

# FUNCTIONAL MORPHOLOGY OF FEEDING AND GROOMING IN CRUSTACEA

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# Morphology of feeding structures in the Conchostraca with special reference to *Lynceus*

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## ABSTRACT

Structures involved in conchostracan feeding are described for representatives of the five known families (Cyclestheriidae, Cyzicidae, Leptestheriidae, Limnadiidae, and Lynceidae). The labrum is a short thick process that contains several glands of unknown function. In most families the distal labrum is slightly bilobed. In the Lynceidae the labrum is larger, is not bilobed, and extends posteriorly more so than in other families. The general morphology of the mandible is similar for all families, but the lynceid mandible differs in details of the triturating surface and the mandible-fornix articulation. The maxillule is known for all families except the Lynceidae, where it is possibly represented by a small duct-like process. The maxillae are setose and well developed in all families; maxillary simple setae are directed posteriorly and may play a role in filtration, whereas stout serrate setae are directed orally and are probably for mechanical manipulation of food particles. The coxal endites of the thoracopods bear stout simple and stout serrate spines and setae and are directed orally. It is hypothesized, based upon morphology, that food is mechanically passed along the ventral food groove by these endites. A narrow esophagus leads from a comb-like fringe of setae surrounding the mouth to a wide tube-shaped foregut. In all families except the Cyclestheriidae, a large hepatopancreas filling much of the head region is connected by short ducts to the anterior foregut. The foregut of conchostracans is apparently unique in containing cells with cilia in addition to a microvillous border. The midgut lining is highly convoluted to aid in absorption. For the genus *Lynceus* the path of ingested food is inferred and diagrammed based on morphological observations.

## 1 INTRODUCTION

Conchostracans (clam shrimps) are small freshwater branchiopod crustaceans inhabiting lakes, ephemeral ponds, and occasionally streams (Retallack & Clifford 1980) on all continents except Antarctica (Belk 1982). The order consists of 5 extant families: Cyclestheriidae Sars, 1899 (monotypic), Cyzicidae Stebbing, 1910 (4 genera), Leptestheriidae Daday, 1923 (5 genera), Limnadiidae Baird, 1849 (6 genera), and Lynceidae Stebbing, 1902 (3 genera); characters used to distinguish among the families are given by Belk (1982). Conchostracans may be among the most primitive of the Crustacea (but see Schram 1986 for

an alternative view). Fryer (1983) argued that, because of the purely anamorphic development in some Anostraca, the Branchiopoda are at least as primitive as the slightly metamorphic cephalocarids. Several authors (e.g., Lauterbach 1975) have suggested that a conchostracan-like crustacean was ancestral to all of the Malacostraca. Yet we know very little of conchostracan morphology, most modern texts (e.g., Pennak 1978) opting to reproduce the excellent figures of Sars (1896a).

The majority of morphological studies on conchostracans have centered on the eyes and frontal organs (see Elofsson 1966 and references therein), reproduction and development (e.g., Sars 1896b, Cannon 1924, Gurney 1926, Linder 1945, Anderson 1967, Strenth & Sissom 1975), or characters of taxonomic significance (e.g., Packard 1883, Linder 1945, Mattox 1959). Accounts of feeding are largely anecdotal, and with few exceptions the feeding appendages have not been described in detail. Previous accounts of feeding morphology or behavior include the works of Bishop (1969) on larval and postlarval feeding behavior in a limnadiid; Cannon (1933), Eriksson (1934), and Lundblad (1916, 1920) on feeding mechanisms and phylogenetic inferences in the Branchiopoda; Cannon (1924) and Cannon & Manton (1927) on the development of the maxillary gland; Larink (1972) on the labrum of a cyzicid; Mahoon (1960) and Shakoori (1968) on morphology and skeletomusculature of *Caenestheria*; Mathias (1937) on branchiopod natural history; Karande & Inamdar (1961) and Royan (1976) on gut contents in leptestheriids; Sars (1887, 1896a) on general morphology and biology of several families; and Schlecht (1979) and Rieder et al. (1984) on the fine structure of the foregut and midgut of a leptestheriid.

The present paper is an attempt to broaden our knowledge of clam shrimp feeding structures. The antennae, labrum, mandibles, and maxillule are described for representatives of the five extant families. The path of ingested food is inferred for the genus *Lynceus* on the basis of known external and internal morphology and compared to previous accounts of feeding in other conchostracan families.

## 2 MATERIALS AND METHODS

Members of the Lynceidae (*Lynceus gracilicornis*) and Limnadiidae (*Eulimnadia* sp.) were collected from shallow ephemeral ponds in north Florida, USA. Preserved specimens of the Cyclestheriidae (*Cyclestheria hislopi* from Laos and Paraguay), Leptestheriidae (*Leptestheria compleximanus* from Arizona and *Eoleptestheria ticinensis* from Czechoslovakia), and Cyzicidae (*Cyzicus californicus* from California and *Caenestheriella setosa* from Arizona) were kindly loaned by Dr. Denton Belk, Our Lady of the Lake University, San Antonio, Texas, USA. Additional members of the Limnadiidae (*Eulimnadia texana* from Arizona) and Lynceidae (*Paralimneta* sp. from Mexico) were also supplied by Dr. Belk.

Specimens to be illustrated were preserved in 10% formalin for 24 hrs and transferred to 70% ethanol. Illustrations were made with the aid of a Wild M-5 stereoscope and M-11 compound microscope both equipped with camera lucida. Specimens used for scanning electron microscopy were fixed in 3% glutaraldehyde for 3 hrs in 0.1 M phosphate buffer (*Lynceus* and *Eulimnadia* sp.) or formalin (all others) and postfixed in 2-3% osmium tetroxide an additional 2 hrs before dehydration in a graded ethanol series. Specimens were then critical-point dried and coated with 10-20 nm of gold-palladium for observation in a Cambridge S4-10 and JEOL 100CX II TEMSCAN at accelerating voltages of 10-30 kV.

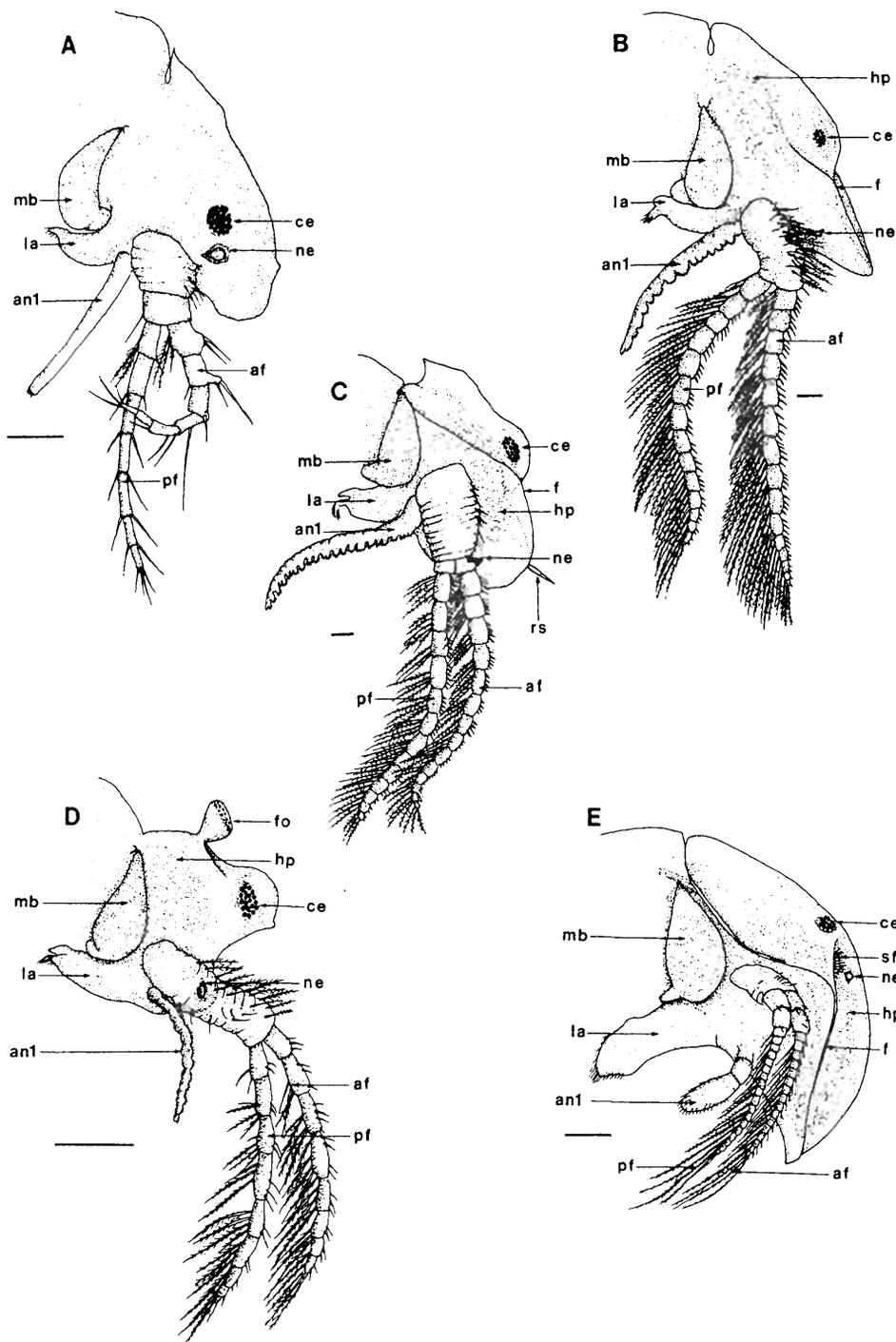


Figure 1. Representatives of 5 families of Conchostraca, anterior region. A. *Cyclestheria hislopi* (Cyclestheriidae). B. *Caenestheriella setosa* (Cyzicidae). C. *Leptestheria compleximanus* (Leptestheriidae). D. *Eulimnadia texana* (Limnadiidae). E. *Lynceus gracilicornis* (Lynceidae). Scale bar = 0.25 mm.

