

Fig. 119. Nerve fibers in the supraesophageal and optic ganglia of *Daphnia schoedleri*. (From Bohm and Parker, 1968.) **A:** Cross section of nerve fibers in supraesophageal ganglion, showing neurofilaments in cross section (long arrows) that bear minute radiating strands (small arrows.)  $\times 48,000$ . **B:** Large (at lower left) and small concentric lamellar structures in the optic ganglion.  $\times 13,860$ . 2, small whorl; G, glial cytoplasm; M, mitochondrion associated with large whorl; S, synapse.

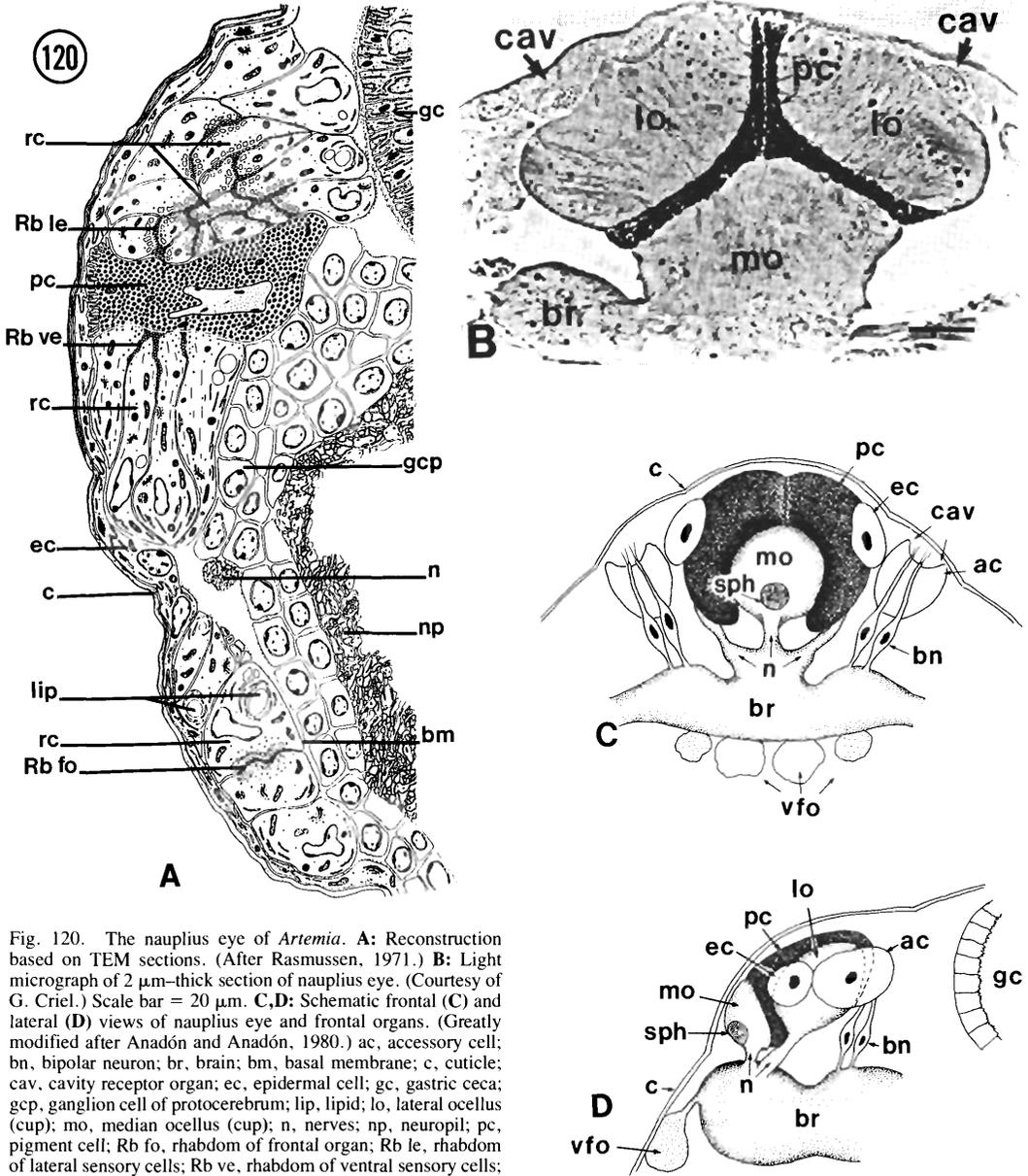


Fig. 120. The nauplius eye of *Artemia*. **A**: Reconstruction based on TEM sections. (After Rasmussen, 1971.) **B**: Light micrograph of 2 μm-thick section of nauplius eye. (Courtesy of G. Criel.) Scale bar = 20 μm. **C,D**: Schematic frontal (**C**) and lateral (**D**) views of nauplius eye and frontal organs. (Greatly modified after Anadón and Anadón, 1980.) ac, accessory cell; bn, bipolar neuron; br, brain; bm, basal membrane; c, cuticle; cav, cavity receptor organ; ec, epidermal cell; gc, gastric ceca; gcp, ganglion cell of protocerebrum; lip, lipid; lo, lateral ocellus (cup); mo, median ocellus (cup); n, nerves; np, neuropil; pc, pigment cell; Rb fo, rhabdom of frontal organ; Rb le, rhabdom of lateral sensory cells; Rb ve, rhabdom of ventral sensory cells; rc, retinula cells; sph, sphere of microvilli; vfo, ventral frontal organ.

is composed of three well-defined cups or ocelli. The three cups are separated by two very large pigment cells, which appear in Figure 120B as an inverted Y. The pigment is melanin, which apparently replaces carotenoid during development (Criel, 1991a).

