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CEPHALOCARIDA

By Robert R. Hessler

[Woods Hole Oceanographic Institution]

[Chapter submitted January, 1962]

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MORPHOLOGY

GENERAL FEATURES

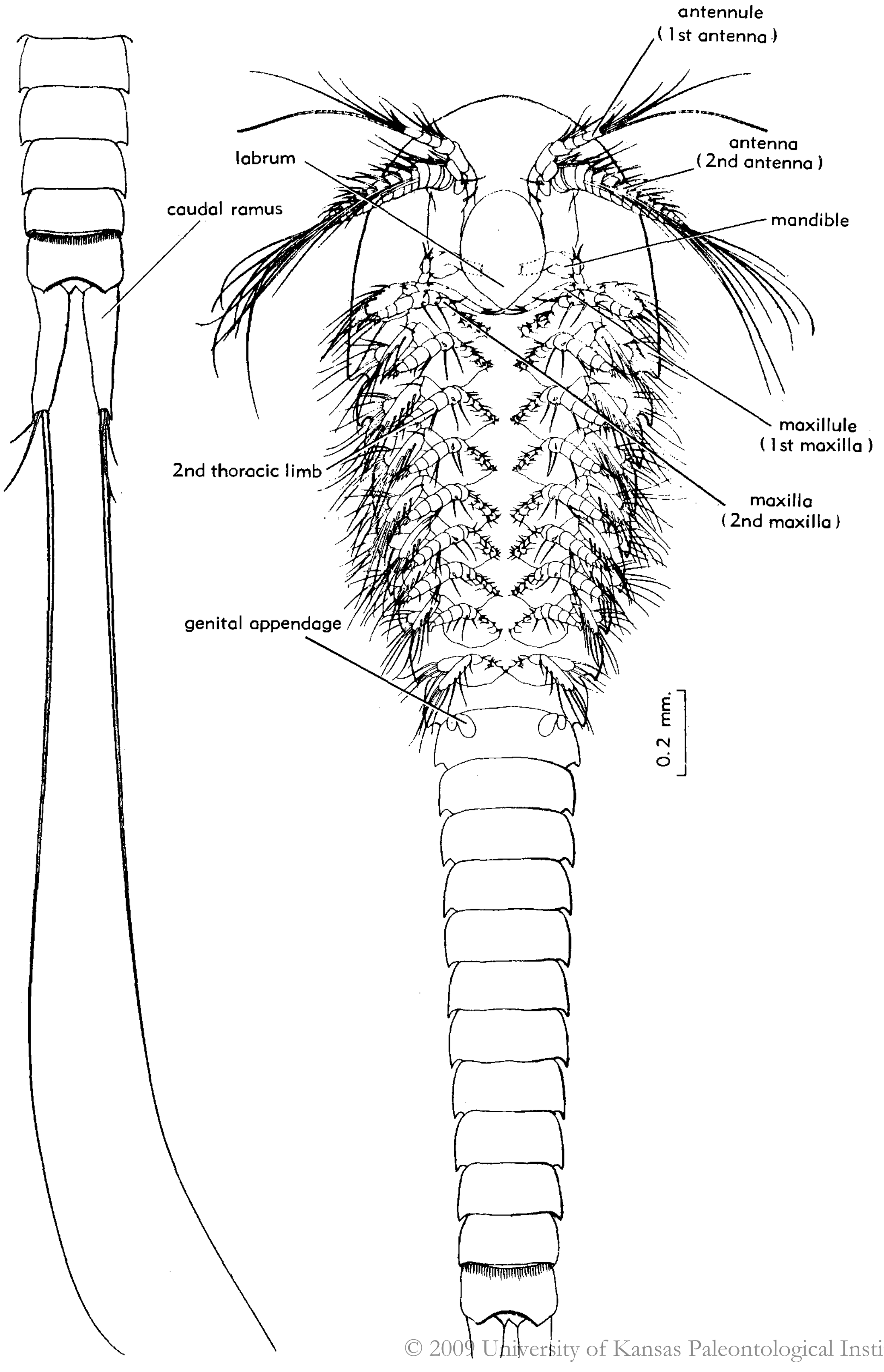
The body (Fig. 40) consists of a horseshoe-shaped cephalon, an eight-somite thorax, and a 12-somite abdomen (including the telson). Both the cephalon and thorax bear flat pleura, which are directed somewhat backward on the thoracic somites. On the cephalon the pleural lobes are continuous with each other anteriorly. Pleural lobes are reduced to posteriorly directed spines on the abdominal somites.

On the middle of the ventral surface of the cephalon is a conspicuous **labrum** which projects distinctly ventrally and posteriorly past the mouth, forming the floor of the **atrium oris.** There are five pairs of cephalic appendages: two pairs of antennae, a pair of mandibles, and two pairs of maxillae (Fig. 40).

Each thoracic somite bears a limb, except in *Lightiella,* where they are absent on the eighth. The first abdominal somite has a pair of reduced limbs which form genital appendages. The telson bears a well-developed caudal furca. The other abdominal somites lack appendages.

(On facing page.)

Fig. 40. Morphology of adult cephalocarid, *Hutchinsoniella macracantha* Sanders, ventral view, showing striking similarity of maxillae and all thoracic limbs, ×64 (9).


antennule
(1st antenna)
antenna
(2nd antenna)
labrum
caudal ramus
mandible
maxillule
(1st maxilla)
2nd thoracic limb
maxilla
(2nd maxilla)
genital appendage
0.2 mm.

