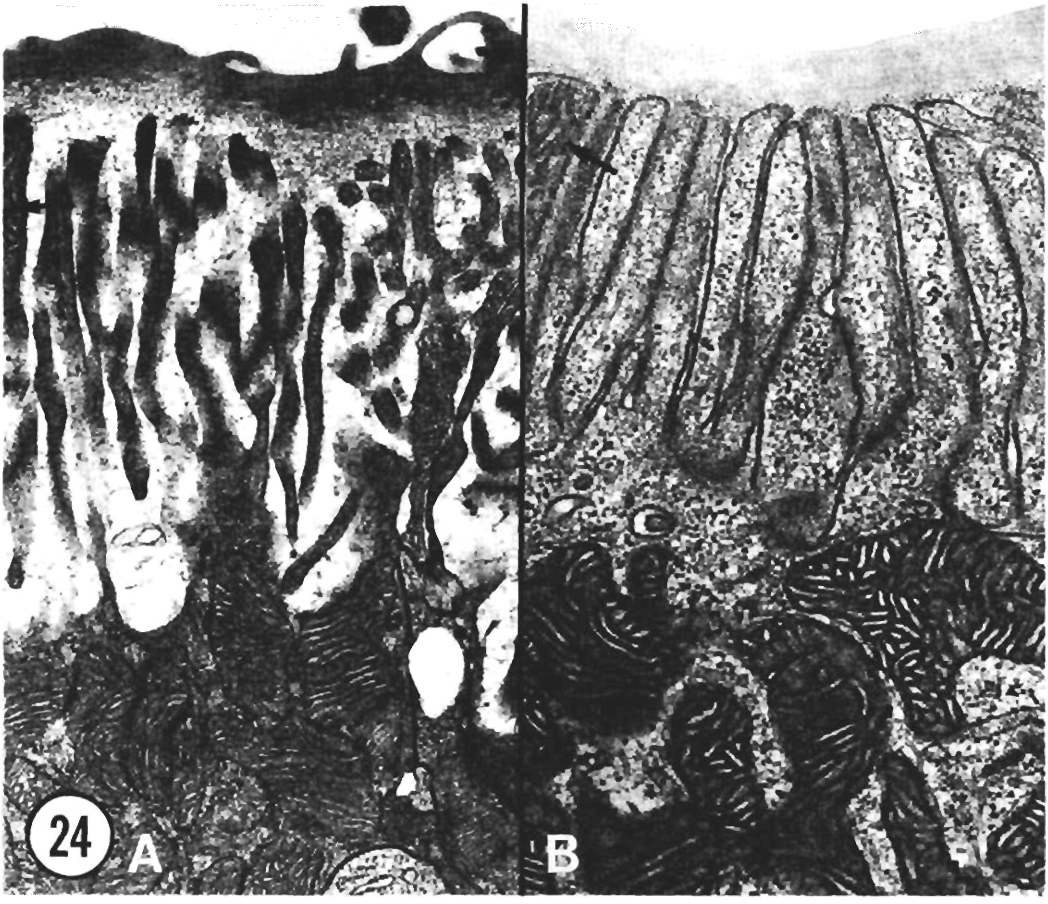


Fig. 24. Microvilli of light and dark cells in dorsal organ of *Daphnia*. (From Halcrow, 1982.) **A:** Dark cell. Note mitochondrion within microvillus (arrow) and branching of some microvilli. ×24,100. **B:** Light cell. Note close packing of microvilli (arrow). ×35,700.

two cell types differ also in the type and amount of apical microvilli. Dark cell microvilli may branch irregularly, are smaller in diameter, and are not as close to one another. In most of the above features, the dorsal organ of *Daphnia* resembles that of larvae of *Artemia*. But they differ in that *Daphnia* has no mitochondrial pump (Copeland, 1966, 1967), the microvilli are more distinct and uniform in appearance, and mitochondria are found within the apical microvilli (Halcrow, 1982). The overlying cuticle is lamellate, seen more easily in oblique sections (Fig. 23B), but is much thinner than that of the surrounding epidermal cells.

The organ in the Haplopoda (*Leptodora*) is a dorsal oval or saddle-shaped structure located posteriorly to the eye, closer to and between the bases of the second antennae (Fig. 25A). Halcrow (1985) noted that in gross morphology it is similar to the organ in other branchiopods, in that the epidermis has two types of squamous cells that differ in electron density (dark and light cells, Fig. 25B), abundant mitochondria containing tubular cristae, extensive interdigitations and infoldings of the basal membranes (Fig. 25C,D), and a thin overlying cuticle separated from surrounding cuticle by a narrow, very dense border (Fig. 25C, arrow). However, the organ in *Lepto-*