The large pigment cells are variable in shape. The nucleus is lobate or indented, ventrally located, and contains up to five nucleoli (Rasmussen, 1971; Anadón and Anadón, 1980). Pigment granules are membrane-bound ellipsoids ranging from 0.5–1.1 μm in

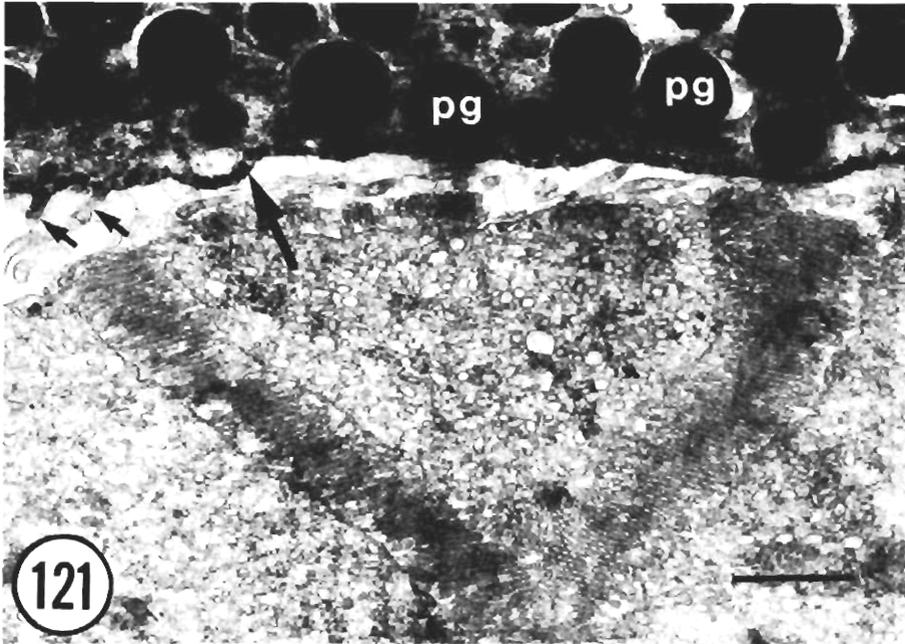


Fig. 121. Confluent rhabdom areas adjacent to pigment cell in nauplius eye of *Artemia*. (After Anadón and Anadón, 1980.) Pigment cell is at top and has large pigment granules (pg), layer of finer peripheral granules (large arrow), and stereocilia (smaller arrow). Scale bar = 1  $\mu$ m.

length. Occasionally, smaller dense granules (120–250 nm diameter) are seen in a series along the plasma membrane of the pigment cell (Fig. 121). Other pigment cell inclusions are “crested” mitochondria, small amounts of ER, microtubules, and lamellated and vesicular bodies (Rasmussen, 1971). The plasma membrane also bears “stereocilia” in areas close to the rhabdoms of retinula cells (Anadón and Anadón, 1980). Because few ER cisternae are seen, Anadón and Anadón (1980) assumed that little or no secretory activity occurs in these cells. Other cellular inclusions were described by Anadón and Anadón (1980), who additionally noted that the cell membrane of the pigment cells is increased between the two cells and between each cell and the surrounding hemocoel, suggesting to them that this increase in cell surface area might be for facilitation of metabolic exchange of the pigment cells.

Each cup houses “inverse” sensory cells

(Elofsson, 1966) that function as photoreceptors. The exact number of cells comprised by each cup varies according to species and according to author. In *Artemia*, each cup may contain 25–75 sensory (retinula) cells (Criel, 1991a), although Anadón and Anadón (1980) estimated only 8–12 cells in the median ocellus and 17–29 in each lateral ocellus. These same authors even noted differences between the two lateral cups in one individual, so that the exact number of cells is probably of little importance. The retinula cells form closed-type rhabdoms between adjacent cells (Rasmussen, 1971; Criel, 1991a). Rasmussen (1971) described several cellular inclusions of these retinula cells, including numerous vesicles, tubular mitochondria, small Golgi complexes, microtubules, multivesicular and lamellar bodies, and lipid inclusions (Fig. 120A). The retinula cells are variably shaped and irregular in location and disposition. They are in contact in certain areas with the

surface of the large pigment cell, except occasional cells at the periphery of the ocellus that Anadón and Anadón (1980) interpreted as undeveloped photoreceptors. There is, at least in the retinula cells of the median ocellus in *Artemia*, a morphological (and presumed physiological) polarity, with rhabdomeres found closest to the pigment cell (Fig. 121) and axons toward the periphery of the ocellus (Anadón and Anadón, 1980). Rhabdomeres only rarely directly face the pigment cell, most often being formed by adjacent retinula cell surfaces just peripheral to their contact with the giant pigment cell (Anadón and Anadón, 1980) (Fig. 121). Rhabdomeres consist of cell membrane microvilli, each being 50–65 nm in diameter, that interdigitate tightly, leaving no interstitial space. This association of tightly packed interdigitating microvilli forms a closed rhabdom (Anadón and Anadón, 1980). Typically, these appear wedge-shaped in horizontal sections, with the wide end toward the pigment cell and the narrow end closed by a zonula adherens (Fig. 121) (Anadón and Anadón, 1980). According to Debaisieux (1944), the rhabdoms are partly resorbed under daylight conditions but fully developed in the dark.

The median ocellus, which always has fewer retinula cells than do the lateral ocelli, additionally has, at least in some individuals of *Artemia*, an unusual component recognized first by Anadón and Anadón (1980) and termed a sphere of microvilli (Fig. 120C,D). Microvilli composing this sphere are 120–130 nm in diameter, approximately twice the diameter of microvilli in the rhabdoms, and they are arranged in a complex jumble of tightly packed lamellae (Fig. 122A,B). The sphere is always found close to the cuticle and adjacent to retinula cells (Figs. 120C,D, 122A,B) (Anadón and Anadón, 1980). Its function is unknown.

From each cup, a nerve composed of the gathered axons of the retinula cells (described in more detail by Elofsson, 1966; Anadón and Anadón, 1980) runs to a recognizable center in the protocerebrum (Elofsson, 1966). This

center is composed of one (Elofsson, 1966) or three (Dahl, 1959; Benesch, 1969) neuropils, surrounded by ganglion cells (Criel, 1991a).

Reconstructions of the nauplius eye, as evidenced in Figure 120, often are not in agreement. Elofsson (1966) illustrated all three ocelli in *Branchinecta paludosa* as situated at the posterior (median ocellus) or posterolateral (both lateral ocelli) sides of the large pigment cells (Fig. 123A). However, Rasmussen (1971) and Anadón and Anadón (1980) illustrated for *Artemia* a condition in which the median ocellus is located on the anterior face of the eye, very near the cuticle (Fig. 120A,C,D), and the entire organ is located just above and slightly posterior to the protocerebral neuropil. This striking difference in arrangement and location between two genera in a single order may be nothing more than the result of crowding of cephalic components; Elofsson (1966) noted that *Artemia*, like *Tanyrastix*, has less available room in the head, with the result that organs of the head are crowded. However, in *Polyartemia forcipata*, another species with more room in the head, the components are relatively spaced out, yet the nauplius eye itself is smaller than in other species, and the ventral cup is composed of only four or five cells (Elofsson, 1966).

