

Functional organization of dermal coelomic canals in *Sipunculus nudus* (Sipuncula) with a discussion of respiratory designs in sipunculans

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Abstract. *Sipunculus nudus* is a large sipunculan that burrows actively in porous marine sands. The body surface is folded into approximately 30 longitudinal ridges that extend along the length of the trunk and introvert. A dermal canal lies beneath each of the ridges and circulates coelomic fluid and hemerythrocytes to within a few micrometers of the body surface. Coelomic fluid enters and leaves the dermal canals through pores leading from the trunk coelom and flows unidirectionally at approximately 0.7 mm/s from posterior to anterior. The flow is generated by cilia on peritoneal cells lining the canals. The volume of the canals is approximately 8% of the total coelomic volume.

We suggest that sipunculan species fall into three functional categories based on the body region or regions used for environmental gas exchange. "Tentacle breathers," such as species of *Themiste*, bore into rocks or micro-oxic sediments and extend their numerous tentacles into the water. Dissolved gases are transported between the tentacular and trunk coelomic cavities via well-developed contractile vessels. "Tentacle and introvert breathers," such as species of *Aspidosiphonidae* and *Phascalosomatidae*, lodge the trunk region of the body in the substratum and extend an elongated, thin-walled introvert and tentacles into the water. Their contractile vessels are usually simple unbranched tubes. "Integumentary breathers," such as *Sipunculus nudus* and other species of *Sipunculidae*, have integumentary specializations for gas exchange across the entire body surface, but usually small tentacles and often weakly developed contractile vessels.

Additional key words: respiration, tentacles, introvert, integument

The body wall of a sipunculan worm typically consists of an outer cuticle, epidermis, connective-tissue dermis, circular musculature (and nerves), longitudinal musculature, and, lining the coelom, a peritoneum (Rice 1993). In some species the coelom is extended into the body wall in the form of either sacs or canals. Such coelomic extensions occur in 4 of the 17 genera recognized in the recent classification of the phylum by Gibbs and Cutler (1987): *Sipunculus*, *Xenosiphon*, *Siphonosoma*, and *Siphonomecus*. In *Sipunculus* and *Xenosiphon* the circular and longitudinal musculature of the body wall is divided into distinct bands, whereas in *Siphonosoma* and *Siphonomecus* the muscle bands are not so distinctly separated, but rather show varying degrees of anastomosis. In *Sipunculus*, the coelomic extensions take the form of longitudinal canals that lie between the longitudinal muscle bands over most of

the length of the trunk; in *Xenosiphon*, they occur as short, diagonal subcutaneous canals, no wider than a single band of circular muscle. In *Siphonosoma* and *Siphonomecus*, coelomic spaces in the body wall are in the form of sacs. Between the bands of longitudinal and circular muscles, pores connect the coelom with the extensions into the body wall. Coelomocytes, including hemerythrocytes (cells bearing the respiratory pigment hemerythrin), occur within the coelomic extensions (Ruppert & Rice 1990). The integument overlying the coelomic spaces is thin, consisting only of epidermis and cuticle.

As a taxonomic character, the presence of integumental coelomic spaces has been important in establishing the family Sipunculidae (Stephen & Edmonds 1972; Cutler & Gibbs 1985) and the form of these structures has been useful in distinguishing genera (Spengel 1912; Fisher 1947). Moreover, the comparative morphology of the coelomic spaces was the pri-

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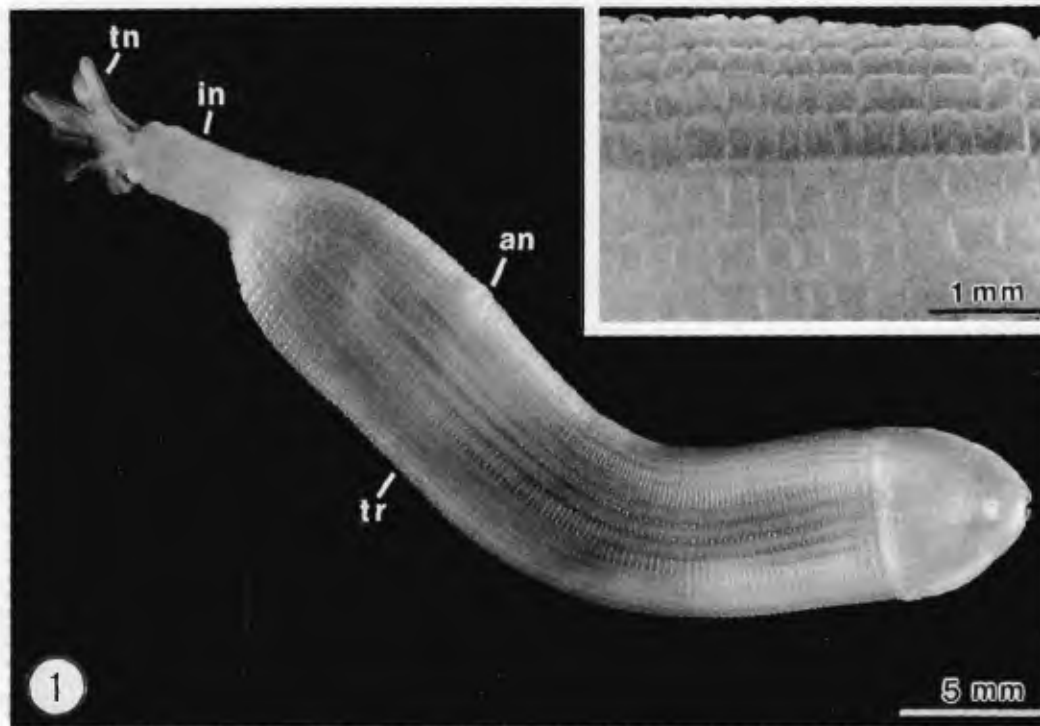


Fig. 1. Photomicrograph of living juvenile specimen, approximately 3 cm long. Inset: body surface showing longitudinal ridges (left to right) which enclose the dermal canals. Anus (an); introvert (in); tentacles (tn); trunk (tr).

mary basis for a recent phylogenetic scheme (Cutler 1986) of relationships within the Sipunculidae.

Andreae (1882) and Metalnikoff (1990), in studies of the anatomy and histology of *Sipunculus nudus*, described the lining of the coelomic canals as peritoneal and the free cells enclosed in the canals as the same as those in the coelom. Shitamori (1936) examined the wall of the integumental canals of *Siphonosoma cumanaense* and noted connective-tissue fibrils and small, round or spindle-shaped nuclei. In an account of the comparative histology of epidermal organs in sipunculans, Åkesson (1958) noted the presence of coelomic extensions in the integument of *Siphonosoma cumanaense* and *Sipunculus nudus*; his figure of a transverse section of the body wall of the latter illustrates the position of the epidermal glands relative to the canals. Cutler (1986), in a comparative study of the body wall in the Sipunculidae, clarified the form and ramifications of the integumental spaces and their relationship to the other components of the body wall. In two ultrastructural studies on the body wall of sipunculans, de Eguileor and Valvassori (1977) elucidated the fine structure of body wall musculature of *Sipunculus nudus*, and Goffinet et al. (1978) reported on the cuticle of two species, including *S. nudus*. In neither paper, however, were the coelomic extensions in the body wall considered.

