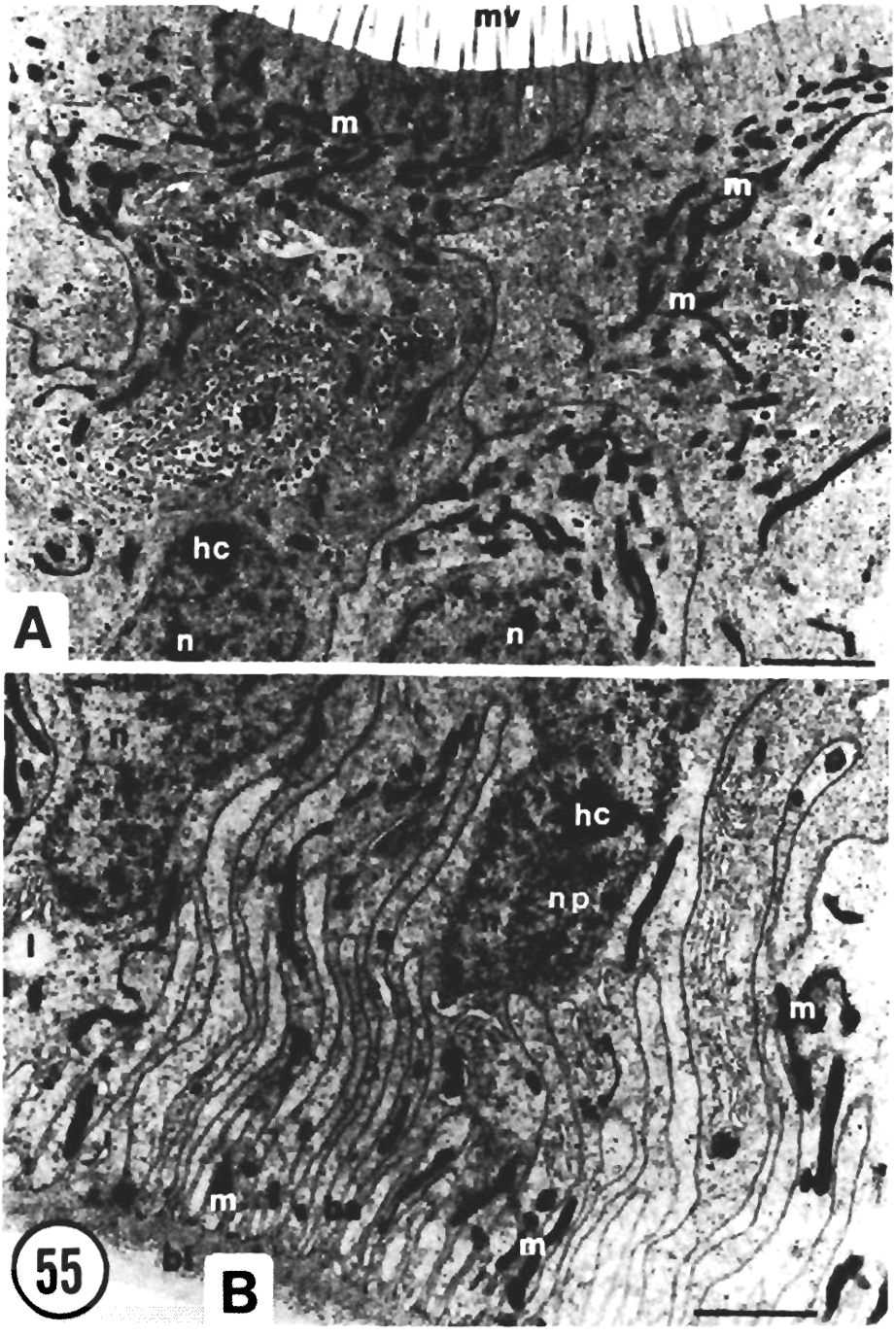

Fig. 55. Apical and basal portions of midgut cells in *Artemia*. (From Schrenhardt, 1987b.) **A:** Apical portion showing extensive mitochondria and glycogen fields. Scale bar = 2 μm. **B:** Basal portion with infoldings of basal and basolateral cell membrane. Scale bar = 2 μm. ba, basal labyrinth; bl, basal lamina; gy, glycogen; hc, heterochromatin; m, mitochondria; mv, microvilli; n, nucleus; nm, nuclear membrane; np, nuclear pore.