### 3 RESULTS

#### 3.1 *Antennae*

The antennules (an1, Fig. 1) are uniramous and reduced, with few or no segments, and in all families, except the Cyclestheriidae, bear numerous short setae. These setae are sensory in nature (see Rieder & Spaniol 1980) and are often referred to as sensory or olfactory papillae. The antennules play no known role in feeding.

The antennae are elongate biramous appendages (af, pf, Fig. 1) that vary in morphology among the families. Their function is primarily locomotory, but they may also function in burrowing, climbing, flotation, and grasping of the female carapace (Karande & Inamdar 1961, McLaughlin 1982). In the Lynceidae and in larval and postlarval stages of some species of *Estheria*, they may function in gathering food (Martin et al. 1986, Cannon 1933). It is possible that they play a minor role in feeding in addition to locomotion in other families, and for that reason they are described here. In all families the peduncle (scape) is a thick cylindrical stalk with poorly marked segments. Thick muscles extend from the cuticle of the head in the area of the occipital notch into the peduncle and into the paired flagella. The paired flagella are more or less equal to each other in length and always longer than the peduncle. Cyclestheriids have relatively short (6-7 segments) flagella with long simple dorsal setae on each segment (Figs. 1A, 2A). These setae arise from slight protuberances of the cuticle on the proximal segments. The ventral setae are similar, with those on the proximal segment plumose. In the Cyzicidae (Figs. 1B, 2B, C) and Leptestheriidae (Figs. 1C, 2D) the dorsal surface of each segment bears stout sharp spines, each of which is minutely setose (Fig. 2C). Ventral setae on these segments are long and plumose. In the Limnadiidae (Figs. 1D, 2E) the flagella are long but lack the spines of the cyzicids and leptestheriids. The dorsal surface of each segment bears 2-4 short setae. The ventral surface is similar and bears long plumose setae only on the distal 4-5 segments. Lynceids (Figs. 1E, 2F) have relatively short flagella, which bear long plumose setae on the ventral surface of each segment. The dorsal surface of each segment of the anterior flagellum (af) bears short stout setae. The dorsal surface of the segments of the posterior flagellum (pf) is unarmed.

#### 3.2 *Labrum*

The conchostracan labrum (la, Figs. 1, 2) is a large thick process that extends ventrally and posteriorly to cover the mouthparts. In the Cyclestheriidae the labrum is short and terminates in a small posteriorly directed protuberance that bears scattered simple setae (Figs. 1A, 2G). In the Cyzicidae, Leptestheriidae, and Limnadiidae, the labrum is similar to that of the Cyclestheriidae but with the distal tip slightly bilobed (Figs. 1B-D, 11C). The posterior lobe, which probably corresponds to the protuberance mentioned above for cyclestheriids, is blunt and lightly setose. The posterior surface of this lobe has been shown to have an excretory duct for one of several labral glands (see Larink 1972 for *Caenestheriella* (sic)). The anterior lobe is smaller and conical (the 'distal spike' of Larink 1972, tentacular projection of Sars 1896a) and bears numerous short simple setae. The labrum of the Lynceidae is quite different from that seen in the other families as it is much longer, less recurved, and not bilobed (Fig. 1E, 2H, I, 11A, B, 12A). In addition it bears simple setae on its distal and posterior surfaces. Within the lynceid labrum are large labral glands (Figs. 11A, 12A) similar to those described by Larink (1972) for cyzicids. Glandular bodies can be seen through the labral cuticle of all other

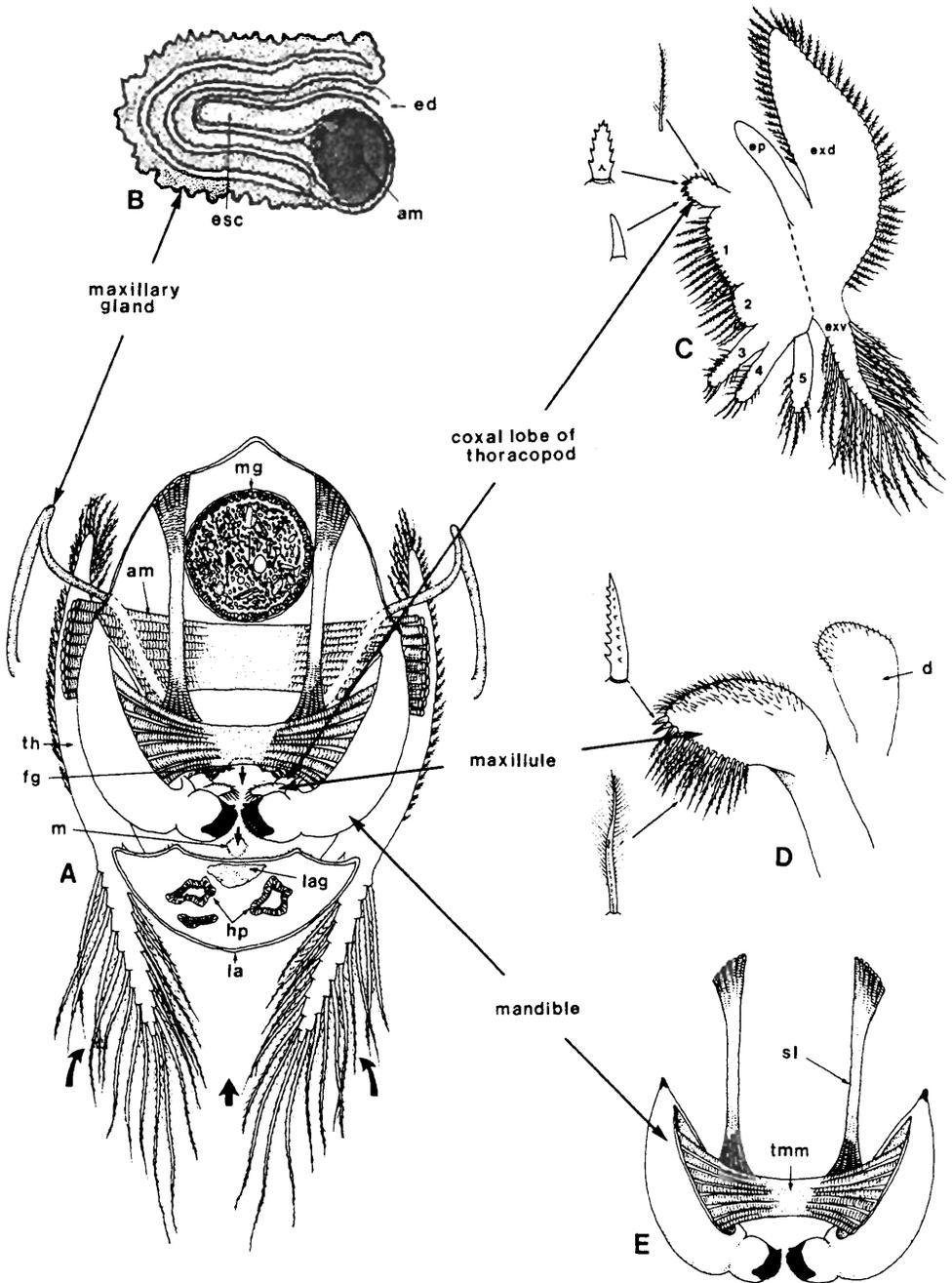


Figure 10. Main feeding structures in *Lynceus gracilicornis*. A. Schematic view of cross section taken just anterior to mandibular somite. Heavy arrows represent water and food influx from surrounding medium; smaller downward-directed arrows indicate transfer of food particles along food groove via coxal lobe of thoracopods, through maxillules and mandibles and into mouth. B. Right maxillary gland, lateral view. C. Typical thoracopod with exemplary setal types drawn for coxal lobe; dashed line indicates axis of folding (see text), numerals refer to endite numbers. D. Maxillule and 'duct' of unknown function, with examples of serrate and plumose setae. E. Mandibular apparatus with sclerotized areas indicated in black. Figures not drawn to scale.

