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Ultrastructure of Auricularia Larval Coeloms: Evidence for the Presence of an Axocoel

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Abstract. A hallmark feature of echinoderm larvae is the development of the left anterior coelom. This coelom, called the axohydrocoel, consists of the morphologically distinct, but undivided, left axocoel and hydrocoel. The axocoelic portion forms a duct that opens to the exterior via a pore on the dorsal surface of the animal. Holothuroid larvae are thought to lack an axocoel, but develop an anterior coelom, duct, and pore that are regarded as parts of the hydrocoel. New ultrastructural data, however, show that holothuroid auricularia larvae possess an axocoel and hydrocoel united together into an axohydrocoel. During development the anterior coelom consists of an interconnected left somatocoel, hydrocoel, and axocoel. The left somatocoel separates from the axohydrocoel and subdivides into left and right somatocoels. The somatocoels and hydrocoel region of the axohydrocoel are lined by a monociliated mesothelium having characteristics of transporting epithelia. The axocoel epithelium, like that of asteroid larvae, is composed of mesothelial podocytes. A duct connects the *axocoel* directly to the open dorsal pore and is lined with a columnar transporting epithelium. The occurrence of a specialized podocyte-lined cavity between the surface pore and the hydrocoel in echinoderm larvae is indicative of an axocoel. That similar structures occur in auricularia larvae supports the identification of an axocoel in holothuroids.

Introduction

Holothuroids with indirect development typically have a planktonic feeding auricularia larva that undergoes metamorphosis to produce a pentactula, or pelagic juvenile. In most holothuroids, the juvenile settles shortly after metamorphosis and assumes an adult lifestyle. The auricularia larva is restricted to the family Synaptidae in the order Apodida and to the families Holothuriidae and Stichopodidae in the order Aspidochirotida (Smiley *et al.*, 1991).

Auricularia larvae have a large blastocoel that houses the J-shaped gut, the paired body coeloms, and the left anterior coelom. In most larval asteroids, ophiuroids, and echinoids, a right anterior coelom is also present, but its developmental fate varies among groups. It reportedly either fuses with the right somatocoel, becomes the pulsatile vesicle (dorsal sac, madreporic vesicle) of the heart, or disappears at metamorphosis (Hyman, 1955; Hendler, 1991; Pearse and Cameron, 1991). The right anterior coelom does not develop in holothuroids and crinoids, which are believed to lack a pulsatile vesicle (Hyman, 1955; Holland, 1991; Smiley *et al.*, 1991).

The left anterior coelom is a unifying feature of echinoderm larvae and, despite differences in specific details of morphogenesis, is positionally and anatomically similar in five of the six extant classes (Hyman, 1955; Dan, 1968; Ruppert and Balser, 1986; for review see chapters 4–8 in Giese *et al.*, 1991); no information exists on the larval development of the Concentricycloidea. In echinoderm larvae, with the reported exception of holothuroids (Smiley *et al.*, 1991), the left anterior coelom represents a fusion of the left axocoel and hydrocoel (Bury, 1885, 1889; Ruppert and Balser, 1986; Giese *et al.*, 1991). Hyman (1955), drawing principally on the work of earlier researchers, emphasized this connection and retained the term axohy-

drocoel. The axohydrocoel is open, if only transiently, to the larval somatocoels and to the exterior via a duct and dorsal pore.

Holothuroid auricularia larvae develop an anterior coelom, duct, and pore, but are believed to lack any vestige of an axocoel (Hyman, 1955; Smiley, 1986, 1989). If holothuroids do not have an axocoel, then the anterior coelom, unlike that of other echinoderms, consists only of the hydrocoel and the somatocoel primoridium. The left somatocoel arises from the anterior coelom and later divides forming the right and left larval somatocoels. A recent study of the development of the aspidochirotid *Stichopus californicus* (Smiley, 1986) suggests that the left anterior coelom and duct consists solely of the hydrocoel and the somatocoel primoridium. Based primarily on the ultrastructure of the madreporic vesicle and the hypothesis that adult holothuroids lack any axoelic derivatives (Smiley, 1986, 1989), Smiley *et al.* (1991) conclude that holothuroid auricularіae have no "identifiable axocoel as part of their complement of coelomic primordia at any stage of development."

Several ultrastructural examinations of axocoelic derivatives in adult echinoderms (Bachmann and Goldschmid, 1978; Welsch and Rehkämper, 1987; Balser, 1990; Balser *et al.*, 1993, unpubl. data) and one of the axohydrocoel of a larval asteroid (Ruppert and Balser, 1986) indicate that podocytes typify the lining of the axocoel. This study was undertaken to search for podocytes and other evidence of an axocoel in holothuroid larvae and is part of a larger investigation that attempts to reconstruct the phylogeny of extant echinoderms using a distinctive echinoderm organ, the axial gland, as a systematic character. Specific objectives of this investigation include examination of the ultrastructure of the larval coeloms of *Holothuria grisea* and different species of field-collected auricularia larvae. A comparison of the coeloms of these larvae with those, particularly the axohydrocoel, of other echinoderms will be used to test the hypothesis that an axocoel is present in holothuroid auricularia larvae.

Methods and Materials

Auricularia larvae of the holothuriid *Holothuria grisea* were obtained from fertilization of freely spawned gametes. Adults were collected in June 1992 from rock rubble beneath the Ft. Pierce South Seaway Bridge and transported to the Smithsonian Marine Station at Link Port, Ft. Pierce, Florida. Specimens were kept in buckets of unaerated seawater until spawning occurred. Fertilized eggs were washed and transferred to culture dishes with clean seawater. Cultures were maintained at 26°C and provided daily with clean water and the marine alga *Isochrysis galbana* (Tahitian strain) as food.

