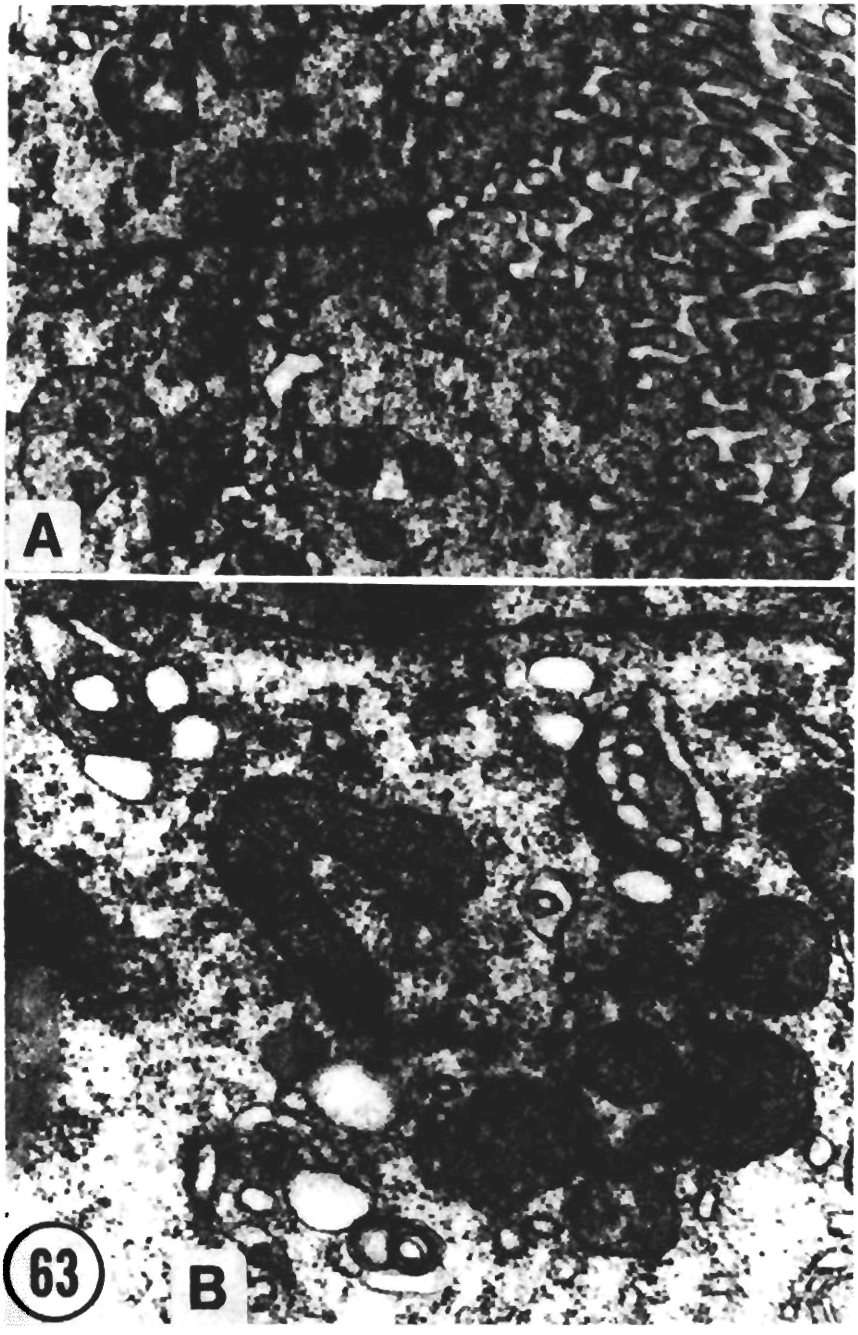


Fig. 63. Apical region of gastric cecal cells of *Artemia*. (From Hootman and Conte, 1974.) **A:** Cell surfaces and microvilli (mv) are less rigidly structured than are those in cells of the midgut. ×26,000. **B:** Golgi complexes (G) and mitochondria (m) are numerous in the apical cytoplasm. ×35,000. SD, septate desmosome.

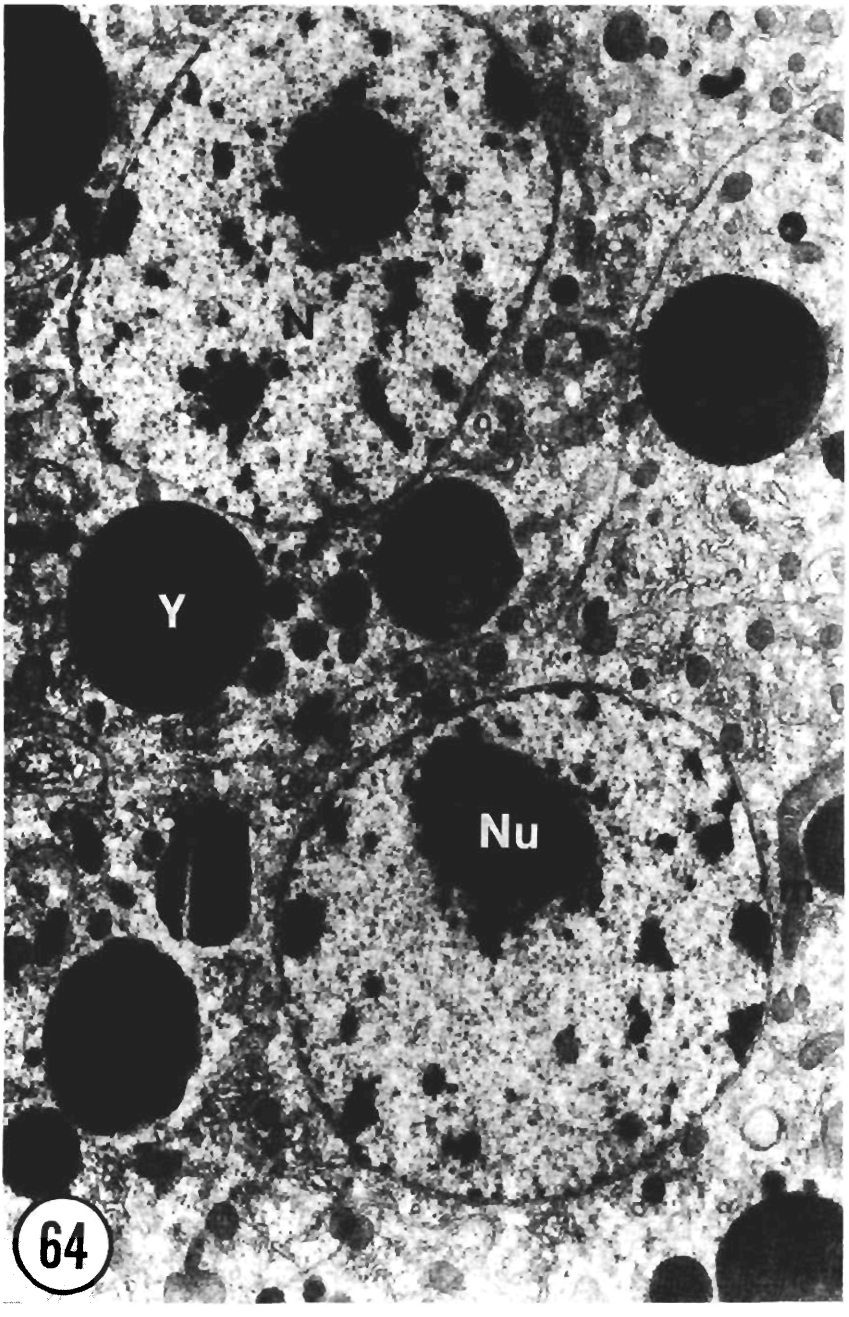


Fig. 64. Transverse section through central regions of two gastric cecal cells of *Artemia*. (From Hootman and Conte, 1974.) m, mitochondrion; N, nucleus; Nu, nucleolus; Y, yolk droplets. ×8,400.

