebral organs. Blood vascular system with single cephalic lacuna; two lateral vessels and one middorsal; supra-anal anastomosis. Cyrtocytes single and clustered, projecting into lateral vascular lacunae; one pair of collecting ducts and nephric pores.

##### *Riserius pugetensis* gen. n., sp. n.

##### Specific diagnosis

Characters of the genus. Cephalic glands and frontal organ lacking. Inner circular musculature reduced and longitudinal muscle plate lacking.

Blood vessels simple, lacking cross-connections, middorsal vessel enters rhynchocoel, precerebral lacuna a single, medial sac. Cerebral organs large; openings deep lateral pits. Rhynchodaeum thin-walled. Rhynchocoel approximately one-quarter of body length. Stomach and intestine histologically distinct, without constrictions or diverticula. Gonochoric.

#### *Type specimens*

Holotype (USNM 149925), and single paratype (USNM 149926) deposited in the Division of Worms, National Museum of Natural History (USNM), Smithsonian Institution, Washington, DC; both specimens were collected 17 July 1981, anaesthetized in magnesium chloride, fixed in Hollande's cupri-picri-formal-acetic fixative and subsequently transferred to 70% ethyl alcohol.

#### *Additional specimens*

Two sets of serial sections of specimens, from the Richmond Beach site, in the author's possession will be deposited in the USNM at a later date. One is a set of three slides bearing transverse serial sections (stained with Heidenhain's iron hematoxylin) of the anterior one-fifth of a specimen. The other consists of eight slides bearing transverse serial sections of two specimens side by side (stained with Heidenhain's azan or Heidenhain's iron hematoxylin).

#### *Type locality*

The top 10 cm of moderately coarse sand at 10 m depth near a reef known locally as Minnesota Reef (near Friday Harbor), San Juan Island, Washington (48°31'48"N, 122°58'55").

#### *Etymology*

The generic designation recognizes the contributions to the study of both nemertines and mesosammic animals by Prof. Nathan W. Riser. The specific designation refers to Puget Sound.

#### **External features**

Gliding specimens reach 15 mm in length and 0.15 to 0.2 mm in diameter. Those with numerous

eggs are somewhat stouter. The epidermis is translucent white with transmitted light and opaque white with reflected light. The body is moderately flattened dorsoventrally when gliding but the cephalic region is cylindrical and has a cephalothricid appearance (Fig. 1). The cephalic region is relatively elongate; in a 10 mm specimen, the pair of conspicuous pits leading to the cerebral organs is about 500  $\mu\text{m}$  from the cephalic tip. An epidermal furrow encircles the body 500  $\mu\text{m}$  farther posteriad, but anterior to the mouth (Figs. 1–3). This furrow is directed posteriad dorsally and antieriad ventrally. The cephalic tip bears a small dimple, the rhynchodaeal pore, which is surrounded by a few elongate cilia, but these are shorter than typical sensory cilia. With gentle squeezing of living specimens under a coverslip one can occasionally observe the pair of dorsolateral nephric pores and also individual mucoid strings emanating from large gland cells. These appear to account for the sticky, multi-point haptic reaction exhibited by this species. When severely agitated, members of this species have a tendency to coil. There is no indication of a caudal cirrus.

#### **Body wall**

Epidermis in sections is 6–10  $\mu\text{m}$  thick, with a ciliary border of 4–5  $\mu\text{m}$ . Two cell types predominate and are about equally represented (Figs 4–11). One is a homoserous glandular cell (Norenburg, 1985), which forms slender to spherical goblets. The content of this cell is first an azanophilous or eosinophilous (non-metachromatic with toluidine blue) matrix containing many fine, more densely-staining granules. Upon contact with seawater the goblet content changes appearance, starting with the portion outside the goblet and proceeding inward. The exposed secretion is homogeneously metachromatic with toluidine blue, intensely azanophilous or olive-green to blackish-brown with hematoxylin. The goblet cells are separated by attenuate ciliated cells with an expanded distal surface. The goblet cells do not have a uniform distribution and there are numerous patches of ciliated cells without goblets.

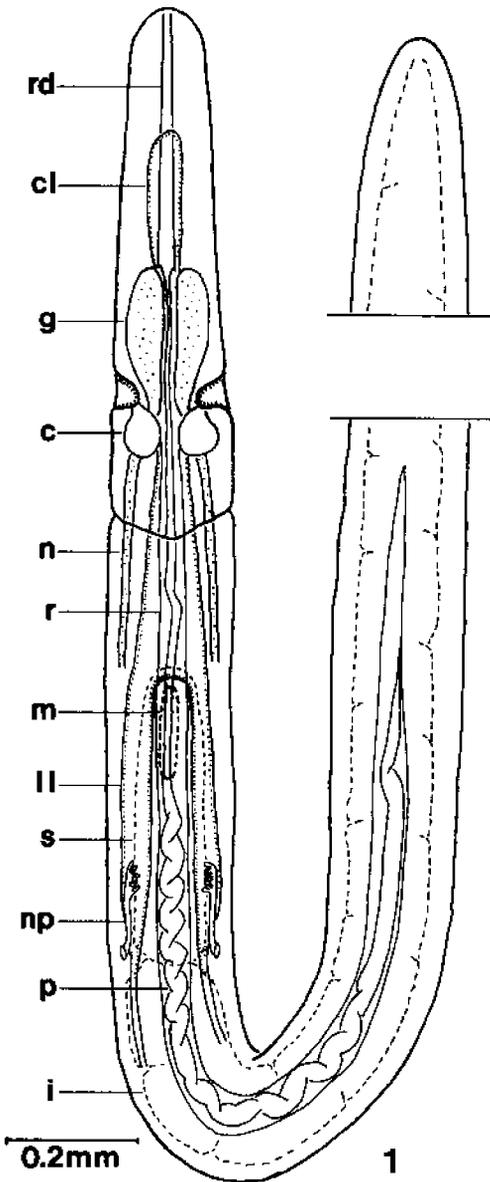
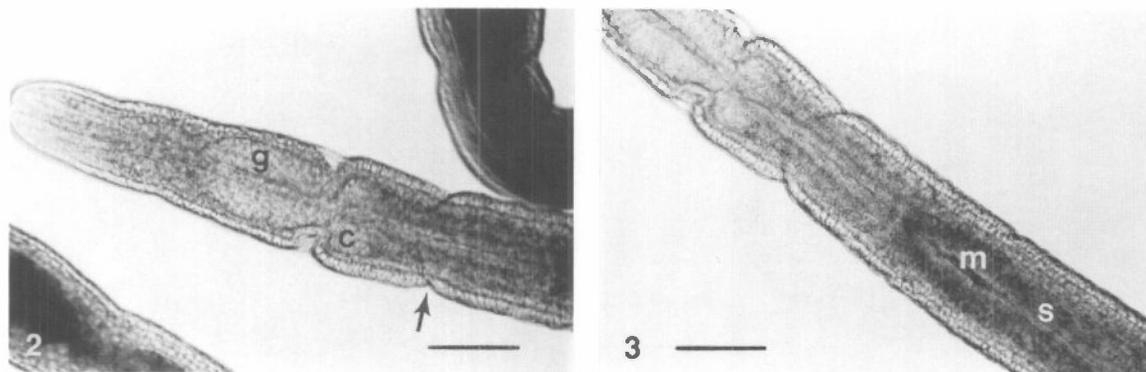


Fig. 1. *Risertius pugetensis*. Schematic figure of anterior one-quarter and posterior terminus of body showing organization of major structures as seen from dorsal perspective. Abbreviations: c = cerebral organ; cl = cephalic blood lacuna; g = cerebral ganglion; i = intestine; ll = lateral blood lacuna; m = mouth; n = lateral nerve cord; np = nephridial complex; p = proboscis; r = rhynchoeol; rd = rhynchodaeum; s = stomach.