Some of the earliest literature in which coelomic canals were described suggested that their function was respiratory (e.g., Andreae 1882). Manwell (1960), in a study on oxygen transfer in sipunculans of different life habits, implied a respiratory function for the coelomic sacs of *Siphonosoma ingens*. No direct observations, however, have been made on the functional morphology of coelomic extensions, nor have there been any observations or measurements of flow through the canals.

In this paper we reconstruct the three-dimensional anatomy, describe the ultrastructure, and measure the flow within the coelomic canals of *Sipunculus nudus* Linnaeus 1766, as well as rationalize the diversity of sipunculan body forms in terms of their gas-exchange surfaces.

Methods

Adult specimens of *Sipunculus nudus* were collected at Hobe Sound, Jupiter Inlet, Florida in 1973 and at Fort Pierce Inlet in 1982. Several juveniles, approximately 4 cm long (Fig. 1), were collected from a tidal sand flat at Sebastian Inlet, Florida in June 1990. They were transported in seawater-filled plastic bags to the laboratory facilities of the Smithsonian Marine Station at Link Port and maintained for several days on a sub-

stratum of natural sand in culture dishes filled with seawater. Another juvenile (Figs. 2, 3) was collected along the Pinellas Bayway in St. Petersburg, Florida in 1982.

Flow in the coelomic canals of living specimens was observed and recorded using a Zeiss photomicroscope equipped with a Dage-MTI NC-67M videocamera and Panasonic AG-1830 videorecorder. Flow velocity was determined by tracking, frame-by-frame, individual hemerythrocytes through the canals.

Specimens were preserved in 2.5% glutaraldehyde in 0.2 M Millonig's phosphate buffer (pH 7.6) for 1 h at room temperature. After a brief buffer rinse, a few specimens were dehydrated through an ethanol series and stored in 70% ethanol. Others were postfixed in 2.0% osmic acid in 0.2 M phosphate buffer for 1 h at room temperature. Following a brief rinse in distilled water, the specimens were dehydrated through an ethanol series and embedded in Polybed 812 (Polysciences, Inc.) using propylene oxide as the infiltration solvent. The polymerized blocks were sectioned for transmission electron microscopy (TEM) using a Diatome diamond knife. Electron micrographs were obtained using a JEOL 100-C transmission electron microscope operating at 60 kV. For scanning electron microscopy (SEM), specimens were preserved in 5% formaldehyde made up in 70% ethanol, and after 3 days, transferred to 70% ethanol for storage. Before examination with the Nova-Scan 30 SEM, they were dehydrated and dried in a Denton critical point drier.

Corrosion casts of two glutaraldehyde-fixed juveniles were prepared by injecting the coelom with blue Microfil silicone rubber (Canton Biomedical Products, Inc.) using a hand-held 5-cc disposable syringe. After approximately 2 h of curing time, the injected specimens were immersed in 5% sodium hypochlorite (Clorox) until the desired amount of digestion was obtained. The completed corrosion casts were stored in 70% ethanol, and later photographed on Kodak Plus-X and Kodachrome 25 films using a Nikon photomacrographic system.

Results

The body wall of *Sipunculus nudus* is a thick dermomuscular sheath that encloses a spacious coelom and the internal organs (Figs. 2,4). Shallow circumferential annulations and deep longitudinal grooves divide the body surface of uncontracted animals into approximately 30 (28–31) continuous longitudinal ridges. In longitudinally contracted animals, the annulations deepen and divide each longitudinal ridge into a series of short segment-like regions (Fig. 1 inset).

The outermost layer of the body wall is a well-developed fibrous cuticle, which in life is translucent, flexible, colorless, and iridescent. The cuticle is finely fibrous throughout but a layer of coarse fibers, wound in a crossed-helical pattern, occupies its outermost half (Figs. 8, 9). The fibers are at approximately 54.5 degrees to the longitudinal body axis. The outer surface of the cuticle is a thin (80 nm) electron-dense lamina.

The epidermis, composed of pavement cells and glands, underlies the cuticle. Although the low, cup-shaped cells lack cilia, they bear long, branched microvilli, which extend apically into, but not through, the cuticle. The pavement cells comprise most of the epidermis and secrete the cuticle (Figs. 7–9). Large epidermal glands occur predominantly in the walls of the longitudinal surface ridges (Figs. 4, 7). The glands are submerged below the epidermal pavement into the connective-tissue dermis but remain in communication with the surface via slender necks and permanent pores in the cuticle. Each pyriform gland is composed of several cells that together enclose an extracellular space, the gland reservoir (Fig. 7). A fine muscular network encloses each gland and is probably responsible for discharging the contents of the reservoir to the exterior. The function of the glands is unknown.

Circular and longitudinal muscles are arranged in a series of uniformly spaced bands, which cross each other like the rails and crossties of a railroad track (Fig. 3). The longitudinal bands bulge into the body cavity to form rail-like strips, each of which lies below a longitudinal groove on the body's surface (Fig. 4). Each circular muscle is innervated by a lateral nerve that originates on the ventral cord and encircles the body within the belly of the muscle (Fig. 7). Although we lack direct evidence, these same nerves may also innervate the longitudinal muscles. All body wall muscles are smooth.

The coelom is lined by a squamous peritoneum composed primarily of non-ciliated and multi-ciliated cells (Figs. 7–9). A basal lamina underlies the peritoneum. The voluminous, fluid-filled cavity contains coelomocytes and motile micro-organs, called ciliated urns (Fig. 10). The predominant coelomocytes are the respiratory hemerythrocytes. These are nucleated, biconcave cells, containing hemerythrin, that are circulated by the action of body wall muscles and especially by cilia on the coelomic lining.