During the spring and summer of 1992, auricularia larvae were collected from the waters off Grand Bahama Island (approx. 23°N 79.8°W) and from the Gulf Stream off the coast of Florida (approx. 26.5°N 78.8°W). Auriculariae were hand-sorted from plankton tows conducted aboard the R/V *Sunburst* of the Smithsonian Marine Station at Link Port and aboard the R/V *Seadiver* during expeditions 3 (4/27/92) and 4 (6/22/92) headed by Dr. Tammy Frank, Harbor Branch Oceanographic Institution, Ft. Pierce, Florida. Larvae were identified as apodids or aspidochirotids based on the presence or absence of wheel ossicles. Within the order Apodida, only synaptids have an auricularia larva, and only larvae in this family possess wheel ossicles (*e.g.*, Smiley *et al.*, 1991). Based on larval characters, further classification of the aspidochirotids was not possible.

Morphological data for *H. grisea* and field-collected auriculariae were acquired from living larvae and from light and electron microscopy of plastic-embedded specimens. Live auriculariae were photographed with a Zeiss Photomicroscope II loaded with T-max (Kodak) black and white film. Serial developmental stages of *H. grisea* larvae were fixed for microscopy using 2.5% glutaraldehyde in Millonig's phosphate buffer adjusted to 1080 milliosmoles with NaCl. Post fixation in 1.0% OsO_4 in 0.2 *M* Millonig's buffer was followed by alcohol dehydration, propylene oxide and Epon 812 infiltration, and embedment in Epon 812 (Electron Microscopy Sciences). Field-collected auricularia larvae were prepared for microscopy by the same method.

Serial thick (1 μm) and representative thin sections were cut with a Porter-Blum Sorvall or Reichert-Jung Ultracut E ultramicrotome. Thick sections were stained with aqueous 1% toulidine blue in 0.5% borax and were observed and photographed with a Zeiss Photomicroscope I. Thin sections were stained with aqueous uranyl acetate followed by lead citrate and examined either with a Zeiss EM 9S or a Hitachi 600 electron microscope.

Results

Coelomic organization

The development from fertilized egg to auricularia larva of *H. grisea* follows that described for other indirect-developing holothuroids (*e.g.*, Smiley *et al.*, 1991). The first 24 h postfertilization are marked by the formation of a uniformly ciliated blastula that hatches from the egg envelope and further develops into a gastrula. Gastrulation is followed by differentiation of the archenteron into a gut and a single unpaired anterior coelom. This anterior coelom arises from the apex of the archenteron and is the primordium of all other larval coeloms. Between the second and third day of development, the archenteron bends

toward and fuses with the ventral epidermis to form the mouth. At the same time, the anterior coelom produces a duct, which grows towards the dorsal surface and eventually opens at a pore just to the left of the larval midline. By day 4, the now recognizable auricularia larva has an unbroken epidermal ciliary band and a complete functional gut (Fig. 1). The gut is C-shaped and consists of a ventral mouth and anus separated by an esophagus, stomach, and intestine. In addition to the gut, the blastocoel is occupied by mesenchymal cells and by the anterior coelom (Figs. 1, 2).

Data from a developmental series of *H. grisea* auricularia larvae and from field-collected larvae show that the anterior coelom forms an undivided cavity consisting initially of three morphologically distinct regions (Figs. 1, 3). These regions are the primordia of the hydrocoel, the axocoel, and the paired somatocoels. The somatocoel primordium grows posteriorly along the left side of the large bulbous stomach and eventually separates from the original anterior coelom (Figs. 1, 3, 6). This cavity later subdivides (Fig. 6) to form both the left and right somatocoels flanking the larval stomach (Dan, 1968; Smiley *et al.*, 1991).

The remaining two regions of the anterior coelom, located dorsal to the gut, correspond to the axohydrocoel found in other echinoderm larvae (Fig. 3). The medial lobe, or hydrocoel, extends toward the middle of the larva and grows to encircle the esophagus. This lobe gives rise to the water vascular system of the pentactula and adult.

The third lobe, or axocoel, is situated between the hydrocoel and the dorsal pore and includes the duct connecting the axohydrocoel to the exterior (Figs. 3, 4, 5). The axocoel varies in size among examined species. In *H. grisea,* the axocoel appears to be restricted to the duct and a few cells at the proximal inner end of the duct. In field-collected aspidochirotids and apodids, the axocoel cavity, which is largest in the synapids, is oval and extends either anteriorly or concentrically from the inner part of the duct (Figs. 4, 5). Dissimilarity in the size of the axocoel may be a reflection of differences in the size of the auricularia of each species. *H. grisea* auriculariae are considerably smaller (0.75 mm in length 15 days postfertilization) than field-collected aspidochirotids (1–3 mm in length) and synaptids (up to 5 mm in length).

Coelomic ultrastructure

Following morphogenesis of the duct and its connection to the exterior, further growth and differentiation of the anterior coelom results in the three ultrastructurally distinct, but continuous cavities representing the somatocoel primordium, the hydrocoel, and the axocoel. The mesothelium lining all three lobes of the anterior coelom is composed of monociliated cells that rest on a continuous basal lamina and are interconnected by cellular junctions. Ultrastructural dissimilarities in the lining of each cavity are principally differences in cellular junctions, apical microvilli, and basal modifications. Although differentiation is evident, at the latest developmental stage of auricularia examined, the epithelium of each region had not yet acquired all the characteristics of juvenile mesothelia. For example, the hydrocoel and the somatocoel primordial cells lack basal myofilaments typical of cells lining the juvenile water vascular system and body cavity.

