

Structure of the Nemertine Integument with Consideration of Its Ecological and Phylogenetic Significance^{1,2}

JON L. NORENBURG

Mount Desert Island Biological Laboratory, Salsbury Cove, Maine 04672

SYNOPSIS. The phylum Nemertina, with more than 800 described species, occupies a wide range of habitats and figures prominently in theories of bilaterian evolution. Integuments of nemertines, from a number of habitats and representing the major orders, are compared and the general cell types constituting the epidermis are reviewed and defined. The general construction and cell demography of the integument are more or less characteristic for each order, but are not readily generalized to lower taxonomic levels. Similarly, the general structure of the integument has correlations with broad environments, but there are few conspicuous, uniquely adaptive, morphological specializations; e.g., the adhesive plate and ciliary bristles of interstitial nemertines, the tube-forming cells of *Carcinonemertes epialti* and various palaeonemertines, the epidermis of the pilidium larva. It is proposed that there are three generalized types of integumentary glandular cells, mucous, serous and bacillary, and that these and the ciliated cells vary only modestly across taxonomic and environmental lines. However, it is also proposed that the major structural variations of the integument not only are diagnostic for the orders but also suggest and correlate with two major evolutionary radiations of the extant nemertines, one epibenthic, the other infaunal—in that sequence. Similarities of the nemertine integument to that of turbellarians are superficial or at best plesiomorphous; i.e., they are also found in other taxa.

INTRODUCTION

Historically, nemertines have been considered an evolutionary zenith of a turbellarian acoelomate body plan (Bürger, 1897-1907; Hyman, 1951; Gibson, 1972). Characteristics found in both groups include: protonephridia; parenchymatous body-filling instead of a coelom (but see Turbeville and Ruppert, 1985); intracellular digestion (Gibson, 1972); vermiform body; a ciliated, glandular epidermis; and the larvae lack an anal pore, although it is present in adult nemertines. Each of these characteristics, up to now, must be considered plesiomorphous; i.e., they are inadequate to support the hypothesis that the Turbellaria and Nemertina comprise a monophyletic group.

The treatises by Bürger (1895, 1897-1907), Böhmig (1929) and Hyman (1951) describe the nemertine integument as consisting of ciliated cells, two types of glandular cells, mucous and serous, and interstitial cells. Taxonomic works do not add to this superficial description. The integumentary glandular cells of the heteronemertines *Lineus viridis* and *L. ruber* are known in some detail (Boie, 1952; Gontcharoff and Lechenault, 1966; Oaks, 1978), while selected details of the integument of other nemertines are presented by Pedersen (1968), Storch and Moritz (1971), Storch (1972), Storch and Welsch (1972), Anadón (1974), Tyler (1979), Stricker and Reed (1981), Turbeville and Ruppert (1983), Vernet (1983), and Vernet *et al.* (1983). Characteristics of integumentary cells are used in a comparative sense in very few instances (e.g., Hylbom, 1957; Gibson, 1979a). One purpose of this paper is to review and attempt to unify the isolated published observations in the context of recent comparative work with nemertine species representing all four orders (*sensu* Iwata, 1972) and a variety of habitats and lifestyles (Norenburg, 1982). Furthermore, I hope to demonstrate that a) most of the nemertine integumentary glandular cells may be assigned to one of three categories, each represented in each of the taxonomic orders, b) the demography of these categories has functional and phy-

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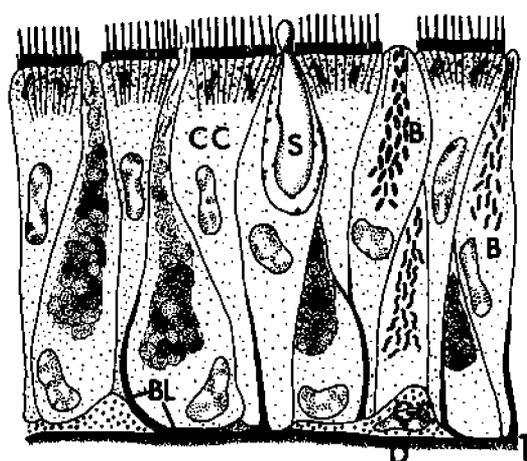


FIG. 1. Diagram of integument with stylized cell types of archi- and palaeonemertines.

logenetic implications, and c) the present data suggest that the integuments of nemertines and turbellarians do not share synapomorphies (uniquely derived characters). Generalizations on ultrastructure made in the following brief text are based on limited observations and therefore should be taken as working hypotheses; many more taxonomically and morphologically interesting nemertines have yet to be investigated critically.

MORPHOLOGY

General structure

The integument is a non-syncytial, columnar or cuboidal epithelium of multiciliated cells and glandular cells that rests on a more or less discrete basal lamina which grades into or is contiguous with a dermis (Figs. 1-3). Epidermal cells are joined apically by zonulae adherentes and septate junctions (Stricker and Reed, 1981; Norenburg, 1982; Turbeville and Ruppert, 1983) (Fig. 9). The septate junction in *Lineus ruber* is of the "pleated sheet" variety (Vernet *et al.*, 1983). Basal (interstitial) cells, often containing granules and associated with the basal lamina, may be seen with light microscopy in many species (Coe, 1905), but in others electron microscopy is necessary. A basiepithelial nerve supply generally is present (Bürger, 1895;

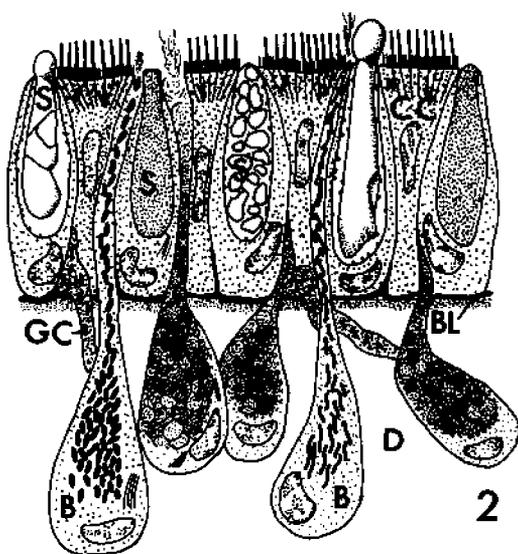


FIG. 2. Diagram of integument with stylized cell types of heteronemertines. B: Bacillary cell. BL: Basal lamina. CC: Multiciliated cell. D: Dermis. GC: Granular basal cell. M: Mucous cell. S: Serous cell.

Stricker and Reed, 1981; Norenburg, 1982; Turbeville and Ruppert, 1983).