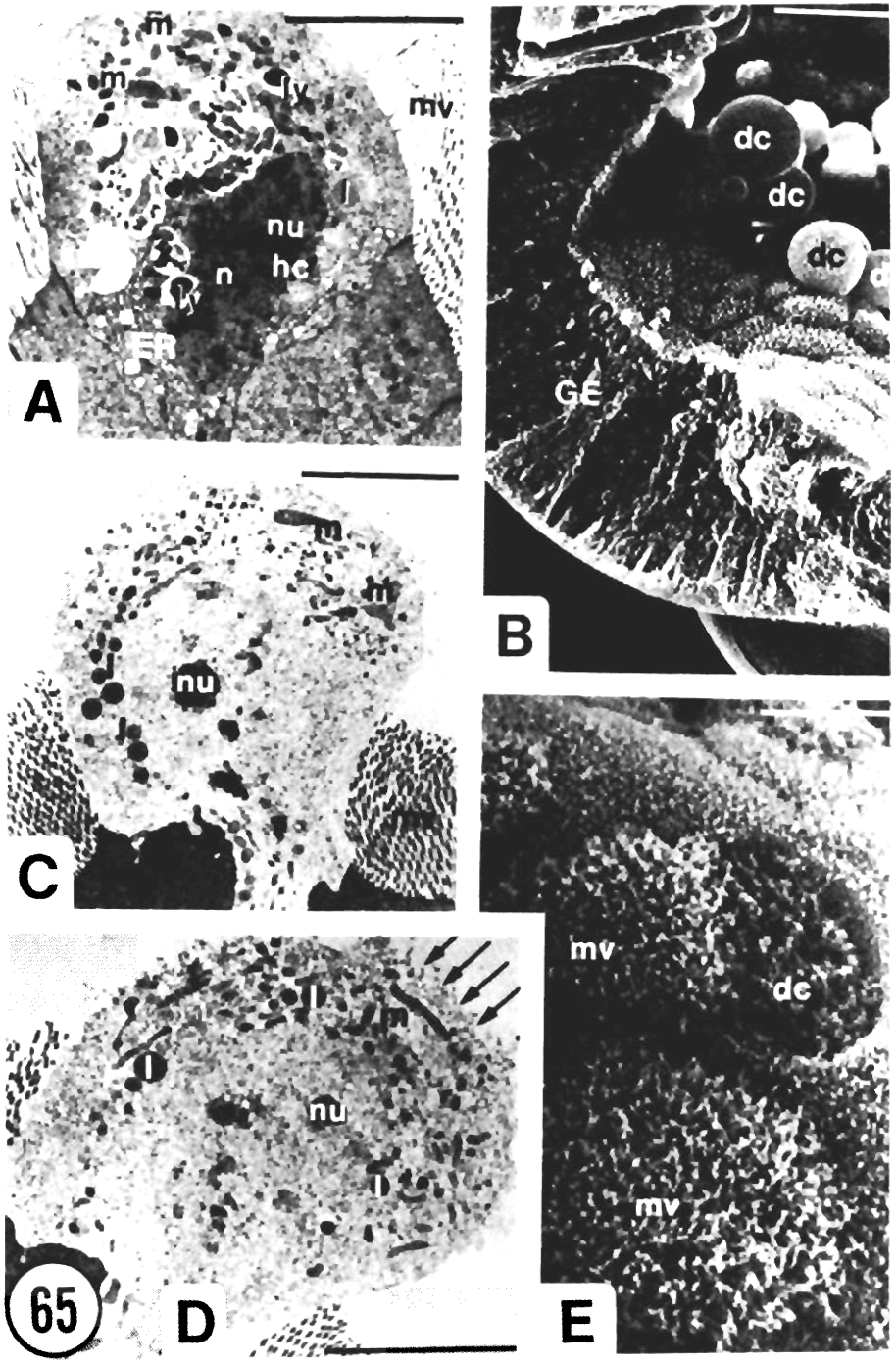


Fig. 65. Degeneration of cecal cells in *Artemia*. (From Schrehardt, 1987b.) **A:** Beginning degeneration of a hepatopancreatic cell. Scale bar = 5 μm. **B:** SEM of degenerating cells. Scale bar = 40 μm. **C:** Advanced degeneration of a hepatopancreatic cell. Note electron-transparent cytoplasm and degeneration of organelles. Scale bar = 5 μm. **D:** More advanced degeneration in epithelial cell. Note disintegration of the apical cell membrane (arrows). Scale bar = 5 μm. **E:** Cytoplasmic rudiments of degenerated cell after releasing of the cell body. Scale bar = 10 μm. dc, degenerating cell; ER, endoplasmic reticulum; GE, gland epithelium; hc, heterochromatin; l, lipid; ly, lysosome; m, mitochondrion; mv, microvilli; n, nucleus; nu, nucleolus.

the anus of a 6-mm animal; Foster and Wolfe, 1986). This "membrane" (Fig. 67A,B) is actually produced by the cells of the midgut, not in any specialized region but by cells all along the length of the midgut (Snyder and Wolfe, 1980; Foster and Wolfe, 1986). The secretory droplets seen in midgut cells probably consist of mucus, which acts as a lubricant for the food mass (Foster and Wolfe, 1986), and possibly explains why Foster and Wolfe (1986) could not detect any fibrillar pattern to the peritrophic membrane, whereas Schlecht (1979) documented extensive fibrillar patterning in the peritrophic membrane of *Leptestheria*. The peritrophic membrane surrounds fecal matter in the gut, and possibly aids with its elimination.

The interesting process of taking in water via the rectum, or "anal drinking," occurs at least in some anomopods (Fryer, 1970; Günzl, 1991), some of which have a diverticulum partially lined with cuboidal epithelial cells stemming from the posterior region of the midgut. It occurs also in laevicaudatans (personal observation), which have no posterior gut diverticulum, and in *Artemia* (Croghan, 1958d). Although not entirely understood, the process may aid in maintaining body turgor pressure and in the retention of digestive products, which otherwise would be lost with defecation, by recirculating water and ingested particles into the anterior region and even the ceca of some species where they can be absorbed (Fryer, 1970). Hypo-osmotic regulation has been suggested for some anostracans (Croghan, 1958d), whereas Günzl (1991) suggests removal of excretory products.

