# The cyphonautes larva of the marine bryozoan *Membranipora membranacea*. I. General morphology, body wall, and gut

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The cyphonautes larva of *Membranipora membranacea* (phylum Bryozoa, order Cheilostomata) is a laterally compressed, planktotrophic larva covered by a triangular, bivalved shell. In this paper, the general morphology of the larva and the cytology of the body wall and gut are examined by light and electron microscopy. The outer part of the body wall underlying the shell consists of an essentially nonciliated layer, called the aboral epithelium. At the larval apex, the aboral epithelium forms a knob-shaped apical organ. The apical organ contains putative sensory cells, a basal nerve plexus, and a group of undifferentiated epithelial cells that probably corresponds to a blastema. The body wall at the base of the larva constitutes the larval locomotory organ or corona. The corona consists of two rows of multiciliated cells, which are flanked by myoepithelial cells and monociliated cells. A large mantle cavity, referred to as the vestibule, occupies the central region of the larva. The vestibule is partially divided into an anterior inhalant chamber and a posterior exhalant chamber by two ciliary ridges that run along the sides of the mantle cavity. At the base of the larva, the inhalant chamber is surrounded by a horseshoe-shaped flap of tissue, called the velum. Apically, the inhalant chamber forms a densely ciliated preoral funnel. Food particles filtered by the ciliary ridges are conveyed to the larval mouth by cilia in the preoral funnel. The mouth in turn leads into a tripartite gut consisting of an esophagus, stomach, and intestine. Two types of ciliated lining cells occur in the esophagus and stomach. The intestine appears to be lined by nonciliated epithelial cells and empties into the exhalant chamber by way of an anus. Morphological features of the cyphonautes larva are compared with those described for other bryozoan larvae in an attempt to define homologous structures among the various larvae of bryozoans.

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La larve cyphonautes de *Membranipora membranacea* (Phylum Bryozoa, Ordre Cheilostomata) est une larve planctonophage contenue dans une coquille bivalve triangulaire. La morphologie générale de la larve de même que la cytologie de la paroi du corps et celle du tube digestif ont été étudiées aux microscopes photonique et électronique. La partie externe de la paroi du corps, sous jacente à la coquille, consiste en une couche essentiellement non ciliée appelée épithélium aboral. À l'apex de la larve, l'épithélium forme un organe apical en pommeau. Cet organe contient les cellules sensorielles précurseurs, un plexus nerveux basal et des cellules épithéliales non différenciées qui constituent probablement le blastème. À la base de la larve, la paroi du corps contient l'organe locomoteur de la larve, ou corona, qui se compose de deux rangées de cellules multiciliées flanquées par des cellules myoépithéliales et des cellules monociliées. La région centrale de la larve est occupée par la cavité du manteau, très grande, qui porte le nom de vestibule. Le vestibule est partiellement divisé en une chambre antérieure inhalante et une chambre postérieure exhalante par deux crêtes ciliaires qui longent les côtés de la cavité du manteau. À la base de la larve, la chambre inhalante est entourée par un repli de tissu en forme de fer à cheval appelé velum. À l'apex, la chambre inhalante forme un entonnoir pré-oral très cilié. Les particules de nourriture filtrées par les crêtes ciliaires sont acheminées vers la bouche de la larve par les cils de l'entonnoir pré-oral. La bouche conduit à un tube digestif tripartite constitué de l'oesophage, de l'estomac et de l'intestin. L'oesophage et l'estomac sont tapissés par deux types de cellules ciliées. L'intestin semble tapissé par des cellules épithéliales non ciliées et son contenu est évacué dans la chambre exhalante par l'anus. Les caractéristiques morphologiques de la larve cyphonautes sont comparées à celles qui existent chez les larves d'autres bryozoaires, de façon à établir l'homologie des structures chez les diverses larves de bryozoaires.

[Traduit par la revue]

## Introduction

Bryozoans are sessile, colonial organisms that typically produce short-lived, lecithotrophic larvae. In a few marine species belonging to the class Gymnolaemata, however, the larva possesses a functional gut and spends a prolonged period feeding in the plankton. Such long-lived planktotrophic stages are referred to as "cyphonautes larvae" and are markedly dissimilar in external morphology to the anenteric "coronate larvae" produced by the vast majority of gymnolaemate bryozoans (Ryland 1974; Zimmer and Woollacott 1977*a*; Woollacott and Zimmer 1978). Unlike the ovoid, fully ciliated coronate larvae that are typical of gymnolaemates, cyphonautes larvae are laterally compressed, triangular larvae that are covered by a bivalved shell. Several unique specializations in their internal anatomy have also been noted in the few histological studies that have been conducted on cyphonautes larvae (e.g., Prouho 1892; Kupelwieser 1905; Atkins 1955*a*).

To describe the cytology of various larval organs, we have undertaken an ultrastructural investigation of the cyphonautes larvae produced by the cosmopolitan bryozoan *Membranipora membranacea* (class Gymnolaemata, order Cheilostomata). In the present paper, we include information on the general mor-

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phology of the larva and on the fine structure of tissues constituting the body wall and digestive tract. A companion paper contains details on the internal sac, larval muscles, and pyriform organ (Stricker *et al.* 1988). One aim of our ultrastructural studies is to present comparative information that will supplement previous reports on the fine structure of coronate larvae (e.g., Woollacott and Zimmer 1971, 1978; d'Hondt 1975; Reed and Cloney 1982*a*, 1982*b*; Reed and Woollacott 1982, 1983; Reed 1984). In addition, we describe the morphology of the free-swimming cyphonautes larva to provide a foundation for studies focussing on larval metamorphosis in *M. membranacea* (Stricker 1988).

## Materials and methods

Larvae were collected with a 250-μm mesh plankton net during the summers of 1985 and 1986 in the vicinity of the Friday Harbor Laboratories on San Juan Island, Washington, U.S.A. The plankton tows were usually taken within 5 m of the surface.

Each metamorphosed larva formed a twin ancestrula, a developmental stage characteristic of the genus *Membranipora* (O'Donoghue 1927). According to other workers, the membraniporid cyphonautes larvae found in the vicinity of San Juan Island probably belong to *M. membranacea* (Strathman and McEdward 1986). There are, however, no reliable guidelines for identifying the adult colonies of membraniporid bryozoans in the Pacific Northwest, since variations in colony morphology previously used to distinguish species can be greatly affected by environmental factors such as predation (Yoshioka 1982*a*; Harvell 1984). Thus, as discussed by Stricker (1987), the cyphonautes larvae examined in this study are designated as belonging to *M. membranacea* (Linnaeus) s.l., until the taxonomy of this genus is more clearly defined.

For scanning electron microscopy (SEM), free-swimming larvae were relaxed briefly in 7.5% magnesium chloride, fixed in bicarbonate-buffered osmium tetroxide, dehydrated in ethanol, and dried by the critical-point method using carbon dioxide (Stricker and Reed 1985). Specimens were also processed for transmission electron microscopy (TEM) as described by Stricker and Reed (1985). In most cases, the primary fixative consisted of a ruthenium red – sodium cacodylate solution of glutaraldehyde (Cavey and Cloney 1972). Occasionally, the larvae were initially fixed in phosphate-buffered glutaraldehyde (Stricker and Reed 1981) or bicarbonate-buffered osmium tetroxide. All glutaraldehyde-fixed specimens were postfixed in bicarbonate-buffered osmium tetroxide, dehydrated in ethanol, and embedded in LX-112 plastic resin (Ladd Research Inc.). Unless stated otherwise, the micrographs in this paper are of material initially fixed in the ruthenium red – sodium cacodylate solution of glutaraldehyde.

## Results

*General morphology*

The cyphonautes larva of *Membranipora membranacea* is covered by a translucent, chitinous shell (Fig. 1). To clarify the terminology used in the following descriptions of the larva, Fig. 2 depicts the larval axes and the orientation of sectioning planes as defined in this paper.

Larvae examined in this study averaged 461 ± 27 μm long ($N$ = 12; range = 410–540 μm) and 363 ± 22 μm high ($N$ = 12; range = 330–420 μm). The posterior margin of the larval shell typically measured about 340 μm long, whereas the anterior margin was usually about 400 μm long. The ovoid apical opening in the shell was situated at a level about 150 μm anterior to the posteriormost tip of the shell.

The major features of the cyphonautes larva are diagrammed in Fig. 3 and summarized briefly below. The anterior end of the larva contains a large neuroglandular complex, termed the pyriform organ. The pyriform organ consists of a glandular field, a median ciliated groove, and an anteriorly positioned tuft of long cilia, called the vibratile plume. Conspicuous lipid-like droplets occur near the pyriform organ.

In bryozoans, the larval epidermis arises from three regions of the embryo: (*i*) aboral ectoderm in the animal hemisphere, (*ii*) oral ectoderm in the vegetal hemisphere, and (*iii*) a band of presumptive coronal cells situated near the border between the aboral and oral hemispheres (Zimmer and Woollacott 1977*a*). During development of the cyphonautes larva, the center of the oral ectoderm becomes invaginated into the aboral hemisphere to form a large mantle cavity, termed the vestibule (Marcus 1926). Concomitantly, the presumptive coronal cells become located at the future base of the larva (Cook 1962). Thus, the outer layer of the body wall in the fully formed cyphonautes larva comprises three main components: (*i*) an aboral epithelium derived from the aboral field, (*ii*) the corona, and (*iii*) the vestibular epithelium derived from the invaginated part of the oral hemisphere.

The outer epithelium of the body wall occurring directly beneath the shell is derived from ectoderm in the former aboral half of the embryo and is thus referred to as the aboral epithelium. At the apex of the larva, the aboral epithelium forms a ciliated, knob-shaped structure, called the apical organ. A mesodermal compartment lies directly beneath the aboral epithelium. Along the anterior and posterior margins of the larva, the mesodermal compartment contains a median band of striated muscles. These muscles run from the apical organ anteriorly to the pyriform organ and posteriorly to the posteriormost part of the corona.

The corona of the cyphonautes larva constitutes the larval locomotory organ. Near the midtransverse plane of the larva, the coronal ciliation is greatly reduced (Figs. 3, 4). This gap presumably allows food-laden water to pass into the vestibule without being disturbed by the beating of the coronal cilia (Atkins 1955*a*). In the vicinity of reduced ciliation, a thin flap of tissue, called the velum, extends more or less perpendicular to the shell and thereby reduces the opening into the anterior part of the vestibule.