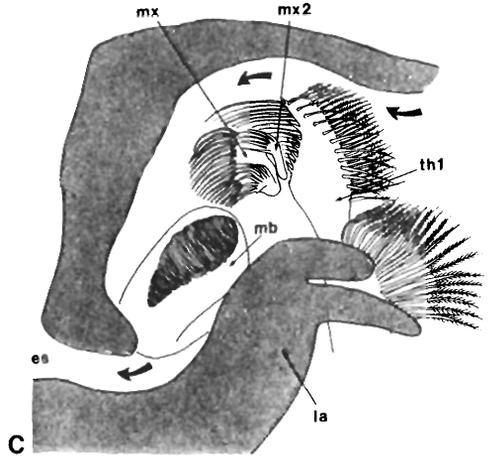
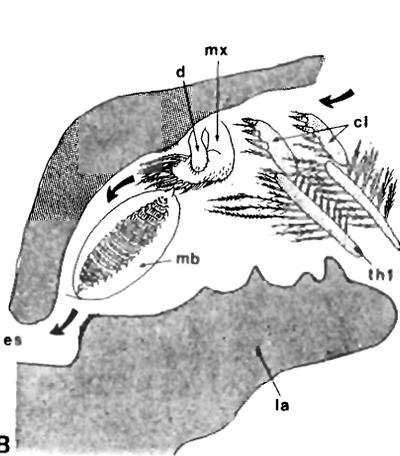
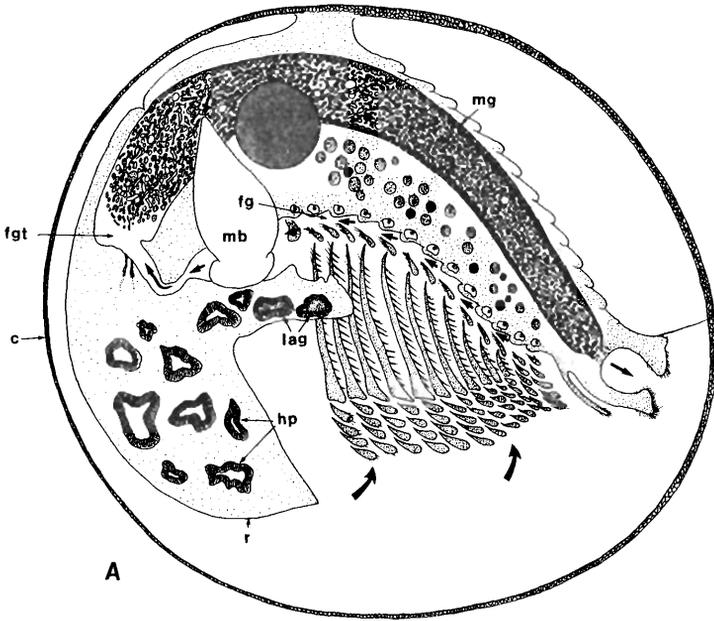


Figure 11. Schematic view of food movement in *Lynceus gracilicornis* based upon histological sections. A. Entire body with proposed food movement indicated by dark arrows. B. Oral section of *Lynceus* with food movement indicated by heavy arrows. C. Oral region of *Estheria* with food movement indicated by heavy arrows (redrawn and modified after Cannon 1933).

families as well. In all families, the labrum is connected by thin paired muscles to the cuticle of the head region just posterior to the compound eyes. Additional musculature encircles the labrum and connects anterior to posterior surfaces (see Larink 1972 and Shakoori 1968 for the Cyzicidae). The exact function of the labrum and of its glands is unknown. Cannon (1933) suggested that the elongated labrum in the Branchiopoda is for secreting a viscous entangling secretion onto food particles filtered out by the thoracopods, thus facilitating food transfer to the mouth. Similar glands in certain cladocerans have been shown to produce just such a

substance (Fryer 1962, 1963, 1968, 1974). The musculature and the numerous labral glands known for the Conchostraca (e.g., Shakoory 1968, Larink 1972, Martin et al. 1986) indicate a similar masticatory and secretory role.

### 3.3 Mandibles

The mandibles are large thick appendages lacking palps. In all families these appendages consist of a narrow conical dorsal part and a stout ventromedial molar process, thus conforming to Manton's (1964, 1977) description (based on the anostracan *Chirocephalus*) of a basic crustacean 'rolling' mandible 'used for primitive grinding movements.' The distal (ventral) portion of the mandible is separated from the proximal portion by a distinct constriction and by an abrupt medial curve (see Fig. 10E). The distal margin differs among the families, with two easily recognizable types of triturating surfaces. The first type consists of a slight terminal groove flanked on the outer surface by comb-like scales. These scales fuse and become a smooth surface of connected pits on the slight groove on the triturating surface. This type of mandible is seen in the Cyclestheriidae (Fig. 3A, B), Cyziciidae (Fig. 3C, D, E), Leptestheriidae (Figs. 3F, 4A, B), and Limnadiidae (Fig. 4C). *Leptestheria compleximanus* has a strong posterior tooth on the outer border (pt, Fig. 3F). The second type of triturating surface is seen in the Lynceidae. Here, the distal mandibular border bears a double row of relatively large teeth (Fig. 4D, E). The area between these two rows is slightly depressed but bears numerous small spinules (Fig. 4E, F) rather than a pitted surface as in the other families. Lynceids possess a slight posterior tooth, similar to that seen in the Leptestheriidae, and a cluster of small spines on the distal dorsal border (see Fig. 4E). The proximal half of the mandible is similar in all families with, again, the Lynceidae excepted. The dorsal part of this region is conical and narrows posteriorly to form a blunt point. This point articulates in all families except the Lynceidae with a slightly cornified protuberance arising from the wall of the mandibular somite (Fig. 5A-D). In the Lynceidae the point of articulation is not on any raised knob of the cuticle but instead on a slight ridge that represents a dorsal continuation of the well developed fornix (Fig. 5E). Functionally this difference is probably of no significance. The axis of swing of the mandible on the body (see Manton 1977) is still in a transverse plane with a dorsolateral point of articulation (which Manton referred to as a ball-and-socket articulation), and the associated musculature is virtually identical to that described for *Estheria clarkii* by Snodgrass (1950) (and *Caenestheria propinqua* by Shakoory (1968)). A strong thick transverse muscle connects the two mandibles and can be seen through the mandibular cuticle in living and preserved individuals as a reticulated pattern (see Fig. 1). This muscle was termed the ventral mandibular muscle by Snodgrass (1950) but the transverse mandibular muscle by Manton (1964, 1977) and Fryer (1983, for *Branchinecta ferox*; the latter terminology is retained here (imm, Fig. 10E). Connecting the mandibles to the overlying cuticle of the head is a pair of strong muscles termed by Snodgrass the suspensory ligaments (sl, Fig. 10E). Manton (1977) referred to a similar structure in *Chirocephalus* as the dorsal suspension of the mandibular tendon, as she believed the transverse mandibular muscle to originate in a transverse tendon. In addition to these easily seen structures conchostracans possess what appears to be a complex series of promoter and remoter muscles. The similarity of the musculature system and the plane of axis to descriptions of anostracan and cladoceran mandibular systems indicates a 'sweeping and rolling' action for these appendages as described in beautiful detail by Fryer (1983) for *Branchinecta ferox*. This similarity in function is further supported by the close resemblance of the

tritulating surface of the mandible in conchostracans (Figs. 3, 4) and anostracans (see Fryer 1983 plate 8-11).

### 3.4 *Maxillae*

The maxillule is a simple unsegmented appendage. Cannon & Leak (in Cannon 1933) note that throughout the Branchiopoda this appendage 'exhibits a remarkably uniform structure.' In all families of the Conchostraca (although not verified for the Cyclestheriidae) the maxillule arises from a stout base in the same plane as the posterior thoracopods, but turns sharply toward the mouth region. The following description is based on *Lynceus*, but applies to all other families as well. The posterior surface bears numerous simple setae. These setae together appear to form an effective filtering device (Fig. 6C, D), although this assumption is not yet supported by any evidence. The ventral border of the appendage has been twisted so that it is directed orally (Figs. 6B, C, 10D). This border bears stout plumose setae that appear to be jointed; that is, there is a midlength thickening of the setal shaft corresponding with a dark node visible under light microscopy (Fig. 10D). These setae overlie a second shorter row of stout serrate setae, also directed orally (Fig. 6E, F). This pattern exists in all other clam shrimp examined, sometimes with the row of serrate setae appearing to be on a second lobe of the appendage.

The maxilla is extremely small and not easily seen. According to Cannon (1933) there are two types of maxillae in the Branchiopoda, one found in the Notostraca and Conchostraca and the other found in the Anostraca, Cladocera, and Lipostraca. Claus, as cited by Cannon (1933), described for the Notostraca a maxilla composed of two parts: 'an inner setose lobe or endite, and an outer tubercle on which opens the duct of the maxillary gland.' The maxillary gland is well developed in all families of the Conchostraca and is composed of a series of winding tubes near the insertion of the adductor muscle (am) on the carapace (Fig. 10A, B). The end sac (esc) of the gland occurs just posterior to the adductor muscle, and its efferent duct appears to bend medially just above this muscle (ed, Fig. 10B). The development of this gland in conchostracans has been described by Cannon (1924) and Cannon & Manton (1927), but its function is not understood. The maxillary gland is most often described as part of the excretory system (e.g., see McLaughlin 1983, Parry 1960), but its proximity to the mouth region may indicate a possible secretory rather than (or in addition to) an excretory role. Of the families examined by me, the Cyzicidae, Leptestheriidae, and Limnadiidae possess a maxilla. The Cyclestheriidae probably possess this appendage (see Sars 1887), although I did not see it. I was unable to confirm visually that the maxillary gland in fact opens on a tubercle of this appendage in any family. In the Lynceidae there is some controversy over the presence or absence of the maxilla. Sars (1896a) illustrated a reduced flabellate appendage for *Lynceus brachyurus*, but Linder (1945) described instead a 'long tubular process of a delicate and membranous consistency' that he regarded as the opening duct of the maxillary gland and that he felt was not a constituent part of the maxilla, of which he stated there is 'no trace to be found.' My findings for *Lynceus gracilicornis* (Figs. 6E, 10D) agree better with Linder's observations than with Sars's. I can see no evidence of a maxilla, but there is a tubular and lightly setose process that may correspond to that described by Linder. However, it is not clear to me that there is an internal duct in this process as was illustrated by Linder (his Fig. 9). This process (d, Figs. 6E, 10D) does not seem to arise from behind the maxillule but rather beside or even in front of it, suggesting further that it is not homologous with the maxilla in other families.

