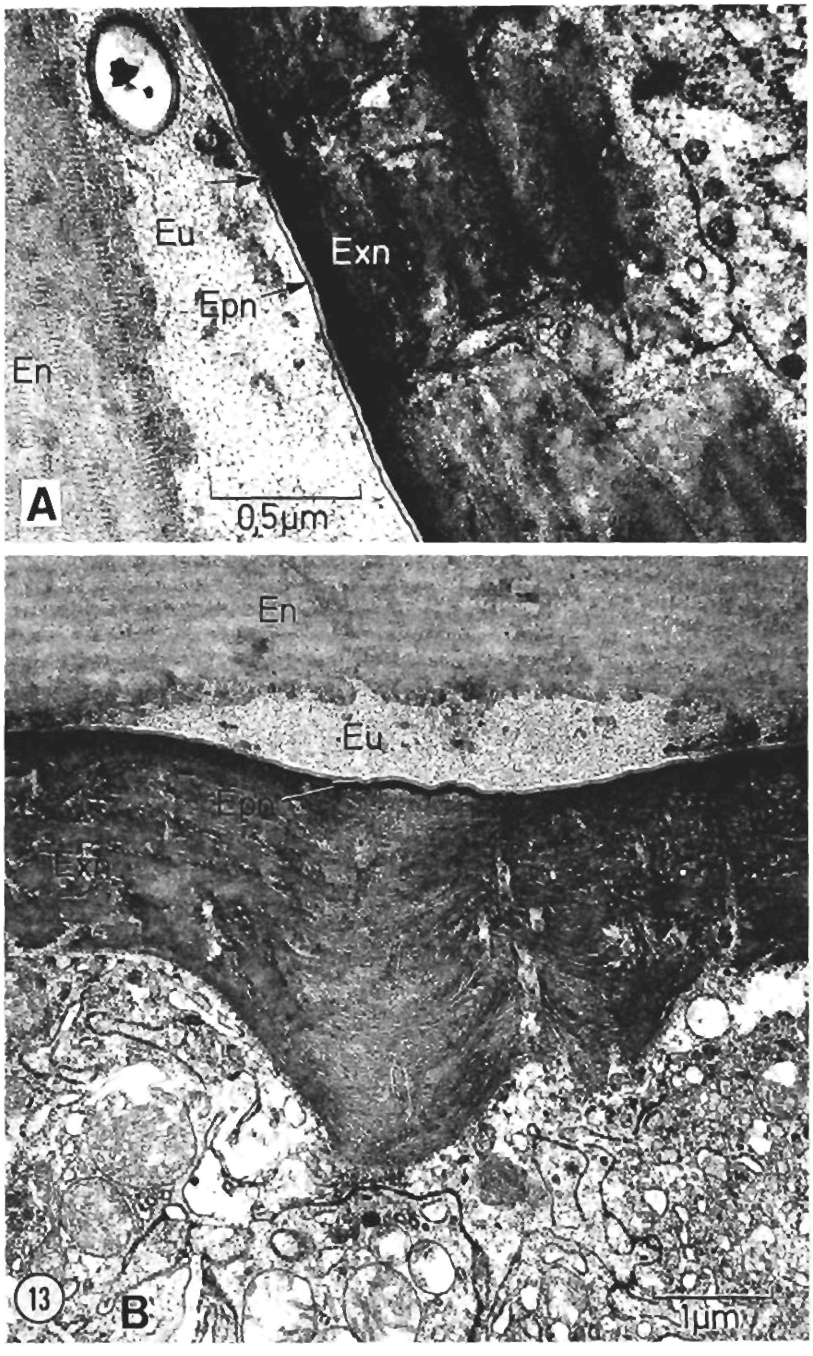


Fig. 13. Integument of *Triops cancriformis* (From Rieder, 1972b.) **A:** Old endocuticle (En) with lamellae in partial cross and longitudinal section and showing funnel-like pores (arrows) ending at the surface of the new epicuticle (Epn). **B:** Exuvial chamber (Eu) just beginning to develop between old and new layers of integument. Exn, newly formed cuticle; Po, pore channel; S, secretory droplets.

