Morphological adaptations of the Cratenemertidae (Nemertea, Enopla, Hoplonemertea) to the epipelagic habitat and lifestyle

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Abstract

Four species (in three genera) of the family Cratenemertidae are found in the epipelagic (depth: <300 m) habitat. These species share many morphological differences from the benthic and intertidal majority of cratenemertids: the change in habitat (and, consequently, in lifestyle) can account for some, but not all, of these differences. The organ systems most affected are the body wall, musculature and sensory structures, particularly, the proboscis apparatus and alimentary canal, where the modifications can be attributed to a shift from active predation to passive feeding.

Keywords: Epipelagic habitat, morphologic adaptation, Achoronemertes, Korotkevitschia

Introduction

A taxonomic revision of the family Cratenemertidae is in progress. Four species (in three genera) occur only in epipelagic habitats. Korotkevich (1961) was the first to recognize one species as probably epipelagic; later Crandall and Gibson (1998) discussed a second such species. Many morphological characteristics shared by these four species are very different from those found in most cratenemertids. The present paper suggests that modification of a number of characters (or, rather, morphological complexes) in the epipelagic forms are adaptations to an altered lifestyle imposed by the habitat.

Other than these four species, most cratenemertids, indeed the majority of hoplonemerteans, are active benthic or intertidal predators, depending on a firm substrate over which they can crawl. This substrate provides a firm base from which to push the body forward, making it possible to thrust the armed proboscis forward to stab and immobilize prey (see the elegant feeding studies of McDermott (1975, 1984, 1987, 1993) and McDermott and Roe (1985)). In contrast, the free-floating epipelagic forms have no firm surface against which to push. Predictably, there are major modifications in the...
musculature and in the feeding apparatus. The present paper relates the distinctive morphology of the four species to their probable feeding method in the epipelagic habitat. A number of the differences from other members of the family are seen as adaptive modifications, while other differences, shared by all four species, are not easy to explain.

Nomenclature presents a problem. Two of the four species discussed here have not yet had full descriptions published in the scientific literature since they form part of the monographic revision of the family, now in progress. Provisionally, these species are referred to as “Atlantic H” and *Achoronemertes* species 2. The restriction of *Nipponnemertes* to the northern Pacific Rim (Crandall 2001) invalidates some other generic names not yet formally replaced; these are shown in quotation marks.

**Description**

**Habitat**

Many species of the family Cratenemertidae are known only from a single specimen or a few specimens collected from a single location; thus, it is difficult to characterize with confidence the habitat range for most of the species. Members of the family have been found in three primary habitats: (1) most are benthic forms found from a few to 500-m depths, (2) a few species appear to be intertidal to shallow subtidal, (3) three genera with a total of four species, which are being treated as a single subfamily-level clade, are epipelagic, living in the top 200 m in mid-ocean above ~5000 -m bottoms.

Swimming behavior has been mentioned for several benthic species, most notably by Berg (1972) and by McDermott (2005, pers. comm.) for “Amphiporus” pulcher, by Coe (1905) for *Nipponnemertes punctatula*, and by Iwata (2001) for *Nipponnemertes fernaldi*. However, the energy requirements associated with swimming preclude its use over anything but relatively short distances. It is, therefore, impossible for these four species to be benthic forms that have swum 5000 m vertically to the surface layers. Moreover, they lack the musculature and body configuration found in actively swimming forms.

We can speculate about the mode of existence of these four epipelagic species, three of which occur in Antarctic waters. The three Antarctic species all occur in the top 200 m, in the layer of water between the Antarctic convergence and divergence (Figure 1). This mass of water, known as the West Wind Drift, moves eastward around the continent. At the same time the belt moves eastward, its surface layer moves northward toward the Antarctic convergence, whence it moves deeper and reverses direction to return toward the divergence (Figure 2). Thus, these species are presumed to float in that flat toroidal belt as it follows its flat spiral pathway around the continent.

Likewise, “Atlantic H”, whose type locality is given as *Michael Sars* Sta. 64, is a mid-ocean form from less than 300 m depth above a ~5000-m bottom. The location of this station, at 34°48’ N, 47°52’ W, is toward the northwestern portion of the Subtropical Gyre, which rotates in a clockwise direction in the temperate northern Atlantic. Once again, the speculation is that this species finds itself largely confined to this slowly rotating surface water mass.