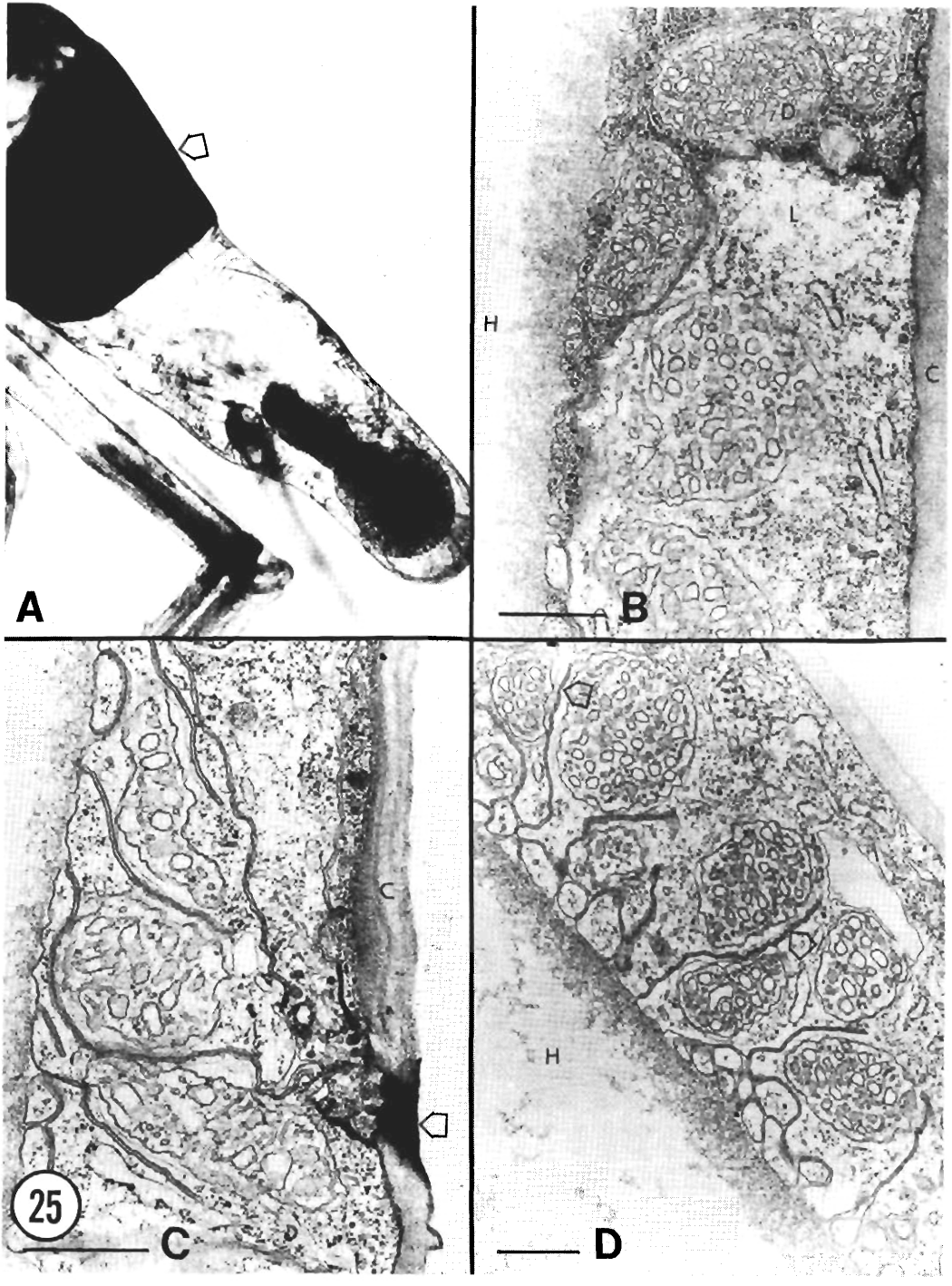


Fig. 25. Dorsal organ in *Leptodora kindtii* (Haplopoda). (From Halcrow, 1985.) **A:** Head, silver stained, showing heavily stained dorsal organ (arrow). ×50. **B:** Transverse section through part of dorsal organ showing junction between light (L) and dark (D) cells. Scale bar = 1 μm. **C:** Transverse section through perimeter of organ. Arrow indicates densely stained cuticle (transition band of some authors) separating organ from surrounding cuticle. Scale bar = 1 μm. **D:** Transverse section through light cell showing two of several infoldings of basal membrane (arrows). Scale bar = 1 μm. C, cuticle; H, hemocoel; L, light cell; P, perimeter cell.

dora differs in that on the apical surface of the cells there are no microvilli, whereas these nearly cover the apical epidermal cell surface in larvae of *Artemia* (e.g., Hootman and Conte, 1975) and in juvenile *Daphnia* (Halcrow, 1985). Halcrow (1985) suggested that this difference might indicate a difference in metabolic activity and/or the fact that the organ in *Leptodora* is so large (and therefore there is less of a need to increase cell surface area to the extent seen in the other taxa). Function was assumed by Halcrow (1985) to be in ion regulation, based on cell structure and similarities with the *Artemia* organ, rather than respiratory, as had been suggested earlier (e.g., Sebestyen, 1931).

The marine genera *Evadne* and *Podon* (Onychopoda) and some related genera also bear a dorsal organ (Fig. 16K,L), which earlier was assigned a respiratory function (Mordukhai-Boltovskoi, 1968) or a glandular function (Monoyer and Bussers, 1978), but in these genera the organ has since been shown to function in ion transport (Potts and Durning, 1980). The cuticular border in both genera is obvious (Fig. 22B), and like the above-mentioned groups there are no pits or pores evident. But there are some differences from what has been described for the dorsal organ of *Artemia*. In *Evadne* and *Podon*, the organ consists of only eight cells found "beneath a thin window in the exoskeleton" (Potts and Durning, 1980) (Fig. 22B). As in *Artemia*, the cells are rich in mitochondria, which, along with an elaborate endoplasmic reticulum, occupy almost the entire cell. The ER tubules or lacunae are confluent with the extracellular fluid through infoldings of the basal and lateral cell membranes (Potts and Durning, 1980), and in this aspect the cells are similar to the salt-regulating cells of *Artemia*'s salt gland and thoracic epipods. Indeed, Potts and Durning (1980) assumed homology with the *Artemia* salt gland and believed that the presence of this "larval" organ in adult onychopods (which have no larval stages) was a case of paedomorphosis. Potts and Durning (1980) also discussed other circumstantial evidence suggesting an osmoregulatory function; the osmolarity of the hemolymph was shown by Khlebovich and Aladin (1976) to be equal to that of the "marsupial fluid" (within the brood pouch formed by the modified carapace) of *Evadne* prior to development of this organ, after which time the brood pouch fluid rose in concentration compared to the surrounding sea water. Finally, Potts and Durning (1980) noted how easily an organ specialized for salt excretion could be modified for salt uptake, the hypothesized role of this organ in freshwater onychopods and perhaps other branchiopods (Fig. 22C).

In some Laevicaudata, the organ displays a 4 + 1 arrangement of bumps or pits (Fig. 17C,D) (Martin and Belk, 1988), which is remarkably (but perhaps superficially) similar to the structure of the dorsal organ in syncarids and larval decapods (Martin and Laverack, in press). In the syncarids and decapods, a central pit or pore is surrounded by the four peripheral pits, and this is not seen in the Laevicaudata. Although a central "bump" is sometimes seen (Martin and Belk, 1988), there is never a pore.

It is interesting to note that the Upper Cambrian *Rehbachiella kinnekullensis* from the Orsten fauna of Sweden, a marine species close to the anostracan lineage of the Branchiopoda, may have a dorsal organ (Walossek, in press). Early developmental stages of this species bear a conspicuous platelike area on the head shield, and Walossek (in press) describes two pairs of pits or pores on this plate and discusses the similarity of the organ in Upper Cambrian and Recent branchiopods.