### 3.5 Thoracopods

The illustrations of flat phyllopodous appendages often seen in descriptions of clam shrimp (e.g., Martin et al. 1986, Fig. 10C of this paper) are somewhat misleading. The thoracopods are never flat but are strongly curved at a line corresponding to the dashed line on Fig. 10C. This line represents the most convex surface of the appendage, with the lobes of the exopod (exd, exv) bent posteriorly to the outside and endites 1-5 and the coxal lobe bent posteriorly to the inside. However, the coxal lobe is bent again so that it is directed toward the head. The result is that the setation of the endites is directed posteriorly, but that of the coxal lobe is directed toward the mouth (Figs. 11, 12A, B). The endites bear a variety of setal types (see Martin et al. 1986 for the Lynceidae). The coxal lobe bears large stout serrate spines in addition to plumose and stout simple setae (Fig. 10C). It is likely that these spines function in transporting food along the food groove toward the mouth, as was described by Fryer (1983) for the Anostraca.

### 3.6 Mouth and digestive tract

The mouth of *Lynceus* can be seen when the labrum and mouthparts are removed. The orifice is small and lined with a border of stiff setae termed by Martin et al. (1986) the oral comb (Fig. 7A). The narrow esophagus (es, Figs. 11, 12) leads from the mouth for a short distance before turning posteriorly to become the slightly enlarged foregut (fgt, Figs. 11A, 12A). The walls of the foregut are thin and are connected by a pair of ducts to the large hepatopancreas in the rostrum and labrum (hp, Figs. 1, 11A, 12A). Sars (1896a) noted that food entering the foregut via the esophagus undergoes a color change from lighter in the foregut to darker in the more posterior part of the intestine; he attributed this change to the yellowish secretions of the hepatopancreas. Schlecht (1979) has described microvilli on the cells lining the foregut in *Leptestheria*. In addition to microvilli, it appears that some cells lining the foregut of *Leptestheria* have true cilia that extend into the gut lumen (Fig. 8, CZ). Schlecht (1979) noticed that there are occasional cytoplasmic extrusions into the lumen and that the arrangement of the microvilli can vary (Fig. 9). Microvilli and cilia have also been described by Rieder et al. (1984), who noted that some hormones are secreted by cells of the foregut. The midgut region is surrounded by a relatively thick network of muscle fibers (Fig. 7B). Sars (1896a) noted occasional peristaltic motions of the intestine that are undoubtedly brought about by this muscle network. The lumen of the intestine in the midgut is lined with a convoluted membrane of presumably absorptive cells (Fig. 12B, C). The thick-walled midgut terminates in an anus that in most families lies between the caudal furcae. In the Lynceidae, which lack caudal furcae, the anus terminates in a slightly muscular rectum in the anal somite (as, Fig. 12B).

### 3.7 Gut contents

Conchostracans appear to be omnivorous. Although few studies describe the gut contents, those that do mention plant and animal matter among the ingested particles. Karande & Inamdar (1961) mention a predominance of algae and plant detritus in the diet of *Leptestheriella gigas*. Bishop (1969) successfully reared larval and postlarval *Limnadia stanleyana* on the alga *Gymnodinium*; this alga was noted also in the guts of field-collected fourth and fifth naupliar stages of the clam shrimp. Other rearing studies have employed a commercial cream

substitute ('Coffee-mate') and bacteria grown on hard boiled eggs (Stern & Stern 1971) or a supply of dirt from the collecting site (Strenth & Sissom 1975). The most informative study on conchostracan gut contents is that of Royan (1976) on *Leptestheriella maduraiensis*. Royan showed that the gut contents, which included phytoplankton (Bacillariophyceae, Chlorophyceae, and Cyanophyceae) and zooplankton (Protozoa, Ostracoda, Rotifera, Cladocera, and Copepoda) varied with the abundance of those foods in the water column. This relationship between food items in the gut and those in the overlying waters was noted for the entire five-month existence of the clam shrimp population and probably reflects the non-selective bottom grazing feeding habits of this species (Royan 1976). In the present study all families were noted to have guts packed with detritus and plant matter and occasionally animal matter. *Lynceus* appeared to have somewhat larger particles and a greater abundance of animal matter, including arthropodal spines and cuticle, in the gut.

### 3.8 Feeding mechanisms

Cannon (1933) described in detail the feeding mechanism of the Branchiopoda, including *Estheria* as a typical conchostracan. His proposed method involved a complex system of water currents such that water (and particulate food) was drawn into the food groove by the action of the thoracopods. Food particles arriving in the food groove or deposited on the specialized setae of the endites were then intermittently moved toward the mouth by spurts of water forced out of the inter-limb spaces of the thoracopods. Cannon's view thus supported and extended the findings of Lundblad (1920) and others (see review by Mathias 1937) of a ventral food current in the Conchostraca, although other workers (e.g., Storch 1924-25) maintained that the coxal lobes (gnathobases) mechanically moved particles toward the mouth.

Cannon's view has recently been challenged by Fryer (1983). Fryer, while admitting that some orally directed current may be produced by the action of the thoracopods, noted that the subdivision of inter-limb spaces envisioned by Cannon is not present in the anostracan *Branchinecta* and would not in any case explain how food particles could accumulate in the food groove (see further arguments by Fryer 1983). All known conchostracans possess well-developed coxal lobes that I believe function as gnathobases to move food particles along the ventral groove toward the mouth. The food groove (= 'innere Rinne' or 'Hohlrinne' of Lundblad 1916, 1920; 'gouttière ventrale' of Mathias 1937) is well defined in all families.

It is important to note that no experimental work was done in the present study, so the following scenario is inferred from morphology alone. However, previous descriptions of feeding and especially the recent work of Fryer (1983) have convinced me that what follows is the most probable course of ingested food. Food particles most likely arrive in the food groove by slight suction of water into the inter-limb spaces and by suction into the area between the thoracopods (Figs. 7C-E, 10A). Lynceids observed swimming in the aquarium will occasionally open the valves and extend and withdraw the antennae, similar to the cirral feeding of barnacles (Martin et al. 1986). At other times, lynceids will swim rapidly over the bottom of the aquarium and over alga-covered rocks and debris on the bottom; they appear to graze on the algal coating. These actions probably aid in bringing food particles into the area between the thoracopods, where particles may be filtered by long plumose setae on the ventral lobe of the exopod (Fig. 7D). Food particles in the food groove (fg, Fig. 10A) are then mechanically passed toward the mouth region by the strong spines and setae of the thoracopod coxal lobes (gnathobases) (Figs. 10A, C, 11A). The oral orientation of these gnathobases

(see Figs. 11A, 12A) would seem to favor this view rather than one dependent on water currents. Once in the oral region, food is passed through the maxillules and between the mandibles. Secretions from the maxillary gland may be added by way of the duct (d, Figs. 6E, 10D, 11B). Secretions from the labral glands mix with the food at this point and help form it into a cohesive mass. After maceration by the mandibles, food is then passed into the esophagus by peristaltic actions of the labrum, esophagus, and foregut as was observed by Sars (1896a). Secretions from the large hepatopancreas are added in the foregut and immediately begin to break down food particles, which are finally absorbed by the convoluted lining of the midgut (Fig. 12B, C).

#### 4 DISCUSSION

There is a striking similarity in the form of the feeding appendages in all families of the Conchostraca, except the Lynceidae, despite a variety of feeding habits. Some members of the Cyzicidae are known to burrow through mud. Emberton (1980) suggested that *Caenestheriella gynecia*, which he routinely found half buried in the mud with its ventral side up, might be a filter feeder. Yet the mouthparts and even the antennae of the cyzicids appear identical to those of the Leptestheriidae, which are, as far as is known, detrital grazers (Royan 1976, but see Karande & Inamdar 1961). The monotypic Cyclestheriidae has long been considered a highly modified conchostracan family with characteristics of the Cladocera. However, the structure of the mandible does not differ from that seen in any of the other non-lynceid families. An argument could perhaps be made that the Lynceidae are modified for a different mode of feeding. Sars (1896a) noted that they are active swimmers and do not attach themselves to plant matter (as do the limnadiids), and Martin et al. (1986) describe what appears to be a planktonic feeding behavior. Kaestner (1970) singles out the lynceids as the only planktonic feeders among the Conchostraca, although he cites no primary reference, whereas Cannon (1933) refers to *Lynceus* (as *Limnetis*) as a 'mud-eater.' In this paper I report that lynceids (at least *L. gracilicornis*) are also known to 'graze' on benthic algae. Thus it appears that the feeding behavior of lynceids is not unique or even particularly specialized and probably does not account for their different morphology.

Two other alternative explanations could explain the difference in the lynceid feeding structures. First, it could be argued that the feeding structures are another neotenic character possessed by the Lynceidae. The absence of growth lines of the carapace, the enormous labrum, the lower numbers of trunk segments, and the absence of dorsolateral spines and terminal claws are all characters reminiscent of larval conchostracans. Second, it could be argued that the form of the mouthparts reflects phylogenetic affinity with the Notostraca, as was suggested by Linder (1945). Linder noted that the surface of the lynceid mandible was very similar to that of the Notostraca. Cannon & Leak (in Cannon 1933) noted the same similarities, but attributed the similarity of the mandible to similarities in feeding habits in lynceids and notostracans. Lynceids likely are similar in feeding habits to notostracans in that both groups are known for scavenging, deposit feeding, and omnivory. However, notostracans are also raptorial predators readily taking living anostracans (see Horne, 1966); they are also known to catch and eat small fish (D. Belk, personal communication). Other characters seeming to unite these two groups (lynceids and notostracans) are the form of the antennule, elongated maxillary gland (compared to those of other clam shrimp) and the form of its associated duct, and the absence (in large adults of the Notostraca) of the maxilla. It seems

almost unnecessary to state, as a conclusion, that further studies on conchostracans are badly needed to answer these and other questions on clam shrimp morphology.