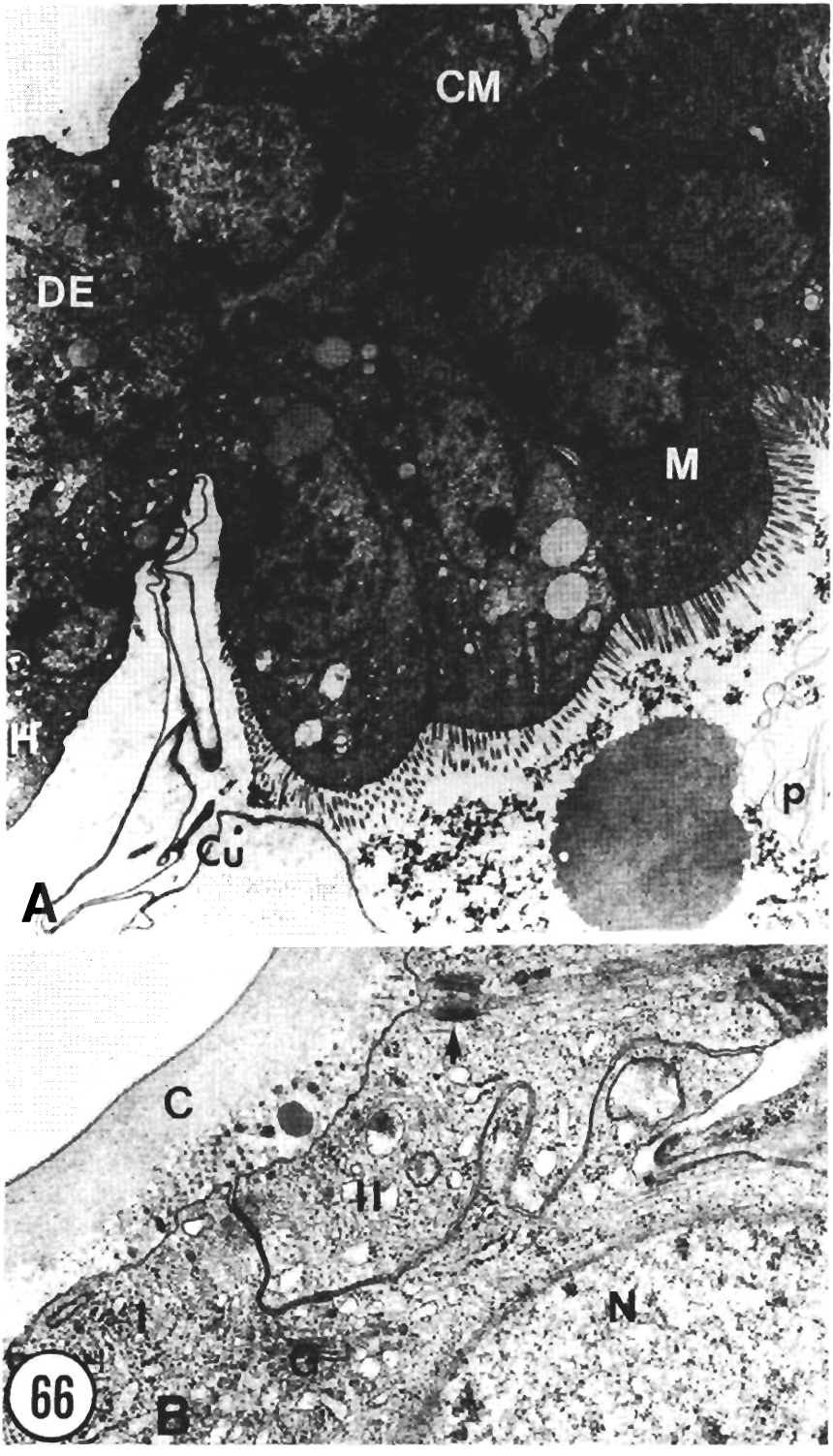
Hindgut

Columnar epithelium of the midgut stops abruptly, marking the beginning of the ectodermally derived (and thus cuticle-lined) hindgut (Fig. 66A,B). In *Artemia,* the cuticle is as thin as in the esophagus (approximately 0.25 μm; Schrehardt, 1987b). Epithelial cells are again cuboidal, as in the esophagus, and almost identical in their ultrastructure and in the surrounding muscle layers.

Both foregut (esophagus) and hindgut basal lamina are single-layered, and the cuboidal epithelial cells that underlie the cuticle contain less lipid and glycogen than the midgut cells (Schrehardt, 1987b). There are also occasional tendinous cells for the attachment of the gut to the dilator musculature (Criel, 1991a: fig. 8).

RESPIRATORY SYSTEM AND OSMOREGULATION

Considering that the name Branchiopoda (literally "gill footed") stems from the presumed ability of these crustaceans to exchange oxygen across limb surfaces, it is surprising how little is known about gas exchange across the cuticle. Physiological studies on respiration abound (e.g., for *Artemia* see Eriksen and Brown, 1980, and reviews by Clegg and Conte, 1980; Decleir et al., 1980; Moens et al., 1991; and papers cited therein), and many have assumed that gas exchange occurs across the very thin cuticle of the epipods of the thoracic appendages. Indeed, these structures are often referred to as gills or branchiae, and the constant rhythmic beating of the thoracic limbs in most taxa has been cited as evidence of the need to produce a constant flow of oxygenated water over the limb surfaces (in addition to bringing in food particles in some taxa). However, there is a growing body of evidence, some of which has existed for quite some time, suggesting that the thoracic epipods cannot bear the full responsibility for respiration and indeed may be less well equipped for this role than other parts of the body. Peters (1987) has pointed out that in *Daphnia,* although the cuticle of the "branchial sacs" (epipods) is very thin (0.2–0.5 μm) compared to other parts of the leg (the cuticle of which is usually 1–3 μm thick), the epithelium underlying this cuticle may be 15–20 μm thick, compared to ordinary epithelial layers elsewhere in the body that are only 3–5 μm thick. Thus, total diffusion distance is greater here, and it seems unlikely that these epipods could be the primary site of gas exchange. Physiological studies also support the idea that thoracic limb


CM
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epipods are not crucial to gas exchange. For example, the rate of limb beating in *Daphnia* is independent of ambient oxygen concentrations, and oxygenation of the hemolymph does not increase with an increase in limb activity (see Peters, 1987). In a now-famous series of papers on *Artemia,* Croghan (1958a–d) demonstrated that the cuticle of the epipods is extremely permeable to salts, and is osmoregulatory in function rather than respiratory, and he also demonstrated (1958c) that "burning" the surface of the gills with $KMnO_4$ did not unduly affect survival of animals in isotonic sea water, some surviving a week or more despite the "browning and distortion of the epithelium of the first ten pairs of branchiae" (Croghan, 1958c: 236). However, surviving *Artemia* did lose the ability to osmoregulate. This finding has been supported by Holliday et al. (1990), who demonstrated by silver staining of the epipods (Fig. 68A–C) that these structures are much more permeable than any other part of the body to chloride and/or silver ions (although the maxillary gland and midgut were also implicated in osmoregulation by having high Na^+/K^+–ATPase enzyme-specific activities). Staining of the epipods occurred in a reticulated pattern, possibly suggesting the pattern of the epithelial cells underlying the cuticle (see discussion of light and dark cells of the epipod epithelium). Moreover, crude homogenates of the epipods had very high Na^+/K^+–ATPase enzyme-specific activity that increased in proportion to the salinity of the medium (and thus in proportion to the need to transport ions out of the epipods). Analyses of hemolymph ions and transepithelial potential differences showed that chloride is transported out, whereas sodium is "very close to electrochemical equilibrium" on either side of the cuticle, and Holliday et al. (1990) noted the apparent functional similarity of the *Artemia* cells to the branchial chloride cells of teleost fishes. Obviously, oxygen exchange in *Artemia* must occur across other areas of the integument, as suggested to be the case in *Daphnia* (Peters, 1987), whereas ion transport occurs almost exclusively across the epipod cuticle (and to some extent across the

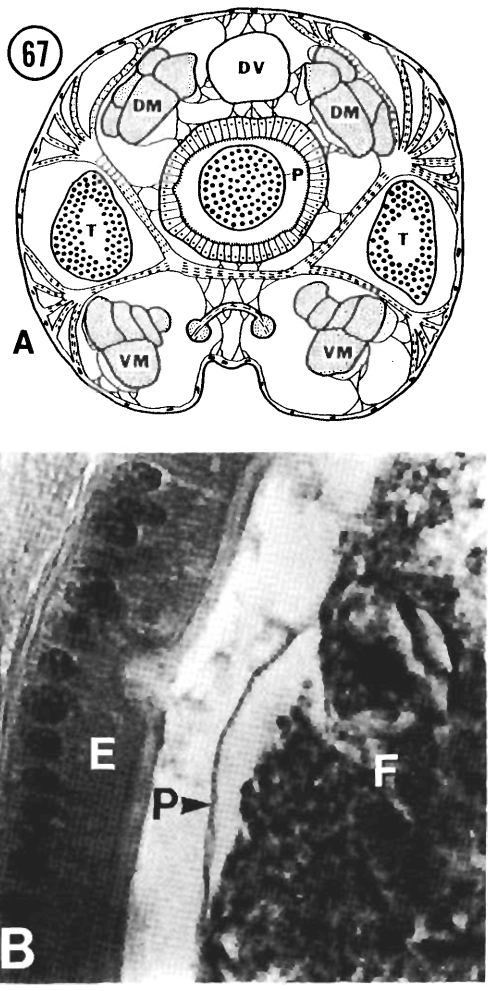

Fig. 67. The peritrophic membrane of *Artemia*. (After Snyder and Wolfe, 1980.) **A:** Diagram of cross section through second abdominal segment of male showing peritrophic membrane (P) within gut. **B:** Longitudinal section of gut showing peritrophic membrane (P) between simple columnar epithelial cells (E) and food mass (F). DM, dorsal longitudinal muscles; DV, dorsal vessel (heart); T, testes, VM, ventral longitudinal muscles.

Fig. 66. Abrupt transition of midgut and beginning of hindgut in *Artemia*. **A:** Median sagittal section showing posterior of midgut and start of hindgut. (From Hootman and Conte, 1974.) **B:** Hindgut epithelial cells and overlying cuticle. (Courtesy of G. Criel.) Arrow, dense apical rod characteristic of tendonal cells; C, cuticle; CM, circular muscle; Cu, cuticle lining hindgut; DE, dorsal ectoderm; G, Golgi complex; H, hindgut; I, gut epidermal cell; II, tendonal cell; M, midgut; N, nucleus; p, peritrophic membrane.