GLANDS AND SECRETIONS

Branchiopods exhibit a wide diversity of glands or glandlike structures, the function of which in many cases is incompletely known. Several of these structures are treated in other sections (e.g., see Reproductive Components for shell and accessory glands; Excretory System for antennary and maxillary glands; Integument for integumentary glands and dorsal

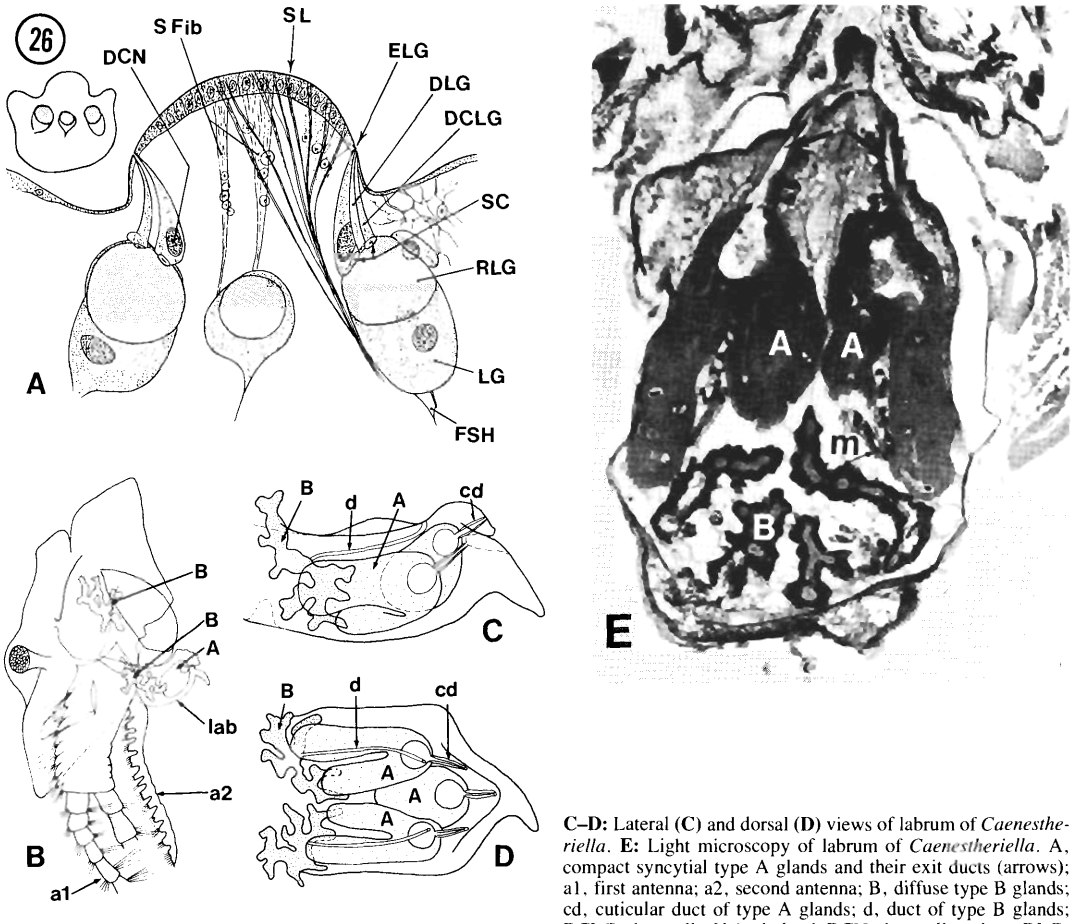


Fig. 26. Labral glands in the Anostraca and Spinicaudata. **A:** Labrum of developing (stage 24) *Branchinecta ferox* (Anostraca). (From Fryer, 1983.) **B–E:** Labral glands of the spinicaudatan *Caenestheriella*. (After Larink, 1972.) **B:** Head of *Caenestheriella*, showing location of labral and similar head glands. **C–D:** Lateral (**C**) and dorsal (**D**) views of labrum of *Caenestheriella*. **E:** Light microscopy of labrum of *Caenestheriella*. A, compact syncytial type A glands and their exit ducts (arrows); a1, first antenna; a2, second antenna; B, diffuse type B glands; cd, cuticular duct of type A glands; d, duct of type B glands; DCLG, duct cell of labral gland; DCN, duct cell nucleus; DLG, exit duct of labral gland; ELG, exit of labral gland reservoir; FSH, fibrous sheet suspending labral glands; lab, labrum; LG, labral gland; m, muscle; RLG, reservoir of labral glands; SC, sphincter cells; S Fib, suspensory fibrils; SL, upper (morphologically ventral) surface of labrum.

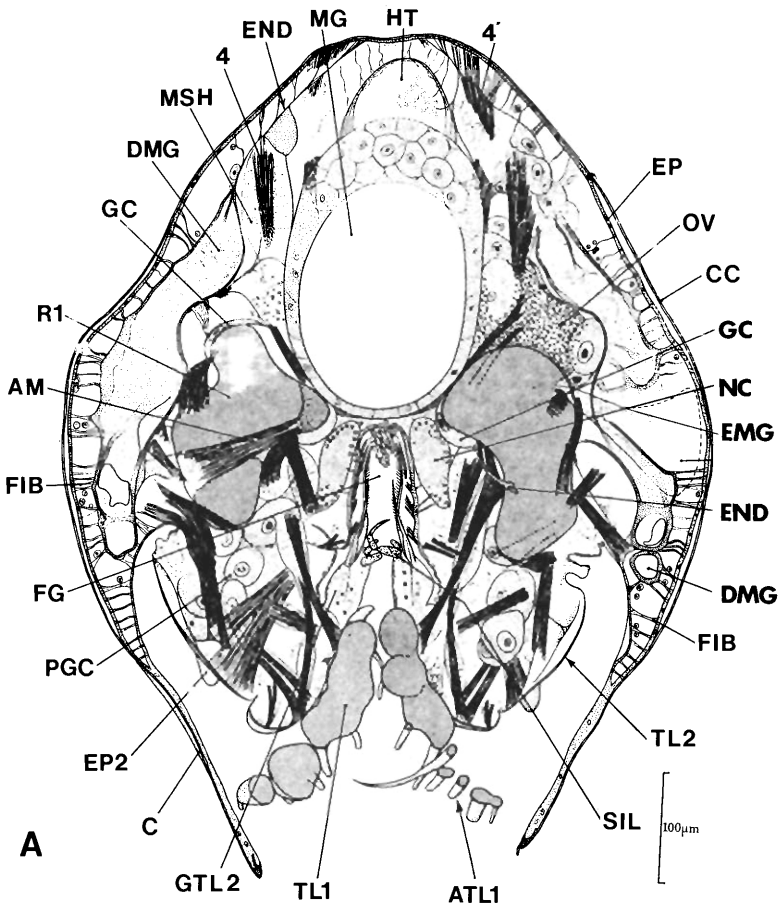
organs; and Digestion for digestive ceca). A few known glands have been omitted because I have been unable to locate adequate anatomical treatments; an example is the transitory mandibular gland that appears early in ontogeny but has disappeared by the adult stage in *Artemia* (Warren, 1938).