The dermis of non-heteronemertines consists of connective tissue fibers, extracellular matrix with few cell processes passing through, and few fixed cells (Bürger, 1895; Pedersen, 1968). The dermal organization of heteronemertines is a key diagnostic for the order and some of its families (Bürger, 1895; Friedrich, 1960; Gibson, 1982); the significant feature being the arrangement of epidermal-type glandular cells lying in the dermis (also termed cutis) either among the dermal musculature or as deep as the primary body-wall muscles (Figs. 2 and 7). These cells open to the epidermal surface individually or in clusters (packet glands) (Bürger, 1895; Boie, 1952). Thus, the heteronemertine integument, typically, is considered to be "pseudostratified," although the cells penetrate the basal lamina.

The integument of some palaeonemertines also appears pseudostratified in the region between the cerebral ganglia and foregut, but it is only a greatly thickened epidermis in which the broad bases of single glandular cells or packet glands domi-

nate the basal region and all of the epidermal cells attach to the basal lamina (Bürger, 1895; Hylbom, 1957; Turbeville and Ruppert, 1983). In some species of the genus *Hubrechtella*, a few cells do penetrate the basal lamina (as in the heteronemertines) in the cerebral region (Gibson, 1979a).

Several other features of the nemertine integument should be mentioned but will not be treated in detail. Most nemertines have specializations of the epidermis that function as or are related to putative sensory structures (Bürger, 1897-1907; Coe, 1905; Gibson, 1972; and many others) and usually are virtually devoid of glandular cells. Pigment may be distributed in the epidermis, dermis, or the body-wall musculature (Gibson, 1972; Vernet, 1983) but has not been studied in great detail (Kennedy, 1979). Intraepidermal muscle fibers arising from subepidermal perikarya are characteristic for several species of palaeonemertines (Coe, 1905; Turbeville and Ruppert, 1983). Fibers that apparently are similar are observed in a number of heteronemertines (Gibson, 1979b).

Coe (1905) described two types of cells at the base of the epidermis, one epithelial and the other a type of anastomosing connective tissue. Electron micrographs show basal granule-containing cells that in some cases are between the epidermis and basal lamina (Fig. 14) (Norenburg, 1982; Turbeville and Ruppert, 1983) whereas in others the granules are predominately below the dermis. Some of these cells appear to be associated with the nervous system and similarity to the gliointerstitial systems described by Nicaise (1973) and Rieger (1981b) seems evident (see also Turbeville and Ruppert, 1985). The hoplonemertines examined, with the exception of *Carcinonemertes epialti*, have a more or less conspicuous zone of vacuolate-appearing, cup-like structures between the epidermis and the basal lamina (Figs. 3, 21 and 22) (Coe, 1905; Pedersen, 1968; Berg, 1972; Norenburg, 1982). With light microscopy, it usually can be resolved in sections 1 to 4 μm thick and in some it is associated with azanophilous granules (Norenburg, 1982) (Fig. 21). With electron microscopy, the

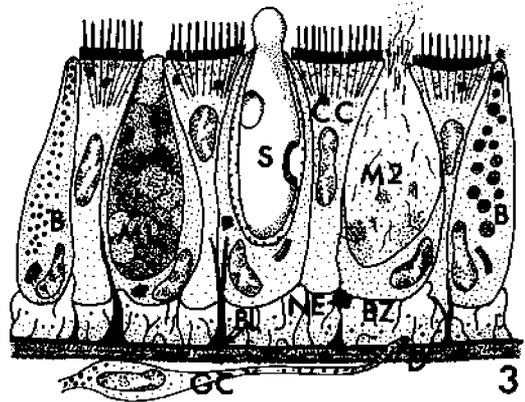
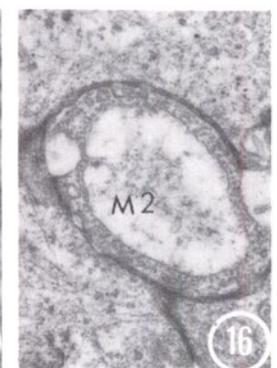
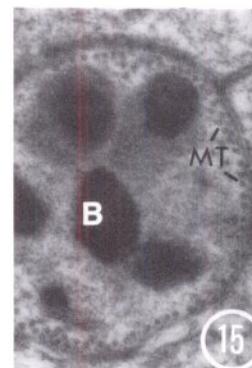
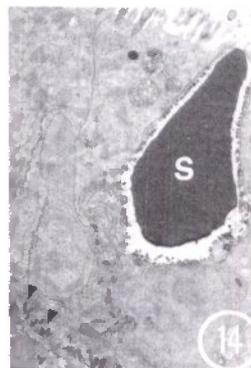
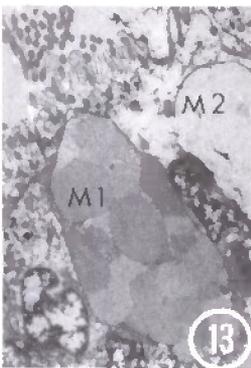
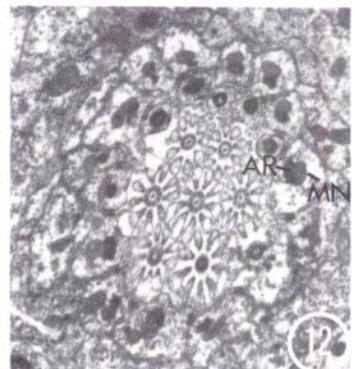
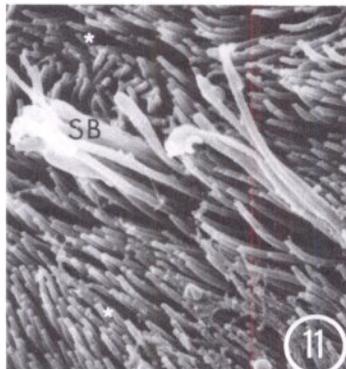
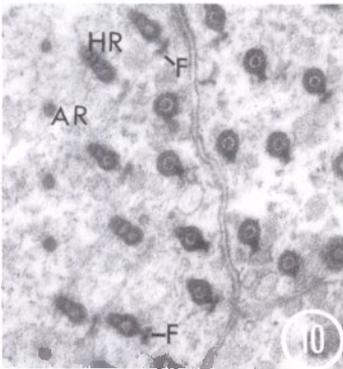
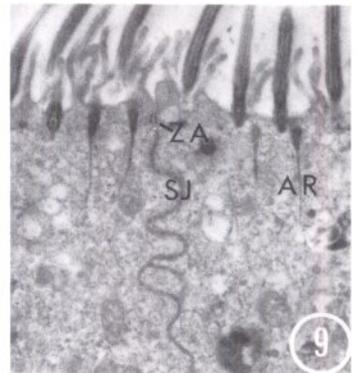
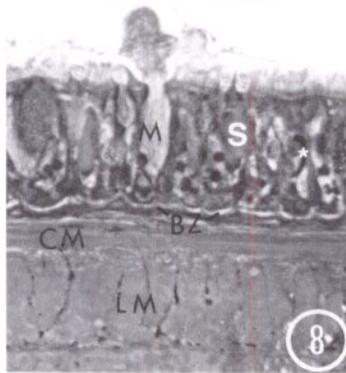
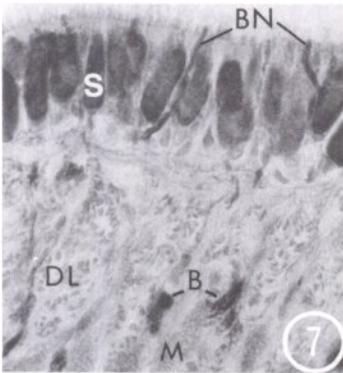
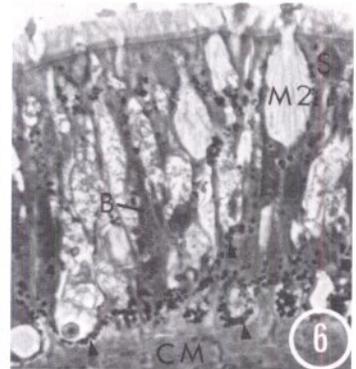
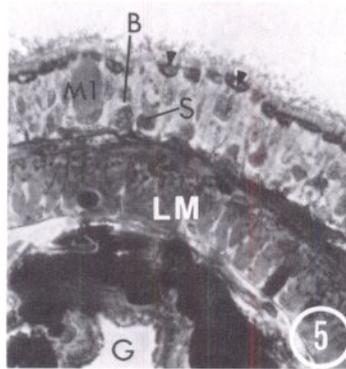
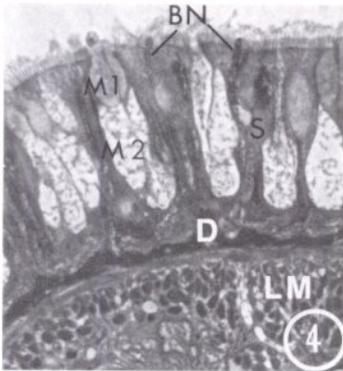