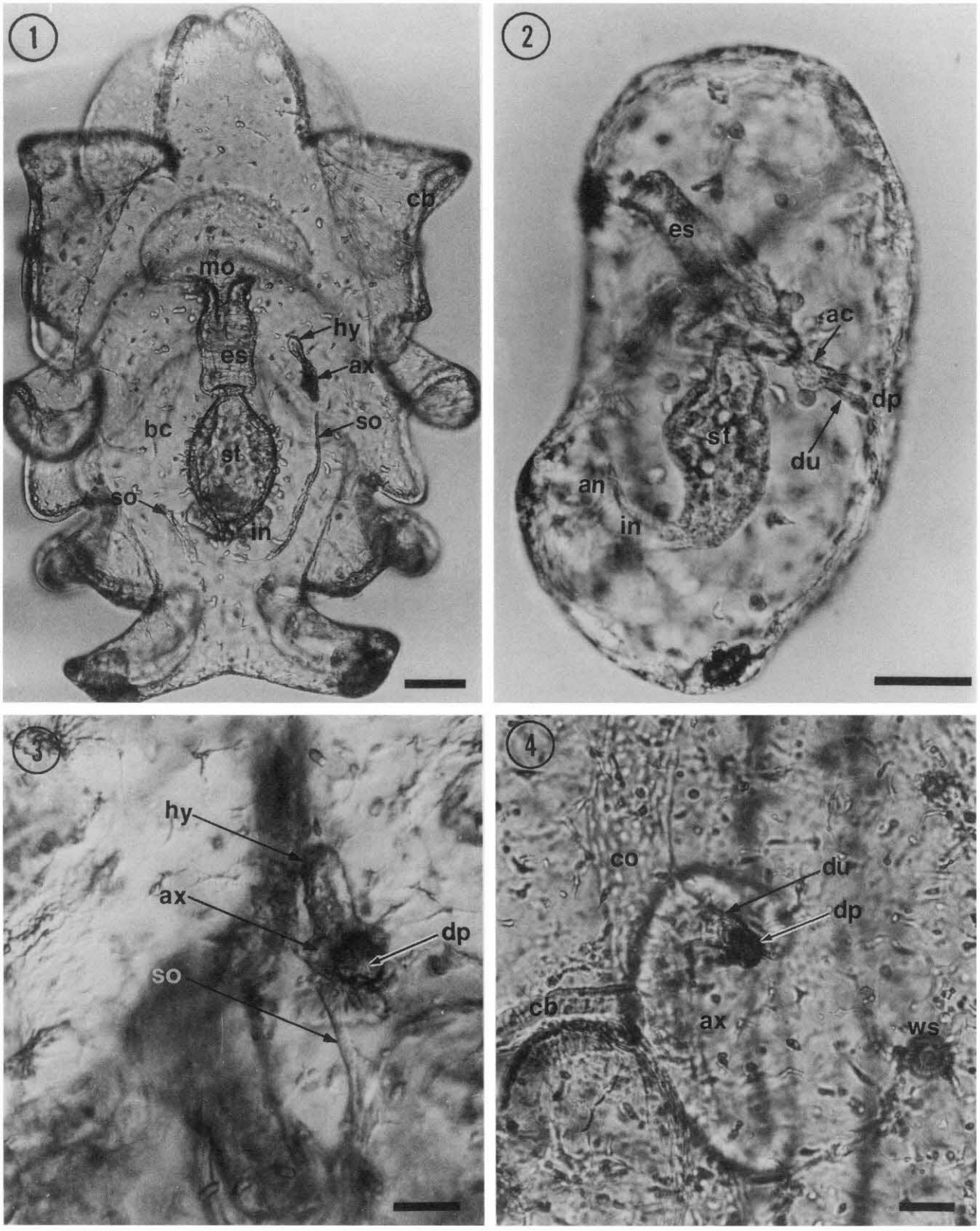
After the somatocoel primordium loses its connection to the anterior coelom, the initially oval cavity becomes elliptical and asymmetrical as it grows posteriorly along the length of the stomach. The cellular lining of the medial surface of the coelom closest to the stomach becomes flat and squamous, while that of the lateral surface remains columnar (Fig. 7). Regardless of shape, somatocoel cells are characterized by apical adhering and septate junctions, scattered apical microvilli, extensive paracellular spaces, and basal, vertebrate-like, tight junctions (Figs. 8, 9, 10). Not all somatocoel cells are coupled by basal tight junctions. In some cases, only basal adhering junctions were observed or basal junctions were absent (Fig. 9). The paracellular spaces often extend to the basal junctions or to the basal lamina. The lateral membranes lining these spaces possess coated pits, endocytic pits, and invagina-

Figure 1. Ventral view of a field-collected aspidochirotid auricularia. The axohydrocoel consists of the axocoel (ax) and hydrocoel (hy). This coelom is situated on the left dorsal side of the animal at the level of the junction between the esophagus (es) and the stomach (st). The somatocoels (so), which are initially connected to the axohydrocoel, lie lateral to the stomach. Scale bar = 0.1 mm; bc, blastocoel; cb, ciliated band; in, intestine; mo mouth.