Goblet cells are lacking entirely in the first 15–20  $\mu\text{m}$  of the cephalic tip. The ciliated cells of these patches are short (6  $\mu\text{m}$ ), columnar cells

and can be seen to contain large spherical nuclei and granular cytoplasm. A third cell type, the bacillary cell, is irregularly scattered among the goblet cells but is present in much lower numbers. It is slender and contains small, discrete granules that are weakly azanophilous or eosinophilous. Beneath the epidermis is a thin zone (0.5  $\mu\text{m}$ ) of granules, followed by a thin dermis (1  $\mu\text{m}$ ), and then by a sparse, subepidermal, outer circular musculature (OCM) consisting of widely spaced single fibers (only poorly observable, even in tangential sections). The latter is followed by a relatively well developed outer longitudinal musculature (OLM) (5–10  $\mu\text{m}$ ); both are sparse precerebrally (Fig. 4). Precerebrally, the OLM gradually thins as it proceeds anteriorly by sending fibers into the cephalic medulla (Fig. 12); thus, there is not a discrete split of the OLM. Some of these fibers are closely associated with nerve tracts. Others bend in front of the cerebral ganglia, where some comprise a very diffuse proboscis insertion and others become confluent with either the inner longitudinal musculature (ILM) or the longitudinal muscles of the rhynchoeol. Posterior to the cerebral ganglia OLM is underlain by the lateral nerve cords and a nerve plexus (Figs 8–11). Below this is a single layer of middle circular musculature (MCM) followed by a well developed ILM. These layers surround the rhynchoeol, gut, blood vessels and gonads. The MCM extends anteriorly to about the rhynchodaeum. The ILM forms a prominent band along the dorsolateral surface of each of the two anterior lacunar portions of the lateral blood vessels (Figs 7–9, 11), but is lacking along a narrow, dorsomedian strip of the rhynchoeol wall between the two lacunae (Fig. 11). This strip extends for the entire length of the rhynchoeol and at this site the circular muscles of the rhynchoeol are confluent, but apparently not interwoven, with the MCM of the body wall. The rhynchoeol has separate outer circular and inner longitudinal musculature. The circular muscles form occasional slings which insert dorsolaterally in the OCM of the body wall. The stomach is invested by a sparse musculature of circular fibers. Some of these extend laterally to the OCM. In the vi-



Figs 2–3. *Riserius pugetensis*. Photomicrographs of live specimen. 2. Anterior, cephalic region showing large lateral cerebral organ openings and dorsal aspect of annular cephalic furrow (arrow). 3. Ventral view of posterior cephalic region showing annular furrow and mouth. Abbreviations as in Fig. 1. Scales = 150  $\mu\text{m}$ .

cinity of the stomach, some of the inner circular muscle fibers extend to the OCM and act as dorsoventral muscles. A longitudinal muscle plate between gut and rhynchocoel was not discerned.

In the region between the cerebral organs and the mouth, there are 8 to 10 large gland cells (10–12  $\mu\text{m}$ ) located in the parenchyma on each side of the body. These are reminiscent of cephalic gland cells of palaeonemertines, staining weakly with aniline blue and appearing pale yellow with hematoxylin. These may be the same as cells referred to as salivary cells in other species. A communication with the body surface could not be identified for these cells. In the vicinity of the two excretory ducts there are several clusters of various-sized droplets. These also are in the parenchyma and are reminiscent of neurosecretory material. The typical heteronemertine subepidermal glands are lacking entirely.

