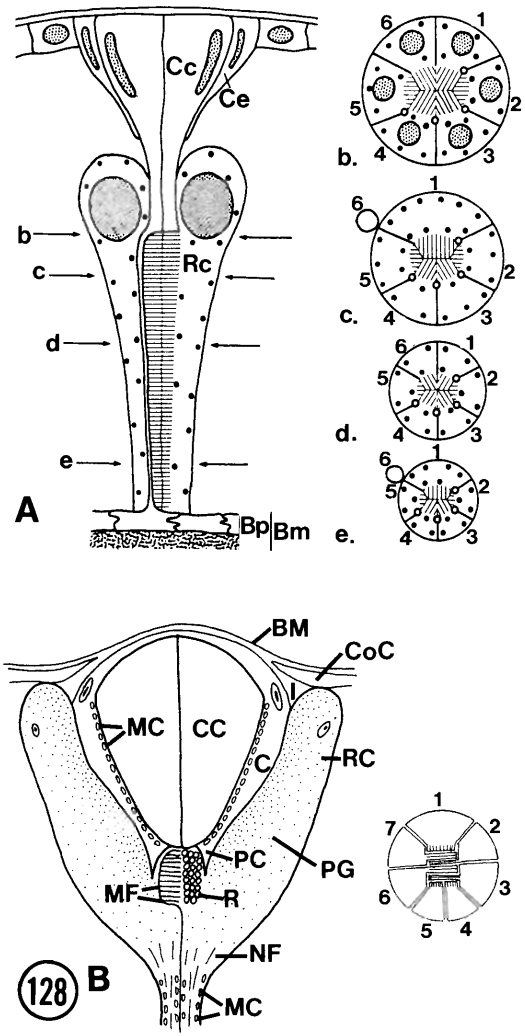



Fig. 128. Comparison of schematic diagrams of the anostracan and anomopod compound eye ommatidia. **A:** *Artemia salina* ommatidium, with cross sections at various levels indicated to the right (b–e) with retinular cells numbered from 1–6. Note cone cell roots drawn as circles close to the rhabdom. (After Elofsson and Odselius, 1975.) **B:** *Daphnia* ommatidium, with cross section at midrhabdom level at right. Note bidirectional pattern of microvilli as compared to multidirectional pattern in *Artemia* rhabdom above. (After Ringelberg, 1987, from various sources.) BM, basilar membrane; Bm, basement membrane; Bp, basal plate; C, cone cell; CC, Cc, crystalline cone; Ce, "cellules epidermiques juxta-cristallines"; CoC, covering cell; I, intercellular space; MC, mitochondria; MF, microvilli; NF, neurofilaments; PC, process of cone cell; PG, pigment granules; R, rhabdom; Rc, RC, retinular cells; nuclei dotted in A.

tinction led Elofsson and Odselius to refer to this as the "anostracan type" of rhabdom, which occurs in some other branchiopods and also in some ostracodes, isopods, and amphipods (Shaw and Stowe, 1982). The microvilli of one cell never span the entire rhabdom diameter, although those of *Daphnia* apparently do (Waterman, 1966; Ringelberg, 1987). Formation of the rhabdom by the rhabdomeres of each cell shows a characteristic contribution from each cell, differing in the extent that each contributes to the rhabdom and in the angle of the microvilli (Elofsson and Odselius, 1975). Three or four directions are exhibited by rhabdoms of *Artemia* (Figs. 127, 128A), although in cladoceans there are just two perpendicular directions (e.g., Wolken and Gallik, 1965; Ringelberg, 1987). Each microvillus measures approximately 50 nm, and arises along with eight others from a 70–75 nm–diameter outgrowth of the retinula cell wall. The rhabdomeric space between adjacent retinula cells is sealed off by zonulae adherentes, and the roots of the cone cells pass just outside of these zonulae (Figs. 127A,B, 128). Typical of retinula cells in a variety of organisms, *Artemia*'s retinula cells contain well-developed smooth ER, Golgi apparati, tubular mitochondria, lamellated vesicles, and multivesicular bodies. Pigment granules (measuring 0.6–0.7 μm) are found throughout these cells and even into the axons. The pigments are ommochromes (ommin and ommatin) (Kiyomoto et al., 1969). Possibly, movements of the rhabdom observed by Debaisieux (1944) upon adaptation to light and dark could be interpreted as a sliding of the rhabdom along the extended cone cell roots mentioned above (Elofsson and Odselius, 1975).

The *Daphnia* eye, a single eye resulting from the fusion of paired embryonic eyes, differs from the above account in having five cone cells forming the crystalline cone in some species (Ringelberg, 1987), although *Daphnia pulex* apparently has four, as does *Artemia* (Guldner and Wolff, 1970). There are seven, rather than six, retinula cells (Fig.