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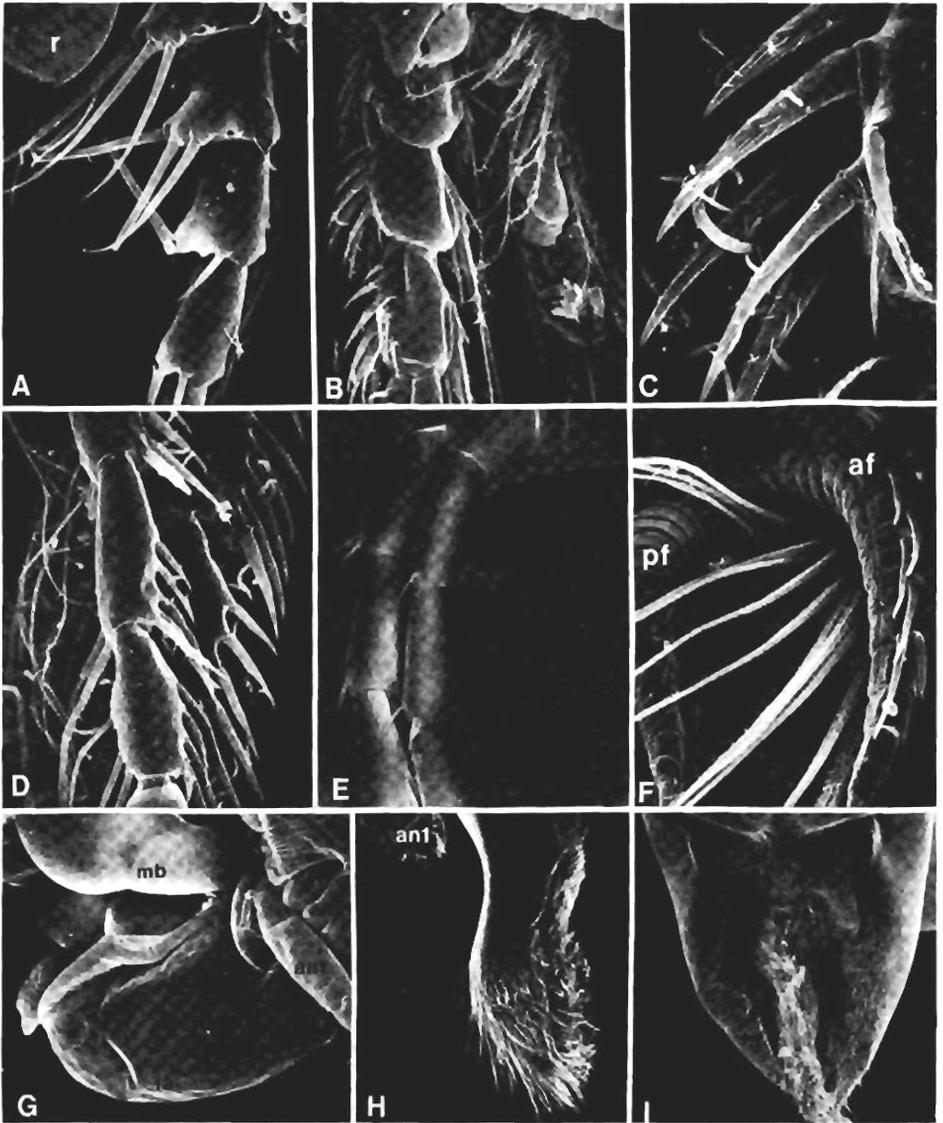


Figure 2. Antennae and selected labra of conchostracans. A. Rostrum and antenna, *Cyclestheria hislopi*;  $\times 100$ . B. Antenna, *Caenestheriella setosa*;  $\times 50$ . C. Spines on dorsal border of segment of antenna, *C. setosa*;  $\times 250$ . D. Antenna, *Leptestheria compleximanus*;  $\times 100$ . E. Antenna, *Eulimnadia texana*;  $\times 50$ . F. Antenna, *Lynceus gracilicornis*;  $\times 100$ . G. Labrum, *Cyclestheria hislopi*;  $\times 100$ . H. Labrum, *Lynceus gracilicornis*, lateral view;  $\times 65$ . I. Labrum, *L. gracilicornis*, posterior view;  $\times 75$ .

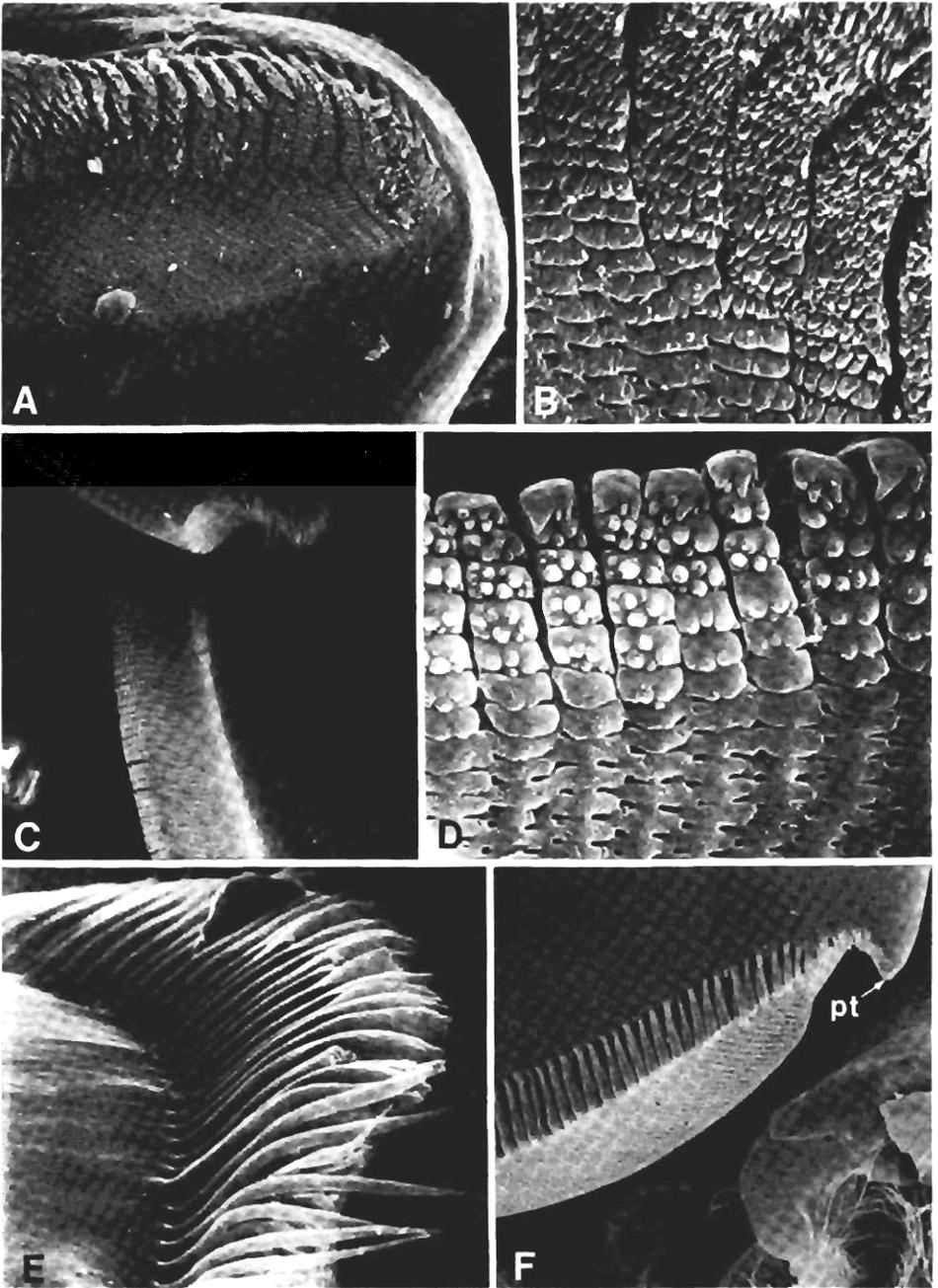


Figure 3. Conchostracan mandibles. A. *Cyclestheria hislopi*, distal end of right mandible;  $\times 750$ . B. Detail of mandible in A;  $\times 3750$ . C. Right (upper) and left mandibles, *Caenestheriella setosa*;  $\times 225$ . D. Detail of mandibles in C;  $\times 2250$ . E. Outer margin of elongate scales of mandible, *C. setosa*;  $\times 1125$ . F. Left mandible, *Leptestheria compleximanus*;  $\times 375$ .