During growth, a coelomic outpocket pushes through each of the spaces between the criss-crossed circular and longitudinal muscles (Fig. 3) and enlarges in the connective-tissue space immediately below the epidermis (Fig. 7). Because of the orthogonal pattern

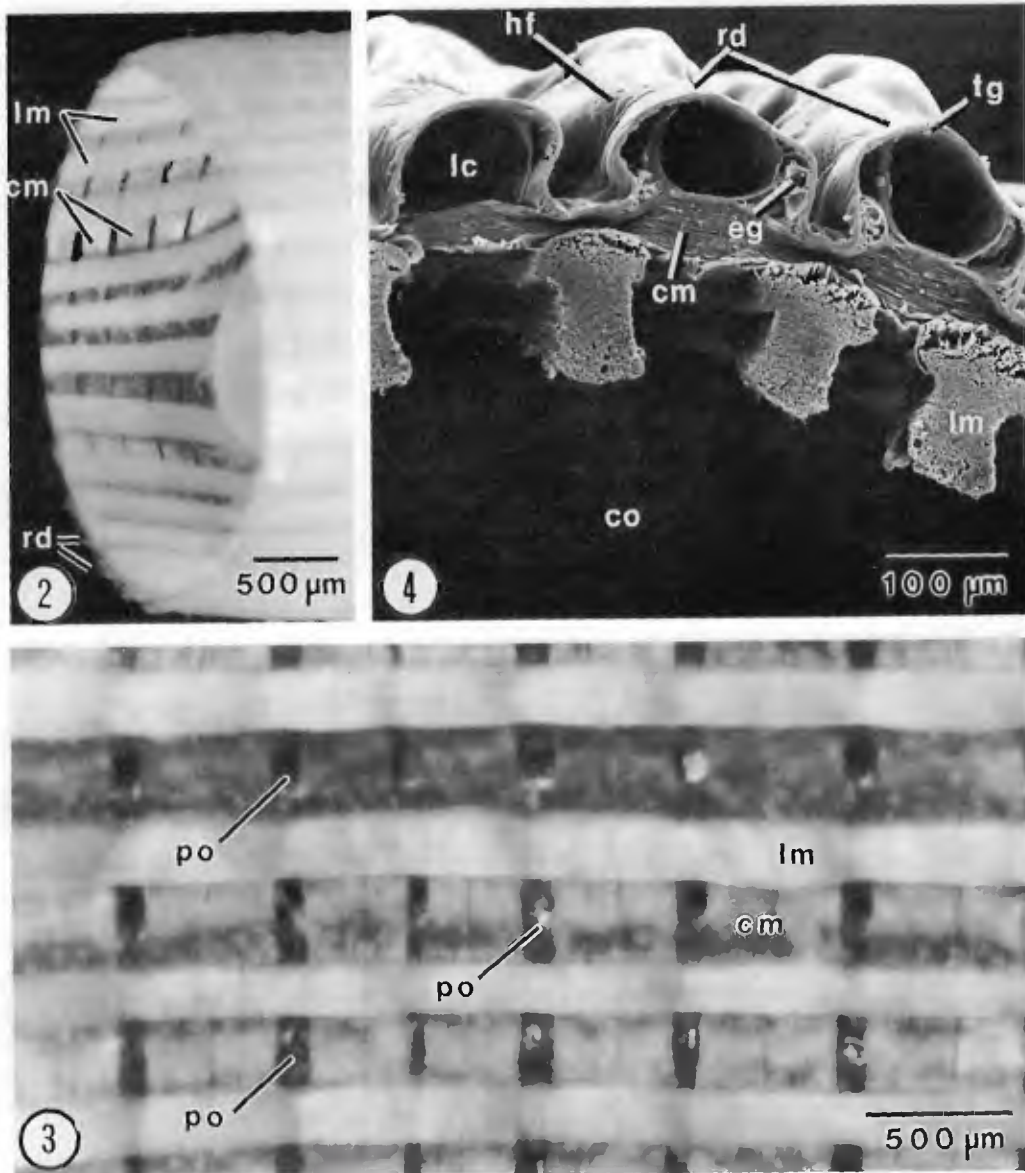


Fig. 2. Cut trunk of preserved juvenile specimen. Circular muscle (cm); longitudinal muscle (lm); body wall ridges (rd). **Fig. 3.** En face view of coelomic musculature of preserved juvenile. Gaps in the musculature are the sites of pores (po) opening from the coelom into the dermal canals (not visible). Circular muscle (cm); longitudinal muscle (lm). **Fig. 4.** SEM of body wall of an adult in transverse section. Dermal longitudinal canals (lc) are situated within the body wall ridges (rd), which alternate with the longitudinal muscles (lm). Circular muscle (cm); coelom (co); epidermal gland (eg); helical cuticular fibers (hf); integument of cuticle and epidermis (tg).

of the circular-muscle bands and longitudinal-muscle strips (Fig. 3), the outpockets are arranged in longitudinal rows alternating with the strips of longitudinal muscles (Fig. 4). As the animal grows, successive pockets in each longitudinal row fuse to form a continuous longitudinal canal, one beneath each of the ridges on the body's surface (Figs. 4–6). Each longitudinal canal remains in communication with the coelom by way of a short radial canal and pore formed

by the original outpocket (Fig. 6). In one juvenile specimen, 3 mm in diameter, the body wall thickness at its maximum was 0.2 mm and the canals extended to within 10 μm of the exterior.

Although each of the approximately 30 longitudinal canals continues unbroken along the length of the animal, flow between the canal and coelom may occur through any of the radial canals. Thus any section of the longitudinal canal between two radial canals can

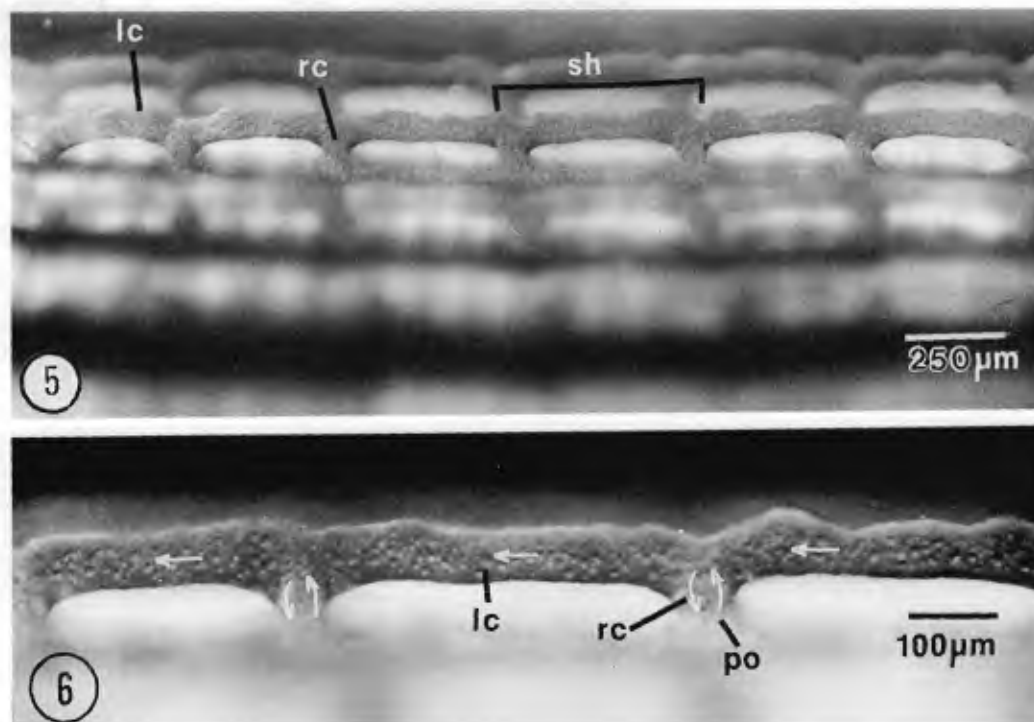


Fig. 5. Silicone rubber corrosion cast of dermal canals of a juvenile. The longitudinal body axis is oriented from left to right. Longitudinal canal (lc); radial canal (rc); shunt, or short circuit (sh). **Fig. 6.** Silicone rubber corrosion cast of dermal canal of a juvenile. Anterior is to the left. Arrows indicate the general direction of fluid flow. This 4-cm long specimen had 30 longitudinal canals, all of which produced a posterior-to-anterior flow of coelomic fluid. Longitudinal canal (lc); pore (po); radial canal (rc).