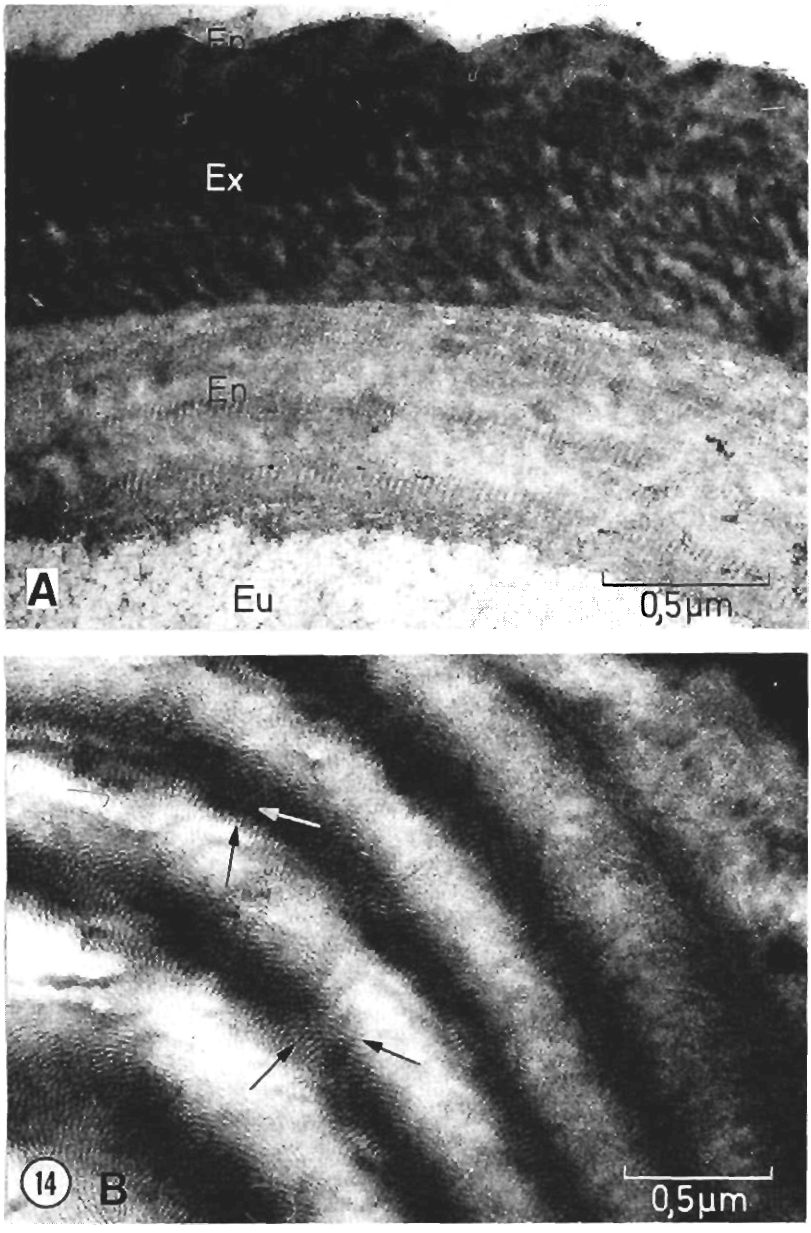
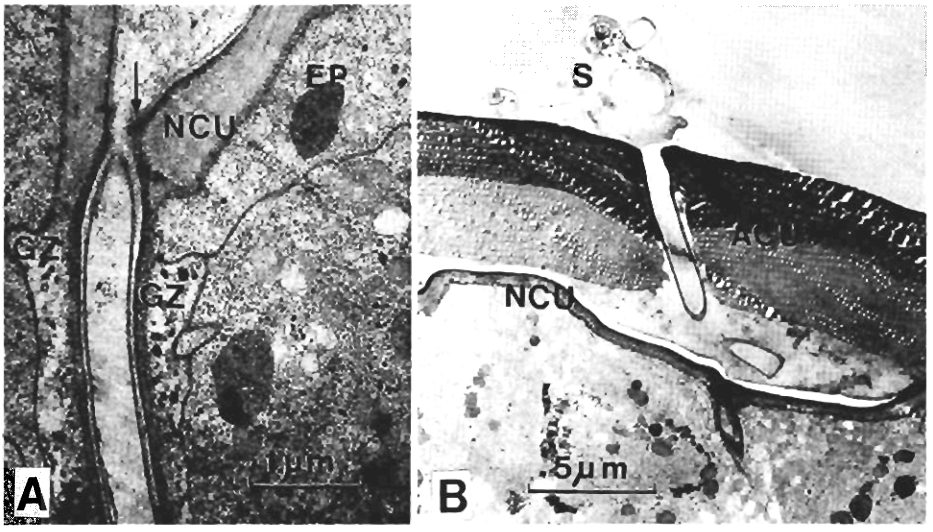


Fig. 14. Specialized areas of integument, *Triops cancriformis*. (From Rieder, 1972b.) **A:** Integument surrounding a sensory seta is basically similar to that of the trunk. **B:** Criss-crossing microfibrils forming several of the 60–80 layers in a nearly tangential section from the endocuticle of an endite, with nearly perpendicular orientation of microfibrils (arrows). Scale bar = 0.5 µm. En, endocuticle; Ep, epicuticle; Eu, exuvial chamber; Ex, exocuticle.



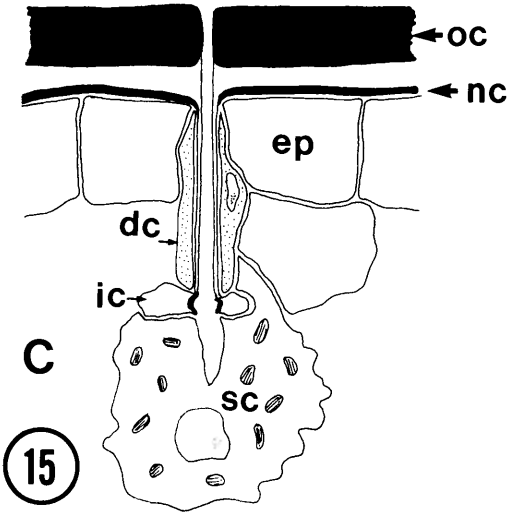


Fig. 15. Integumental glands in *Triops cancriformis* (Notostraca). (After Rieder, 1977.) **A:** Section through duct cell (GZ) and epidermal cell (EP). **B:** Exit duct of integumental gland showing secretory product (S). **C:** Diagram of integumental gland based on sections. ACU, old cuticle; dc, duct cell; ep and EP, epidermal cell; ic, intermediate cell; nc and NCU, new cuticle; oc, old cuticle; sc, secretory cell.

cretion of the epicuticle in other crustaceans. A separate section is devoted to discussion of the dorsal organ, a cuticular specialization found in all branchiopods but understood in relatively few.

Cuticular Specializations

Cuticular specializations are numerous, and include such various structures as the spines and cuticular cones on the male anostracan antenna (Wolfe, 1980; Tyson and Sullivan, 1979a, 1980a; Tyson et al., 1991), unusual components of conchostracan claspers (e.g., Martin, 1989b), and a variety of different setal types. Almost all types of setae known in other crustaceans (e.g., see Jacques, 1989; Watling, 1989) can be found in branchiopods, which additionally bear several possibly unique setal types. As one of many possible examples of branchiopod setal diversity, Martin et al. (1986) illustrated eight structurally and functionally different setal

types on one thoracopod in the genus *Lynceus* (Laevicaudata). Sensory setae are discussed in the section on the nervous system.