It is worth noting that although the adult anostracan nauplius eye is distinguished by having three cups, the naupliar larval stages of *Artemia* have been described as having a bipartite eye (Moroff, 1912; Horridge, 1965b). Along these same lines, it is noteworthy that the notostracans, and probably other branchiopods, which differ from anostracans in their possession of a nauplius eye of four cups, have only three cups in their naupliar stages (Dahl, 1959).

The nauplius eye of the notostracans is quite different from the above description (Elofsson, 1966). It is large and consists of four, rather than three, ocelli or cups: the posterior medial cup, ventral medial cup, and paired lateral cups (Fig. 123B). Each lateral cup is large, contains several hundred sensory

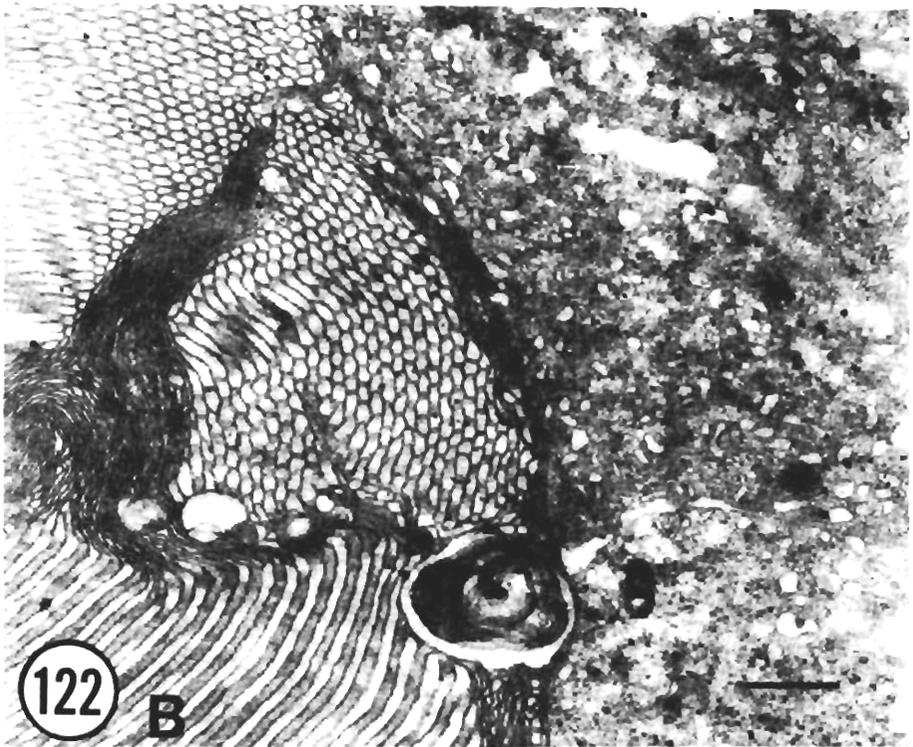
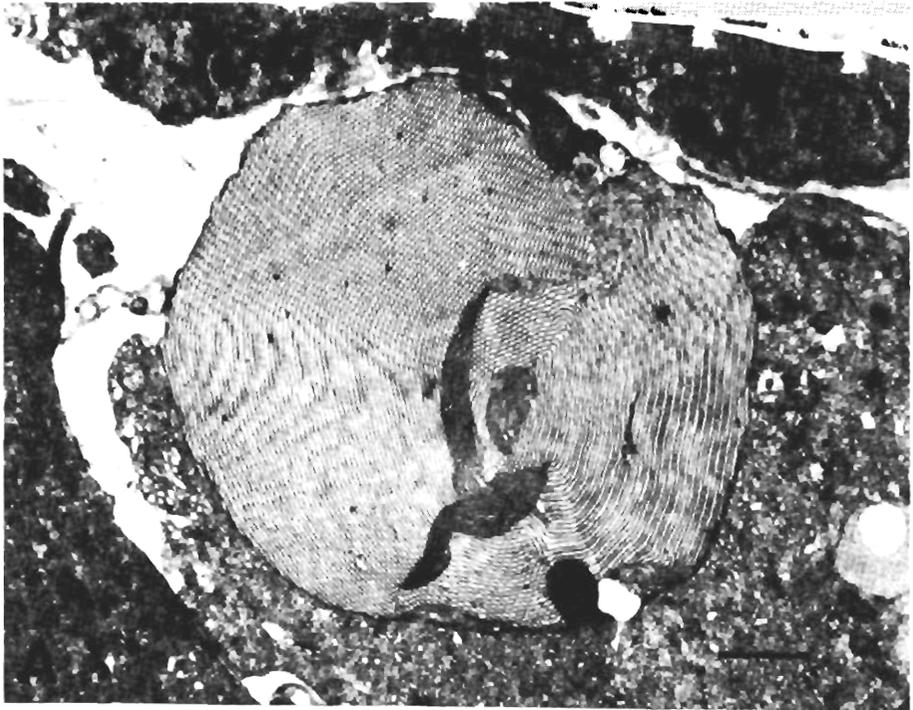


Fig. 122. Sphere of microvilli found in the nauplius eye's median ocellus in some specimens of *Artemia*. (From Anadón and Anadón, 1980.) **A**: Entire sphere adjacent to cuticle (visible as light line at upper right). Scale bar = 2  $\mu\text{m}$ . **B**: Detail of sphere where it contacts retinula cells. Scale bar = 1  $\mu\text{m}$ .