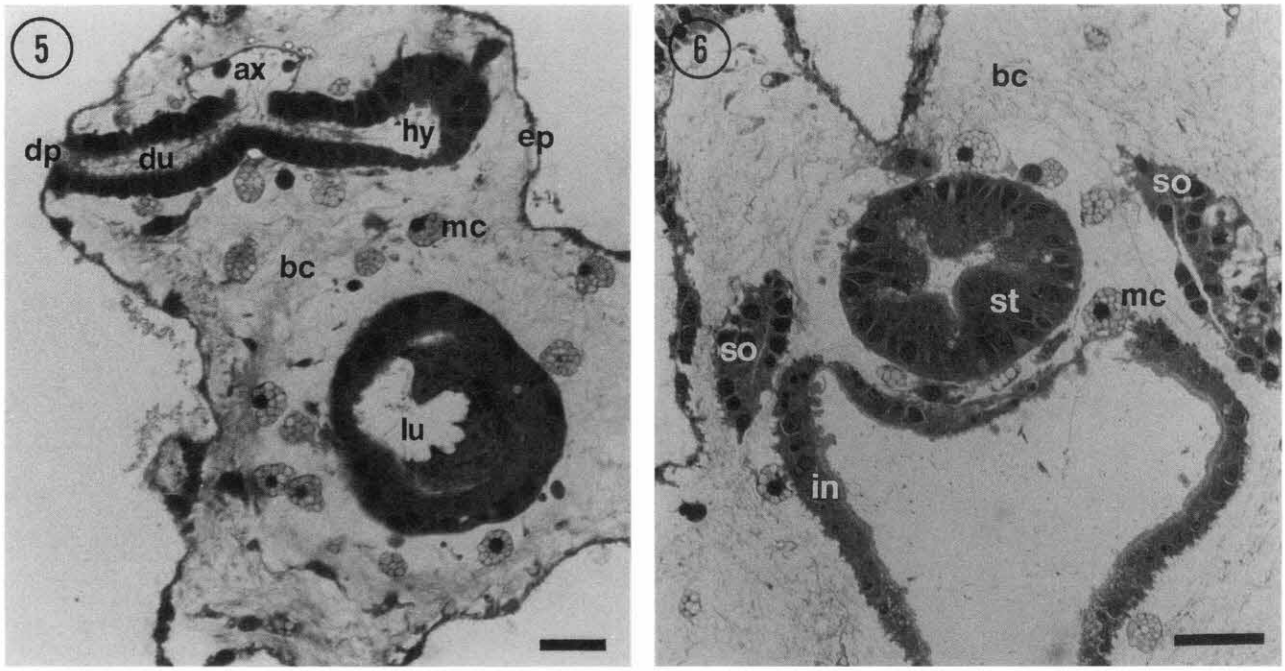
Figure 2. Lateral view of a 7-day-old larva of *H. grisea.* At this stage of development, the anterior coelom (ac) consists of the duct (du) and the undivided and undifferentiated left axocoel, hydrocoel, and somatocoel primordium. The duct provides an open connection between the anterior coelom and the dorsal pore (dp). Scale bar = 0.05 mm; an, anus; es, esophagus; in, intestine; st, stomach.

Figure 3. Dorsal view of the coeloms of a field-collected aspidochirotid auricularia larva showing the interconnected left axocoel (ax), hydrocoel (hy), and somatocoel (so). Scale bar = 0.05 mm; dp, dorsal pore.

Figure 4. Dorsal view of the axocoel (ax), duct (du), and pore (dp) of a field-collected synaptid auricularia larva. Scale bar = 0.05 mm; cb, ciliary band; co, coelom (hydrocoel?); ws, wheel ossicle.



Figures 1–4. Light micrographs of living auricularia larvae.



Figures 5–6. Light micrographs of tangential sections through the larval coeloms of a field-collected aspidochirotid auricularia.

Figure 5. Shows axocoel (ax) and hydrocoel (hy). The axocoel consists of a thin-walled cavity and a ciliated axocoelic duct (du), which opens at the dorsal pore (dp) on the left dorsal side of the animal. Scale bar = 0.01 mm; bc, blastocoel; ep, epidermis, lu, lumen of the stomach; mc, vesiculated mesenchyme cell.

Figure 6. The somatocoels (so) lie lateral to the stomach (st) and the upper intestine (in). Scale bar = 0.025 mm; bc, blastocoel; mc, vesiculated mesenchyme cell.

tions suggestive of transfer tubules (Fig. 8). Somatocoel cells, like those of the other coelomic mesothelia, are monociliated (Fig. 7). The cytoplasm contains coated vesicles, numerous other vesicles, mitochondria, and a large nucleus.

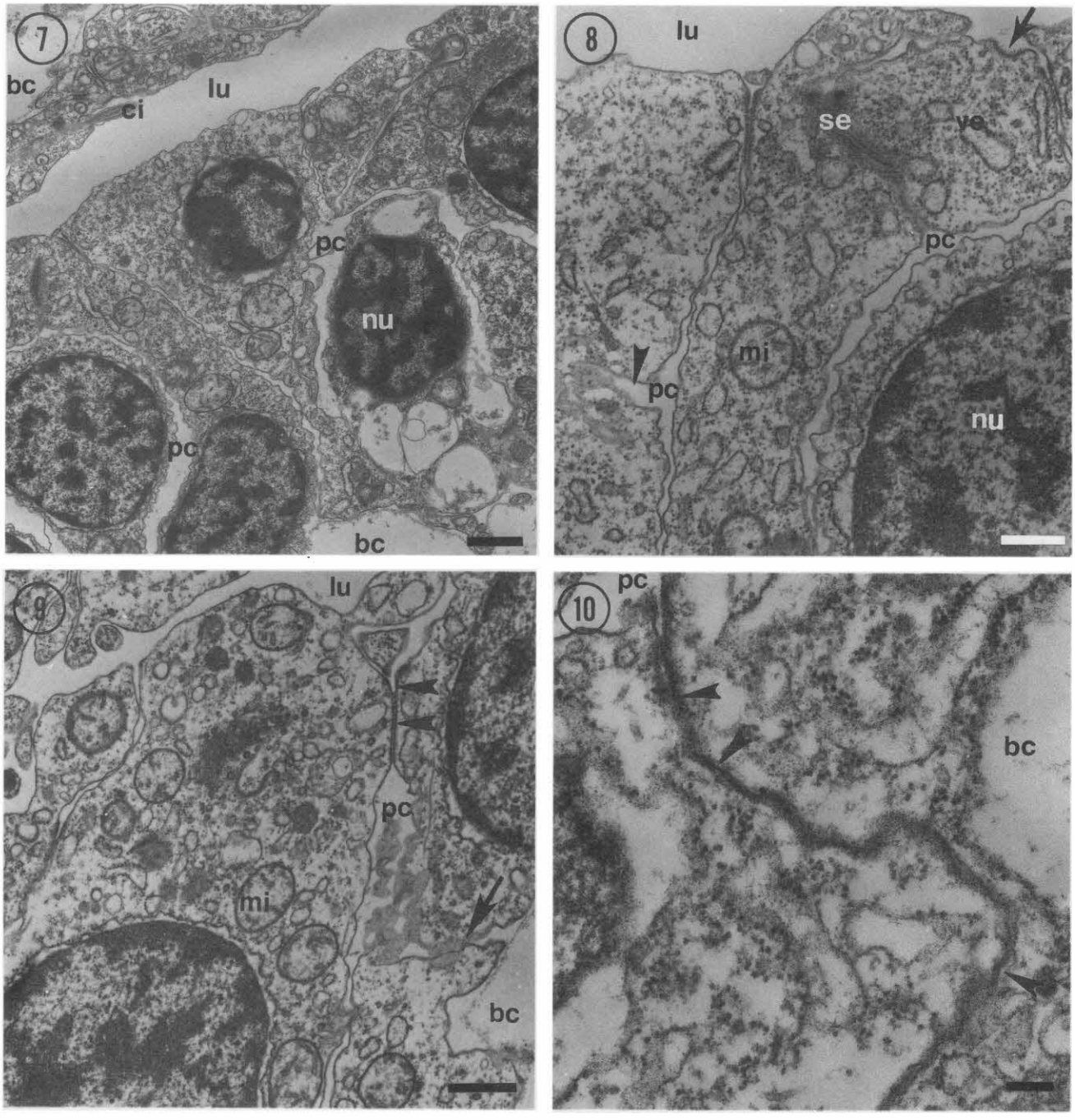
The hydrocoel lobe of the axohydrocoel is lined by squamous and cubodial epithelial cells joined by apical adhering junctions followed by septate junctions (Figs. 11, 13). Basally, the lateral membranes are extensively interdigitated and are interconnected by tight junctions (Figs. 12, 14). The cytoplasm is replete with basal mitochondria, putative lysosomes, and vesicles. The nucleus is basal and is elongated. Apical microvilli were infrequently observed.