function as a short circuit, or shunt, between the canal and coelom (Figs. 5, 6, 12).

Flow in the longitudinal canals results from the action of cilia on the coelomic lining and is always posterior to anterior in direction (Figs. 6, 8, 9, 11). Flow in the radial canals is bidirectional: fluid flows from the coelom into the longitudinal canal along the posterior wall of the radial canal, and from the canal into the coelom along the anterior wall of the radial canal (Fig. 7). Both fluid and coelomocytes enter the dermal canals from the coelom. The median flow rate in a longitudinal canal is 0.7 mm/s ($N = 7$, 0.56–0.77 mm/s; Fig. 11). The body wall musculature acts in valving the flow in the longitudinal canals. While the body is extended, the flow continues uninterrupted along the length of the canal before being returned to the coelom. In longitudinally shortened regions of the body, however, flow between the coelom and canal is local and restricted to the shunts.

Approximate volumes were calculated for the coelom and dermal canals of one preserved adult. The body was 185 mm in length and ranged from 6 to 10 mm in diameter. The body wall thickness ranged from 0.5 to 1.0 mm and each of the 31 dermal canals had

a diameter of approximately 0.25 mm. The coelomic volume was approximately 3900 μl and the aggregate volume of the dermal canals, 300 μl , or roughly 8% of the coelomic volume.

Discussion

Sipunculans are vulnerable, soft-bodied worms that occupy a variety of protective habitats, including sandy or muddy sediments, seagrass beds, and algal clumps, as well as oyster and mussel beds. In rocky environments, they may be found in crevices, under boulders, or in galleries or borings in coralline rubble and calcareous rock. Species living in sediments are active burrowers, feeding on organic matter in sand engulfed as they burrow and rarely emerging onto the surface. In such mobile sand-burrowing species, exemplified by the genera *Sipunculus*, *Xenosiphon*, *Siphonosoma*, and *Siphonomecus* of the family Sipunculidae, gas exchange may be accomplished through coelomic sacs or canals in the body wall, as described above for *Sipunculus nudus*. In contrast, the more sedentary species associated with rocky habitats, especially those dwelling in deep galleries or borings, have

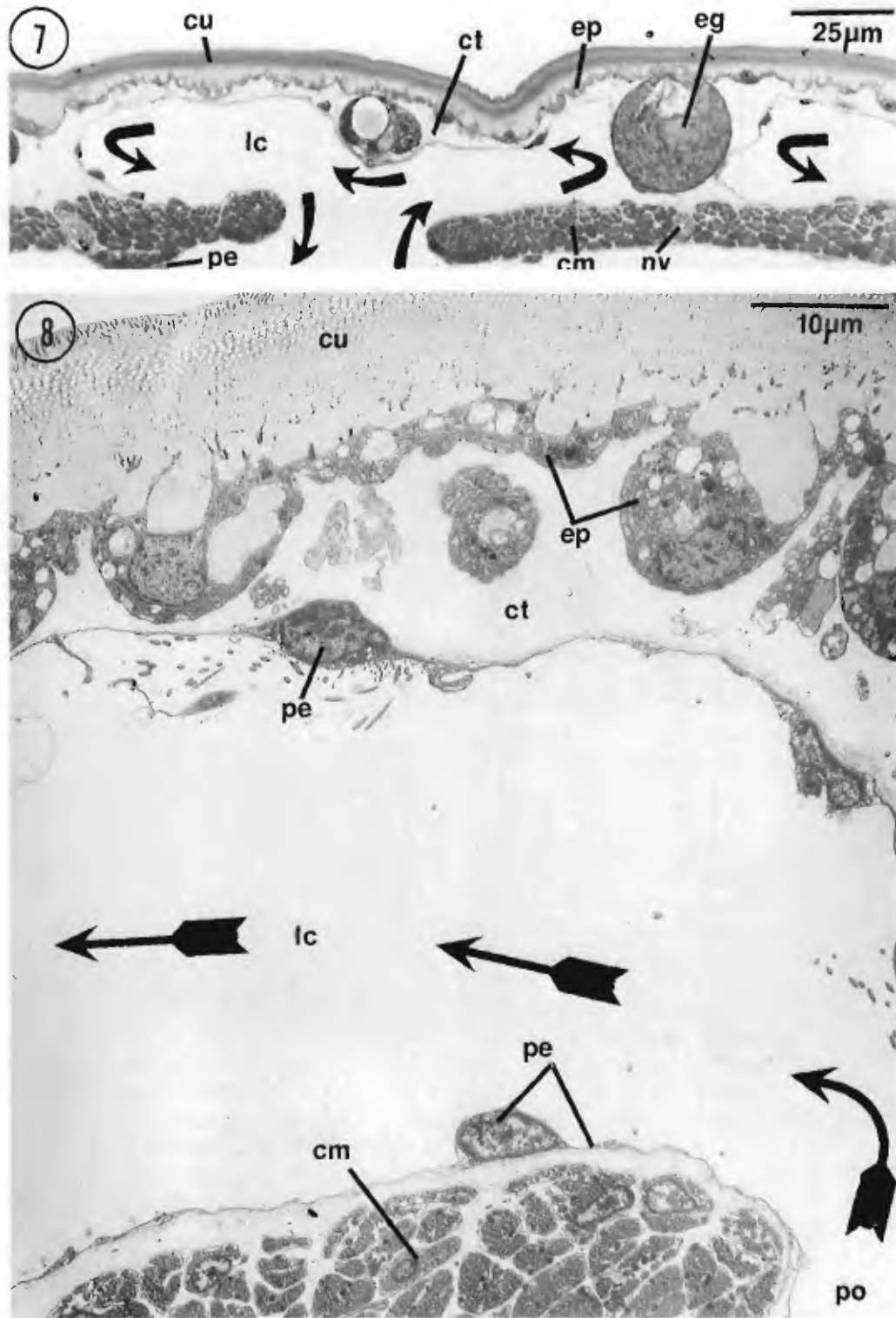


Fig. 7. Longitudinal section of the body wall of the trunk of a juvenile (light micrograph). Developing dermal canals arise as a longitudinal series of individual coelomic outpockets, one of which is shown here (lc). Later, successive pockets along the length of the body fuse to form a continuous longitudinal canal, as shown in Figs. 5 and 6. Glands (eg), also known as epidermal organs, open onto the surface of the cuticle. Arrows indicate direction of fluid flow. Anterior is to the left. Circular muscle (cm); connective tissue dermis (ct); cuticle (cu); epidermal pavement cells (ep); longitudinal canal (lc); lateral nerve (nv); peritoneum (pe). **Fig. 8.** Longitudinal TEM section of a dermal canal (lc) and coelomic pore (po) of a