**Probable feeding mode**

In the few epipelagic species so far found, feeding has not been observed directly. Probably feeding is accomplished by everting the proboscis for extended periods until plankton
adhere to the adhesive surface of the papillae whereupon the proboscis is withdrawn, stripping the plankton off into the atrium where the mouth is located (Figures 10–12). This premise is supported by the variety of organisms adherent to the papillae of a specimen fixed with the proboscis in an everted position (see Figures 13 and 14).

Body size and shape

Compared to other cratenemertids, the four epipelagic forms have a much smaller aspect ratio (i.e. body length to body width). Cratenemertids have been reported from about 3 mm in length up to some 240 mm. Widths have been reported from less than 1 mm to as much as 1 cm. The family has been noted occasionally for extreme degrees of contraction during preservation, e.g. Bürger’s (1895) figures of *Amphiporus virgatus* and *Amphiporus marmoratus*. Conversely, specimens in active locomotion are often considerably longer and slimmer than when at rest. The literature contains no reports suggesting that aspect ratio (in normal specimens) might be a useful taxonomic character.

My investigations have shown that all presently known cratenemertids fall into one of three groups with respect to aspect ratio. The preferred condition of the animal for determining the dimensions is the anesthetized live specimen, as well as when it is extended and actively locomoting. However, except for a very few cases of extreme over-contraction upon preservation without first anesthetizing, specimens fall within a particular group regardless of the degree of extension or contraction.

This aspect ratio of cratenemertids has been found to fall into the following three discrete ranges:

1. The great majority of cratenemertids, are characterized by moderate length and robust girth. The cross-section varies from rounded anteriorly and flattened posteriorly (like a narrow-bladed oar), to triangular, with a rather flat “sole” ventrally and the apex in the...
dorsal midline above the rhynchocoel, to elliptical, with the posterior portion somewhat flatter than the anterior. Usually, the anterior end tapers slightly and is rounded at the tip, while the posterior end has a short somewhat rounded taper. An aspect ratio in the range of 8:1 to 25:1 has been selected as a principal diagnostic character for this group. Preserved specimens with some degree of contraction often fall toward the lower part of the range, while active specimens will tend toward the upper part. Extremely contracted or extended specimens may fall a little outside this range but that is regarded as an abnormal condition.

(2) The epipelagic species are very short, plump in midbody, tapering somewhat toward each end. In lateral view, most specimens resemble a clove of garlic with a straight dorsum and deeply curved belly; transverse sections are nearly round (Figure 3). This body form is confined to the three epipelagic genera and is interpreted as morphological adaptation to the pelagic habitat. Preserved specimens have ranged between 1.19:1 and 2.31:1 (Table I) and it is estimated that, given the body wall configuration, living specimens would be unlikely to exceed double the preserved length. Therefore, an aspect ratio of less than 4:1 has been designated a principal diagnostic character for this group. Severely contracted specimens of some species of group 1 above, such as preserved specimens of *Duosnemertes marmoratus* and "*Amphiporus*" virgatus figured by Bürger, should not be confused with members of this subfamily, and, indeed, Bürger's (1895) figures of living specimens of these two taxa have aspect ratios typical for the first group above.

(3) The third group, currently consisting only of "*Amphiporus*" peruvianus, is very long, very slim, and mainly round in cross section. Aspect ratio of greater than 40:1 has been designated a principal diagnostic character for this group, but even preserved specimens are usually greater than 50:1. The two preserved type specimens have aspect ratios of 51:1 and 72:1, respectively.
**Table 1.** Length:width ratio* of epipelagic cratenemertidae.