FIG. 3. Diagram of integument with stylized cell types of hoplonemertines. B: Bacillary cell. BL: Basal lamina. BZ: Basal-cup zone. CC: Multiciliated cell. D: Dermis. GC: Granular basal cell. M1: Mucous cell with neutral mucus. M2: Mucous cell with emptying goblet. NE: Neurite bundle. S: Serous cell.

cup-like structures contain sparse, undefined floccules (Fig. 22) but in some species these cups contain sparse material suggestive of neurofilaments or microtubules (*ibid.*). There is no evidence yet to support Pedersen's (1968) suggestion that these basal cups are parts of the overlying glandular cells. The cup-like structures also are found under the proboscis epithelium (Norenburg, 1982) which suggests that they are not a fixation artifact. Perhaps they are analogous to the "space" layer in the epithelium of the limpet *Patella vulgata*, that Grenon and Walker (1982) consider to be made up of degenerating cells; but they are unable to specify a function. In nemertines, a separate, extensive system of neurites lies between the basal cups and the epidermal cells.

Ciliated cells

With the exception of putative sensory cells, the ciliated cell is relatively uniform among all species examined ultrastructurally (Norenburg, 1982). Usually they are interspersed with glandular cells and are attenuated basally and have broad apical surfaces (Figs. 1-9), thereby maximizing ciliated surface (Bürger, 1895; Coe, 1905). The nucleus is basal or in the middle third of the cell.



Length of the cilia is uniform within a species and from 3 to 10 μm in the species examined, with 5 μm being the most frequent value. The diameter ranges from 0.20 to 0.26 μm (Norenburg, 1982). There appears to be wide species-variation in the number of cilia per cell and per unit surface area of the cells as determined from tangential electron micrographs (*ibid.*). For instance, *Otocyphlonemertes lactea* has about 64 cilia per cell with a density of about 5.2 cilia per μm^2 whereas *Prostomatella obscura* has about 391 cilia per cell with a density of about 1.6 cilia per μm^2 (*ibid.*). Not enough accurate measurements are available yet to detect any phyletic or environmental correlates. As noted by Tyler (1979), the cilia of a number of nemertines have a slight subapical constriction (Fig. 11) when viewed with scanning electron microscopy but more information is needed.

A zone of microvilli (Fig. 9), 1 to 1.5 μm high, is present in all species examined and is stained red or violet with alcian blue/periodic acid-Schiff technique (Norenburg, 1982). Electron microscopy demonstrates a moderately developed glycolyx and, in a few species, a web-like mat is present between the microvillar tips (*ibid.*); here, also more detailed study is necessary. Microvilli often appear bifurcate, but in most cases where the branch point is somewhat basal it can be shown that this is actually a "branching" of microvilli from

basal ridges that traverse the apical surface of ciliated cells (*ibid.*) (Fig. 9).

The apical cytoplasm of ciliated cells is stained pink with periodic acid-Schiff procedure, except when preceded by diastase treatment, thus suggesting glycogen stores (*ibid.*). Oaks (1978) demonstrated that the apical cytoplasm contains glycogen granules as well as ciliary rootlets, mitochondria, coated and crescent vesicles, smooth endoplasmic reticulum and dictyosome cisternae. Ciliary roots include a slender axial rootlet, 1.5 to 2.5 μm long, and a stocky, rostral horizontal rootlet, both of which are striated (Oaks, 1978; Sticker and Reed, 1981; Norenburg, 1982) (Figs. 9 and 10). A small basal foot is opposite the rostral rootlet. Turbeville and Ruppert (1983) report only single, axial rootlets for *Carinoma tremaphoros*. There is no evidence of interconnections between ciliary rootlets or of an apical web, comparable to that found in many Turbellarians (see Rieger, 1981a). However, a dense zone can be observed with light microscopy in the apical cytoplasm of the palaeonemertine *Hubrechtella cf. dubia* (Fig. 5); this is similar to the light microscopic appearance of the epidermis of the turbellarian *Nemertoderma* (unpublished observations).

