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## Chapter 3

# Branchiopoda

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### INTRODUCTION

The great morphological diversity seen among branchiopod crustaceans very nearly prohibits generalizations about form and function. Branchiopods are among the most diverse of the classes of Crustacea, which in turn is the most morphologically diverse (although not the most speciose) taxon on earth. No single character or group of characters uniquely defines the Branchiopoda, and for any given suite of characters there are many exceptions. Early schemes of branchiopod classification, and many of the characters upon which they were based, were reviewed by Fryer (1987c), who commented on the impressive heterogeneity of extant branchiopods, a problem recognized by many previous students of the Crustacea, and discussed the difficulties in formulating an unambiguous definition that would apply to all members of the group. Perhaps as a consequence of the group's morphological diversity, the monophyletic status of the branchiopods is still questioned by some workers (e.g., see Wilson, in press), although arguments for monophyly based on larval characters (e.g., Sanders, 1963), sperm morphology (Wingstrand, 1978), and feeding apparatus (Walossek, in press) seem strong.

Most branchiopods are small, freshwater animals with numerous, similar, phyl-

lopodous limbs, although many of the diverse "cladocerans"—making up half of the eight extant orders, accepting Fryer's (1987c) classification—do not conform to this description. Although many branchiopods possess numerous body somites, others exhibit rather extreme fusion and tagmatization. Appendages are often flat and leaflike, sometimes termed "phyllopods"; however, trunk limbs are more or less stenopodous in two predatory orders (Haplopoda and Onychopoda). Although as a taxonomic name meant to include all branchiopods the term Phyllopoda has been abandoned (Fryer, 1987c), it still is occasionally employed, in a very different capacity, to encompass various crustacean assemblages (Schram, 1986) or component groups of the Branchiopoda (Walossek, in press). Usually there are no appendages on the "abdomen" (which is often defined as the postgenital somites but is a rather meaningless term in this group), other than characteristic caudal rami (sometimes termed furcae or cercopods) on the telson or anal somite (see Bowman, 1971; Schminke, 1976; and Walossek, in press, for terminology) in most groups. A carapace is present in many groups, and may be a univalve shield (notostracans and the extinct *Rehbachella*), or bivalved, reduced, or absent (adult anostracans). Among the bivalved groups, where the valves actually represent a secondary shield over-

growing the initial one (Walossek, in press), it is hinged only in the Laevicaudata (and simply folded in the others); in haplopods and onychopods the carapace valves are greatly reduced and can no longer enclose any part of the body. A small cuticular "dorsal organ" (= neck organ) is present in all groups at some stage of development (usually larval), but the homology is, in my opinion, uncertain (Martin and Laverack, in press). Most (not onychopods or haplopods) possess a rather deep ventral food groove, extending posteriorly from the cephalic feeding groove and formed by an invagination of the cuticle of the thoracic sternites. Associated with this food groove are certain unique modifications of the feeding appendages and thoracopods (Walossek, in press). In those orders that have retained the nauplius larval stage (all groups except the anomopods, ctenopods, and onychopods), the nauplius is recognizable in its possession of the following combination of features: (1) an unsegmented first antenna that bears only distal setation (although segmentation is evident in larvae of some taxa and in some extinct forms), (2) a second antenna with an elongate protopod that is more than half the total length of the appendage, (3) a single spine on the distal article of the second antennal protopod, (4) an absence of setae on the medial surface of the second antenna endopod, and (5) a uniramous mandible (Sanders, 1963). Finally, all species examined possess an ameoboid sperm lacking on acrosome and flagellum; this combination is unique among the Crustacea (Wingstrand, 1978).

Most species have adapted to life in temporary or permanent freshwater ponds, small streams, and occasionally lakes. Many of the habitats are ephemeral, i.e., they are dry during certain seasons, but are permanent in the sense that they persist from year to year. It is unclear whether multiple radiations into freshwater occurred, as perhaps suggested by the discovery of a marine anostracan-like branchiopod from the Upper Cambrian (Walossek, in press), vs. a single invasion that preceded the extensive morphological radiation (see Potts and Durning, 1980; Kerfoot

and Lynch, 1987). Consequently, some branchiopod peculiarities may represent convergent adaptations to the freshwater habitat.

Traditional classifications divided the approximately 800 species of living branchiopods (Belk, 1982) among four major groupings, usually given ordinal status: Anostraca (fairy and brine shrimps), Notostraca (tadpole shrimps), Conchostraca (clam shrimps), and Cladocera (water fleas). The Branchiopoda is now recognized as consisting of eight, rather than four, extant orders (Fryer, 1987c). These eight extant groups are the result of recognizing that the "Conchostraca" consists of two rather different assemblages of bivalved crustaceans, the orders Laevicaudata (family Lynceidae) and Spinicaudata (all other families formerly included as conchostracans), and that the "Cladocera" encompasses four morphologically disparate taxa (the orders Anomopoda, Ctenopoda, Onychopoda, and Haplopoda). Cladocerans encompass the widest range of morphological and behavioral habits of any branchiopod grouping, and in retrospect it is surprising that the group was not formally reorganized into four distinct orders until recently (Fryer, 1987a,c). In general, I agree with Fryer's (1987c) classification, although I might argue, based on naupliar characters of lynceids that were not available to Fryer (C. Sassaman, unpublished data), that the Conchostraca might still be retained as a valid taxon despite the many peculiarities of adult lynceids (Fryer, 1987c; Martin and Belk, 1988). Occasionally in this review, for the sake of conserving space, I employ the terms conchostracan and cladoceran when discussing the above orders. The orders Anostraca and Notostraca are still believed to be valid monophyletic groupings. There are also several fossil taxa of ordinal or subordinal status (Lipostraca, Kazacharthra, and possibly *Rehbachella*; see Fryer, 1987c; Müller, 1983; Walossek, in press; Müller and Walossek, in press); these are not discussed further here but are of tremendous importance in phylogenetic considerations (see Walossek, in press). Also crucial for understanding branchiopod evolution, and for understanding much of the anat-

TABLE 1. Classification of the Extant Branchiopoda Followed in This Chapter\*

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Order Anostraca
Family Branchinectidae (1, <i>Branchinecta</i> )
Family Artemiidae (1, <i>Artemia</i> )
Family Branchipodidae (5 or 6)
Family Streptocephalidae (1, <i>Streptocephalus</i> )
Family Thamnocephalidae (3, <i>Branchinella</i> , <i>Dendrocephalus</i> , <i>Thamnocephalus</i> )
Family Chirocephalidae (7)
Family Polyartemiidae (2, <i>Polyartemia</i> , <i>Polyartemiella</i> )
Family Linderiellidae (2, <i>Linderiella</i> and <i>Dexteria</i> , both monotypic)
Order Notostraca
Family Triopsidae (2, <i>Triops</i> , <i>Lepidurus</i> )
Formerly "Conchostracans":
Order Laevicaudata
Family Lynceidae (3, <i>Lynceus</i> , <i>Lynceiopsis</i> , <i>Paralimnetis</i> )
Order Spinicaudata
Family Cyclestheriidae (1, <i>Cyclestheria</i> , monotypic)
Family Cyzicidae (4, <i>Caenestheria</i> , <i>Caenestheriella</i> , <i>Cyzicus</i> , <i>Eocyzicus</i> )
Family Leptestheriidae (5)
Family Limnadiidae (6)
Formerly "Cladocerans":
Order Anomopoda
Family Daphniidae (6)
Family Moinidae (2, <i>Moinodaphnia</i> (monotypic) and <i>Moina</i> )
Family Bosminidae (2, <i>Bosmina</i> and <i>Bosminopsis</i> (monotypic))
Family Macrothricidae (16 or 17)
Family Chydoridae (over 30)
Order Ctenopoda
Family Sididae (6 or 7)
Family Holopediidae (1, <i>Holopedium</i> )
Order Onychopoda
Family Polyphemidae (1, <i>Polyphemus</i> )
Family Podonidae (6 or 7)
Family Cercopagidae (2, <i>Bythotrephes</i> , <i>Cercopagis</i> )
Order Haplopoda
Family Leptodoridae (1, <i>Leptodora</i> , monotypic)

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\*After Belk, 1982; Mordukhai-Boltovskoi and Rivier, 1987; Fryer, 1987c; Dodson and Frey, 1991; and other sources. No phylogenetic relationships are implied. Numbers in parentheses are approximate number of extant genera, names of which are provided for those families with four or fewer. For reviews of various previous classification schemes and the characters on which they were based, see Fryer (1987c).

omy of adults, but given only brief mention in this review, are branchiopod larval features.

Unfortunately, Fryer (1987c), although hinting at the affinities of some taxa, proposed no explicit relationships among the eight extant orders, and although Walossek (in press) suggests relationships among many of the branchiopods, he does not attempt to resolve relationships among the six orders formerly comprising the "cladocerans" or "conchostracans." For the present chapter I have simply listed the extant families under the orders proposed by Fryer (Table 1), which I assume will be accepted by most carcinologists, without giving any indication of phylogenetic relationships within the Branchiopoda as a whole.

Because of the tremendous amount of time that branchiopods have existed (see Linder,

1945; Tasch, 1963, 1969; Smirnov, 1971; Briggs, 1976 [although *Branchiocaris* is no longer believed to be a branchiopod]; Bergström, 1979, 1980; Müller, 1983; Fryer, 1985, 1987c, 1991a,b; Walossek, in press), which, as noted by Fryer (1987c), is longer than the time during which all radiations of terrestrial vertebrates took place, it is not surprising that extensive morphological diversification has occurred, and the relationships among the constituent groups may be obscured by homoplasies. Another problem for the phylogenist or comparative morphologist is that the branchiopods exhibit a curious combination of morphological plasticity and evolutionary stasis. The external and cellular morphology of some extant branchiopods can be modified by altering the conditions under which they are reared. Developing daphniids

(Anomopoda) will produce spines in response to waterborne chemical cues of predators, with the number of spines increasing with predator density (e.g., see Krueger and Dodson, 1981; Havel, 1986; Havel and Dodson, 1987; Dodson, 1989; Walls and Ketola, 1989; Harvell, 1990). Cyclomorphosis is common (reviewed by Jacobs, 1961, 1987; Kerfoot, 1980), and the sex ratio of developing embryos and the reproductive switch from producing embryos vs. resting eggs in some branchiopods can be influenced by a variety of environmental stimuli (reviewed by Hobaek and Larsson, 1990). Other branchiopods have been shown capable of rapid and striking changes in morphology caused not by external cues but by mutation. Bowen et al. (1966) documented a single mutation in the anostracan *Artemia franciscana* that produces, instead of the normal brine shrimp with two widely separated eyes borne on stalks, a cyclopean mutant with a single, median eye, complete and entirely functional, with all musculature and nerves operational. In stark contrast, one species of notostracan, known from fossils from the Triassic (Trusheim, 1938), was considered conspecific with extant *Triops cancriformis* by Longhurst (1955) despite a time difference of some 200 million years. If these fossils are indeed conspecific with extant *Triops cancriformis* (which now seems unlikely in light of ongoing electrophoretic studies [C. Sassaman, personal communication] that indicate divergence despite morphological similarity), then *Triops cancriformis* is the oldest continuous species of any animal on earth (Fryer, 1985).