been observed in the laboratory to extend the anterior introvert or tentacles over the surface of the rock or into the overlying water while feeding (Rice 1969). Because the galleries or rocky enclosures may be low in oxygen, the excursion of introvert and tentacles into the water may be significant not only for feeding, but also for gas exchange. Thus, external respiratory surfaces of sipunculans may include the entire body, introvert and tentacles, or tentacles alone. Respiratory specializations are most likely to reflect the specific habitat, the availability of oxygen, and the behavior or life habit of each species.

Internally, the respiratory organs of sipunculans consist of the spacious trunk coelom and, in many species, a more or less conspicuous contractile vessel (compensation sac), a tubular evagination of the tentacular coelomic cavity (Pilger 1982) into the coelomic cavity of the trunk. This vessel is usually a single blind sac that extends along the dorsal surface of the esophagus; in some species a second vessel runs ventral to the esophagus. The contractile vessels form an internal transport system and gas-exchange surface between tentacular and trunk coelomic cavities. Because these vessels mediate gas exchange between the tentacles and introvert-trunk, their degree of development should be greatest in those species that rely primarily on the tentacles as an external respiratory surface. An intermediate degree of development might be expected in those species that use both tentacles and introvert as gas-exchange surfaces. The least development should be found in sipunculans that use the entire body surface for gas exchange.

We propose, therefore, that sipunculans fall generally into three functional categories based on the body region or regions used for environmental gas exchange. The examples given to relate morphology, habitat, and behavior are as known from the literature or from personal observation.

1. Tentacle breathers (Fig. 13A–C): Tentacles are well developed, the introvert is short, and the trunk body wall is thick and dense. The contractile vessels, as the principal exchange surfaces between tentacles and trunk coelom, are elaborated into numerous diverticula (villi), which may appear as short, simple tubules or as elongate, sometimes branching extensions.

This category is best exemplified by the genus *Themiste* of the monogeneric family Themistidae. This genus is characterized by the most elaborately developed tentacular crown in the phylum Sipuncula, consisting

of dichotomously branched tentacles that bear small tentacles palmately or pinnately arranged. The tentacles remain extended for long periods over the substratum at the opening of the animal's burrow or other refuge (Pecbles & Fox 1993; Tarifeno 1975). Habitats include sand, rock fissures, and tunnels in coral rock or oyster shells. In studies of sipunculan respiratory pigments, Manwell (1960) demonstrated that the hemerythrin of the tentacular system (including the contractile vessel with its numerous villar extensions) had a lower oxygen affinity than that of the trunk coelom, suggesting that oxygen is transported from the seawater through the tentacular system to the main coelom.

Based on habitus, structure, and behavior, other species can be deduced to be tentacle breathers. For example, the large sand-burrowing species *Thysanocardia* (= *Golfingia*) *pugettensis* of the family Golfingiidae, with numerous, filiform tentacles and conspicuous, thick, sometimes branched villar projections on the contractile vessel, meets structural criteria for this category. Moreover, in both the laboratory and field, this species extends its tentacular crown for long periods above the surface of the fine, muddy sand in which it burrows (M.E.R., pers. observ.). *Antillesoma antillarum*, a member of the Phascolosomatidae and the sole species of *Antillesoma* (Gibbs & Cutler 1987), occupies rocky habitats in tropical and subtropical waters. Unlike other phascolosomatids, but like species of *Themiste*, it has a thickened trunk, relatively short introvert, and tentacular crown of numerous elongate tentacles. Internally, the contractile vessel bears clusters of slender, dichotomously branched villi. In the laboratory, specimens have been observed to extend the tentacular crown from their burrows in coral rock for long periods (Rice 1969, 1975, 1976).

2. Introvert and tentacle breathers (Fig. 13D–F): The introvert is generally elongate and the tentacles vary from few and small to moderately well developed. The body wall of the extended introvert is noticeably thinner than that of the trunk, which is often thick and abundantly ornamented with dense structures used in boring, anchorage, and protection, such as papillae, holdfasts, and anterior and posterior shields. The contractile vessels lack villi and are usually simple tubes. These sipunculans occupy a wide variety of habitats, including calcareous rock or coralline rubble, rock fissures, discarded molluscan shells, and sand. Typically, they extend the introvert and tentacles far

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juvenile. Anterior is to the left. Arrows indicate direction of fluid flow. Circular muscle (cm); connective tissue dermis (ct); cuticle (cu); epidermis (ep); peritoneum (pe).