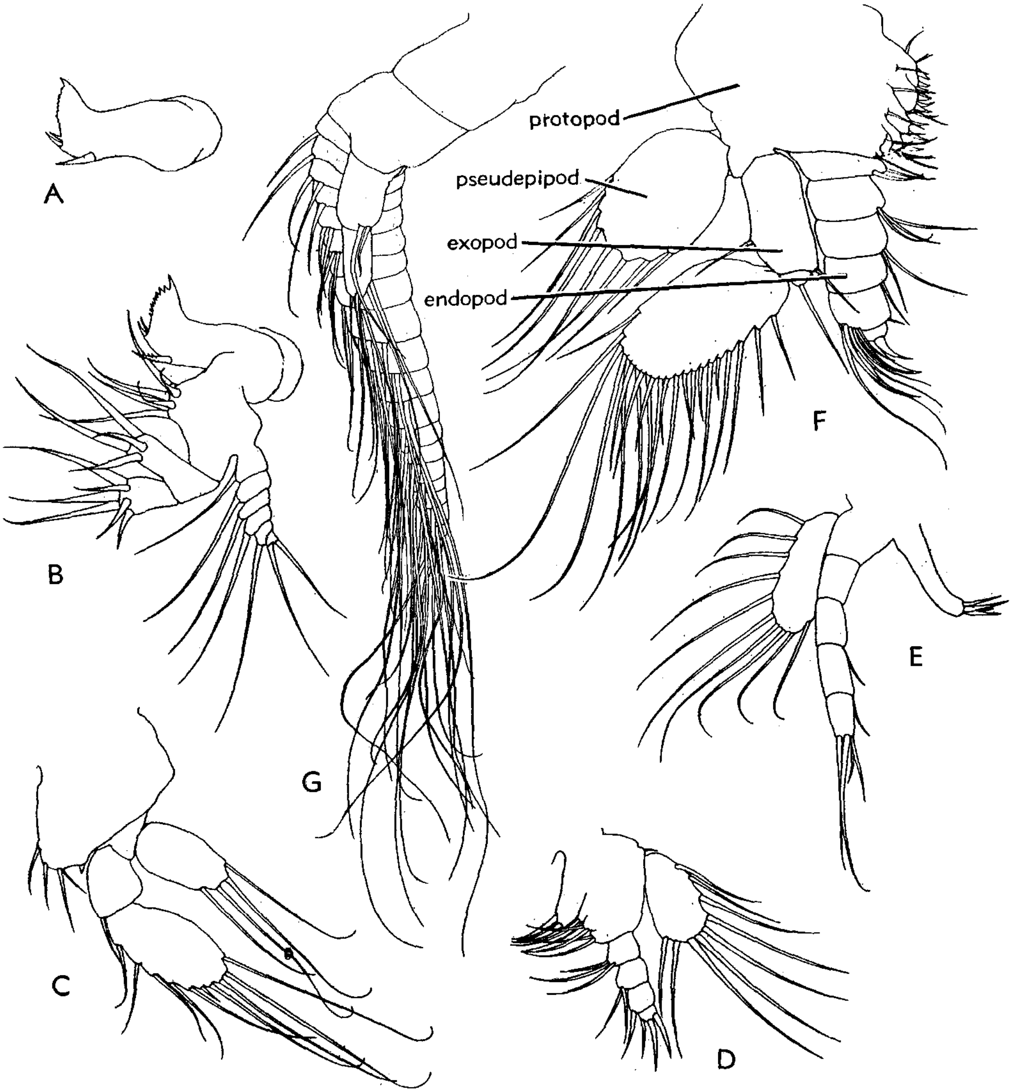


FIG. 41. Limbs of *Hutchinsoniella macracantha.*——*A.* Adult left mandible, ventral view.——*B.* Left mandible of stage 4 larva, ventral view.——*C.* Left 8th thoracic limb of adult, anterior view.——*D.* Left maxillule of stage 4 larva, anterior view.——*E.* Adult right maxillule, anterior view.——*F.* Adult right 4th thoracic limb, anterior view.——*G.* Adult right antenna, medial view. All figures of adults *(A, C, E-G)* ×150; those of larvae *(B, D)* ×170 *(A, B, D,* 9; *C, E-G,* Hessler, n).

APPENDAGES

The maxillae (2nd maxillae) and first seven thoracopods are alike except for details (Fig. 41,*F*). A foliaceous protopod bears three rami distally—a slightly flattened ambulatory endopod with five or six segments, and a three-segmented exopod, which gives rise to a single-segmented pseudepipod from its basal segment. SANDERS (9) considers the exopod to have four segments. However, the penultimate one is poorly developed and is more probably part of the segment proximal to it. The protopod bears six movable, medial endites (five on the maxilla) and an ill-defined transverse furrow by which the distal half of the protopod may bend somewhat with relation to the proximal half. The medial edge of the endopod is continuous with the median endites of the protopod. Both bear rows of setae, the orientation and morphology of which vary depending on their task in the capture and transport of food particles toward the mouth. Terminally the endopod bears three claws, except on the 7th thoracopod. Sanders (8) considered the medial claw to be the terminal segment and called it a dactylus. However, no muscles extend to this claw and therefore it cannot properly be considered a limb segment. The basal segment of the exopod is broadly joined to the protopod. The 2nd segment of the exopod is rodlike, with a few distal setae. Both the distal exopodal segment and the pseudepipod are paddle-like and have a distal fringe of setae.

The 8th thoracic limb (Fig. 41,*C*), when present, is basically like the preceding except that the endopod is missing.

The adult maxillule (Fig. 41,*E*) differs from the basic pattern of the thoracic limbs in that the pseudepipod is missing, the exopod is unjointed, the anteriorly oriented endopod is four-segmented, and the much-reduced protopod bears only a single endite, which forms a long, anteriorly curved finger. The larval maxillule (Fig. 41,*D*) is much more similar to the basic thoracic plan. The endopod curves posteriorly, and four normally developed endites occur on the proportionately larger protopod.

The adult mandible (Fig. 41,*A*) is a palpless, masticatory process. However, the morphology of the palp-bearing larval mandible (Fig. 41,*B*) is clearly based on the pattern of the thoracic limbs. Here the masticatory process is seen to be an endite of the coxa. The palp consists of the basis bearing a single endite, a two-segmented endopod, and a six-segmented exopod. The basic difference from the thoracic limbs is that the exopod is multisegmented.

The antennae (Fig. 41,*G*) are also interpretable in terms of the basic limb pattern. The protopod consists of coxa and basis. A two-segmented endopod and 19-segmented exopod are observed, the ventral surface of the latter being richly supplied with long setae. On the larval antenna the basis has a single endite, and a long naupliar process arises from the coxa. The naupliar process is homologous to the masticatory process of the mandible, the single endite of the maxillule, and the basal endite of the subsequent limbs.

The antennules have six segments and are uniramous. Each bears a long, multiarticular, sensory flagellum on its distal end.

INTERNAL ANATOMY

The digestive tract is a simple tube which ascends anteriorly from the mouth and then bends posteriorly to traverse the entire trunk. A pair of simple, glandular diverticula located in the cephalon open posteriorly into the anterior end of the mesenteron.

The excretory organ of the later larval stages and adult is a noncoiled maxillary gland with an external pore located on the posterior surface of the base of the maxilla. Antennary glands are present in the larva, and possibly in the adult as well.

The paired tracts of the ventral nerve cord form a simple ladder, as in the Branchiopoda, but with much shorter commissures. In each somite are large ganglia. The ganglia of the mandibular and two maxillary somites are somewhat coalesced.

Movement of the trunk is effected by paired dorsal and ventral longitudinal muscles, which run the length of the body, attaching at each intersomitic boundary, and by paired intrasomitic dorsoventral muscles. Each limb, except for the antennules and antennae, is moved by body-limb muscles having four origins; anterior and posterior dorsolateral origins, and anterior and posterior ventromedial origins. Intrinsic limb muscles move the rami and endites.

The heart extends the length of the thorax, with paired ostia in each somite.

Hutchinsoniella is hermaphroditic. Both the testes and ovaries are paired, finger-like organs located in the abdomen. The vas deferens opens on the protopod of the 6th thoracic limb; the oviduct opens on the genital appendages of the 1st abdominal somite. Only two large yolky eggs can be carried at a time, one on each genital appendage.

DEVELOPMENT

Development is gradual. The first free-living stage is a benthonic metanauplius

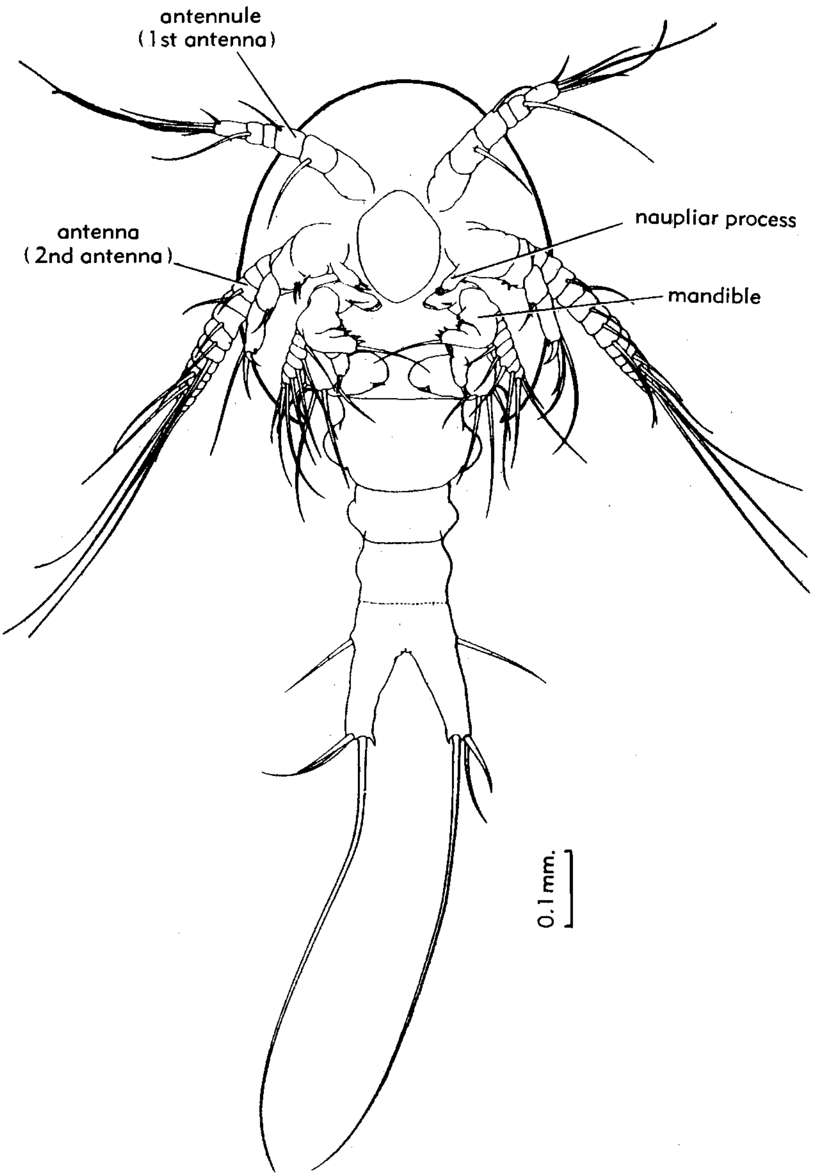


FIG. 42. Stage-1 larva (metanauplius) of *Hutchinsoniella macracantha,* ventral view, ×95 (9).