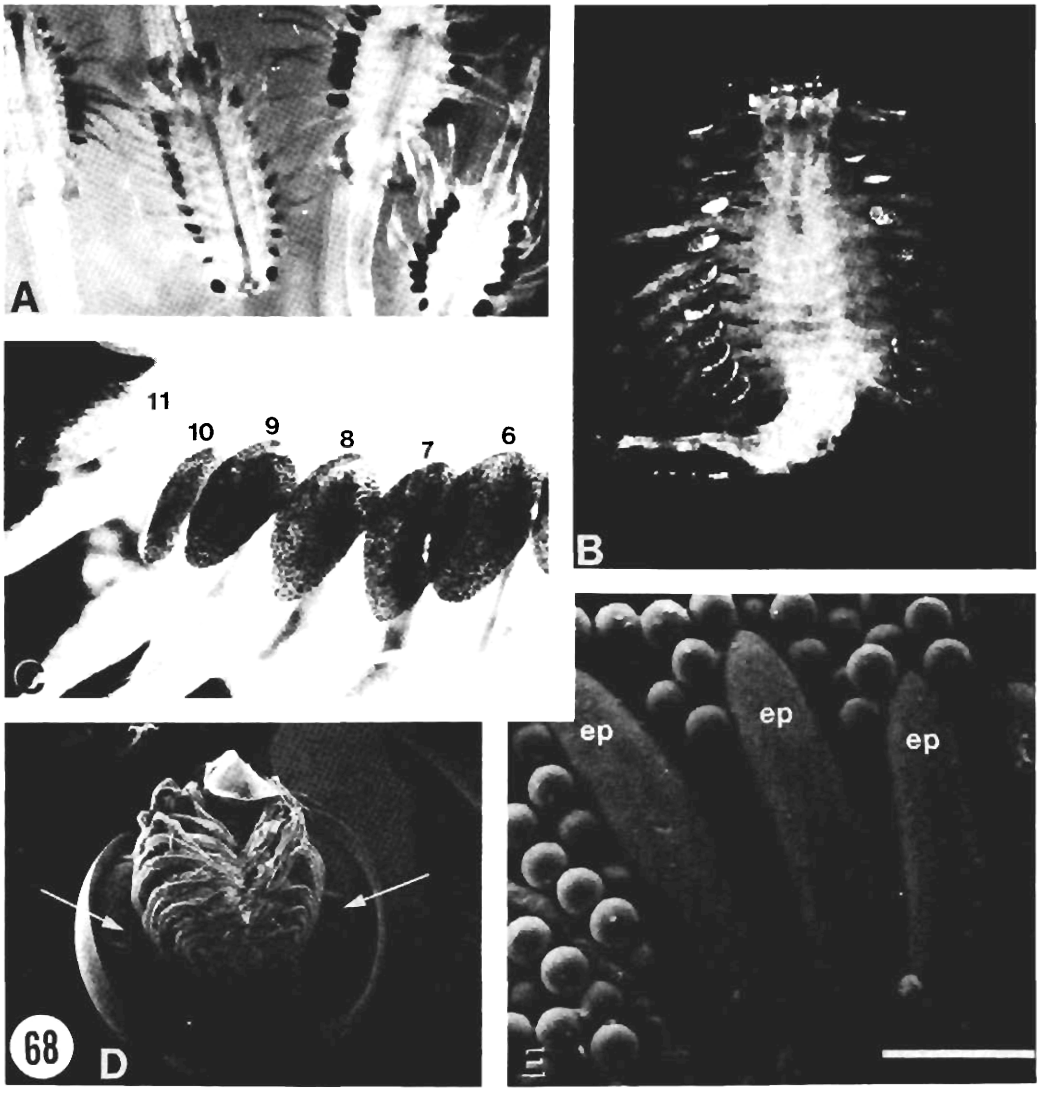

Fig. 68. Presumed respiratory and osmoregulatory surfaces. **A:** Dorsal view of four adult *Artemia* with silver-stained epipods, indicating permeability to salts. Note darker staining of epipods of two animals at right, caused by acclimation to higher salinity (400% sea water) (compared to 50% sea water for two animals on left) prior to staining. (Courtesy of C. Holliday.) **B:** Ventral view of young *Artemia* with thoracic limb epipods (arrows) silver-stained. (Courtesy of C. Holliday.) **C:** Thoracic limb epipods 6–11 showing reticulated staining pattern after silver staining. Note 11th pair never stains. (Courtesy of C. Holliday.) **D:** Laevicaudatan *Lynceus gracilicornis*, ventral view with "respiratory membrane" (inner layer of cuticle) showing (arrows). **E:** Inflated epipods (ep) of the spinicaudatan *Leptestheria dahalacensis*. (From Scanabissi Sabelli and Tommasini, 1990b.) Scale bar = 0.3 mm.

midgut and maxillary gland epithelium) in adults. Thoracic "respiratory" epipods are lacking in the Onychopoda and Haplopoda (*Leptodora*) (and on some thoracic limbs of the ctenopod *Holopedium*). In these taxa, gas exchange obviously occurs across the thin cuticle of some other area of the body. Finally, some groups use the epipods as reproductive structures, storing the ripe eggs. While this is hardly a sacrifice in the Notostraca, where it could be argued that there are plenty of remaining epipods that could handle respiratory demands, it is harder to explain the benefit to leptestheriid conchostracans, which employ

four or five epipods per side as egg storage and transfer devices (Tommasini and Scanabissi Sabelli, 1989). If the epipods were critical to respiration, then committing this many on each side of the body would seem a high price.

We are left with the assumption that oxygen uptake and carbon dioxide elimination are occurring by way of passive diffusion (as in all Crustacea; McMahon and Wilkens, 1983) across the general body surface, possibly over the thin, permeable cuticle overlying the epipods but more likely across the cuticle of other parts of the body. One such area is the thin layer of cuticle that lines the inner surface of the carapace in the bivalved taxa (Fig. 68D) and in the Notostraca. This thin layer has been termed a respiratory membrane or respiratory organ in some conchostracans and cladocerans and has been suggested to be a probable site for gas exchange (e.g., Kaestner, 1970; Schram, 1986). Respiratory areas on the inner surface of the carapace are known in branchiurans (e.g., McLaughlin, 1980, 1983), and something similar may occur in branchiopods; patterns of blood flow within the carapace folds of the Notostraca were diagramed as long ago as 1841 (Zaddach, 1841: pl. 1). The location of the inner carapace fold would seem to favor such a role, since fresh oxygenated water brought into the area between the valves would directly contact this thin layer of cuticle. This function has yet to be demonstrated. In larval stages of *Artemia,* the cuticle may be only 0.1–0.3 μm thick (Freeman, 1989), and epipods are not yet developed. Gas exchange must occur across the general body surface, and this is probably the case in many of the very small branchiopods.

However it arrives, once in the hemolymph, oxygen can then bind to the extracellular respiratory pigments, which in branchiopods consist of three structurally different hemoglobins that range from 230,000–700,000 molecular weight units (Weber, 1980). Although a review of the structure of these pigments is beyond the scope of this treatise, I mention them briefly here because they are of phylogenetic and comparative importance, since they differ from known respiratory pigments in all other arthropods. In Terwilliger's (1980) review of invertebrate hemoglobins, he noted that hemoglobin is known in the Anostraca, Notostraca, Conchostraca (spinicaudatans only, although laevicaudatans certainly appear red and probably contain hemoglobin also; personal observation), and anomopod cladocerans (Terwilliger, 1980: table 2). Branchiopod hemoglobin is polymeric and similar in some ways to that of several insects. For example, it contains 1 heme per 17–20,000 grams of protein. However, branchiopod hemoglobin forms larger polymeric aggregates, not known among insects, and there is tremendous variation in molecular weight of the smallest subunit, ranging from 15,500 in the spinicaudatan *Cyzicus,* 23,000 in the cladoceran *Moina,* 30–35,000 in the notostracan *Lepidurus,* to 125,000 in *Artemia.* It is possible that branchiopod hemoglobin is unique among arthropods (Terwilliger, 1980) in not being divisible into heme-containing subunits of 15–17,000 dalton units.