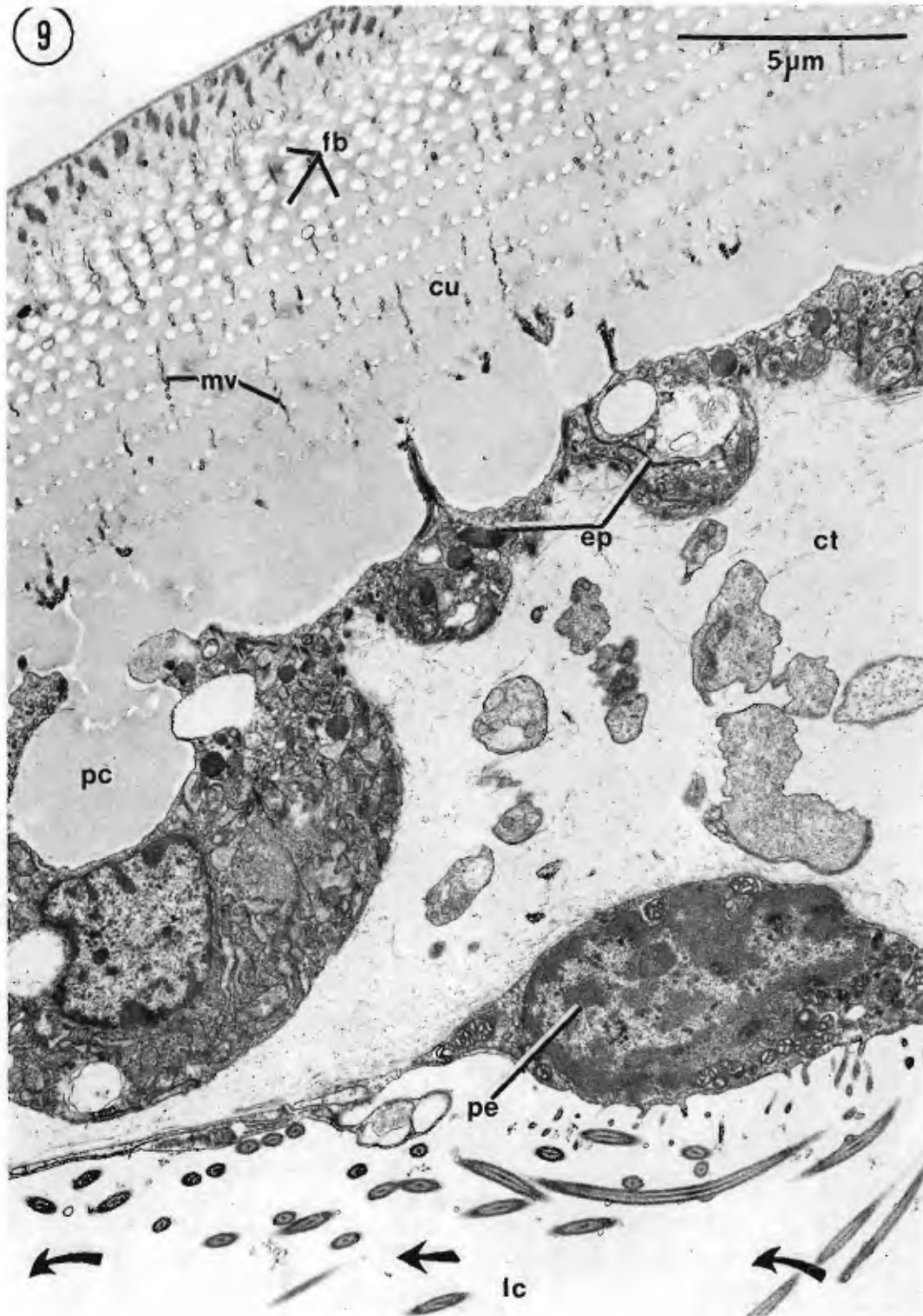


Fig. 9. Longitudinal dermal canal and overlying tissues. Longitudinal section of juvenile specimen (TEM). Multiciliated peritoneal cells (pe) generate flow (arrows) in the canal (lc). Anterior is to the left. Connective-tissue dermis (ct); crossed-helical fibers (fb); cuticle (cu); epidermal pavement cell (ep); microvilli (mv); precursor cuticle (pc).

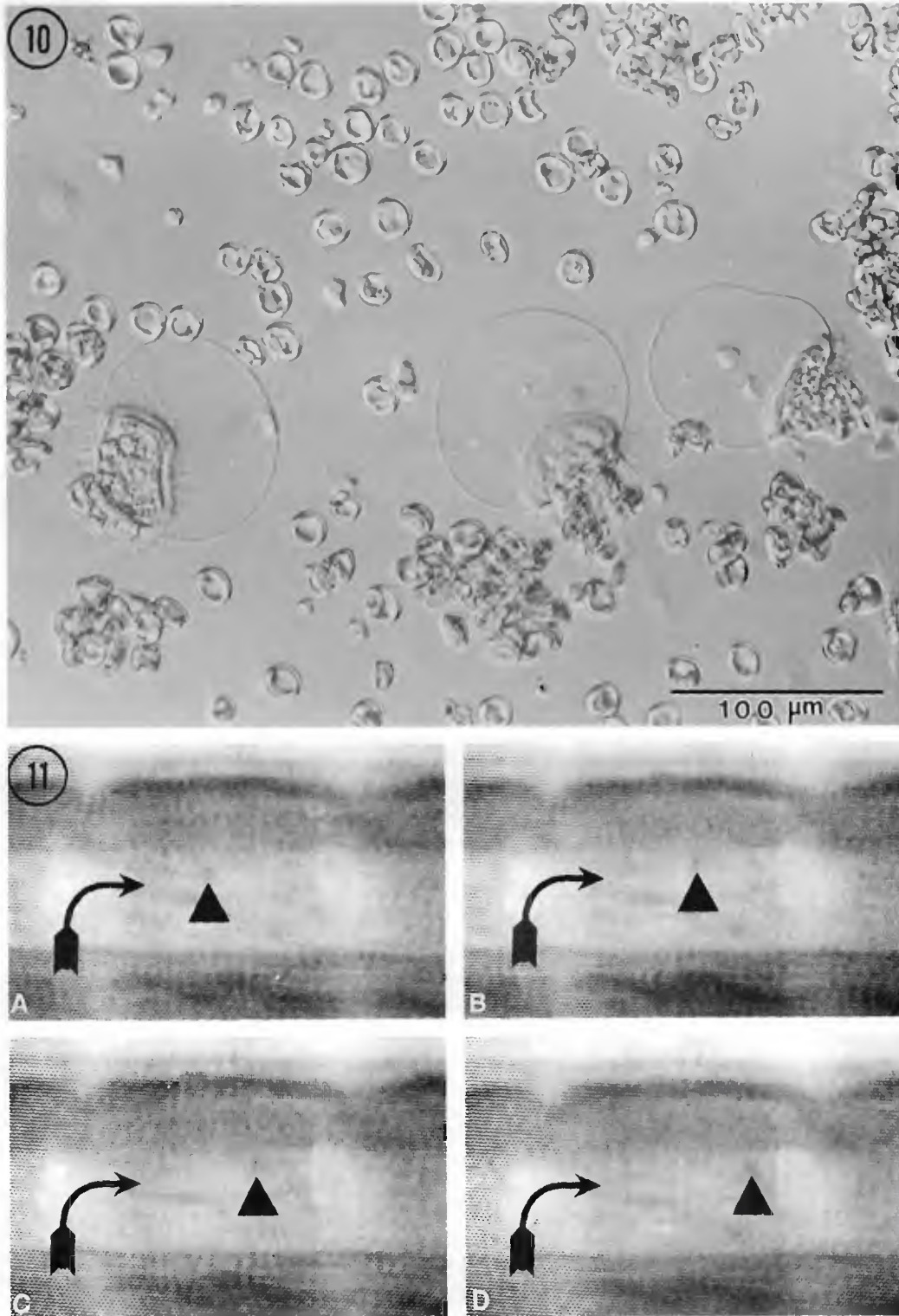


Fig. 10. Coelomocytes and ciliated urns of an adult (light micrograph of living cells). Small, biconcave cells are respiratory hemerythrocytes. The medusoid ciliated urns are motile micro-organs that police the coelom for spent cells and particulate wastes, which they entangle in trailing mucous threads. Coelomocytes circulate freely to and from the coelom via the dermal canals. **Fig. 11. A–D.** Video recording of coelomocyte (arrowheads) being transported from posterior to anterior (left to right) along one section of a longitudinal canal. Coelomocyte enters the longitudinal canal through a pore (arrows), which is a stationary reference in A–D. Interval between frames is 0.1 s.