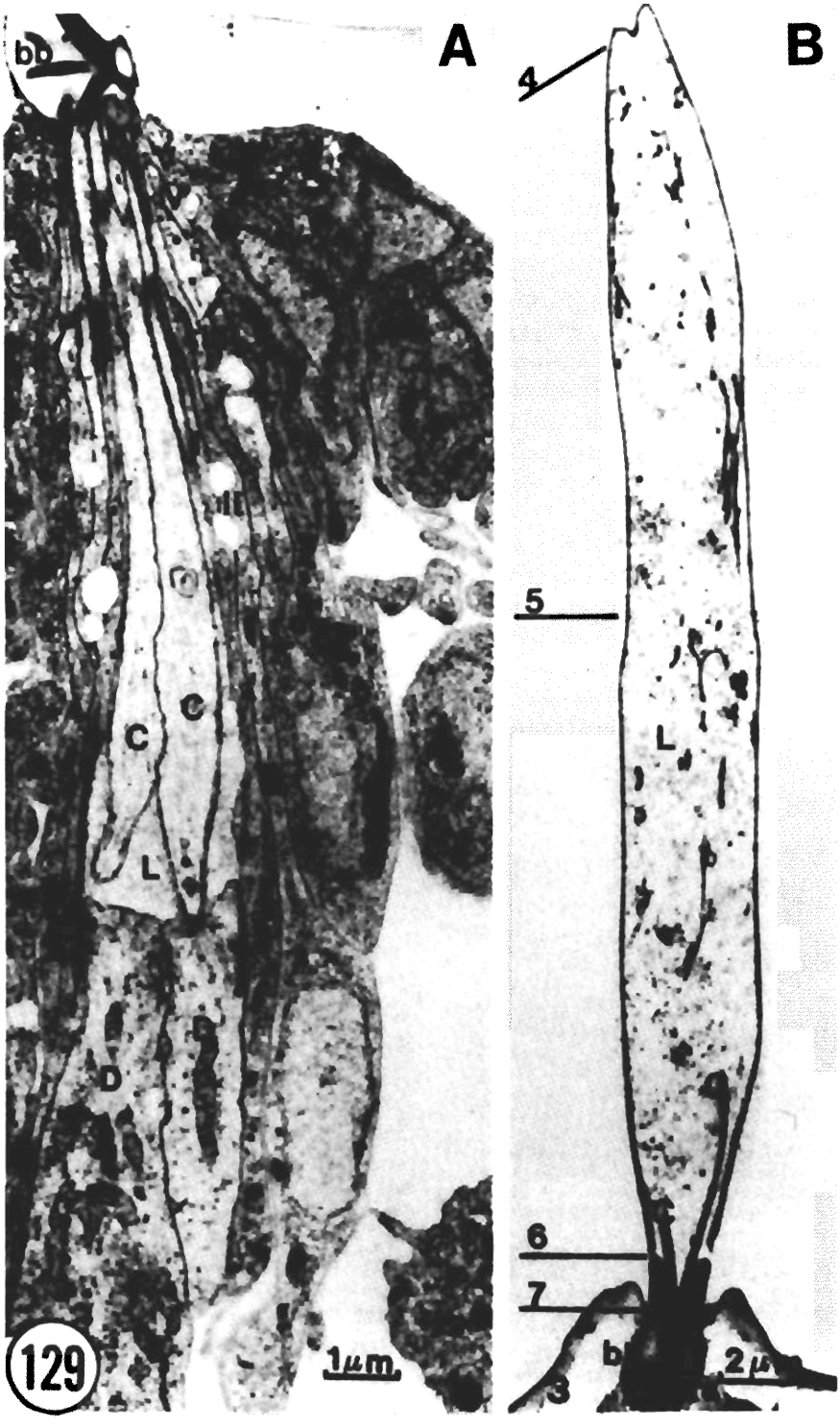



Fig. 129. Sensory setae (aesthetascs) of the antennule of *Leptestheria dahalacensis* (Spinicaudata). (From Rieder and Spaniol, 1980.) **A:** Proximal part of seta terminates in a basal bead (bb), below which are sheath cells, receptorcilia (C), and dendrites (D). **B:** Entire seta showing receptorcilia extending upward through basal bead into the seta where they branch. Numbers 4–7 correspond to sections shown in Figure 130A–D, respectively. I–V, sheath cells 1–5; L, liquor space (fluid chamber).