The literature on some branchiopods is vast, while other groups have escaped serious attention for many years. The genus *Artemia*, probably the best known genus in all of the Crustacea (rivalled only by *Daphnia*, another branchiopod), has been the subject of over 4,000 primary references (Browne et al., 1991), and is so well known at the cellular level that it has aided our understanding of the function of the eukaryotic cell (MacRae et al., 1989). Several recent and extensive compila-

tions (e.g., MacRae et al., 1989; Warner et al., 1989; Browne et al., 1991; Belk et al., 1991; and a series of six volumes under the direction of the *Artemia* Reference Center in Ghent, Belgium [Persoone et al., 1980; Sorgeloos et al., 1987]) provide access to the vast *Artemia* literature. The attention lavished on *Artemia* is a result of its abundance, economic importance, ease in laboratory rearing, and importance as a model crustacean for comparative morphological studies. Similarly, "cladocerans," primarily the Daphniidae (Anomopoda), have been the focus of numerous experimental studies, in part because of their value as test organisms for toxicity studies, ease in manipulation, and abundance (e.g., see papers in Peters and De Bernardi, 1987). References to morphological studies on anomopods can be found in the works of Fryer on the Daphniidae (1991a), Chydoridae (1963, 1968) and Macrothricidae (1974).

Because the majority of previous studies have centered on *Artemia* and some of the daphniids, and because my own knowledge is severely restricted to a few conchostracans, many of the following examples are from these taxa. But I strongly caution the reader against making any generalizations based on examples presented here. The diversity of branchiopod anatomy and ultrastructure cannot be deduced from a few selected illustrations. For example, it would be misguided to extend an observation made on the feeding and absorption mechanisms in *Artemia*, so often depicted as a "typical" branchiopod, to all other anostracans, some of which feed by predation rather than filtration, and meaningless to impose such generalizations upon other orders, such as members of the anomopod family Chydoridae, where there are known filter feeders, scrapers, scavengers, and even ectoparasites on freshwater hydras (Fryer, 1968). Several sections, such as those on excretion and osmoregulation, are based on the brine-inhabiting *Artemia*, a species with diametrically opposed needs in these areas compared to most other branchiopods, which inhabit fresh waters. Examples pre-

sented here must be viewed with the great functional and anatomical diversity of branchiopods in mind.

## EXTERNAL MORPHOLOGY

### Anostraca

Anostracans (fairy shrimp) (Fig. 1A) inhabit fresh or saline inland waters or (rarely) marine lagoons. The habitat is most often an ephemeral one, although some species inhabit permanent larger bodies of water in the Arctic and Antarctic; these habitats tend to have few predators. There are eight extant families: Artemiidae (one genus, *Artemia*), Branchinectidae (one genus, *Branchinecta*), Branchipodidae (five or six genera), Chirocephalidae (seven genera), Linderiellidae (two mono-

typic genera), Polyartemiidae (two genera), Streptocephalidae (one genus, *Streptocephalus*), and Thamnocephalidae (three genera). This group includes the largest branchiopods, reaching lengths of up to 100 mm in *Branchinecta*, but most are 15–30 mm as adults (e.g., see Linder, 1941).

Anostracans are characterized by an elongate body with little regional specialization (tagmatization) within the three obvious tagma (head, thorax, and abdomen). There is no carapace, although it has been argued that a headshield is present in early larval stages (e.g., see Schrehardt, 1986, 1987a, for figures; Walossek, in press, for discussion). There are 19–27 postcephalic segments (fewer in some extinct taxa; see Fryer,

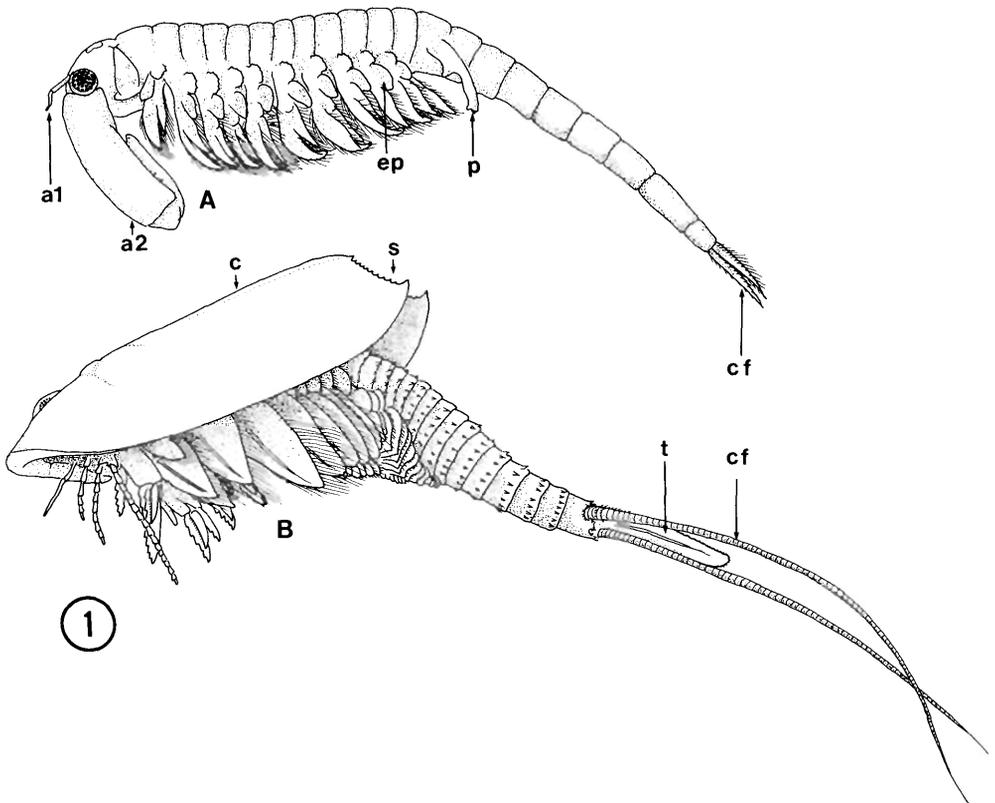


Fig. 1. Orders Anostraca and Notostraca. **A:** *Branchinecta conservatio* (Anostraca). **B:** *Lepidurus packardii* (Notostraca). a1, first antenna (antennule); a2, second antenna; c, carapace; cf, caudal furca or ramus (= cercopod); ep, epipod of thoracic limb; p, external penis; s, sulcus of carapace; t, supra-anal plate of telson.

1987c). Fryer (1987c) stated that there is a pair of dorsal sensory setae on each segment, but I have not seen these in all taxa. The head is short and frontally rounded or even flattened. The paired compound eyes are well developed and borne on movable stalks, a condition unique among branchiopods. The antennules of adults are simple, one-segmented structures that are uniramous and more or less tubular in design. The antennae exhibit extreme sexual dimorphism, being less mobile (Fryer, 1987c) and often simple in females (with several exceptions) but modified as highly movable claspers in males. The modified male antennae may be enormous grasping structures, often with species-specific basal outgrowths and elaborate ornamentation. The labrum is large and fleshy, with functional, secretory labral glands often persisting into the adult stage. The mandible is of the grinding and rolling type, but in some taxa may be secondarily modified for biting (e.g., *Branchinecta*). The maxillules are greatly reduced in extant forms, existing only as modified gnathobases that bear a single row of long, denticulate spines and a single stout spine (Fryer, 1987c). The maxillae consist of a single lobe (the proximal endite) with two or three anteriorly directed setae and a variable number of distal setae. Postcephalic limb-bearing somites (which traditionally have been termed the "thoracic" segments) are easily recognizable (i.e., there has been little or no fusion) and may number 11, 17, or 19 (excluding the two often-fused genital somites), although as few as eight are known in one extinct species. Appendages of these somites are foliaceous, phyllopodous limbs that beat with a distinctive metachronal rhythm and that display considerable serial similarity. Each limb has an exopod, endopod, and a series of endites and in most species is modified for filtering. Additionally, each thoracic limb bears a "respiratory" epipod (actually osmoregulatory; see later) and one or two exites proximal to the epipod. The more distal exopod is clearly demarcated from the rest of the limb. The food groove between the limbs is narrow and deep. The

"abdomen" consists of 9 segments, the first two of which are genital and fused, and often considered part of the thorax (see Benesch, 1969; Walossek, in press), and the last of which is the telson or anal somite. The post-genital region consists of six cylindrical segments plus the telson and bears no appendages other than a pair of rather flattened caudal rami (fused into paired plates extending forward along the abdomen in the genus *Thamnocephalus*) borne on the telson. Other external features include an elongate brood pouch in females and an extensible penis in males, both of which are borne on the first post-thoracic segment (= the twelfth thoracic of Benesch, 1969, and Walossek, in press), which typically is fused in both sexes to the following segment.

#### Notostraca

The Notostraca (Figs. 1B, 2), commonly called tadpole shrimps, are all members of a single extant family, Triopsidae, consisting of two genera, *Triops* and *Lepidurus*. There are approximately ten extant species (Linder, 1952; Longhurst, 1955; Belk, 1982). Species inhabit inland freshwater pools, which are sometimes slightly alkaline or even brackish. Most pools are temporary, but as with anostracans some are found in predator-poor permanent bodies of water. Notostracans are omnivorous, and are predominantly benthic, although they can swim well. They may attain lengths of 100 mm (Belk, 1982), although most often they are smaller, 30–50 mm. They do not filter but rather feed on detritus or on other organisms, living or dead, and will even pursue and catch anostracans and small fish (Horne, 1966; Martin, 1989a). Their various anatomical modifications reflect these basic functional and ecological differences from anostracans and other branchiopods.

Notostracans superficially resemble anostracans that have acquired a shieldlike carapace (Fig. 1B). But the resemblance goes no further. Although the body is elongate, with a variable number of cylindrical trunk somites (varying even within a species or population), they are functionally and morphologically

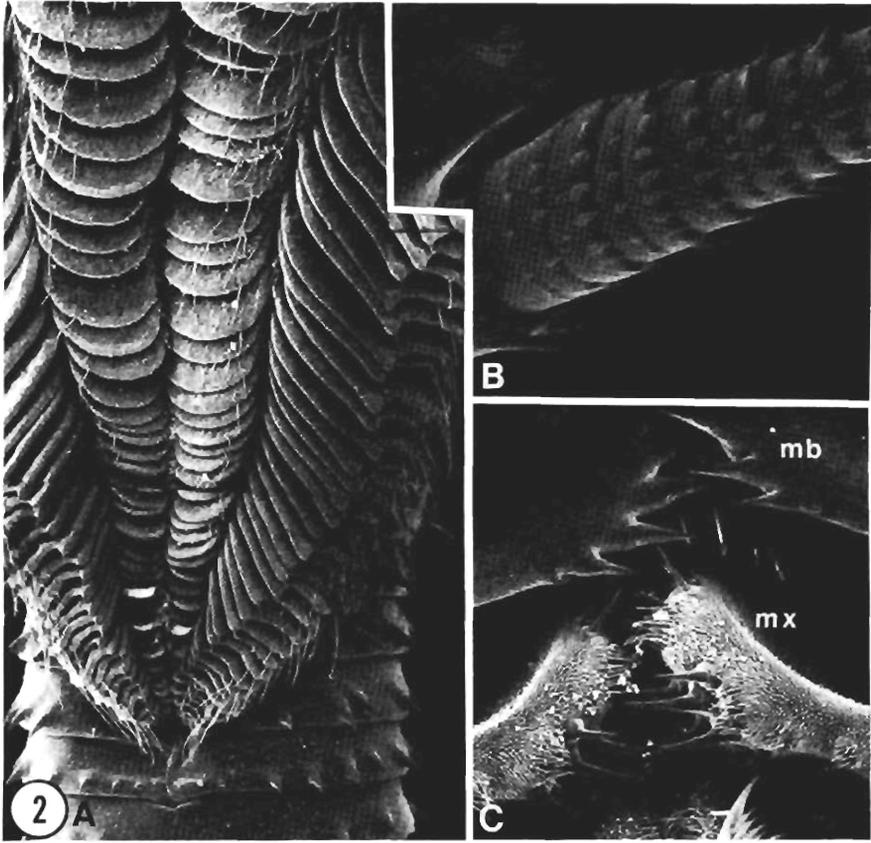


Fig. 2. Order Notostraca, SEM of selected external features. A: Ventral view of "thoracic" limbs and cylindrical rings of anterior region of "abdomen," *Triops longicaudatus*. Note high numbers of limbs per body somite. B: Base of single branch of caudal rami (= cercopod). (Courtesy of B. Felgenhauer.) C: Heavily spined mandible and first maxilla, *Triops longicaudatus*. mb, mandible; mx, first maxilla.