Near the posterior edge of the velum, two laterally positioned ciliary ridges extend into the vestibule. The ciliary ridges partially divide the vestibule into an anterior inhalant chamber and a posterior exhalant chamber. According to Atkins (1955*a*), a larva in the process of feeding draws water into the inhalant chamber by cilia on the ciliary ridges. The water is then passed between the two ridges and out the exhalant aperture. Protists of appropriate size are filtered by the ciliary ridges and conveyed to the "preoral funnel," a densely ciliated region of the inhalant chamber underlying the larval apical organ. The tapered end of the preoral funnel leads into the larval mouth, which in turn opens into a tubular digestive tract located at the posterior end of the larva. The gut comprises three regions: the esophagus, stomach, and intestine.

A large ovoid organ, called the internal sec, lies anterior to the intestine along the midline of the former oral field of the larva. At the anterior edge of the internal sac, an adductor muscle extends across the larva and attaches to the aboral epithelium underlying each valve of the shell. Figure 3 also depicts the attachment sites of two other sets of muscles, the sac muscles and lateral muscles.

*Body wall*

*Shell*

Most of the larval shell measures 2–5 μm thick. When

viewed by SEM, each valve exhibits a posterior curved band that marks the positions of the shell apex at earlier stages in development (Atkins 1955*a*). In addition, faint growth lines are evident. The growth lines appear to be arranged in a concentric fashion anterior to a posterobasal region representing the initial shell secreted by the larva (Fig. 4).

Each valve of the shell is bilayered. The outer layer consists of a thin (~250 nm) sheet of electron-dense material (Fig. 5). The rest of the shell contains relatively electron-lucent material which appears filamentous, especially when viewed in grazing sections (Fig. 6).

In most cases, the posterior margin of the shell lies directly above the aboral epithelium. Anteriorly, however, the shell is often separated from underlying tissues by a space of varying size, depending on the state of larval contraction (Fig. 1). At advanced stages of development, the basal margin of each valve forms an inwardly directed row of a few dozen tubercles that appear reddish brown in living specimens (Fig. 7).

*Aboral epithelium*

The aboral epithelium underlying the shell valves consists of an essentially nonciliated simple layer resting upon a thickened basal lamina. Toward the base of the larva, the epithelial cells tend to be squamous, whereas epithelial cells situated near the larval apex are cuboidal to columnar (Figs. 8–10). Occasionally, the aboral epithelium appears stratified, since the apical ends of some cells extend over the apices of neighboring cells (Fig. 9). The aboral epithelial cells lack an overlying cuticle and typically contain Golgi bodies as well as numerous arrays of rough endoplasmic reticulum (RER).

A distinct type of aboral epithelial cell is tightly associated with the basal half of each valve. These cells have been designated as constituting a "Polster" (cushion) by Kupelwieser (1905). The polster cells of *M. membranacea* extend from a level near the midtransverse plane of the pyriform organ to a few micrometres beyond the anterior edge of the internal sac. They reach apically from the basal margin of the shell to about the level of the adductor muscle. Thus, a "Polster-free zone" exists in the apical half of the larva as well as along the anterior and posterior margins.

Each polster cell is filled with tightly packed granules containing homogeneous material (Fig. 8). The granules vary in shape and size but tend to be ovoid and about 5 μm long. As described above for other regions of the aboral epithelium, squamous cellular processes occasionally overlie the granule-containing cytoplasm of the polster cells. In all larvae examined, however, the polster granules lie above the basal lamina of the aboral epithelium and hence will be considered part of that epithelium.

At the posterior and anterior margins of the shell, the aboral epithelium contains unusual monociliated cells that lie between the shell valves (Fig. 10). The apices of these cells are elaborated into stout projections that protude into the external milieu. The cilium extending from each cell possesses a rootlet and arises from a deep, narrow pit.

*Apical organ*

The aboral epithelium is highly specialized at the apex of the larva and forms a knob-shaped apical organ that measures about 50 μm in diameter. The apical organ is completely covered by a cuticle and can protrude slightly through the ovoid opening between the shell valves (Figs. 11–13). The ultrastructure of the apical organ in the cyphonautes larva of *M. membranacea* has been described by Stricker (1987) and will be summarized only briefly here. Figure 12 diagrams the cytological organization of the organ.

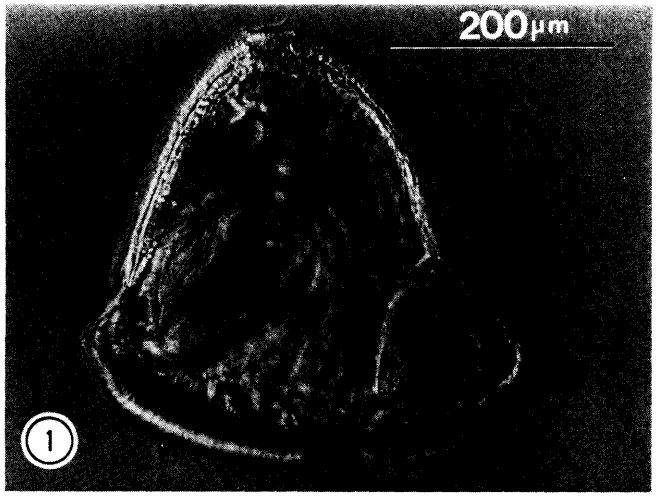
The core of the apical organ contains 5–15 bipolar neurons which are continuous with a well-developed nerve plexus lying directly above the basal lamina of the organ. The nerve plexus is connected with nerves in the pyriform organ by a bundle of neurons that run beside the anterior median muscle. At least some of the neurons within the apical organ possess a cilium and thus appear to represent primary sensory cells (Fig. 14). The neural core contains a single myoepithelial cell with a stri-

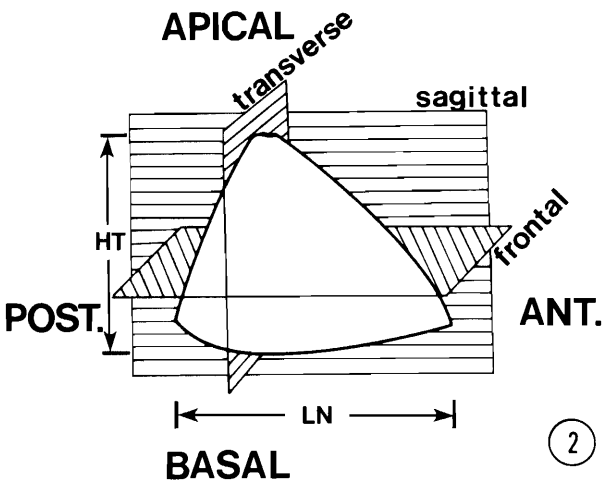


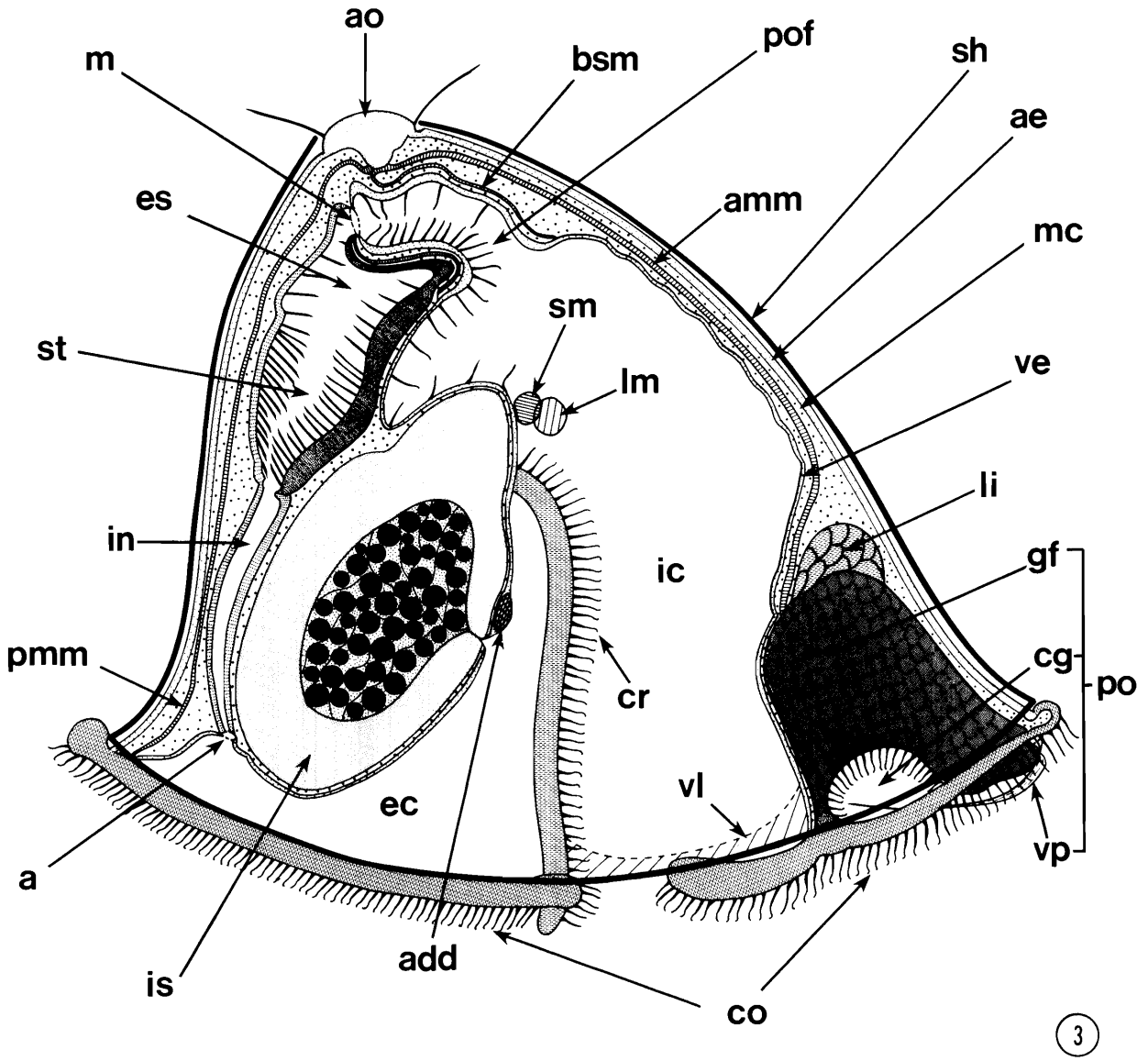
FIG. 1. Photomicrograph of a living cyphonautes larva of *Membranipora membranacea*. The anterior end of the larva is oriented to the right. Note that parts of the anterior body wall have pulled away from the larval shell. Differential interference contrast optics. FIG. 2. Diagram of the larval axes. The larva is oriented as in Figs. 1 and 3. ANT., anterior; HT, height; LN, length; POST., posterior. FIG. 3. Diagram of a lateral view of a cyphonautes larva, showing the major morphological features. *a*, anus; *add*, adductor muscle; *ae*, aboral epithelium; *amm*, anterior median muscle; *ao*, apical organ; *bsm*, basket of striated muscle; *cg*, ciliated groove of pyriform organ; *co*, corona; *cr*, ciliary ridge; *ec*, exhalant chamber of vestibule; *es*, esophagus; *gf*, glandular field of pyriform organ; *ic*, inhalant chamber of vestibule; *in*, intestine; *is*, internal sac; *li*, lipid-like droplets; *lm*, lateral muscle attachment; *m*, mouth; *mc*, mesodermal compartment; *pmm*, posterior median muscle; *po*, pyriform organ; *pof*, preoral funnel; *sh*, shell; *sm*, sac muscle attachment; *st*, stomach; *ve*, vestibular epithelium; *vl*, velum; *vp*, vibratile plume of pyriform organ.