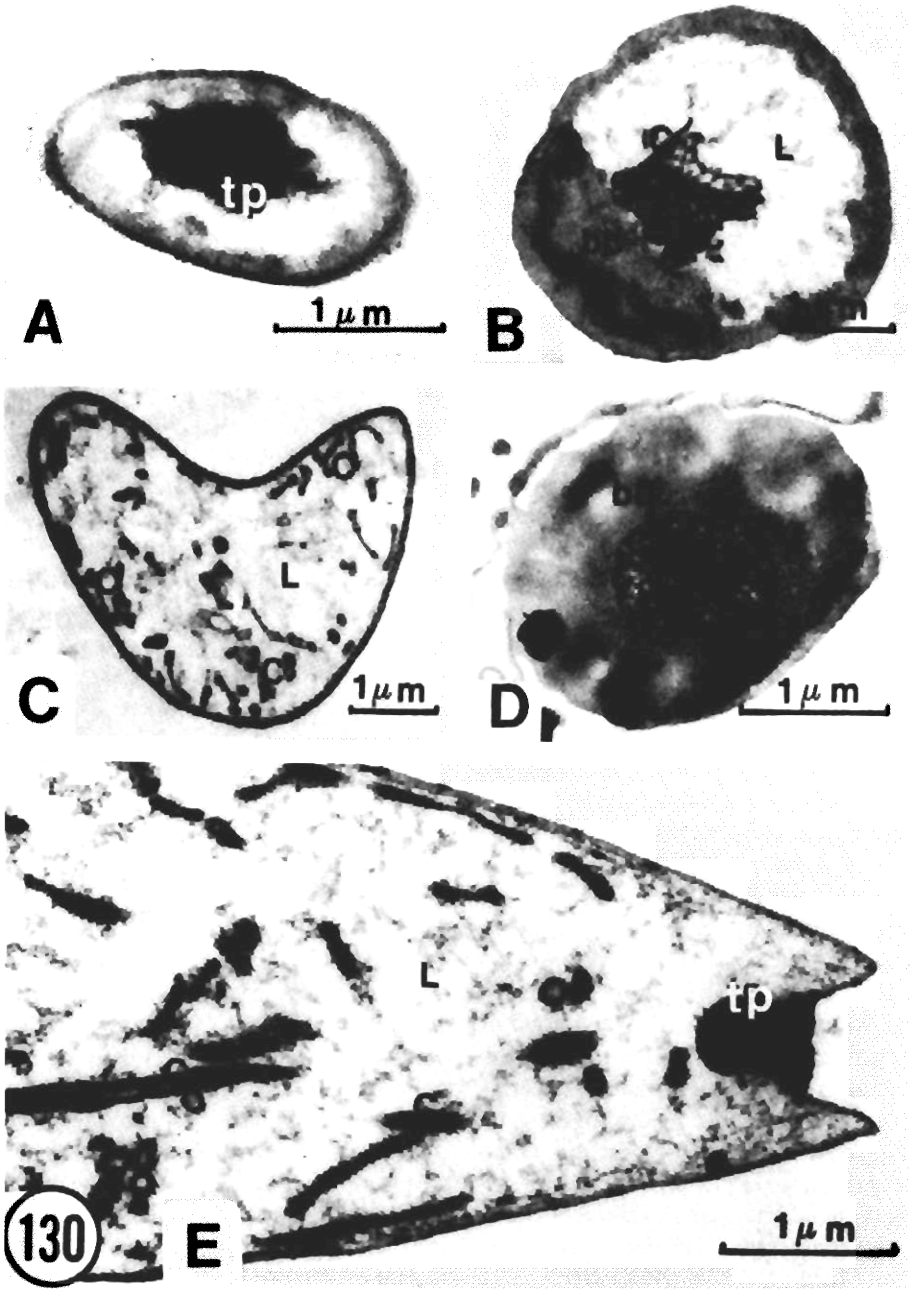



Fig. 130. Sensory seta of antennule of *Leptestheria dahalacensis*. (From Rieder and Spaniol, 1980.) **A–D:** Cross sections at points 4–7 in Figure 129B. **E:** Longitudinal section through distal extremity showing recessed terminal pellet (tp) composed primarily of epicuticle. bb, basal bead; c, receptorcilia; L, liquor space (fluid chamber).

128B), arranged radially around the optic axis of the ommatidium, with an eighth cell, also containing a rhabdomere (Macagno et al., 1973), occupying a different position. The microvilli composing the rhabdom are oriented in only two directions (Fig. 128B) (Elofsson and Odselius, 1975; Ringelberg, 1987).

Downing (1974) described what appears to be a unique feature of the *Daphnia* eye. The eye is suspended in position not by ligaments or tendons but by a large circular membrane (Fig. 116A), which forms a watertight seal between the eye and the surrounding carapace (Downing, 1974), and consequently separates the hemocoel from the external medium. A combination of hemocoelic pressure, muscle tensions (there are six muscles that produce eye movement), and tensions in the suspensory membrane result in eye rotations but very little translationary movement. Downing compared the function of this hydraulic system to that of a universal joint, and noted that this feature would allow for the continual rotary tremor seen in the *Daphnia* eye and also for some of the larger rotations (up to 160° in the sagittal plane, and about 60° in the coronal plane and 50° in the transverse plane) documented for this eye. (Laevicaudatans also exhibit a continual slight eye tremor, but such a universal eye joint has not been described.) Young and Downing (1976) demonstrated that the focal length far exceeds the length of the very short rhabdom in *Daphnia,* with the result that image formation is not possible.

Neurons departing from the ommatidia pass through the basement membrane into the lamina ganglionaris. Each ommatidium "projects in register to a single distinct columnar synaptic structure, the optic cartridge" (Shaw and Stowe, 1982: 301).

### Sensory Setae

The aesthetascs or sensilla of the first antenna (antennule) (reviewed by Hallberg et al., in press) are best known among branchiopod sensory setae. These setae are relatively simple structures usually found along one edge of the antennule (e.g., Notostraca, most Spinicaudata) or confined to the tip (e.g., *Artemia* [Anostraca], *Daphnia* [Anomopoda], and *Cyclestheria* [Spinicaudata]). The most detailed study of these setae of which I am aware is that of Rieder and Spaniol (1980) on the spinicaudatan *Leptestheria dahalacensis* (see also Hallberg et al., in press, for *Daphnia*). Like most other spinicaudatans, these clam shrimp have long, lobate antennules that bear up to 600 setae in groups of 25–30 on each lobe. Each seta is divisible into two parts by a "basal bead," an epicuticle-derived cuticular socket to the seta that provides for movement in several planes (Fig. 129A,B). The walls of the basal bead are formed from thickened epicuticle. The tip of the seta is recessed but appears closed by what Rieder and Spaniol (1980) called a terminal pellet (Fig. 130E). The sensillum is innervated with four to ten dendrites, each with a "receptorcilium" that extends from the interior part of the sensillum through the basal bead and into the setal lumen, where they branch before terminating in the terminal pellet (Figs. 131, 132) (Rieder and Spaniol, 1980). Five sheath cells (Figs. 129A, 131) surround the basal portion of the seta (interior to the basal bead). These cells can be seen during the molting process to form the socket (cell 5), the basal bead (cell 4), and the setal shaft (cell 3) of the sensillum, with sheath cell 3 dividing to form two additional sheath cells responsible for formation of the tip and the cuticular sheath of the newly formed seta. These setae appear very similar in external morphology to those on the antennule of many other branchiopods, all of which have at least some sensory setae on the antennule, but the paucity of knowledge of the ultrastructure in other orders prevents comparisons (but see Hallberg et al., in press).