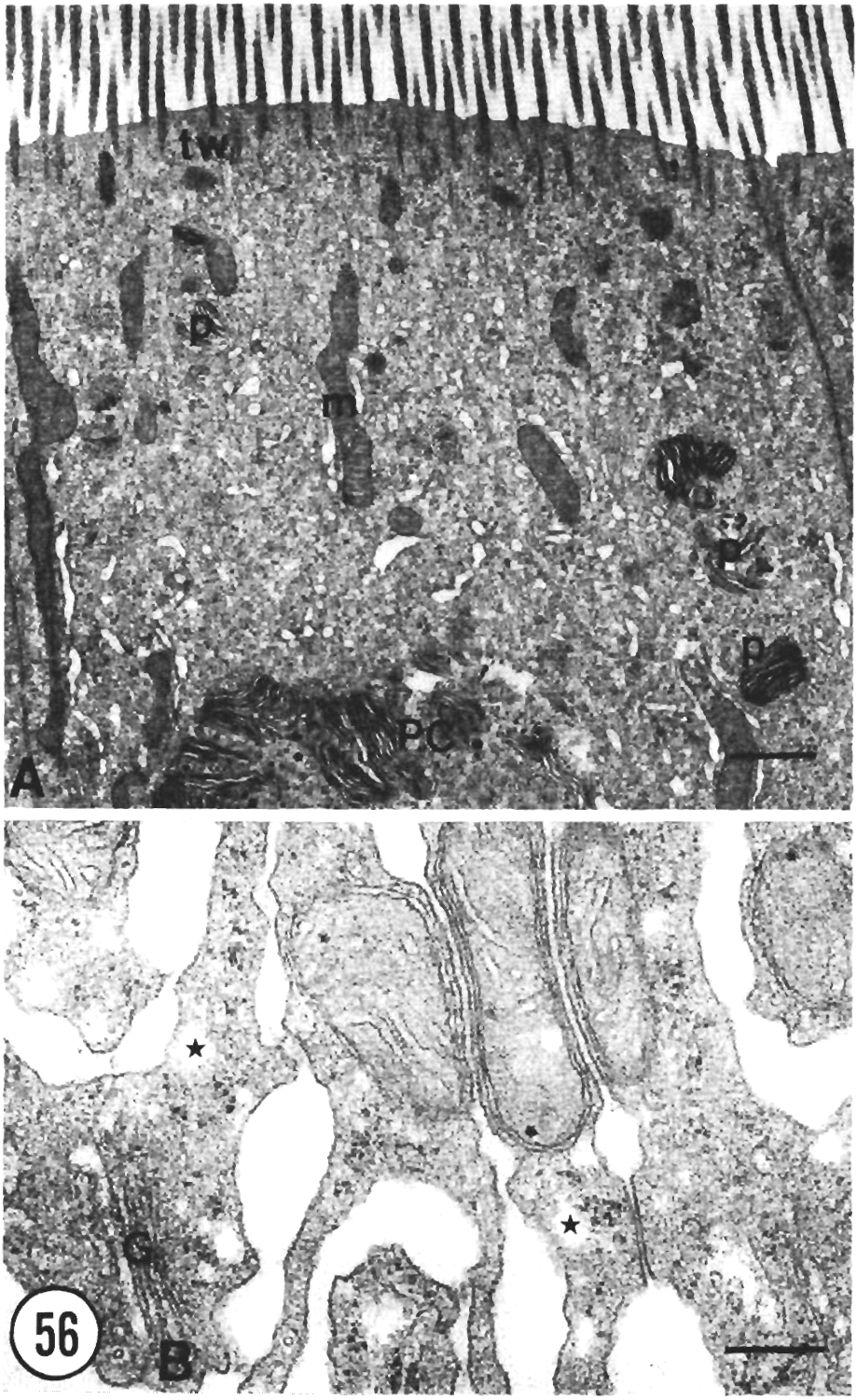

Fig. 56. Higher magnification of apical and basal regions of midgut cells in *Artemia*. (After Criel, 1991a.) **A:** Extensions of microvilli into apical cell region forming "terminal web" (tw). Note phagolysosomes (p) coalescing to form large phagolysosomal body (PC). Scale bar = 1 μm. **B:** Close association between mitochondria and basal infoldings of the cell membrane. Clear spaces (★) caused by loss of glycogen during fixation. Scale bar = 200 nm. G, Golgi apparatus; m, mitochondrion.