In cysts or resting eggs, which in anostracans, notostracans, and (to a lesser extent) conchostracans have been shown to be remarkably resistant to extreme temperatures, low pressure, extreme dehydration, and irradiation (Moens et al., 1991) during the resting or "dormant" state, respiratory metabolism is either completely halted (Clegg and Conte, 1980) or occurs at very low levels. This fascinating phenomenon is not reviewed here; for reviews of cyst metabolism and respiration (mostly in *Artemia*) see Clegg and Conte (1980), Clegg and Jackson (1989), Moens et al. (1991), and papers in Persoone et al. (1980) and Decleir et al. (1987).

The "respiratory" epipods of the thoracic appendages are treated next, but as osmoregulatory rather than respiratory structures in light of the above discussion.

Thoracic Limb Epipods

The "respiratory" epipods (= branchiae, gills, metepipods, metepipodites) are naked, balloonlike processes that stem from the bases

of the thoracic appendages just proximal to the exopod. They may be oval and flattened, or elongate and nearly tubular (Fig. 68E). They have been illustrated for many taxa and are easily recognizable. In *Artemia,* the epipods have been described as having a "finely dimpled" surface (Copeland, 1967; Moens et al., 1991), but that condition might result from slight wrinkling during critical-point drying (see Felgenhauer, 1987), because in some taxa the surface of the epipods appears smooth (e.g., Fig. 68E). Apparently the cuticle overlying the epipods is extremely thin, only 0.2–0.5 μm thick on the epipods of *Daphnia* (Peters, 1987). Additionally, the cuticle here may not contain all three layers of the typical crustacean integument (see Integument).

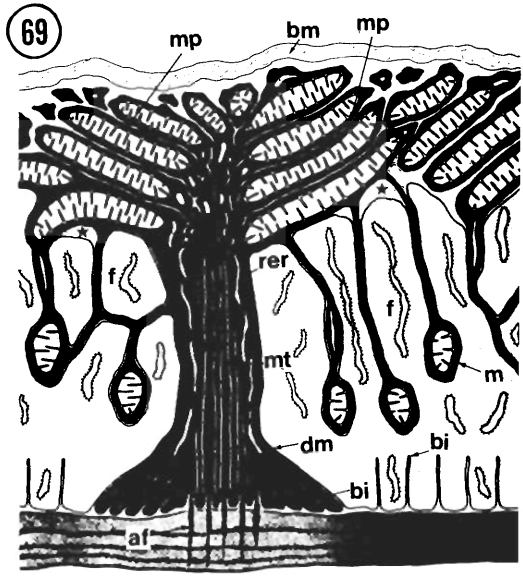

Fig. 69. Schematic view of "mitochondrial pump" of thoracic epipod epithelium of *Artemia*. (After Copeland, 1967.) Cuticle is at bottom of picture. af, anchor fibers connecting cell to cuticle; bi, basal indentations of light and dark cell membranes; bm, basement membrane; dm, dense membrane between light and dark cells; f, light cell interdigitation with rough ER; m, mitochondria; mp, mitochondrial pumps; mt, microtubules and microfibrils; rer, rough endoplasmic reticulum; star, intercellular spaces.

Light and Dark Cells of the Epipod Epithelium

A single layer of epithelial cells lies just internal to the epipodal cuticle. Copeland (1967) classified these cells in *Artemia* into two types based on electron density: dark cells, which contain numerous mitochondria, and light cells, with few mitochondria (Fig. 69). The dark and light cells occur in approximately equal numbers and are arranged in "an alternate interdigitating manner" (Copeland, 1967; Criel, 1991a). Both cell types have marked indentations of the plasma membrane of the cell surface that faces the cuticle, but otherwise they differ markedly in their morphology.

Dark cells contain large numbers of mitochondria, some of which are very flattened and in close association with the cell membrane, forming the "mitochondrial pumps" of Copeland (1967). Dark cells are more or less columnar, and in frontal sections they appear to surround the light cells. Consequently, their microtubules, which are more numerous than in the light cells, and microfibrils are oriented more or less perpendicular to the cuticle (Fig. 69), to which they appear to be anchored by thin fibers that extend from distal infoldings of the plasma membrane into the cuticle. Dark cell cytoplasm is separated from that of the light cell (apically, prior to the first intracellular interdigitation) by the two apposed plasma membranes; the space between these membranes, which extends from the cuticular area to the level of the first cellular interdigitation (Copeland, 1967), contains a dense material. At the cuticular end of this dense region, the membranes are connected to one of the basal indentations (an unfortunate term, as the indentations are at the apical end of the cell) by a "simple, compact desmosome (zonula occludens)" (Copeland, 1967). Further from the cuticular surface, in the area of interdigitation of dark and light cell processes, the dense material between the membranes exhibits periodicity more characteristic of septate desmosomes (Copeland, 1967). Thin cytoplasmic processes, recognizable as belonging to dark cells by their electron density and numerous mitochondria, extend "be-

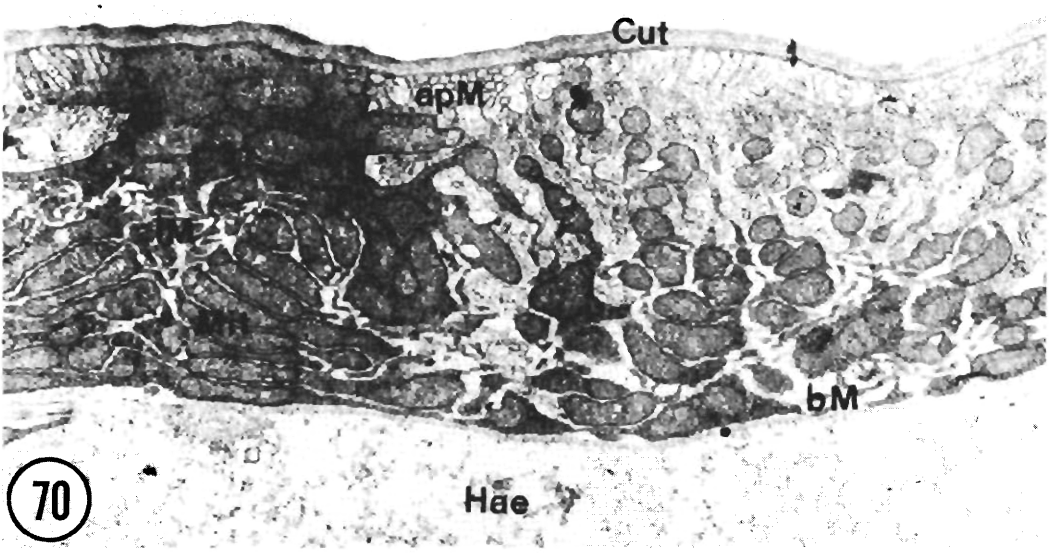

Fig. 70. Osmoregulatory epithelium of thoracic limb epipod of *Artemia*. (From Conte, 1980.) Transverse section through epipod of adult. Note membrane amplification (apM) and prominent array of mitochondria (Mit) adjacent to hemocoelic cavity (Hae). bM, basement membrane; Cut, cuticle; lM, lateral membrane.

tween evaginations of the light cell" (Copeland, 1967: 370) and surround similar processes of the light cells. Only the dark cells have sinusoids (extensions of the extracellular space) and are in direct contact with the circulating hemolymph.

The mitochondrial pumps of *Artemia* dark cells were defined by Copeland (1967: 380) as "a metabolically linked ion pump located in the cell plasma membranes intimately associated with the mitochondrial membranes at a distance of several hundred angstroms or less." These areas are characterized by the flattened mitochondria, the shape of which affords a larger surface area for association with lamellar membranes (Figs. 70, 71). The lamellar spacing is remarkably constant, ranging from 15 to 20 nm, suggesting to Copeland (1967) some sort of physical binding or molecular attraction between these layers. The gap between the lamellar membrane and the outer mitochondrial membrane is also constant (10–15 nm).

Light cells appear more cuboidal, lack mitochondrial pumps, contain fewer mitochondria (the ratio of dark to light mitochondria is 15 or 20:1), do not fix well (possibly indicating that they are more highly hydrated; Copeland, 1967), and their apical plasma membrane indentations are less regularly organized than those of dark cells. However, they have a more regular pattern of RER that could serve a transfer function (Copeland, 1967). Light cells are always separated from the hemocoel by at least a thin sheet of dark cell cytoplasm, and they contact the hemolymph only indirectly, via intracellular canaliculi that penetrate the dark cells.