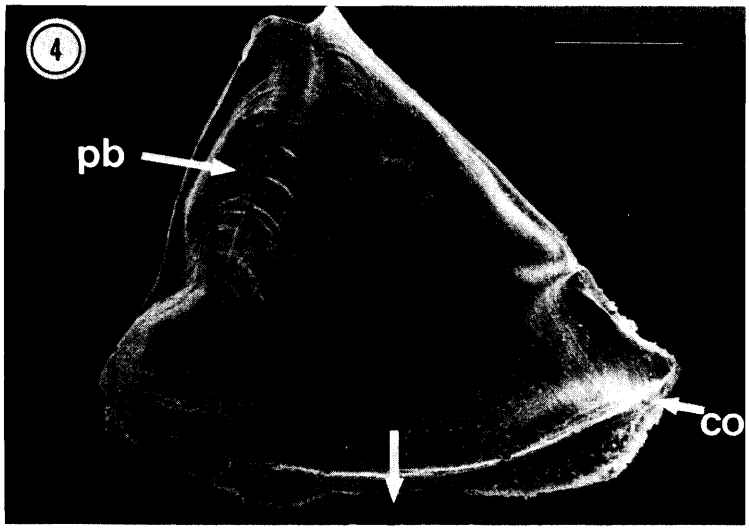
FIG. 4. Scanning electron micrograph (SEM) of a cyphonautes larva. The asterisk marks the site of the initial shell secreted by the larva, and the unlabelled arrow points to the central gap in coronal ciliation. *co*, corona; *pb*, posterior band on shell. Scale bar = 100 μm. FIG. 5. Transmission electron micrograph (TEM) of a longitudinal section of the shell. The double arrowheads mark the thin outer layer of the shell. Scale bar = 1 μm. FIG. 6. TEM of a grazing section of the shell, showing its filamentous nature. The arrowhead marks the apical tip of an aboral epithelial cell. Scale bar = 1 μm. FIG. 7. Photomicrograph of the basal edge of the shell. The arrowheads mark inwardly directed tubercles along the margin of the shell. Differential interference contrast optics. Scale bar = 100 μm. FIG. 8. TEM of a sagittal section through polster cells (*pl*) in the aboral epithelium underlying the shell (*sh*). Scale bar = 1 μm. FIG. 9. TEM of a sagittal section of the aboral epithelium (*ae*). The double arrowheads mark apical processes extending over neighboring cells. *bl*, basal lamina; *mc*, mesodermal compartment; *sh*, shell. Scale bar = 5 μm. FIG. 10. TEM of a sagittal section near the posterior margin of the shell (*sh*). The arrowheads mark stout projections arising from monociliated cells in the aboral epithelium (*ae*). *bl*, basal lamina. Scale bar = 5 μm.

FIG. 11. Low magnification TEM of the apical organ (*ao*). *ae*, aboral epithelium; *ms*, mesodermal cells; *np*, nerve plexus; *sh*, shell. Scale bar = 10 μm. FIG. 12. Diagram of the cytological organization of the apical organ. *ae*, aboral epithelium; *bl*, basal lamina; *cu*, cuticle; *me*, myoepithelial cell; *ms*, mesodermal cells; *nc*, neural core; *np*, nerve plexus; *pr*, peripheral ring of monociliated cells; *sh*, shell; *spr*, subperipheral ring of monociliated cells; *tc*, transitional cells; *udc*, undifferentiated cells. FIG. 13. SEM of the apical organ. The double arrowheads mark debris entangled in the cilia (*ci*) of the organ. Scale bar = 10 μm. FIG. 14. TEM of a neuron (*ne*) in the apical organ, showing a cilium (*ci*) arising from the cell. Phosphate-buffered glutaraldehyde primary fixation. Scale bar = 1 μm. FIG. 15. TEM of lipid-like (*li*) droplets in the mesodermal compartment surrounding the pyriform organ. Scale bar = 5 μm. FIG. 16. TEM of the relatively undifferentiated mesodermal cells underlying the apical organ. Scale bar = 1 μm.