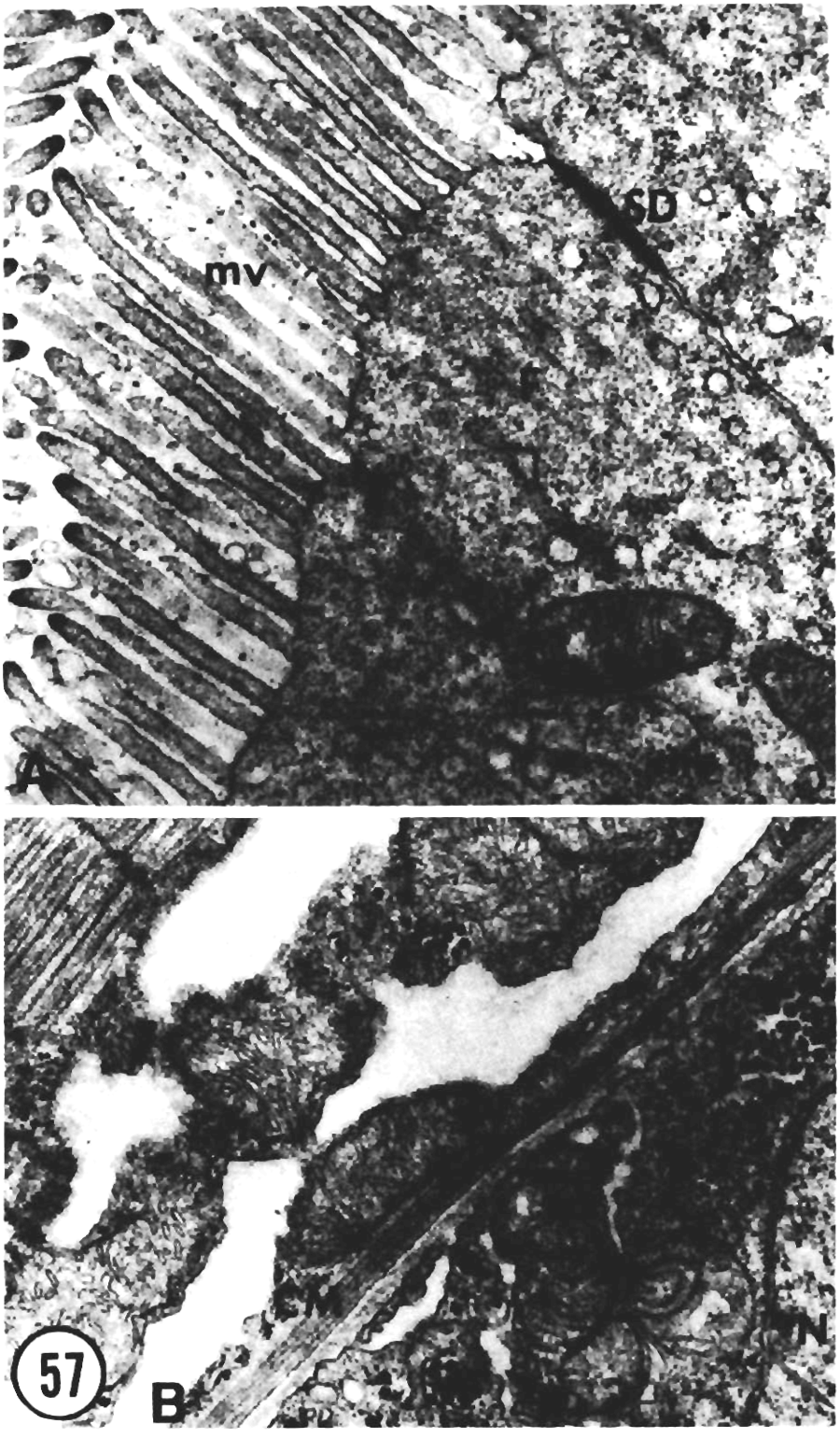

Fig. 57. Details of midgut cells in *Artemia*. (From Hootman and Conte, 1974.) **A:** Junction of two midgut cells showing septate desmosome (SD). ×26,500. Note fusion of one of the multivesicular bodies (mb) with plasma membrane (arrow). **B:** The basal lamina (bl) separates circular muscle (CM) from the hemocoel. ×28,000. F, filaments that extend into microvilli (mv); N, nucleus of midgut cell.