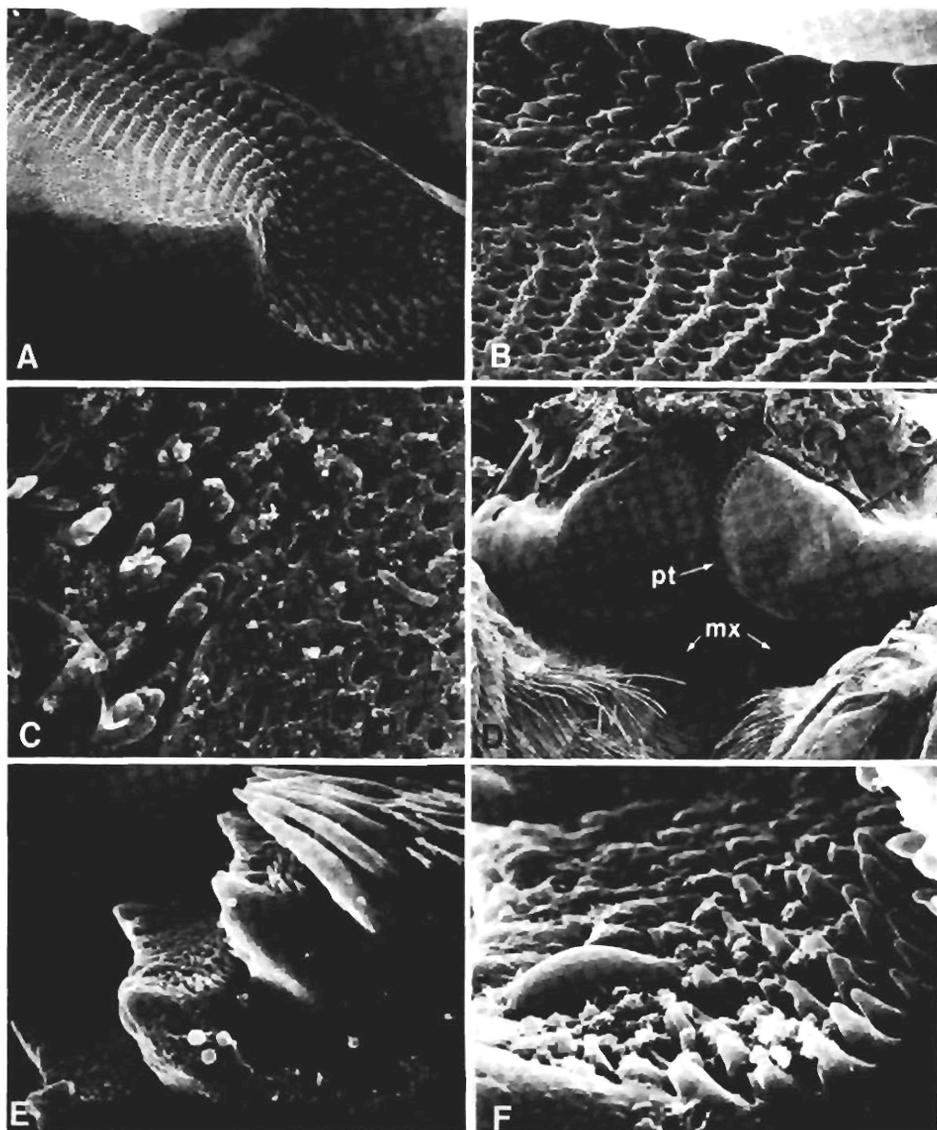


Figure 4. Conchostracan mandibles, continued. A. Anterodistal end of right mandible, *Leptestheria compleximanus*;  $\times 600$ . B. Detail of mandible in A;  $\times 2250$ . C. Triturating surface of mandible, *Eulimnadia texana*;  $\times 4500$ . D. Mandibles, *Lynceus gracilicornis*, in situ;  $\times 100$ . E. Anterodistal end of triturating surface of mandible, *L. gracilicornis*; note double row of teeth;  $\times 750$ . F. Minutely dentate area between rows of teeth seen in E;  $\times 3750$ .

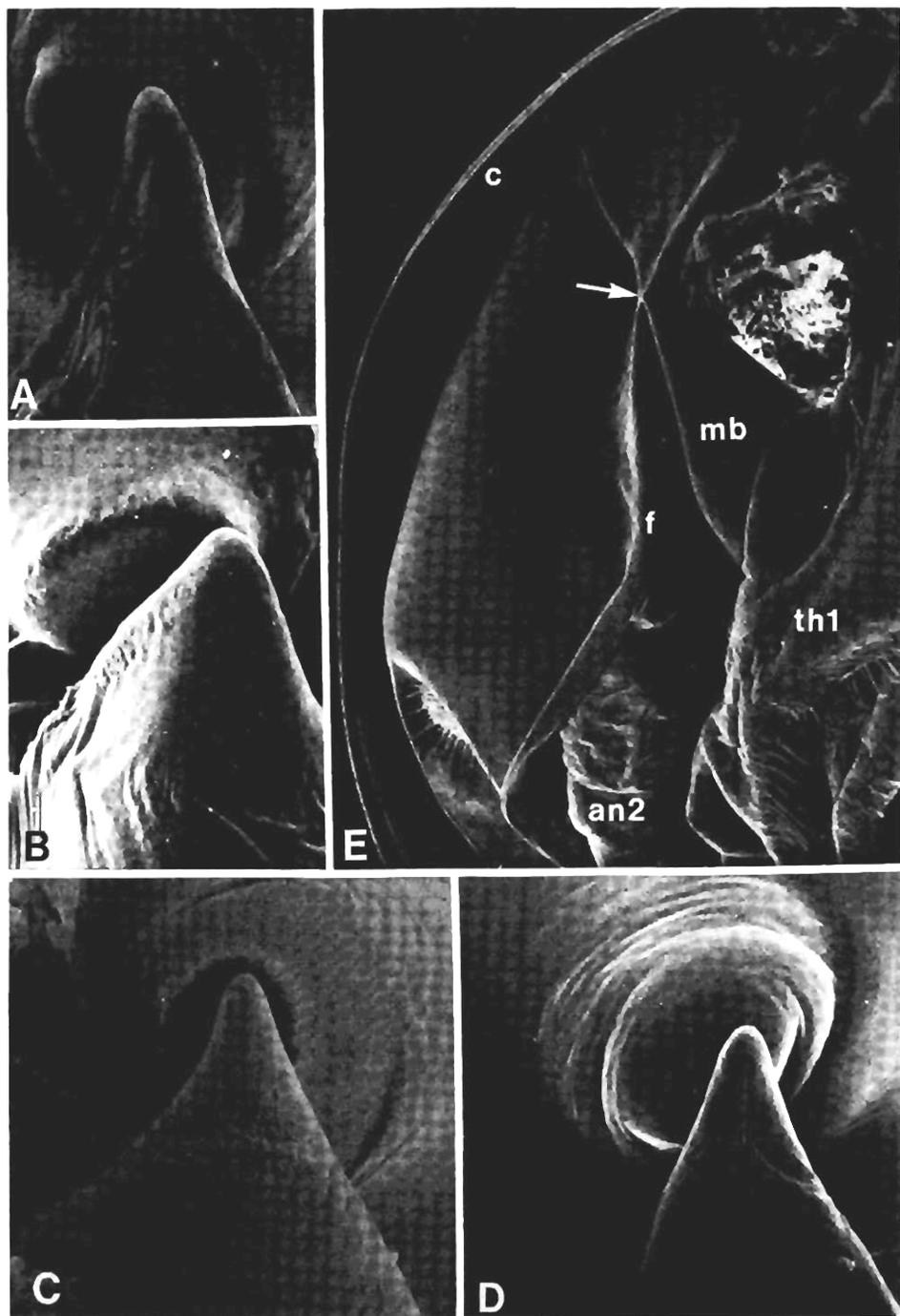


Figure 5. Articulation of mandible with sclerotized protuberance arising from wall of mandibular somite. A. *Cyclestheria hislopi*,  $\times 400$ . B. *Caenestheriella setosa*;  $\times 350$ . C. *Leptestheria compleximanus*;  $\times 300$ . D. *Eulimnadia texana*;  $\times 250$ . E. Anterodorsal part of head region, *Lynceus gracilicornis*; note articulation (heavy arrow) of mandible on raised ridge extending from fornix;  $\times 50$ .