(Fig. 42) having well-developed antennules and antennae and mandibles, and rudimentary maxillules and maxillae. Three postcephalic somites are seen in *Hutchinsoniella* but eight in *Lightiella incisa.* The dorsal carapace is of the same form as that of the adult. From this stage on, both somites and limbs are added gradually. The limbs first appear in a rudimentary form, and require about three instars to attain functional maturity.

The antennae, mandibles, and maxillules undergo correlated metamorphic change from larval to adult morphology. This change occurs after the 13th stage in *Hutchinsoniella* and marks the end of the larval period and the naupliar mode of feeding. At this time the naupliar process of the antennae disappears. The palp disappears from the mandible, having undergone some previous reduction. The maxillules rotate anteriorly so that their endopods become directed forward. All protopodial endites of the maxillules disappear except for the basal endite, which appeared in the eighth larval stage and gradually became longer throughout the rest of the larval period. The antennules and limbs behind the maxillules undergo no change once they have developed.

The pleura of limbless larval thoracic somites are like those of the adult abdomen. Each thoracic somite develops adult thoracic pleura only as its limbs develop.

MODE OF LIFE

ENVIRONMENT

The known Cephalocarida are wholly benthonic marine crustaceans occurring from the intertidal zone to depths of 300 m. *Hutchinsoniella macracantha* Sanders (7) is a nonselective deposit-feeder living in the loose, organic-rich zone on the surface of subtidal silt-clay sediments. *Lightiella serendipita* Jones (6) has been found subtidally on silty sands. *Lightiella incisa* Gooding (4) was found associated with the fine sediments trapped by the roots of *Thalassia* (turtle grass).

FEEDING

The method of feeding is known only for *Hutchinsoniella* (8). Feeding results from a metachronal anteroposterior beating of its limbs. The motion is initiated posteriorly and passes forward from limb to limb in a smooth wave.

The two pairs of antennae sweep backward with an oarlike motion. Their setae, particularly the numerous large setae on the ventral surface of the antennae, sweep food and detritus posteriorly and medially into the region of the thoracic limbs.

In the cycle of movement of the thoracic limbs and maxillae, the volume of the space between the limb and one behind it increases and decreases. The three rami of the limb alternately fold backward against the following limb and extend forward again. This action acts as a valve, rhythmically closing off the interlimb space laterally and ventrally, and then opening again. The thoracic pleura serve to block flow of water dorsolaterally. As the volume of the interlimb space increases on the forestroke, the valves are closed, resulting in a current of water that enters the median space between the paired rows of limbs from below, and proceeds into the interlimb space. The valves are open as the interlimb space decreases on the backstroke, allowing the water to flow out laterally and ventrolaterally. Food and detritus carried by the inflowing current is trapped by the spines and setae on the median surface of the endopods and endites of the protopods. Interdigitation of these setae with other setae on the median edge of the following limb brushes this material loose and concentrates it dorsally along the ventral surface of the thorax between the two rows of limbs (i.e., in the food groove). The endites of the protopods move this food forward toward the posterior end of the labrum. Here the long endites of the maxillules push the food into the atrium oris, where it is broken down by the mandibles and swallowed. All these actions occur simultaneously within the metachronal cycle, so that the feeding process is continuous.

During early larval life, thoracic limbs are insufficient to sustain the kind of feeding employed by the adult. Instead, food is swept toward the body by the antennules and antennae and exopods of the mandibles. It is concentrated at the posterior end of the labrum by means of setae on the antennae and endopods of the mandibles. From here it is passed to the molar processes of the mandibles by endites of the maxillules and naupliar processes of the antennae.

As thoracic limbs are added, the adult mode of feeding becomes increasingly effective, until finally at the 14th stage it becomes the sole method of food collection. Up until that time both methods of feeding function simultaneously.

LOCOMOTION

Hutchinsoniella cannot swim. It moves along the bottom by means of the same metachronal movement by which feeding takes place. Forward movement results from the backward thrust of the distal claws of the thoracic endopods on the substrate, the paddle-like action of the thoracic exopods and pseudepipods, and the oarlike action of the two pairs of antennae.

EVOLUTIONARY SIGNIFICANCE

Although the Cephalocarida are represented by few species and are unknown in the fossil record, they are of extreme interest because of their central position in the evolution of the Crustacea. Cephalocarids are the most primitive known crustaceans, as judged by their high degree of serial homology and the generalized nature of their morphology. Furthermore, where the cephalocarids show similarities to members of other classes, it is to the most primitive members that the resemblance is closest (SANDERS, 8, 9; HESSLER, 5).

In no other known crustacean is there less serial specialization of the limbs. Except for reduction or loss of the last thoracic limb, all thoracopods are alike. Whereas in the Copepoda, Mystacocarida, and most of the Malacostraca, the first thoracopods are modified as mouth parts, here they are totally unmodified, and even the maxillae conform precisely to the thoracic-limb pattern, a condition unique to the Cephalocarida. In addition, the pattern expressed by the thoracic limbs is easily seen in all of the more anterior adult or larval cephalic appendages except the antennules. In contrast to the Branchiopoda, often considered quite primitive, there is little reduction of the two pairs of maxillae and the antennules. The cephalocarid antennae stand in contrast to those of the Notostraca, where they are reduced, and to those of the Anostraca, which are modified as a copulatory structure.

With exception of the adult mandibles and maxillules, all limbs share equally in trophic and locomotory functions. There is no modification for copulation other than slight alteration of the distal setae of the endopod of the seventh thoracic limb for clasping.

The skeletomuscular system displays the same high degree of serial homology seen in the external morphology. The muscles of the maxillae and thoracic limbs are alike, and the pattern found in the maxillules and mandibles are easily derived from that of more posterior appendages. The extrinsic limb muscles and the serially repetitious ventral longitudinal muscles of the trunk take origin from transverse, endoskeletal bars which are the same in all thoracic somites. The complex ventral cephalic tendon which gives rise to all the ventral extrinsic limb muscles of the head is clearly derived from the fusion of three transverse bars.

The heart and the ventral nerve cord also repeat the same form from somite to somite.

The simple cephalocarid development, in which both limbs and somites are added gradually, stands in contrast to that of other Crustacea, wherein limbs and somites are added in blocks.

The Cephalocarida are not only primitive, but probably stand near to the protocrustacean stock; it is possible to derive the limbs of all classes of crustaceans from a cephalocarid type of limb. With *Lepidocaris* as an intermediate, the thoracic limbs of living branchiopods result from the loss of the endopod and shifting of the exopod and pseudepipod. (This conclusion is in great contrast to the classically held notion of the composition of the branchiopod limb.) The thoracic limbs of copepods may have a similar origin. The head appendages of calanoid Copepoda, Mystacocarida, cladocopan Ostracoda, and larval Cirripedia bear strong similarity to those of larval Cephalocarida. The appendages of adult Eumalacostraca bear little resemblance to those of the Entomostraca. However, during early larval stages of euphausiids and pennaeids the appendages show close similarity to those of the cephalocarids. During later development of these groups, the cephalocarid-like larval limbs are altered through secondary replacement of parts or profound modification, to form the typical, adult, malacostracan appendages. Thus the adult morphology of these forms is clearly secondary. The form of the leptostracan thoracic limb is quite similar to that of the cephalocarid.