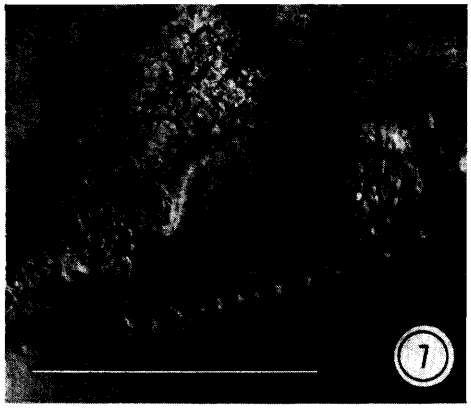


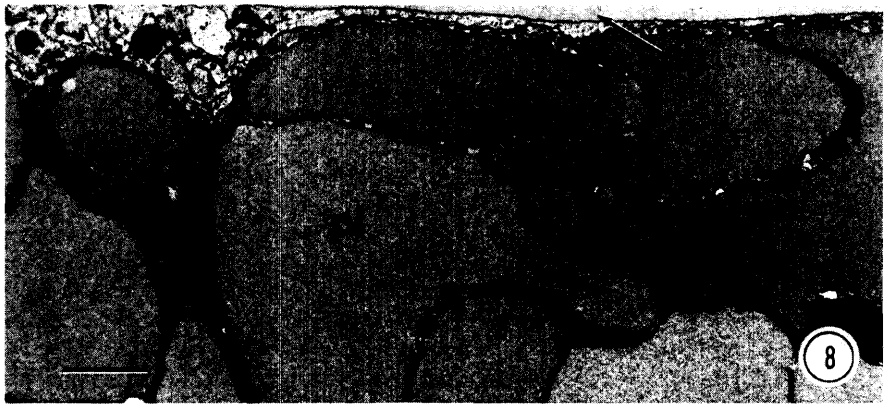



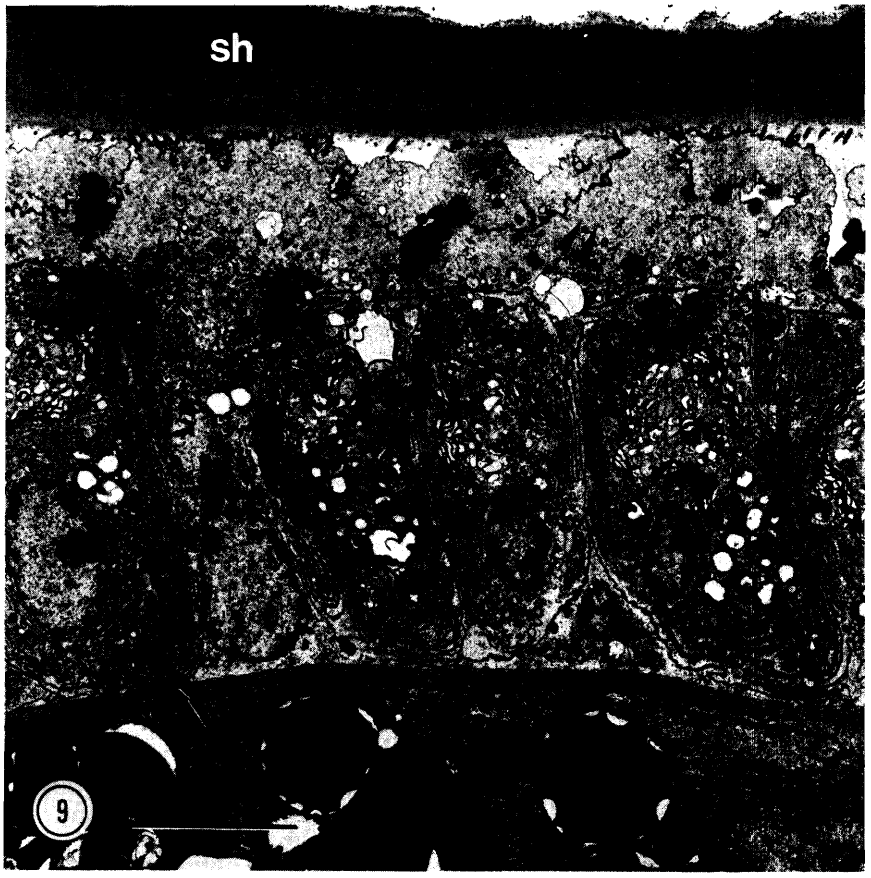





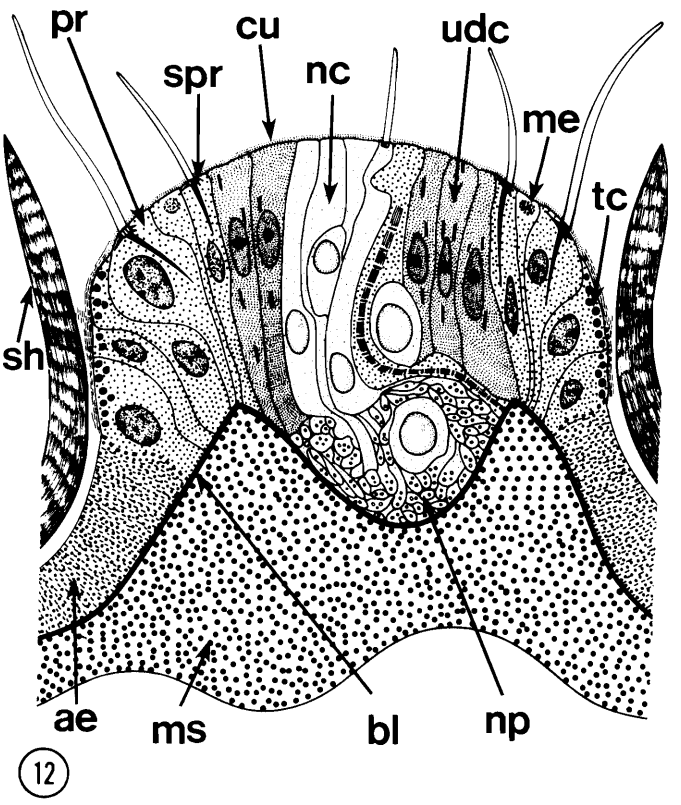


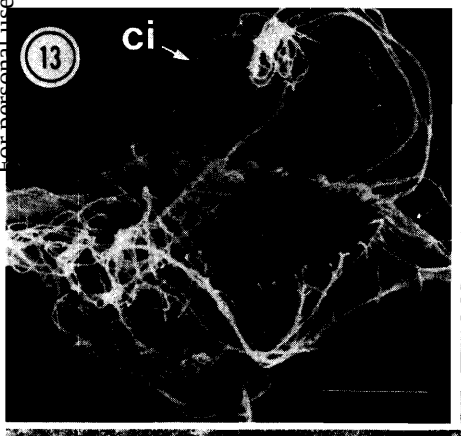



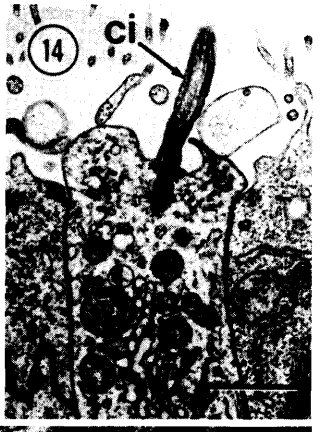



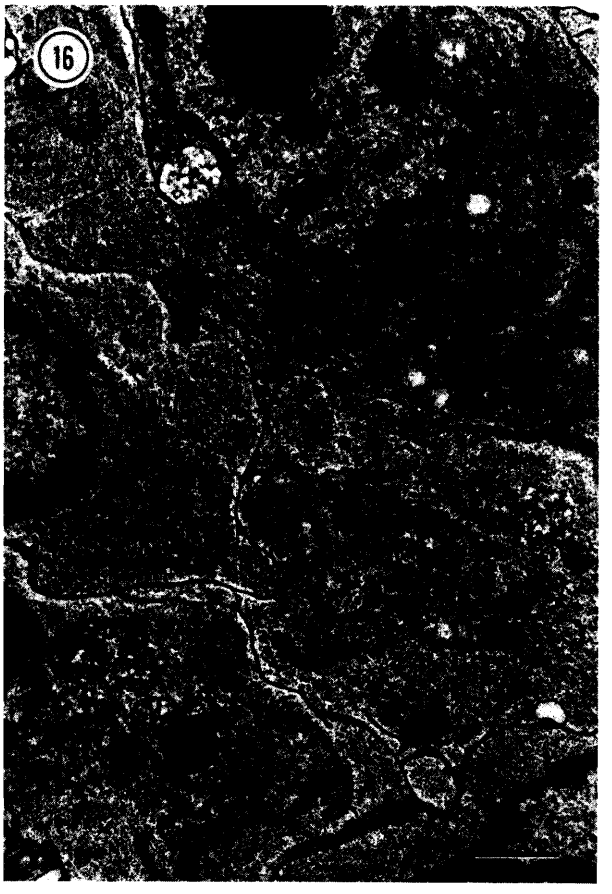








ated myofibril that extends along the apical–basal axis of the organ. The central neurons are surrounded by several types of nonpigmented epithelial cells. These cells constitute a nonstratified epithelial layer consisting of (*i*) undifferentiated cells that contain bundles of microfilaments, (*ii*) a pair of concentric rings of monociliated cells, (*iii*) a thin band of myoepithelial cells lying between the rings of monociliated cells, and (*iv*) a peripheral ring of so-called transitional cells that are covered by a layer of mucus-like material.

*The mesodermal compartment underlying the aboral epithelium*

Virtually no extracellular connective tissue occurs within the cyphonautes larva. Instead, the mesodermal compartment of the body wall is packed with cells. In most regions, the aboral epithelium occurs above a sheet of mesodermal cells that appear relatively undifferentiated (Figs. 15, 16). Each mesodermal cell typically possesses (*i*) abundant glycogen particles and free ribosomes, (*ii*) scattered mitochondria and arrays of RER, and (*iii*) many thickened regions in its plasmalemma, which may represent extensive gap junctions. Occasionally, these cells also contain large spherical granules of unknown significance (Fig. 11).

The subepithelial band of mesodermal cells is generally quite thin, but a large aggregation of these cells occurs directly beneath the apical organ. A somewhat smaller mass of undifferentiated cells also occurs in the mesodermal compartment enveloping the pyriform organ. In the posterior part of the larva, the mesoderm lies between the aboral epithelium and the viscera (i.e., the posterior edge of the gut and the posterolateral margins of the internal sac). Anteriorly, the mesoderm is sandwiched between the aboral epithelium and the epithelium lining the vestibule.

In addition to the undifferentiated mesodermal cells, the aboral epithelium overlies cells that resemble lipocytes (Fig. 15). Such cells tend to be located in two main regions: (*i*) around the pyriform organ, especially in a cap-like region above the organ, and (*ii*) on either side of the proximal part of the gut.

The lipocyte-like cells contain mitochondria and Golgi bodies toward their periphery. The central region of each cell is typically packed with large droplets that lack a surrounding membrane. Smaller, less electron-dense droplets can often be seen at the margins of the larger droplets.

*Corona*

The corona is composed of two juxtaposed rows of multiciliated cells. The outermost row of coronal cells faces the shell and is flanked by a row of monociliated cells. The inner row of coronal cells occurs toward the vestibule and is flanked by a row of myoepithelial cells. Figure 17 diagrams the topographic relationships of these three types of cells as viewed in transverse section.

The apical surfaces of the coronal cells are covered by a prominent cuticle which is continuous with the cuticle overlying the vestibular epithelium. Neighboring myoepithelial cells and monociliated cells are also covered by a cuticle. A clear demarcation is visible between the monociliated cells and adjacent epithelial cells bordering the shell, since the cells in this part of the body wall lack an overlying cuticle (Fig. 18).

Coronal cells are pyramidal in shape and are tapered toward the basal lamina. The cells are packed with mitochondria and typically possess 20–60 cilia (Figs. 18, 19). The ciliary rootlets in these cells are extremely well developed. Each basal body gives rise to a vertical rootlet that reaches the basal plasmalemma (Fig. 20). A horizontal rootlet, which appears to be composed of braided strands, extends from the basal body on the side opposite to the basal foot process. Judging from the average size of the coronal cells and the overall length of the corona, each larva possesses several hundred coronal cells.

The monociliated cells contain irregularly shaped vesicles of unknown significance. Unlike the multiciliated coronal cells, the monociliated cells possess relatively few mitochondria. The cilia of these cells are typically located near the lateral border that abuts the outer row of coronal cells (Fig. 18).

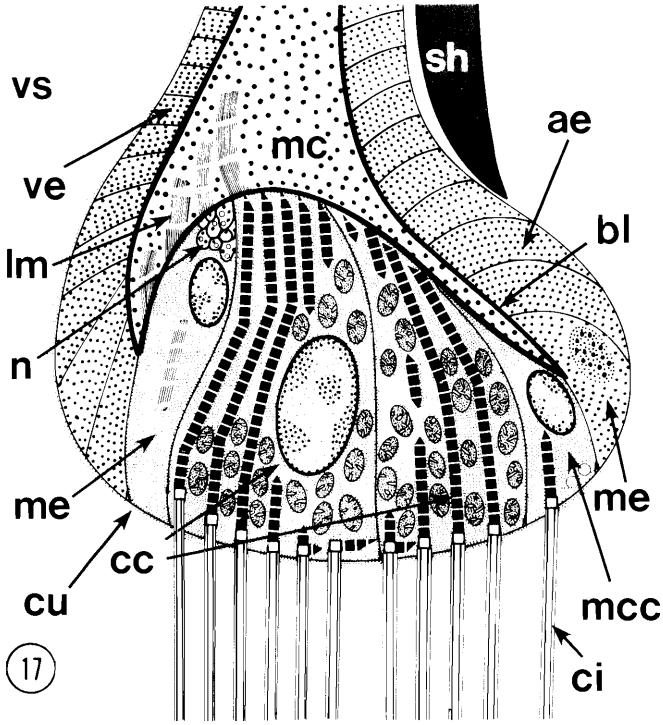
The myoepithelial cells that flank the inner row of coronal cells contain few cytoplasmic organelles other than striated myofibrils, which tend to be oriented along the apical–basal axis of the cells (Fig. 21). Similarly, the cells that abut the outer margin of the monociliated cells contain striated myofibrils, but these are arranged parallel to the long axis of the corona, rather than along the apical–basal axis of each cell (Fig. 22).