Many nemertines have specialized ciliated regions *e.g.*, cephalic slits, grooves and pits (see Gibson, 1972) but only isolated ultrastructural observations are available

Figs. 4-16. Integuments of representative nemertines. FIG. 4. Archinemertine *Procephalothrix spiralis*. $\times 540$. FIG. 5. Palaeonemertine *Hubrechtella cf. dubia*. Note apical densities (arrows) in ciliated cells. $\times 540$. FIG. 6. Palaeonemertine *Tubulanus rhabdotus*. Note irregular pigment granules (arrows) throughout integument. $\times 540$. FIG. 7. Heteronemertine *Cerebratulus lacteus*. $\times 880$. FIG. 8. Hoplonemertine *Zygonemertes viridis*. Note sickle-shaped granule (*). $\times 540$. FIG. 9. Apical region of pair of ciliated cells, *Prostomatella obscura*. $\times 11,800$. FIG. 10. Tangential section along apical surfaces of ciliated cells, *Otocyphlonemertes lactea*. $\times 15,700$. FIG. 11. Pair of sensory bristles with 6-10 cilia each. Note slight bilobed apices and subapical narrowing (*) of regular cilia, *Tetrastemma* sp. $\times 6,250$. FIG. 12. Transverse section through basal region of sensory bristle, showing cilia with modified microvilli. Note outer cell apices with single rootlet and mitochondrion, *Otocyphlonemertes* sp. $\times 7,150$. FIG. 13. Longitudinal section of mature goblet with neutral mucus spherules and part of empty goblet nearby, *Otocyphlonemertes lactea*. $\times 4,100$. FIG. 14. Longitudinal section of mature serous goblet. Note ovoid basal granules (arrows) lying above a thin basal lamina. Undescribed interstitial heteronemertine. $\times 2,800$. FIG. 15. Transverse section through apical neck of bacillary cell, *Prostomatella obscura*. $\times 28,600$. FIG. 16. Transverse section through apical neck of mucous cell, *P. obscura*. $\times 15,760$. AR: Axial rootlet. B: Bacillary cell granules. BN: Bacillary cell neck. BZ: Basal-cup zone. CM: Body wall circular muscle sheath. D: Dermis. DL: Dermal longitudinal muscle. F: Foot process of cilium. G: Gut. H: Horizontal or rostral rootlet. LM: Body wall longitudinal muscle sheath. M: Mucous cell. M1: Mucous goblet at neutral phase. M2: Mucous goblet at acid phase and emptying. MN: Mitochondrion. MT: Microtubule. S: Serous cell. SJ: Septate junction. ZA: Zonula adherentes.

(Storch and Moritz, 1971). In general, these regions are the sites of specialized, putative sensory cells with elongate cilia (unpublished observations). So-called sensory bristles, usually consisting of several extra-long cilia, are found in most larvae and many adults. The apical plate of the pilidium larva consists of either monociliated or multiciliated collar cells and its cilia may be more than 1 mm long (Cantell *et al.*, 1982). Cephalic bristles (Figs. 11 and 12), so characteristic of metazoans inhabiting the interstices of marine sands, also are prominent in the interstitial hoplonemertines of the genus *Ototyphlonemertes*. Their spatial arrangement is varied and seems to be a potent species specific character (Kirsteuer, 1977; unpublished observations). These bristles consist of monociliated collar cells and preliminary observations suggest that the ultrastructure of these and the bristles of other nemertines has potential value in phylogenetic comparisons at several taxonomic levels.

Glandular cells

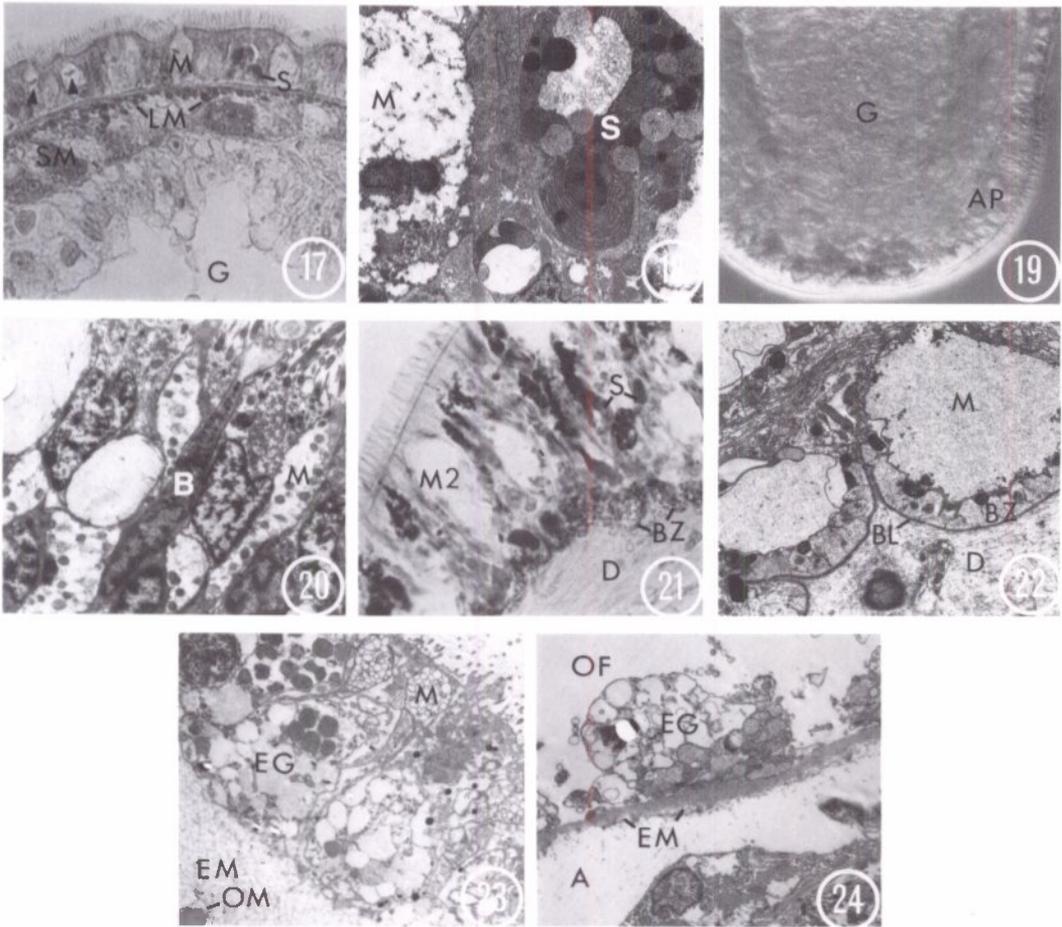
Generally, two types of epidermal glandular cells, mucous and serous, are recognized (Gibson, 1972). The deep glandular cells (packet or clustered glands) are sometimes considered a third category. Various workers recognize more types: four in the heteronemertine *Zygeupolia rubens* (Thompson, 1901), five in several palaeonemertines (Hylbom, 1957; Gibson, 1979a), and eight subepidermal types in *Lineus gesserensis* (Anadón, 1974). Thus far, glandular cells with apical cilia or microvilli have not been described for nemertines, but all appear to have apical microtubules accompanying the secretory material (Norenburg, 1982). The integument of many species is described as "usual" for that group or as displaying a "variety of glandular cells" but a unified, descriptive classification of integumentary glandular cells for the Nemertina is lacking. Based on the relatively detailed descriptions of glandular cells available for a variety of nemertines (Thompson, 1901; Nawitzki, 1931; Hylbom, 1957; Gibson, 1979a; and others) and personal observations of many species, I propose a framework of three

broad categories, mucous, serous and bacillary. These categories were defined initially by morphology and two or three key histochemical reactions, but a given glandular cell usually may be referred to one of them with just morphological information.