DORSAL ORGAN

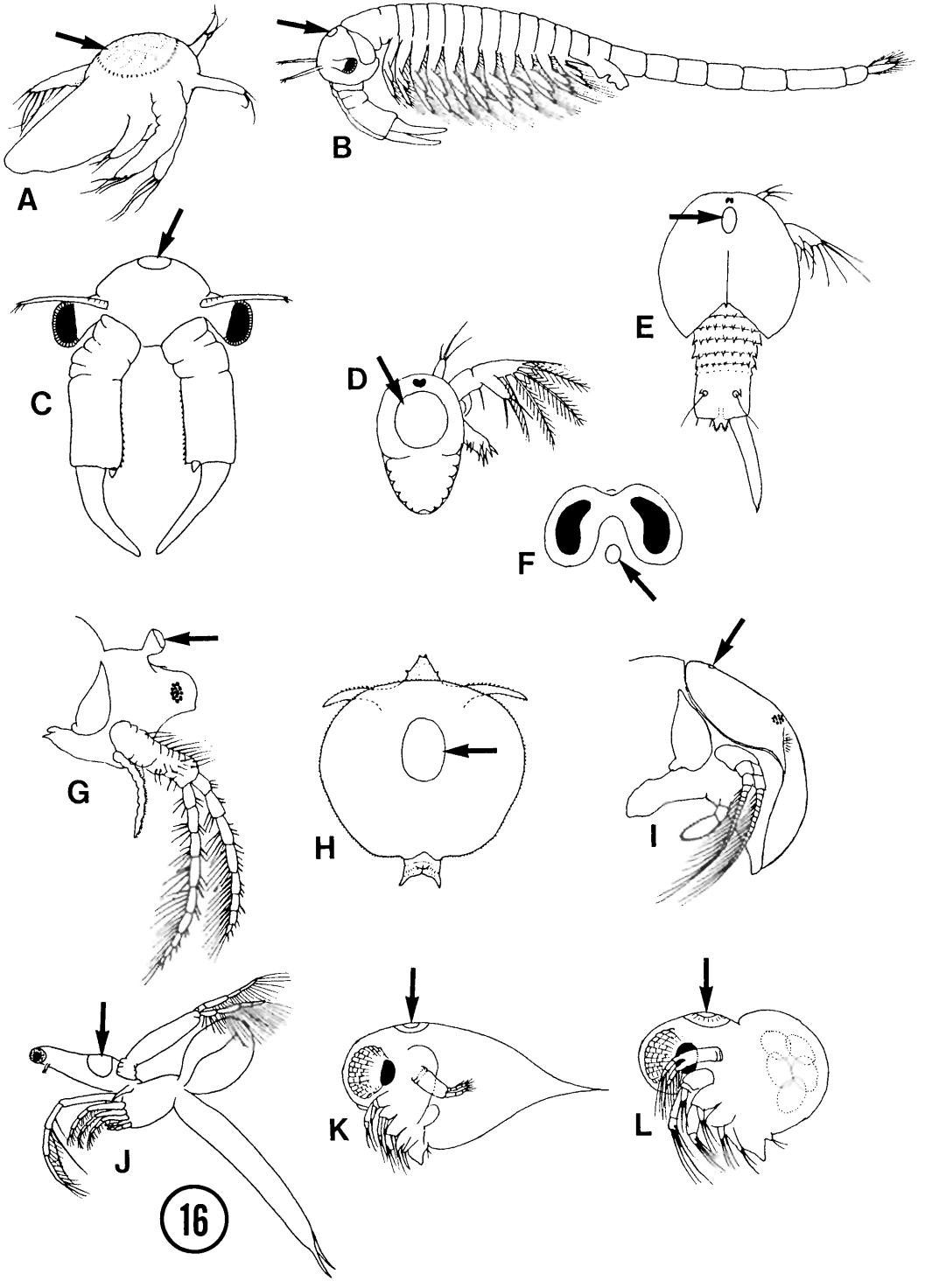
One interesting component of the integument in branchiopods is a structure termed the dorsal organ, Nuchalorgan, neck organ, Haptorgan, neck shield, cephalothoracic organ, or salt gland. It is found on the anterior region of the cephalic shield or head in all branchiopod taxa (Walossek, in press) at least at some point in development (Figs. 16, 17), but in some it degenerates before adulthood. The extensive literature on this structure in *Artemia* usually describes it as a larval salt gland, because it is restricted to larval stages in that genus and its function in hypo-osmoregulation is well known. But the term salt gland may be inappropriate for marine taxa that need not osmoregulate, and it exists in adults in many taxa (e.g., *Leptodora*). Additionally, ion regulation, although clearly the function of this organ in some orders, has yet to be demonstrated for others, and other functions (e.g., attachment in *Sida*) are known or suspected. The rather vague term *dorsal organ* is used here (see also Martin and Laverack, in press). Although there are similarities in structure and location, homology is uncertain, either among branchiopod orders (but see Walossek, in press, for arguments in favor of homology) or between branchiopods and other classes that have a similar organ (e.g., syncarids and larval stages of decapods; Barrientos and Laverack, 1986; Laverack, 1990; Martin and Laverack, in press).

In anostracans the organ is known from larval *Artemia* (Fig. 16A) and from adults in several families (Figs. 16B,C, 17A) (Martin and Laverack, in press). It probably occurs in larval stages of all families but persists to the adult stage (where it may not be functional) only in some species. It has been thoroughly studied in nauplii of *Artemia*, where it is particularly obvious in early stages, as evidenced by several scanning electron microscopical (SEM) studies such as Conte et al. (1972), Hootman et al. (1972), Hootman and Conte (1975), Conte (1984), Lowy and Conte (1985), Schrehardt (1986, 1987a), and Go et al. (1990).

In nauplii of *Artemia*, the organ is a dome-like structure on the cephalon (Fig. 16A), approximately 130–200 μm across, composed of 50–60 to perhaps 75 cuboidal epithelial cells that are larger than the surrounding epidermal cells (Hootman et al., 1972; Hootman and Conte, 1975; Conte, 1984; Lowy and Conte, 1985). The organ changes during ontogeny from a flat, caplike structure to a raised, domed organ with deep invaginations coursing through the epithelium, with the entire organ covered by a thin layer of cuticle (Hootman et al., 1972; Conte, 1984). The organ is demarcated from the adjacent cuticle by a border of thicker cuticle termed the transition band (Hootman et al., 1972; Lowy and Conte, 1985). The epithelial layer, from apical (cuticular) surface to hemocoel, is 25–30 μm thick (Hootman and Conte, 1975; Conte, 1984).