very different from anostracans (see Fryer, 1988). The carapace is a shieldlike expansion of the dorsal cuticle, presumed to be of the maxillary somite, and contains between its inner (ventral) and outer (dorsal) surfaces the coils of the maxillary glands. It is not hinged or folded, but a longitudinal carina and a posterior carapace sulcus allow considerable flexibility and mobility of the trunk. The carapace extends anteriorly to shield the head and posteriorly to shield the anterior half of the trunk. It differs from the carapace of the bivalved branchiopod orders, in which the carapace overgrows the head, in that, in notostracans, the head is incorporated into the shield, with the compound eyes visible dor-

sally. The compound eyes are technically external but become internalized during ontogeny; in adults the now-sessile compound eyes remain in contact with the external environment via a small median opening (Fig. 124F, G), seen also in some conchostracans. The antennules are short and uniramous. The antennae also are uniramous and are reduced or absent. The labrum is a flat, stiff plate that does not bear secretory glands in the adult. The mandibles are enormous and well developed for biting, with sharp denticles along the molar region (Fig. 2C). The maxillules have two segments and are robust and heavily muscled and sclerotized, the only maxillules in the Branchiopoda capable of true biting. The

maxillae are reduced to small lobes, probably representing remnants of the former gnathobases (Fryer, 1987c, 1988), with the opening of the maxillary gland on an adjacent tubular outgrowth. The distinction between thorax and abdomen is unclear; altogether the trunk may bear 35–72 pairs of limbs, of which 24–60 occur posterior to the genital segment (segment 11) and are usually termed abdominal. Posterior to the genital segment there may be up to six pairs of limbs on one cylindrical somite or body ring (Fig. 2A). The “thoracic” limbs (those anterior to the genital somite) are nonfiltratory and extend laterally rather than ventrally from the axis of the body. Although somewhat phyllopodous, these limbs have clearer distinctions among the various endites than do the anostracan thoracopods. In the anterior one or two postcephalic limbs, some endites may be elongate and filiform. The gnathobases of the trunk appendages are thick, sclerotized, and impressively armed with a variety of spines and setae. Thoracic appendages also bear an exopod and an inflated epipod. In females, the limbs of the genital somite are modified as oostegopods, in which the endopod has become fused with the “apical lobe” (Fryer, 1988) to form an egg-bearing pouch; the cover of this pouch is formed by the modified exopod. The food groove between the gnathobases of the thoracopods is well developed but is broad and shallow. More posterior appendages are less complex, becoming simple and flaplike eventually. The long, cylindrical “abdomen” terminates in a telson that bears a pair of long, thin, cylindrical, multiarticulate caudal rami (Fig. 2B), between which extends a platelike process in *Lepidurus*.

### **Laevicaudata**

This order contains one extant family, the Lynceidae (Fig. 3C–E), with approximately 40 species (Martin and Belk, 1988) in three genera: *Lynceus*, *Lynceiopsis*, and *Paralimnetis*. Species are known from ephemeral ponds and occasionally streams on all continents except Antarctica (Martin and Belk, 1988). Lynceids are small to medium-sized (to about 8 mm) branchiopods that spend most

of their time at or just above the bottom and feed primarily by scraping, scavenging, or “grazing” on detritus (Martin et al., 1986; Martin and Belk, 1988; Martin, 1989a).

Laevicaudatans were for many years grouped with other families of “clam shrimp” (see below) in the Conchostraca. Although they resemble other conchostracans in the possession of a bivalved carapace, strong carapace adductor muscle, telsonal filaments (= postabdominal setae), and modified male first thoracopods, there are many more differences than similarities (Linder, 1945; Fryer, 1987c; Martin and Belk, 1988). The bivalved carapace is globose, nearly spherical, almost circular in lateral view, and lacks an “umbo” or any growth lines or other external ornamentation (Fig. 3C). The two valves are joined dorsally by a true hinge in a recessed groove, although the valves are not entirely separate but are fused for a short distance along the dorsal border. The head region is enormous (Fig. 3D,E), taking up nearly a third of the space between the valves, and articulates with the trunk, thereby becoming capable of extending beyond the valves, which it often does. The eyes are sessile and “internal,” in contact with the external environment via a median pore (Fig. 135C) (as in notostracans); they characteristically quiver back and forth, much as in some anomopod cladocerans. The head is produced into an elongate “rostrum” more so than in other clam shrimps, and bears distinctive paired fields of sensilla on either side of the midrostral carina just posterior to the above-mentioned pore (Figs. 3E, 135C). The antennules are short, uniramous, and two-segmented, and bear sensory setae on the expanded distal segment. The antennae are large and natatory, with the anterior flagellum bearing short spines and with both rami bearing plumose, posteriorly directed natatory setae, one per segment. The labrum is huge and fleshy, and bears large internal secretory glands. The mandibles are large and heavy, of the grinding/rolling type, but the masticatory surfaces are narrow and bear stout teeth; the proximal end of the mandibles articulates with a cuticular ridge (the fornix) rather than on a protrusion of the head cuticle (as is the

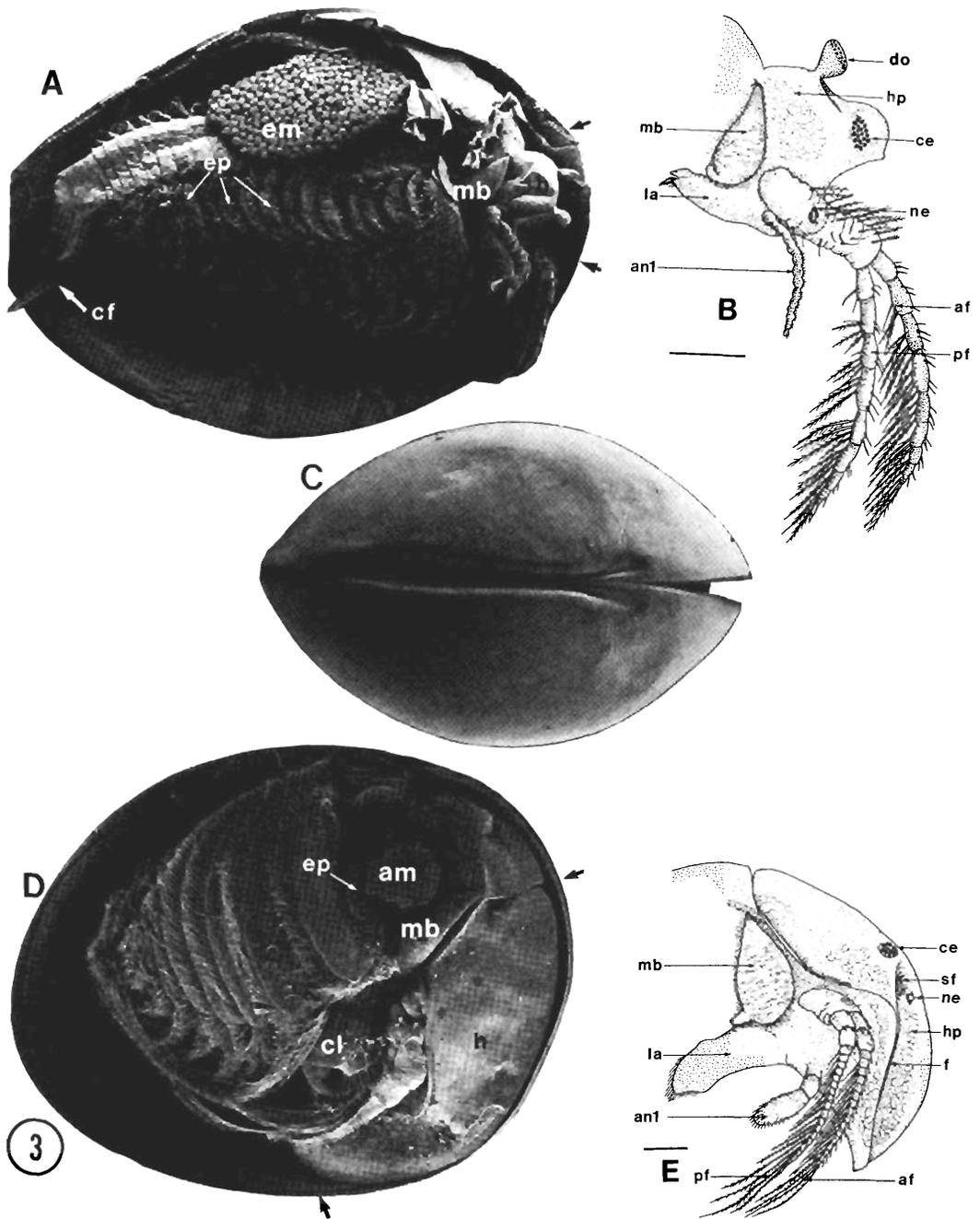


Fig. 3. The two conchostracan orders Spineauctada and Laevicaudata. **A:** *Eulimnadia ovisimilis* (Spineauctada), lateral view with right valve removed. (After Martin, 1989b.) **B:** *Eulimnadia texana* (Spineauctada), enlargement of head region (approximately the area between arrows in A.) (After Martin, 1989a.) **C:** *Lynceus gracilicornis* (Laevicaudata), dorsal view of carapace. Note recessed hinge between valves, lacking in A, and absence of growth lines. (After Martin and Belk, 1988.) **D:** Lateral view of *Lynceus brachyurus* with right valve removed. (After Martin and Belk, 1988.) **E:** Enlargement of head region of *Lynceus*

*gracilicornis* corresponding approximately to region marked by arrows in D. Note relatively large head size. (After Martin, 1989a.) af, anterior flagellum of second antenna; am, adductor muscle of carapace (present also in A but not visible in this photograph); an1, first antenna; cf, caudal furca; cl, male clasper; ce, compound eye; do, dorsal organ; em, egg mass; ep, epipod; f, fornx of head region; h, head region; hp, hepatopancreas (digestive ceca); la, labrum; mb, mandible; ne, nauplius eye; pf, posterior flagellum of second antenna; sf, sensory field.

case with spinicaudatans). The maxillules are reduced to a small, thin, setose lobe. The maxillae are vestigial, with no obvious masticatory function, and carry the duct of the maxillary gland. The trunk is short, consisting of only 10 segments in males and 12 in females, with all segments bearing appendages. The first trunk appendage is modified in males as a clasper for grasping the female carapace during mating; however, the clasper components are derived from different endites from those in the Spinicaudata. The second male appendage is sometimes modified as well (*Paralimnetis*, *Lynceiopsis*), but never as a clasper. More posterior appendages are foliaceous, directed ventrally, and display marked serial similarity (e.g., Martin et al., 1986), differing mostly in size and development of the various endites. The gnathobase is well developed, with stout spines and setae, and is directed anteriorly. The food groove is broad and V-shaped. Each limb has a well-developed exopod, an inflated "respiratory" epipod (Fig. 3D), and several endites; these often bear large scraping setae and perform a variety of functions (although not filtration). The trunk terminates in an anal somite (= telson?) that bears telsonal filaments (postabdominal setae) but lacks caudal rami, and is ventrally shielded by opercular lamellae of the penultimate trunk somite. There are no spines on the dorsal surface of the trunk somites. Oviducts of females open on the 11th somite; those of the male open either alongside the anus (claimed by Linder, 1945) or at the base of a posterior trunk limb (Sars, 1896). In females, unique lateral flaps of the body wall work in conjunction with exopods of trunk limbs nine and ten to support the egg mass.