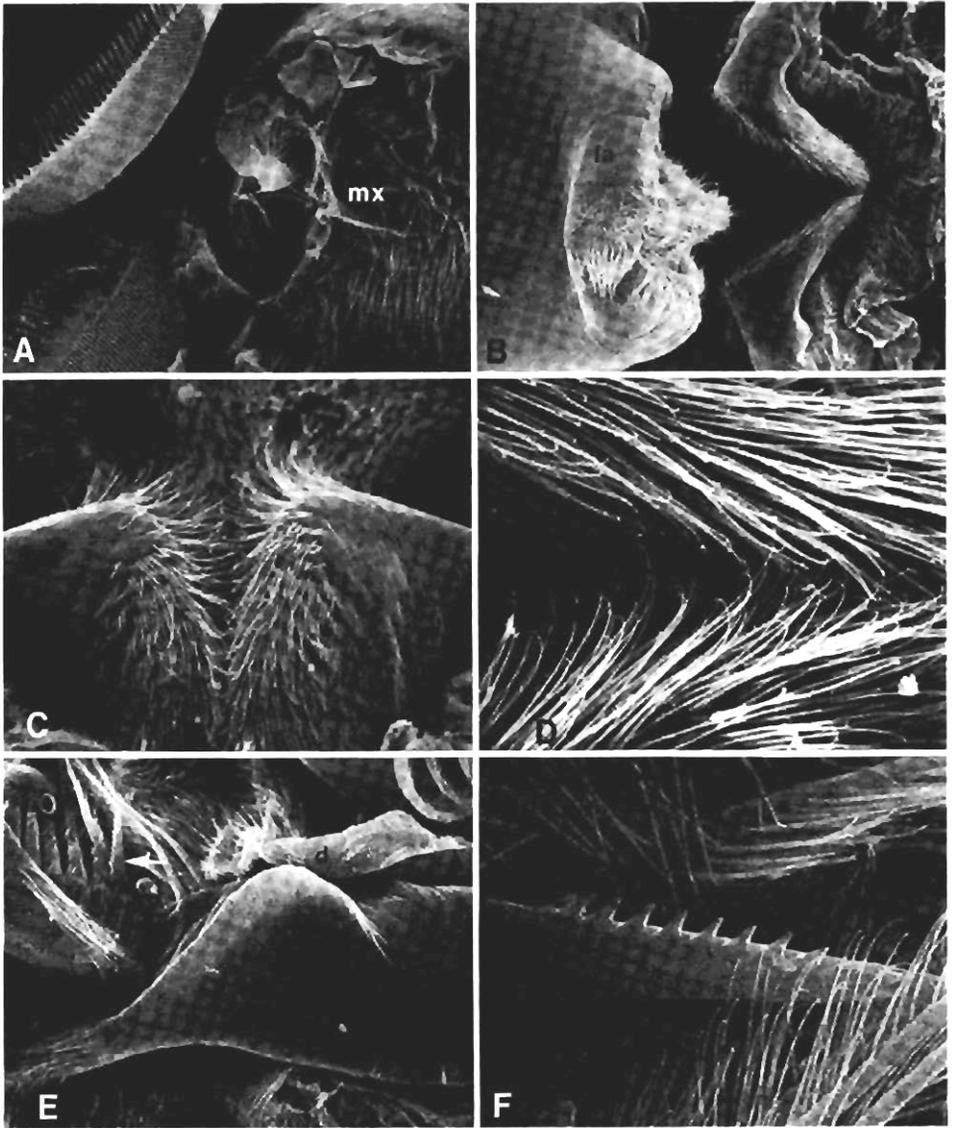


Figure 6. Maxillules of selected conchostracans. A. Maxillule and mandibles (to left), *Leptestheria compleximanus*;  $\times 225$ . B. Ventral view of the labrum and maxillule, *Lynceus gracilicornis*;  $\times 150$ . C. Outer (posterior) surface of maxillules, *L. gracilicornis*;  $\times 240$ . D. Close up of 'filtering' area composed of simple setae of maxillules seen in C;  $\times 410$ . E. Ventral view of maxillules and 'duct', *L. gracilicornis*;  $\times 225$ . F. Close up of serrate setae indicated by arrow in E;  $\times 1,500$ .

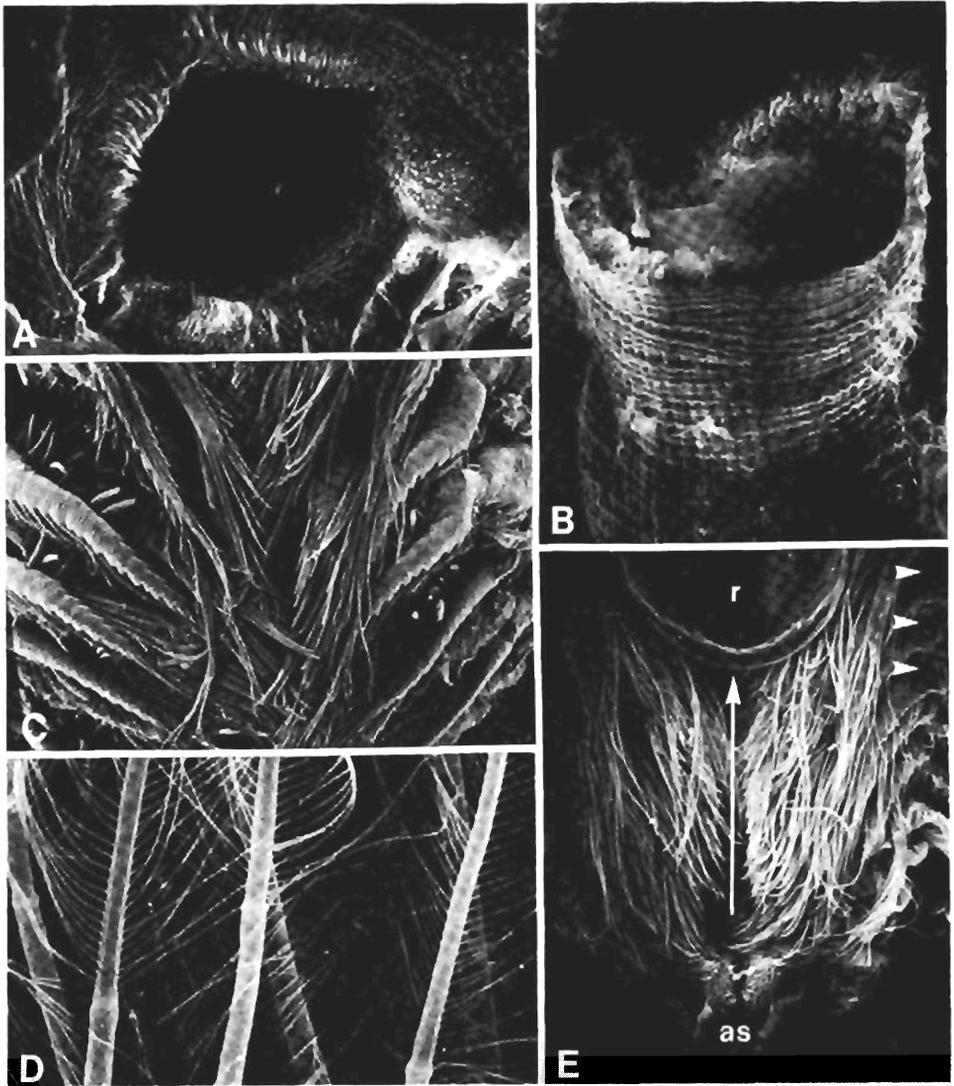


Figure 7. Mouth, midgut, and thoracopods of *Lynceus gracilicornis*. A. Mouth with all mouthparts removed; arrow indicates direction of labrum;  $\times 150$ . B. Section of midgut showing network of muscle fibers;  $\times 225$ . C. Ventral view of thoracopods coming together at midline below the food groove;  $\times 45$ . D. Example (from *Cyclestheria hislopi*) of plumose setae on lobes of exopod. E. Ventral view of *L.gracilicornis* showing rostrum and thoracopods. Large arrow indicates direction of food movement in food groove (obscured by thoracopods), arrow heads indicate inter-limb spaces.  $\times 38$ .

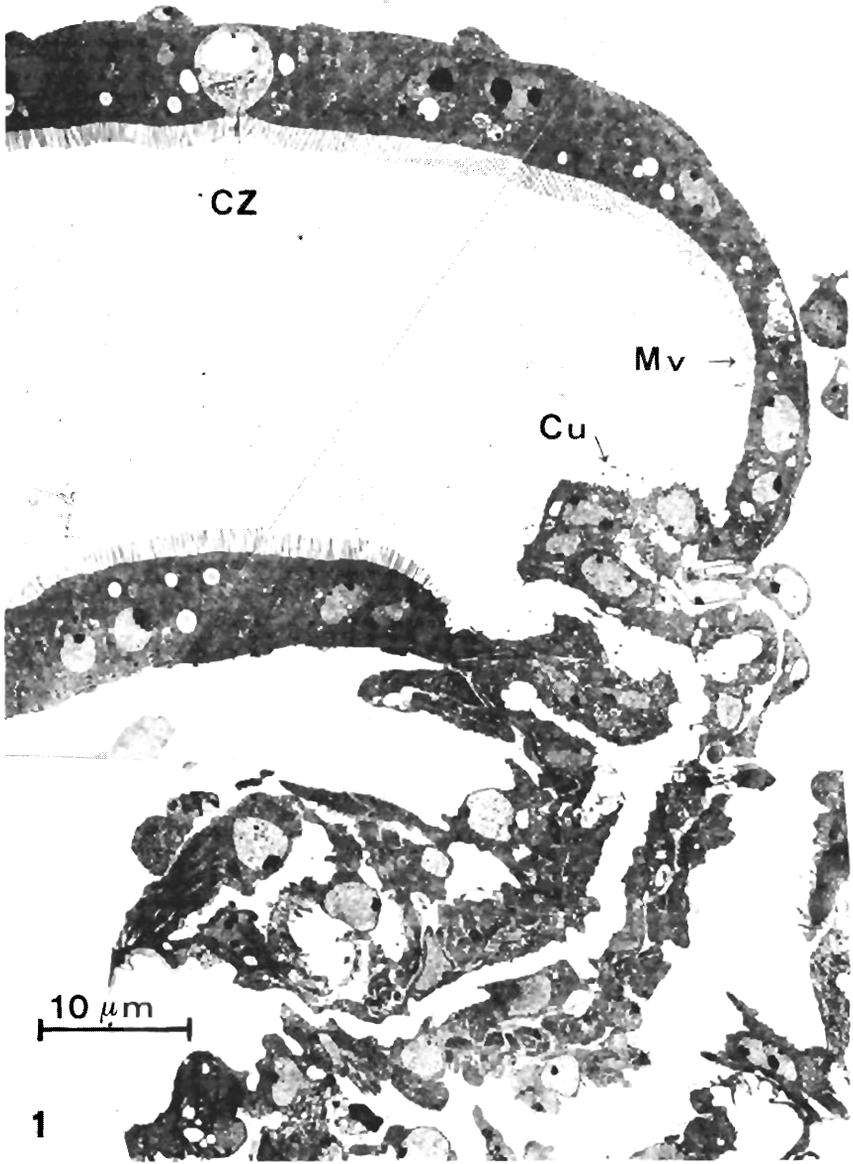


Figure 8. Sagittal section through naupliar stage of *Leptestheria dahalacensis*, esophagus and anterior region of foregut, the latter lined with microvilli (Mv);  $\times 2,000$ . Note cell with cilia (CZ). After F. Schlecht, 1979, *Zoomorphologie* 92:161-181, Springer-Verlag, by permission.