Although *Daphnia* epipod epithelium also contains dark and light cells, the former with many mitochondria and the latter with few, as in *Artemia,* the ultrastructure of these cells differs from the above description (Kikuchi, 1982a,b, 1983, 1984). Osmoregulatory problems faced by *Daphnia* and other freshwater branchiopods are opposite to those faced by

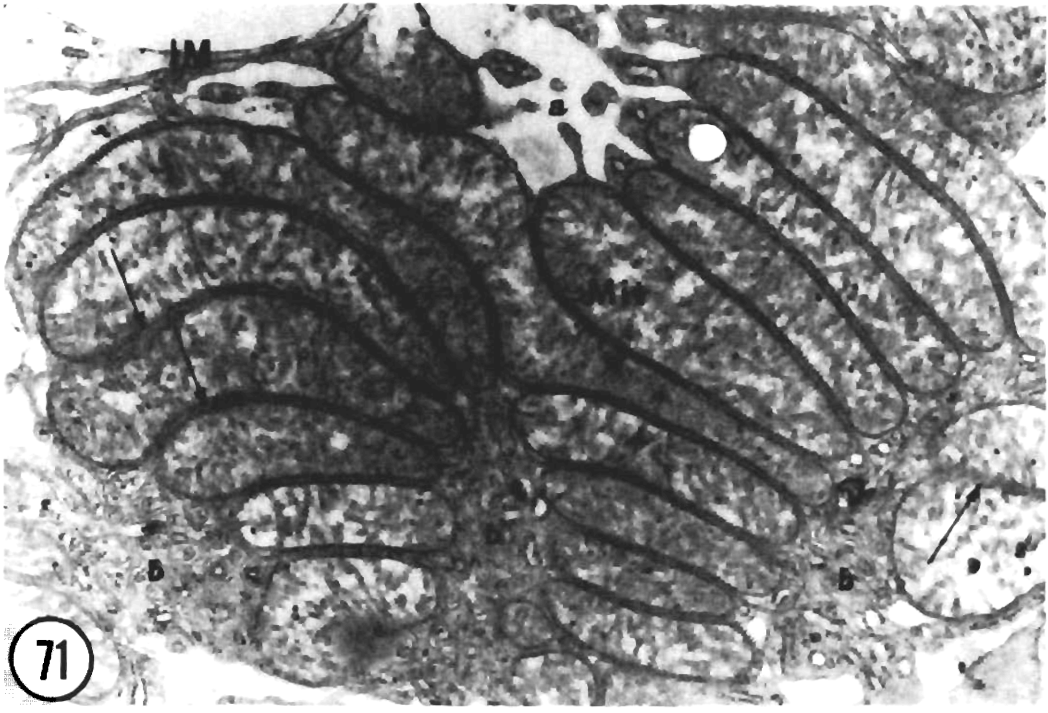

Fig. 71. Detail of mitochondrial pump and associated infoldings of plasma membrane in "dark" cell of *Artemia* epipod. (From Conte, 1980.) Note unique array of mitochondria and juxtaposition of plasma membranes. a, sinusoidal system of "dark" cell; b, tubular labyrinth; lM, lateral membrane; Mit, mitochondria; arrows, lamellar spaces.

brine-inhabiting *Artemia*. Water entering by osmosis must be removed, and internal ion concentrations must be maintained by inward transport of ions. This has been demonstrated for Na^+ uptake in *Daphnia* (Stobbart et al., 1977), and the site of inward transport has been assumed to be the epipod epithelium (Gicklhorn and Keller, 1925; Stobbart et al., 1977). Consequently, differences in the ultrastructure of the transport mechanism of *Daphnia* and *Artemia* might be expected.

In epipod epithelial cells of *Daphnia,* there is an elaborate system of cytoplasmic tubules of two types. Large (about 130 nm diameter) tubules contain flocculent material, have a spiraled, ridgelike surface coat (Kikuchi, 1982a), and are directly connected with the basal and lateral cell membranes. These were regarded by Kikuchi (1982a, 1983) as extensions of the basal and lateral cell membranes. Therefore, the lumen of these tubules corresponds to the extracellular spaces and surface coat of the cell membrane. Smaller cytoplasmic tubules (about 70 nm diameter) occur in bundles and seem to be smooth-surfaced ER. The dark cells have a unique cell membrane lined with repeating subunits on the cytoplasmic side of the apical cell border (Kikuchi, 1982b, 1983), and are known to accumulate chloride ions on their apical surfaces beneath the cuticle (Kikuchi, 1983). The apical membrane of the dark cells forms microvilli in the "subcuticular space" (Kikuchi, 1982b), unlike *Artemia*. There are microvillous projections on the lateral and basal surfaces of dark cells as well. And although the dark cells have

numerous "ordinary" mitochondria, they also have "giant" mitochondria (up to 3 μm, compared to a width of about 0.5 μm for ordinary mitochondria) that contain "crystalline matrices" (Kikuchi,1984). The crystalline matrices were seen as hexagonal, pentagonal, or irregular in profile (Kikuchi, 1984). As in *Artemia,* the dark cells were suggested by Kikuchi to play the more important role in osmoregulation, but obviously in reverse direction from what occurs in *Artemia* (Kikuchi, 1983).

There is also a relationship between the salinity of the habitat and the morphology of these cells. At low salinities, there is a predominance of light cells (few mitochondria), and the epithelial layer is thin; *Artemia* raised in dilute sea water (approximately isotonic with body fluids) have normal-sized epipods with a greatly reduced epithelial lining with few mitochondria. In more saline waters the epithelial cell layer is thicker, there are many more mitochondria, and cellular complexity is greater (Copeland, 1967). This finding supports the mitochondrial pump hypothesis (Copeland, 1966, 1967). The function of these two cell types is in the regulation of salts. This has been demonstrated by several workers and is now well accepted (e.g., see Copeland, 1967; Holliday et al., 1990). Thus, this epithelial layer perhaps should be discussed under the heading Excretion, but I have elected to discuss it here because of the possibility (unproven) that some gas exchange does occur across the epipod cuticle, and therefore across this cell layer, and because of the historical precedent of referring to the thoracic epipods (erroneously it now seems) as gills or branchiae. Moens et al. (1991: 210) stated that "oxygen has only to cross the cuticle of the metepipodites [epipods]; once in the intercellular space of the monolayer it reaches the hemolymph and can bind to the respiratory pigments," thus inferring that the epithelial cells have occasional gaps between them through which hemolymph can contact the cuticle directly. Direct contact between hemolymph and cuticle has been implied for the cells of the larval salt gland of *Artemia,* which are morphologically very similar to epipod cells. Hootman and Conte (1975: 373) noted that "sinusoids from the labyrinth open directly into the hemocoel . . . providing numerous avenues by which hemolymph may enter the tubules." If true for the epipod epithelial cells, this might explain the reticulated staining pattern noted by Holliday et al. (1990) and others, although the work of Croghan (1958a–d) firmly established the fact that *Artemia,* if indeed it employs the epipods for any gas exchange, certainly is not dependent upon them for such; he also demonstrated that the epipods are the sites of active ion excretion in a hypertonic medium and probably of active uptake in hypotonic media, being permeable to Na^+, K^+, and Mg^{++}.

In larvae, where the epipods have not yet developed, ion regulation (at least in *Artemia*) is by the dorsal organ (= salt gland; see section on Dorsal Organ).

EXCRETORY SYSTEM

Excretion occurs across general body surfaces and by several organs, the functions and development of which change during ontogeny. Although this section is devoted to specific organs of excretion, Peters (1987) noted that, at least in *Daphnia,* it is unlikely that most solutes would be excreted by a single organ or at a distinct site. Rather, Peters suggested that daphniids, because of their small size and short diffusion distances, exhibit "direct release to the environment," supported indirectly by studies showing constant, slow release of nitrogen and phosphorus, rather than pulses of these products that would be more indicative of glandular secretion. It is possible that this sort of excretion occurs also in other branchiopods, in addition to the documented excretory activity of the glands discussed below. Salt regulation via the epipods of thoracic limbs (in those taxa having epipods) and dorsal organ (in larval stages) is discussed under Respiratory System and Osmoregulation (epipods) and Dorsal Organ.