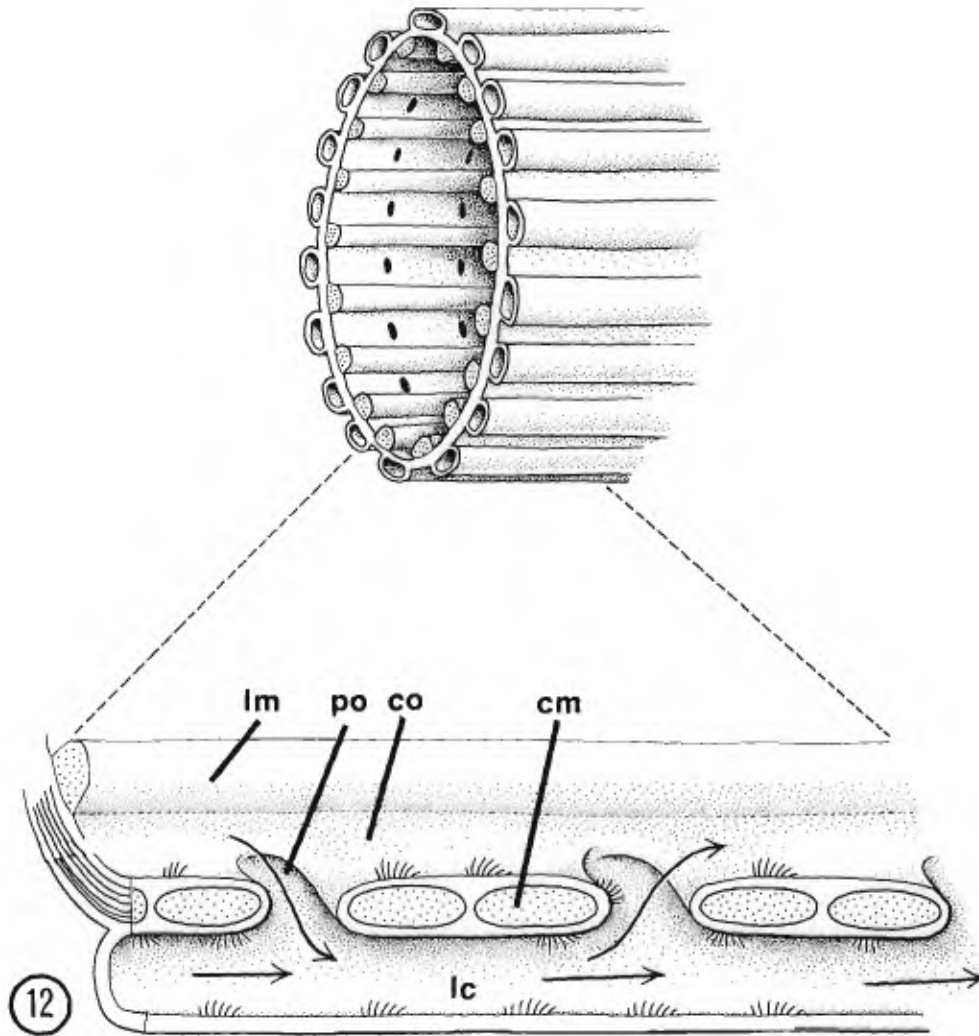


Fig. 12. Reconstruction of the body wall and dermal canals. Arrows indicate direction of coelomic fluid flow. Circular muscle (cm); coelom (co); dermal canal (lc); longitudinal muscle (lm); pore (po).

into the surrounding water while the trunk remains lodged in the retreat. Examples of this category are species from the families Phascolosomatidae and Aspidosiphonidae. *Phascolosoma perlucens*, a rock-boring species common throughout the Caribbean and other tropical waters, has short, digitiform and relatively few tentacles, a highly extensible introvert. Maintained in the laboratory within its burrow in coral rock, this sipunculan periodically extended the introvert for great distances over the surface of the rock and subsequently retracted it into the burrow (Rice 1975, 1976). These observations were reported relative to feeding behavior, but this activity probably also provides for respiratory exchange, not only through the tentacles, but especially through the greatly distended, relatively thin body wall of the introvert. A deep-sea species, *Phascolosoma turnerae*, has also been ob-

served in the laboratory to extend its introvert to great lengths. Maintained in sand in which they burrow, the animals stretch their introverts vertically above the sediment, retaining this position for long periods. Whereas the introvert is usually equal to or slightly greater in length than the trunk, under these conditions it may be extended to three or more times the length of the trunk.

Another phascolosomatid that fits this category is *Apionsoma misakiana*, which inhabits holes in coral-line rubble. Smaller than in those species described above, the trunk is only 2 to 3 mm long and in living specimens the introvert may be extended 10 times that length. In the laboratory, specimens maintained in sand have been documented by time-lapse cinematography (M.E.R., unpubl.) to burrow into the sand, extending the introvert out over the surface, presumably