| Specimen                        | Length | Width | Depth | L/W ratio |
|---------------------------------|--------|-------|-------|-----------|
| *Achoronemertes scoresbyi*     |        |       |       |           |
| Sta. 302, holotype              | 5.0 mm | 2.5 mm| -mm   | 2.00      |
| Sta. 302, paratype              | 3.7    | 1.6   | –     | 2.31      |
| Sta. 550, paratype              | 4.5    | 2.0   | –     | 2.25      |
| *Achoronemertes sp2*           |        |       |       |           |
| Sta. 548, holotype              | 3.3    | 2.5   | 2.5   | 1.32      |
| Sta. 548, paratype              | 2.5    | 2.1   | 2.1   | 1.19      |
| *Korotkevitschia pelagica*      |        |       |       |           |
| Holotype                        | 9.0    | 4.0   | 3.0   | 2.25      |
| “Atlantic H”                    |        |       |       |           |
| Holotype                        | 4.6    | 2.5   | 2.5   | 1.84      |
| Paratype 1                      | 4.2    | 2.7   | 2.0   | 1.56      |
| Paratype 2                      | 4.1    | 2.0   | 2.5   | 2.05      |

*All measurements in this table are of preserved specimens.*
These three ranges are discontinuous and the top of one is separated from the bottom of the next by a factor of \( \sim 2:1 \). This separation is regarded as adequate to establish the discreteness of these three groups and thereby substantiate aspect ratio as a legitimate multistate taxonomic character for the family Cratenemertidae.

Great body sinuosity is of no advantage to an animal that spends its life passively floating and passively feeding, and sinuosity carries with it the requirement for a greater aspect ratio which actually may be a distinct disadvantage to a pelagic animal. For example, the pelagic polystilifera (believed to be a polyphyletic assemblage) all have modest aspect ratios, while the reptantic polystilifera, with a lifestyle much like the majority of cratenemertids, have an aspect ratio similar to the first group of cratenemertids above.

Table I gives the measurements and computed ratios for the specimens depicted in Figure 3.

\[ \text{Modified musculature and body wall} \]

\textit{Reduced body wall thickness, reduced longitudinal muscle layer.} With the change from active predation to a passive floating lifestyle, the need for a powerful body wall musculature was greatly diminished. The thick and well-developed integumentary epithelium and dermis are substantially the same as in the benthic members of the family. The circular layer is thinner, but the longitudinal layer shows the greatest reduction. While the longitudinal layer is divided into wedges as in the rest of the family, the wedges are only about one-quarter as deep as in the benthic forms. Also, the wedges do not show the extensive substructure present in those species with deep and powerful wedges. Where the deep wedges of the benthic forms have significant spaces between them, through which run diagonal muscles and nerves, the spaces between wedges in the epipelagic forms are much reduced, due in part to the paucity of diagonal musculature.

\textit{Reduced diagonal muscle layer.} The diagonal musculature enables different parts of the body, particularly the head end, to twist about the longitudinal axis with respect to the rest of the body. This capability is extremely important to an active predator but not to a passively feeding animal. Moreover, as the body shortens and the aspect ratio decreases, twisting any part of the body about the longitudinal axis becomes less and less possible. In these epipelagic forms, the diagonal musculature is reduced to a sparse lattice-type array of reduced-diameter fibers (Figure 18).

\textit{Near absence of dorso-ventral musculature.} The extremely well-developed dorso-ventral muscle found in many, if not most, cratenemertids is all but absent in the epipelagic forms. What little is present consists of a few very thin, poorly developed fibers positioned near the margins of the body. Unlike other members of the family where the fibers extend into the dermis and are firmly anchored, in the epipelagic forms the fibers penetrate just into, but not through, the circular muscle layer. The foreshortened and chunky body shape would render impossible the anguilliform swimming motions known from several of the benthic species, since this requires dorso-ventral flattening of the posterior portion of the body. Thus, dorso-ventral musculature serves little or no functional purpose and one may regard its major reduction as readily understandable.

\textit{Almost total lack of parenchyma.} Gelatinous parenchyma (or extracellular matrix) appears to act as a readily deformable padding between body wall and various internal organs. A
sufficient thickness of this material allows structures to move with respect to one another without binding or tearing. This in turn facilitates the range of motions needed by an active benthic or intertidal predator. While most cratenemertids have a significant zone of parenchyma between the body wall longitudinal muscle layer and the internal structures, the epipelagic forms show almost complete reduction of such parenchyma. This reduction may be regarded as a further adaptation to a passive feeding lifestyle and the various morphological adaptations that strongly indicate major reduction of range of body wall motion. Throughout much of the body length the intestine is situated tightly against the longitudinal muscle layer with no trace of intervening parenchyma.