Different types of sensilla (differing from each other and from those described above) are known for the antennule of the Anostraca. Tyson and Sullivan (1979b) documented two types of sensory setae on the tip of the *Artemia* antennule, neither of which is particu-

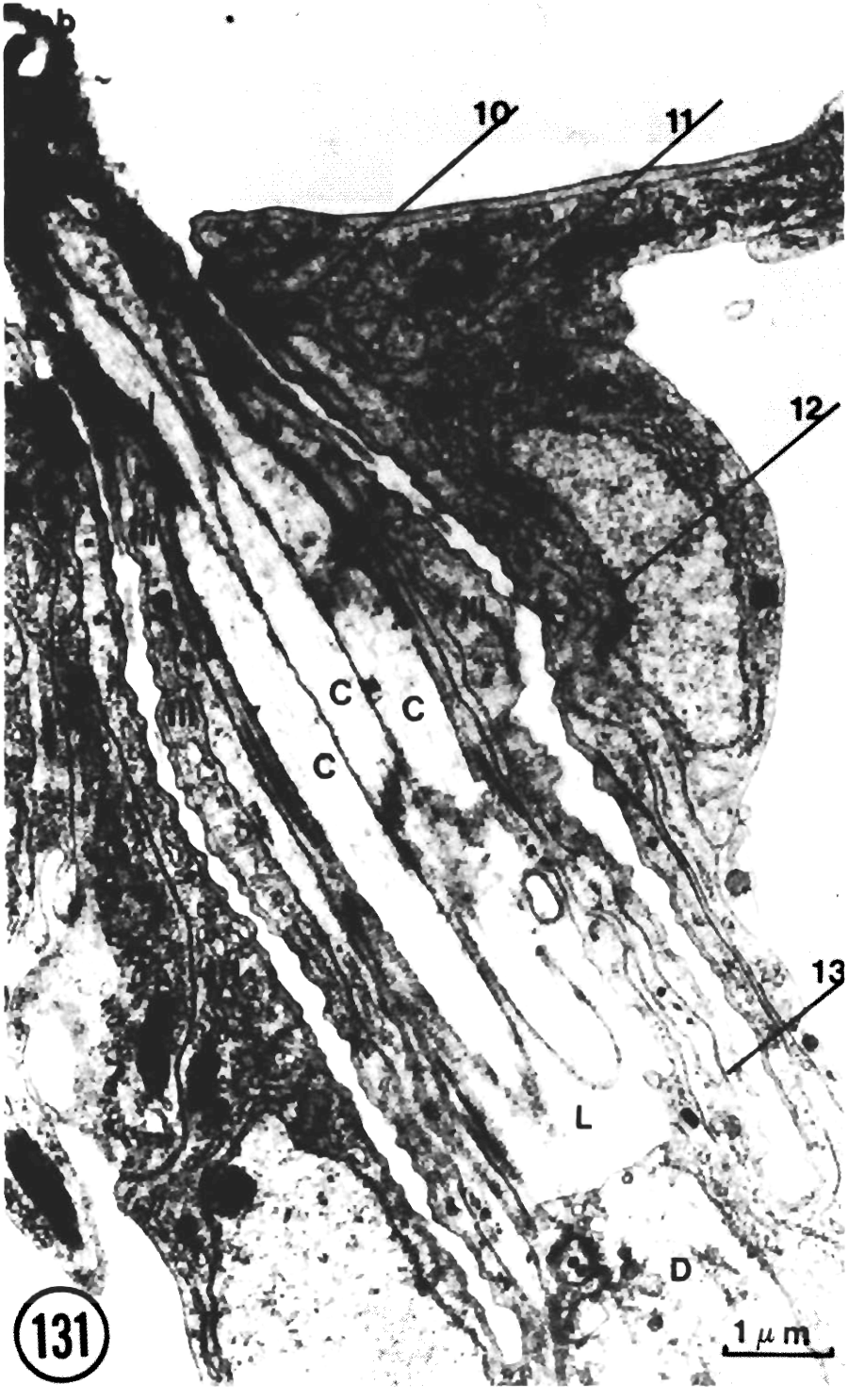



Fig. 131. Basal and interior portions of sensory seta of antennule of *Leptestheria dahalacensis* later in the molt cycle. (From Rieder and Spaniol, 1980.) Note sheath cell III divided by receptorcilia (C) of newly forming sensory seta. Numbers 10–13 refer to cross sections shown in Figure 132A–D, respectively. (From Rieder and Spaniol, 1980.) bb, basal bead; cs, cuticular sheath; D, dendrite; I–V, sheath cells 1–5; L, liquor space (fluid chamber).