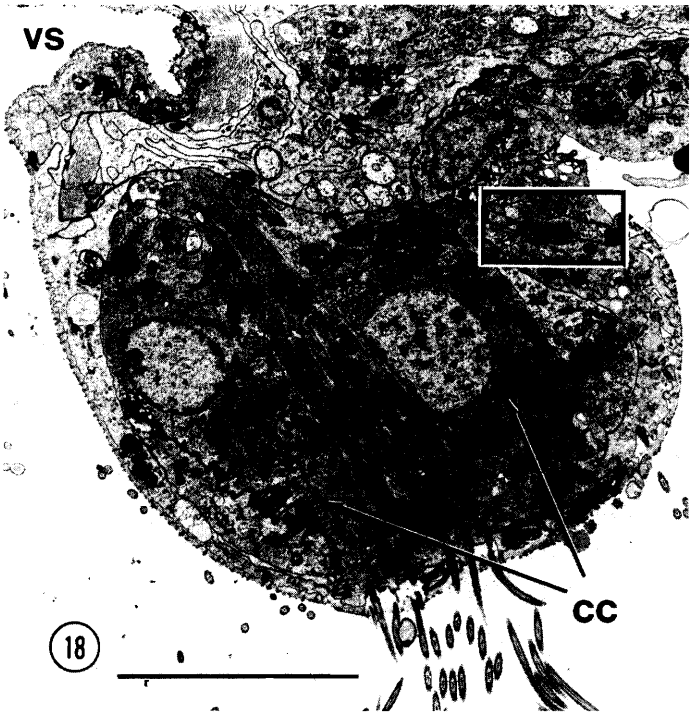
At the base of the coronal cells, there is a bundle of neurons that constitute a coronal nerve (Fig. 21). The coronal nerve lies above the basal lamina delimiting the border of the corona. Situated near the coronal nerve are the terminal ends of striated muscle fibers (Fig. 21). These fibers represent the ends of the lateral muscles that attach to the coronal basal lamina and serve to retract the locomotory organ when the larva is disturbed.

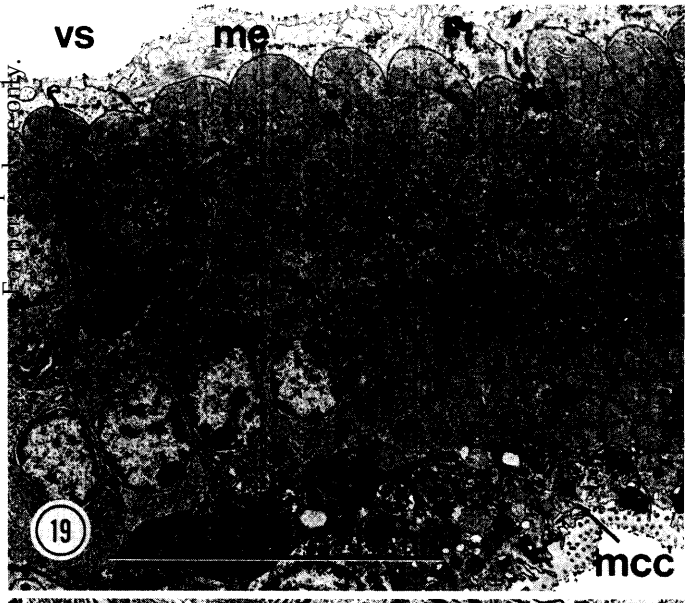
*Ciliary ridges, vestibular epithelium, and velum*

Near the midtransverse plane of the larva, two curved ciliary ridges run along the sides of the vestibule and thus partially divide the larval mantle cavity into an anterior inhalant chamber and a posterior exhalant chamber (Fig. 23). Each ciliary ridge extends into the vestibule from slightly below the corona and gradually bends toward the midsagittal plane of the larva. Posteriorly, the ridges meet at the anterior end of the internal sac at a level near the apicalmost extension of this organ. In specimens relaxed before fixation, the ciliary ridges can be separated from each other by as much as 60 μm. Each ciliary ridge is completely covered by a cuticle. When viewed in frontal sections, the ciliary ridge consists of an ovoid ciliated band that measures about 20 μm along its major axis (Fig. 24). The ciliated cells of the ridge are partially flanked on their anterior and posterior sides by squamous, nonciliated cells.

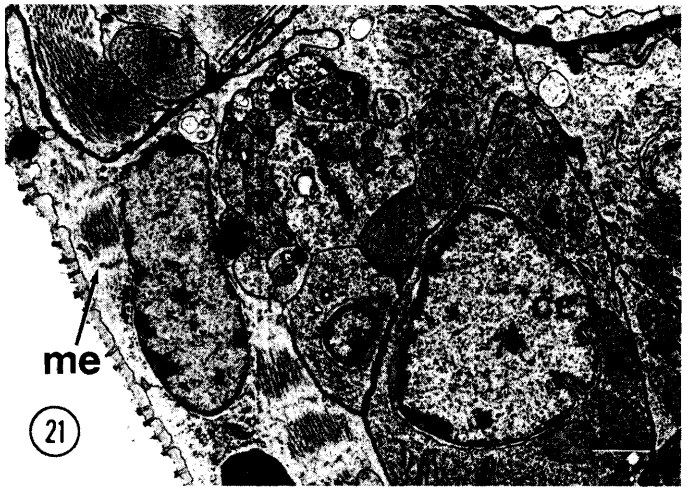
FIG. 17. Diagram of a transverse section through the corona and neighboring tissues. *ae*, aboral epithelium; *bl*, basal lamina; *cc*, coronal cell; *ci*, cilium; *cu*, cuticle; *lm*, lateral muscle; *mc*, mesodermal compartment; *mcc*, monociliated cell; *me*, myoepithelial cell; *n*, nerve; *sh*, shell; *ve*, vestibular epithelium; *vs*, vestibule. FIG. 18. TEM of a transverse section through the two rows of coronal cells (*cc*). The rectangle outlines the region shown at higher magnification in Fig. 22. *ae*, aboral epithelium; *mc*, mesodermal compartment; *vs*, vestibule. Scale bar = 10 μm. FIG. 19. TEM of a frontal section through the two rows of coronal cells (*cc*). *mcc*, monociliated cell; *me*, myoepithelial cells; *vs*, vestibule. Scale bar = 10 μm. FIG. 20. TEM of a sagittal section of the coronal cells, showing the vertical rootlets (*ro*) of the cilia extending toward the basal lamina (*bl*); *lm*, lateral muscle; *n*, nerve. Scale bar = 5 μm. FIG. 21. TEM of a transverse section through a myoepithelial cell (*me*) lying next to the inner row of coronal cells (*cc*). *lm*, lateral muscle; *n*, nerve. Scale bar = 1 μm. FIG. 22. TEM of a transverse section through the bundle of myofilaments (*mf*) in the myoepithelial cells lying next to the monociliated cells. Scale bar = 1 μm.

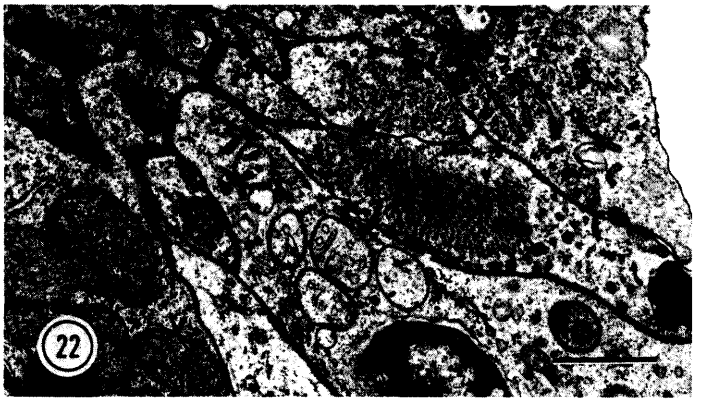






The nonciliated cells in turn cover the thin mesentery that connects the ciliary ridge to the vestibular wall.

The ciliation on each ciliary ridge is arranged into three discrete tracts (Fig. 24). The posterior edge of the ciliary ridge contains a column of multiciliated cells with large mitochondria. These cells resemble coronal cells and give rise to the so-called "lateral cilia" of the ciliary ridge (Atkins 1955*a*). Anterior to the multiciliated cells is a column of densely staining cells that contain the "laterofrontal cilia" of the ciliary ridge (Atkins 1955*a*). These cells possess one, two, or three cilia and are in turn flanked along their anterior margin by a column of multiciliated cells that possess relatively few mitochondria. The cilia of the anteriormost multiciliated cells are referred to as the "frontal cilia" of the ciliary ridge (Atkins 1955*a*).

A longitudinally oriented band of neurons occurs between the row of lateral cells and the row of laterofrontal cells in each ridge (Fig. 25). In addition, a striated muscle runs beneath the basal surfaces of the laterofrontal cells and the frontal cells (Fig. 24).

The vestibule is lined by a simple squamous to cuboidal epithelium, which is covered throughout by a prominent cuticle. The vestibular epithelium lining the preoral funnel is composed of relatively tall ciliated cells (Fig. 27). The preoral cilia occur mainly on the posterior side of the funnel that lies next to the proximal end of the gut, but a few cilia are also present on the anterior wall. The epithelium that lines the funnel is underlain by a thin basket of striated muscle cells. These muscles are continuous with the median striated muscles that run beneath the anterior and posterior margins of the shell (Fig. 28). The vestibular epithelium lying between the preoral funnel and the apicalmost extension of the ciliary ridges is also ciliated. The rest of the vestibule is essentially nonciliated, except for scattered cilia arising from nipple-like projections along the anterior wall of the inhalant chamber and some ciliation occurring in the perianal region of the exhalant chamber.

The velum forms a posteriorly opening, horseshoe-shaped ring around the inhalant entrance to the vestibule (Figs. 26, 29). A prominent cuticle completely covers the velum. In fixed specimens, the distal edge of the velum is typically bent toward the larval apical organ. The inner wall of the velum faces the vestibule and comprises a single layer of nonciliated squamous cells that are confluent with, and similar in ultrastructure to, the cells of the vestibular epithelium proper. The outer wall of the velum is composed of a simple cuboidal epithelium which is continuous with the corona. The terminal and subterminal cells in the outer wall are ciliated. The tuft of cilia arising from each terminal cell is typically directed toward the apical organ of the larva, whereas the cilia arising from the subterminal cells tend to project away from the vestibule. Lying between the corona and the ciliated cells of the outer velar wall are myoepithelial cells associated with a small aggregation of neurites.

The mesodermal compartment adjacent to the velum is packed with undifferentiated cells and the terminal ends of striated muscle fibers. Near the distal edge of the velum, a circumferential band of striated muscle cells occurs between the inner and outer walls of the velum (Fig. 29). Contraction of this muscle presumably serves to reduce the aperture of the inhalant opening in a drawstring-type fashion.

*Gut*

The digestive tract is situated toward the posterior end of the larva and consists of a simple, slightly curved tube. In our studies, three regions of the gut were recognized: the esophagus, stomach, and intestine (Figs. 30, 31).