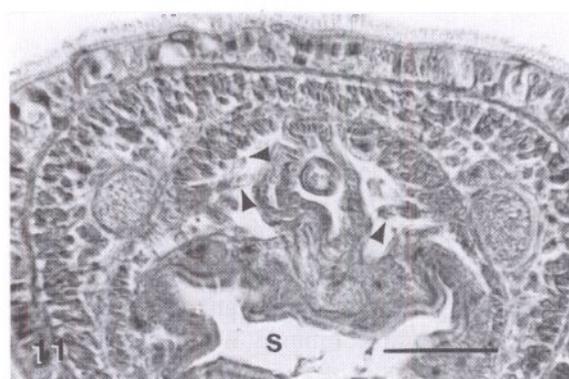
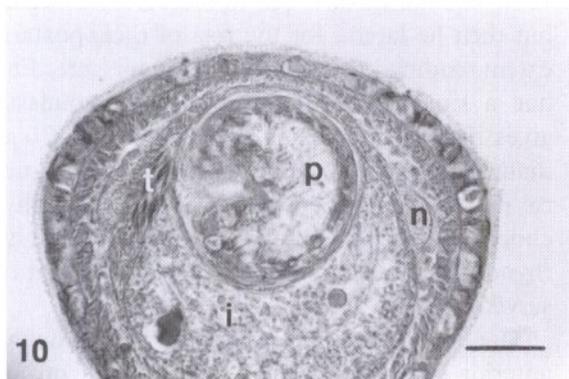
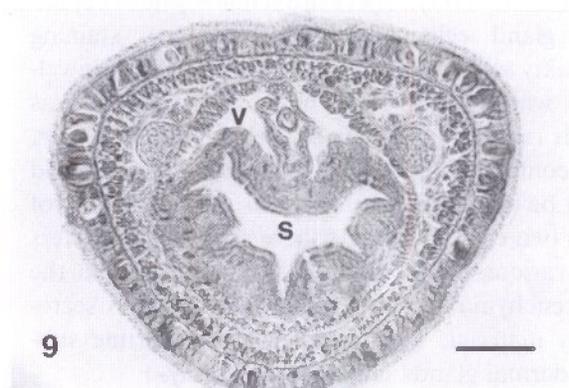
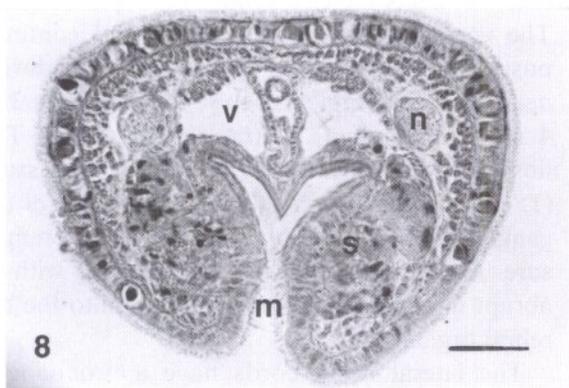
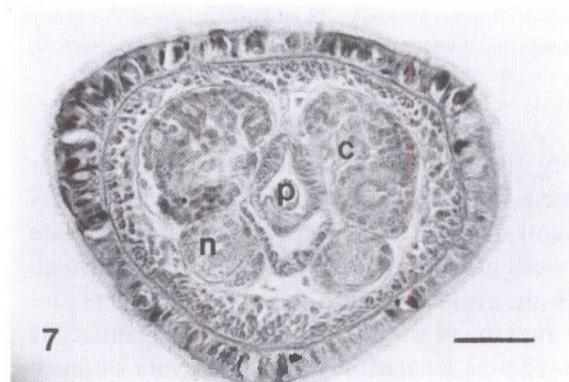
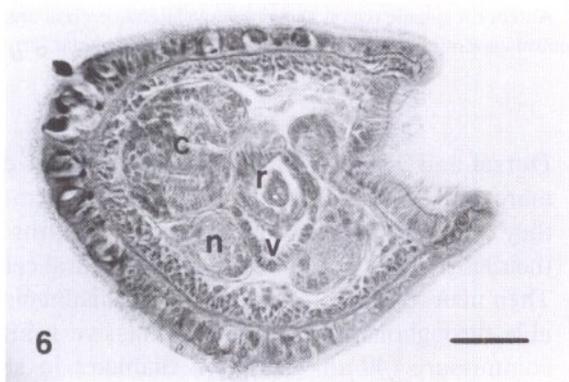
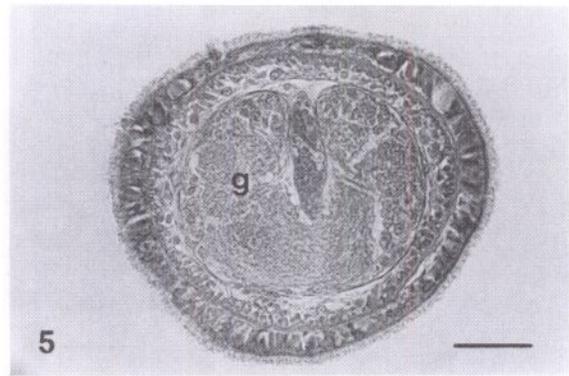
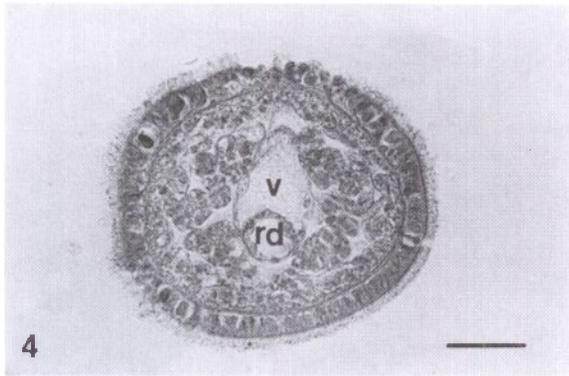
### Nervous system and sensory structures

The central nervous system, consists of four cerebral ganglia, two lateral nerve cords and a dorsal nerve. Each of the two lateral lobes consists of a fused dorsal and ventral ganglion and is an elongate structure about 250–300  $\mu\text{m}$  long (from anterior margin to cerebral organ). In transverse section, maximum combined width of the two lobes is about 60% of cephalic width (Fig. 5).

Dorsal and ventral ganglia of a lobe are not demarcated from each other externally. Internally they are separated for the posterior two-fifths of their length by a horizontal wedge of neural cells. Their neuropils fuse anteriorly but are distinguishable throughout their length. A massive ventral commissure (40  $\mu\text{m}$  minimum diameter in section) connects the two ventral neuropils (Fig. 5). The ventral neuropils are simple and continue posteriorly as the lateral nerve cords. The dorsal neuropils are complex, each presenting from 2 to 4 major fiber tracts in transverse section. The dorsal ganglia are united by a dorsal commissure (15  $\mu\text{m}$  diameter) near the anterior margin of the ganglia, slightly anterior to the ventral commissure. The dorsal neuropil ends posteriorly with an abrupt lateral flexure which extends into the cerebral organ.

The lateral nerve cords have a pronounced ventromedial flexure below the cerebral organs, but then lie lateral for the rest of their posterior extent, ending in a supra-anal commissure. Each has a single neuropil. The dorsal commissure gives rise to a nucleated dorsal nerve (5–10  $\mu\text{m}$  diameter) which extends posteriorly, in the neural plexus, along the dorsal midline of the rhynchocoel. It could not be detected beyond the rhynchocoel. A rhynchocoelic nerve was not observed.

The cerebral ganglia do not have well-defined anterior faces from which nerve tracts project.



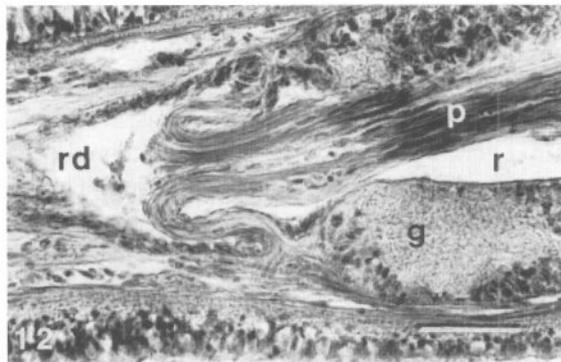


Fig. 12. *Riserius pugetensis*. Histological sagittal section through proboscis insertion. Scale = 25  $\mu\text{m}$ .

Rather, each lobe gradually dissolves to form 3 to 4 major tracts that extend anteriorly to the cephalic tip. Each tract is accompanied by muscle fibers and abundant neural cells that are continuous with the neural cell coat of the ganglia. Neurochord elements are lacking. A pair of nerves extends along the ventrolateral margins of the stomach and are usually somewhat embedded in its gland cell layer. There are at least two cross connections (commissures) between these. Their origin and distal extent were not determined. Presumably these are the homologues of oesophageal nerves.