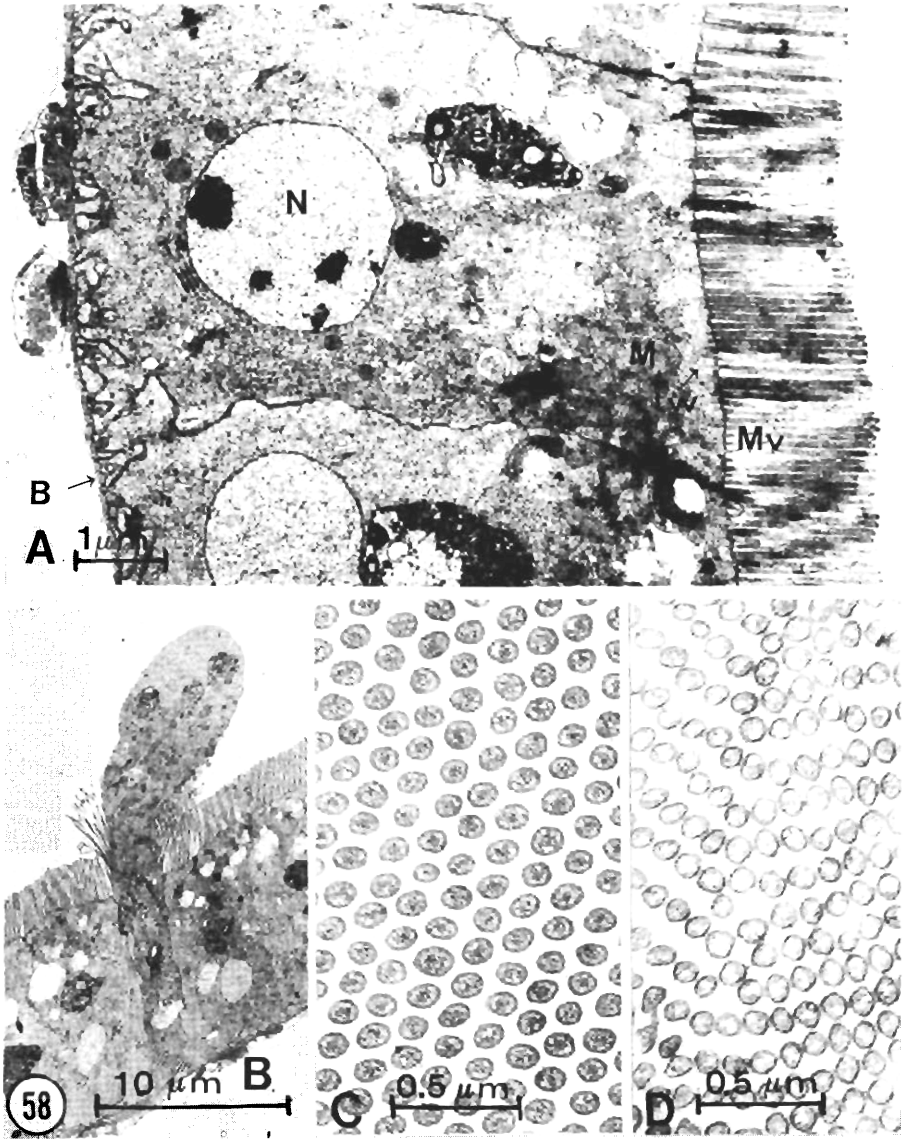

Fig. 58. Ultrastructure of the midgut region, *Leptestheria dahalacensis* (Spinicaudata) nauplius. (From Schlecht, 1979.) **A:** Single cell of the midgut wall. **B:** Cytoplasm extending into the intestinal lumen. **C,D:** Cross sections through the microvilli showing different patterns of arrangement. B, basal lamina; eM, electron-dense material; M, mitochondria; Mv, microvilli; N, nucleus; tw, terminal web.

circular muscles in *Artemia* lie directly on the surface of the bilayered basal lamina of the epithelial cells (Figs. 54, 58A). Each muscle cell contains a long nucleus, striated myofibrils, smooth endoplasmic reticulum (SER) cisternae, and few mitochondria (Schrehardt, 1987b). Unlike muscle cells of the gastric ceca, these cells are innervated by multipolar neurons (Schrehardt, 1987b; figs. 42–44). This circular muscle in anostracans is characterized by having nine filaments surrounding a central thick filament (Kikuchi, 1971) rather than the 6 + 1 arrangement seen in anostracan appendage musculature (Reger, 1962).

All of the midgut, including the covering layer of circular muscles, is covered by a thin layer of connective tissue separating it from the hemocoel.

In most groups, the surface area of the midgut is further increased by having paired gastric ceca or hepatopancreatic ceca (Figs. 49A,B, 52A, 60) that branch from the anterior region of the midgut and often extend into the head and/or labrum. In daphniids, these are simple evaginations of the midgut (Schultz and Kennedy, 1976). In anostracans, these relatively simple pouches receive food from the esophagus and anterior midgut via contraction of esophageal and midgut circular muscles and closure of the esophageal sphincter. Upon contraction of the muscles lining the ceca (Figs. 60, 61E), food is then propelled posteriorly into the midgut (Snyder and Wolfe, 1980). As noted above, there is some controversy concerning the number of recognizable cell types in these ceca in *Artemia,* with Schrehardt (1987b) recognizing only one type, morphologically nearly identical to cells lining the midgut, but with Foster and Wolfe (1986) recognizing three (Fig. 62). Although Schrehardt (1987b) did not recognize different cell types in the midgut as opposed to the gastric ceca, he did observe slight differences (Fig. 61). These included, in the midgut cells, shorter microvillous borders, longer nuclei (10–11 μm), a single nucleolus, and only scattered small lipid drops, glycogen being the main storage product. Cellular inclusions in general (i.e., ribosomes, Golgi complexes, ER cisternae) are less common in the midgut cells, and the basal cell membranes exhibit narrow infoldings, with associated mitochondria, that extend into the cytoplasm to about the level of the nucleus (Fig. 63A,B). In addition, Schrehardt (1987b) noted that occasionally peroxisomes with a fine granular matrix are seen in cells of the hepatopancreas. The three cell types of Foster and Wolfe (1986), termed dark, light, and mature light based on staining properties (Fig. 62), differ in the cytoplasmic inclusions. Darker staining cells contain multivesicular bodies and more extensive RER and glycogen granules. Light cells contain RER and glycogen but in smaller amounts. Mature light cells consist of a large vacuole, an apical complex, and deep tight junctions, and these cells were sometimes seen to empty their contents into the lumen (see below). Foster and Wolfe (1986) equated these cells with the three cell types of true digestive glands in higher crustaceans, the dark cells being equivalent to Restzellen, light cells to Fibrillenzellen, and mature light to Blasenzellen. If these cells function as do those of higher crustaceans, then the ceca are digestive glands and not merely storage areas to increase surface area for better absorption. Foster and Wolfe (1986) suggested that the dark cells absorb nutrients into the multivesicular bodies, where they are broken down by lytic enzymes from the RER, and also store lipids and glycogen. Light cells produce digestive enzymes and store them in large vacuoles, eventually becoming mature light cells that pinch off their apical regions, emptying the vacuolar digestive contents into the lumen (Foster and Wolfe, 1986). In some taxa (e.g., Notostraca and almost all conchostracans), the hepatopancreatic ceca can be extensively developed, with numerous convolutions almost filling the head (e.g., Figs. 3B,E, 52A), and so must function in a different manner from the relatively simple "storage" function assigned by some workers to the anostracan gastric ceca. Lipid is the main storage substance in *Artemia* cecal cells and is arranged either as nearly circular drops (Fig. 64) or as irregular fields, and glycogen is also stored in small amounts. Adjacent cells are joined by septate desmosomes and tight junctions (Schrehardt, 1987b). The underlying basal lamina is finely granular and bilayered. Bundles of striated muscles circle the ceca (Fig. 60), but Schrehardt (1987b) could not detect any innervation of these muscle cells, as opposed to those of the midgut. As in the midgut, the overlying muscle fibers are covered by a thin basal lamina that appears continuous with the basal layer of the basal lamina of the epithelial cells (Schrehardt, 1987b).