The epithelial cells (Figs. 18, 19) are cuboidal or even nearly spherical, with a diameter of approximately 34 μm (Lowy and Conte, 1985). In many ways the cells are similar to epithelial "chloride" cells of the thoracic limb epipods, which also function in ion regulation (see section on respiration). These similarities include extensive plasma membrane amplification (Figs. 19, 20), a "hallmark of epithelial cells destined to transport electrolytes" (Conte, 1984: 74). Infoldings of

Fig. 16. Location of dorsal organ (arrows) in selected branchiopods. **A:** Nauplius of *Artemia*. (From photograph in Schrehardt, 1986.) **B:** Adult *Branchinecta paludosa*. **C:** Frontal view of head of *Branchinecta paludosa*. (B,C after Sars, 1896.) **D:** Hatching larva (metanauplius) stage of *Triops cancriformis*. **E:** Later ("neonatal") stage of *Lepidurus arcticus*. **F:** Dorsal view of eyes and organ in adult notostracan (*Triops cancriformis*). (D–F after Longhurst, 1955.) **G:** Lateral view of head of adult limnadiid clam shrimp (Spinicaudata). (After Martin, 1989a.) **H:** Dorsal view of "heilophore" larval stage of *Lynceus* (Laevicaudata). (After Gurney, 1926.) **I:** Lateral view of head of adult laevicaudatan. (After Martin, 1989a.) **J:** *Leptodora kindtii* (Haplopoda). (After Calman, 1909, from Lilljeborg, 1901.) **K:** Female *Evadne spinifera* (Onychopoda). **L:** Female *Pleopis polyphemoides* (Onychopoda). (K,L after Smirnov and Timms, 1983.)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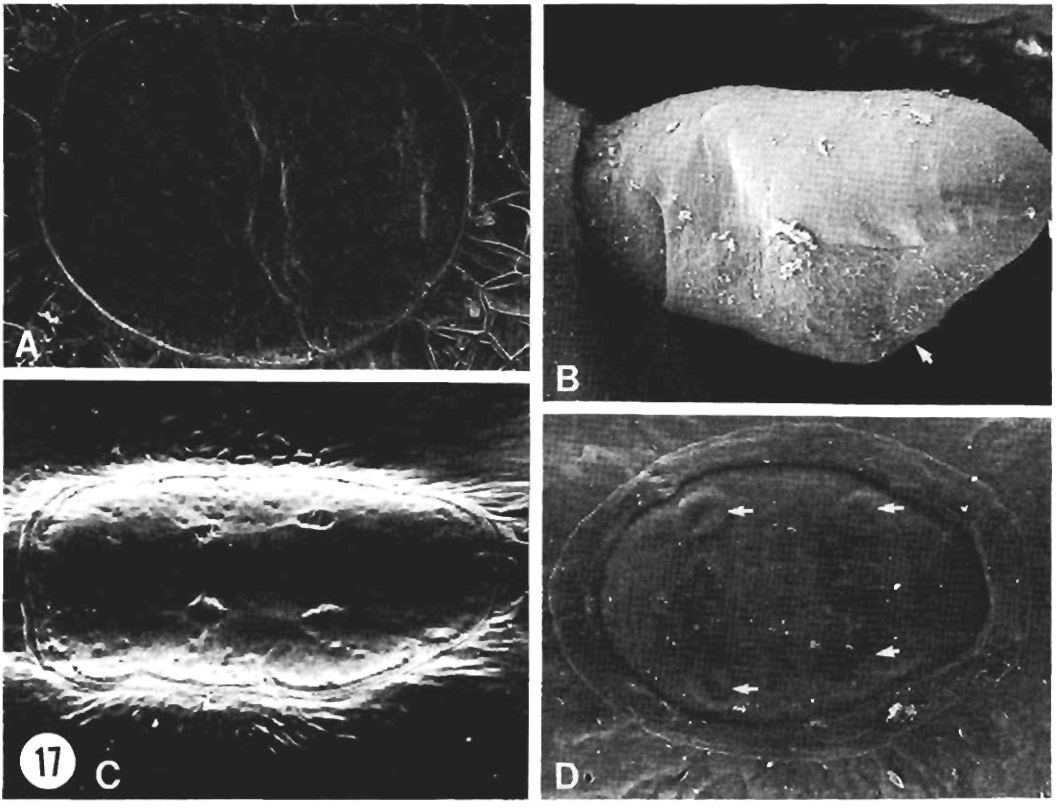

Fig. 17. SEM of dorsal organ in Anostraca, Spinicaudata, and Laevicaudata. **A:** *Branchinecta conservatio* (Anostraca). **B:** *Limnadia lenticularis,* with cuticular edges of organ marked (arrows). **C:** *Paralimnetis mapimi*. Note four peripheral depressions. **D:** *Lynceus gracilicornis*. Note four peripheral "bumps" (arrows) and possibly fifth, more central, bump.

the apical plasmalemma form irregular loops that are not closely associated with mitochondria, and the plasma membrane extends into large numbers of irregular tubular tufts that differ from true microvilli (Conte, 1984; Lowy and Conte, 1985). Basal and lateral infoldings form an extensive network of tubular reticulum, termed the cytoplasmic labyrinth, that is in direct contact with the hemocoel and is closely associated with numerous mitochondrial complexes (Fig. 19) (Hootman and Conte, 1975; Conte, 1984). These membrane infoldings occupy most of the cell (Figs. 19, 20) (Hootman and Conte, 1975). The cells are also very rich in mitochondria. However, unlike the epithelial layer underlying the epipod cuticle, and contrary to earlier reports that mentioned two distinct cell types (light and dark), the salt gland epithelium consists of a single cell type that exhibits apical to basal polarity (Hootman and Conte, 1975; Lowy and Conte, 1985; Criel, 1991a). These cells also differ from epipod epithelial cells in having large numbers of yolk platelets (Figs. 18, 19) (each of which contains a unique storage product, a symmetrical pyrophosphate ester) and large quantities of glycogen granules (Hootman and Conte, 1975; Lowy and Conte, 1985). These two features apparently provide the larvae with "unique metabolic advantages" for adenosine triphosphate (ATP) production (see Conte, 1984). The cells can be divided into three zones: basal, central, and apical (Fig. 19) (Hootman