**Modified proboscis**

The architecture of the cratenemertid proboscis is typical of the hoplonemerteans generally, i.e. proboscis insertion, anterior chamber, bulb region, posterior chamber and retractor muscle. While the apparent size of the proboscis with respect to the overall size of the animal is affected by the rigors of preservation, there is considerable variation in actual size among the various species of the family. In the epipelagic species, the proboscis is considerably shorter than in other members of the family and this is attributed to adaptation to a passive feeding mode. A long proboscis would be more likely to be damaged and would not be as readily stripped of adherent food material. Another adaptation is major modification or entire loss of central armature and bulb region but, except for shortening, only minor or no modification of other components.

**Proboscis insertion and septum.** The proboscis insertion of the epipelagic species exhibits no substantial differences from other members of the family. Septa are of the closed type with essentially all parts of the longitudinal layer contributing fibers. This is the most prevalent condition in the family.

**Anterior chamber.** In the cratenemertids, generally, the anterior chamber, which becomes the exterior of the proboscis when everted, is lined with papillae largely covered with an epithelium consisting of adhesive cells. Each papilla also contains some sensory elements connected to a nerve lying in the dermal core of the papillar stalk. Although the size, height and shape of these papillae vary somewhat among the various species of the family, among the epipelagic species the papillae are notably smaller, shorter and more fungiform in shape than in the other groups and the distal portion is flattened so that they form a dense mat of adhesive cells. This is interpreted as an adaptation to the different feeding mechanism employed in the pelagic environment. In a specimen of "Atlantic H" with an everted proboscis, bits of plankton are seen adhering to the surface of the papillae (Figures 12–14).

**Bulb region.** Most cratenemertids have the typical monostiliferan bulb region, which joins the anterior and posterior chambers of the proboscis and forms the supporting structure for the central armature. It is constructed primarily of fibrous and muscular elements arranged in radial and spiral arrays, often with some small interspersed glands. It contains a duct running from the posterior chamber forward into the anterior chamber near the base of the central stylet. The duct is presumed to convey venom produced by the glandular epithelial lining of the posterior chamber to bathe the central stylet, thus, creating a "poisoned dagger" with which to stab prey.
Two of the epipelagic genera, *Achoronemertes* and *Korotkevitschia*, have completely lost the bulb region so that the anterior and posterior chambers are directly joined with virtually no transitional structure between them. The third genus, “Atlantic H”, has lost all of the usual components of the bulb except for the duct. The diameter of this remaining structure has increased so that it forms the connection of the anterior and posterior chambers (Figures 10–12). However, its lining epithelium appears histologically identical with that of the bulb duct in the other species of the family.

**Armature.** The normal hoplonemertean armature consists of the central stylet and basis, often referred to as the “central armature”, plus the pouches of reserve stylets. While the central armature is embedded in, and supported by, the bulb region structure, the reserve stylet pouches lie in the posterior-most part of the anterior chamber, just where it joins the bulb structure. In the four epipelagic species, the central armature is entirely absent as are all of the supporting elements of the bulb structure, but the two reserve stylet pouches are present and usually contain only two to four poorly formed stylets (Figures 6, 8, 9 and 17). The reserve stylet pouches are largest in *Achoronemertes*, intermediate in *Korotkevitschia*, and smallest in “Atlantic H”.

Without a firm substrate against which to push, a free-floating animal everting its proboscis would simply propel the rest of the body backward, and any stabbing thrust would be ineffective. Since it cannot be employed in the usual manner, the central armature presumably has been abandoned due to loss of functional significance. Why the reserve stylet pouches remain, although arguably in some degree of reduction, is not clearly understood.

**Posterior chamber.** The posterior chamber is regarded as the site of venom production. It is lined with a relatively thick glandular, or secretory, epithelium (Figures 11, 12 and 19) and is connected to the anterior structures by the bulb duct, which passes through the bulb to open very near the base of the central stylet where the anterior face of the bulb structure joins the anterior chamber. The posterior chamber of the epipelagic forms does not appear histologically different from other species in the family, but it is not possible to tell whether the secretory activity is maintained at the same level.