Schrehardt (1987b) described an unusual process of cell degradation and degeneration

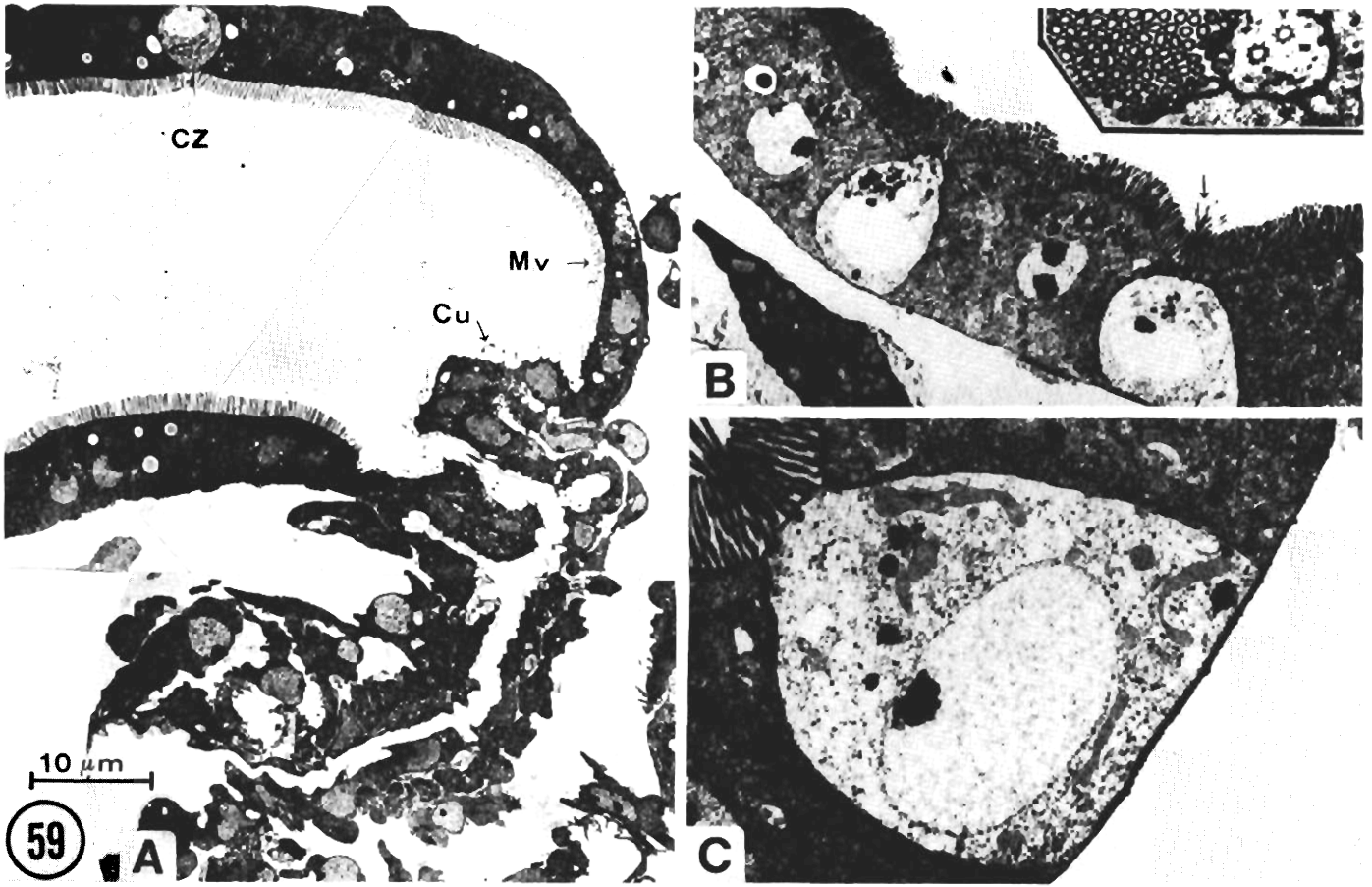

Fig. 59. The gut of a larval spinicaudatan *Leptestheria dahalacensis,* showing unique cilia-bearing cells (CZ) in midgut. **A:** Sagittal section through foregut and anterior region of midgut. (From Schlecht, 1979.) **B,C:** Sections of the midgut. (From Rieder et al., 1984.) **B:** Several midgut cells, those bearing two cilia (arrow) appearing less dense. **Inset** (upper right) is a cross section through the two cilia of one cell and the microvilli of adjacent cells. ×3,500 (inset ×19,000). **C:** The large, low-density cell bearing two cilia. ×11,000. Cu, thin cuticle of foregut; CZ, cilia-bearing cells; Mv, microvilli.

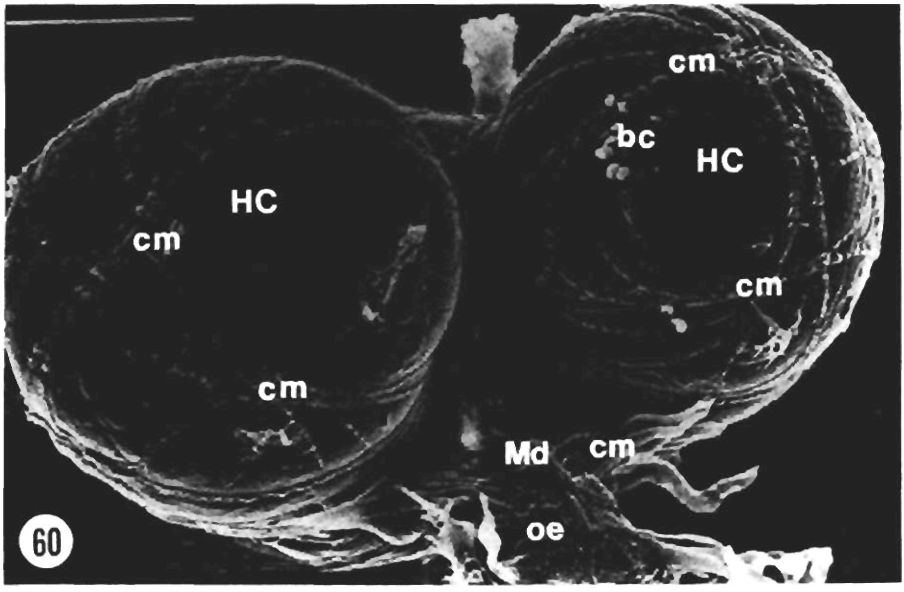

Fig. 60. The hepatopancreatic (gastric) ceca in anostracans are simple globular protrusions from the anterior margin of the midgut. Note circular muscles (cm) apparently lacking innervation. (From Schrehardt, 1987b.) Scale bar = 100 μm. bc, adhering blood cells; HC, hepatopancreatic ceca; Md, dilator muscle of esophagus; oe, esophagus.

in the gastric ceca, and less frequently in the midgut, of *Artemia*. Epithelial cells from time to time are seen to extend out into the cecal or midgut lumen, and Schrehardt (1987b) marked this as the onset of cell degeneration (Fig. 65). Associated with the intrusion of the cell into