The mouth opens into a capacious, sparsely ciliated esophagus. The anterior wall of the esophagus protrudes into the vestibule and thus forms a small caecum. The esophagus is slightly constricted at its distal end where it joins the densely ciliated stomach. The stomach is about as long as the esophagus and forms a prominent constriction at its junction with the intestine. The intestine runs a straight course and empties into the exhalant chamber of the vestibule by way of an anus.

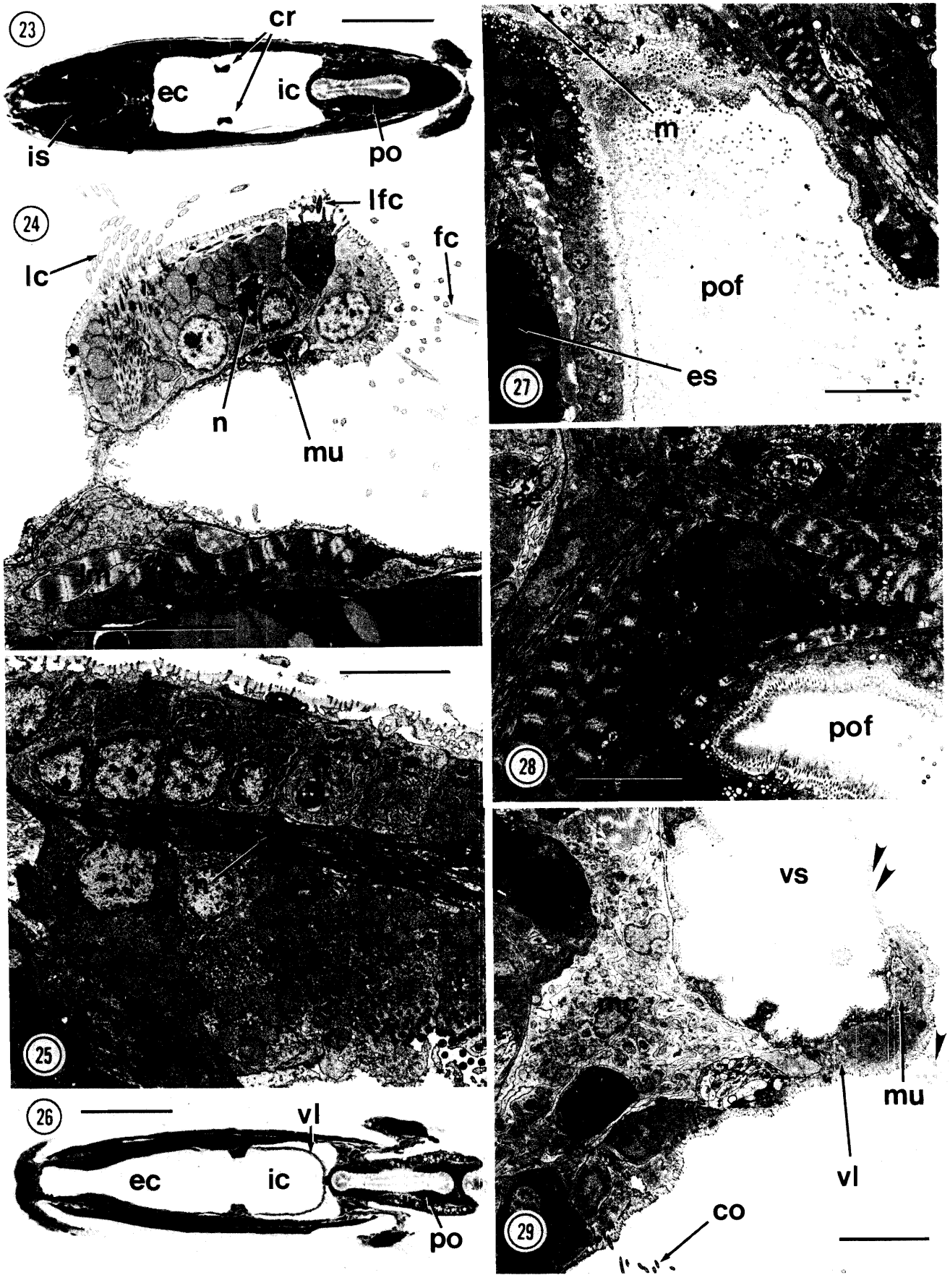
Two types of cells are present in the lining of the esophagus and stomach (Figs. 32–34). Type A cells lack an overlying cuticle and occur near the mouth as well as along the posterior and lateral walls of the esophagus. These cells contain (*i*) a relatively electron-lucent cytoplasmic matrix, (*ii*) scattered lysosomes, and (*iii*) various vacuoles that probably represent endocytosed food particles. Type B cells also lack an overlying cuticle. Such cells line the esophageal caecum and contain a dense matrix as well as a prominent rough endoplasmic reticulum. A few electron-dense granules occur toward the apices of the cells. Both types of cells occur throughout the lining of the stomach.

The lining cells of the esophagus typically possess elaborate apices consisting of densely packed, interdigitated microvilli. These microvilli form a spongiosa-like stratum that occupies much of the esophageal lumen (Fig. 35). Cilia arising from both types of lining cells lie interspersed among the network of microvilli. Type A cells tend to be more densely ciliated than type B cells. The cilia occurring within the stomach form an interdigitated sieve that virtually obliterates the gastric lumen (Fig. 36).

The intestinal lining is composed of cells that apparently lack cilia, as no intestinal ciliation was observed in any of the thin sections we examined. The intestinal cells resemble the type A cells in the esophagus and stomach but possess a less elaborate layer of apical microvilli.

Several types of mineralized and nonmineralized protists are typically visible within the lumen of the larval gut. Some

FIG. 23. Photomicrograph of a frontal section through a larva showing the two ciliary ridges (*cr*) that partially divide the vestibule into an anterior inhalant chamber (*ic*) and a posterior exhalant chamber (*ec*). *is*, internal sac; *po*, pyriform organ. Bicarbonate-buffered osmium tetroxide fixation. Scale bar = 100 μm. FIG. 24. TEM of a frontal section through a ciliary ridge. *fc*, frontal cilia; *lc*, lateral cilia; *lfc*, laterofrontal cilia; *lm*, lateral muscle; *mu*, muscle; *n*, nerve; *pl*, polster cell. Scale bar = 10 μm. FIG. 25. TEM of a sagittal section through a ciliary ridge in the vicinity of the internal sac (double arrowheads). *lf*, laterofrontal cell; *lt*, lateral cell; *n*, nerve. Scale bar = 5 μm. FIG. 26. Photomicrograph of a frontal section through a larva, showing the velum (*vl*) surrounding the opening to the inhalant chamber (*ic*). *ec*, exhalant chamber; *po*, pyriform organ. Bicarbonate-buffered osmium tetroxide fixation. Scale bar = 100 μm. FIG. 27. TEM of the preoral funnel (*pof*). *es*, esophagus; *m*, mouth. Scale bar = 10 μm. FIG. 28. TEM of the basket of striated muscle (double arrowheads) surrounding the preoral funnel (*pof*). *ae*, aboral epithelium; *amm*, anterior median muscle; *np*, nerve plexus of apical organ; *pmm*, posterior median muscle. Scale bar = 10 μm. FIG. 29. TEM of a transverse section through the velum (*vl*). Cilia arise from the terminal (double arrowheads) and subterminal (arrowhead) cells in the outer wall of the velum. *co*, corona; *mc*, mesodermal compartment; *mu*, muscle; *vs*, vestibule. Scale bar = 10 μm.



ingested phytoplankton measure 20 μm in diameter, whereas the smaller ingested microbes are only one to several micrometres long (Figs. 37, 38). Whether or not all sizes and types of ingested protists and microbes are actually absorbed by the epithelial cells lining the gut remains to be determined.

## Discussion

*Comparative larval morphology*

As discussed by Zimmer and Woollacott (1977*a*), marine bryozoans produce two main kinds of larvae: (*i*) nonshelled lecithotrophic larvae, and (*ii*) shelled, planktotrophic cyphonautes larvae. In addition, lecithotrophic larvae that superficially resemble cyphonautes larvae in possessing an external shell are known for the ctenostome gymnolaemates *Flustrellidra hispida*, *Pherusella brevitata*, and *Pherusella tubulosa* (for review, see Zimmer and Woollacott 1977*a*). The nonshelled lecithotrophic type of larva, referred to as a coronate larva, is the typical larval form of the class Gymnolaemata and generally remains free-swimming for less than a few hours. Morphologically similar larval types have been described for cyclostome bryozoans (Nielsen 1971). True cyphonautes larvae, on the other hand, have been reported for (*i*) members of the cheilostome genera *Biflustra*, *Conopeum*, *Electra*, and *Membranipora*, (*ii*) the cheilostomes *Pyripora catenularia* and *Tendra repiachowi*, and (*iii*) the ctenostomes *Alcyonidium albidium*, *Farrella repens*, and *Hypophorella expansa* (for reviews, see Zimmer and Woollacott 1977*a*; Taylor 1987). In addition to the rather abundant membraniporid cyphonautes larvae found near San Juan Island, a much smaller and rarer cyphonautes larva produced by *Alcyonidium* sp. is occasionally present in the plankton during the summer months (R. L. Zimmer, unpublished observation).

The external morphology of the cyphonautes larva produced by *Membranipora membranacea* in the vicinity of Great Britain has been described in detail by Atkins (1955*b*) and Ryland (1964). The shape, ornamentation, and proportions of the larval shell reported by these authors are similar to those observed in this study. One major difference is that the larvae described by Atkins and Ryland are much larger than those examined in this study and typically reach a maximum size of 700–840 μm. In addition to such large specimens, Ryland (1964) has diagrammed a few relatively small cyphonautes larvae of *M. membranacea* from Øresund, Sweden, and has concluded that these forms represent incompletely developed larvae.

We also believe that the larvae collected in this study correspond to specimens that had not reached maximum size, because other workers have reported that the cyphonautes larva presumably produced by *M. membranacea* in the vicinity of San Juan Island can reach lengths of 650 μm (McEdward and Strathmann 1987). It should be noted, however, that the larvae we examined often underwent a normal metamorphosis in the laboratory when the proper stimuli were provided, and subsequently formed functional colonies. Thus, these specimens possessed the requisite organs for postlarval life and should be considered well developed, albeit smaller than the maximum size. The average dimensions at which cyphonautes larvae first become competent to metamorphose are not known.