Ocelli and statocysts are lacking. Besides the pair of cerebral sensory organs (CSO) and their associated lateral pits, the only other potential sensory structures are the few short cirri adjacent to the rhynchodaeal pore. A frontal organ (pore) was not observed. The CSO lie posterior to and are not fused with the cerebral ganglia and do not penetrate the ILM or the vascular system. Maximum length and diameter of the CSO is about 250  $\mu\text{m}$  and 50  $\mu\text{m}$  respectively. The entrance to each CSO is in a deep lateral pit in the body wall

even with the posterior margin of the cerebral ganglia (Figs 1–3, 6). Each pit is shaped somewhat like a postero-medially directed funnel, with a surface opening of about 50  $\mu\text{m}$  diameter and a gradual indentation of the body wall anteriorly but an abrupt margin or lip posteriorly. The pit is lined with specialized ciliated cells (12  $\mu\text{m}$  tall) bearing few very elongate cilia (14  $\mu\text{m}$  long) and narrows to give rise to the ciliated canal of the CSO. The CSO nerve lies immediately dorsal to the canal at this point. A little further posterior (5–7  $\mu\text{m}$ ) the canal twists abruptly back to the body wall and abuts the OLM. This portion of the canal is surrounded by neural (bipolar?) cells. The canal extends posteriorly along the outer longitudinal musculature for another 35–40  $\mu\text{m}$  and is flanked medially by more neural cells that surround the cerebral organ nerve in this region. The ciliated canal ends blindly and the cerebral organ nerve ends against this blind terminus. There is a relatively large pool of non-stained secretory droplets accumulated at the terminus but there are very few glandular cells in evidence in the rather large cerebral organ (Fig. 7). These are scattered individually throughout the organ and their content did not stain with azan or hematoxylin techniques. Most of the bulk of this organ is made up of relatively small neural cells.

### Proboscis complex

The proboscis and rhynchocoel extend for about 20 to 25% of body length. The proboscis is frequently somewhat coiled and is up to 40% of body diameter (Fig. 10), but about the first millimeter is extremely slender (Figs 6–9). The proboscis is described in its everted position. The lining epidermis is up to 10  $\mu\text{m}$  thick and consists

Figs 4–11. *Riserius pugetensis*. Histological transverse sections. 4. Section through precerebral region, showing cephalic blood lacuna and rhynchodaeum flanked by longitudinal muscle bundles. 5. Section through cerebral ganglia and ventral commissure. 6. Oblique section showing opening to cerebral organ on the right and, more posteriorly, cerebral organ with ciliated canal on left. 7. Section showing glandular region of cerebral organ on right. 8. Section through mouth at bifurcation of medial blood lacuna into two lateral lacunae. 9. Section through stomach and lateral lacunae. 10. Section showing intestinal region and mature testis. 11. Section through lateral blood lacunae showing clusters of cyrtocytes (arrows). Abbreviations: t = testis; v = vascular system; others as in Fig. 1. Scales = 25  $\mu\text{m}$ .

of: modified ciliary cells with few, stout bristles; large, goblet gland cells with characteristics similar to those of the epidermis; and cells containing pseudocnidae (terminology after Martin, 1914: 272), usually arranged in parallel in clusters of 4 or 5. The pseudocnide appears as a slender, clavate capsule ( $0.5 \times 13 \mu\text{m}$ ) enclosing an eversible, thread-like tubule (about  $30 \mu\text{m}$  long). The epidermis is underlain by a sparse nerve plexus: in one specimen at least one longitudinal nerve could be consistently recognized. Underneath the neural plexus, in only a few longitudinal sections, occasional circular fibers seemed to be present. I am not convinced that this is musculature. The remaining neural plexus is underlain by a well-defined, single layer of longitudinal muscle fibers. Inner circular musculature and distinct endothelium were not detectable even in longitudinal sections, nor were muscle crosses. Rhynchocoel musculature is described earlier; a distinct endothelium was not recognized here either. The proboscis retractor muscle ends in the longitudinal muscles of the posterior extremity of the rhynchocoel. The rhynchodaeum is thin-walled (Fig. 4) and (about 50 to  $100 \mu\text{m}$  posterior to its invagination) is invested posteriorly by longitudinal muscle fibers confluent with that of the rhynchocoel and some that extend into the body wall OLM.

#### Alimentary canal

The mouth is an elongate opening,  $80 \mu\text{m}$  long, located about  $300 \mu\text{m}$  posterior to the cerebral ganglia. Its interior margin (lip) is a zone of large columnar cells bearing a sparse border of relatively long cilia (Fig. 8). This zone is surrounded by glandular cells indistinguishable from those of the stomach proper. Immediately above this lip the buccal cavity is lined by a very dense 'brush border' (cilia or microvilli) and its epithelium rapidly grades into that of the stomach. The stomach's moderately convoluted wall is 10 to  $20 \mu\text{m}$  thick and comprises large spherical gland cells whose necks project to the luminal surface through the proximal 'brush border' (Fig. 9). The

gland cells are predominantly of one type, containing finely granular, yellowish-brown material that does not stain well with azan or hematoxylin techniques. A few cells are vacuolate and contain a variable quantity of small, unstained droplets. The stomach is  $350\text{--}400 \mu\text{m}$  long. There is a gradual diminution in thickness of the wall and in number of gland cells posteriorly. The posterior limit of the stomach is demarcated by an abrupt change, without constriction, to an intestinal epithelium of tall, vacuolate, columnar cells with few cilia. The intestine (Fig. 10) is a simple tubular structure having no diverticula, although it may be slightly constricted at sites of mature gonads.

#### Blood vascular system

The vascular system is simple, consisting of a middorsal vessel and two lateral vessels; all three unite anteriorly and posteriorly. Its precerebral portion is a thin-walled, elongate lacuna that lies medially over the rhynchodaeum to near the cephalic tip (Fig. 4). This passes posteriorly through the cerebral ring and comes to lie ventral to the rhynchocoel; presumably it bifurcates around the rhynchodaeum and then re-anastomoses ventrally. The middorsal vessel arises between the cerebral ganglia and passes immediately through the musculature of the rhynchocoel wall (Figs 6–8), where it forms a relatively thick-walled construction of cells with dense cytoplasm. The latter may represent a rhynchocoelic villus, although a discrete villus could not be identified. The vessel lies completely within the rhynchocoel cavity until it reaches the posterior limit of the stomach. Here it passes back through the musculature of the rhynchocoel wall, becomes thin-walled and continues posteriorly, between the rhynchocoel and intestine, to a supra-anal anastomosis with the lateral vessels. A voluminous post-cerebral lacuna lies above the foregut, almost enveloping the rhynchocoel so that it appears to be suspended from the dorsum of the lacuna. The lacuna becomes bifurcated in the vicinity of the mouth by the descending rhynchoc-

oel (Fig. 8). The resulting pair of lacunae continues posteriorly, bordered by inner longitudinal muscles, stomach, and rhynchocoel (Figs 9, 11). At the posterior limit of the stomach, which also is the posterior limit of the nephridia, the vessels narrow markedly and are difficult to detect for most of the rest of their course to the supra-anal anastomosis. The endothelial lining of the lacunae contains numerous vacuolate cells containing various quantities of minute droplets. Some of these form a more or less continuous longitudinal tract along the outer edge of each lacuna, adjacent to the lateral nerve cords. The inner longitudinal musculature, which lies along the outer margin of the lacunae, is lacking along these two tracts. Valves were not found.