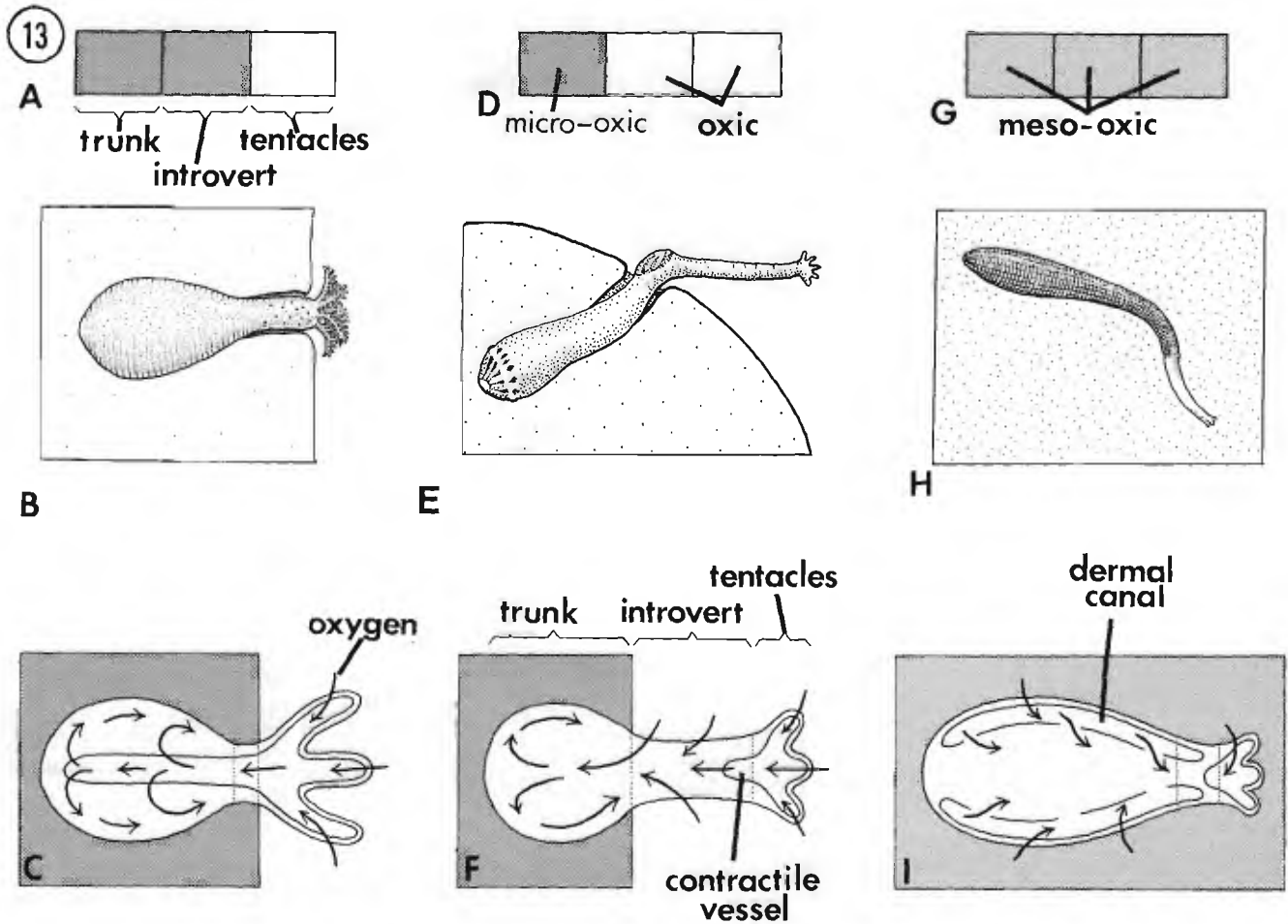


Fig. 13. Speculative model that correlates habitat, oxygen availability, and body structure in sipunculans. Arrows indicate possible paths of oxygen diffusion and internal transport. A–C. Tentacle breathers, illustrated by *Themiste alutacea*. D–F. Introvert and tentacle breathers, illustrated by a species of *Aspidosiphon*. G–I. Integumentary breathers, illustrated by *Sipunculus nudus*.

for both feeding and respiration. Tentacles of this species are few and minute and the contractile vessel is reported either as small or missing.

Species of *Aspidosiphon* with elongate, extensible introverts, few short tentacles, and simple contractile vessels fall into this category. Characterized by thickened cuticular structures, termed shields, at the anterior and posterior trunk, these species often inhabit burrows, presumably of their own formation, in calcareous rock. When the introvert is retracted, the anterior shield serves as an operculum, closing off the mouth of the burrow. Although the in-situ behavior of species of *Aspidosiphon* is unknown, specimens of *A. albus*, *A. brocki*, *A. fischeri*, *A. spinosocutatus*, and *A. steenstrupi*, removed from their burrows, have been extensively observed in the laboratory (M.E.R., unpubl.). Under these conditions, their activity consists mainly

of extension of the introvert, which in some species, may be two or more times the length of the trunk.

3. Integumentary breathers (Fig. 13G–I): Characteristic of species in this category is the similarity of the body wall in introvert and trunk regions and the presence of coelomic evaginations into the body wall. Four of the five genera in the family Sipunculidae are included in this category: *Sipunculus*, *Xenosiphon*, *Siphonosoma*, and *Siphonomecus*. In *Sipunculus* the coelomic evaginations are long, continuous canals, as described in this study for *S. nudus*. In *Xenosiphon* there are short, diagonal coelomic canals from which finger-like filaments or gills extend to the exterior of the body, increasing the external surface area available for oxygen uptake. Each evagination of *Siphonomecus* consists of a sac (“vestibule”) from which arises a group of short, small, parallel, longitudinal mini-canals

(Cutler 1986). *Siphonosoma* differs in that the coelomic evaginations consist of sac-like outpocketings. The contractile vessel of certain species of *Siphonosoma* is distinguished by villi, but in the other three genera contractile vessels are simple. Tentacular development varies considerably. Species of all four genera are large, sand-burrowing species that actively move and feed within the sediment, only rarely coming to the surface.

Studies of oxygen affinity in the respiratory pigment hemerythrin of *Siphonosoma ingens* confirm that the skin is the primary site of gas exchange (Manwell 1960). In this species the coelomic hemerythrin has a lower oxygen affinity than the tentacular, suggesting that the flow of oxygen is through the body wall into the main coelom and from the coelom to the tentacular system.

The monotypic genus *Phascolopsis*, also of the Sipunculidae, is an apparent exception to the proposed body structure for integumentary breathers. Unlike other members of the Sipunculidae, *Phascolopsis gouldii* lacks integumentary coelomic spaces, although behavioral observations indicate that it may respire through the integument. According to Mangum and Kondon (1975) and Mangum (1992), the species remains burrowed completely in the sediment under normal conditions in the field and laboratory. Under laboratory conditions in which the flow of water over the sediment was discontinued, however, the animals extended their tentacles above the surface of the sediment into the overlying water.

A singular occurrence in the family Phascolosomatidae, reported in the Indo-Pacific species *Phascolosoma arcuatum* (= *P. lurco*), is the intrusion into the body wall of coelomic sacs, similar to those of *Siphonosoma* (Rice & Stephen 1970). This species of *Phascolosoma* inhabits burrows in mud in or near mangrove swamps from the intertidal to the highest level of the mangrove swamp where the mud is covered by seawater only at the most extreme high tides (Green 1975; Green & Dunn 1976). In such a muddy, often semi-terrestrial habitat, low in available oxygen, the coelomic extensions would function to increase respiratory exchange through the surface of the body wall.

Thus, it is evident that in addition to the dermal coelomic canals of *Sipunculus nudus*, described here in terms of structural and functional organization, a diversity of mechanisms achieve gas exchange and transport within the phylum Sipuncula. Data on the respiratory physiology of sipunculans and the availability of environmental oxygen in different habitats are limited, however, despite a large literature on the molecular structure of hemerythrin, the respiratory

pigment common to this group (cf. Kurtz 1992; Mangum 1992). It is our intent that the generalized categories proposed above may serve as a basis to stimulate further comparative anatomical and physiological investigations on sipunculan respiration.

Acknowledgments. The technical assistance of Julianne Piraino is acknowledged with gratitude. The research was supported in part by NSF grant BSR-9006599 to E.E.R. This is contribution #357 of the Smithsonian Marine Station at Link Port.

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