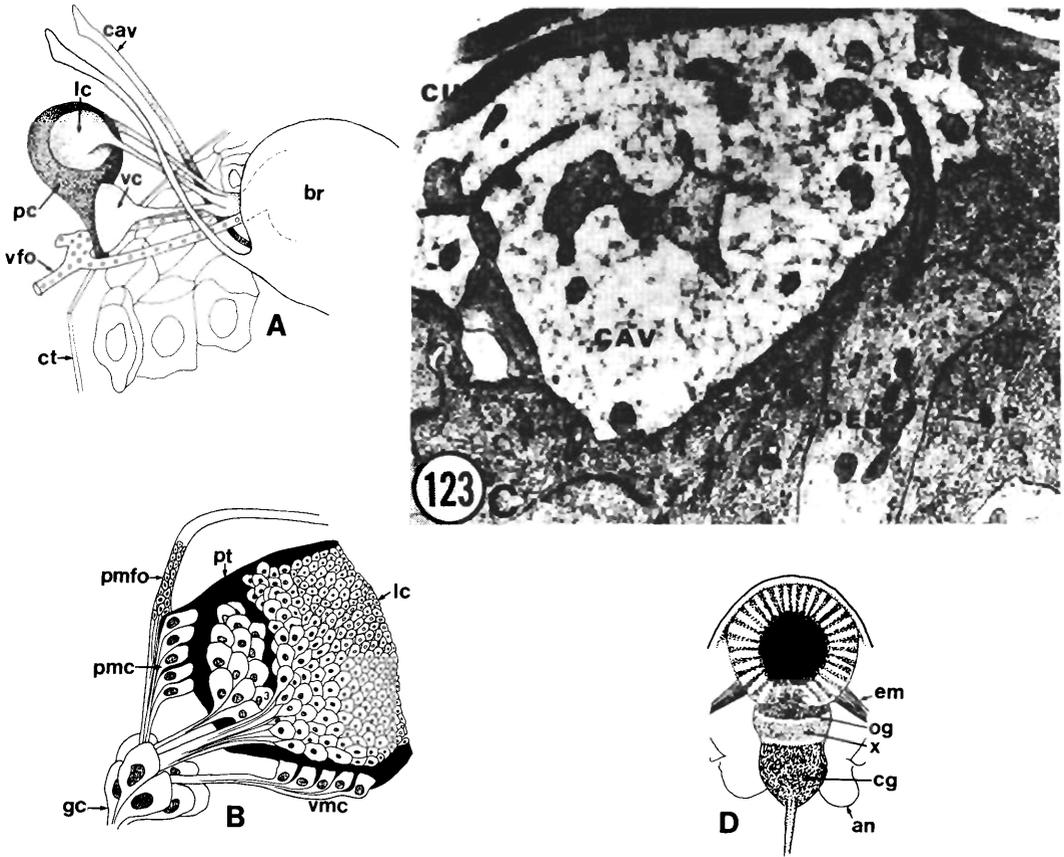


Fig. 123. Various frontal organs and nauplius eyes. **A:** Anterior brain, nauplius eye, and frontal organs of *Branchinecta paludosa* (Anostraca). **B:** Nauplius eye of *Lepidurus arcticus* (Notostraca). (A,B modified after Elofsson, 1966.) **C:** Cavity receptor organ of *Artemia salina*. (From Elofsson and Lake, 1971.) **D:** Brain and compound eye of *Leptodora kindtii* (Haplophoda), which lacks nauplius eye and any frontal organs. (From a photograph in Scharer, 1964a.) ARB, arborizations of epider-

mal cells; an, antennule nerve; br, brain; cav, CAV, cavity receptor organ (cavity only in C); cg, cerebral ganglion; CIL, cilia; ct, connective tissue; CUT, cuticle; DEN, dendrites; EP, epidermis; em, eye muscles; gc, giant cells; lc, lateral cup; og, optic ganglion; pc, pigment cell; pmc, posterior medial cup; pmfo, posterior medial frontal organ; pt, pigment tissue; vc, ventral cup; vfo, ventral frontal organ; vmc, ventral medial cup; x, X-body of brain.

cells that tend to increase in size toward the base of the cup, and is divisible into two distinct regions, each with its own nerve, such that an argument could almost be made for six total cups (Fig. 123B). The ventral and posterior medial cups are smaller, with about 30 cells in the latter, and contain sensory cells similar to those of the lateral cups. All sensory cells contain rhabdoms, and all cups connect to the brain via nerves at their posteroventral borders. Pigment is contained not in a

few large cells but in a tissue that more or less envelops the sensory cups, sometimes seen between individual sensory cells, and follows the course of the nerves, occurring among the axons and even extending into the nauplius eye center of the brain (Elofsson, 1966). The pigment tissue is thick and contains membrane-filled lamellae, which are tighter peripherally, leaving a "pigment cavity" with pigment but only loose lamellar folds in the center (Elofsson, 1966). The pigment layer

and the lateral cups are in direct contact with the epidermis. Nerves from the cups (totaling six) pass through a cluster of "giant cells" (Elofsson, 1966), where they contact the brain. These large cells are similar to the large sensory cells of the optic cups and could even be mistaken for such, although Elofsson (1966) noted that, although the cells themselves are in contact with the nauplius eye center of the brain, nerves from these cells do not terminate there but pass ventrally to the hind margin of the brain. Elofsson suggested the possibility of neurosecretion of these cells. Closely associated with the notostracan nauplius eye is a small, unpaired, posterior medial frontal organ that arises from the posterior medial cup (Fig. 123B, pmfo). The cells of this organ extend in a tube that apparently terminates in an "outlet at the epidermis" (Elofsson, 1966: 12). This unusual feature is seen also in some conchostracans (Elofsson, 1966). Elofsson (1966) considered this frontal organ a reduced frontal eye, as all cellular components are the same as seen in the ocellar cups and the nerve from this organ ends in the nauplius eye center of the brain. In fact, Elofsson (1966) argued that a case could be made for five frontal eyes in branchiopods, the various frontal organs representing remains of some of these frontal eyes (see below).

Conchostracans (both Spinicaudata and Laevicaudata) have nauplius eyes similar to those of the Notostraca, with four cups: two large laterals, one small posterior medial, and one small ventral. The ocellar cups contain fewer inverse sensory cells than do those of notostracans (e.g., approximately 50 in lateral cups, and 25 in the ventral cup, of *Caenestheria*, but only two in the medial and four in the posterior cup of the laevicaudatan *Lynceus*). As in notostracans, pigment is in a lamellar tissue, including the internal "pigment cavity," and in some spinicaudatans there is a posterior medial frontal organ stemming from the posterior medial cup, a unique synapomorphy of conchostracans (at least *Limnadia*) and notostracans (Elofsson, 1966),

although its presence in laevicaudatans and other families of the Spinicaudata has yet to be demonstrated.