Mucous cells

In general, the mucous cell is readily recognized as a classic goblet cell (Figs. 1-6, 8, 13, 16 and 17). The secretory material has staining reactions that indicate a high proportion of mucopolysaccharides (glycosaminoglycans) and may be described as foamy, flocculent, finely granular or fibrous (Gontcharoff and Lechenault, 1966; Norenburg, 1982). Although it often is difficult to stain, the goblet mucus staining affinity tends to be blue with Heidenhain's azan, weakly to strongly alcian blue-positive, paraldehyde-fuchsin-positive, and is often metachromatic with toluidine blue or azure II, but very weakly or not at all with iron hematoxylin or mercuric bromphenol blue (Norenburg, 1982). With electron microscopy, mucous goblets contain finely granular, membrane-bound spherules (Fig. 13) of various electron densities or appear vacuolate and contain diffuse fibrous and membranous material (Fig. 18). They also occur in states appearing intermediate to these two conditions. The histochemical and ultrastructural work of Gontcharoff and Lechenault (1966), with the heteronemertines *Lineus ruber* and *L. viridis*, suggests that there are in fact two phases in mucus production characterized by "neutral" and "acid" mucopolysaccharides, successively, but that each may be secreted. The finely granular spherular material appears to represent the early, neutral phase, whereas goblets with fusing spherules and releasing mucus usually are reactive for acid mucopolysaccharide (Norenburg, 1982). Often, goblets with "neutral" mucus basally show "acid" mucus reactions apically if mucus is being released (*ibid.*).

The mucous cell is epidermal in each order except the Heteronemertina, in which the major portion of the cell normally is subepidermal (Figs. 2 and 7) (*i.e.*,



FIGS. 17-24. Integuments of representative nemertines. FIG. 17. *Carcinonemertes epialti* showing azanophilous, suspended nuclei (arrows) in empty mucous goblets and submuscular mucous cell. $\times 440$. FIG. 18. The unusual, putative serous secretory complex of *C. epialti*. $\times 2,930$. FIG. 19. Hind-end of *Ototyphlonemertes lactea* squeezed under coverslip to show thickened epidermal adhesive plate. $\times 300$. FIG. 20. Section through adhesive plate of *O. lactea* showing similarity of bacillary and specialized mucous cells to duo-gland releasing and viscid glands. $\times 1,250$. FIG. 21. Oblique section of integument of *Drepanophorus cf. crassus* showing basal cups with azanophilous granules. $\times 780$. FIG. 22. Basal-cup zone of *Prostomatella obscura* in tangential section showing flocculent content. $\times 1,980$. FIG. 23. Section through outer surface of oral lappet of pilidium larva, *Cerebratulus* sp., showing epidermis and extracellular matrix with portion of larval muscle. $\times 1,330$. FIG. 24. Section through inner surface of same oral lappet showing incomplete epidermis and dense layer of extracellular matrix. $\times 1,930$. A: Amnion cavity surrounding anlage in pilidium larva. AP: Adhesive plate. B: Bacillary cell. BL: Basal lamina. BZ: Basal-cup zone. D: Dermis. EG: Epithelio-glandular cell. EM: Extracellular matrix. G: Gut. LM: Body wall longitudinal muscle. M: Mucous cell. M2: Evacuated mucous goblet. OF: Oral funnel. OM: Obliquely striated larval muscle. S: Serous cell. SM: Submuscular mucous cell.

in the dermis) (Thompson, 1901; Gontcharoff and Lechenault, 1966; Anadón, 1974; Norenburg, 1982) and extends to the surface (individually or jointly) via a slender cell neck. Most of the deep glandular cells or packet glands of the thickened epidermis present in some palaeonemertines

appear to be mucous cells that also open via narrow cell necks (e.g., type 4 cell of Hylbom, 1957; and Gibson, 1979a; cells with "no particular staining affinity" of Gibson, 1979b; fig. 3 in Turbeville and Ruppert, 1983; unpublished observations). In both orders the mucous cell necks often

include an apical, empty goblet. The mucous cells of the archinemertine *Procephalothrix spiralis* usually have an apical, empty goblet overlying a larger mass of mucous spherules (Norenburg, 1982). In contrast, the empty goblets of hoplonemertine mucous cells usually are almost the full size of the cell. It appears that in the anoplan orders mucus is released from a given cell in relatively small amounts while in hoplonemertines it is released in a single burst (*ibid.*).

Some species also have putative mucous cells that are not in the usual position. In the region of the cerebral ganglia of palaeonemertines these mucous cells are found below the basal lamina, but cell necks extending to the surface have been found in only a few species (Hylbom, 1957; Kirsteuer, 1967; Gibson, 1979a). Many hoplonemertines have glandular cells that open to the body surface (Coe, 1905), but these cells are located below the primary body wall musculature, not in the dermis. In at least some of these hoplonemertines (*e.g.*, *Carcinonemertes epialti*, *Nemertopsis bivittata*, several *Ototyphlonemertes* species, *Paranemertes peregrina*) most of these cells contain material similar to that of the epidermal mucous cells as well as the cells of the cephalic gland (unpublished observations). Usually these cells are restricted to the cerebral or foregut region but in a few species they extend far into the intestinal region (Bürger, 1895; Coe, 1905; unpublished observations). Whereas electron microscopic study of heteronemertine development suggests that their dermal gland cells are epidermally derived (unpublished observations), I believe that hoplonemertine submuscular cells are derived evolutionally from the cephalic gland, but developmental study is required to resolve this point. However, the subepidermal mucous cells of the aberrant hoplonemertine *Malacobdella grossa* may indeed be submerged epidermal cells (Riepen, 1933; Storch and Welsch, 1972).