larly similar to Rieder and Spaniol's (1980) description of the spinicaudatan sensillum. Type 1 sensilla (always three per antennule) of *Artemia* are long (43–80 μm) and tapering, with a simple external morphology. There is no apparent socket where the cuticle of the setal shaft merges with that of the antennule, and the only external difference is in the surface rugosity (Tyson and Sullivan, 1979b). These setae bear no apical pores, and are similar in some ways to antennular setae of the nauplius larval stages. Type 2 setae, which vary in number, differ in being shorter (12–23 μm), in having a distinct modification of the cuticle where the shaft meets the antennule (the shaft is recessed within a small knoblike outgrowth of the antennule cuticle, forming a socket), in having a midlength groove or annulation, and in having a distal pore (average diameter of which is 0.4 μm; Tyson and Sullivan, 1979b; Tyson, 1980). The edge of the pore bears small cuticular projections that vary in number and shape. The two types of sensilla also differ in their permeability to certain dyes; a solution of crystal violet was taken up by the type 2 setae only, inferring that these may be chemoreceptors. Tyson and Sullivan (1979b: 389) stated that both setal types are innervated, and they illustrated this for type 2 (their fig. 7). Lent's (1977) work indicated that *Artemia* does possess mechanosensory capability, and Tyson and Sullivan (1979b) suggested that one or both of these setal types of the antennule might be responsible. They further suggested that type 2 sensillae, with both a terminal pore and a socketlike base, may have a dual role in chemo- and mechanoreception, but they noted that such a sensillum has never before been documented in any other crustacean.

Anostracans additionally have paired segmentally arranged setae on the dorsal surface of the trunk somites, and Fryer (1987c) employed this character as a diagnostic feature of the order. Tyson and Sullivan (1980b) noted that these setae occur also along the ventral surfaces of trunk somites (at least in *Artemia*), and speculated that the two series (dorsal and ventral) may be chemo- or (more likely) mechanosensory in function, although internal anatomy is unknown. Most other orders have setae on parts of the trunk and/or abdomen, and it is possible that many of these are sensory.

Unique to anostracans are the spinelike outgrowths of the frontal knobs of the male second antenna, which is used for clasping in this order. These outgrowths include noncellular, conical spines as well as sensory setae in *Artemia*. The more numerous conical spines are rather unremarkable and are not innervated, consisting only of an epidermal core covered by cuticle (Wolfe, 1980; Tyson et al., 1991), and therefore presumably they are not sensory. The setae are innervated, although their exact role has not yet been elucidated (Wolfe, 1980). Each sensory unit consists of a large, dome-shaped supporting cell (Fig. 134A), a seta-producing cell, and a sensory neuron, embedded within the hypodermis (Fig. 134 B–D). The sensory neuron is completely enclosed by the seta-producing cell and contains four groups of microtubules (Fig. 134C) that Wolfe (1980) believed were modified ciliary processes. The seta itself extends through the large supporting cell approximately 4 μm above the surface of the dome (Wolfe, 1980).

As Fryer (1988) pointed out, the natural history of notostracans (being predominantly benthic, and employing a variety of feeding modes for a variety of food items) requires considerably more sensory input than does life in open waters, and it is not surprising that these animals exhibit a greater array of sensory setae than is known for most other branchiopods (see Fryer, 1988, for comparison of notostracan and anostracan sensilla). The function of most of these notostracan setae is unknown; innervation has been demonstrated for relatively few (Fig. 133) (Rieder, 1974, 1978, 1979). However, their probable role as mechano- or chemosensory setae often can be inferred by their location and external design. Thus, Fryer (1988: 51) was able to demonstrate among the "profusion of sensillae" in notostracans some that were clearly tactile