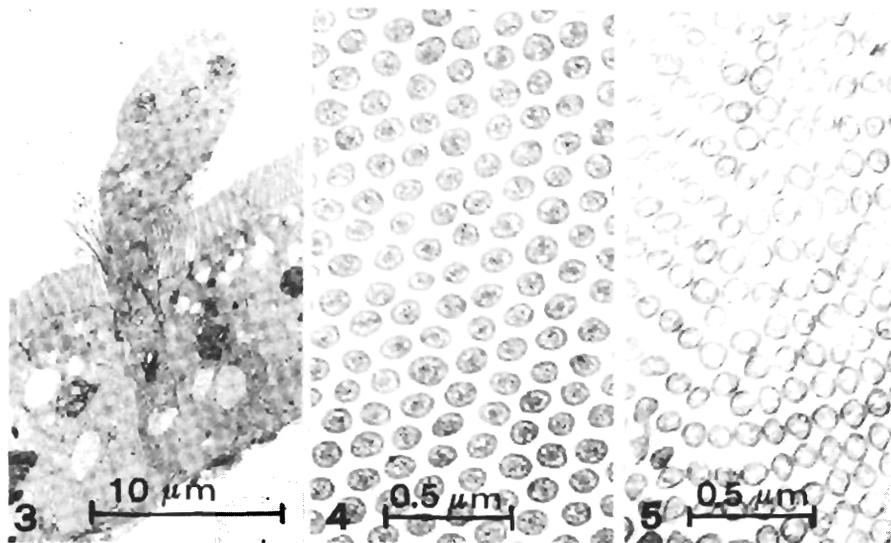
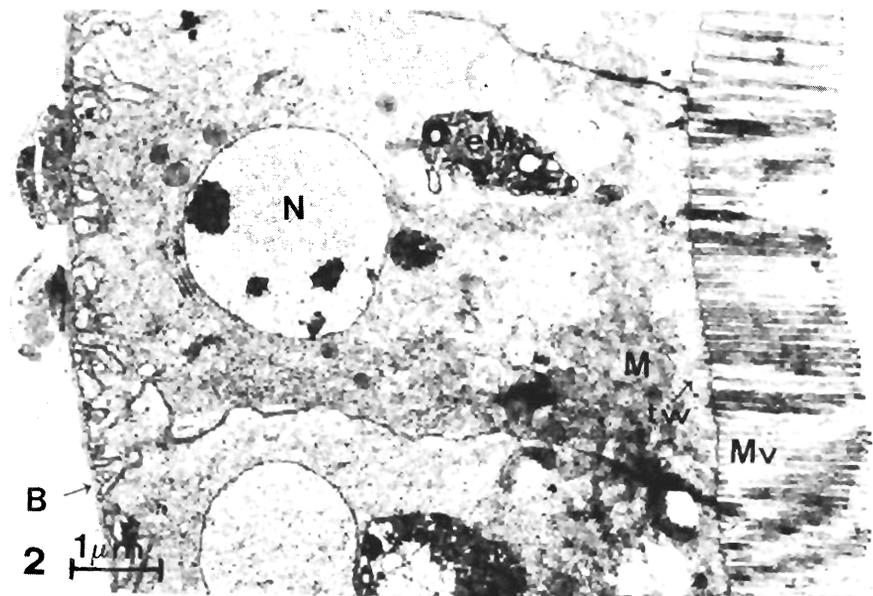


Figure 9. Ultrastructure of the midgut region, *Leptestheria dahalacensis*. 2. Single cell of the midgut wall, overview;  $\times 11,000$ . 3. Cytoplasm extending into the intestinal lumen;  $\times 2,500$ . 4 and 5. Cross section through microvilli of nauplius, showing different patterns of arrangement;  $\times 37,000$  and  $33,000$ , respectively. After F. Schlecht, 1979, *Zoomorphologie* 92:161-181, Springer-Verlag, by permission.

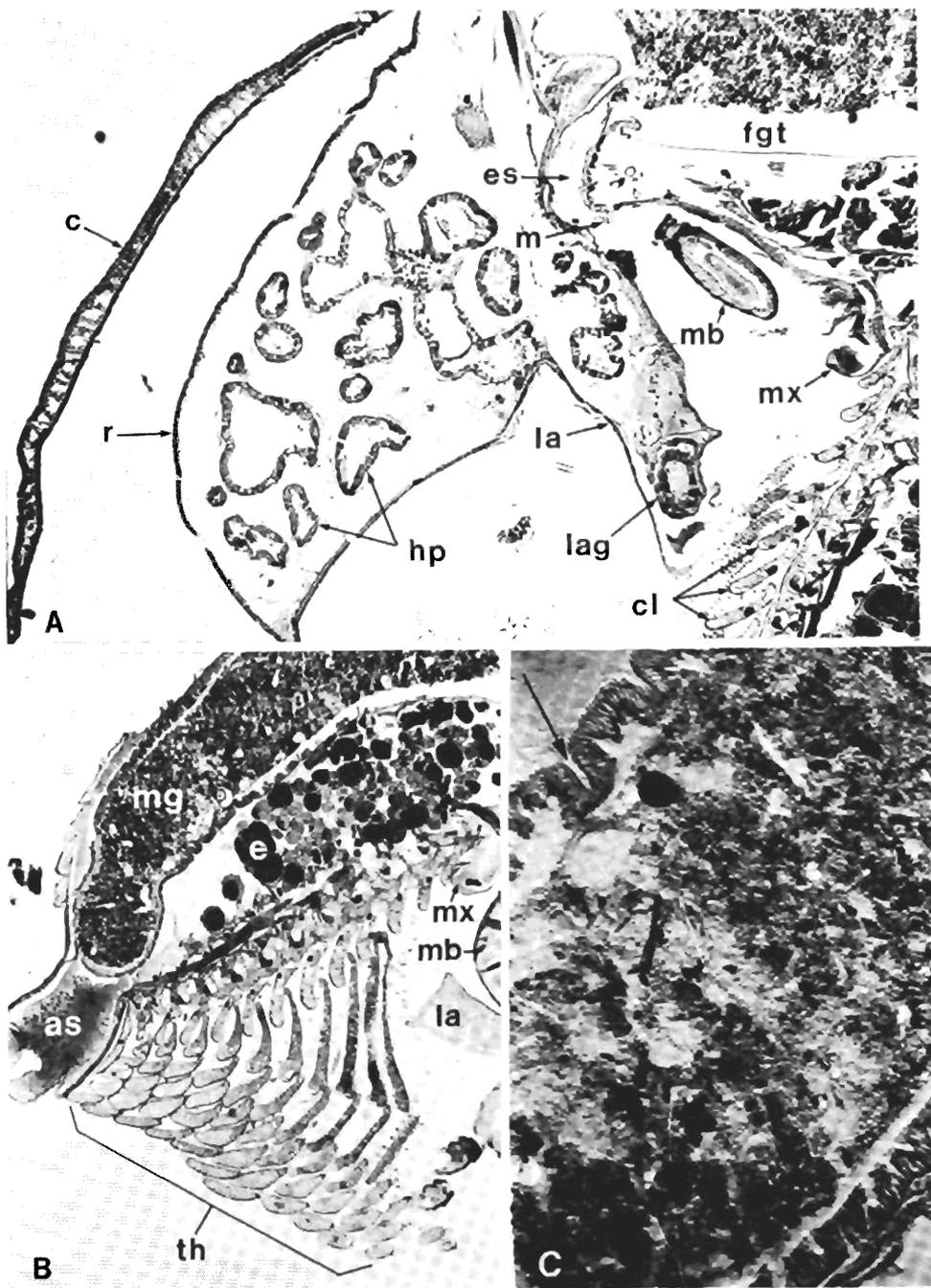


Figure 12. Sagittal sections through female *Lynceus gracilicornis*. A. Head region showing mouth, esophagus, and foregut and with feeding appendages indicated by abbreviations (see Appendix). B. Posterior region showing packed midgut, anus, and nature of thoracopods. C. High magnification of midgut; arrow indicates convoluted lining of gut wall.

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## APPENDIX I: List of abbreviations used in the figures

af	anterior flagellum of antenna	fo	pyriform frontal organ
am	adductor muscle	hp	hepatopancreas
an1	antennule	la	labrum
an2	antenna	lag	labral gland
as	anal somite	m	mouth
B	basement membrane	M	mitochondria
c	carapace	mb	mandible
ce	compound eye	mg	midgut
cl	coxal lobe of thoracopod	Mv	microvilli
Cu	cuticle lining of foregut	mx	maxillule (first maxilla)
CZ	cell with cilia	mx2	maxilla
d	duct (?) of maxillary gland	N	nucleus
e	egg	ne	naupliar eye (ocellus)
ed	efferent duct of maxillary gland	pf	posterior flagellum of antenna
eM	electron-dense material	pt	posterior tooth of mandible
ep	epipod	r	rostrum
es	esophagus	rs	rostral seta
esc	end sac of maxillary gland	sf	sensory field
exd	dorsal lobe of exopod	sl	suspensor ligament of mandible
exv	ventral lobe of exopod	th	thoracopod
f	fornix	th1	first thoracopod
fg	food groove	tmm	transverse mandibular muscle
fgt	foregut	tw	'terminal web' (see Schlecht 1979)

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