In the four cladoceran orders, reduction of the nauplius eye is common, perhaps as a consequence of increased reliance on the relatively large compound eyes, and variation of the nauplius eye and frontal organs is great. However, all have four cups of inverse cells, in those species where a nauplius eye is recognizable, and Elofsson (1966) had no difficulties in establishing homologies with eyes of the notostracans and conchostracans. In *Daphnia*, where the nauplius eye and frontal organs are reduced, each of the four cups contains only 2–4 sensory cells (Horridge, 1965b; Ringelberg, 1987). The function of the nauplius eye in *Daphnia* is uncertain; removal of it did not in any way alter the behavior of adult *Daphnia* (Schultz, 1928; Ringelberg, 1987), although Baylor and Smith (1957) found it to be light-sensitive, and Debaisieux (1944) noted changes in the amount of pigmentation upon exposure to light.

*Leptodora* has lost all vestiges of a nauplius eye (Fig. 123D) and all frontal organs, although perhaps the remnants of these organs are to be found in a "disorganized heap of cells" that bears rhabdoms and is located on the anterior of the brain (Elofsson, 1966). Incorporation of some components of the nauplius eyes and/or frontal organs into the brain is also suggested by Scharrer's (1964b) finding of brain cells in *Leptodora* that bear microvillous borders (Fig. 116F), originally called trophosphongia by Scharrer (1964a), which are typical of all arthropod photosensitive cells (Elofsson, 1966) but otherwise unknown in branchiopod brains.

### Frontal Organs

Many branchiopods possess frontal organs, some of which should perhaps be termed frontal eyes, as they possess many of the characteristics of retinula cells of the nauplius eye (Elofsson, 1966). Indeed, Elofsson (1966) argued that branchiopods might have originally

**TABLE 3. Distribution of Various "Frontal Organs," and Number of Ocellar Cups in the Nauplius Eye, in the Branchiopoda\***

	Anostraca	Notostraca	Spinicaudata	Laevicaudata	Anomopoda
Ventral frontal organ	yes	no	no	no	no
Cavity receptor organ <sup>a</sup>	yes	no	no	no	no
Posterior medial frontal organ	no	yes	yes <sup>b</sup>	no	no
Wenke's organ	no	yes	yes <sup>b</sup>	no	no
Distal frontal organ	no	no	yes <sup>b</sup>	yes	no
Frontal organ	no	no	no	no	yes
Nauplius eye, cups	3	4	4	4	4

\*Onychopods and haplopods, which lack nauplius eyes and frontal organs, and ctenopods, for which I could find no detailed information, are excluded. Data mostly from Elofsson (1966), Elofsson and Lake (1971), and Anadón and Anadón (1980).

<sup>a</sup>X-organ or organ of Bellonci of older literature; see Elofsson and Lake (1971).

<sup>b</sup>Known only for *Limnadia*; other spinicaudatans (e.g., *Caenestheria*) studied by Elofsson (1966) lack this.

possessed several frontal eyes, some of which have degenerated to become "frontal organs" of one sort or another. Perhaps supporting Elofsson's belief, Rasmussen (1971) remarked on the ultrastructural similarities (e.g., perirhabdomeric vacuoles and the degree of pinocytotic processes at the base of the rhabdom) between the rhabdoms of the nauplius eyes, rhabdoms of the frontal organs, and retinula cells of the compound eyes. Most of the frontal organs or eyes appear to be innervated by the protocerebrum.

The distribution of the various frontal organs, whether or not they appear to be frontal eyes, is summarized in Table 3. Onychopods and haplopods are not included, since no remnants of these organs or of the nauplius eye exist in these orders (but see above for possible nauplius eye vestige in *Leptodora*). Detailed information is available for few of these structures. One interesting frontal organ, unique to the Anostraca, where it was originally termed the X-organ (e.g., Menon, 1962; Hentschel, 1965; Elofsson, 1966) or organ of Bellonci (Lake, 1969), is now known as a cavity receptor organ (Fig. 123A,C) (Elofsson and Lake, 1971). This paired organ exists on either side of the nauplius eye within a small cavity just under the cuticle. Neuronal dendrites enter the cavity by passing through an enormous "accompanying cell" and epi-

dermal cells (Elofsson and Lake, 1971; Anadón and Anadón, 1980). Each dendrite has a pair of cilia extending into the cavity, where arborizations of the epithelial cells are also seen (Fig. 123C). Although no homologous organ is known in other branchiopods, Elofsson and Lake (1971) suggested, based on the ciliated neurons and connection with the medulla terminalis, possible homologies with the frontal filament organ of barnacles and the "third unit" organ of copepods. Although function is unknown, it is presumed to be sensory, rather than neurosecretory as indicated by staining before the details of the organ were known (Elofsson and Lake, 1971; Criel, 1991a). Aramant and Elofsson (1976a,b) have shown, via fluorescence, that sensory neurons of this organ are monoaminergic, the first report of monoaminergic sensory neurons in any arthropod. Also unique to the Anostraca is the ventral frontal organ, clearly a photoreceptive organ based on rhabdomal similarities with the nauplius eye, but there is disagreement concerning the details of this probably paired organ (see Elofsson, 1966; Rasmussen, 1971; Anadón and Anadón, 1980). Elofsson (1966) described cells of this organ as small copies of the larger sensory cells of the lateral and ventral cups of the anostracan nauplius eye. There are marked similarities between this organ and

the organ bearing this name in the Malacostraca, but Elofsson (1966) argued that this is a case of convergence because the nauplius eye in the two groups (Anostraca and Malacostraca) differs.

### Compound Eyes

According to Land (1984: 402), crustaceans possess more different kinds of eyes, with different optical mechanisms, than any other phylum or subphylum in the animal kingdom. Branchiopod compound eyes are quite diverse in form, but detailed information is available for relatively few taxa. All branchiopod compound eyes are of the apposition type. They differ from those of decapods in that they lack special pigment cells of the shielding or reflective type (Elofsson and Odselius, 1975; Hertel, 1980; Nilsson and Odselius, 1981), and they lack corneagen cells and distal pigment cells, although possibly one or both are homologous with the specialized epidermal cells surrounding the crystalline cone (Elofsson and Odselius, 1975). The compound eyes are stalked in the Anostraca (Fig. 124A,E) but sessile and occasionally fused in other taxa (most "cladocerans" [e.g., see Nilsson et al., 1983] and cyclotheriid clam shrimps). Although appearing internal, the compound eyes of notostracans migrate inward during ontogeny, leaving a small pit connecting the outside environment to the space just over the now-internalized eye (Fig. 124F,G). This pit also is seen in all laevicaudatans (visible in Fig. 135C) and most families of spinicaudatans, and I assume its existence in these groups indicates a similar process in the ontogeny of the compound eyes. The cuticle overlying the branchiopod compound eye is more or less unspecialized, i.e., it does not function as a lens, although it is obviously faceted externally in anostracans (Fig. 124B). Ommatidia are of the "eucone" type (after Grenacher, 1879), i.e., beneath each ommatidium there is a transparent refractile crystalline cone (Fig. 124D,E), secreted by surrounding cells with laterally displaced nuclei (Horridge, 1965b). The number

of ommatidia varies widely. Anostracans have about 300, as does the single huge eye of *Leptodora* (500 according to Kaestner, 1970), and the entire head of *Bythotrephes* (Onychopoda) is filled by its eye, whereas *Simcephalus vetulus* has 60–70 (Zahid, 1981) and *Daphnia* has only 22 (Ringelberg, 1987). Apparently even with such a small number there are no gaps in *Daphnia*'s visual field (Young and Downing, 1976).