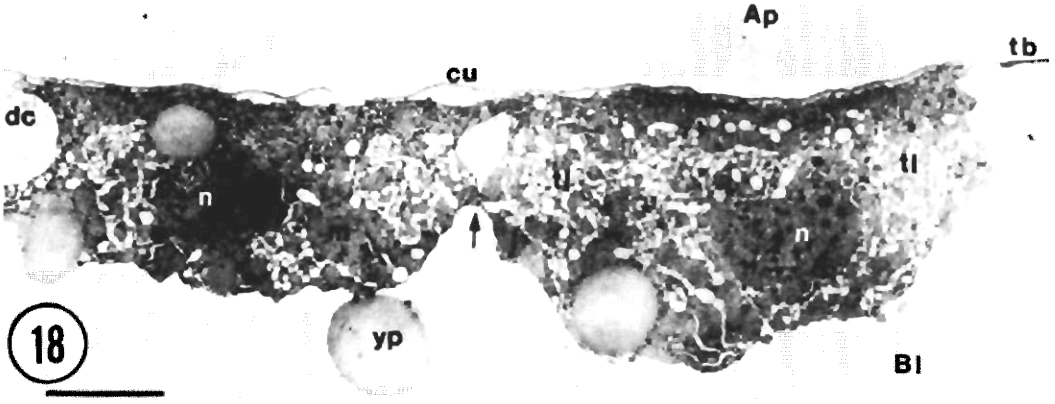

Fig. 18. Low-magnification TEM of an isolated dorsal organ (salt gland) from an *Artemia* nauplius. (From Lowy and Conte, 1985.) Arrow indicates contact between two cells. Ap, apical surface; Bl, basolateral surface; cu, cuticle; dc, damaged cytoplasm (caused by removal of organ from animal); m, mitochondria; n, nucleus; tb, transition band; tl, tubular labyrinth; yp, yolk platelets. Scale bar = 10 μm.

and Conte, 1975). The basal zone contains most of the nuclei, yolk platelets, and other storage products. The central zone contains lightly staining cytoplasm, an abundance of mitochondria, and fewer yolk and storage products. The apical zone has darker staining cytoplasm than the central area and fewer mitochondria. Each cell has a large nucleus with two to five prominent nucleoli. Other cytoplasmic inclusions observed by various authors are Golgi complexes, multivesicular bodies, and smooth and rough ER. Interestingly, most authors state that there is no basement membrane underlying these epithelial cells (Fig. 19), so that the cells are directly bathed by the hemolymph. Consequently, their only contact is with adjacent cells (via apical septate junctions) and with the overlying cuticle, but attachment to the cuticle is strong, evidenced by the fact that disruption of the cell–cell attachment by removal and bending of the entire gland does not result in detachment of cells from the cuticle (Lowy and Conte, 1985). The hemocoelic cell surface is relatively smooth and rounded, with slight protrusions possibly representing tubular labyrinth and internal yolk platelets (Lowy and Conte, 1985).

The necessity of a salt regulatory organ in *Artemia* is underlined by the dramatic shift from reliance on the larval salt gland to reliance on thoracic epipods, accompanied by the disappearance of the larval salt gland, which occurs immediately upon completion of the last instar (Clegg and Conte, 1980).

Function of the organ is now well known in *Artemia,* where it is justifiably called a larval salt gland based on numerous physiological as well as morphological studies (e.g., see review in Conte, 1984). This function is also supported by "micropuncture studies" (Russler and Mangos, 1978) and by the finding of Na^+/K^+-activated ATPase in the organ, mostly on the apical and basolateral cell boundaries (Conte et al., 1977; Conte, 1984; Criel, 1991a). The presence of a small muscle that apparently inserts in the central region of the gland is curious (Hootman and Conte, 1975, fig. 1). Lowy and Conte (1985) note flexion of the organ, probably as a result of this muscle, during naupliar swimming, perhaps helping to force water across the cuticular surface. The organ probably functions in osmoregulation in other orders as well, but there may be other functions. Adhesion has been suggested in some cladocerans, and oc-

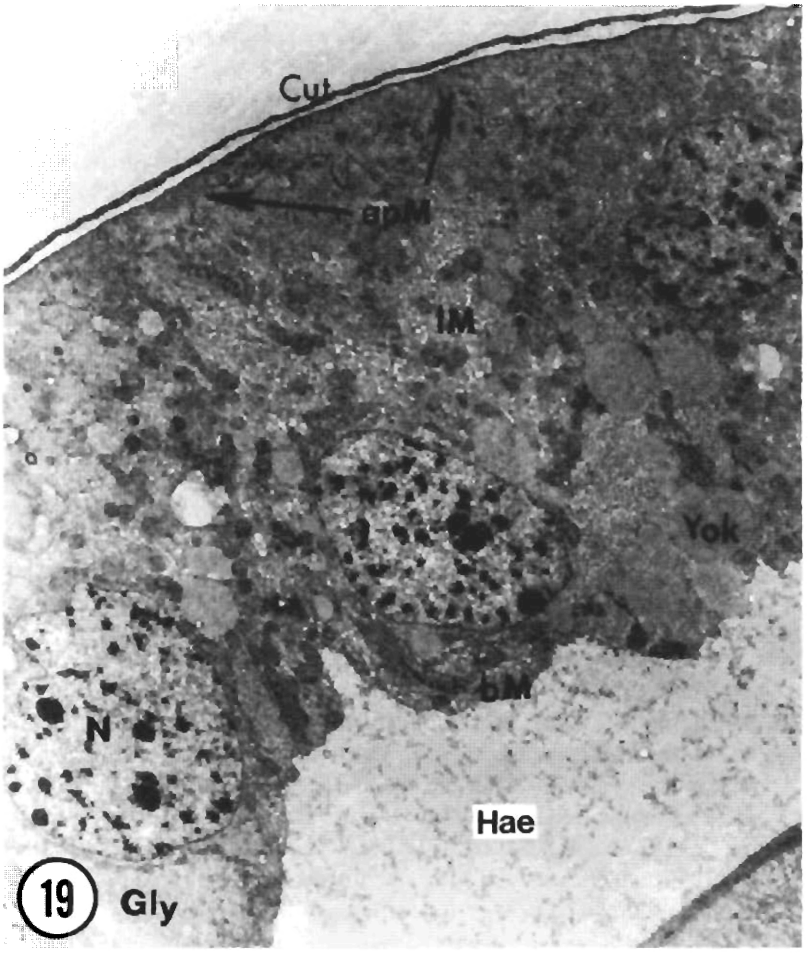

Fig. 19. Transverse section through dorsal organ (salt gland) of *Artemia* nauplius in situ. (From Conte, 1980.) apM, apical membrane amplification; bM, basal cell membrane; Cut, cuticle; Gly, glycogen granules; Hae, hemocoel; lM, lateral cell membranes; N, nucleus; Yok, yolk platelet. ×4,800.

curs at least in *Sida,* but the ultrastructural details of the attachment mechanism, and thus the role of the dorsal organ, are unknown.