the lumen is the synchronous breakdown of the microvillous border and cisternae of the ER, deformation of the nucleus, and loss of glycogen and lipid as storage products (Fig. 65). Lysosomes surrounded by an "increasingly electron transparent" border appear in the cytoplasm. Following these ultrastructural changes, the cell extends further into the lumen (Fig. 65B), at which point only the nucleoli, a few mitochondria, and some lipid drops are still visible (Fig. 65C,D). Further decay involves breakdown of the remaining products and continued extrusion into the lumen, culminating in release of cytoplasm into the gut (Fig. 65C,D), with only cytoplasmic rudiments, themselves eventually released into the lumen later, remaining where the cell used to be (Fig. 65E). This cell degeneration may be what Foster and Wolfe (1986) saw (their fig. 3) in cells of the ceca, stating (1986: 29) "some mature light cells were found emptying their vacuolar contents into the lumen of the gut." A similar process is seen in Schlecht's (1979) figure of the gut of the spinicaudatan *Leptestheria dahalacensis,* where some cells extrude their cytoplasm into the gut lumen (Fig. 58B). This process is in some ways similar to the action of presumed secretory cells described in the midgut of higher crustaceans (Dall and Moriarty, 1983), although differentiation of midgut cells into two or more distinct types does not occur in *Artemia*.