**Retractor muscle and attachment.** The proboscis retractor muscle is essentially a prolongation of the proboscis longitudinal musculature beyond the termination of the posterior chamber. In the cratenemertids, it attaches to the dorsal wall of the rhynchocoel and individual fibers can usually be traced through the rhynchocoel wall and into the body wall musculature (Figure 22). Although the attachment seems always to be located in the posterior half of the rhynchocoel, the attachment point along the length of the rhynchocoel appears to be more or less characteristic for each particular species. There does not appear to be significant modification of the retractor muscle in the epipelagic forms.

**Nerves**

The proboscis nerves arise, in the usual manner, from a nerve trunk on each side that emanates from the medial side of the ventral ganglion a little in front of the ventral commissure. The nerve trunks rise dorsally and branch as they enter the proboscis insertion to form the separate longitudinal nerves that run the length of the proboscis. The
longitudinal nerves are connected by a radial layer of fine fibers and glial material that is thinner than the nerves and forms the so-called neural sheath. Midway between the nerves there are aggregations of neuroganglionic cells that form longitudinal belts in the sheath that are thicker than the neural sheath but not as thick as the nerves themselves. The neural sheath divides the longitudinal muscle layer (in the normal inverted position of the proboscis) into a thinner outer portion and a thicker inner portion (Figures 6 and 17). The nerves are thickest and most prominent in the anterior chamber and continue as thinner strands down the length of the posterior chamber.

All section series of epipelagic species studied have 12 proboscis nerves in the anterior chamber. The sectioned specimen of Achoronemertes sp2 has only 11 nerves in the posterior chamber.

Modified alimentary canal

**Apparent foreshortening of intestinal region.** Comparison of the proportion of body length occupied by the intestine, from the pyloric junction to the beginning of the hindgut, in the epipelagic forms and the rest of the family shows extreme foreshortening of the intestine in the former. Coupled with the decrease in length of the intestine is a major increase in girth, so that the intestine occupies nearly all of the volume bounded by the body wall. Moreover, instead of a central canal with distinct lateral diverticula, the intestine is essentially circular in cross-section and does not appear to have diverticula, at least not in the usual sense.

These major changes in length and girth of the intestine account largely for the greatly altered body aspect ratio. For example, in Achoronemertes sp2, the foregut from the tip of the head to the pyloric-intestinal junction is 33% of the body length, while the hindgut from the end of the intestine to the posterior tip is 12%. Thus, the intestine or midgut is only 55% of the total length, where normally it would occupy a much larger percentage. At the same time, the reduced body wall thickness and the greatly increased girth of the intestine cause it to occupy some 85% of the total mid-body diameter (Figures 4 and 7).

**Foregut opens into atrium.** The majority of cratenemertids have the esophagus opening into the rhynchodaeum, which in turn opens through the rhynchostome. Several species have both rhynchodaeum and esophagus opening together through a common pore, still referred to as the rhynchostome. One species, Duosnemertes marmoratus, has the esophagus and rhynchodaeum passing to the exterior through separate openings. The epipelagic forms have a dorsal rhynchostome and ventral mouth opening separately, but close together, into a shallow bowl-like atrium lined with an epithelium differentiated from the lining of both tubes and from the surrounding integumentary epithelium. This morphological arrangement is entirely consistent with the hypothesis concerning feeding, i.e. that the proboscis is left in the everted position until a quantity of planktonic organisms have stuck to it and then withdrawn, stripping the collected material off into the bowl-like atrium, whence the food runs down into the mouth opening for ingestion. Figures 12–14 show plankton adherent to the proboscis. In the epipelagic forms, the esophagus is short to almost nonexistent, with the definitive stomach epithelium beginning at or just inside the mouth opening (Figures 11 and 12). The small amount of esophageal epithelium is confined to the ventral side of the tube. The stomach is likewise short and without the pouches and diverticula present in many other members of the family (Figures 10–12).