Labral Glands

The labrum in most branchiopods is large and fleshy, and labral glands typically exist as paired structures with clearly defined ducts exiting on the posterior (functionally upper) labral surface (e.g., Bernard, 1892; Nowikoff, 1905; Cannon, 1922, 1935b; Eriksson, 1934; Nicholson and Yonge, 1935; Dornesco and Steopoe, 1958; Fryer, 1962, 1983, 1991a; Martin, 1989a). The exception is the Notostraca, where the labrum is a flat shield-like plate that apparently contains no glands in adults (Fryer, 1987c, 1988). Although labral glands might best be considered part of the integument, as the ducts actually exit the body, or perhaps part of the feeding system,

as they clearly play a part in ingestion of particulate matter in several groups, I have treated them separately here because their exact function(s) remain uncertain in some taxa. Labral glands occur in all anostracans, at least in developmental stages. Even in nonfiltering species such as *Branchinecta ferox,* the glands exist but degenerate by the adult stage, not surprising in light of the fact that adults of *Branchinecta ferox* are predators and no longer need an entangling fluid for binding particulate matter (see Fryer, 1983), but the glands persist in filtering species. For early stages of *Branchinecta ferox,* Fryer (1983) described three glands (Fig. 26A), with the medial one degenerating before the two lateral glands during ontogeny. Each gland has an associated duct formed by two duct cells and exiting on the ventral (functionally upper) surface of the labrum, and a rather large reservoir presumably acting as a storage site for the secretory product (Fig. 26A). Labral glands are present in all conchostracan families (e.g., Shakoori, 1968; Martin et al., 1986; Martin, 1989a) and were described in some detail by Larink (1972), who recognized, in spinicaudatans, two different types (Fig. 26C–E). Type A glands are compact and form a syncytium containing numerous and "often ramified" nuclei; Larink (1972) found three of these, each with a "cuticular duct," in the distal region of the labrum in the cyzicid *Canestheriella.* More basally located are type B glands, described by Larink (1972) as being diffuse, with small unramified nuclei and with no reservoirs but with two ducts per gland. Curiously, Larink also reported additional type B glands on either side of the head, but these apparently have no connection with the labral glands (Fig. 26B). Labral glands are also well known for all of the "cladoceran" groups (Figs. 27, 28). Cannon (1922) first adequately described the gland cells in *Simocephalus,* and Sterba (1957a) added the observation that the large nuclei of the gland cells become highly polyploid through endomitosis; indeed at 2,048-ploid these cells have "perhaps the highest ploidy of any known cells" (Fryer, 1991a: 39). Labral glands and their secretions in the Anomopoda have been extensively discussed in a series of papers by Fryer (1962, 1963, 1968, 1974, 1991a). Although present in nearly all taxa, they may not always be secretory; Fryer (1968) mentioned several curious cases, such as *Alonopsis elongata,* in which the labral glands and associated ducts are well developed (Fig. 28C) but no secretions have ever been observed. It is possible in this and other species that copious secretions from the trunk limb glands (see below) have assumed the role of the labral gland secretions. In some macrothricids (Fig. 27A,B), the reservoirs of these glands are enormous, sometimes extending dorsally into the head (e.g., some species of *Macrothrix, Onchobunops,* and *Streblocerus;* Fryer, 1974). Recent ultrastructural studies of labral glands in daphniids (Zaffagnini and Zeni, 1987) indicate that at least some anomopod labral glands exist as three "distinct functional units on each side" of the labrum, the units being: (1) several cells at the base of the head, (2) two large cells at the base of the labrum and a large cell ("cell A") in the median part of the labrum, and (3) one large cell ("cell B"), also located medially (Fig. 29A). These three functional units, which are comparable to the class 3 category of insect exocrine glands (Noirot and Quennedey, 1974), do not appear to correspond closely to Larink's (1972) description for cyzicid spinicaudatans. Contrary to previous accounts of cladoceran labral glands, the gland cells in *Daphnia* do not occur in a syncytium (Zaffagnini and Zeni, 1987). All cells except "cell B" (which contains a distinctive and unusual cytoplasmic ultrastructure that is not yet fully understood) contain well-developed rough endoplasmic reticulum and Golgi complexes (Fig. 29B). Activity of the Golgi complexes changes during the molting cycle and differs among the cell types.

Cells at the base of the head have well-defined plasma membranes and are usually in close contact, but occasionally may be separated by a slight space containing electron-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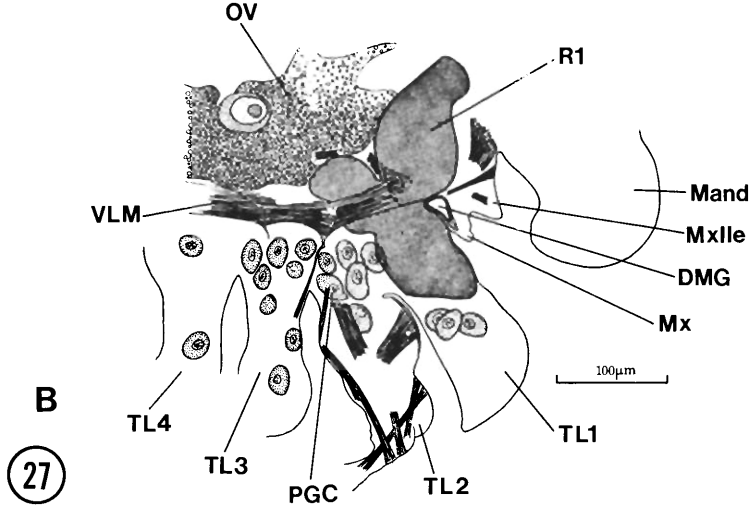
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dense material (Fig. 29C). Their cytoplasm contains free ribosomes, polymorphous mitochondria (some of which are "giant," according to Zaffagnini and Zeni), numerous tubular cristae, many large Golgi complexes (dictyosomes), and well-developed RER organized in parallel tubes; the latter are especially obvious in the more interior cells bathed directly by the hemolymph (Fig. 29B–D). Those cells at the base of the head that are in contact with the cuticle additionally contain pinocytotic vesicles.

The pair of large anterior gland cells near the base of the labrum bears several interesting features (Fig. 30), including a visible plasma membrane (in contrast to Cannon's [1922] view) that is thin, sinuous, and widely separated in the middle region of the zone of contact (Fig. 30A), possibly delimiting what Cannon (1922) thought was a poorly defined reservoir of secretion (Zaffagnini and Zeni, 1987). However, at the beginning of this zone and intermittently along its length, the cell membranes are bound by intermediate junctions, or "zonulae adherentes" (Zaffagnini and Zeni, 1987: 24). Cytoplasm of these cells is rich in free ribosomes, RER, Golgi complexes (Fig. 30C) with associated electron-dense microvesicles (some of which are interconnected by a tubular component) adjacent to distal cisternae, variously shaped (sometimes cup-shaped) mitochondria, and autophagic vacuoles (Fig. 30D) (see Zaffagnini and Zeni, 1987, for further details).