### Spinicaudata

The Spinicaudata (Fig. 3A,B) encompasses those taxa most commonly referred to as "clam shrimp," formerly grouped with laevicaudatans in the Conchostraca. There are four extant families: Cyclestheriidae (monotypic, *Cyclestheria hislopi*), Limnadiidae (six genera), Leptestheriidae (five genera), and Cyzicidae (four genera). Some species,

mostly in the Cyzicidae and Limnadiidae, can attain lengths of 18 mm (mature females), but most are on the order of 8–10 mm. All inhabit ephemeral freshwater pools or prairie streams, and they are commonly found with other branchiopod species. *Cyclestheria* also frequents permanent bodies of water.

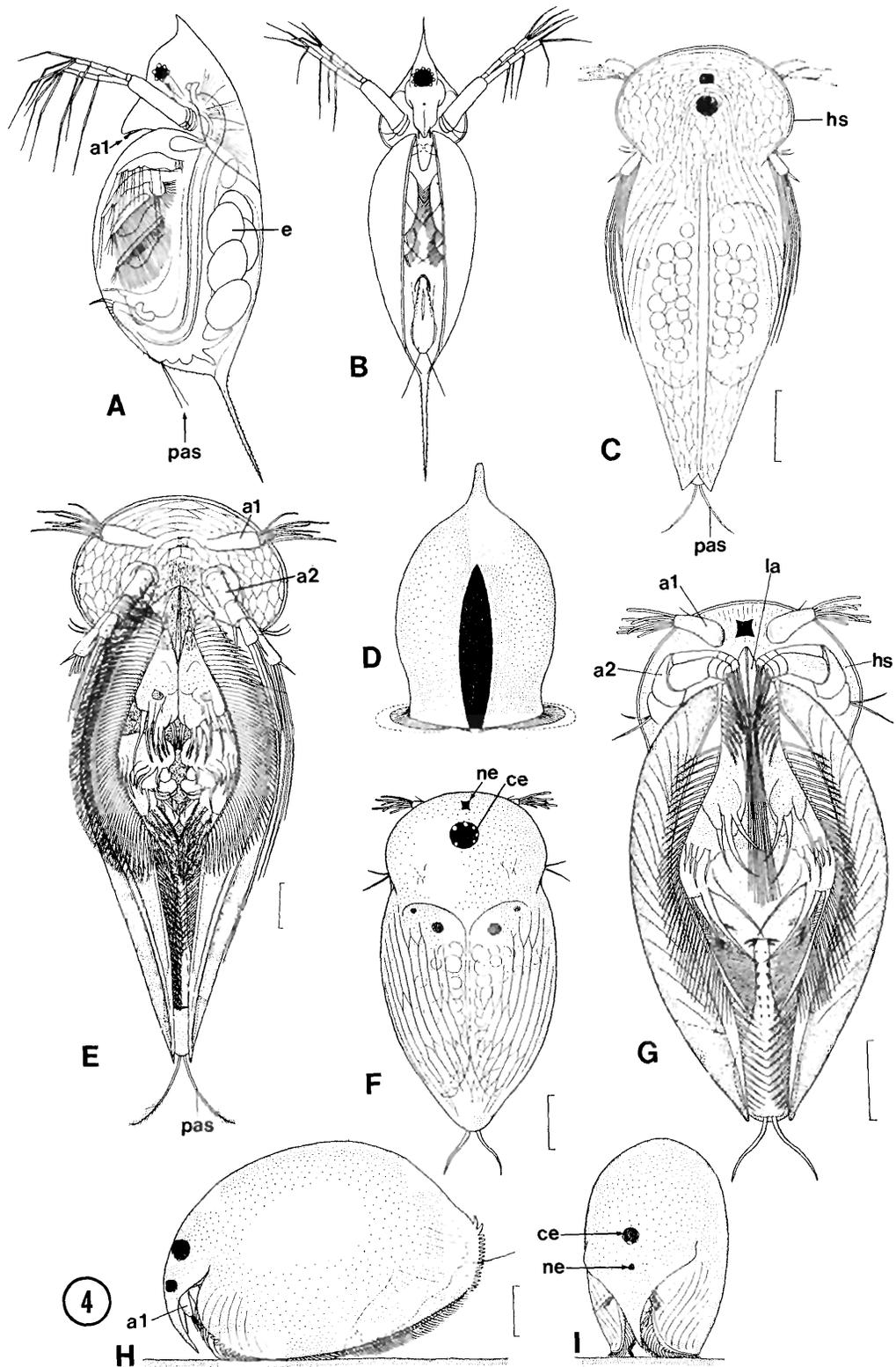
Like the lynceids, all spinicaudatans have a bivalved carapace and powerful adductor muscle, but the nature of the valves and the external and internal morphology differ significantly. The valves are joined dorsally by a simple fold; there is no true hinge. All species have external growth lines on the carapace. The carapace encloses the entire body, and the small and usually narrow head region (Fig. 3A,B) is not capable of articulating with the trunk and extending beyond the valve margins, although in large individuals of *Cyzicus* the head may protrude slightly. The compound eyes are assumed to have become "internalized" during ontogeny at least in some families, since the same median pore as described above for notostracans and laevicaudatans exists. These eyes are paired, but in some species, and especially in *Cyclestheria*, they appear very close together and may even be fused into one functional unit. The labrum is small, often tipped with setal tufts, and contains secretory glands. The antennules are elongate and subdivided into several lobes, each of which bears sensillae, except in *Cyclestheria*, which has a straight, tubular antennule with the sensory setae confined to its tip. The antennae are large and natatory with plumose setae and sometimes with dorsal spines. Although in some ways similar to laevicaudatan antennae, the musculature apparently differs significantly (see Fryer, 1987c). Mandibles are of the rolling/grinding type, but they lack the heavy teeth seen in notostracans and laevicaudatans, and they articulate with a protuberance of the head cuticle (Martin, 1989a). The maxillules are reduced and probably represent only the remaining gnathobase, being armed with stout spines and setae. The maxillae are reduced to small lobes with distal setae. The trunk, although short, is comprised of 16–32 somites; and thus there are 16–32 pairs of trunk limbs. The first and

second trunk limbs of males are modified as claspers (only the first in the Cyclesteriidae, in which males are rare), which superficially resemble those of the laevicaudatans (the clasper components are derived from different endites; Fryer, 1987c). More posterior trunk limbs are foliaceous, directed ventrally, and are composed of an exopod, endopod, and protopod (corm) subdivided into endites. The trunk limbs display serial similarity, differing mostly in size. Each has a "respiratory" epipod (Fig. 3A), elongate endopod, and well-developed gnathobase, which differ slightly in spination from anterior to posterior limbs. The food groove between the gnathobases is broad and shallow, and usually somewhat U-shaped. In females, trunk limbs 9–11 often bear "dorsal filaments" (actually modified dorsal lobes of the exopods) to which the eggs are attached. The external openings of the male and female genital ducts are at the base of the 11th pair of trunk limbs, and caudal rami and spines (Fig. 3A) occur in all species.

#### Anomopoda

The Anomopoda (Figs. 4, 5) contains the five families that are perhaps most often considered "typical" cladocerans: Daphniidae (six genera), Bosminidae (two genera), Chydoridae (over 30 genera), Macrothricidae (approximately 16 genera), and Moinidae (two genera). They are small, from less than 0.3 mm to perhaps 6 mm in adult females (all display sexual dimorphism, with smaller males). The group includes one of the smallest known arthropods (the chydorid *Alonella nana*, with an adult female maximum length of 0.26 mm; Fryer, 1968). All inhabit fresh water, with a few exceptions in inland saline bodies for some bosminids and daphniids. Habits are extremely diverse, and include benthic, planktonic, interstitial, moist terrestrial (rainforest leaf litter and mosses, e.g., Frey, 1980), and even cave (Brancelj, 1990) environments. Most feed by filtration or scraping, or by some combination of these modes, but others are scavengers on other crustaceans (*Pseudochydorus*) and one genus (*Anchistropus*) is ectoparasitic on freshwater hydras (see Fryer, 1968).

Anomopods are characterized by having a short body exhibiting extreme fusion. The carapace, which is often elaborately modified or ornamented (e.g., Fig. 5D, and Frey, 1982a,b, 1987) and may bear numerous pores, is bivalved but lacks a true hinge, and it does not enclose the head, which is short and often expanded dorsally into a protective headshield (Fig. 4C,E,G). The compound eyes are fused into a single median eye (also true in some spinicaudatans), which may be variously reduced or absent, but there is no known connection to the external environment via a median pore (although some species have a median head pore; e.g., see Kerfoot et al., 1980, for *Bosmina*). The labrum is short and fleshy, and bears secretory glands. Female antennules are variable, either tubular and of one or two segments, or reduced to small vestiges, or in some cases enlarged; male antennules very often are modified as clasping structures with a large grappling spine (but only slightly so in the Macrothricidae and Chydoridae). The antennae are well developed, biramous, and natatory, with three or four segments per ramus and often with plumose setae on all segments, although it is common to have one or more segments without setae. The mandibles are stout and of the rolling/grinding type. The maxillules are reduced and bear four or fewer spines. The maxillae are reduced to small, nonsetose protrusions, or are absent. The trunk limbs display none of the serial similarity seen in the more "phyllopodous" branchiopods (the above-mentioned taxa), and are fewer in number, usually numbering only five or six. These limbs are widely diverse in form and function in the various taxa. All have an epipod, but the first trunk limbs bear unique "ejector hooks," and they lack a true gnathobase basally. The trunk limbs (see Watts and Petri, 1981) perform functions as diverse as grasping, scraping, mechanically transferring food particles, and filtration, or some combination of these duties, although the first and sixth (when present) are never filtratory, and the limbs never beat in a metachronal rhythm. The first is most often used in locomotion. The food groove tends to be deep and