Knowledge of ultrastructure in nonanostracan orders is restricted to the Spinicaudata (Rieder et al., 1984), Anomopoda (Halcrow, 1982), Onychopoda (Monoyer and Bussers, 1978; Potts and Durning, 1980; Meurice and Goffinet, 1982, 1983), and Haplopoda (Halcrow, 1985). Rieder et al.'s (1984) description of the organ in the spinicaudatan *Limnadia lenticularis,* in which the organ is borne on a peduncle (diagnostic of the family Limnadiidae, Figs. 16G, 17B), differs from the above account of *Artemia*. For this species, Rieder et al. described five different cell types in the organ's epithelium (Figs. 21, 22A). A central cell, containing many mitochondria and ribosomes and having well-developed microvilli, is surrounded by a ring of two other cell types, which have fewer organelles. Unlike *Artemia, Limnadia* has four nerve fibers (Figs. 21C, 22A) that extend through the epithelium to the overlying cuticle (Rieder et al.,

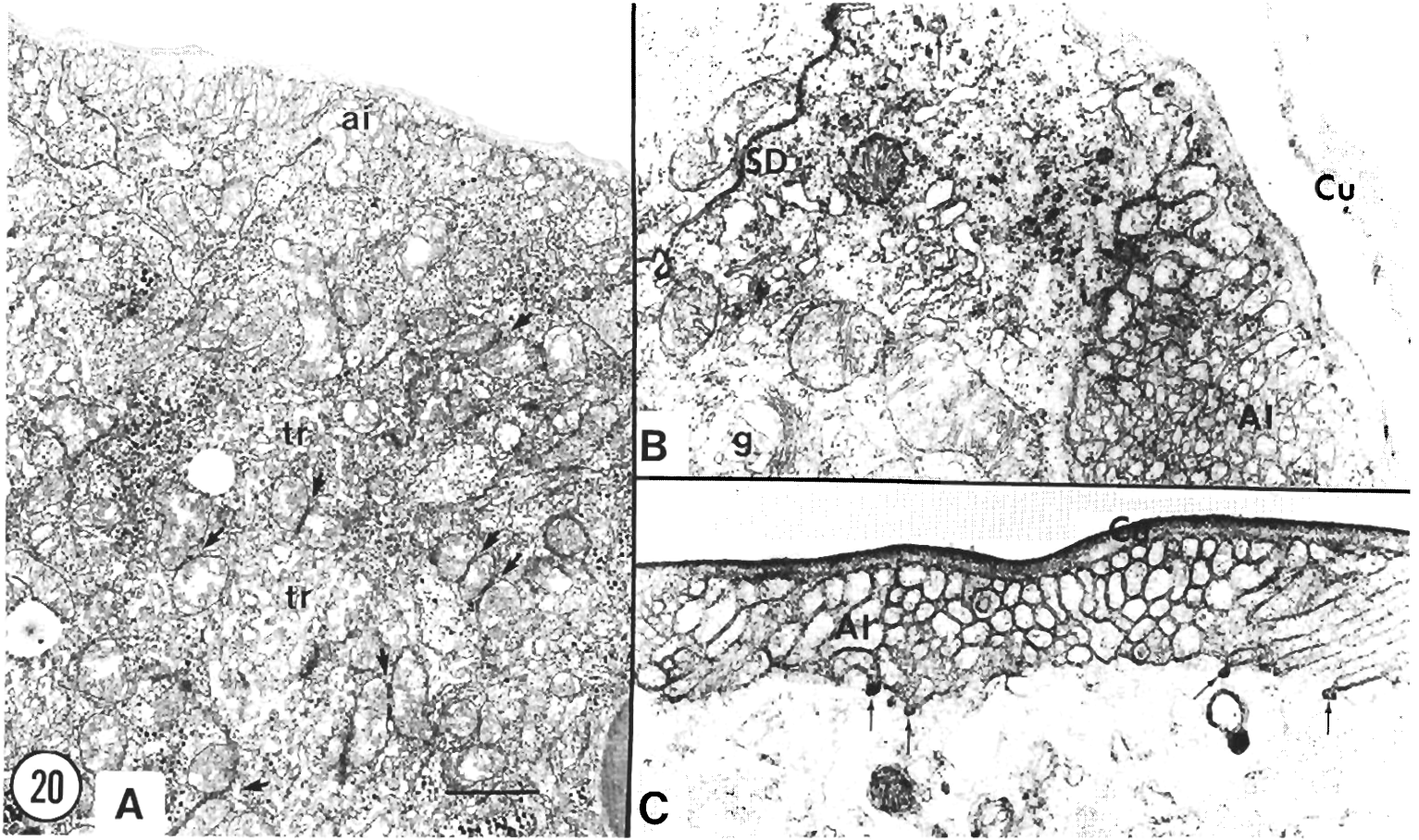

Fig. 20. Dorsal organ (salt gland) of *Artemia*, details of apical region. **A:** TEM showing apical infoldings (ai), tubular reticulum (tr), and areas of mitochondrial pumps (arrows). (After Criel, 1991b.) Scale bar = 1 μm. **B:** Apical zone near cell boundary marked by septate desmosome (SD). Apical infoldings (AI) are not uniform over cell surface. Arrows indicate dense vesicles beneath apical plasmalemma. g, Golgi complex. ×32,000. **C:** Portion of apical zone in which cuticle (Cu) has not detached during preparation. Note extensive apical membrane infoldings (AI), some of which appear in contact with dense vesicles (arrows). ×24,500. (B,C from Hootman and Conte, 1975.)