Many parts of the cephalocarid musculature and its skeletal support are generalized in form. For example, the pattern of trunk muscles in the various crustacean classes is diverse, yet in all they can be derived easily from the generalized condition found in the Cephalocarida. The basic processes involved in these changes are loss of connection of muscles with the body wall and endoskeleton, or shifting of the position of these origins, commonly to form spiraled muscular bundles. Even the complex caridoid musculature in the abdomen of the Eumalacostraca can be derived from a cephalocarid-like condition. The caridoid musculature is found in the basic members of the Syncarida, Eucarida, and Peracarida, that is, in all Eumalacostraca except the Hoplocarida. The latter group, which is thought to have branched off early in eumalacostracan evolution, has an abdominal musculature like that of the caridoid facies, but simpler in form and reflecting an earlier grade of evolutionary development. The hoplocarid condition can in turn be derived from a cephalocarid-like musculature, such as is found in the most primitive malacostracans, the Leptostraca.

Cannon (3), in a detailed study of the feeding mechanisms of the Branchiopoda, postulated the ancestral type from which the various branchiopod feeding types could be derived. This theoretical ancestor corresponds closely to the actual condition in the Cephalocarida. In the cephalocarids the food groove is not invaginated into the trunk as in the Anostraca and Diplostraca. There is no specialization among the protopodial endites such as occurs in all Branchiopoda. The enditic setae are relatively unspecialized, suited only for the retention of coarse particles, not a highly developed filter bed, as in the Diplostraca and Anostraca.

SYSTEMATIC DESCRIPTIONS

Class CEPHALOCARIDA
Sanders, 1955

Body consisting of cephalon, thorax with eight somites, and abdomen with 12 somites; cephalon and thorax with well-developed pleura. Labrum projecting strongly backward to form atrium oris. Telson bearing caudal furca. Thoracic limbs and maxillae all similar, mixopodial; foliaceous protopods bearing several endites; multisegmented, ambulatory endopods; jointed paddle-like exopods; unjointed, paddle-like pseudepipods. Eighth thoracic limb reduced or absent. Maxillules reduced but of thoracic limb type. Mandibles palpless in adults, but with biramous palp in larvae. Antennae biramous, with large, multisegmented exopods. Antennules uniramous. Total size of adult about three to four mm. *Rec.*

Extant representatives of the Cephalocarida are found on the northeastern and western coasts of North America, in the Caribbean, in the Pacific off Japan, and in the South Pacific (N. Caledonia) (Delamare Deboutteville, personal communication).

Tesnusocaris goldrichi Brooks is the only known fossil crustacean included in the Cephalocarida (2). Later Birshteyn (1) made this species the basis for a new cephalocarid order, named Enantiopoda. This species should be rejected from the Cephalocarida. The two pairs of maxillae are too greatly reduced, being reminiscent of the Branchiopoda in this respect. The entire structure of the thoracic limbs is so different as hardly to allow comparison with the cephalocarid condition.

Order BRACHYPODA
Birshteyn, 1960

Characters of subclass. *Rec.*

Birshteyn mistakenly included the maxillae with the thoracic limbs. That they are truly maxillae is shown by the presence of openings for the maxillary glands.

Family HUTCHINSONIELLIDAE
Sanders, 1955

Characters of type genus. *Rec.*

Hutchinsoniella Sanders, 1955, p. 61 [**H. macracantha*; OD]. Eighth thoracic somite with limb and well-developed pleura. Basal segment of endopods of thoracic limbs clearly defined from protopods. Ventral comb on abdominal somite preceding telson. *Rec.*, NE.N.Am.——Fig. 40-42. **H. macracantha*; 40, ventral view of adult showing morphological features, ×64 (9); 41, *A, C,* *E-G,* limbs of adult, ×150 (*A,9; C, E-G,* Hessler, n); 41,*B,D,* limbs of larva, ×170 (8); 42, stage-1 metanauplius, ×95 (9).

Family LIGHTIELLIDAE Jones, 1961

Characters of type genus. *Rec.*

Lightiella Jones, 1961, p. 32 [**L. serendipita*; OD]. Eighth thoracic somite without limb, and with pleura weakly developed or absent. Basal segment of endopods of thoracic limbs not defined from protopods or defined only posteriorly. No ventral comb on abdominal somite preceding telson. *Rec.,* W.N.Am.-Carib.

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BRANCHIOPODA

By Paul Tasch

[Wichita State University]

[Chapter submitted June, 1956; revised 1961, 1963]

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INTRODUCTION

The phyllopod crustaceans (exclusive of the malacostracan phyllocarids) have been classified until recently in five orders; Notostraca, or tadpole shrimps; Conchostraca, or clam shrimps; Cladocera, or water fleas; Anostraca, or fairy shrimps; and Lipostraca, known only as fossils. In general, all are characterized by the nature of their swimming appendages, which are flattened, leaflike, and lobate (83). Two additional orders —Kazacharthra and Acercostraca—now are known from the fossil record, both with affinities to the Notostraca.

Besides presence of a head and trunk, gross morphological features of the better-known branchiopod orders can be summed up briefly as follows (83, p. 4; 107, p. 324). Anostraca are characterized by a cylindrical body. Notostraca typically have a dorsoventrally depressed shieldlike carapace that covers most of the body. Conchostraca have a body enclosed by a bivalved carapace that is laterally compressed. Cladocera have an obscurely segmented laterally compressed body, covered by a folded carapace, and possess a postabdomen. All mentioned orders have a telson and caudal rami except the Cladocera, which have a postabdomen and claws. Like the Anostraca, the Lipostraca lack a carapace. A considerable range in size, as indicated by length, is seen within the orders: Anostraca, 7 to 100 mm.; Notostraca, 10 to 58 mm.; Conchostraca, 2 to 16 mm.; Cladocera, 0.2 to 18 mm.; Lipostraca, adults about 3 mm. (107).

Examination of the five branchiopod orders having a carapace calls attention to certain similarities. Equivalents of the shieldlike carapace of notostracans, kazacharthrans, and acercostracans occur in conchostracans and cladocerans at one stage or another. Thus, SARS (122) showed that in the later larval stage of *Limnadia lenticularis* (conchostracan) a hood-shaped carapace occurs. It consists of two symmetrical halves without any distinct division and bears a notostracan-like posterior emargination. A line of weakness is thus marked off on the carapace and a dorsal break occurs in postlarval development that separates the carapace into two distinct valves. In the Cladocera, too, the carapace is a single folded piece (107, p. 350). Although it presents a bivalved appearance, separation into two distinct valves does not occur.

Close relationships between cladocerans and conchostracans, as noted subsequently, is indicated by the presence on cladoceran shells of the kind of surface markings (ornamentation) that is so characteristic of conchostracans. These consist of reticulations, striations, and other types of ornament (19). The morphology, anatomy, and other aspects of each order will be discussed separately, and therefore elaboration of these topics is deferred.

BRANCHIOPOD TAXONOMY

LINDER (70) has presented convincing evidence and argument in support of a regrouping of the Branchiopoda according to affinities found to exist between the orders. His proposed arrangement, which divides the Conchostraca into two "tribes" named Laeviscaudata and Spinicaudata, here designated as suborders, and which isolates the Anostraca and Lipostraca in a separate series equivalent to a superorder, is followed in the *Treatise*. Modifications introduced here include placing cyzicid-like fossil forms in the Spinicaudata and adding two fossil orders.

An alternate grouping used by PENNAK (107), which is stated to be accepted by the majority of carcinologists, recognizes two "divisions" ("superorders" of F. LINDER) of the subclass Branchiopoda; these are named the Eubranchiopoda and the Oligobranchiopoda. The Cladocera are placed in the latter division, whereas the Anostraca, Notostraca, and Conchostraca are assigned to the former. This grouping fails to take account of the fossil orders and, further, it is insensitive to sharp distinctions that separate the Anostraca from all other branchiopod orders.