The overall size of the larvae we examined is comparable to that of a Japanese form, designated *Membranipora serrilamella* (Mawatari and Ito 1972; Mawatari and Mawatari 1974). To determine whether or not the larvae we examined actually belong to the species of bryozoan studied by Ryland (1964) and Atkins (1955*b*) requires further taxonomic studies of adult colonies that take into account morphological variations such as predator-induced polymorphisms (Yoshioka 1982*a*). Similarly, until the systematics of this genus is more clearly defined, we cannot preclude the possibility that cyphonautes larvae of more than one species of membraniporid occur in the vicinity of San Juan Island. In our studies, however, we have not recognized great variability in morphological traits, which might be indicative of larvae arising from multiple species of membraniporids.

Internally, the cyphonautes larva of *M. membranacea* contains all the features of a generalized gymnolaemate larva as hypothesized by Zimmer and Woollacott (1977*a*). The major organs that the cyphonautes larva has in common with other gymnolaemate larvae are (*i*) an internal sac situated along the midline of the former oral field of the larva, (*ii*) an anterior pyriform organ, (*iii*) an apical disc complex arising from a modified region of the aboral epithelium, and (*iv*) a neural cord running between the apical disc and pyriform organ.

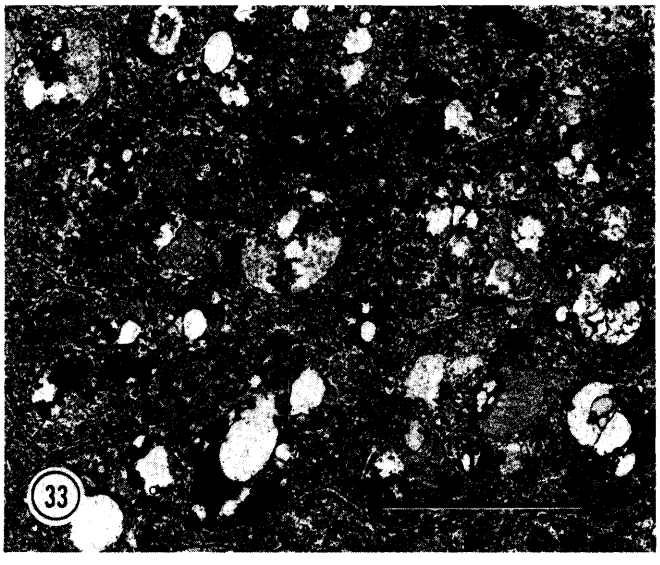
The cyphonautes larva is distinguished from other gymnolaemate larvae by the possession of a functional gut and the development of several unique features, including (*i*) an extremely well-developed set of muscles, (*ii*) a vestibule with associated structures, and (*iii*) large aggregations of lipid-like droplets. The well-developed musculature of the cyphonautes larva functions during larval life by retracting larval tissues within the shell and during metamorphosis by changing the shape of the larva (Stricker *et al.* 1988). The vestibular cavity, ciliary ridges, and velum, on the other hand, represent adaptations that aid in the collection of food during a protracted planktotrophic phase. Similarly, the large deposits of lipid-like material may represent food reserves stored by the larva during its free-swimming existence. The length of time spent in the plankton by the cyphonautes larvae of *M. membranacea* in the vicinity of San Juan Island has not been determined. The larvae of *M. membranacea* in southern California are estimated to be free-swimming for about a month (Yoshioka 1982*b*), whereas cyphonautes larvae of other species reportedly remain planktonic for 2 months (Marcus 1926).

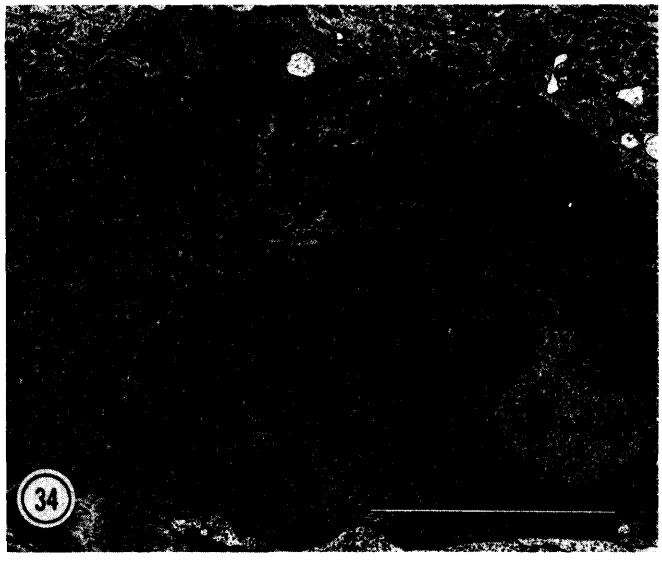
*Cytology of the body wall*

The shell covering the outer surface of the body wall in the cyphonautes larvae we examined resembles the bilayered shell described by Atkins (1955*a*). In both cases, the outermost layer is extremely thin and stains differently than the much thicker inner layer. The filamentous nature of the shell

FIG. 30. Photomicrograph of a sagittal section of the posterior end of the larva. *ao*, apical organ; *es*, esophagus; *esc*, esophageal caecum; *is*, internal sac; *m*, mouth; *vs*, vestibule. Bicarbonate-buffered osmium tetroxide fixation. Scale bar = 50 μm. FIG. 31. Photomicrograph of a sagittal section through the region adjacent to that shown in Fig. 30. *in*, intestine; *st*, stomach. Bicarbonate-buffered osmium tetroxide fixation. Scale bar = 50 μm. FIG. 32. TEM of a sagittal section through the esophagus, showing type A (tA) and type B (tB) cells in the epithelial lining. *pof*, preoral funnel. Scale bar = 10 μm. FIG. 33. TEM of a grazing section through a group of type A cells in the epithelium lining the esophagus. The double arrowheads mark an endocytotic vacuole. Scale bar = 5 μm. FIG. 34. TEM of a section through type B cells in the lining of the esophagus. The double arrowheads mark an apical inclusion. *bl*, basal lamina. Scale bar = 5 μm.



observed in electron micrographs supports the notion that the shell is composed of chitin, but no chemical analyses have been performed to confirm this view.

Early stages in shell formation were not observed in this study. The arrangement of the concentric growth lines suggests, however, that new shell material is added mainly along the anterior and apical margins of the shell. The reddish brown tubercles occurring along the basal margin of each valve are characteristic ornaments of the shell in older *M. membranacea* larvae (Atkins 1955*b*; Ryland 1964). The possible functions of these bumps remain obscure.

The aboral epithelium underlying the basal half of the valves contains a distinct type of cell, termed the polster cell (Kupelwieser 1905). In *Electra pilosa*, polster cells are described as occurring (*i*) along the basal margins of the shell, (*ii*) next to the ciliary ridges, and (*iii*) beneath the anterior and posterior edges of the shell to the level of the apical organ (Kupelwieser 1905). Thus, the polster cells of *Electra* extend more along the anterior and posterior margins of the larva than they do in *M. membranacea*, but a larger mass of these cells occurs beneath the basal half of the shell in *M. membranacea*.

Polster cells have been hypothesized to cushion the larva from mechanical damage (Kupelwieser 1905). Based on studies of metamorphosing specimens, however, it seems more likely that these cells remain tightly adherent to the shell and thus function analogously to tendons by dispersing the forces of muscular contractions during metamorphosis (Stricker 1988).

The monociliated cells occurring along the anterior and posterior margins of the aboral epithelium lie between the two shell valves and are thus exposed to the external milieu. Such cells may constitute sensory regions in the aboral epithelium of the body wall, but we have not observed a well-developed innervation in the vicinity of these cells to support this view.

The apical organ in the cyphonautes larva of *M. membranacea* is similar to that described for *E. pilosa* (Kupelwieser 1905) except that it lacks pigmentation. As discussed by Stricker (1987), the well-developed neural core and basiepithelial nerve plexus of the apical complex may constitute a primary sensory organ as well as a larval brain that mediates the actions of other larval systems such as the muscles and the pyriform organ.

In many bryozoan larvae, the apical disc region of the body wall contains undifferentiated cells that represent epidermal and mesodermal blastemas (Zimmer and Woollacott 1977*a*). These blastemas contribute to the ancestrular polypide following metamorphosis (for review, see Zimmer and Woollacott 1977*b*). In the cyphonautes larva of *M. membranacea*, the undifferentiated cells directly surrounding the central neurons probably constitute the epidermal blastema of the apical organ, but no true mesodermal blastema occurs within the apical organ proper. Instead, undifferentiated mesodermal cells lying below the basal lamina of the apical organ are believed to represent a mesodermal blastema (Stricker 1987). Kupelwieser (1905) was unable to discriminate cellular boundaries within the apical organ of *E. pilosa*, but his histological descriptions suggest that the organ is a bilayered structure containing both epidermal and mesodermal blastemas (Zimmer and Woollacott 1977*a*). Our observations of a single layer of undifferentiated cells within the apical organ proper indicate, however, that the cyphonautes larva of *M. membranacea* falls in an intermediate position between vesicularioid ctenostome larvae that possess simple apical discs without blastemas (Reed and Coney 1982*a*) and cellularioid cheilostome larvae that contain a compound apical disc in which both epidermal and mesodermal blastemas are present (Woollacott and Zimmer 1971, 1978).