In *Artemia*, each ommatidium is composed of four cone cells, each of which contains glycogen (Fig. 125) (Elofsson and Odselius, 1975). The cone cells are enveloped by two "peripheral" epidermal cells, termed by Debaisieux (1944) the "cellules épidermiques juxtacrystallines," that extend down about four-fifths of the cone length, tapering to a thickness of 0.1–0.2  $\mu\text{m}$ . The distal tips of the ommatidia are separated by large extracellular spaces (\* in Fig. 125A) where hemocytes are sometimes seen (Elofsson and Odselius, 1975); such spaces are known also in *Daphnia* (Guldner and Wolff, 1970). The crystalline cone normally is composed of four cells (but three, five, and six are known; Debaisieux, 1944) that form the distal body of the cone, which tapers proximally and eventually abuts on the rhabdom (Fig. 128A) (Elofsson and Odselius, 1975). The cone, which clearly is an intracellular creation (Elofsson and Odselius, 1975), has an electron-light inner portion containing glycogen granules of 25–50 nm, and a denser outer zone containing mitochondria, Golgi apparatus, and the flat nuclei (Fig. 125A). The glycogen-containing inner zone is the functional lens (Elofsson and Odselius, 1975).

The elongate "root" of each cone cell extends down through intercellular spaces among the retinula cells (see below) to the basal lamina. Upon reaching the basal lamina, the root flattens and widens and interdigitates with similar root cells. This layer of interdigitating cone cell roots constitutes a "basal plate" that composes the upper layer of the basal lamina (Figs. 126A, 128) (Elofsson and Odselius, 1975). The basal

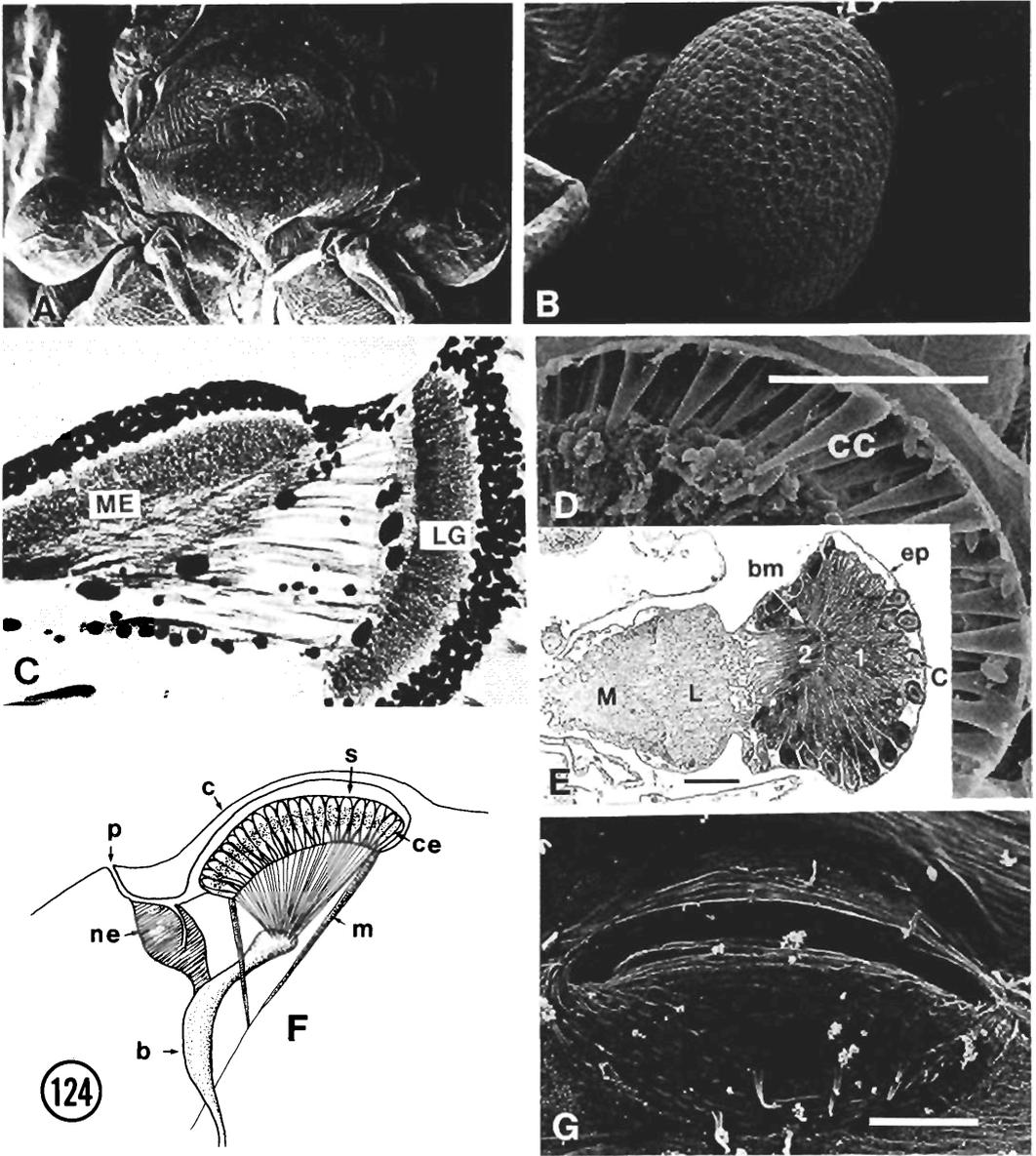


Fig. 124. The compound eyes of Anostraca (A–E) and Notostraca (F,G). A,B: SEM of *Branchinecta conservatio*. C: *Branchinecta paludosa*, horizontal section showing medulla externa (ME) and lamina ganglionaris (LG). Note straight course of fibers between them. (From Elofsson and Dahl, 1970.) D: Fracture through *Artemia* eye showing crystalline cones (CC). Scale bar = 100 µm. (From Schrehardt, 1987a.) E: Light micrograph of 2 µm section through *Artemia* eye. Scale bar = 50 µm. (Courtesy of G. Criel.) F: Diagram of “internalized” eye of