The defining feature of the axocoel mesothelium is the presence of podocytes (Figs. 15–19). Podocytes are epithelial cells that exhibit basal modifications forming foot processes, or pedicels (Figs. 16, 18, 19). Pedicels rest on the underlying basal lamina and provide breaks, or fenestrations, in an otherwise continuous epithelium. Pedicels are bridged by the extracellular matrix of the underlying basal lamina (Figs. 18, 19). In addition to the basal lamina, some pedicels are bridged by diaphragms similar to filtration-slit membranes found across the pores of the fenestrated epithelia associated with the vertebrate nephron (Bulger, 1983). The cell bodies of podocytes are generally interconnected only by adhering junctions, but short septate junctions were occasionally observed connecting podocytes to hydrocoel or somatocoel cells or to axocoelic duct cells (Fig. 17). In addition to scattered microvilli (Fig. 17), the apical membrane possesses a single cilium and endocytic and coated pits. The cytoplasm contains vesicles, mitochondria, lysosomes, and a large circular nucleus (Figs. 16, 17).

Columnar monociliated epithelial cells line the lumen of the axocoelic duct which directly connects the axocoel lobe of the axohydrocoel to the dorsal pore (Fig. 20). The apices of these cells have a single cilium, many microvilli (Figs. 20, 21), and coated pits. Coated vesicles, numerous other vesicles, mitochondria, putative lysosomes, and a basal nucleus were observed (Fig. 21). Apical adhering and subapical septate and basal tight junctions are typical of this epithelium (Figs. 22, 23).

Discussion

The left axohydrocoel develops similarly in all echinoderm larvae except crinoids (Hyman, 1955; Balser and



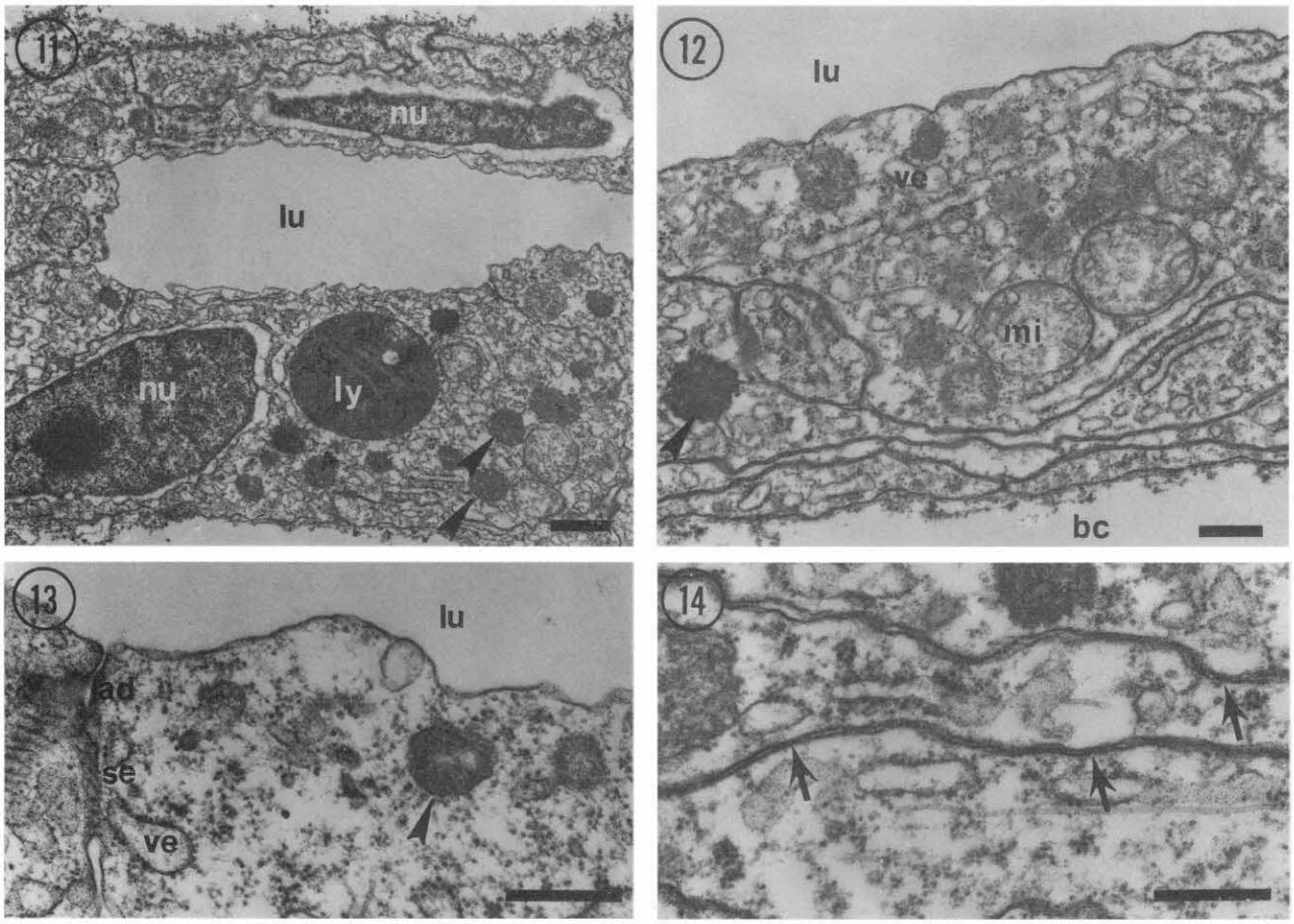
Figures 7–10. Transmission electron micrographs of sections through the somatocoels of aspidochirotid auriculariae.