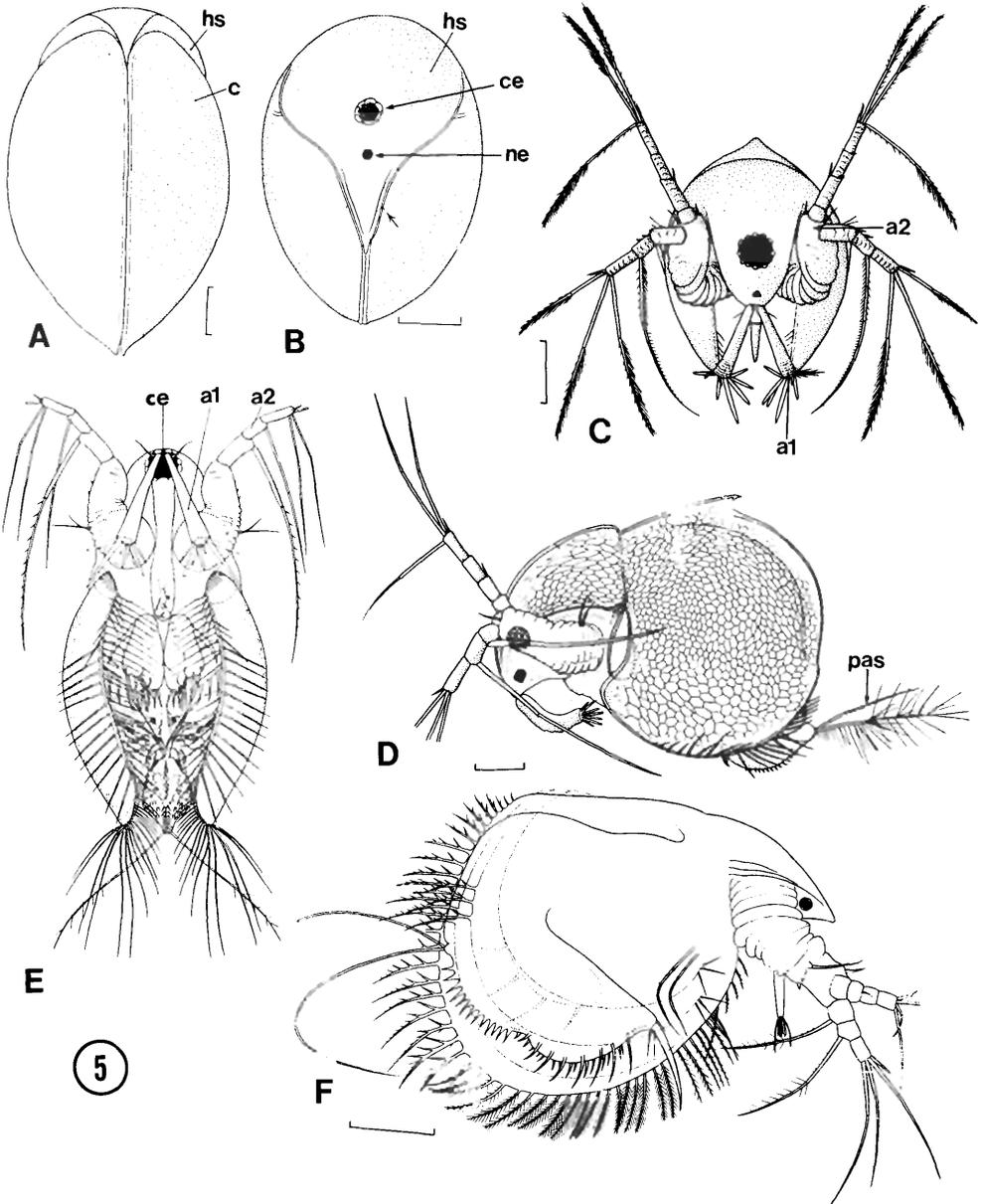


Fig. 5. External morphology of Anomopoda, families Chydoridae and Macrothricidae. **A,B**: Chydoridae. (After Fryer, 1968.) **A**: Ventral view of the scavenger *Pseudochydorus globosus*. **B**: Anterior view of *Pseudochydorus globosus* in "closed" position. **C-F**: Macrothricidae. (After Fryer, 1974.) **C**: Anterior view of the primitive *Acantholeberis curvirostris*. **D**: Adult

female of a burrowing species, *Drepanothrix dentata*. **E**: Ventral view of *Acantholeberis curvirostris*. **F**: A mud-frequenting burrower, *Ilyocryptus sordidus*. Not to scale. a1, first antenna; a2, second antenna; c, carapace; ce, compound eye; hs, head shield; ne, nauplius eye; pas, postabdominal setae.

Fig. 4. External morphology of the Anomopoda. **A,B**: Lateral (**A**) and ventral (**B**) views of an open water species, *Daphnia galeata* (Daphniidae). (After Fryer, 1991a.) **C-I**: Family Chydoridae. (After Fryer, 1968.) **C**: Dorsal view of a gliding gastropodlike species, *Graptoleberis testudinaria*. **D**: Posterior view of *Graptoleberis testudinaria*. **E**: Ventral view of *Graptoleberis testudinaria* as animal glides over substrate. **F**: Dorsal view of

*Alonella exigua*. **G**: Ventral view of *Alonella exigua* gliding over substrate. **H**: Lateral view of *Peracantha truncata*. **I**: Oblique anterior view of *Peracantha truncata*. Not to scale. a1, first antenna; a2, second antenna; ce, compound eye; hs, head shield; la, labrum; ne, nauplius eye; pas, postabdominal setae (= telsonal filaments).

narrow. There are never any postgenital limbs, and the telson or postabdomen terminates in a pair of strong terminal "claws" (caudal rami) and bears a pair of dorsal sensory "telsonal filaments" or "postabdominal setae" (Figs. 4A–C, E–G, 5D–F). The telson is usually bent under, so that its ventral surface is functionally dorsal, and it may articulate with the trunk.

### Ctenopoda

The Ctenopoda (Fig. 6A, B) contains only two families, Sididae (seven genera) and Holopediidae (one genus, *Holopedium*). All are small (to about 4 mm) microphagous filter feeders that are found mostly in open water, although they also may be benthic or associated with vegetation (Fryer, 1987a–c). All are in fresh water except for *Penilia*, which is marine.

Ctenopods at first glance appear rather similar to anomopods, and indeed Fryer (1987a–c) discussed some deep-seated similarities between the two orders. Like anomopods, the body is short, somite boundaries are obscured by fusion, and the trunk is enclosed in a bivalved, hingeless carapace. But the head, although short and extending beyond the valves of the carapace, differs from the anomopod condition in that there is never a headshield (Fig. 6A, B). The compound eye is single and internal, with no sign of having become "internalized" during ontogeny. The labrum is large and rather fleshy. The antennules are tubular in females and are large and modified for grasping in males. The antennae are biramous and natatory (secondarily uniramous in females of *Holopedium*, Fryer, 1987a, b), with endopod and exopod each of two or three segments bearing natatory setae. The mandibles are of the grinding/rolling type. Maxillules are small and spinose, and the maxillae are reduced to small lobes that may or may not bear setae. There are six pairs of trunk limbs, all of which are pregenital and display serial similarity, although the last pair is always reduced and is not filtratory, which the others are. Additionally, the sixth limb

lacks a functional gnathobase, whereas limbs one through five have a gnathobase that functions in transferring food toward the mouth. The first trunk limb lacks the basal "ejector hooks" known in anomopods, and in males often bears distal hooks or other modifications for grasping. "Respiratory" epipods are present (although not on all limbs of *Holopedium*), and the limbs beat with an obvious metachronal rhythm and are never used for grasping, scraping, or locomotion. The food groove between the limbs is deep and narrow. The telson, which bears caudal rami and a pair of postabdominal setae, does not articulate with the trunk as in anomopods.

### Onychopoda

Onychopods (Fig. 6C, D) are freshwater and marine predators variously modified for grasping prey, although some may ingest particulate detrital matter (Fryer, 1987a, b). They may reach 12 mm in length, but this measurement includes an extremely long caudal process found in some taxa (e.g., see Fig. 6C); most are 2–6 mm. There are three families: Polyphemidae (one genus, *Polyphemus*), Cercopagidae (two genera), and Podonidae (six or seven genera) (Mordukhai-Boltovskoi and Rivier, 1987).

Onychopods have a short head and trunk, the segments of which have become obscured by extensive fusion. The carapace has been reduced to a dorsal brood pouch (Fig. 6C, D). The single, median eye is composed of many ommatidia, of several different structural types in some taxa (e.g., 130 ommatidia of four types in *Polyphemus*), and occupies nearly all of the head region, but there is no external indication of facets. The labrum is large and bears secretory glands. The antennules are uniramous and more or less tubular, varying in length among taxa. The antennae are biramous and natatory, with a three-segmented endopod and four-segmented exopod each bearing plumose natatory setae. The mandibles are modified versions of the grinding/rolling type and allow biting. The maxillules are reduced, and the maxillae ap-

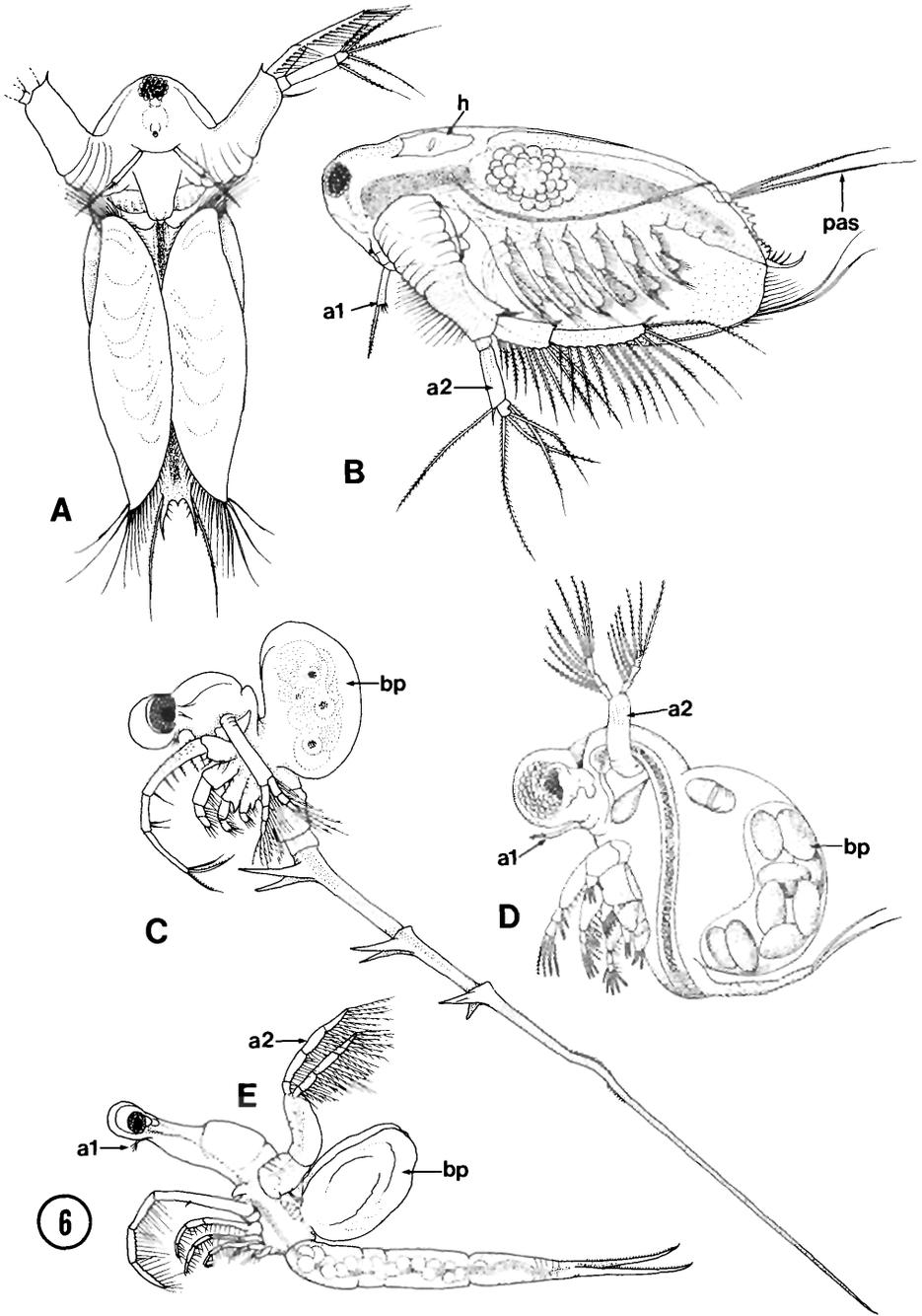


Fig. 6. The orders Ctenopoda, Onychopoda, and Haplopoda. **A:** *Latonopsis serricauda* (Ctenopoda), ventral view. (After Sars, 1901.) **B:** Lateral view of *Latonopsis serricauda*. (After Sars, 1901.) **C:** The onychopod *Bythotrephes cederstroemi*, a species with an extremely long abdomen. **D:** The onychopod