### Nephridial system

The nephridial system is largely confined to the lumen of the two lateral blood lacunae. Its posterior limit is marked by a single exit pore on each side of the body just above the lateral nerve cord and slightly posterior to the stomach (Fig. 1). From each pore a ciliated duct (8–10  $\mu\text{m}$  diameter) extends directly to and penetrates the blood lacuna. The duct extends anteriorly, lying along the dorsolateral surface of the lacuna. This entire portion of the duct (15–18  $\mu\text{m}$  diameter) is relatively thick-walled (4–5  $\mu\text{m}$ ), densely ciliated and extends for about 140  $\mu\text{m}$  before abruptly narrowing (5–8  $\mu\text{m}$  diameter) in cell thickness and lumen diameter. This thin duct extends anteriorly another 140  $\mu\text{m}$  and at irregular intervals receives the terminal tubules of cyrtocytes. The cyrtocytes project into the vascular lumen singly and in clusters (Fig. 11). Each cyrtocyte is about 4  $\mu\text{m}$  in diameter and 18  $\mu\text{m}$  long, has a single lateral nucleus located proximally and a central cluster of long cilia.

### Reproductive structure

The species is gonochoric with gonads arranged linearly along each side of the intestine, and

bounded externally by the middle circular musculature. Testes open via individual pores located dorsolateral to the rhynchocoel and intestine. Maturation of the testes of a given individual is synchronous. In most testes there is a single cluster of mature sperm (Fig. 10) with all their heads parallel and their flagella extending dorsally into the gonoduct. Motile sperm have a head-piece about 16  $\mu\text{m}$  long and 0.5  $\mu\text{m}$  in diameter with a flagellum of about 30  $\mu\text{m}$ .

Females obtained at the same time as mature males had ova in clusters of 2 to 6, each ovum 50 to 60  $\mu\text{m}$  in diameter with a 20  $\mu\text{m}$  germinal vesicle. A 10 mm female had about 50 irregularly spaced ovaries with a total of about 300 ova. No ovaries were observed in sectioned material.

### Natural history

The species has been found intertidally at Richmond Beach on Puget Sound; at San Juan Island it was found subtidally. It occurs in the top 5 cm of relatively poorly sorted sand at both sites. The sand is moderately coarse (200–450  $\mu\text{m}$ ) but has a significant silt component. In August of 1979, six specimens, 10–15 mm long, were collected at Richmond Beach. Two were mature males, but the others lacked recognizable gonads. Of three specimens collected at Minnesota Reef in mid-July of 1981, one was a mature male and two were females with ova (50–60  $\mu\text{m}$ ).

### Discussion

Currently, structure of the body wall is the principal diagnostic feature for the orders Palaeonemertina (*sensu* Iwata, 1960) and Heteronemertina. That is, the body wall of Heteronemertina includes between epidermis and nerve plexus an outer longitudinal musculature (OLM) and a well-developed cutis of connective tissue and glandular cells (Gibson, 1982); these three elements may have various structural relationships to each other (Riser, 1993). The primary feature defining, but not necessarily uniting, Palaeonemertina is lack of these elements. Position of the

nervous system is often cited as a distinction; in fact, it is in homologous position in both groups – overlying the original body wall circular musculature (Stiasny-Wijnhoff, 1923). Transverse sections of the body wall of *Riserius pugetensis* are convincingly heteronemertinean in appearance until one realizes that there is no dermis and there are no subepidermal glandular cells. In the absence of other patently heteronemertinean features, this condition could represent loss of the latter two by a heteronemertine or gain of OLM by a palaeonemertine. The latter is not a novel suggestion. Cantell (1969), in showing that *Hubrechtella dubia* Bergendal, 1902, possessed a pilidium larva, suggested that this might demonstrate 'the pilidium larva as primitive among the Nemertini' or that *Hubrechtella* 'is a heteronemertine which has ... lost its outer longitudinal muscles.'

Few adult heteronemertines are as small as *Riserius pugetensis*; most are much larger. Possibly as a consequence of large size, heteronemertines tend to have relatively complex and diverse anatomies. Simplicity or absence of features will tend to characterize a taxon as relatively plesiomorphic unless one can infer reduction or loss. Smaller nemertines are frequently classified in groups that are generally considered to be 'primitive,' with the notable exception of the Tubulanidae, which includes some very large members. Meiobenthologists accept implicitly that reduction and/or loss of structure has a very appreciable probability for mesopsammon (see especially Swedmark, 1964). I conclude that *Riserius pugetensis* is mesopsammonic (interstitial) based on its size, habitat, and its association with other typical mesopsammonic species (these include *Cephalothrix cf. pacifica* Gerner, 1969, at Richmond Beach and one undescribed species each of *Ototyphlonemertes* Diesing, 1863, and *Annuloneemertes* Berg, 1985, at Minnesota Reef). The visage of living *R. pugetensis* is strongly reminiscent of some smaller palaeonemertines, including *Hubrechtella*. Is this a function of convergence or recency of common ancestry? Evaluating this phylogeny problem is hampered by absence or ambiguity of information for many nemertinean

characters. The problem is compounded by the prevalence of references to *ad hoc* assemblages of characters in constructing taxa. Phylogeny of *R. pugetensis* can be examined only with reference to phylogeny of palaeo- and heteronemertines. A full cladistic analysis of that relationship is not available and is outside the scope of this paper, but a start in that direction is made in the following discussion, wherein relevant characters are discussed, if somewhat broadly, in terms of Hennigian principles of homology analysis.

Most palaeonemertines have a short rhynchocoel lined only by circular muscles and most have a proboscis with outer circular musculature and inner longitudinal musculature (palaeotype). But the rhynchocoel of some, including *Hubrechtia* Bürger, 1892, *Hubrechtella* (Hylbom, 1957; Kirsteuer, 1967; Gibson, 1979a) and *Tetramys* Iwata, 1957, is invested by outer circular and inner longitudinal musculature as in *Riserius pugetensis* and heteronemertines. These also share the presence of a medial blood vessel. Therefore, it is not surprising that *Hubrechtia* and *Hubrechtella* lack the body-wall inner circular musculature (Kirsteuer, 1967; Gibson, 1979a) found in other palaeonemertines. I will postulate at the outset that 1) it is evident from a hierarchy of similarities that the cerebral sensory organ is a synapomorphy for all nemertinean groups where it is present or may be inferred to have been present ancestrally; 2) the medial (mid-dorsal) blood vessel is a synapomorphy for a smaller group of palaeo- and heteronemertines; 3) the pilidium larva is a synapomorphy uniting *Hubrechtella* and Heteronemertina; and 4) parallel losses are much more likely than parallel gains. These points are addressed to various extents in the remaining discussion.