A superior arrangement in three superorders which expand LINDER's grouping has been proposed by BROOKS (17, 19). The superorder Diplostraca GERSTAECKER, 1866 (=*Onchyura* ERIKSSON, 1934) was erected to embrace the orders Conchostraca and Cladocera. BROOKS pointed out that the "close similarity between the structure of adult Cladocera and the larvae of certain conchostracans strongly suggests that the Cladocera are neotenic (paedomorphic) derivatives of some early conchostracan." He also noted that "the fossil Lipostraca are very much more like the Anostraca than they are like the other orders." Accordingly, he proposed that a superorder (unnamed by him) should be defined to embrace the last two-mentioned orders (equal to LINDER's Series B) and that the Notostraca alone should constitute a third superorder. The two recently discovered fossil orders, Kazacharthra and Acercostraca, would have to be associated with the Notostraca in such a superorder. In my opinion this indicates the basic soundness of LINDER's grouping and does not accord with the classification used by PENNAK.

An outline of classification of the branchiopod crustaceans adopted in the *Treatise* is given in the tabulation on pages R112-113, which shows suprageneric taxa down to subfamily rank, accompanied by records of geologic occurrence and numbers of included genera. The last-mentioned data provide information on numbers of subgenera additional to nominotypical ones which are differentiated in some family groups, as well as numbers of doubtfully recognized genera.

SYSTEMATIC DESCRIPTIONS

Class BRANCHIOPODA Latreille, 1817

[=order Branchiopoda Latreille, 1817, p. 59; 1829, p. 149; order Phyllopoda Latreille, 1825, p. 301] [*emend.* G. O. Sars, 1867; raised to subclass, Calman, 1909] [Assignment of taxonomic rank in this section is a responsibility of the editor and is based on consistency with other major divisions of the Crustacea]

Crustacea in which carapace may form dorsal shield or bivalve shell, or may be entirely absent; number of trunk somites varying greatly; posterior part of trunk without limbs and usually ending in caudal furca; antennules generally reduced and unsegmented; mandibles lacking palp or with only vestige of one; maxillae reduced or absent; trunk limbs, which vary greatly in number, generally of uniform structure, rarely pediform, generally foliaceous and lobed; position of genital apertures varies greatly; paired eyes rarely absent; development usually with metamorphosis; young hatched in nauplius or metanauplius stage (21). *L.Dev.-Rec.*

Subclass CALMANOSTRACA Tasch, new subclass

Carapace broad shieldlike, with or without telson-furca development. *L.Dev.-Rec.*

Order NOTOSTRACA Sars, 1867

[*nom. transl.* Calman, 1909 (*ex* suborder Notostraca Sars, 1867)] [=tribe Monostraca Gerstaecker, 1866; tribe Notophylla Stebbing, 1902]

[For specific technical advice on notostracans I am indebted to Dr. James E. Lynch, of the University of Washington, and to Dr. Alan Longhurst, of Bedford College, University of London. Mr. Wilhelm Bock, of the Philadelphia Academy of Natural Sciences, and Prof. B. F. Howell, Princeton University, provided some needed literature.]

Body elongate, more or less covered dorsally by broad, shieldlike (univalve) carapace, attached anteriorly to head, tapering backward and ending in long, caudal furca; posterior somites varying in number lack legs (apodous). Two sessile compound eyes occur close together on dorsal surface of head, with minute obscure ocellus in front of them. Antennae greatly reduced or absent. Body appendages (legs), 35 to 71 pairs, of which 29 to 52 are postgenital; first pair with endites filiform, commonly very long. Rami of caudal furca very long, multiarticulate. Genital ducts open on 11th somite. Ova retained in capsular ovisac formed by 11th pair of trunk limbs. No special prehensile organs occur in males. Young hatched in the metanauplius stage (7, 71, 74). *U.Carb.-Rec.*

ANATOMY

The appendages of notostracans, like those of other branchiopods, appear to be leaflike. Due to this feature, the name Phyllopoda (leaf feet) was originally given to the entire group (Latreille, 1803).

Tadpole shrimps have a shieldlike, arched carapace (Fig. 43,*1*; 44,*2*). This "univalve" ends in a posterior emargination (notch or sinus) that may or may not be denticulate. On its outer surface, the carapace bears sessile **compound eyes,** a **median eye,** and a dorsal, **nuchal organ** (71, pl. 7, figs. 3-6; 74, fig. 4) (Fig. 43,*1b*). Also visible on the surface is a cervical groove. Behind the groove, a carina extends along the mid-dorsal line to the posterior emargination. The arched carina may bear short spines along its length. In flattened specimens these appear as a ladder-like series of flattened spines. Behind the cervical groove, coiled tubes of the shell gland extend diagonally on either side of the carina. These glands serve as excretory organs and empty at the base of the maxillae. They can be seen through the dorsal surface of the carapace and may be preserved as internal casts (e.g., *Triops beedei,* Fig. 43,*2*).

Exclusive of the terminal telson, notostracans have 25 to 44 body somites (or body rings) (71). These rings may bear more than two pairs of legs each and toward the rear some bear ten or more pairs. All body rings are of comparable length. The **thorax** consists of the first 11 rings, the remainder constituting the abdomen.

In all species of the genus *Triops* the supra-anal plate is absent, excepting *T. cancriformis,* in which it is rudimentary (74). In species of *Lepidurus* it is invariably present and prominent.

The notostracan **telson** is heavily chitinized.[1] This can account for its occurrence as a fossil in the sparse record of the order.

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[1] A. G. Richards (1951, Table 2) indicates that *Triops* gives a positive test for chitin in its body wall (see footnote, p. *R*168).

It is difficult to determine a "normal" adult size in notostracans because of the wide range of variations within species. The usual adult size for all species of *Triops* is between 15 and 30 mm. for carapace length. A "giant" species has been reported from Siberia. Large individuals up to 40 mm. in carapace length are also known elsewhere. In general, species of *Lepidurus* tend to be smaller than those of *Triops.* The growth of the carapace is isometric in *Triops,* that is, the ratio of carapace length to total body length remains constant during growth (74, p. 6, fig. 1).

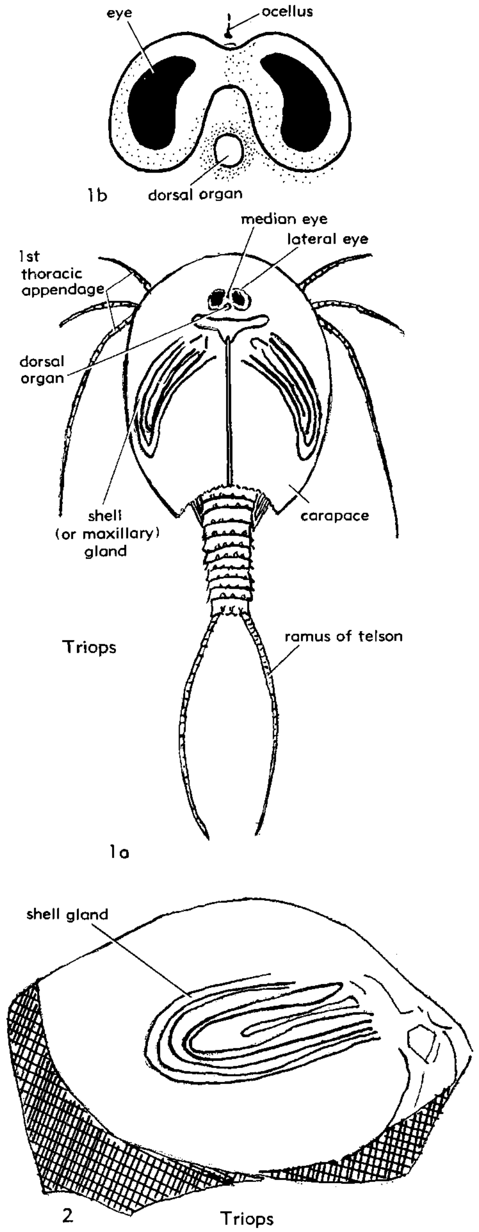

FIG. 43. Morphological features of living and fossil notostracans.——*1.* **Triops cancriformis* (SCHAEFFER); *1a,* complete individual seen through carapace, enlarged (15); *1b,* detail of eye region, enlarged (74).——*2. T. beedei* (RUEDEMANN), shell gland and cervical fold on half of carapace, ×3.5 (170a).