Figure 7. The epithelium lining the lumen (lu) of the somatocoel is composed of squamous and columnar monociliated cells. Scale bar = 1.0 μm; bc, blastocoel; ci, cilium; nu, nucleus; pc, paracellular space.

Figure 8. Large paracellular spaces (pc) lead to channels suggestive of transfer tubules (arrowhead). Scale bar = 0.5 μm; lu, lumen of somatocoel; mi, mitochondrion; nu, nucleus; se, grazing section through a subapical septate junction; ve, vesicle; arrow indicates apical coated pit.

Figure 9. Somatocoel epithelial cells are joined by apical adhering junctions followed by subapical septate junctions (arrowheads). Basal junctions are absent between some cells (arrow). Scale bar = 0.5 μm; bc, blastocoel; lu, lumen of somatocoel, mi, mitochondrion; pc, paracellular space.

Figure 10. The basal portion of some somatocoel cells are interconnected by tight junctions. Arrowheads indicate points of membrane contact. Scale bar = 0.1 μm; bc, blastocoel; pc, paracellular space.



Figures 11–14. Transmission electron micrographs of tangenital sections of the hydrocoel region of the axohydrocoel of field-collected synaptid auricullariae.

Figure 11. Hydrocoel epithelial cells have elongated nuclei (nu), numerous putative small (500–750 nm in diameter) lysosomes (arrowheads), and larger lysosomes (ly). Scale bar = 1 μm; lu, lumen of hydrocoel.

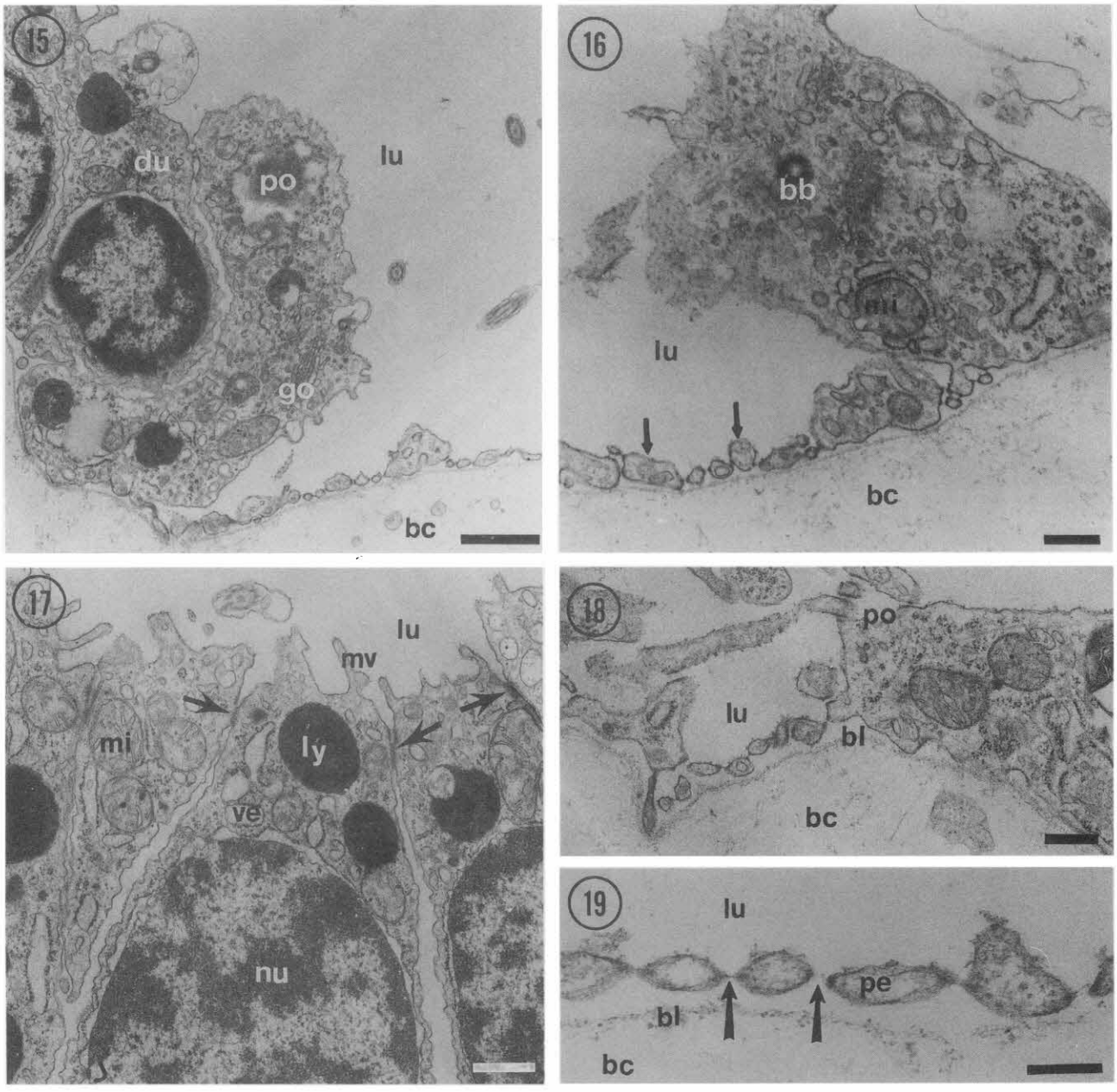
Figure 12. Hydrocoel epithelial cells show extensive basal interdigitation. Basally located mitochondria (mi) are often associated with these digitations. Scale bar = 0.5 μm; bc, blastocoel; lu, lumen; ve, vesicle; arrowhead indicates putative lysosome.