Conspicuous external features of *Riserius pugetensis* are an annular cephalic furrow encircling the body anterior to the mouth and a pair of deep, lateral cephalic pits leading to the cerebral sensory organs. An annular cephalic furrow is characteristic of most hoplonemertines, at least one palaeonemertine, *Carinomella lactea* Coe, 1905 (personal observation), the heteronemertines *Cephalomastax* Iwata, 1957, *Diplopleura*

Stimpson, 1857 (Bürger, 1895), *Oxypolella* Bergendal, 1902, *Oxypolia* Punnett, 1901 (see also Cantell, 1972; Gibson, 1982), *Poliopsis* Joubin, 1890, and *Pontolineus* (Müller & Scripcariu, 1964). Coe (1895) reports that the head of *Zygeupolia rubens* (Coe, 1895) is 'marked off from the body by a slight constriction formed by a pair of shallow, lateral, transverse grooves', which are separate from the openings of the cerebral sensory organs. These grooves may correspond to the annular furrow, but neither Coe nor Thompson (1901) offers clear evidence for this. The furrow is anterior to the mouth in each of the heteronemertines (cf. Iwata, 1957; Cantell, 1972), including *R. pugetensis*, whereas it is intersected by the mouth in *Pontolineus*, and it is posterior to the mouth in *C. lactea*. This relationship in hoplonemertines is obscured by the enigmatic morphogenetic history of the mouth. The cerebral sensory organs of *Oxypolella* and *Oxypolia* open into the annular furrow (Cantell, 1972; Punnett, 1901), and open anterior to the furrow in hoplonemertines and the heteronemertines *R. pugetensis*, *Cephalomastax*, *Pontolineus*, and, I presume, the other heteronemertines cited above. Thus, this landmark bolsters the likelihood that this furrow is a synapomorphy for a group encompassing at least the hetero- and hoplonemertines; it may be a more plesiomorphic link for all three orders.

Nothing is obviously unique about the cerebral sensory organ (CSO) of *Riserius pugetensis*. They are not intimately joined to the cerebral ganglia, a feature shared with most other palaeonemertines, some baseodiscids and most hoplonemertines. Thus, this may be a plesiomorphic condition. Intimate apposition of CSO and cerebral ganglia is typical for lineids and Gibson (*in litt.*) notes that a similar degree of intimacy is found in some reptant Polystilifera and some species of *Nipponnemertes*. Presumably this represents two or three instances of convergence, unless there is a definable shared structural expression of this intimacy. The CSO of *R. pugetensis* are not embedded in vascular lacunae, unlike those of *Hubrechtia* and some other palaeo- and heteronemertines. However, I am not aware of clear

evidence that any CSO actually penetrates the vascular epithelium. This criterion seems only to describe a particular degree of contact with vasculature and could also be a function of vascular volume. The CSO of *R. pugetensis* opens into a large lateral pit, or depression of the body wall, which is similar to that of most palaeonemertines, baseodiscids (the pits tend to be more ventral in these) and other heteronemertines lacking horizontal fissures. The cerebral sensory openings of most hoplonemertines present relatively minor variation from this construction, which probably represents the plesiomorphic condition. The shape and relatively large size of these pits in *R. pugetensis* speaks for some degree of specialization. I do not believe this to be an artifact of perception caused by the small size of the animal; *Hubrechtella* tends to have similarly well-developed CSO pits. Müller & Scripcariu (1964) argue that the cephalic fissures of *Pontolineus* are reduced because of its endopsammic habit, but I believe this may as easily be plesiomorphic. This follows from my contention (Norenburg, 1985) that the primary ancestral radiation of heteronemertines was infaunal, and from the fact that the greatest development of cephalic fissures is seen in infaunal forms showing a high degree of apomorphy, such as species of *Cerebratulus* Renier, 1804. Further, there is no evidence of reduction in several macrofaunal lineiform species that live in the coarse sand of relatively high-energy beaches (personal observations), e.g. *Parvicirrus dubius* (Verrill, 1892) (see Riser, 1993). As there is no vestige of modified cephalic epidermis and there is no other obvious synapomorphy with lineiforms, I conclude that the CSO openings of *R. pugetensis* represent a unique form of a basically plesiomorphic condition.

The epidermis of *Riserius pugetensis* is simple, in terms of the elements present and structural complexity, when compared to hetero- and many palaeonemertines. There is some superficial similarity with species of *Hubrechtella*, but *R. pugetensis* lacks the diversity and localization of glandular cells reported from *Hubrechtella* (Hylbom, 1957; Gibson, 1979a). Lack of a definitive cutis, especially lack of subepidermal glandular cells,

distinguishes the new species from all other heteronemertines except *Colemaniella albulus*, which appears otherwise to be a typical 'lineid' (Gibson, 1981). Norenburg (1985) concluded that presence of subepidermal mucous cells is the plesiomorphic condition for heteronemertines, leaving the epidermis dominated by homoserous cells (with isolated other kinds of glandular cells). This is supported by structure of the epidermis in *Hubrechtella*, in which it is also the mucous cells that tend to be submerged. It is the homoserous cell that dominates the epidermis of *R. pugetensis*; there appears to be a complete lack of integumentary mucous cells. In contrast, the epidermis of macrofaunal and mesopsammic hoplonemertines is dominated by mucous cells, as is the epidermis of *Arhynchonemertes* (Riser, 1988). Thus, I conclude that absence of subepidermal glandular cells (and perhaps a cutis) is a derived condition in *R. pugetensis*.

Pseudocnidae very similar to those of *Riserius pugetensis* are also found in the proboscis epidermis of interstitial cephalothricid archinemertines (Gerner, 1969; personal observations), in all but one of the five species of the palaeonemertine genus *Hubrechtella* (Hylbom, 1957; Gibson, 1979a; personal observations), and in the heteronemertines *Cerebratulus urticans*, *Micrura purpurea* (Bürger, 1895) and *Paralineus elisabethae* Schütz, 1911 (Schütz, 1912). It is not clear how or whether these structures relate to the much smaller heteronemertinean proboscis 'spines' of other authors. This enigmatic character invites phylogenetic speculation, but its taxonomic distribution reduces its systematic value for our purposes, at least until there is a comparative study of pseudocnidae.

The nephridial system of *Riserius pugetensis* is simple, resembling that of several palaeonemertines (e.g., *Hubrechtia*) and heteronemertines (e.g., *Paralineus*). This is probably the plesiomorphic state for most, if not all nemertines (absence of nephridia in *Hubrechtella* must be considered apomorphic).

The presence of an outer circular musculature, albeit sparse, would by classical diagnoses set *Riserius pugetensis* apart from other heteronemer-

tines except *Cephalomastax*, which does have well-developed subepidermal gland cells and cutis. However, outer circular muscles are found in the cutis or among the subepidermal glandular cells of many heteronemertines, as has been mentioned by many authors, including: *Baseodiscus delineatus* (Delle Chiaje, 1825) (cf. Gibson, 1979b), *Lineus coccinus* Bürger, 1892, and *Valencinia longirostris* Quatrefages, 1846 (cf. Bürger, 1895). It has been treated implicitly as 'different' from the so-called primary body wall musculature, in effect as a variable of the connective tissue. It seems to represent a plesiomorphic layer for at least the heteronemertines; its absence in some, if any, heteronemertines probably is secondary and more likely to be a homoplasious condition than is its presence. It is not apparent how this body wall musculature relates to that of palaeonemertines (with a subepidermal nervous system), especially a form such as *Tetramys* Iwata, 1957, which has the same sequence of body wall muscle strata as *R. pugetensis*.