*Polyphemus pediculus*. (After Belk, 1982.) **E:** Sole member of the order Haplopoda, the predatory *Leptodora kindtii*. a1, first antenna; a2, second antenna; bp, brood pouch formed by modified carapace; h, heart; pas, postabdominal setae.

parently have been lost. The trunk is short, and segmentation is obscured; however, all species have four pairs of "thoracic" (pregenital) limbs, and so at least primitively the trunk may have been composed of four somites. The trunk limbs (Fig. 6C,D) are ste-nopodous, segmented, grasping appendages with exopods and small gnathobases but without an inflated epipod. Despite the presence of small (but presumably functional) gnathobases, there is no true food groove. In males, the first trunk limb is sometimes modified for grasping the female, and paired external penes are occasionally found just posterior to the base of the last trunk limb. The form of the abdomen varies among taxa. It may be short and unsegmented, or long and revealing some indication of former somite boundaries. The telson may terminate in "typical" cladoceran caudal rami, or the postabdomen may be produced into a long, thin caudal process, possibly derived from a fusion of furcal elements (e.g., Fig. 6C).

### Haplopoda

The order Haplopoda has long been recognized as being very different from all other "cladocerans" and, even before the rearrangement of the Branchiopoda suggested by Fryer (1987c), was treated apart from ctenopods, anomopods, and (less frequently) onychopods. The order contains a single family, Leptodoridae, with a single species, *Leptodora kindtii* (Fig. 6E), a nearly transparent predator on freshwater plankton in holarctic lakes. Females may reach 18 mm, whereas males do not exceed 9 mm. *Leptodora* is a highly specialized predator, as are members of the Onychopoda, and many if not all of its unusual features can be seen as adaptations to its predatory life style.

The head is long, narrow, and cylindrical; probably as a consequence the compound eye is a single, median structure that completely fills the anterior of the head and is composed of "about 500 specialized radially arranged ommatidia" (Fryer, 1987c), but there are no external indications of facets. The carapace has been reduced in females to a dorsal brood

pouch that appears to be situated near the posterior extremity of the thoracic region; in males the carapace is absent. The antennule is uniramous, and is short in females but long (modified for grasping) in males. The antenna is biramous, large, and natatory in both sexes. Both the exopod and endopod of the antenna are four-segmented, with each segment bearing numerous natatory (plumose) setae. The labrum is short and broad. The mandibles are styli-form, not grinding, and are thus unique among the Branchiopoda. Both maxillules and maxillae are absent. The thoracic region (the actual limits of the thorax are uncertain) has undergone extensive fusion; somite boundaries are indistinct. The six appendages of the thorax are grasping appendages, all of which lack exopods and branchial epipods. Only the first bears a modified coxal lobe (gnathobase), which is rather reduced, and there is no food groove. The abdomen is long, slender, and cylindrical. Segmentation is more or less clear; there are three rather long segments, the last of which has been termed a telson with caudal rami, but these do not articulate with the somite as do "true" caudal rami as seen in ctenopods, anomopods, spinicaudatans, etc. There are no paired telsonal filaments or setae. The cuticle is exceedingly thin and transparent, and in water *Leptodora* is nearly invisible to the naked eye.

### INTEGUMENT

The branchiopod cuticle is built along the same lines as for most crustaceans, i.e., it consists of a thin outer epicuticle composed mostly of protein, lipids, and calcium salts (mostly in higher crustaceans) and an internal procuticle, usually recognized as being composed of an outer preecdysial procuticle (or exocuticle) and beneath it a postecdysial procuticle (or endocuticle) (see Stevenson, 1985, fig. 1). The procuticle is much thicker than the epicuticle and is composed of layers of fibrous lamellae parallel to the surface; often the two component layers of the procuticle are themselves divided into sublayers. However, the cuticle is typically very thin in bran-

chiopods, with no calcification of the exocuticle and with little sclerotization. Cuticle covering the thoracic epipods in *Daphnia* may be only 0.2–0.5  $\mu\text{m}$  thick (Peters, 1987). In larval *Artemia*, where embryonic development and proliferation of epidermal cells has been the subject of several excellent papers by Freeman (1986, 1988, 1989), the cuticle may be as thin as 0.3–1.0  $\mu\text{m}$  (Freeman, 1989), and the inner “procuticle” has not yet differentiated into an exo- and endocuticle. In adults the thickness of the cuticle varies according to functional requirements; it is of course extremely thin on presumed respiratory structures (epipods; see below) and flexure zones and thickest on areas that undergo heavy use, such as the masticatory surfaces of the mandible and on male claspers. In the male anostracan “clasper” (the antenna), the cuticle may be 7  $\mu\text{m}$  thick, whereas in the anostracan trunk and thoracopods it is often only 1–1.5  $\mu\text{m}$  (Criel, 1991a). It is possible that in regions where gas exchange is important all layers are not present. Criel (1991a) points out that no endocuticle is visible in Copeland’s (1967, fig. 4) figure of the gill (thoracopodal epipod) cuticle, and apparently the epicuticle is absent in some areas of the *Daphnia* integument (Schultz, 1977; Schultz and Kennedy, 1977; Stevenson, 1985).

The following account is based primarily on Halcrow’s (1976) study on the integument of the anomopod *Daphnia magna*, which has a relatively simple integument. *Daphnia*, because it is a bivalved animal, has the carapace folded back on itself in the region of the valves, much as in the branchiostegal region of decapods (see also Fig. 68D for both sides of the valves in a conchostracan). Thus, a section through the carapace in this region shows integument facing the inner (facing the animal) and outer (facing externally) surfaces, with a thin hemocoelic space sandwiched between them (Fig. 7A). The two layers of cuticle are connected by “pillars” of connective tissue that extend through the hemocoelic space and probably serve as support (Anderson, 1933).

The epicuticle is thicker on the outer carapace surface, usually about 1.6  $\mu\text{m}$ , compared to about 0.5  $\mu\text{m}$  on the inner surface. It is composed of three layers (four in *Triops*; see Rieder, 1972b) and has a layer of material loosely attached to its surface (Fig. 7B). The procuticle is not readily subdivided into an obvious exo- and endocuticle, possibly because there is a greater similarity between pre- and postexuvial synthetic mechanisms than is seen in higher crustaceans such as decapods. The procuticle at times appears distinctly lamellate (e.g., Fig. 7B) and at other times relatively homogeneous in its electron density (Figs. 7C, 8A); Halcrow (1976) interprets this variability as nothing more than an artifact of the angle or thickness of the section. The procuticle is traversed incompletely by thin, rod-shaped structures (approximately 15–36 nm diameter) that appear to extend from the underlying epithelium into the procuticle (Fig. 7B,C). These rods are associated with invaginations of the apical plasma membrane (conical hemidesmosomes; Halcrow, 1976) of the epidermal cells (Fig. 7B,C).

During the intermolt period, the epidermal cells are squamous and appear narrow in cross section. Golgi bodies and mitochondria are present, and the nucleus is disc-shaped. The endoplasmic reticulum is loosely organized, and ribosomes “lie freely in the cytoplasmic matrix” (Halcrow, 1976: 2). Large numbers of microtubules are present and pass obliquely through the cytoplasm to the apical region, where they become associated with invaginations of the plasma membrane. These invaginations are lined by electron-dense material, and each contains the base of a rod (see above) that extends into the overlying procuticle. Below each invagination are microtubules and granular (microfibrillar) material associated with invaginations in other planes. In cross section, these invaginations appear to occur in clusters. The plasma membrane of the lateral cell border is highly convoluted, and septate junctions occur along the apical regions of the lateral borders. Halcrow (1976) noted similarities with the apical regions of