**Apparent “droplets” in intestine.** All of the epipelagic species exhibit vacuolate spaces in the intestine (Figures 4, 6, 7, 11, 17 and 22). Upon close examination, each of these spaces is
found to be bounded by a very thin membrane that appears to have encapsulated and been permeated by a substance that stains it yellow. These are believed to have originally been oil droplets or globules tinted orange by carotenoids. During histological processing, any oils would have been extracted leaving these empty appearing spaces. The evidence that these species are feeding, at least in part, on small crustaceans (Figures 13 and 14) provides a logical source for such oil droplets. Oil droplets of this kind would be extremely useful in maintaining neutral buoyancy in an epipelagic, drifting animal. In addition, oil droplets provide a concentrated energy store that would be of great advantage to an animal feeding passively with irregularity in timing of food capture.

Extended caecal anterior pouches. In most hoplonemerteans, the first pair of caecal diverticula bend forward to form what are called anterior caecal pouches. In the cratenemertids, these are usually relatively slender and quite short, not reaching very far toward the brain. In the epipelagic forms, the anterior pouches are quite plump and reach the brain, bend upward along its rear side, and then bend forward to extend above the rear part of the dorsal ganglia (Figure 16). There is no apparent reason for this difference from the rest of the family, but it is consistent within this group.

Very long hindgut. Though only sporadically mentioned in the literature, there are important distinctions between intestine, hindgut, rectum and anus. Hindgut is the part of the alimentary canal between the end of the intestine, particularly its lining epithelium, and the exit through the body wall to the exterior. There is always some kind of anus, i.e. the aperture to the exterior. It usually has an epithelium differentiated from both the integument and the part immediately to the interior. In some species, there is a very short simple anus, as the transition between the intestine proper and the exterior. In most cratenemertids, the hindgut consists of a distinct rectum connecting the end of the intestine with the anus. In all of the benthic species, the hindgut is relatively short occupying less than 2% of the total body length. However, in the epipelagic species the hindgut is very long, occupying from 10–20% of the total body length (Figures 10 and 15). This greater relative length is largely due to the great foreshortening of the intestinal (midgut) region, which also reduces the body aspect ratio. When the absolute length of the hindgut is compared with the absolute length of the anterior end back to the pyloric–intestinal junction, the comparative length is not as dramatic.

Modified nephridial ducts

In most cratenemertids, the pair of efferent nephridial ducts leave the posterior portion of the mass of nephridial tubules, move laterally above the lateral nerve cord, bend ventrally along its outer side and exit through the ventro-lateral body wall. These nephridiopores are usually located at the level of the pyloric region of the foregut. In the epipelagic forms, the position and posterior extent of the nephridia are as in other members of the family, but the ducts, as they leave the tubule mass, bend at right angles to run posteriorly just above the lateral nerve cord behind the mid-body point well back in the intestinal region before bending sharply outward to exit through the lateral body wall (Figure 20). Depending on species, the nephridiopores are located from 52–60% of the body length behind the tip of the head. While the reasons for these differences from the rest of the family in both length and radial position are obscure, the condition prevails in all epipelagic specimens.
Modified position of cerebral organ canal openings

In all but three of the benthic cratenemertids, the cerebral organ canals open ventro-laterally, a short distance in front of the brain and precerebral septum. In the exception, the canals open straight laterally near the rear of the brain or straight ventrally near the middle of the brain. In all of the epipelagic species, the cerebral organ canals open dorso-laterally in front of the septum at about the 10:30- and 13:30-h clock positions. There seems no apparent reason for this difference in the radial position of the canal openings, but it is of consistent occurrence.

Simplified cephalic grooves

Most of the cratenemertids have deeply incised complex cephalic grooves with secondary grooves and rugae perpendicular to the main groove structure (Figure 23). However, in the epipelagic species, the groove is a shallow U-shaped depression about half the thickness of the integument (Figure 16), and the lining epithelium is not as noticeably different from the integumentary epithelium as it is in the benthic forms. Since the elaborate groove structure in most cratenemertids appears to be a sensory organ, one can speculate that it is useful in the life of an active predator and that the much simplified groove in the epipelagic forms is consistent with the passive lifestyle.

Absence of eyes

None of the four epipelagic species have eyes. In contrast, the benthic cratenemertids have arrays of highly developed eyes. The pelagic polystilifera also lack demonstrable eyes, though a few species have what some workers interpret as degenerative nerve elements that might once have served as eyes. This would tend to suggest that eyes have been lost as a consequence of adopting the pelagic habitat. The reason for loss in the bathypelagic polystilifera could be attributed to life in the aphotic depths, but in the epipelagic forms the reasons are more obscure.