Serous cells

The serous cell, typically, also forms a goblet of secretory material (Figs. 1-3). The

latter is stable in aqueous and alcoholic fixatives and has staining reactions suggestive of a high proportion of proteinaceous material (Norenburg, 1982). As defined in this paper, all nemertine integumentary serous cells known are entirely epidermal (*ibid.*). The secretory mass initially is an accumulation of finely granular material that progressively condenses to form large, homogeneous, irregular, electron-opaque bodies. There may be several of these bodies in a goblet (Fig. 2), but the typically recognized form is a single, large, club-like inclusion (Figs. 7 and 14) (Bürger, 1895; Coe, 1905; Oaks, 1978; and many others). The latter often has been referred to as rhabditous or rhabdite-like, but it is evident from the recent review and clarification of turbellarian rhabdites by Smith *et al.* (1982) that this is inappropriate. The secretory material is stained intensely with naphthol yellow (Gontcharoff and Lechenault, 1966) and mercuric bromphenol blue (Norenburg, 1982). In all anoplans and many of the hoplonemertines this material has a unique reaction to the paraldehyde-fuchsin-trichrome procedure (Gabe, 1976) *i.e.*, following potassium permanganate and sulfuric acid oxidation they are golden-yellow whereas all other glandular materials are rendered magenta (Norenburg, 1982). The viscid nature of serous secretion is attested to by the discrete, exuded droplets often found at the surface of sectioned and scanning electron microscopic material (*ibid.*). As Oaks (1978) has noted, the material appears to undergo considerable shrinkage and condensation in fixation and usually is pulled away from the goblet wall (Fig. 14). In sum, these observations provide circumstantial evidence for the highly proteinaceous nature of the serous secretion.

Bacillary cells

Bacillary cells comprise a diverse group encompassing most of the remaining integumentary glandular cells (Figs. 1-7, 15 and 20). Their secretory material is in the form of discrete, often paracrystalline (Fig. 15), granules that usually are of uniform size and shape (Figs. 1-3) (Norenburg, 1982).

Bacillary refers to the secretory granules and is used as a convenient morphological descriptor, following similar usage by Pierantoni (1908) with polychaetes. The granules are from 0.2 to 6 μm in diameter or length and usually are membrane-bound. Bacillary granules in all nemertines examined are stained moderately to strongly with mercuric bromphenol blue (Norenburg, 1982). The work of Gontcharoff and Lechenault (1966) demonstrates that two types found in *Lineus ruber* and *L. viridis* have similar positive staining reactions for various protein groups. However, bacillary granules display a heterogeneous set of reactions with other stains, such as periodic acid-Schiff, alcian blue/alcian yellow, toluidine blue, iron hematoxylin and Heidenhain's azan (Norenburg, 1982). The granules also exhibit many kinds of distinctive substructure (*ibid.*; also figures in Anadón, 1974; Storch and Moritz, 1971; Storch and Welsch, 1972; Oaks, 1978; Turbeville and Ruppert, 1983), but they apparently all are membrane-bound, usually appear to be distributed evenly within a cytoplasmic matrix (*i.e.*, not aggregated as in a goblet cell) and are of uniform structure within a species and cell-type (Norenburg, 1982). Light and electron micrographs give the impression that granules are released individually by exocytosis (*i.e.*, no fusion prior to release) and hydrate rapidly (*ibid.*).

Although most nemertine species examined appear to have at least two types of bacillary cells (*ibid.*), the figures of *Lineus gesserensis* in Anadón (1974) suggest as many as four types (her cells 2, 3, 5 and 6) and Oak's (1978) figures of *L. ruber* demonstrate three types. Likewise, light microscopy of several species of the palaeonemertine genus *Hubrechtella* suggests the presence of at least three types (Hylbom, 1957; Kirsteuer, 1967; Gibson, 1979a; unpublished observations). The latter situation is complicated in that a given cell type apparently may stain differently in different regions of the body and may have conspicuously different epidermal distributions in closely related species (Hylbom, 1957; Gibson, 1979a).

Bacillary cells usually are dermal in the heteronemertines (Figs. 2 and 7) but are epidermal in the remaining orders (Norenburg, 1982). However, in a newly metamorphosed lineid heteronemertine, dermal glandular cells were not apparent but bacillary granules were found in the epidermis (unpublished observations), thus potentially confirming the epidermal origin of dermal glandular cells. Elongate, rod-shaped or spiral granules up to 6 μm long have been observed in species of each of the anoplan orders, including *Procephalothrix spiralis*, *Tubulanus* spp., *Hubrechtella cf. dubia*, *Micrura leidy*, *Cerebratulus lacteus*, *Lineus socialis* and *L. vegetus* (Norenburg, 1982; unpublished observations). Such granules have not been found in any hoplonemertines as yet, but bacillary cells with spherular inclusions have been found in all of the orders (*ibid.*). The latter bacillary cells may be divided into those that have uniform, bead-like granules (0.2 to 1 μm) and those that have somewhat larger, more irregularly-sized spherules (1 to 3 μm).

Several glandular cells do not readily fit one of the above categories or they presently are insufficiently described. In the epidermis of *Carcinonemertes epialti* there are large spheres of intense synthetic activity (Figs. 17 and 18), with part appearing homogeneous and azanophilous, characteristic of serous secretion, but with the remainder consisting of secretory vesicles reminiscent of bacillary secretion. Although very incompletely described, the spherical "Wanderdrussenzelle" (wandering gland cell) of the commensal *Malacobdella grossa* described by Riepen (1933) is curiously similar to the spheres of *C. epialti*. Sexually competent female *Lineus viridis* form new cyanophilous glandular cells throughout the entire cutis that appear to be intermediate to the two usual types of dermal bacillary cells (Gontcharoff and Lechenault, 1966). In contrast, Bierne (1970) described azanophilous glandular cells, forming ventrally in the cutis, accompanying sexual competence in male *L. viridis*. The special female cutis glands are implicated in production of the large amount of slime that fills the egg cocoon,

but the function of the special male cutis glands is not evident (Bierne, 1970).