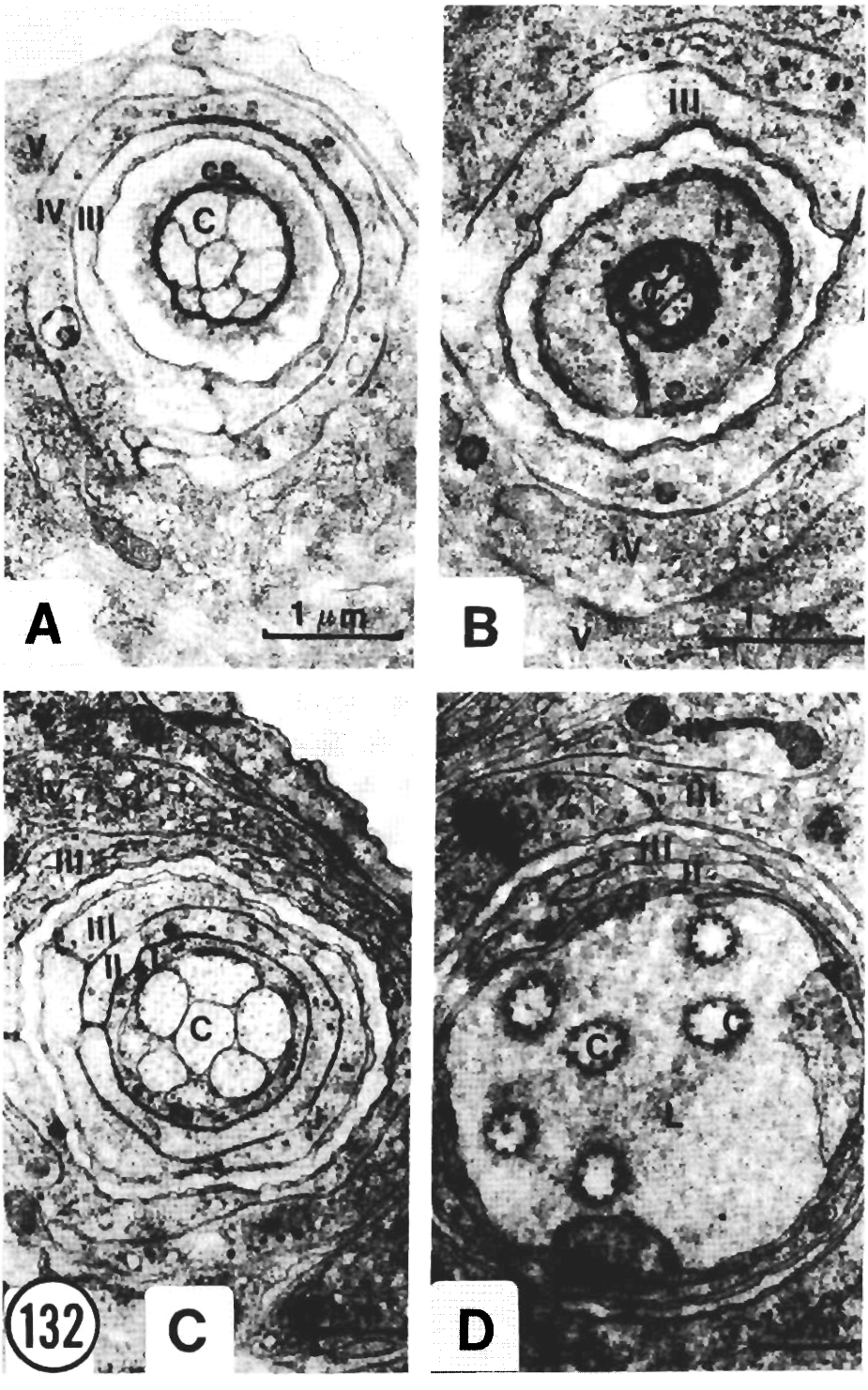



Fig. 132. Cross sections of sensory seta of antennule of *Leptestheria dahalacensis* corresponding to numbers 10–13 in Figure 131. (From Rieder and Spaniol, 1980.) Note ringlike arrangement of sheath cells, varying number of receptorcilia (4–8), and microtubules at periphery of receptorcilia in **D.** C, receptorcilia, cs, cuticular sheath; I–V, sheath cells 1–5; L, liquor space (fluid chamber).

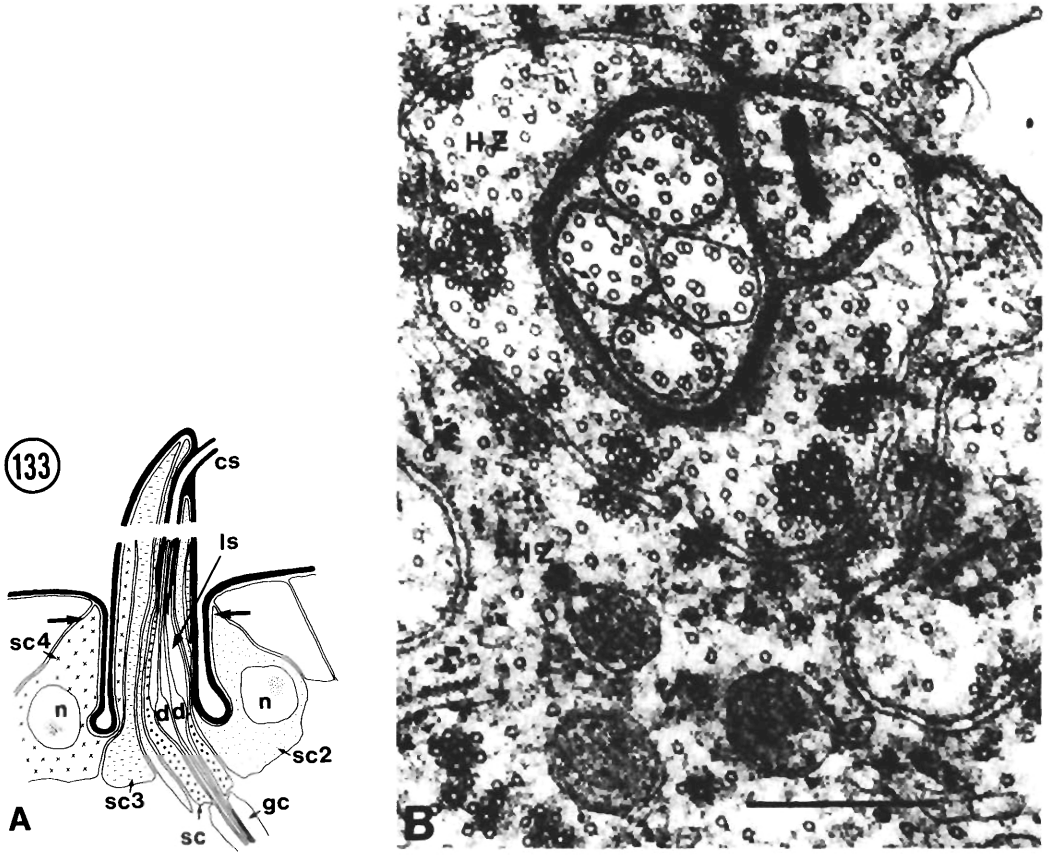
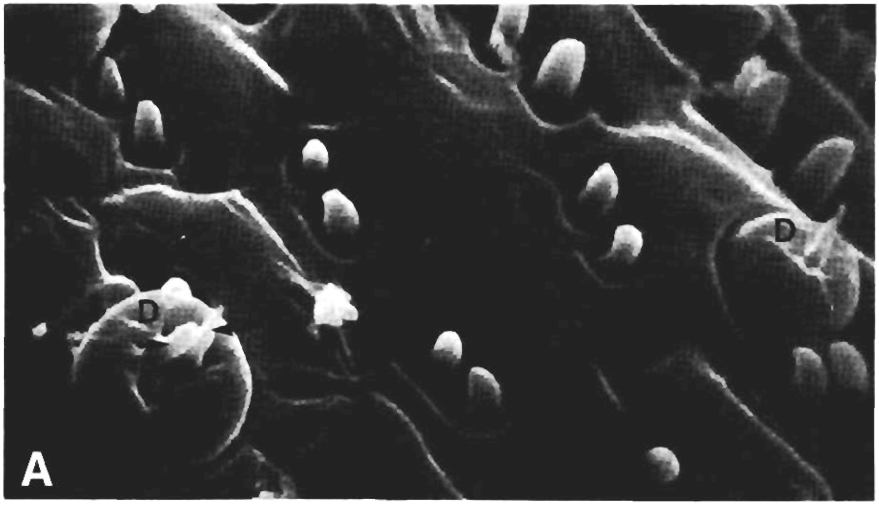