Fig. 27. An example of large labral glands with enormous reservoirs in a macrothricid (Anomopoda), *Ophryoxus gracilis*. (From Fryer, 1974.) **A:** Transverse section through second trunk limbs, anterior view. **B:** Longitudinal section left of midline, as seen from inside, showing extent of large reservoir (R1) of trunk limb 1 containing entangling secretion. 4′, remotor roller muscles of mandible; AM, adductor muscle of carapace; ATL1, armature of trunk limb 1; C, carapace; CC, carapace cuticle; DMG, duct of maxillary gland; EMG, end sac of maxillary gland; END, endoskeleton; EP, epidermis; EP2, epipod of trunk limb 2; FG, food groove; FIB, suspensory fibers; GC, gland cells; GTL2, gnathobase of trunk limb 2; HT, heart; Mand, mandible; MG, midgut; MSH, muscle sheath; Mx, maxilla; Mxlle, maxillule; NC, left ventral nerve cord; OV, ovary; PGC, gland cells within cavity of limb; R1, enormous reservoir of trunk limb 1; SIL, setae of inner lobe of trunk limb 1; TL 1–4, trunk limbs 1–4; VLM, ventral longitudinal trunk muscles.

The posterior pair of cells (Fig. 31A) includes two different types (cell A and cell B of Zaffagnini and Zeni, 1987). The cytoplasmic ultrastructure of the anteroventral cell (cell A) is very similar to that of the cells of the anterior gland cells (above). Cell B differs markedly from cell A, and thus from the anterior gland cells, in that the cytoplasm between the nucleus and the cell membrane closest to cell A contains "large circular areas of a slightly electron-dense granular matter" (Zaffagnini and Zeni, 1987: 27). This area of cytoplasm lacks Golgi complexes, has fewer and smaller mitochondria, contains large circular areas of electron-dense matter, and "probably corresponds to the zone of accumulation of secretion vacuoles described by previous investigators" (Zaffagnini and Zeni, 1987: 27). Remaining cytoplasm in cell B bears few, large Golgi apparati, short tubules of RER, and normal-sized mitochondria.

The labral gland secretions were assumed by Zaffagnini and Zeni (1987) to flow into the hemolymph after accumulation in large intercellular spaces, which, if true, is very unusual. The four larger cells (the pair at the base of the labrum and cells A and B) are in contact with a duct cell (Fig. 31A) or possibly several duct cells characterized by a marked infolding of the plasma membrane (Fig. 31B,C) (Zaffagnini and Zeni, 1987). A narrow lumen is formed by the duct cell(s) (Fig. 31A–C), but no passage of substance from the glands to the duct cell(s) was observed.

The secretory product of the labral glands in many branchiopods functions to entangle food particles to facilitate handling by the mouthparts and ingestion. This function was first suggested by H.G. Cannon for a variety of branchiopod groups (e.g., Cannon, 1922, 1924, 1928, 1933, 1935b) and has been confirmed for many anomopods (e.g., Fryer, 1962, 1963, 1968, 1974, 1991a; Zeni and Franchini, 1990). In anomopods, the copious secretions are mixed with food particles by actions of the maxillules and lobes of the first trunk limbs; these secretions may work in conjunction with secretions from more poste-