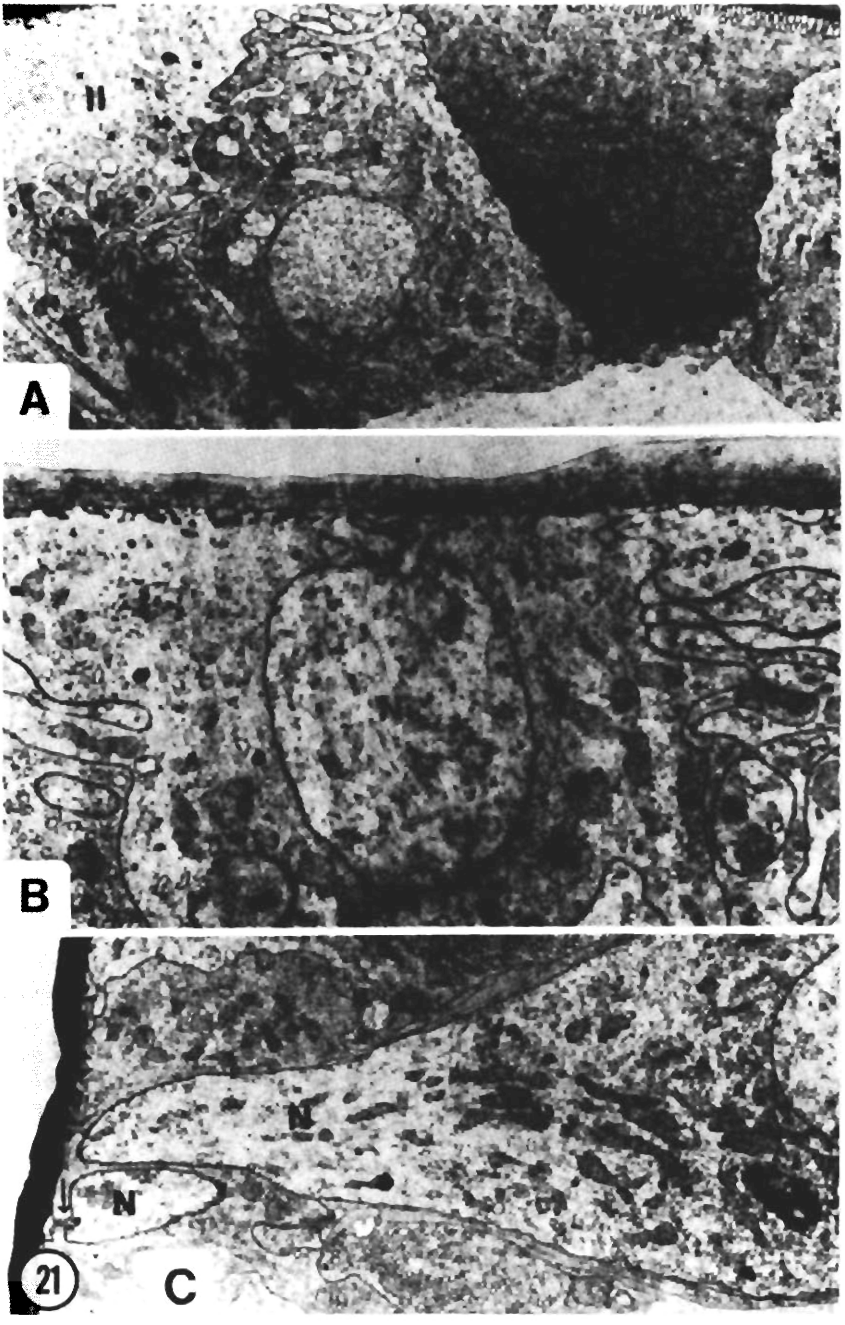

Fig. 21. Pedunculate dorsal organ in the spinicaudatan *Limnadia lenticularis*. (From Rieder et al., 1984.) **A:** Central cell (Z) is rich in mitochondria and appears more dense than surrounding intermediate cells (I, II). Note apical microvilli visible at upper right. ×3,800. **B:** Neurons (N) extending through organ and branching just beneath overlying cuticle. ×3,800. **C:** Higher magnification of neurons (N) extending to cuticle. Arrow marks base of dendrites. ×9,500.

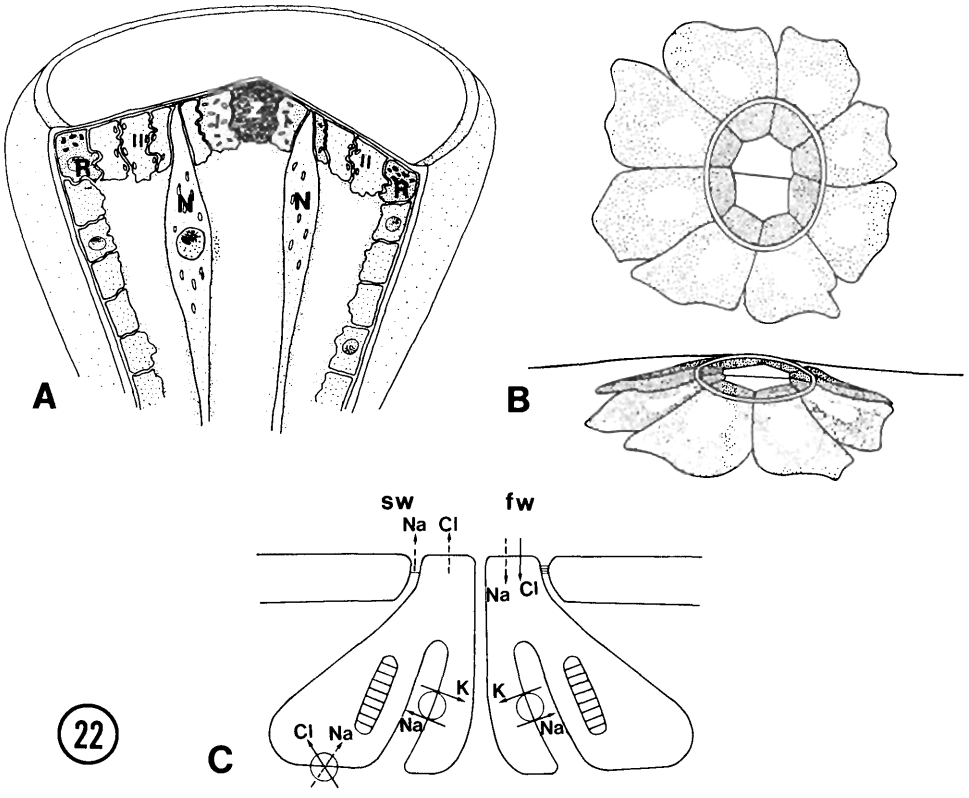

Fig. 22. Reconstruction of dorsal organ in spinicaudatans and onychopods. **A:** Pedunculate dorsal organ of *Limnadia lenticularis* (Spinicaudata). (After Rieder et al., 1984.) Note pair of nerve cells (N) extending to cuticle, central cell (Z), intermediate cells (I, II), and ring cells (R) underlying region of cuticular specialization. **B:** Dorsal and oblique views of organ in *Evadne nordmanni* (Onychopoda) showing eight cells underlying thin "window" of cuticle. **C:** Diagram of possible routes of ion movements through dorsal organ in sea water (sw) and fresh water (fw). Solid lines imply active transport, dashed lines passive diffusion. (B, from Potts and Durning, 1980, after Dejdar, 1931; C, after Potts and Durning, 1980.)