Fig. 133. Structure of one type of sensory seta found on notostracan trunk appendages. (After Rieder, 1979.) **A:** Diagram showing several surrounding sheath cells (sc–sc4). **B:** Cross section at level of arrow in A. Scale bar = 0.5 μm. cs, cuticular sheath; dd, dendrites; gc, glial cell; HZ, sheath cell; ls, liquor space; n, nucleus.

and others that were obviously chemoreceptors. Not all of the notostracan sensory setae are described here (see Fryer, 1988), but the unique "sensory pads" are deserving of attention. These circular arrays of sensory setae occur on the gnathobase and distal endites of the anterior series of trunk limbs, becoming smaller and fewer in the posterior limb series, and almost undoubtedly function in "taste" and food recognition. The pad consists of a cluster of innervated tubular setae (the type 4 bristles of Rieder, 1978) that are surrounded by a circle of stiff, slender spinelike setae (Fig. 135A,B). The pad measures approximately 100 μm across in an average-sized adult, with the central field of tubular sensilla occupying perhaps 70 μm of that (Fryer, 1988). Each tubular sensillum is approximately 2 μm (or slightly more) in diameter, perhaps 20 μm long, and is slightly dilated at the tip (Fig. 135B). The tip bears approxi-

Fig. 134. Sensory setae and spines on the frontal knob of *Artemia*. (After Wolfe, 1980.) **A:** Outer surface of dome-shaped supporting cells (D) with sensory setae (arrows) arising from center. ×3,200. **B:** Diagram of spines (SP) and sensory setae. **C:** Diagram of cross section through sensory seta at level of arrow in B. **D:** TEM through sensory seta showing lightly staining cytoplasm of supporting cell (SC) and darkly staining cytoplasm and microvilli (MV) of hypodermis (HP). Cuticle is at the upper right. ×16,200. F, FB, fibrillar material; MT, microtubules; SN, sensory neuron; ST, setal cell.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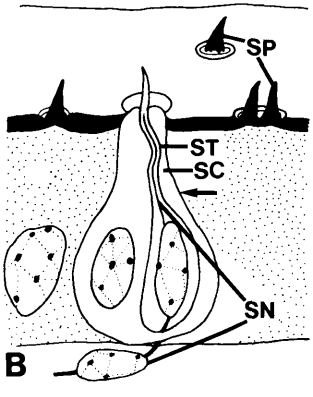
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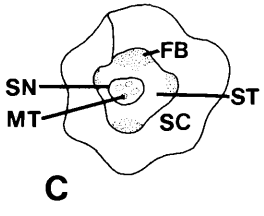
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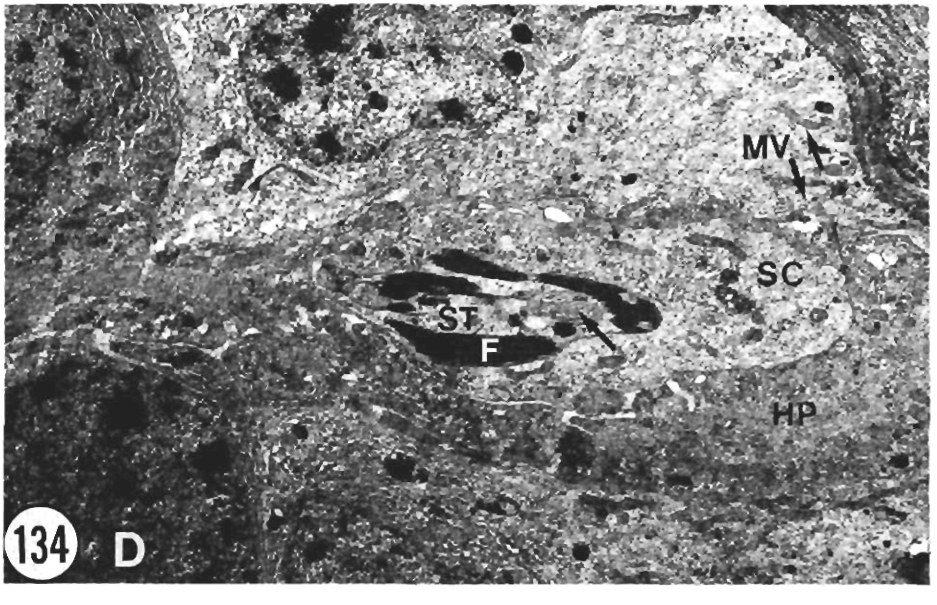
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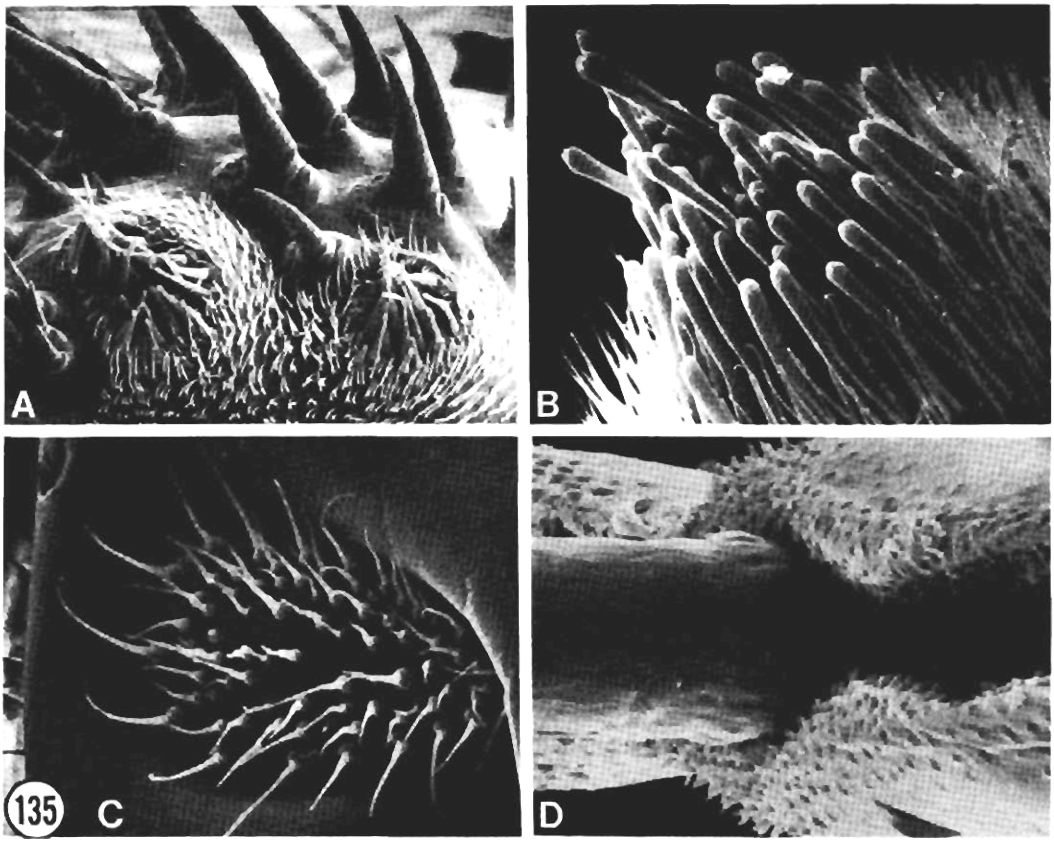