Figure 13. Apical adhering junctions (ad) are followed by septate junctions (se). Scale bar = 0.5 μm; lu, lumen; ve, vesicle; arrowhead indicates putative lysosome.

Figure 14. Basal junctions are similar to vertebrate tight junctions. Arrows indicate definitive points of membrane contact. Scale bar = 0.5 μm.

Ruppert, 1993). Crinoids differ from other echinoderms because the archenteron separates into anterior and posterior cavities. The anterior cavity gives rise to the enteric sac and the axohydrocoel. The posterior cavity gives rise to the left and right somatocoels. A connection, which is maintained in the adult, is secondarily established between the somatocoels and the axohydrocoel.

In noncrinoid larvae, the left anterior coelom separates from the archenteron and is the primordium of the paired somatocoel, hydrocoel, and axocoel. The somatocoel primordium eventually loses its connection to the anterior coelom, but the axocoel and hydrocoel remain united. The axohydrocoel establishes a duct that opens to the exterior via the dorsal pore. In crinoids, asteroids, ophiuroids, and echinoids, the undivided axohydrocoel and its union with the exterior are retained through metamorphosis via the stone canal and madreporic pores. The adult stone canal, which may originate from the axocoel, provides a link between the axial gland coelom and the hydrocoel-derived water vascular coelom. The madreporite opens internally into the ampulla (an axocoelic derivative), which joins the axial coelom to the stone canal. A stone canal and madreporite and, according to Erber (1983), a rudimentary ampulla all develop in juvenile



Figures 15–19. Transmission electron micrographs of podocytes lining the axocoelic region of the axohydrocoel of several different auricularia larvae.

Figure 15. Longitudinal section of the axocoel of a field-collected aspidochirotid larva shows the transition of the cuboidal mesothelium of the duct (du) to the mesothelial podocytes (po) lining the lumen (lu) of the axocoel. Scale bar = 1 μm; bc, blastocoel; go, Golgi body.

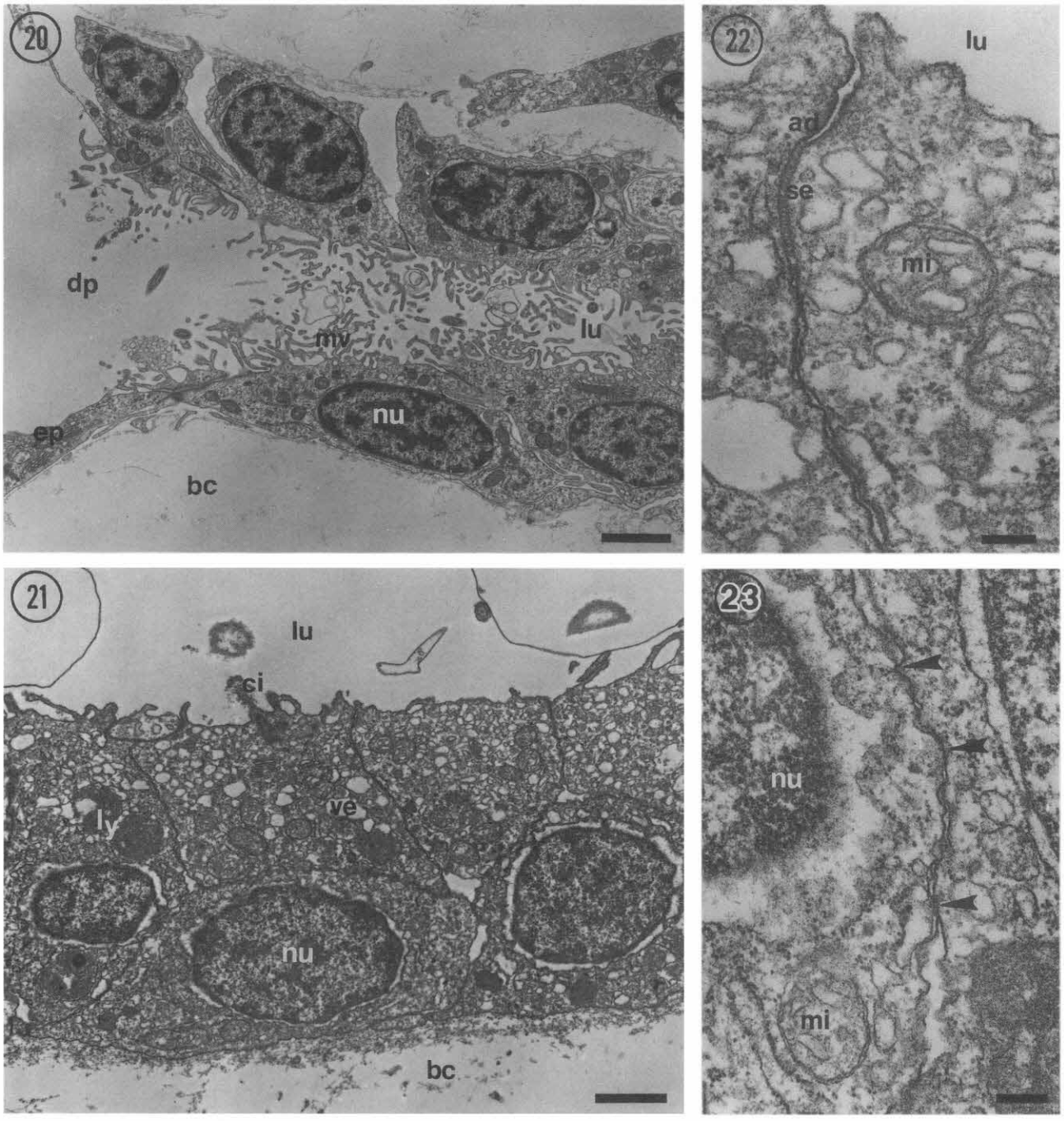
Figure 16. Field-collected synaptid auricularia podocyte. Podocytes are defined by the presence of foot processes or pedicels (arrows). Scale bar = 0.5 μm; bb, ciliary basal body; bc, blastocoel; lu, axocoel lumen.