The heteronemertines are currently divided into five 'convenient families' based primarily on the nature of cephalic furrows (Gibson, 1982, 1985). The Lineidae, the largest 'family' numerically, is characterized by lateral horizontal cephalic fissures (Friedrich, 1960) and generally seems to include the so-called 'most-advanced' heteronemertines. The lateral fissures are a fundamental synapomorphy for this large group of heteronemertines (it seems more appropriate, relative to the remaining 'families', to consider the otherwise morphologically-diverse lineids as a suborder, Lineiformes). The four remaining 'families' (Poliopsiidae, Pussylinaeidae, Valenciniidae and Baseodiscidae) are less-readily defined (cf. Gibson, 1982, 1985), largely because there are numerous information gaps about characters of the more obscure taxa, but some useful comparisons with *R. pugetensis* are possible.

Structure of the proboscis has been a traditional cornerstone for taxonomy of nemertinean, and especially heteronemertinean, genera (Wijnhoff, 1914; Friedrich, 1960; Gibson, 1985). Wijnhoff (1914), in analyzing probable phylogeny of the nemertinean proboscis, makes a strong argu-

ment that the plesiomorphic proboscis (termed 'palaeotype') has two muscle strata, outer circular and inner longitudinal, and a nerve zone between the epithelium and circular musculature. She argues that the addition of outer longitudinal musculature between the epithelium and nerve zone leads to a heterotype proboscis, thereby reflecting in part structure of the body wall. Gibson (1985) suggests that this heterotype is the logical ancestral condition for the heteronemertean proboscis, whereas Riser (1993) states that the two-layer condition (palaeotype) is plesiomorphic for heteronemertines. I support the latter on the basis of outgroup comparison, but this may not be the case for lineiform nemertines. Wijnhoff (1914) argues that the plesiomorphic position of the nerve plexus and central nervous system also is subepidermal for the nemertean body wall (see also Bürger, 1895; Bergendal, 1903); this still is widely accepted (Hylbom, 1957, 1993; Gibson, 1972). The nervous system of the Heteronemertina has not 'migrated' but is in its plesiomorphic position, displaced inward by the addition of outer musculature. However, Wijnhoff and others have since overlooked the importance of the nervous system as a positional reference in determining homologies among proboscidean muscle strata. If one assumes, as most authors imply, that there is a morphogenetic relationship between body wall and proboscis wall, proboscis outer longitudinal musculature (between nerve zone and epithelium) is the homologue of body wall outer longitudinal musculature, but proboscis inner circular musculature (between endothelium and inner longitudinal muscle) has no body wall homologue. Gibson's (1985) group A proboscis (outer longitudinal, middle circular, inner longitudinal) is not homologous to the body wall just because 'outer and inner longitudinal...layers sandwich a middle circular coat'; rather, it is because they have the correct anatomical relationship to other body wall components. For the remaining discussion proboscis muscle strata are defined as follows: outer longitudinal (OLM) is between epidermis and neural tissue, outer circular (OCM) is subneural and is followed by inner longitudinal (ILM), inner circular muscles (ICM)

are subendothelial and have no body wall homologue. I am assuming, without rechecking, that all of the genera in Gibson's (1985) group B have a proboscis with OCM and ILM, and those of group A have OLM in addition. It should be noted that *Parapolia aurantiaca* Coe, 1895, is included in group A (parsimony favors this as the correct interpretation) but position of the proboscis nerves is unknown, nor is it clarified by Wheeler (1934, 1940) or Friedrich (1970) for a second species. Coe (1895) initially described the proboscis of *Zygeupolia rubens* (Coe, 1895) as having OLM, OCM and ILM in its main body, but lacking the OLM (inner by his definition at that time) anteriorly, whereas Thompson (1901), in her very detailed description, cites only OCM, ILM, and a thin 'endothelial' circular musculature (ICM?). Coe (1905) seems to accept Thompson's description by not offering further comment.

Gibson's (1985) group C is more problematical. It may be used to illustrate the organizing strength of phylogenetic analysis and the pitfalls of using parsimony uncritically; e.g., without homology analysis. Group C, although unintended, is founded on parsimony; that is, membership is based on having a proboscis with 'outer longitudinal, inner circular muscle'. *Uchidana parasita* Iwata, 1967, is described as having 'outer longitudinal and inner circular muscle' (Iwata, 1967), but it is clear from the rest of his description and figures that these are OCM and ILM, placing it in group B. *Cephalomastax*, according to Iwata's (1957) description, has OLM and ILM plus a discrete subendothelial circular musculature (ICM); that is, the apparent 'outer longitudinal' is split by the nervous system and OCM is actually absent. Likewise, *Valencinia longirostris*, according to Bürger's (1895) description and figure (Plate 23:9), has OLM, ILM and a subendothelial wickerwork of ILM and ICM comprising the main body of the proboscis. Bergendal (1902) suggests, from personal examination of sections, that Bürger's interpretation of this wickerwork was incorrect and that it is composed only of interlacing obliquely-orientated circular muscle fibers. This opinion is shared by Wijnhoff (1914); but,

she considers this to be the 'result of the dissolving of muscle crosses', which could occur only if there were an intervening LM originally. In the 'middle section' of the proboscis of *Valencinura bahusiensis* Bergendal, 1902, the inner portion of the circular musculature consists of obliquely oriented fibers (Bergendal, 1902). The position of proboscis nerves is unknown for *Chilineus* Friedrich, 1970, but the proboscis is clearly described (using current convention) as containing 'inner circular and outer longitudinal' musculature. Our knowledge of the proboscis in *Poliopsis* consists of Friedrich's (1970) remark 'soweit er erhalten ist,  $\Delta$ Lm und Rm...'. In the absence of contrary data parsimony argues that these are OCM and OLM in the latter two genera (*i.e.*, the nervous system should be between OLM and OCM). Wijnhoff (1914) asserts that the same sequence in baseodiscids, 'outer longitudinal and inner circular' musculature, is derived from the heterotype proboscis by loss of the ILM. However, the 'outer' longitudinal muscles of *Baseodiscus* are subneural, therefore ILM, and the circular muscle is subendothelial (ICM). Unless the nervous system has relocated this proboscis may be derived by loss of OCM of a heterotype proboscis or by loss of OLM from a proboscis such as that of *Cephalomastax* or *Valencinia longirostris*. The proboscis of *Riserius pugetensis* has only the subneural longitudinal musculature, which on the basis of parsimony is likely to be ILM; it has lost at least the OCM. Baseodiscids have a tendency to 'lose' the ICM (*cf.* Gibson, 1979b); in its absence the two proboscides would be considered homologous.