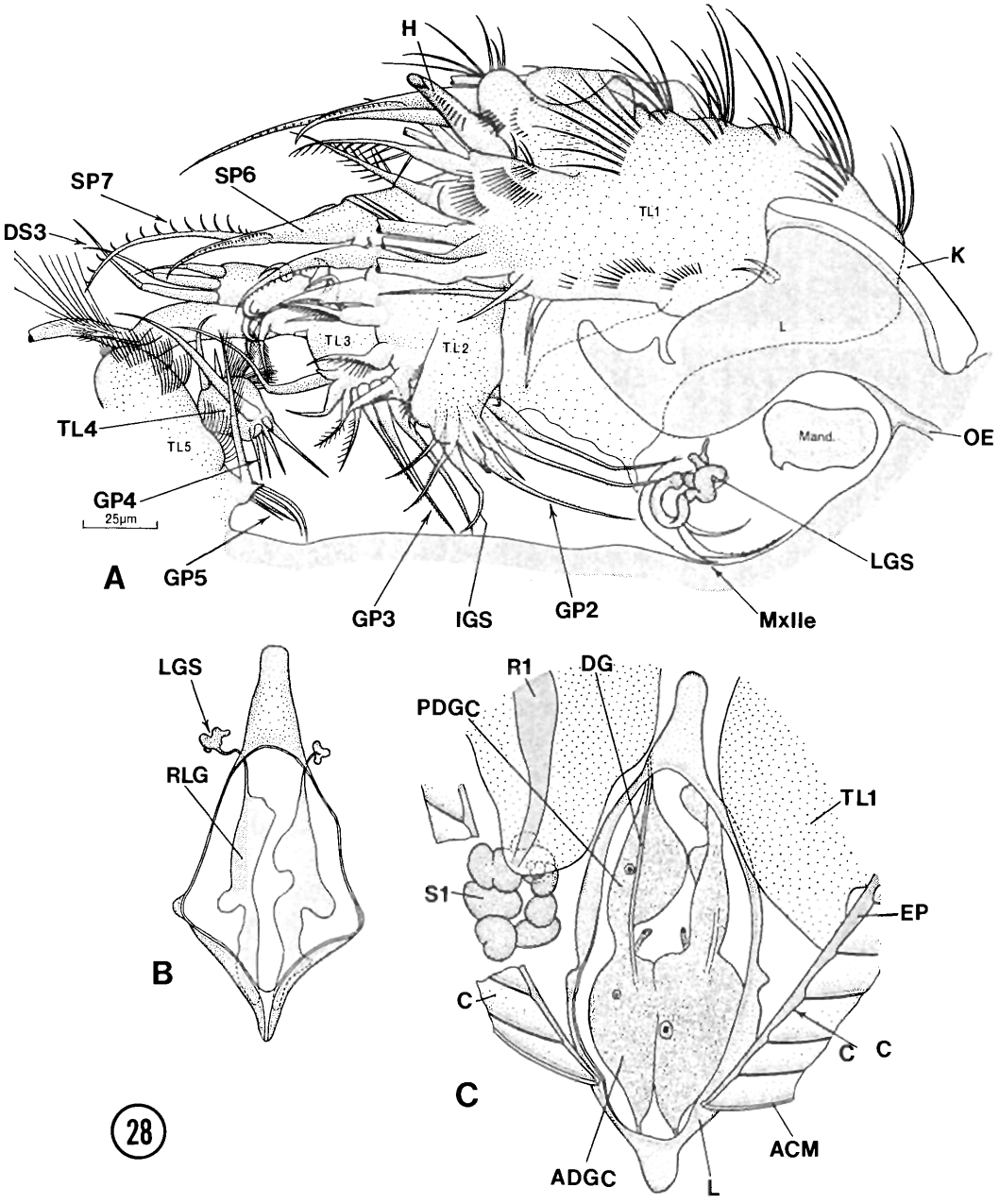

Fig. 28. Labral glands in the Chydoridae (Anomopoda). (After Fryer, 1968.) **A:** Median longitudinal section through *Pseudochydorus globosus* showing limbs modified for grasping, dragging, pushing, and forking, and labral gland secretions (LGS) near maxillule (MxIle). **B:** Horizontal slice through labrum of *Peracantha truncata* showing large reservoirs (RLG) storing entangling secretions of labral glands secretory product (LGS) exiting from ducts. **C:** Horizontal slice through region of labrum and first trunk limbs of *Alonella elongata*, showing well-developed labral glands, which have not been observed to produce secretions, and copious production of entangling secretions from trunk limb 1. ACM, anterior carapace margin; ADGC, anterior distal gland cells; C, carapace cuticle; DG, duct of labral glands; DS3, distal scraping spines of trunk limb 3; EP, epidermis; GP2–5, gnathobasic plate of trunk limbs 2–5; H, large hook of trunk limb 1; IGS, internal gnathobasic spine; K, keel of labrum; L, labrum; LGS, labral gland secretions; Mand., mandible; MxIle, maxillule; OE, esophagus; PDGC, posterior distal gland cell; R1, reservoir of trunk limb 1 containing entangling secretions; RLG, reservoir of labral gland; S1, entangling secretion issuing from trunk limb 1; SP6–7, modified sixth and seventh spines of endite 2 (see Fryer, 1968); TL1–5, trunk limbs 1–5.

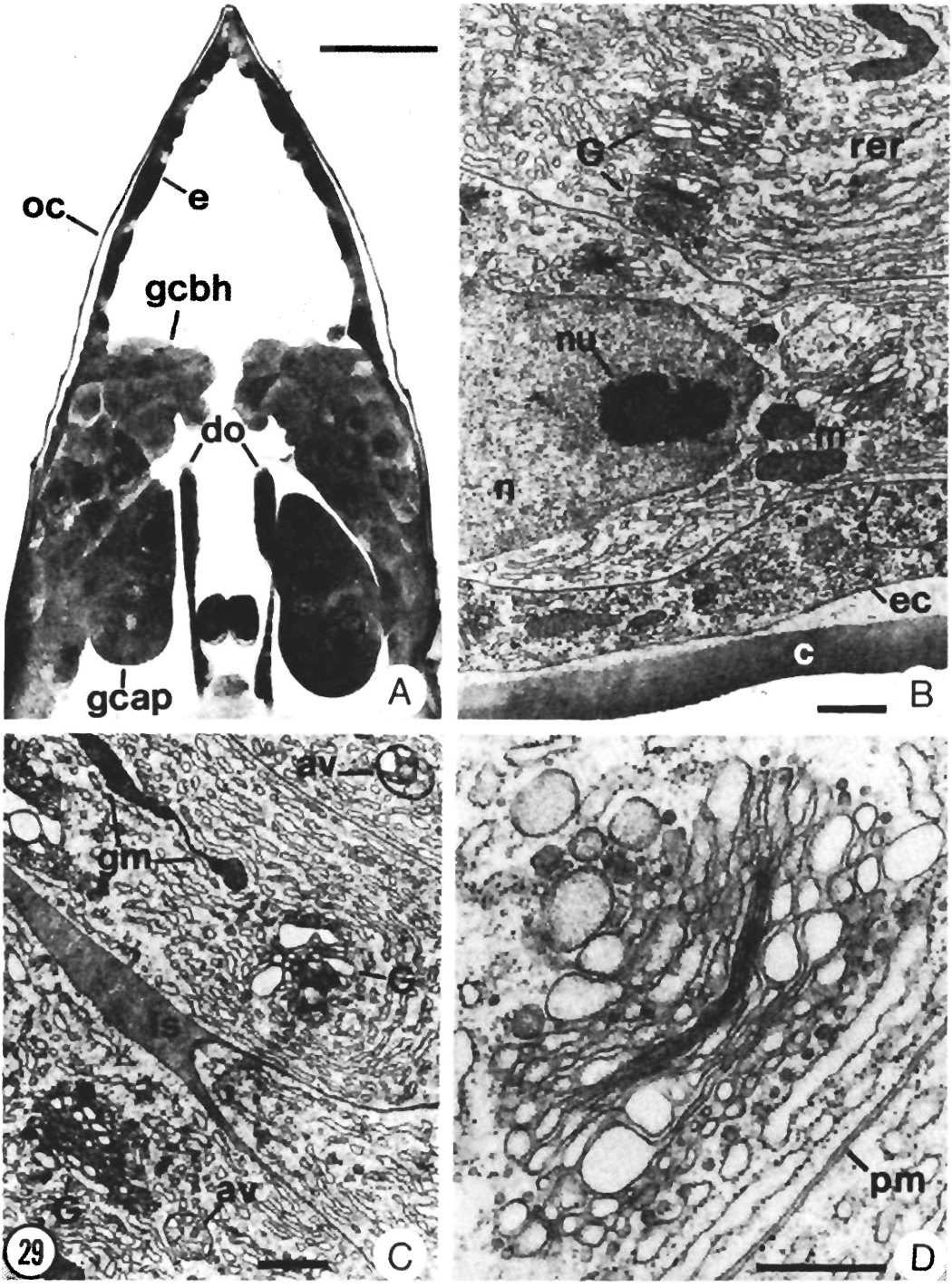

Fig. 29. Labral glands of *Daphnia obtusa* (Anomopoda), base of the head. (From Zaffagnini and Zeni, 1987.) **A:** Cross section at the level of the base of the head. Scale bar = 40 μm. **B:** Gland cells of the head base in contact with epidermis. Scale bar = 1 μm. **C:** Contact zone between gland cells at head base showing enlarged portion of intercellular space (is) filled with slightly electron-dense matter. Scale bar = 1 μm. **D:** Golgi complex of gland cell at head base. Scale bar = 0.5 μm. av, autophagic vacuole; c, cuticle; do, dilator muscles of esophagus; e, epidermis; ec, epidermal cell; G, Golgi complexes; gcap, gland cells of anterior pair of labrum; gcbh, gland cells at base of the head; gm, giant mitochondrion; m, mitochondria; n, nucleus; nu, nucleolus; oc, old cuticle; pm, plasma membrane; rer, rough endoplasmic reticulum.