1984), although there is no external indication of four sensory pits as seen in decapod larvae and syncarids (and perhaps laevicaudatans; Martin and Belk, 1988; Martin and Laverack, in press). Curiously, Henry (1948) (figure repeated in Horridge, 1965c) also figured a nerve extending to this organ in the notostracan *Triops* (as *Apus*), possibly suggesting a sensory role, and daphniids also have such a nerve (Fig. 116A). Based on the ultrastructure of these cell types in spinicaudatans, Rieder et al. suggested that the organ functions in the regulation of chloride ions. The structure is apparently the same in the family Leptestheriidae, although it was not illustrated (see Rieder et al., 1984).

The organ is rather well known in developing daphniids (order Anomopoda). Halcrow (1982) described the organ in an SEM examination of developing *Daphnia magna,* in which species the organ is known only from the first instar, and recognized light and dark cells (Fig. 24A,B) plus peripheral cells (Fig. 23B). As in larvae of *Artemia,* the cuticle on the periphery of the organ (the transition band) stains very darkly (Fig. 23B), and the surface area of the apical and basal cell membranes is greatly increased by microvilli and membrane infoldings (Figs. 23A, 24A,B). Mitochondria with prominent cristae are abundant, much more so in the dark (Fig. 24A) than in the light (Fig. 24B) cells, and the

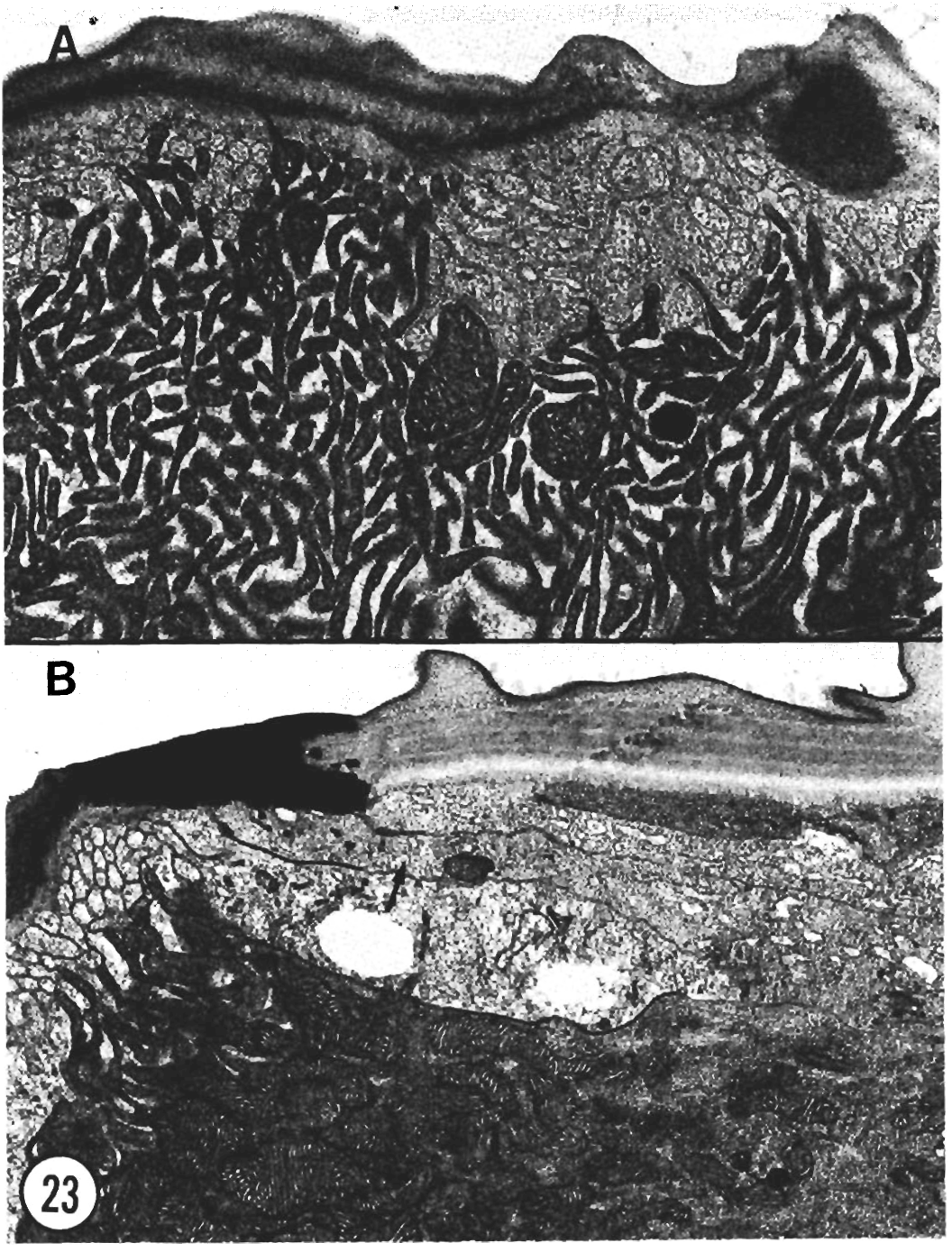

Fig. 23. Dorsal organ in *Daphnia magna*. (From Halcrow, 1982.) **A:** Frontal section of dark and light cell microvilli, some of which contain mitochondria (arrows). ×23,700. **B:** Junction of dorsal organ with adjacent epidermal cell. Perimeter cell (arrow) separates them and is overlain by densely staining cuticle (transition band). ×15,600.