Basal lamina and dermis

Ultrastructure and histochemistry of the dermis of the hoplonemertine, *Amphiporus pulcher*, and two heteronemertines, *Lineus bilineatus* and *L. ruber*, is described by Pedersen (1968). In most species a basal lamina (20 to 40 nm thick) is distinct along the base of the epidermis and may grade more or less smoothly into the underlying dermis (Fig. 22) (Pedersen, 1968; Anadón, 1974; Oaks, 1978; unpublished observations). In small species, such as the interstitial nemertines, the dermis is thin and only a narrow, finely granular zone underlies the basal lamina (unpublished observations). In large nemertines the dermis may be enormously thick and contains collagenous fibers that usually have specific orientations and are embedded in a granular matrix (*ibid.*, Pedersen, 1968). Various cells may be embedded in the dermis and many cell processes such as glandular necks, muscle fibers, and nervous elements pass through (Bürger, 1895; Pedersen, 1968; and others). A dense zone frequently is observed between the dermis and underlying muscles. Dense lamellae from the basal lamina frequently penetrate between epidermal cells (Figs. 1-3). Curiously, a discrete basal lamina is not apparent under the outer epidermis of pilidium larvae whereas a thick deposition of extracellular matrix is found along the oral funnel, although the epidermis of this region is often incomplete (Fig. 24) (unpublished observations).

DISCUSSION

Most nemertines occupy marine habitats, which include infaunal, interstitial, epibenthic, pelagic and commensal habits, but freshwater and terrestrial nemertines also are known. These habits pose very different physical problems; *i.e.*, infaunal nemertines burrow, interstitial nemertines glide and "swim" among shifting sand grains, and epibenthic and commensal forms glide over surfaces. The obvious concerns of the integument relate to loco-

motion and maintaining position. Terrestrial nemertines additionally must resist desiccation while freshwater nemertines evolutionally have had to cope with a major shift in their osmotic regime. The integument is in a position that is basic to mechanisms for coping with each of these conditions. The integument of marine species also has been implicated as a site of nutrient uptake (Fisher and Oaks, 1978; Roe *et al.*, 1981) whereas its slime contains various toxic or distasteful compounds that appear to confer protection against predators (see Kem, 1985).

Glandular cell demography and function

There is considerable variation in the proportions (total volume or numbers) of the three general types of integumentary glandular cells, but some generalizations appear justified at the ordinal level. Thus, it is evident that the mucous cell completely dominates the hoplonemertine epidermis, whereas in the anoplan orders its abundance is similar to that of the other glandular cells (Norenburg, 1982; unpublished observations). Conversely, bacillary cells are abundant in the anoplan orders but a scarce component of the hoplonemertine integument. Serous cells are most abundant in heteronemertines where they are the only fully epidermal glandular cells. They are also prominent, but more variable, in the two other anoplan orders (*ibid.*).

All nemertines leave behind them a continuous slime tube as they move (Pantin, 1950; Norenburg, 1982). Boie (1952) suggested that the slime coating of the heteronemertine *Lineus* has protective and lubricating functions. He believed that the epidermal glandular cells (*i.e.*, serous in this paper) produce the "protective" secretion whereas the secretion of the dermal glandular cells (Paketdrussen) is involved in strengthening the mucus tube, preparation of the egg cocoon, and lubrication. Morphological and histochemical characteristics suggest that mucous secretion is primarily a lubricant, whereas serous and bacillary secretions probably effect or affect structure and viscosity of the outer zone of the slime coat. This assertion is borne out

by comparison of the demography of the glandular cells with the generalized and specialized habits of nemertines.

It is known that ciliary activity requires a watery, lubricating mucus, such as the evanescent slime trail produced by most hoplonemertines, as might be anticipated by the large proportion of mucous goblets in these species (Norenburg, 1982). A vast majority of hoplonemertines lives in a mode that may be described as epibenthic (although they may be cryptic or interstitial) or pelagic (original compilation). The primary resistance that they must overcome in locomotion is aqueous. In fact, the primary mode of locomotion of hoplonemertines appears to be ciliary, whereas muscular activity effects change of direction and rapid, peristaltic movements (unpublished observations). This is true even for the terrestrial *Argonemertes dendyi* (Pantin, 1950). Infaunal hoplonemertines, such as *Paranemertes peregrina*, appear to be the exception and probably make use of sub-muscular glandular cells to provide additional slime for protection against abrasion. However, this species feeds at the surface and the extent of their active burrowing (as opposed to simply occupying a relatively static burrow) appears not to have been investigated. Similar cells also are found in non-burrowing, closely related species (see "Mucous cells" above). (It should be noted here that dermal or sub-muscular glandular cells have not been described from archinemertines.)

Heteronemertines generally are active burrowers, although some appear to be secondarily epibenthic (original compilation). The outer region of the slime tube needs to be viscid and resilient. Amplification of the bacillary and mucous cells into the dermis and the abundance of serous cells in the epidermis of heteronemertines confers upon this group an integument that is well-suited for active burrowing in abrasive habitats. It is among the Baseodiscidae and Lineidae, which have the most highly developed dermal glands, that the largest species of nemertines may be found. A parallel development of epidermal glandular cells is seen in the large burrowing palaeo-

nemertines of the Tubulanidae (personal observations). This evolutionary link with habit seems evident and is confirmed by other adaptive morphological characteristics (Coe, 1905; Turbeville and Ruppert, 1983). The relatively smaller number of bacillary and serous cells in many non-burrowing archi-, palaeo-, and most hoplonemertines further supports the correlation and hypothesis of an evolutionary link between integumentary glandular cell complement and environment (Norenburg, 1982).

The interpretation of function offered above is consistent with our understanding of adhesion and lubrication in other systems. This is especially well shown by Hermans' (1983) dialectic on the dualistic nature of these functions. Hermans (1983) addresses the nature of adhesion and de-adhesion but recognizes that conceptual reversal of this dualistic process also can describe lubrication. He argues that adhesion is by means of polycationic and "multifunctional" substances (glycoproteins) and that it is modulated by controlled release of membrane-bounded polyanionic substances (acid mucopolysaccharides and mucoproteins) serving as de-adhesives or lubricants. Thus, several lines of evidence suggest that the mucous goblets have lubrication as a primary function. The serous and/or bacillary cells may anchor the mucous to the substratum and perhaps provide resistance against which the cilia work. However, any or all of the secretions may and probably do have additional functions as well, particularly as vehicles or modulators for toxins or repellents (see also Kem, 1985), attractants, trail markers, metabolic wastes or physiological regulatory functions.

From the diverse morphology and histochemistry displayed by the bacillary cells one might anticipate a diversity of specialized functions. Parchment-like tubes are correlated with unusual or specialized cell distributions in several nemertine species. The cells implicated in tube construction and described by Hylbom (1957) for several palaeonemertine species appear to be bacillary cells. A sharp transition in col-

oration that occurs at the level of the lateral sensory organs in most of these species (Coe, 1905; Hylbom, 1957; personal observations) also correlates with a disjunction in staining reactions of the bacillary cells (Hylbom, 1957). Several species of *Tubulanus* form a complex of parchment-like, resting or residence tubes but produce a relatively ephemeral mucous tube as they move away from their resting area (unpublished observations). The mucous tube becomes translucent or opaque as the worm is relatively stationary or moves the portion of the body anterior to the lateral sense organs rhythmically back and forth through the region that is becoming fibrous and parchment-like (*ibid.*). A similar relationship between bacillary cells and tube construction may be indicated for the heteronemertines *Zygeupolia rubens* and *Parapolia aurantiaca* (Thompson, 1901). The hoplonemertine *Carcinonemertes epialti* forms parchment-like resting tubes on its host crab (Wickham, 1978). This species has an unusual secretory cell, as well as unusual mucous goblets (Norenburg, 1982). Several species of *Tetrastemma* build similar but more fragile resting tubes (*ibid.*).