Schrehardt (1987b) did not mention the peritrophic membrane described for *Artemia* by Snyder and Wolfe (1980) and Foster and Wolfe (1986). A peritrophic membrane has been noted at least in *Artemia* (Snyder and Wolfe, 1980; Foster and Wolfe, 1986), in the Spinicaudata (*Leptestheria*), and in *Daphnia* (Schlecht, 1979). In *Artemia,* the peritrophic membrane (Fig. 67A,B) can extend posteriorly behind the animal several times the length of the animal's gut (e.g., 80 mm past

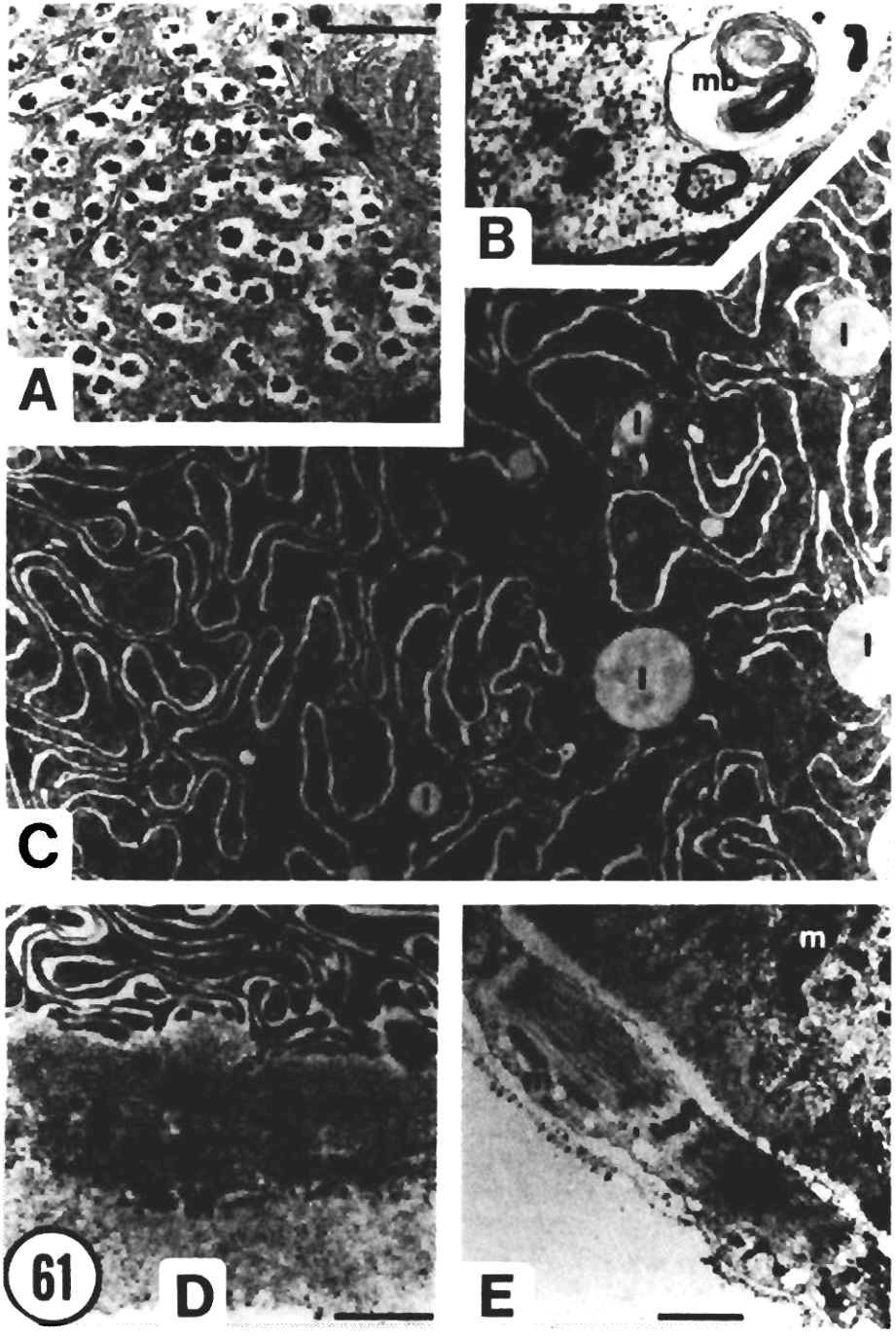

Fig. 61. Cells of the gastric ceca in *Artemia*. (From Schrehardt, 1987b.) **A:** Glycogen field. Scale bar = 1 μm. **B:** Part of a cytoplasmic body containing a myelin body (mb). Scale bar = 2 μm. **C:** Tangential section through basal portion of cell showing infoldings of the basal labyrinth. Scale bar = 2 μm. **D:** Finely granular bilayered basal lamina just below infoldings of basal labyrinth. Scale bar = 1 μm. **E:** Circular muscle separated from epithelium by basement membrane. ba, basal labyrinth; bl, basal lamina; cm, circular muscle; gy, glycogen; is, intercellular space; l, lipid; m, mitochondrion; mb, myelin body.