Modified lateral nerve cord and myofibrillae placement

In most cratenemertids, the lateral nerve cords are situated well below the horizontal midline of the body in a more or less ventro-lateral position for most of their length. By contrast, in the epipelagic forms they lie at, or just slightly below, the horizontal midline (Figures 4 and 7).

All cratenemertids are uniquely characterized by a band of connective tissue in the lateral nerve cord lying between the medial side of the fiber core and the ganglionic cell layer. In most members of the family, the dorsal one-fourth to one-third of this band has a vacuolate space, much like the eye of a needle, within which lie a number of myofibrillae. In the epipelagic species, the vacuolate space extends nearly the entire distance from the top to the bottom of the band and the myofibrillae are distributed along this entire length. In these species, the myofibrillae are of two different diameters with the thinner ones occupying the dorsal portion of the band and the thicker ones the ventral portion (Figures 18 and 21). The reasons for these differences are unknown, but the pattern is consistent, again setting the epipelagic forms apart from the rest of the family.
Discussion

A number of the observed morphological differences between the epipelagic and benthic cratenemertids are interpreted as adaptations of originally benthic cratenemertid ancestors.

Figure 4. *Achoronemertes* sp2, cross section near midbody. Figure 5. *Achoronemertes* sp2, proboscis with reserve stylet pouches. Figure 6. *Achoronemertes* sp2, proboscis with reserve stylet pouches, enlarged view. Figure 7. “Atlantic H”, cross section near midbody. Figure 8. “Atlantic H”, reserve stylet pouch, longitudinal section. Figure 9. “Atlantic H”, reserve stylet pouch, transverse section.
to altered habitat and lifestyle. The alternative explanation, that the epipelagic and benthic lines evolved separately from an even more primitive ancestor, is regarded as being highly improbable. Far too much parallel evolution of many characters to identical character
states would have been required to lend credibility to this alternative. These adaptations, most of which represent reductions from the state in the benthic and intertidal forms, include:
Passive feeding as opposed to active predation.

Body size and shape, particularly the small aspect ratio.

Reduced body wall thickness and reduced longitudinal muscle layer.

Reduced diagonal muscle layer.

Near absence of dorso-ventral muscles.

Near absence of parenchyma.

Total loss of central armature and great reduction or loss of bulb region of proboscis.

Highly modified alimentary canal, including; atrium, reduction of esophagus, foreshortening of intestine, apparent lipid droplets, greatly extended hindgut.

For some of the observed differences, there currently seems no ready causal explanation, though these features are shared by all four species but not by the benthic and intertidal forms. Among these characters are:

- Nephridial ducts extending posteriorly to the mid-body region.
- Cerebral organ canals opening dorso-laterally.
- Simple cephalic groove structure.
- Absence of eyes.
- Placement of lateral nerve cord and myofibrillae.
Extended anterior caecal pouches.

The recent molecular studies of Thollesson and Norenburg (2003) have shown that the Malacobdellidae fall in the midst of the other monostiliferous families. Thus, the morphological modifications of the malacobdellids, which are far more extreme than those of the epipelagic cratenemertids, can, by inference, be attributed to habitat and lifestyle adaptations rather than phylogeny. Therefore, attributing the above morphological changes of these four cratenemertid species to adaptation to habitat and lifestyle offers the most persuasive hypothesis.

In the past, morphological similarities between the cratenemertids and the Polystilifera Reptantia resulted in speculative schemes relating them to one another (cf. Gibson 1988; Sundberg 1990; Crandall 1993), none of which found support. The recent molecular studies of Thollesson and Norenburg (2003) indicate these are the two basal sister groups at the root of the enopla and each has unique characters possessed only by each member of that group. Therefore, despite the diversity of morphology among them, the cratenemertids are regarded as constituting a coherent monophyletic family. At the same time, in each of the three cratenemertid groups, as defined by body aspect ratio, there are numerous other character states found only within that group. Thus, the epipelagic species form one distinct and well supported (cf. Crandall 2001) subfamily clade of the three, into which the Cratenemertidae can conveniently be divided.

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