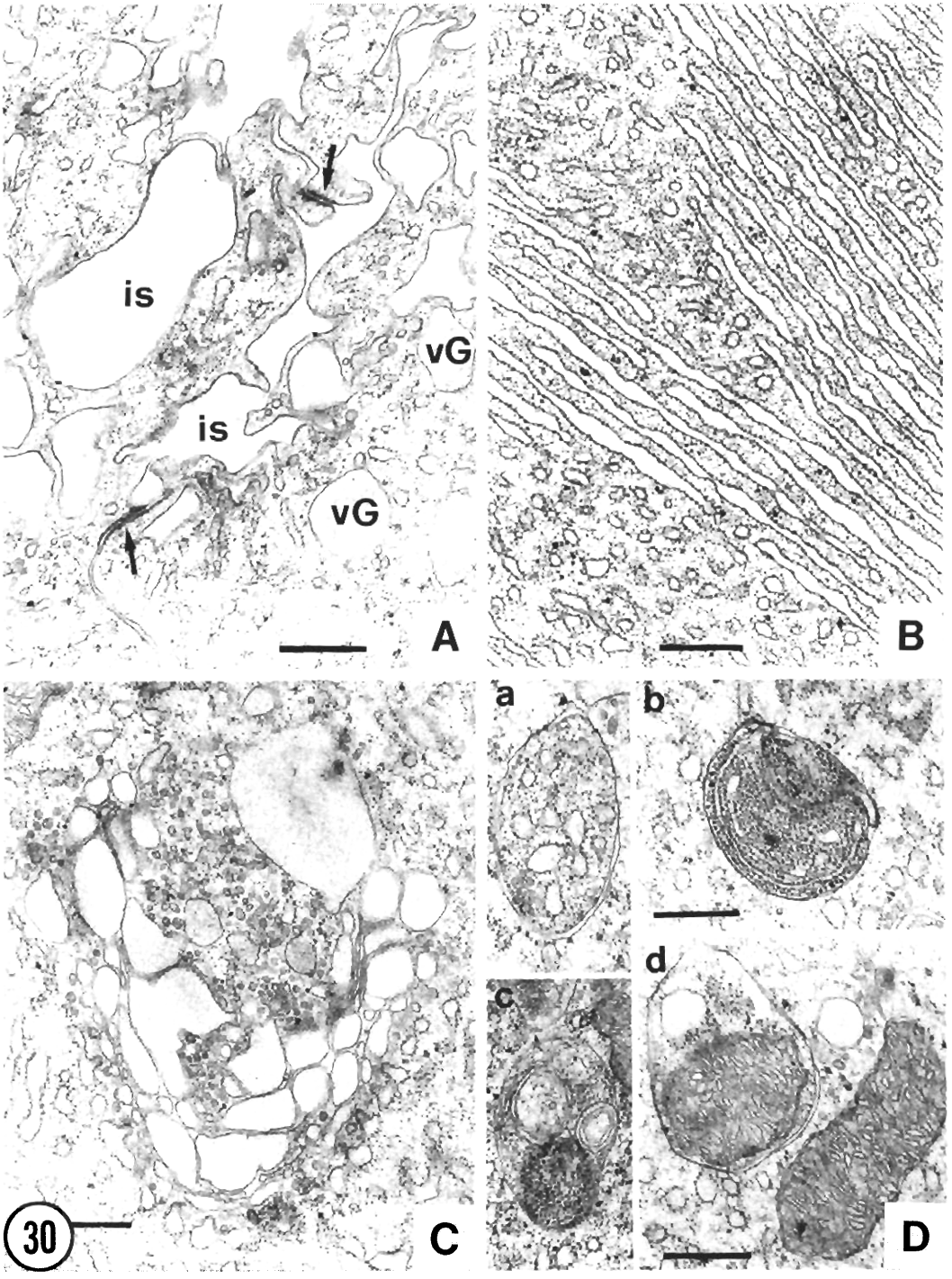

Fig. 30. Labral glands of *Daphnia obtusa,* anterior pair. (From Zaffagnini and Zeni, 1987.) **A:** Detail of central contact zone. Membranes are sinuous and far apart, forming wide intercellular spaces (is) and joined by intermediate junctions (arrows) when in contact. **B:** Cytoplasm of gland cell showing RER arranged in parallel tubules. **C:** Golgi complex of gland cell. **D:** Features of autophagic vacuoles of gland cells, including structures unique to newly formed vacuoles **(a,b),** vacuole in which the cytoplasmic content is undergoing degeneration **(c),** and vacuole containing one mitochondrion not yet degenerated **(d).** Scale bars = 0.5 μm. vG, vesicles from Golgi complex.