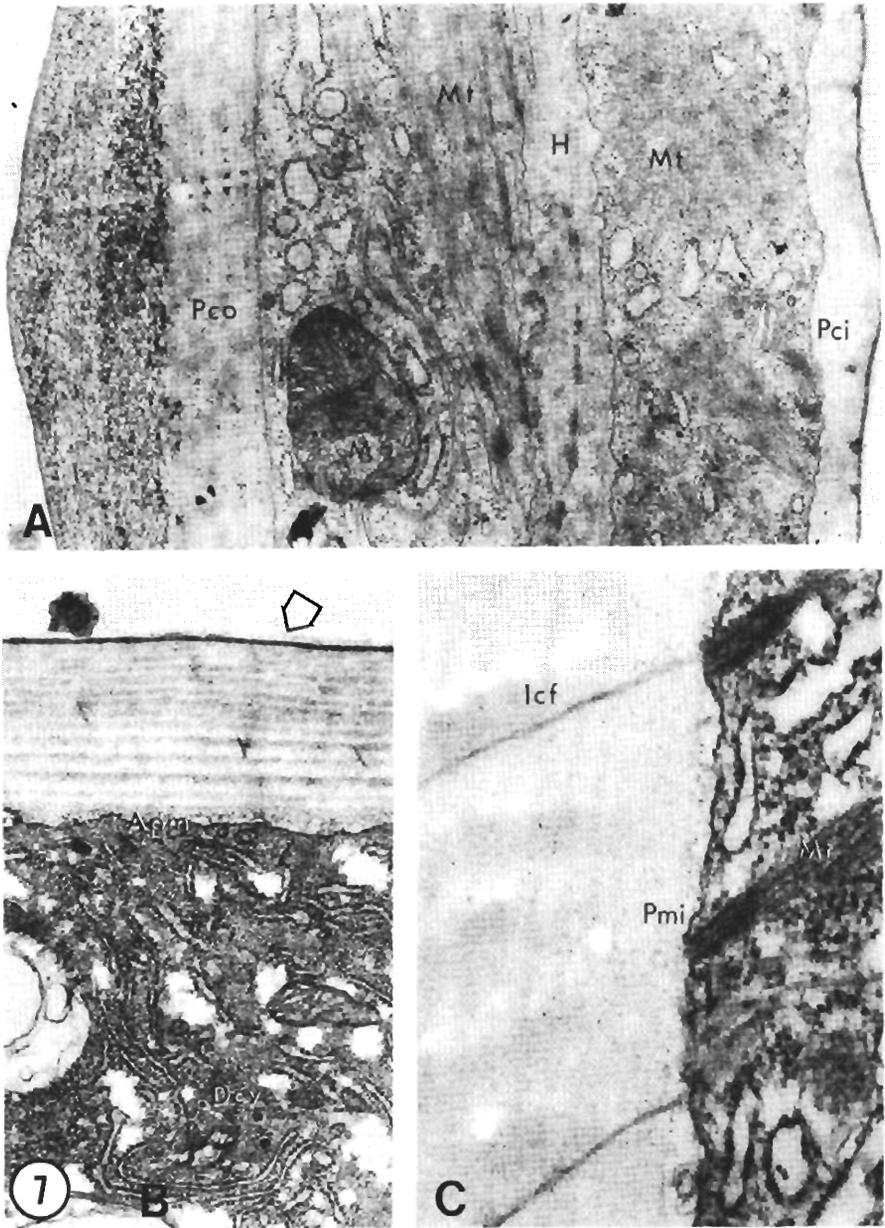


Fig. 7. Integument of carapace valves of *Daphnia magna*. (From Halcrow, 1976.) **A:** Inner and outer integument layers of carapace with hemocoel between.  $\times 24,400$ . **B:** Outer integument layer. Note detached outermost layer of epicuticle (arrow) and portions of intracuticular fibers within procuticle.  $\times 25,500$ .

**C:** Detail of outer integument layer.  $\times 44,500$ . Apm, apical plasma membrane; Dcv, dense core vesicles; H, hemocoel; Icf, intracuticular fibers; M, mitochondrion; Mt, microtubules; Pci, procuticle of inner layer; Pco, procuticle of outer layer; Pmi, invagination of apical plasma membrane.

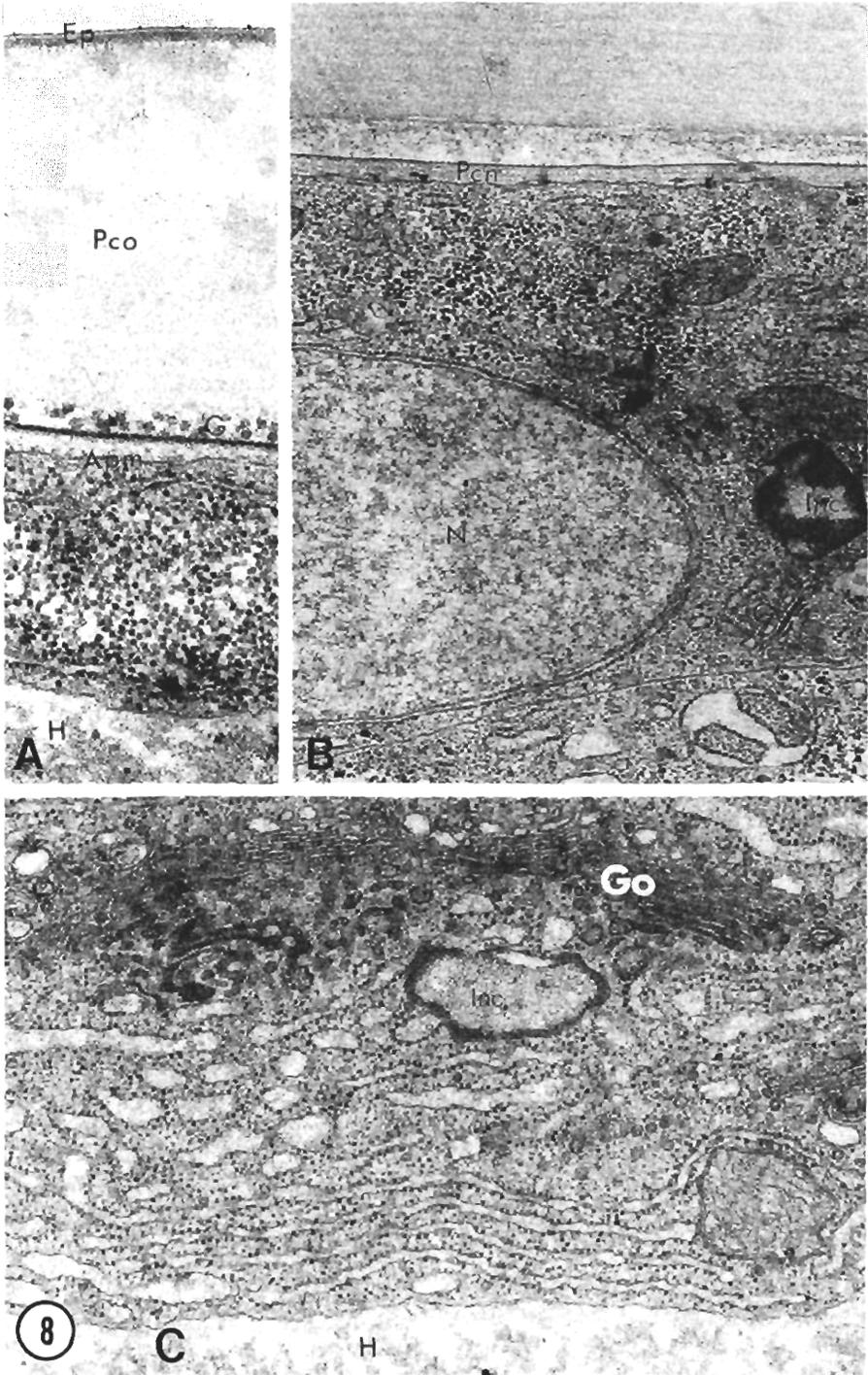


Fig. 8. Integument of *Daphnia magna*. (From Halcrow, 1976.) **A**: Inner integument layer showing granules (G) in narrow exuvial space between new and old cuticle.  $\times 47,500$ . **B**: Outer integument showing inclusion (Inc).  $\times 20,000$ . **C**: Outer layer epidermal cell. Note proximity of inclusion to Golgi complexes.  $\times 35,500$ . Apm, apical plasma membrane; Ep, epicuticle; Go, Golgi apparatus; H, hemocoel; N, nucleus; Pcn, new procuticle; Pco, procuticle of outer layer.

cells in the midgut diverticulum of *Daphnia* (Hudspeth and Revel, 1971). Golgi bodies pinching off dense core vesicles (each about 110 nm in diameter) are seen. These vesicles are similar to others near the apical cell border and to vesicles in tissue fixed immediately after ecdysis. Coated vesicles of approximately 140 nm diameter, usually seen in animals that are halfway through premolt (Fig. 8A), are sometimes seen in just-molted animals as well. The basement membrane separating these cells from the hemocoel is about 0.2  $\mu\text{m}$  thick (Fig. 8C).

During the premolt period, epithelial cells are surprisingly much the same as during the intermolt period. The newly forming epicuticle is visible (Fig. 8A), interrupted in places by the intercuticular fibers extending into the procuticle, and an ecdysial space filled with amorphous matter, suggested by Halcrow (1976) to be the results of enzymatic digestion of the endocuticle, is evident (Fig. 8B). However, in the epithelial cells the only obvious changes are in the more abundant granular endoplasmic reticulum, increased cell height, abundance of glycogen, and presence of irregularly shaped inclusions near Golgi bodies, both seen later in the premolt period (Fig. 8A–C). Apart from the inclusions seen in premolt cells (Fig. 8B,C), no cytoplasmic structures involved in cuticle synthesis were seen to be restricted to any specific period during the molt cycle, and fusion of the vesicles with the apical plasma membrane occurred before and after premolt initiation. These changes are of less magnitude than those seen in many higher crustaceans, where there is a distinct decline in activity and structural organization when synthesis of the new cuticle is complete. This might be because the intermolt period in daphniids is so short (Halcrow, 1976). Thus the mechanism for synthesis of new cuticle is a more continuous process. No microvilli were seen in *Daphnia* epithelial cells during formation of the new epicuticle.

The above synopsis can probably be extended to other parts of the body in *Daphnia*, and possibly to other branchiopods as well.

For example, cuticle of the *Artemia* trunk region (Fig. 9) is basically similar to the above description (Criel, 1991a). However, specializations of the integumental epithelium exist in certain appendages and organs treated elsewhere. Specialized cells of the epithelium of the thoracic epipods are described in the section on respiration, and cells comprising the dorsal organ are described later in this section.

A study of the integument of two spinicaudatan conchostracans revealed a cuticle (Figs. 10A,B, 11A) that in most parts of the body is similar to that of *Daphnia* and *Artemia* (Rieder et al., 1984). However, in these taxa (*Leptestheria dahalacensis* and *Limnadia lenticularis*) the cuticle of the carapace is not shed with each molt, accounting for the growth lines present on spinicaudatans (Fig. 10A). Consequently, the number of layers of cuticle seen in a cross section of the valves reveals the number of molts, and the dorsal region of the valves can become quite thick with accumulated layers of unshed integument (Figs. 10A, 11B). Rieder et al. (1984) also described "ribs" of cuticle on several parts of the spinicaudatan body, attributing the formation of these ribs to small exocuticular granules that swell and eventually extrude the epicuticle and outermost layers of the exocuticle. A similar thickening of the cuticle, including layers like those seen in spinicaudatan clam shrimp, occurs in the formation of the ephippium of anomopods (see Schultz, 1977).

Pore canals extending through the integument are not seen in *Daphnia* (Halcrow, 1976) or spinicaudatans (Rieder et al., 1984) but are present, although uncommon, in *Triops* (Rieder, 1972b), which has a slightly thicker cuticle (approximately 12  $\mu\text{m}$  thick). Possibly there is no need for such cytoplasmic extensions in crustaceans where the cuticle is as thin as in *Daphnia* (Halcrow, 1976).