Figure 17. Apical region of podocytes in a field-collected aspidochirotid auricularia showing apical junctions (arrows) and microvilli (mv). Scale bar = 0.5 μm; lu, lumen; ly, lysosome; mi, mitochondrion; nu, nucleus; ve, vesicle.

Figures 18–19. Basal region of field-collected aspidochirotid auricularia podocytes (po) showing pedicels that provide gaps or fenestrations (arrows) in an otherwise continuous epithelium. Pedicels that are not joined by filtration slit membranes are bridged only by the basal lamina (bl) supporting this mesothelium. Between pedicels the lumen (lu) of the axocoel and the blastocoel (bc) are separated only by these extracellular connective tissue layers.

Figure 18. Scale bar = 0.5 μm.

Figure 19. Scale bar = 0.25 μm.



Figures 20–23. Transmission electron micrographs of the axocoelic duct of an *H. grisea* larva (20) and a field-collected synaptid auricularia larva (21–13).

Figure 20. Longitudinal section through the duct that opens to the exterior via the dorsal pore (dp). Duct cells are cuboidal monociliated epithelial cells that have basal nuclei (nu) and apical microvilli (mv). Scale bar = 2 μm; bc, blastocoel; ep, epidermis; lu, lumen of duct.

Figure 21. Cells lining the duct lumen (lu) possess numerous apical cellular vesicles (ve) and putative lysosomes (ly). Scale bar = 2 μm; bc, blastocoel; ci, cilium; nu, nucleus.

Figure 22. Shows apical adhering (ad) and septate (se) junctions. Scale bar = 0.25 μm; lu, lumen; mi, mitochondrion.

Figure 23. Shows basal tight junctions. Arrowheads indicate areas of membrane contact. Scale bar = 0.25 μm; mi, mitochondrion; nu, nucleus.

holothuroids, but the fate of the larval axocoel reported here is unknown at present.

The ultrastructure of holothuroid larval somatocoels is similar to that of asteroid larvae (unpubl. data) and suggests a transportive function for this epithelium. The presence of paracellular spaces extending from the basal lamina towards the cell apex and the absence of basal junctions in some areas suggest that this epithelium is transporting substances from the blastocoel into the cell or indirectly into the coelom (Berridge and Oschman, 1972). This hypothesis is supported by the presence of apical septate junctions, putative transfer tubules, endocytic and coated pits on the lateral membranes, and numerous vesicles.

The ultrastructure of the hydrocoel also indicates a transporting function. Deeply folded lateral and basal membranes and associated basal mitochondria are typical of osmoregulatory epithelia (Berridge and Oschman, 1972). The presence of occluding apical septate junctions and basal tight junctions and the paucity of apical microvilli suggest that the presumed transport is basally located.

Like that of asteroid larvae, (Ruppert and Balser, 1986), the holothuroid axocoel mesothelium is composed, in part, of podocytes. The presence of podocytes and of the open ciliated duct to the exterior indicates a pressure-driven filtration system and suggests an excretory function (Ruppert and Smith, 1988). Although, at present, no physiological data are available, we predict that blastocoelic fluid is filtered across the basal lamina underlying the podocytes, through the fenestrations between pedicels, and into the coelomic cavity of the axohydrocoel. Modification of the primary urine could be accomplished by the axohydrocoel and duct mesothelium. The occurrence of apical microvilli, endocytic and coated pits, and numerous apical vesicles suggests that the duct epithelium is transporting substances from the lumen.

Results presented in this paper indicate that holothuroid auricularia larvae possess a left axohydrocoel morphologically similar to that of other echinoderm larvae. In contrast, Smiley *et al.* (1991) argue that holothuroids do not have an axocoel and, thus, the anterior coelom is composed of the hydrocoel and the somatocoel primordia only. They base this hypothesis principally on the unusual ultrastructure of the madreporic vesicle and the presumed lack of axocoelic derivatives in the adult (*i.e.,* the axial gland). Unlike the madreporic vesicle (dorsal sac, pulsatile vesicle), which is a muscular sac in other echinoderms, the madreporic vesicle of holothuroids, as described by Smiley (1986), is a syncytium and probably functions in the secretion of the madreporite ossicles.

Smiley (1989) speculates that axocoelic functions such as larval attachment are assumed by the hydrocoel and that the axocoel of other echinoderms arose from differentiation of the epithelium forming the buccal podia. He supports this idea with the fact that the pentactula (as well as juveniles of direct developers) use the buccal podia as attachment organs. The undivided, undifferentiated holothuroid axohydrocoel is regarded as a hydrocoel only. In his view, the axocoel of other echinoderms evolved later from the plesiomorphic holothuroid "hydrocoel."

The discovery of a morphologically distinct region of the holothuroid larval axohydrocoel, combined with the positional and ultrastructural agreement of that region with the axocoelic portion of the left axohydrocoel of other echinoderms, reopens the question of an axocoel in holothuroids. Data presented here show that holothuroid auricularia larvae develop an axohydrocoel, axocoelic duct, and open dorsal pore. The position of the axocoel and duct between the dorsal pore and hydrocoel, the connection of the axocoel to other larval coeloms, and the presence of podocytes indicate the existence of an axocoel in holothuroid larvae.

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