*Triops* showing pore (p) connecting internal eye space (s) to external environment. (After Calman, 1909.) G: SEM of pore in *Lepidurus packardii*, anterior side at top. Scale bar = 20 µm. 1, zone of cone cell roots and retinula cells; 2, zone of photoreceptor axons; b, brain; bm, basement membrane; c, cuticle; C, CC, crystalline cones; ce, compound eye; ep, epidermis and cuticle; L, lamina ganglionaris; M, medulla; m, eye muscle; ne, nauplius eye.

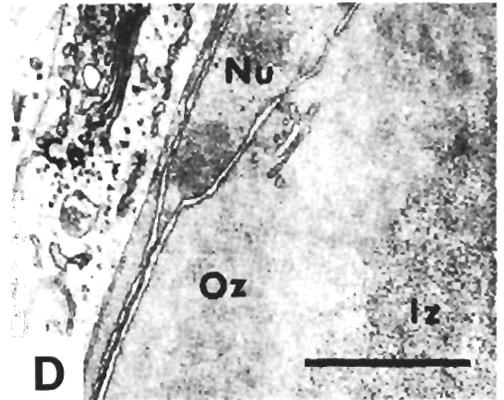
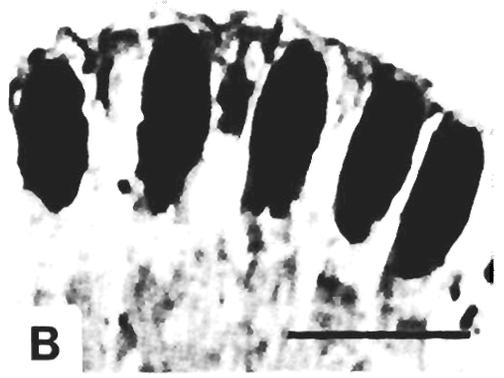


Fig. 125. Ultrastructure of the *Artemia* compound eye. (From Elofsson and Odselius, 1975.) **A**: Paracentral longitudinal section through ommatidium, TEM. Note extracellular space (\*) surrounding crystalline cone. Scale bar = 5  $\mu$ m. **B,C**: Longitudinal light micrographs showing positive reaction (**B**) of crystalline cones to lead tetracetate followed by Schiff's reagent (indicating glycogen) and negative reaction (**C**) of controls. Scale bars = 50  $\mu$ m. **D**: TEM section through border of a crystalline cone. Scale bar = 1  $\mu$ m. Cc, crystalline cone; Ce, "cellule epidermique juxta-cristalline"; Cr, cone cell root; Ep, epidermis; Iz, inner glycogen-rich zone; Oz, outer zone; Nu, nucleus; Rc, reticular cell; Rh, rhabdom.

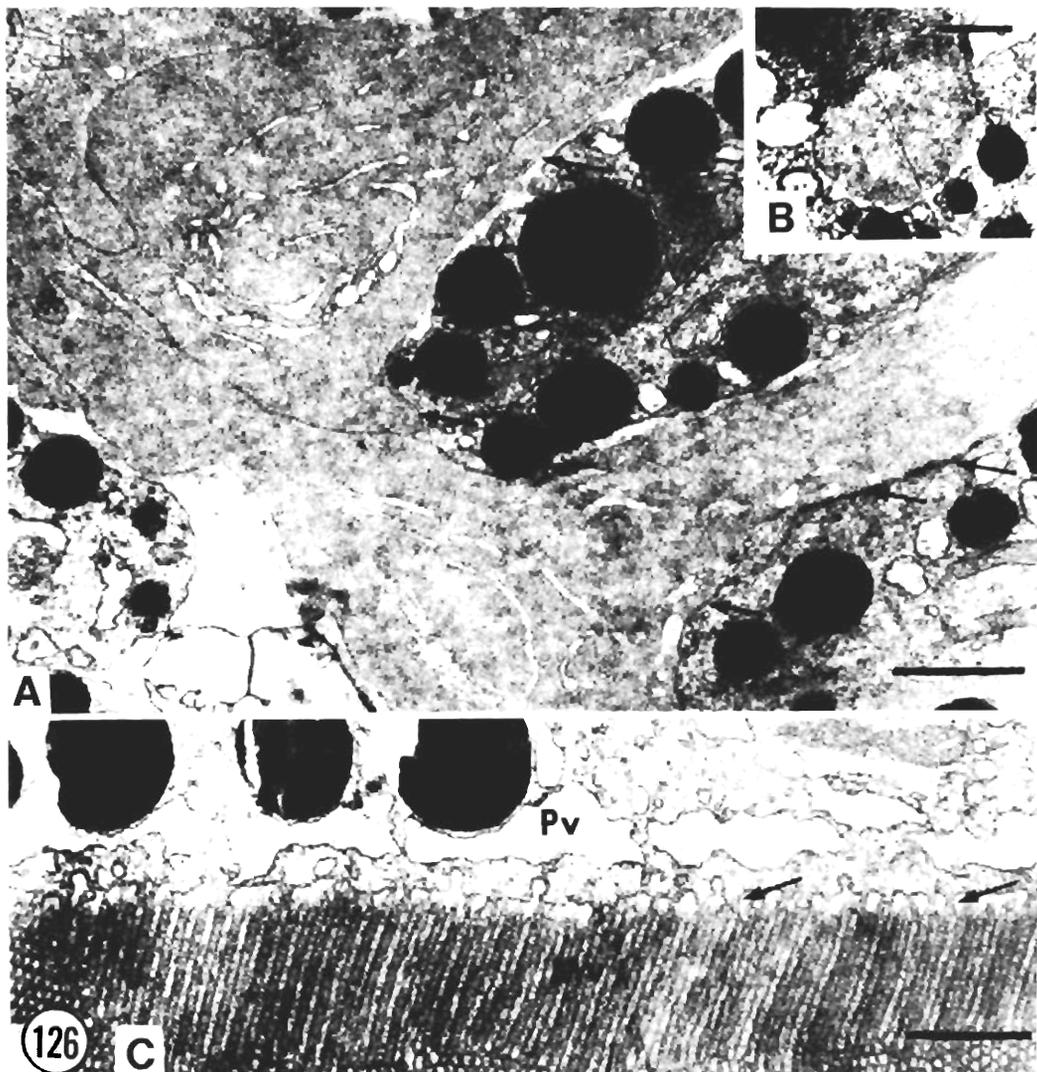
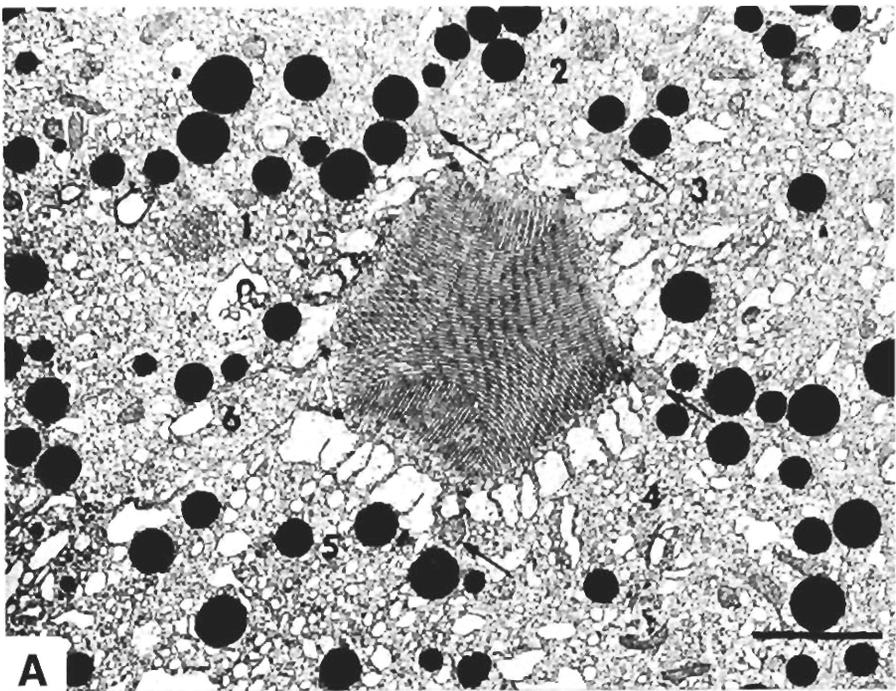