Antennal Glands

Excretion in developing branchiopods is probably via the antennal (or antennary) glands, which are present in all larval branchiopods (although not all taxa have larvae) but degenerate with the onset of development of the maxillary glands (Warren, 1938; Lochhead, 1950; Criel, 1991a). These glands are conspicuous in larval stages of anostracans (e.g., see Warren, 1938: fig. A; Fryer, 1983: figs. 14, 17, 19; Conte, 1984) and are present and presumably functional in stage 2 larvae of *Artemia* (Conte, 1984) and in the notostracans *Triops cancriformis* (Grasser, 1933) and by stage 4 in *Triops longicaudatus* (Fryer, 1988). Fryer (1988) refers to these glands in notostracans as "transient" and illustrates (his fig. 116) the end sac and tubules in a stage 4 larva. In some taxa, a vestige of the gland can be seen in adults; the rudiment of the end sac (clearly nonfunctional, as the duct is no longer present) is evident in *Artemia* and other anostracans (e.g., Claus, 1886; Cassel, 1937; Warren, 1938; Lochhead, 1950) and in certain anomopods and other "cladocerans" (e.g., see discussion in Fryer, 1969). The gross anatomy is similar to that of the only other segmental excretory organ, the maxillary glands (see below), as the antennal gland consists of a blind end sac and an efferent duct. In naupliar larvae of *Artemia*, these glands are located on either side of the head in the area where the second antenna arises and open at the base of the antennal protopodite (Cassel, 1937; Warren, 1938). Reports of the number of cells constituting the end sac vary from 11–14 (Cassel, 1937) to 16 (Warren, 1938) in *Artemia*, whereas the larval efferent duct is composed of three or four syncytial cells and an intracellular duct (Warren, 1938; Cassel, 1937; Benesch, 1969; Criel, 1991a). The excretory function is transferred to large, well-developed maxillary glands, which become functional by about the sixth naupliar instar in anostracans (Warren, 1938).

A poorly known gland referred to by Warren (1938) as the mandibular gland is also transitory, present in the first and second instar nauplius of *Artemia* (Conte, 1984) but disappearing by about the sixth instar. This gland may have some excretory function as well, although Warren (1938) could not locate any external opening of the duct, and Conte (1984) expressed doubts as to its function as a renal organ.

Maxillary Glands

Excretion in adults is primarily via large, paired maxillary glands. These glands consist of a central blind end sac, around which is coiled a rather long efferent excretory duct. The gland lies in the open hemocoel, connected to the adjacent cuticle by strands of connective tissue, and is bathed by the hemolymph. The efferent excretory duct or tubule terminates in a short, ectodermally derived (and, hence, cuticle-lined) exit duct (Goodrich, 1945; terminal duct of Tyson, 1968), which eventually leads to an opening on the maxilla.

These glands are present and conspicuous in all eight extant orders. Although differences exist in the shape of the gland in the various orders, the overall arrangement is roughly similar (Cannon and Manton, 1927) (Fig. 72). In both conchostracan orders, the end sac and ducts are arranged within the folds of the carapace around the rather large carapace adductor muscles (Fig. 72C,D; see also Fig. 38B for *Lynceus*). In notostracans, which lack comparable carapace adductor muscles, the coils of the efferent duct are slightly more compressed and the gland is consequently elongated in an anterior–posterior direction (Fig. 72B). Notostracans also display slight differences in the gross structure of the end sac, which is produced into three small lobes, two of which project into the trunk cavity and one that is an elongated "fenestrated lobe" (Cannon and Manton, 1927), which Claus (1873) mistook for an adductor muscle. In the onychopods (e.g., *Polyphemus*, Fig. 72F), despite the fact that the carapace is greatly reduced and displaced posteriorly, and the reduced adductor muscle now attaches to the coils of the gland rather

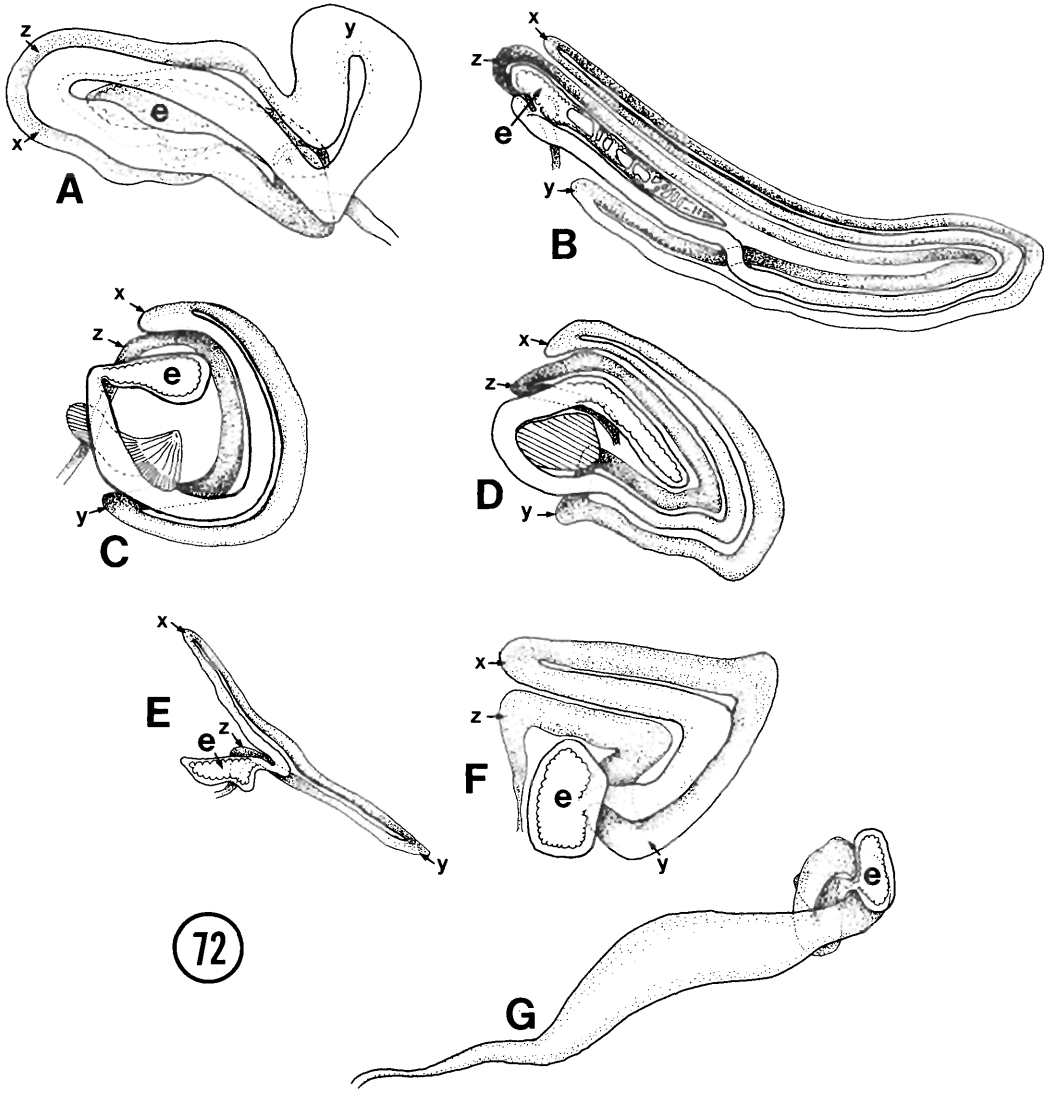

Fig. 72. General form of the maxillary gland. (After Cannon and Manton, 1927.) **A:** *Chirocephalus* (Anostraca). **B:** *Lepidurus* (Notostraca). **C:** *Estheria* (Spinicaudata). **D:** *Lynceus* (Laevicaudata). **E:** *Sida* (Ctenopoda). **F:** *Polyphemus* (Onychopoda). **G:** *Leptodora* (Haplopoda). e, end sac; x, y, and z refer to regions believed homologous in the various orders by Cannon and Manton (1927).