Evolution of heteronemertinean proboscides is more complex than previously entertained. The morphotypes identified above are summarized graphically (Fig. 13) without any indication of relationship. Transformation series are dependent on presumed ancestral state, and many equally parsimonious or 'logical' orderings are possible if the root is unspecified. Recognition of ancestral states is confused significantly by the fact that the proboscides of *Hubrechtella queenslandica* Gibson, 1979, and *Tetramys* have three muscle strata (outer circular, middle longitudinal, and inner cir-

cular) (Iwata, 1957), whereas the four remaining species of *Hubrechtella* have proboscides with outer longitudinal (OLM) and inner circular musculature (ICM) (Hylbom, 1957; Kirsteuer, 1967), and that of *Hubrechtia* is palaeotype (OCM, ILM). Some 'logical' transformations present themselves on the basis of parsimony. I consider parallel or convergent losses as likely but would require significant corroboration from other characters to accept the same as gains. Thus, OLM may be plesiomorphic for heteronemertines of Gibson's groups A and B (except *Zygeupolia*). It seems plausible, and even likely, that some of the generic inconsistencies as shown in Gibson's (1985) groups A and B are due to convergent loss of OLM (bad taxonomy may account for other conflicts). Hylbom (1957) alluded to the possible relationship between muscle crosses in palaeo- and heteronemertines. The broad distribution of muscle crosses in heteronemertines favors a single origin over multiple ones. It seems evident that presence of muscle crosses infers existence of an ICM, as previously suggested by Thompson (1901) and Wijnhoff (1914), although it may be very weakly developed, as in *Zygeupolia*. It is tempting to view *Zygeupolia* as approximating an ancestral heteronemertinean condition, with its lateral sensory organ, and proboscis with OCM, ILM, rudimentary muscle crosses and ICM. Obviously, one would not expect muscle crosses in the absence of an 'inner' longitudinal musculature, but the oblique musculature in the proboscides of *Valencinia longirostris* and *Valencinura bahusiensis*, both of which are reported to have a weak 'endothelial' circular musculature (Bergendal, 1902), may betray its origin as a muscle cross. Although I do not necessarily subscribe to Wijnhoff's (1914) explanation for the developmental differentiation of rhynchocoel sheath and proboscis musculature, it is evident that a relatively minor morphogenetic shift during this differentiation could significantly alter the relative position of the nervous system, as is the case in hoplonemertines.

The proboscis of *Riserius pugetensis* can be derived from group B, *Baseodiscus*, *Zygeupolia*, or *Poliopsis* by one loss, and from group A or *Cepha-*

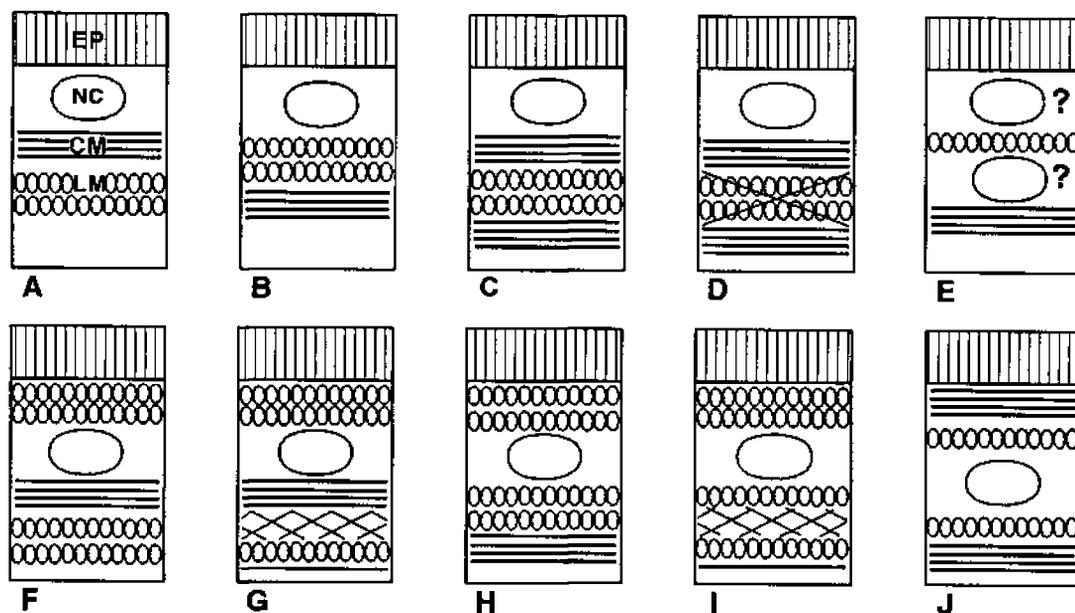


Fig. 13. Schematic representations of nemertean proboscides in transverse section as found in: A. Palaeotype (e.g., Cephalothricidae, *Hubrechtia*, and Heteronemertina of Group B – see text). B. Baseodiscidae, *Hubrechtella* (in part). C. *Tetramys*, *Hubrechtella queenlandica*. D. *Zygeupolia*, mid-region showing the muscle cross between circular and so-called endothelial circular muscle. E. *Poliopsis* (position of nerve cord is unknown). F. Heterotype (e.g., *Valencinina*, Heteronemertina of Group A – see text). G. *Valencinura*, mid-region showing zone of oblique muscle fibers. H. *Cephalomastax*. I. *Valencinia longirostris*, mid-region showing 'obliquely-orientated circular muscle fibers.' J. Hoplonemertina. Abbreviations: CM = circular musculature; EP = outer epithelium; LM = longitudinal musculature; NC = nerve cord. No indication of relative thickness of musculature is intended in any of the figures; 'outer' and 'inner' are respectively to the top and bottom of figures.

*lomastax* by two losses. More importantly, to be derived from any of the advanced 'heterotype' proboscides, *R. pugetensis* must have lost subepidermal glandular cells (and cutis). Alternatively, it may have diverged from an ancestral heteronemertine that had not developed a cutis or subepidermal gland cells, and lost proboscis musculature in parallel with other heteronemertines.

*Riserius pugetensis* cannot be referred to any prior genus or higher taxon of heteronemertines. It shares plesiomorphic features with the palaeonemertines *Hubrechtia*, *Hubrechtella* and *Tetramys* that are also shared with heteronemertines. The putative loss of subepidermal mucous cells and the presence of OLM in the body wall suggest a more recent common ancestry with the heteronemertines, perhaps with the baseodiscids or *Paralineus*.

#### Acknowledgements

I acknowledge with gratitude the support of Sigma Xi for a Grant-in-Aid of Research and the American Museum of Natural History for an award from the Theodore Roosevelt Memorial Fund, both of which funded the field work. I also am grateful to Friday Harbor Laboratories of the University of Washington, the Marine Science Center of Northeastern University, and the Smithsonian Institution for use of facilities. My visits and work on the West Coast were facilitated and enriched by many people – notably, Stephen Stricker, Paul and Ruth Ilg, M. Patricia Morse, Robert Fernald and Christopher Reed. This is Contribution No. 192 from the Marine Science Center, Northeastern University, Nahant, MA.

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