Rieder's (1972a,b) account of the cuticle of the notostracan *Triops* dealt mostly with the layers of the cuticle itself rather than with the epithelial cells. In this predominantly benthic

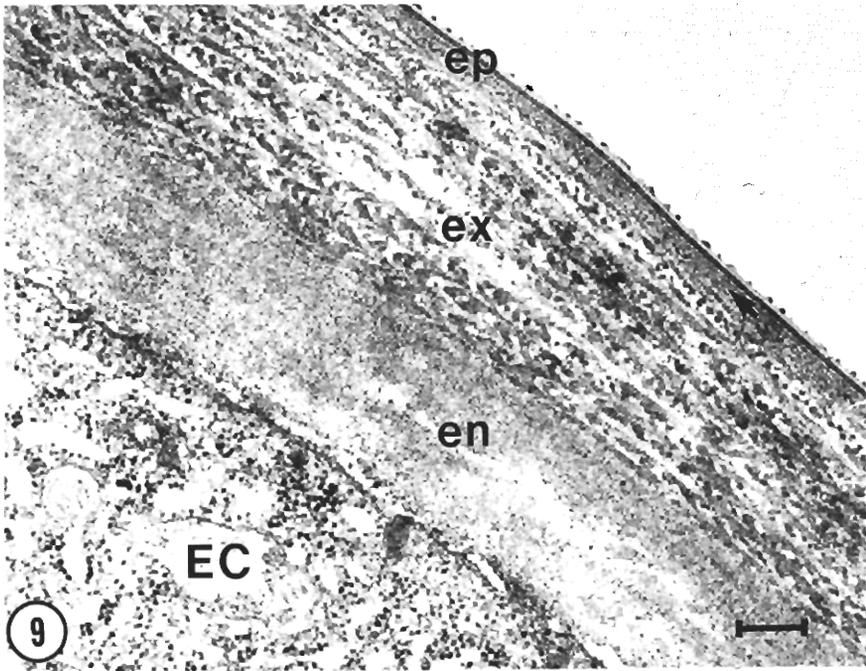


Fig. 9. Integument of trunk region of adult *Artemia* (Anostraca). EC, epidermal cell; en, endocuticle; ep, thin, three-layered epicuticle; ex, exocuticle with thin homogeneous outer layer (arrow) and broad laminated inner layer. Scale bar = 200 nm. (Courtesy of G. Criel.)

order, which might be expected to require a more durable and yet more flexible carapace than in some of the mostly planktonic or open-water orders, the epicuticle consists of four layers, the exocuticle consists of up to ten layers, and the endocuticle may be composed of up to 80 layers (Figs. 12–14), the most known in any branchiopod.

All branchiopods contain chitin in the cuticle. The various pathways for chitin synthesis in *Artemia* were reviewed by Horst (1989). The most likely scenario is that the chitoprotein is synthesized in the rough endoplasmic reticulum (RER), then moves to the Golgi apparatus (where Horst presumes that chitin synthetase is located), where it serves as a “primer” molecule for chitin synthetase, yielding a chitin–protein complex. The chitin–protein complex must somehow be transported to the apical membrane and exported to be incorporated into the cuticle, but the mechanism is unknown.

### Integumental Glands

Knowledge of integumentary glands is fragmentary and is restricted to anostracans and notostracans. In the Anostraca, Dornesco and Steopoe (1958) found proximal thoracopodal glands consisting of one large and two small gland cells linked to the outside by a short duct of three to four cells; the duct opens at the base of a spine on the protoendite in *Branchipus* and *Artemia*. These poorly known structures are treated in the section on glands. Rieder (1977) described well-developed integumental glands in notostracans that consist of three cell types, a rather large secretory cell, a collarlike intermediate cell, and duct cells extending up through the epidermis (Fig. 15). Rieder (1977) suggested that these glands function in the secretion of the epicuticle, but Stevenson (1985) doubted this because of the inadequate number and distribution of these glands and because other studies (e.g., Neville, 1975) indicated epidermal se-

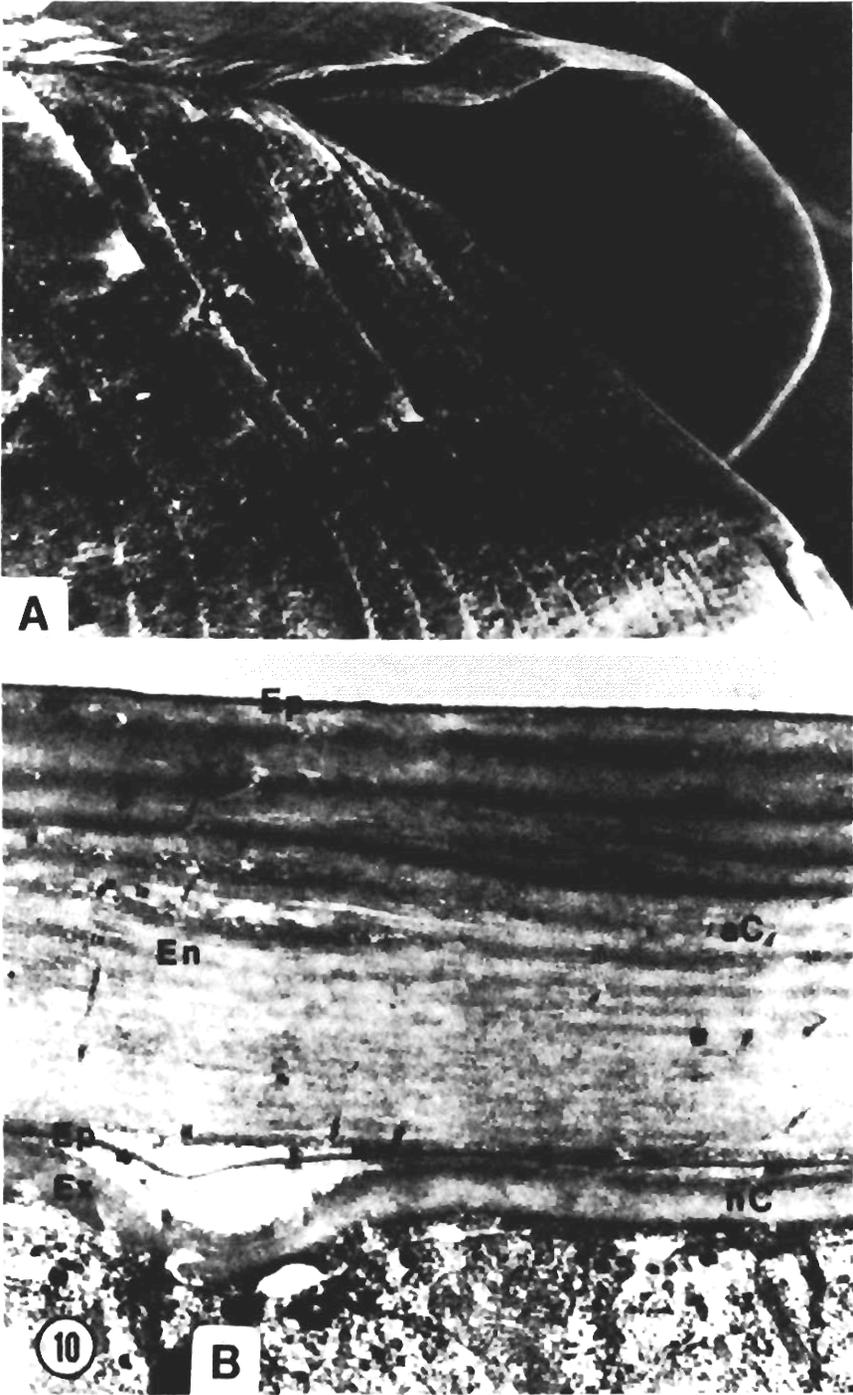


Fig. 10. Integument of the spinnicaudatan *Leptestheria dahalacensis*. (From Rieder et al., 1984.) **A:** Posterior end of valves showing accumulated layers of cuticle retained after ecdysis (forming "growth lines" on the carapace).  $\times 43$ . **B:** New cuticle, consisting at this stage of only the epicuticle and upper layer of the exocuticle, replacing old at edge of carapace.  $\times 32,000$ . aC, old cuticle; Ep, epicuticle; En, endocuticle; Ex, exocuticle; nC, new cuticle.



Fig. 11. Integument of the spinaudatan *Leptestheria dahalacensis*. (From Rieder et al., 1984.) A: Newly forming cuticular ribs (nR) visible under ribs (R) of older carapace.  $\times 4,800$ . B,C: Examples of accumulated layers of old cuticle (not shed during ecdysis). B,  $\times 12,000$ ; C,  $\times 13,600$ .

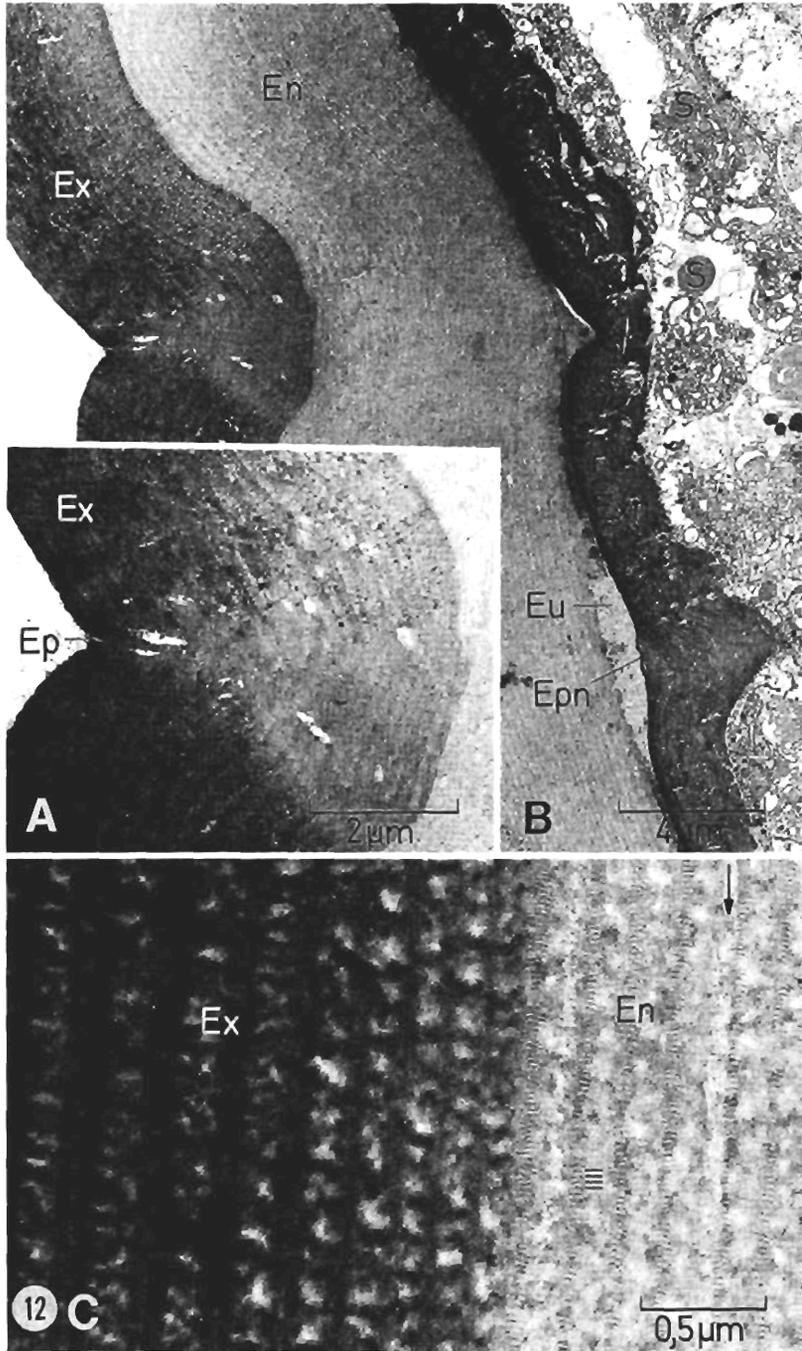


Fig. 12. Integument of *Triops cancriformis* (Notostraca). (From Rieder, 1972b.) **A**: Wedge-shaped "molting suture." **B**: Exocuticle (Ex) and endocuticle (En), distinguished by density and contrast. **C**: Laminations of the exo- and endocuticle. Ep, old epicuticle; Epn, newly formed epicuticle; Eu, exuvial chamber between old and new integument layers; Ex, newly formed cuticle; S, secretory droplets; small arrow, rare archlike structure.