Fig. 126. TEM of *Artemia* compound eye. (From Elofsson and Odselius, 1975.) **A**: Longitudinal section through the basement membrane. Arrows show two cone cell roots widening into "feet" or the basal plate, in which interlocking cell borders are seen (\*). Scale bar = 1  $\mu\text{m}$ . **B**: Double cone cell root. Scale bar = 1  $\mu\text{m}$ . **C**: Longitudinal section through the rhabdom. Mv, microvilli; Pv, perirhabdomeric vesicles in the reticular cell. Arrows indicate microvillar stalks in extracellular space. Scale bar = 1  $\mu\text{m}$ .

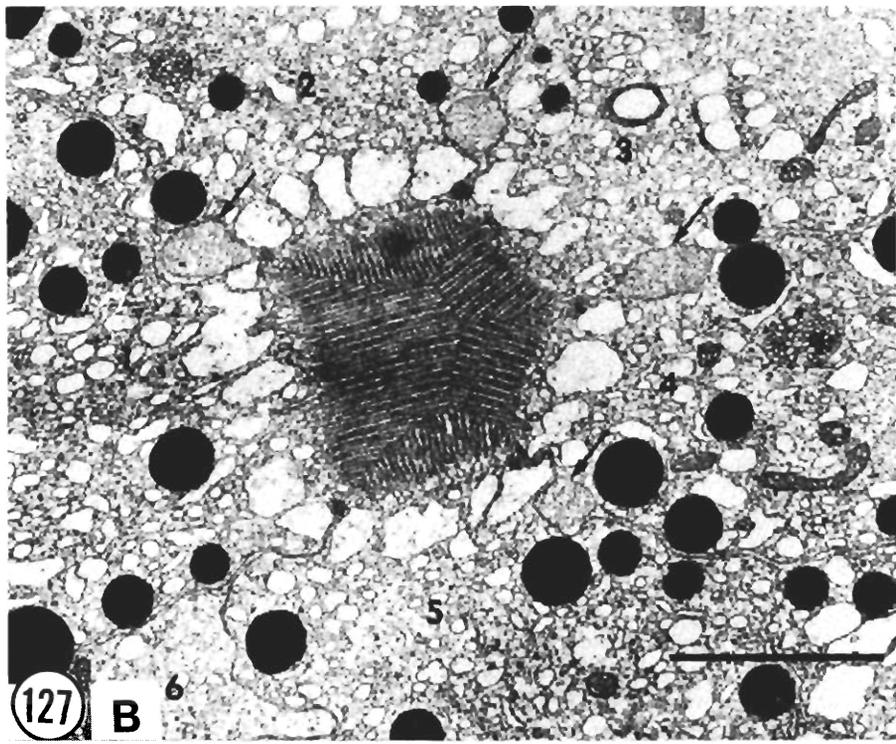
lamina does not completely seal off the ommatidium from the hemocoel, as indicated by the presence of hemocytes among the distal ends of ommatidia (see above).

Six concentrically arranged retinula cells compose the ommatidium and contribute to the rhabdom. The fused rhabdom is about 60

$\mu\text{m}$  long and is tapered, with a distal diameter of approximately 8  $\mu\text{m}$  and a proximal diameter perhaps one-third that size (Elofsson and Odselius, 1975). The rhabdomere is unique in that each rhabdom is continuous, not interrupted as in the "toothed" rhabdom of decapods (Elofsson and Odselius, 1975). This dis-



**A**



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**B**

Fig. 127. Transverse sections through single ommatidium of *Artemia* compound eye. (From Elofsson and Odseius, 1975.) **A**: Transverse section through ommatidium at the level of arrows at "b" in Figure 128A. Reticular cells are numbered 1-6. Arrows indicate cone cell roots. Scale bar = 2  $\mu$ m. **B**: Transverse section at level of arrows at "c" in Figure 128A, showing multivesicular body (\*) but otherwise as in 127A. Scale bar = 2  $\mu$ m.