Evidence for a special function of bacillary cells is seen in the secondary development of glandular, dermal spawning cells in female and male *Lineus* just prior to egg deposition (Gontcharoff and Lechenault, 1966; Bierne, 1970), although it is not clear yet that the male's cells are bacillary. The dense accumulation of bacillary cells adjacent to mucous cells in the adhesive plate (Figs. 19 and 20) of several species of the interstitial *Ototyphlonemertes* must be interpreted as evidence that they participate in the specialized duo-gland-like adhesive function of this region (Norenburg, 1982).

Phylogeny

Detailed analyses of the body wall of turbellarians and other taxa have influenced profoundly our understanding of function and phylogeny at taxonomic levels ranging from species to phyla (e.g., Rieger, 1976; Tyler, 1976; Ehlers and Ehlers, 1977; Storch, 1979; Smith *et al.*, 1982). Whereas about 100 published papers address ultrastructure of the turbellarian body wall

(Rieger, 1981a), only about 12 consider any aspect of ultrastructure of the nemertine integument.

Based on the generalizations formulated in this paper, ultrastructure of the integument supports the traditional histological basis for separating the Anopla and Enopla, and, to a more limited degree, the ordinal classifications presented by Iwata (1972) and Gibson (1982). In asserting a correlation between structure of the integument and general habitat of the higher taxa, I am suggesting that the major evolutionary radiation of the hoplonemertines was in an epibenthic (non-burrowing) mode, whereas that of the heteronemertines was in a burrowing mode. The archinemertines are essentially shallow infauna but do not appear to be strong burrowers and have not achieved the diversity or large size of the heteronemertines. Palaeonemertines, as a group, occupy a diversity of habitats. Many are shallow infauna or occupy confined, cryptic habitats such as crevices in rubble and wood, whereas some are active burrowers. Hylbom (1957) noted the apparent heterogeneity of the Palaeonemertina and a trend toward a heteronemertine-like condition of the integument. He suggests that this is reflected in potential polyphyly of the Heteronemertina. It is likely that many of the extant palaeonemertine genera represent development in parallel with heteronemertines.

Clark (1979) considers burrowing to be derived with respect to an epibenthic habit. Similarly, Jägersten (1972) envisions a pelagic origin for the Metazoa. As suggested earlier, for purposes of locomotion there is little physical difference between these habitats for a small worm propelled by ciliary activity, although solid substratum for anchoring a mucus tube would appear to give an epibenthic worm greater control over its destiny. The structure of the nemertine integument appears to support a non-burrowing ancestry for the nemertines and I suggest that the structure of the hoplonemertine integument approximates the plesiomorph condition for the phylum. Possibly the even simpler integument of the nemertine "planuloid" and pilidium larva should be taken as ple-

siomorph (unpublished observations), but at least that of the pilidium may in fact be quite specialized (*ibid.*) and more observations are required. There is no implication here that a member of an extant order was ancestral to any of the other orders.

There seems little doubt that the relationships of the Nemertina are with the Spiralia. However, the origin and affinities of the Nemertina are still enigmatic even after a century of debate on the evolutionary origins of metazoan groups, the coelom, blood vessels and larvae. Steinbock (1963) declares that "morphological and histological data, it is almost universally agreed, make obvious the relation of the Rhynchocoela to the Turbellaria." Beklemishev (1963) is more cautious, remarking that nemertines "... are so primitive that their relationship to the Turbellaria must place their origin at the very base of the phylogenetic lineages." In fact, even with flexible application of Hennig's (1966) principles of phylogenetic analysis, the epidermis is the only complex structure with a serious possibility of homology for these two groups. Electron microscopy is required to resolve questions of homology at that level (*cf.*, Rieger and Tyler, 1979). However, as Storch (1979) asserts, ultrastructural identity is by no means sufficient to prove homology. With such structurally simple forms as turbellarians and nemertines one may anticipate that coordinate function, structure and position often have obligatory interrelationships for which Storch's (1979) admonition of caution carries special force.

With the exception of the duo-gland system (Tyler, 1976) and rhabdites (Smith *et al.*, 1982), the glandular cells of the turbellarian epidermis are not well known (Rieger, 1981a). According to the criteria of Smith *et al.* (1982) nemertines do not appear to have rhabdites. Remaining, superficial similarities of mucous, serous or bacillary secretions would require much detailed comparison since they are found in great diversity in many different invertebrates (*cf.* Storch and Welsch, 1972; Rieger *et al.*, 1974; Hermans, 1983). The ciliated cell is of considerable interest in

phylogenetic relationships of lower invertebrates (*e.g.*, Rieger, 1976, 1981a). The nemertine ciliated cell does not appear to have a special relationship to any of the four patterns of features that Rieger (1981a) finds characteristic for turbellarians, which include apical cell web, ciliary tips, rootlet organization, basal lamina and ultrarhabdites. Thus far, only *Hubrechtella cf. dubia* shows any promise of having an apical cell web. Using Rieger's (1981a) ultrastructural criteria and Karling's (1974) and Ax's (1963) turbellarian archetypes, a potential, common ancestor for these and a nemertine archetype would be very simple indeed; as Beklemishev (1963) suggested "... at the very base of phylogenetic lineages" (presumably meaning metazoan lineages). Assuming no secondary losses, such a creature would be turbellariomorph with a cellular epidermis and gastrodermis separated by a thin intercellular matrix; epidermal multiciliated cells having single or paired, equal length, rootlets and septate junctions; epidermal mucous, serous and bacillary cells; a simple mouth pore and sac-like gut; anterior and posterior bristles; separate sexes with external fertilization, and possibly protonephridia. I believe that creature would bear a close resemblance to the palaeonemertine "planuloid" larva. This is consistent with but does not prove either the Planuloid-Schizocoel or the Gastraea-Enterocoel theories of evolution for the Bilateria (*cf.*, Turbeville and Ruppert, 1983). It is also consistent with my view that nemertines or nemertoid forms had little to do with the evolution of other extant metazoan lineages (see also Riser, 1985).

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