REPRODUCTION

Notostracan populations in which males are absent have generally been referred to as parthenogenetic (72). Recent cytological work, however, raises questions as to the validity of this assumption. LONGHURST (72, 74) confirmed earlier findings of H. M. BERNARD, that in *Triops cancriformis* and some species of *Lepidurus,* the gonads are ovotestes. Thus, the assumed parthenogenetic females are actually hermaphrodites, self-fertilizing, and hence capable of laying viable eggs in the absence of males (74, fig. 12). This finding is confirmed by chromosome number counts (74, table 2, fig. 14).

The role of hermaphroditism in the distribution of notostracans is discussed below. Note may be made that this reproductive mechanism is rare in Crustacea (72). Other notostracan species appear to be characterized by an invariable bisexuality.

In the female, the limbs of the genital somite (11th thoracic ring) are modified to form brood pouches for carrying eggs ("oostegopods" of PEARSE). Notostracans, like other phyllopods, after leaving the eggs, pass through a free-swimming larval stage. As a newly hatched metanauplius, *Triops cancriformis* has an oval body in which one can discern the beginnings of five trunk somites.

SPECIES VARIATION

Many notostracan species are cosmopolitan and exhibit a wide range of variation. For example, all North American and some South American forms of the living *Triops* have recently been assigned to a single species (71). A similar tendency lumps together different species of *Lepidurus.* Study of LINDER's monograph (71) of North American notostracans indicates that considerable variation will be encountered in the following characteristics (both in fossil and living forms): number of body rings, total number of legs on a particular ring, number of leg-bearing abdominal rings, number of legless abdominal rings, form of the supra-anal plate, and spines on dorsal side of the supra-anal plate.

LONGHURST systematically considered every character previously employed to separate species of *Triops* and found that the most important diagnostic character of this genus is armature of the telson (74, p. 18-23, fig. 5). The only other valid characters recognized by him were: presence or absence of the maxillae, arrangement of the eyes, and nature of the dorsal organ. He ruled out as invalid characters that can be correlated with number of body somites or sex of an individual.

Lepidurus apus has a larger geographic range than any other known notostracan, for it is found in Europe, exclusive of Britain, North Africa, Palestine, Asia Minor, Russia, North and South America, New Zealand, and Australia (74, p. 50). Despite this cosmopolitan distribution, very little morphological variation has been observed in its entire range. LONGHURST recognized five geographic races of this species.

A remarkable homogeneity in almost all characters seems to mark species of *Triops* regardless of geographic distribution. Even in a character like protein specificity, determined by spectrographic study of the blood, little individual variation has been found to exist between apparently different populations (74, p. 29-30, table 1).

ECOLOGY

Much confusion in the literature relates to the ecology of notostracans. Most recent work indicates that the ecological differences beween *Triops* and *Lepidurus* are "slight" (74). Between species of *Triops* almost no difference is found, although in some places (e.g., western Australia) this does not hold. Only *L. arcticus,* from the circumpolar Arctic region, differs from all other notostracans.

HABITAT

Species of *Triops* are known from temporary and brackish waters all over the world. *T. cancriformis* does not extend beyond 60°N (74, p. 42). The annual precipitation appears to affect the distribution of two species of *Triops* in North Africa, *T. cancriformis* being found in steppe and substeppe areas where the annual rainfall is 300 mm. (steppe) or 300 to 500 mm. (substeppe), whereas *T. granarius* is found only in substeppe regions. Species of *Triops* (e.g., *T. longicaudatus*) are also known from rice fields in California and Japan, where they uproot rice seedlings.

A recent collaborator of mine, Dr. J. R. ZIMMERMAN (formerly of Wichita State University), conducted a survey of Kansas-Oklahoma ponds in the general area of the Leonardian clam-shrimp-bearing beds. During the summers of 1958 through 1960 he sampled some 500 ponds and in only two found living *Triops cancriformis*—one observed in the summer of 1958 (Seward County, Kansas), and the other in the summer of 1960 (Sumner County, Kansas). In both occurrences he reported that notostracan ponds—some 180 miles apart—were clear, with soft mud bottoms, and not more than one foot deep. Only in Seward County were conchostracans co-inhabitants with *Triops.*

Triops has been found in large temporary lakes, as well as in persistent saline lakes of the Tibetan Plateau (74, p. 35). In general, species prefer temporary waters that dry out with some regularity. The eggs normally require a period of desiccation to hatch out, although exceptionally *Triops* eggs hatch without prior desiccation.

The clearest picture of the "slight" ecological difference between *Triops* and *Lepidurus* derives from study of their distribution in western Australia (74). Here, *Lepidurus* is restricted to the southwestern coastal belt, which enjoys a regular winter rain. On the contrary, *Triops* is confined to the arid interior, where rainfall is slight or absent.

In North America, *Lepidurus* is known from temporary alkaline pools. *L. lynchi* occurs in muddy lake water 2 feet deep. *L. arcticus* predominates in shallow lakes of melted snow and ice and is reported to show remarkable growth in a few weeks. Eggs of this species from Iceland were observed to hatch after desiccation. This contradicts earlier reports by BRAUER and others that *Lepidurus* eggs cannot withstand desiccation. In Europe, *Lepidurus* species are often found in peat bogs and moors that are always under a cover of clear water (7). Humic acids and noxious gases are apparently so diluted or dispersed that they do not interfere with normal egg development.

TEMPERATURE AND pH

In Algeria it was observed that *Triops cancriformis* tolerates a pH range of 7.4 to 7.6 and a temperature range of 14° to 19°C. *Lepidurus lubbocki* (=*L. apus*) had a pH range of 6.4 to 6.6 and a temperature range of 10.5° to 18°C. (GAUTHIER, in 83). While the temperature ranges overlap, it is apparent that in Algerian pools, *L. apus* is more readily able to survive under lower pH conditions.

Mathias subjected *Triops cancriformis* to a temperature of 80°C. while dry and to 42°C. while in contact with water, without observable adverse effects (83). This bears out Longhurst's report (72) that the Notostraca grown by him in the laboratory under variable conditions of temperature, food, and vessel size, all remained "remarkably uniform" morphologically (74).

FOOD

Members of both genera are detritus-feeders and stir up the bottom detritus with the tips of their thoracic limbs prior to filtering it. Besides consuming microscopic organisms, they have been known to gnaw on the living and dead bodies of larger organisms, such as earthworms, mollusks, and even dead tadpoles. They will also tackle frogs' eggs. Trusheim has reported evidence of cannibalism in fossil forms of *Triops* (149).

LOCOMOTION, HABIT, AND POPULATION DENSITY

Individuals of both genera have a choice of varying modes of locomotion. They can crawl, swim, or clamber. A good deal of the time tadpole shrimps creep or burrow superficially in the soft substrate of their respective habitats. This comes about because they inhabit temporary water basins. During drought periods they can burrow or bury themselves in the bottom mud. In such muds their numbers may be very great. In a shallow, dried depression about 20 feet in diameter in Nebraska, Pearse estimated that almost a half-bushel of dead *Triops* bodies were spread over the bottom. Considering their average size of 15 to 30 mm., this denotes a high population density. Equivalent populations are known from the fossil record. Trusheim found literally thousands of *Triops* fragments in thin beds of Middle Keuper (Triassic) age (148).

These dried Recent muds often contain a varied fauna capable of being awakened to life by the addition of water. The material Longhurst studied came from dried muds from phyllopod pools all over the world. While many of the samples received by him contained no viable eggs, quite a number did (74). An example is on record of one sample of dry mud from East Africa that yielded active larvae when wetted, although it had been kept dry for 15 years.

DISTRIBUTION

Still another effect arises from the drought-resistant habit. Muds of desiccated narrow, shallow temporary basins can adhere to the feet of birds that visit them to feed on notostracans and other fauna (e.g., starlings, gulls, Arctic terns, 74, p. 39), or they can be blown great distances by winds or carried by other means. Longhurst has referred to this as "passive distribution." In this way one can easily account for the cosmopolitan distribution of many notostracan species.