than to the ectoderm of the carapace, the maxillary gland nevertheless shows similarities to the *Estheria* type described by Cannon (1924) and Cannon and Manton (1927). In the haplopod *Leptodora,* the situation is very different. The end sac and one small coil of the efferent duct lie in folds of the posterolaterally displaced carapace, but from that point the efferent duct is uncoiled and rather large (Fig. 72G) and empties on the body wall (Cannon and Manton, 1927). In ctenopods and anomopods, the coils of the efferent duct are often straightened out to the point that the coils appear as long tubes with rather sharp bends

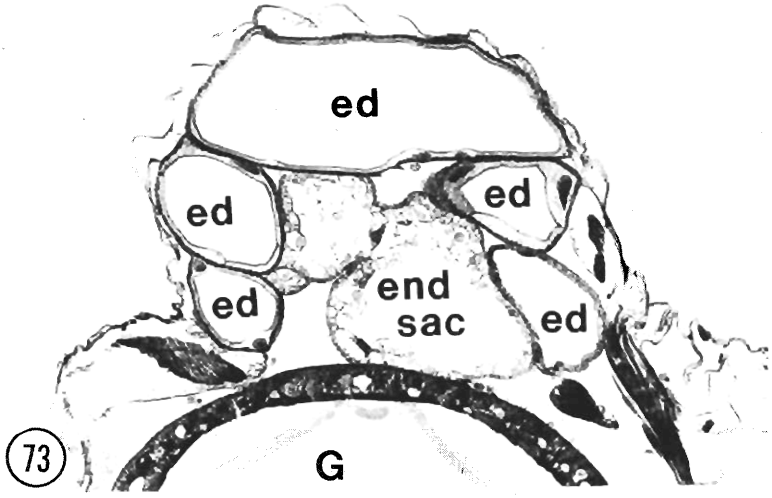

Fig. 73. Light micrograph of section through maxillary gland of *Artemia*. Centrally located end sac is surrounded by coils of the efferent duct (ed). (Courtesy of G.Criel.) G, gut.

at their anterior and posterior extremities (e.g., *Sida,* Fig. 72E). In anostracans, these glands are seen externally as slight bulges just posterior to the mandibles (Lochhead, 1950). Because the glands in anostracans are not bound by the confines of the carapace folds, they are free to extend into the body cavity, where the loops of the efferent duct may overlap (e.g., *Chirocephalus,* Cannon and Manton, 1927, and *Artemia,* Warren, 1938; Tyson, 1969a; Criel, 1991a). In notostracans, conchostracans, and most cladocerans, the end sac and coils of the efferent duct are located within the folds of the carapace, and are shaped according to available space between the inner and outer layers of cuticle. Thus they may appear somewhat more elongate in notostracans than in smaller conchostracans and cladocerans, but no functional or phylogenetic significance is attributable to this difference (Fryer, 1987c). In the ctenopods and anomopods, the glands also are found in the folds of the carapace, much as in the "conchostracans."

Detailed studies on the maxillary glands exist only for the spinicaudatan *Estheria* (Cannon, 1924) and for *Artemia* (Warren, 1938; Tyson, 1968, 1969a,b; Criel, 1991a). In *Artemia,* the gland consists of a centrally located, slightly enlarged end sac, around which the efferent excretory duct makes three loops before passing to the maxilla (Fig. 73).

The end sac is anchored in place by thin strands of connective tissue running from the outer layer of the end sac to the coils of the efferent duct (Tyson, 1968). Furthermore, and more interesting, adjacent coils are connected via "intercoil connections," where the basal laminae of cells in the two coils are continuous and where one or more cytoplasmic extensions from one cell may form a bridge to the cell in the adjacent coil (Fig. 79) (Tyson, 1969b). Connecting processes are branched, and the interdigitation of the two cells is quite complex, similar in some ways to the interdigitations seen between cells in the distal efferent duct (Tyson, 1969b: fig. 13C). The connecting cytoplasmic processes do not penetrate the basal lamina and enter the hemocoel. At the site of these connections, the basal laminae of the two adjacent coils are "clearly continuous with one another, thereby

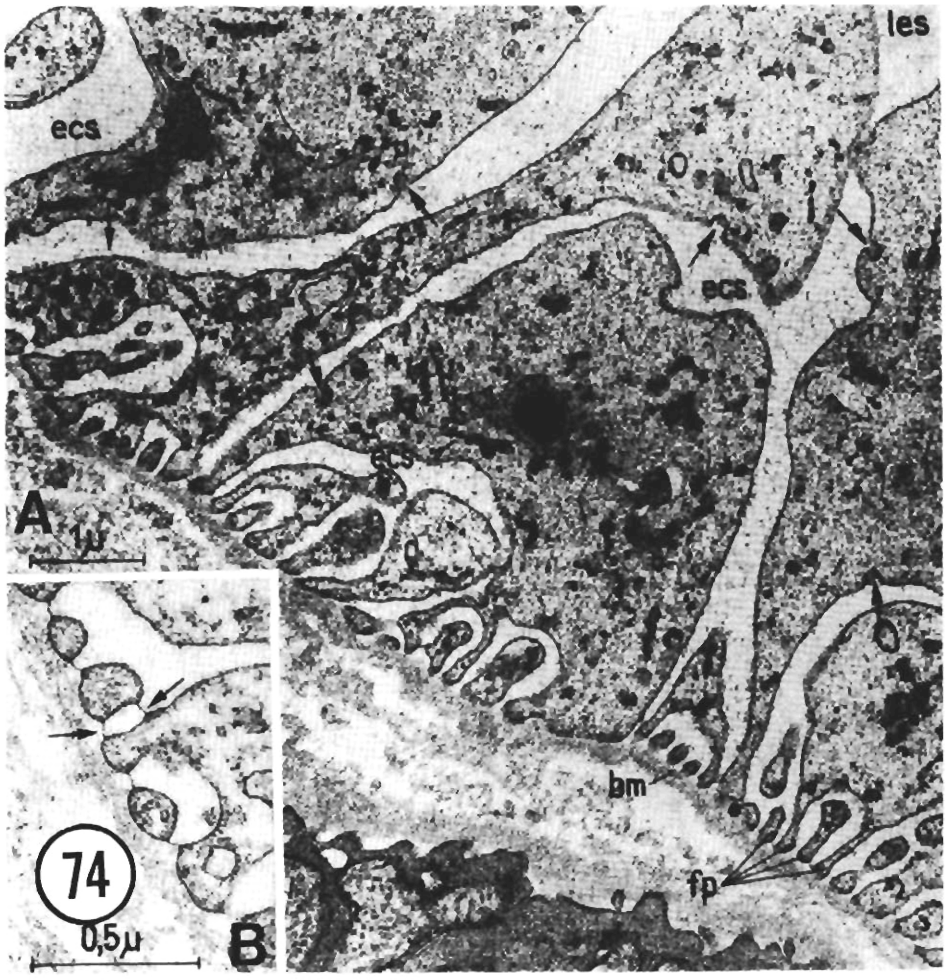

Fig. 74. Epithelium of maxillary gland end sac of *Artemia*. (From Tyson, 1968.) **A:** TEM of basal end of epithelial cell. ×14,500. **B:** Higher magnification of foot process. ×42,300. bm, basement membrane; ecs, extracellular spaces; fp, foot processes; les, lumen of end sac. Arrows denote spiny coated pits in A, junctional specializations between adjacent foot processes in B.

preserving the integrity of the basal lamina as an uninterrupted layer separating the cells of the tubular epithelium from the haemocoel" (Tyson, 1969b: 55).

The epithelium lining the lumen of the end sac (Figs. 74, 75, 80A) consists of a single layer of large, highly branching cells that are remarkably similar to the podocytes (or visceral epithelial cells) of Bowman's capsule of a vertebrate nephron. Cell height is variable, but tends to be greatest where there is a nucleus (e.g., Tyson, 1968: fig. 2). Large cytoplasmic protrusions of these cells may branch often before "coming to rest on the basement membrane as small foot processes" (Tyson, 1968: 133). Interdigitation of neighboring foot processes is common and rather orderly, with the processes lying approximately equidistant to each other at the level of the basal lamina (Fig. 74) (Tyson, 1968). Between adjacent cytoplasmic extensions and branches (Fig. 75), there are often wide extracellular