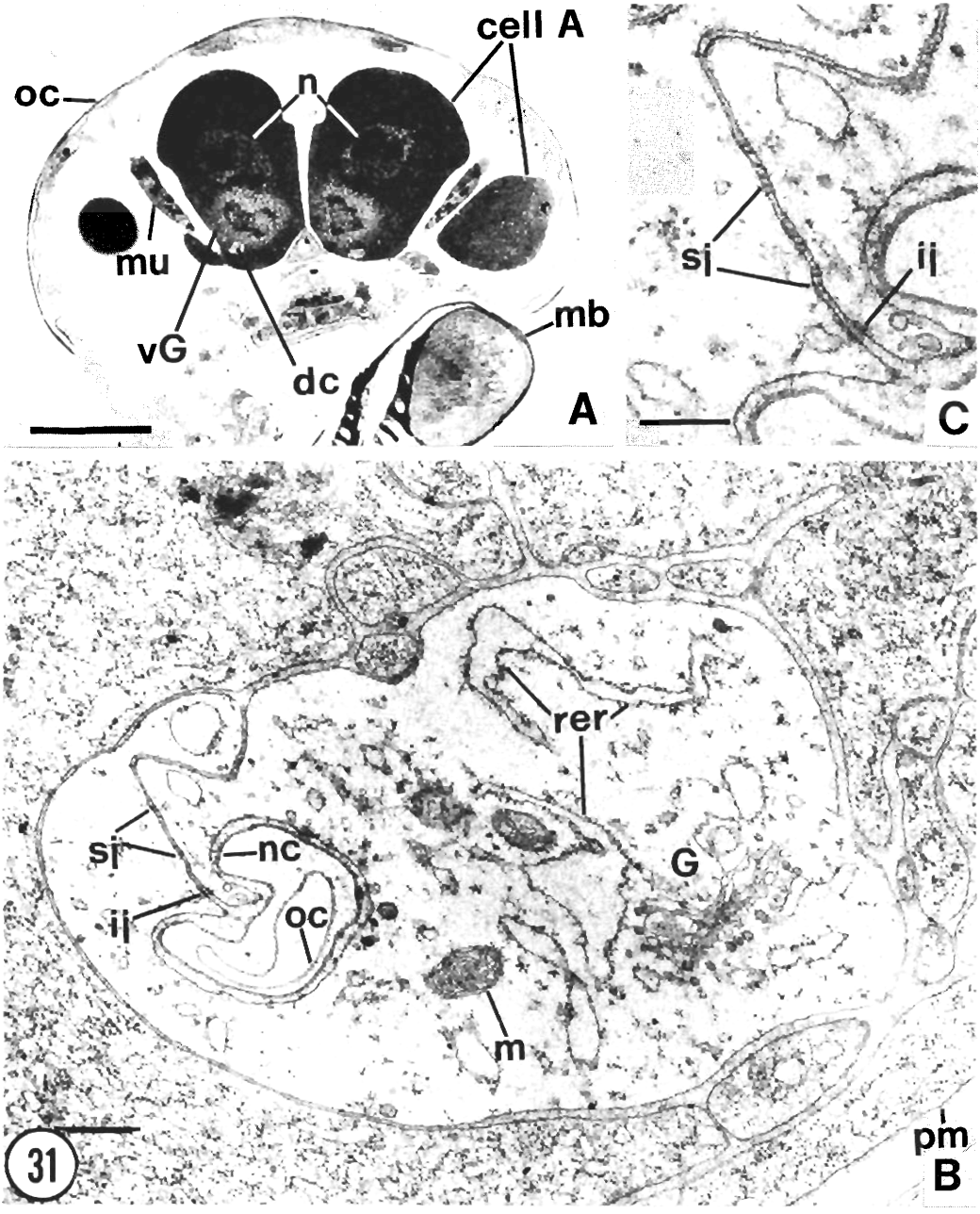

Fig. 31. Labral glands of *Daphnia obtusa*, cross section through labrum during stage of new cuticle secretion. (From Zaffagnini and Zeni, 1987.) **A:** Low magnification showing location of posterior pair of cells (cell A) on either side. Scale bar = 40 μm. **B:** Cross section of duct cells (dc in A) at same level as in A. Note no direct communication between duct cell (delimited by new cuticle, nc) and zone of vesicles from Golgi complex of cell A. Scale bar = 0.5 μm. **C:** Detail of B showing two types of junctions, septate (sj) and intermediate (ij), along infolded portion of plasma membrane of duct cell. Scale bar = 0.25 μm. dc, duct cell; G, Golgi complex; ij, intermediate junction; m, mitochondrion; mb, mandible; mu, muscle; n, nucleus; nc, new cuticle of duct; oc, old cuticle; pm, plasma membrane of gland cell; rer, rough endoplasmic reticulum; sj, septate junction; vG, accumulation zone of vesicles from Golgi complex.

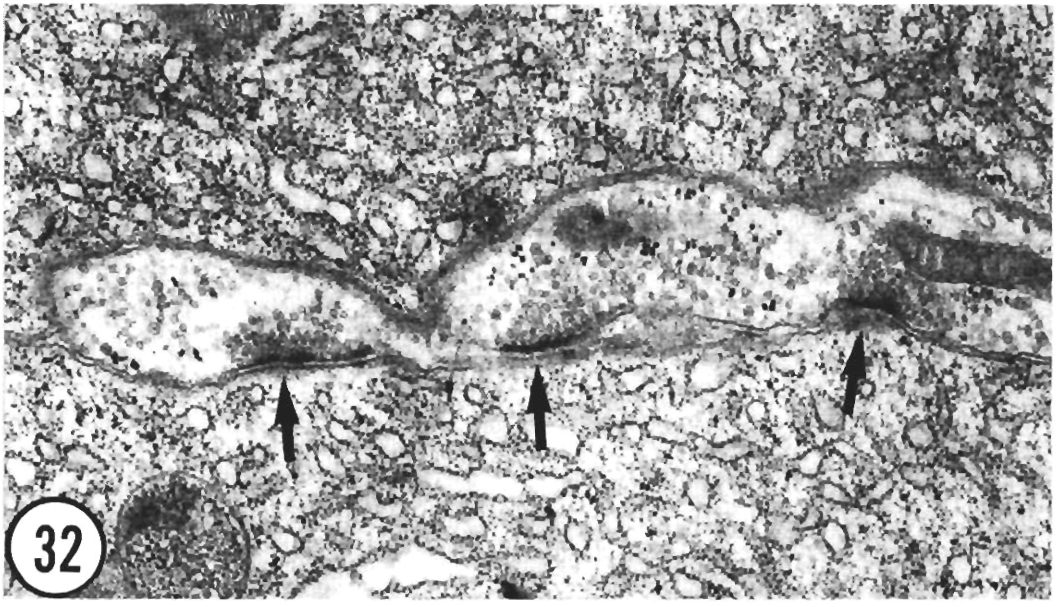

Fig. 32. Nerve fiber between the two cells of the anterior pair of labral glands of *Daphnia*. Three presynaptic zones are visible (arrows). (From Zeni and Zaffagnini, 1988.)

rior trunk limb glands in some anostracans and anomopod cladocerans (Fryer, 1962, 1983, 1991a). The secretions are largely glycoproteins (Zeni and Franchini, 1990). At least in daphniids, the secretory product has been suggested to contain, in addition, proteolytic enzymes and possibly even hormones (Zaffagnini and Zeni, 1987), although neutral polysaccharides that do not seem to be enzymatic are also present (Fryer, 1991a), and Sterba (1957a,b) found no evidence for digestive enzymes. Schram (1986), attempting to explain why some species that on preliminary inspection might not seem to need an agglutinizing agent (e.g., the scavenging *Pseudochydorus globosus*) nevertheless have large glands, suggested the possibility of a surfactant in such secretions, but such a compound has not yet been identified. Finally, "the idea that the labral glands may control the metabolism (molt cycle?) and with it the maturation of the ovaries" was considered a valid hypothesis by Zaffagnini and Zeni (1987: 33). Zaffagnini (1964) attributed to these glands (in particular to the cells at the base of the head) a possible endocrine function, but that has not yet been demonstrated.

Innervation of labral glands was first suggested by Cannon (1922) for the daphniid anomopod *Simocephalus* and recently was confirmed by Zeni and Zaffagnini (1988) for *Daphnia obtusa* (Figs. 32, 33). Nerve fibers innervate both pairs of gland cells of the labrum, but not the gland cells at the base of the head (which may have some endocrine function, and have even been suggested to aid in the formation of cuticle; see Zaffagnini, 1964, and Zaffagnini and Zeni, 1987); neuronal contact is on the cell membranes on the surface of the cell or within infoldings of the plasma membrane. Axonal processes are either single or double and lack glial wrappings, contacting the cells as naked sheaths (Zeni and Zaffagnini, 1988). Nerve fibers contain round or oval vesicles that vary in size and density, ranging in size from 46–100 nm (most often 70–80 nm) for larger, more granular vesicles with electron-dense cores, and