Coupled with "passive distribution" is another notostracan attribute, namely, the occurrence of hermaphroditic populations. Thus, hermaphrodites that were probably passively transported are credited with the postglacial extension of the range of *Triops cancriformis.* This reproductive mechanism may also explain the westward extension of *T. longicaudatus* across the Pacific (74, p. 40). This seems to be indicated since no males have been reported from Pacific notostracan populations.

GEOLOGIC OCCURRENCE

Fossil notostracans are closely similar to living forms and represent a stagnant group, in an evolutionary sense (73). Thus, *Lepidurus stormbergensis,* from the Triassic of South Africa, is very close to the Pleistocene *L. arcticus* and living representatives of this species (8, 50). Chernyshev's Lower Cretaceous notostracans from Turkestan are slight variants of *Lepidurus* species (25).

Although the fossil record of *Triops* (=*Apus*) is more extensive than that of *Lepidurus,* most fossil material parallels living forms. Trusheim's remarkable collection from a thin green shale and sandstone zone (Middle Keuper) astonished him by the near-identity of fossils when compared with the living *T. cancriformis* (149). He was so intrigued by notostracans that he raised living forms in an aquarium for a year to study their life cycle and habits and his study provides the most complete information available on the fossil record of *Triops* (148, 149). By the nature of preservation and the condition of detachment of carapace and body parts, Trusheim inferred that fossil *Triops* had a predilection for cannibalism (148, p. 200).

Schimper's species *Triops antiquus,* from the Bunter Sandstone (L.Trias.) is identical with living *Triops,* as Soergel's species from Keuper (U.Trias.) beds appears to be. Soergel originally assigned his material to Schimper's *Apudites,* suggesting that, like Schimper's species, it too belongs to *T. cancriformis.* Ruedemann's *T. beedei,* from Permian rocks of Oklahoma, is also most likely assignable to living *Triops,* although this cannot be proved from a mere shell gland. This leaves only one fossil species at present that eludes definite assignment to living *Triops*; it is GOLDENBERG's *T. ornatus*, from the Stephanian (U.Carb.) of Germany. GUTHÖRL removed this species, which had been placed with cladocerans, to the notostracans. LONGHURST (personal communication, June 1, 1955) could not place GUTHÖRL's specimens of *T. ornatus* in a modern species because available illustrations were inadequate. In view of the known identity to living forms of other *Triops* fossils, it is quite likely that *T. ornatus* will be found to be a synonym for *T. cancriformis*.

Family TRIOPSIDAE Keilhack, 1910

[=Apodidae BURMEISTER, 1834; Lynceitidae COPELAND, 1957]

Shell shieldlike; abdomen formed of more than 15 rings; terminal spine of last ring long, movable, and articulated. *U. Carb.-Rec.*

Triops SHRANK, 1803 [**Apus cancriformis* SCHAEFFER, 1756, p. 131; OD] [=*Apus* SCHAEFFER, 1756 (pre-Linnaean) (*non Apus* CUVIER, 1798, *pro Apos* SCOPOLI, 1777; *nec Apus* SCHOCH, 1868); *Thriops* GHIGI, 1921; *Lynceites* GOLDENBERG, 1870]. Carapace smaller than that of *Lepidurus*, leaving more somites exposed; no telsonic supra-anal plate; first pair of legs with very long endites; commonly more than 8 apodal somites. *U.Carb.-Rec.*, cosmop. [Fossil species include the following forms: (1) *T. ornatus* (GOLDENBERG), represented by impressions of broadly oval dorsal shield (4 by 4.5 mm.), weakly arched, with elevated keel (49), U.Carb.(Stephan.), Ger.; (2) *T. beedei* (RUEDEMANN), with shell gland visible on interior of carapace, 6 urinary tubes represented by pair of concentric furrows (median and outer longitudinal), and cervical fold (115), Perm., USA(Okla.); (3) **T. cancriformis*, =*Triops cancriformis minor* (TRUSHEIM), represented by some 400 carapace fragments, without marks of body parts, 70 carapace-and-body fragments, 30 fragments of abdomen with impressions of furcal setae, eggs, carapace margins, not distinguishable from Recent *T. cancriformis*, U.Trias.(M.Keuper), Ger.; (4) **T. cancriformis*, =*Apudites* sp. SOERGEL, L.Trias.(Bunter), Ger.; (5) **T. cancriformis*, =*Apudites antiquus* SCHIMPER, with compound and median eyes visible on carapace and paired caudal filaments; L.Trias.(Bunter), Ger. (Vogesian Mts.)].——FIG. 43,*1*. **T. cancriformis*, Rec., Eng.; *1a*, dorsal view, ×1.3 (15); *1b*, detail of eyes, dorsal organ, and ocellus, enlarged (74).——FIG. 43,2. *T. beedei* (RUEDEMANN), Perm., USA(Okla.); shell gland and cervical fold on half of carapace, ×3.5 (170a).

Lepidurus LEACH, 1819 (p. 539) [**Apus productus* BOSC, 1802; OD] [=*Bilobus* SIDOROV, 1924; *Prolepidurus* CHERNYSHEV, 1940]. Carapace very large, leaving only few somites exposed; last somite (telson) produced as thin, flat, supra-anal plate between caudal filaments. First pair of legs with comparatively short endites; never more than 8 apodal somites. *Trias.-Rec.*, cosmop.——FIG. 44,*7*. *L. lynchi* LINDER, Rec., USA; telson, body rings and supra-anal plate, ×8.5 (71).——FIG. 44,*2*. *L. apus* (LINNÉ), Rec., cosmop.; dorsal view, ×1.5 (74). [Fossil species include the following forms.]——FIG. 44,*8*. *L. stormbergensis* HAUGHTON, distinguished by pointed or well-rounded supra-anal plate with well-marked mediodorsal keel (50), Trias.(Stormberg Series), S.Afr.; supra-anal plate and caudal filaments, ×4 (50).——FIG. 44,*5,6*. *L. arcticus* (PALLAS), characterized by very small supra-anal plate (74); *5*, Pleist.; ?♀ telson and supra-anal plate from Isle of Man, ×50 (162); *6a,b*, Pleist.-Rec., Eng., and circumpolar, Rec. ♀ and ♂ telson and supra-anal plate, ×50 (74).——FIG. 44,*1*. *L. daja* CHERNYSHEV, with wide, tongue-shaped supra-anal plate (25), L.Cret., Turkestan (Kelmensk Mts.); supra-anal plate and caudal filaments, ×2 (25).——FIG. 44,*3*. *L. schewija* CHERNYSHEV, with supra-anal plate larger than telson and constricted in anterior part while enlarged near middle (25), L.Cret., Turkestan (Kelmensk Mts.); supra-anal plate and caudal filaments, ×1.5 (25).——FIG. 44,*4*. *L. kuenga* CHERNYSHEV, with very small telson and acutely triangular supra-anal plate equal in length to telson (25), L.Cret., Turkestan (Kelmensk Mts.); supra-anal plate and telson, ×6 (25).