Fig. 135. Examples of sensory or presumed sensory setae. **A,B:** The sensory pads on the endites of notostracan thoracic appendages. **C:** The laevicaudatan "sensory fields" on either side of the rostral carina. Midrostral pore is to upper left. (After Martin and Belk, 1988.) **D:** Base of the frontal seta diagnostic of the spinicaudatan family Leptestheriidae, dorsal view.

mately 15 papillae that surround a central pore, the internal diameter of which is less than 0.3 μm; it is not known if the opening is separated from the setal lumen by a membrane (or plug, as in the antennular setae described by Rieder and Spaniol [1980] for a spinicaudatan) or if it is a true pore, directly opening into the interior of the seta (Fryer, 1988).

A plethora of other setal types exists, not only in notostracans but in many other branchiopods (e.g., see Martin et al., 1986, for pore-tipped setae on the claspers of the Laevicaudata), and detailed knowledge is available for very few. Setae from various parts of the body have been called sensory, but definitive evidence in the form of internal composition and innervation often is lacking. For example, the paired "sensory fields" described for the Laevicaudata (Fig. 135C) (Martin et al., 1986; Martin and Belk, 1988) have yet to be shown to be sensory in function. The same is true for several other setal types, some pore-tipped and therefore likely to be chemosensory (although chemosensory setae do not always bear pores, and not all pore-tipped setae are chemosensory; Laverack and Barrientos, 1985), on various appendages. Examples include the long sensillum of the anostracan gnathobase (Fryer, 1983, figs. 133–136), var-

ious sensilla of some "cladocerans" (Scourfield, 1896, 1905; Dahm, 1976), the presumed sensory pores and/or sensilla on the mandibles of *Artemia* (Tyson and Sullivan, 1981, and Tyson, personal communication), and the diagnostic frontal seta of the conchostracan family Leptestheriidae (Fig. 135D). Many branchiopods also have pores in the integument (e.g., see Frey, 1959, 1962, for chydorid anomopods; Mauchline, 1977, for the marine onychopod genera *Podon* and *Evadne*), and it is possible that some of these serve in a sensory capacity, but I am not aware of any ultrastructural studies on these pores.

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