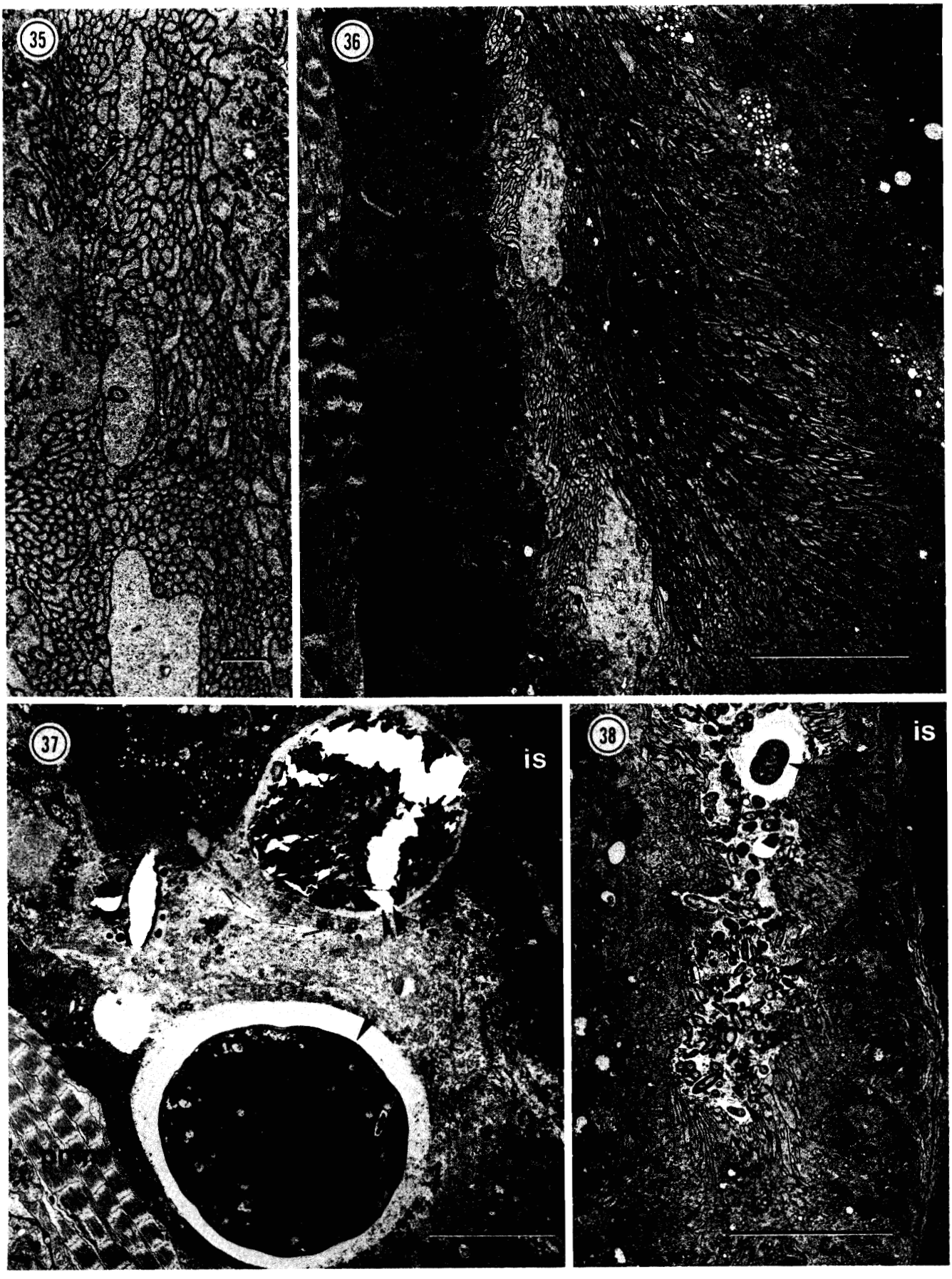
The ciliary ridges observed in the cyphonautes larva of *M. membranacea* resemble those previously described by Kupelwieser (1905) and Atkins (1955*a*) for *E. pilosa* and *M. membranacea*, respectively. The mode by which these ridges develop and the topographical relationship between the ridges and neighboring tissues such as the corona remain obscure. When fully formed, the ciliary ridges possess lateral cilia that serve to move water through the vestibule (Atkins 1955*a*). The frontal cilia, on the other hand, convey filtered food particles toward the preoral funnel (Atkins 1955*a*). The laterofrontal cilia occurring between these two groups of cilia were originally thought to represent sensory organelles (Kupelwieser 1905). Recent studies have shown, however, that these cilia remain stationary during feeding and form a sieve that captures food particles of appropriate size (Strathmann and McEdward 1986).

The vestibular epithelium and velum observed in this study are similar to those described by Atkins (1955*a*). The position of the velum within the larva suggests that this structure serves to control the size of the opening to the inhalant chamber, but the functional significance of such a reduction in the inhalant aperture remains obscure.

The corona at the base of the cyphonautes larva consists of two rows of multiciliated coronal cells, flanked by monociliated cells and myoepithelial cells. In many other bryozoan larvae, the coronal cells are extremely elongated and total only 32 in number (Zimmer and Woollacott 1977*a*). The corona of the cyphonautes larva of *M. membranacea*, however, contains several hundred multiciliated cells that are columnar in shape. These two rows of cells correspond to the juxtaposed rows of type A and type B cells described for the corona in the cyphonautes larva of *Electra pilosa* (Kupelwieser 1905). Neighboring cells, which are similar in structure to the monociliated cells and the myoepithelial cells of *M. membranacea*, have also been diagrammed for *E. pilosa* (Kupelwieser 1905). The monociliated cells directly flanking the outer edge of the corona in *M. membranacea* correspond in position to the "supracoronal cells" of many other gymnolaemate larvae, including the shelled lecithotrophic larva produced by *Flustrellidra hispida* (d'Hondt 1977). Similarly, the cells that abut the inner edge of the corona in *Membranipora* are situated in the same position as the "infracoronal cells" of other bryozoan larvae (d'Hondt 1977).

The coronal cells of *M. membranacea* undoubtedly serve as the locomotory units of the larva. The monociliated cells, on the other hand, probably represent sensory cells that convey

FIG. 35. TEM of a grazing section through the lumen of the esophagus. A spongiosa-like stratum of microvilli (double arrowheads) virtually fills the lumen. *ci*, cilium arising from an epithelial lining cell. Phosphate-buffered glutaraldehyde primary fixation. Scale bar = 1 μm. FIG. 36. TEM of a sagittal section of the stomach, showing the numerous cilia (*ci*). *pmm*, posterior median muscle. Scale bar = 10 μm. FIG. 37. TEM of a sagittal section through the intestine. Mineralized (double arrowheads) and nonmineralized (arrowhead) protists occur within the lumen of the intestine. Phosphate-buffered glutaraldehyde primary fixation. Scale bar = 10 μm. FIG. 38. TEM of the distal end of the intestinal lumen showing numerous small microbes (arrowheads). *is*, internal sac. Scale bar = 10 μm.



impulses to the nerves located near the coronal cells.

In spite of the major morphological differences evident between the lecithotrophic and planktotrophic larvae of bryozoans, certain correlations can be recognized in the organization of the larval body wall. In lecithotrophic larvae with large coronas, the aboral epithelium is typically invaginated around the apical disc region to form an annular sulcus, called the pallial sinus. The epithelium that lines the sinus is referred to as the pallial epithelium and has been homologized with the aboral epithelium that underlies the shell in the cyphonautes larva (Zimmer and Woollacott 1977*a*). The corona and neighboring regions of the larval epidermis in various coronate larvae contain cells that are similar in ultrastructure to several epidermal cell types found in the cyphonautes larva of *Membranipora*. In the vesicularioid ctenostome *Bowerbankia gracilis*, for example, the aboral margin of the corona is joined to the invaginated portion of the aboral epithelium by a ring of monociliated supracoronal cells that correspond in position to the monociliated cells found at the junction between the corona and aboral epithelium in *Membranipora* (Reed and Cloney 1982*a*). In addition, the myoepithelial cells flanking the monociliated cells at the outer edge of the corona in *Membranipora* occur in a comparable position to the so-called aboral collarette of myoepithelial cells that borders the corona in the cellularioid *Bugula neritina* (Woollacott and Zimmer 1971; Reed and Woollacott 1982). Myoepithelial cells also occur next to the inner edge of the corona in *Membranipora*. Whether these cells correspond to the oral collarette of myoepithelial cells in *B. neritina* or the infracoronal cells of other larvae (d'Hondt 1977) remains to be determined.

*Structure of the digestive tract*

Cyphonautes larvae are the only known bryozoan larvae that possess a functional gut. The shelled lecithotrophic larvae of the ctenostomes *Flustrellidra* and *Pherusella* contain an incomplete digestive tract (d'Hondt 1977; Zimmer and Woollacott 1977*a*). As discussed by Strathmann (1985), "most feeding larval forms are of great antiquity." During evolution, the larval feeding apparatus is lost in some cases, and nonfeeding larval types are generated (Strathmann 1978). In the so-called oligomerous phyla (i.e., Echinodermata, Hemichordata, Bryozoa, Brachiopoda, and Phoronida), a feeding apparatus is seldom reestablished in lecithotrophic larval forms (Strathmann 1978). Similarly, we infer that the cyphonautes larva with its unique gut is more primitive than the lecithotrophic larvae of bryozoans and is not secondarily derived from a nonfeeding form.

Other authors have referred to the ciliated region of the inhalant chamber that occurs anterior to the mouth of the cyphonautes larva as the pharynx (Kupelwieser 1905) and (or) the esophagus (Atkins 1955*a*) implying that it forms part of the larval digestive tract. However, the epithelium lining this ciliated region is covered by a cuticle resembling that observed over the corona. Conversely, the gut epithelium lacks a cuticle. Such ultrastructural observations are consistent with previous embryological studies that describe the inhalant chamber as arising from an invagination of the former oral ectoderm of the larva (Prouho 1892; Marcus 1926). The gut, on the other hand, is stated to develop from endodermal cells that secondarily connect with the vestibule (Prouho 1892; Marcus 1926). Thus, we refer to the ciliated region of the inhalant chamber as the preoral funnel rather than the pharynx or esophagus to emphasize the fact that this area lies anterior to the mouth and is not part of the digestive tract proper.

Our ultrastructural observations suggest that the digestive tract consists of three regions. Kupelwieser (1905) and Atkins (1955*a*) recognized only two parts in the postoral portion of the gut of cyphonautes larvae. These authors referred to the proximal end of the digestive tract proper as the stomach, and the distal end as the intestine. In *M. membranacea*, the large proximal region previously referred to as the stomach is actually bipartite, judging from the cytology of the lining cells and the presence of a slight constriction between these two areas. The region directly behind the mouth is referred to in this study as the esophagus. The esophagus in turn connects with a more densely ciliated stomach region.

Both the esophagus and stomach are lined by two types of cells that perhaps function differently in digestion. Type A cells, with numerous phagosomes and a relatively sparse matrix, probably represent the primary absorptive cells in the gut. Type B cells, on the other hand, may be secretory cells that exocytose products used in extracellular phases of digestion.

The intestine constitutes the third part of the larval gut. This region is lined by cells that resemble the type A cells found in the esophagus and stomach. Contrary to a previous report (Atkins 1955*a*), the intestinal cells do not appear to be ciliated.

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