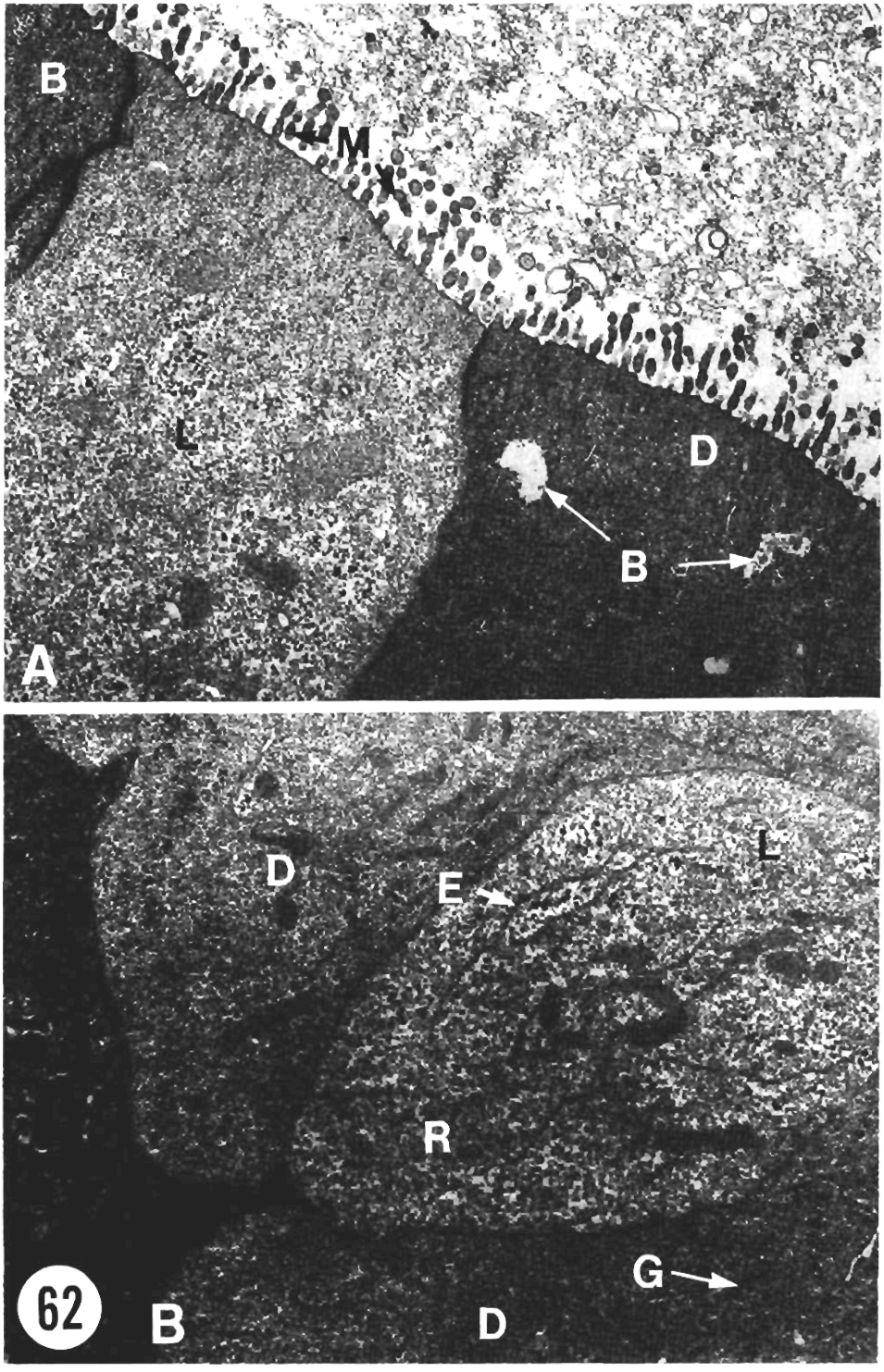

Fig. 62. Epithelial cells of gastric ceca of *Artemia*. (After Foster and Wolfe, 1986.) **A:** TEM of light (L) and dark (D) cells with microvilli (M) along apical surface and multivesicular bodies (B). ×18,000. **B:** TEM of light (L) and dark (D) cells showing rough endoplasmic reticulum (E), glycogen granules (G), and free ribosomes (R). ×26,000.