Order KAZACHARTHRA Novozhilov, 1957

Six pairs of crustacean-type appendages. Cephalothorax more or less semicircular, incurved at front and rear, or with elongated leaf form, with or without spines on margins; two ocular tubercles bear paired contiguous eyes. Abdomen with two longitudinal rows of spines on dorsal and ventral surfaces; lateral margins of somites with pleura or spines; segmentation visible also on ventral anterior portion of abdomen; number of abdominal somites variable, ranging from 32 to 40. Telson oval or more or less round, with spines on lateral margins and dorsal and ventral surfaces, with or without cerci. Antennae unknown (97). *L.Jur.(Lias.).*

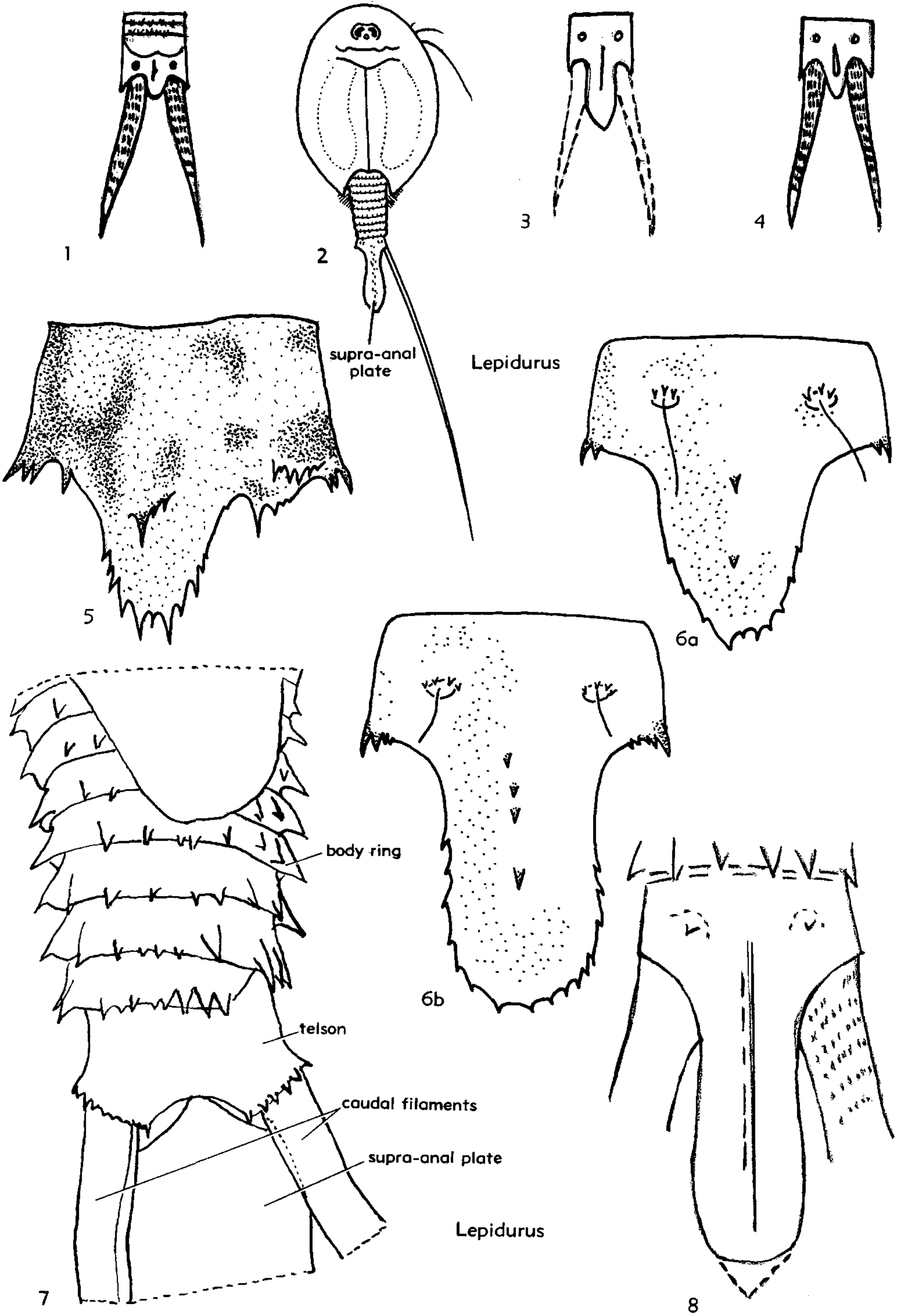

Fig. 44. *(Continued on facing page.)*

ANATOMY

Novozhilov (100, p. 266) has observed that in ventral view, the mouth parts of *Almatium,* a genus classed by him in the order Kazacharthra, are of the same type as in true notostracans—that is, they have the general form of a horseshoe that reaches the posterior margin of the cephalothorax. Study of published photographs shows (100, pl. 7, fig. 4) the presence on one specimen of a labrum, antennule, and three somites apparently displaced anteriorly, somites which could correspond to the paragnathum, maxillule, and maxilla of notostracans; another figure (100, pl. 7, fig. 5) shows a labrum, antennule, and ?mandible, which are notostracan-type mouth parts.

For the appendages, Novozhilov (100, fig. 2) provided a line drawing, which indicates that these possess three branches (proepipodite, epipodite, exopodite) in addition to several endites. The number of short appendages attached to the anterior portion on the ventral face of the abdomen is fewer than found in notostracans. In the Kazacharthra Novozhilov has noted that the segmentation of the anterior part of the abdomen is complete on two sides—dorsal and ventral. Genera of the Kazacharthra are also distinguished by structure of the telson, which, though possessing cerci, lacks a terminal segment. In certain genera *(Panacanthocaris)* the telson has a complex structure.

D. G. Sharov (cited 100, p. 266), who helped in collecting materials from the Sajkan Mountains, is of the opinion that two features—cerci on the telson and similarity of appendages—warrants assignment of the kazacharthrans with notostracans. Novozhilov explained that he rejected the "presence of cerci" as a character having taxonomic importance, since they occur in many arthropod orders, as well as in the Trilobitomorpha. As for swimming appendages, notostracan resemblances lose taxonomic importance in Novozhilov's view because the Kazacharthra lack the greater number of short appendages found in notostracans.

It is certainly clear that in shield characteristics, mouth parts, appendage structure, and some abdominal features, the Kazacharthra rather closely resemble notostracans. Only additional material and further study can determine if the smaller number of short appendages and variable characteristics of the telson merit assignment of ordinal rank.

As yet, evidence on which the order is based has not been adequately analyzed by specialists in the study of crustacean evolution. Hence, the order is simply reported here for completeness.

GEOLOGIC OCCURRENCE

Specimens of the Kazacharthra are so far known only from the Ketmen and Sajkan Mountains of southeastern and northeastern Kazakhstan. *Ketmenia gusevi* Chernyshev (1940) was originally based on poorly preserved fossils, but a fortunate discovery in 1957 by L. F. Belzhankin yielded abundant new and better-preserved specimens which permitted Novozhilov (100) to distinguish a new genus *(Almatium),* with the above-named species as type. According to Novozhilov, *Almatium* is based on more than 200 cephalothoraxes, dozens of abdomens (some with telson attached), as well as isolated body parts (e.g., labra, mandibles, appendages). In addition, parts of several new genera were more

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(Continued from facing page.)

Fig. 44. Morphological features of living and fossil notostracans.——*1. Lepidurus daja* Chernyshev, showing wide, tongue-shaped supra-anal plate and caudal filaments, ×2 (25).——*2. L. apus* (Linné), showing eye region, dorsal shield with shell glands outlined, body rings, supra-anal plate and caudal filament, ×1.5 (74).——*3. L. schewija* Chernyshev, with supra-anal plate larger than telson and constricted in anterior part while enlarged near middle, ×1.5 (25).——*4. L. kuenga* Chernyshev, with very small telson and acutely triangular supra-anal plate equal in length to telson, ×6 (25).——*5. L. arcticus* (Pallas), characterized by very small supra-anal plate, ×50 (74).——*6. L. arcticus* (Pallas), *6a,b,* ♀ and ♂ telson and supra-anal plate, ×50 (74).——*7. L. lynchi* Linder, showing telson, body rings and supra-anal plate (spines omitted on caudal filament), ×8.5 (71).——*8. L. stormbergensis* Haughton, characterized by pointed or well-rounded supra-anal plate with well-marked mediodorsal keel, ×4 (50).

recently made available. The finding of abundant fossil remains of any branchiopod is always of great interest and where a new order seems to be indicated, such discoveries are noteworthy for the light they may shed on branchiopod evolution and ultimately on crustacean evolution also.

The lithology of the Jurassic beds yielding specimens of the Kazacharthra is sketchily given by SCHULTZ (cited 97, 1957) for the Kyzyl-Tam ravine section, in which Bed 3, bearing the crustacean fauna, occurs 120 m. above the base. It overlies a bed of alternating red and gray-yellow shale with beds of sandstone, conglomerates, and disseminated and bedded carbon containing a Lower Jurassic flora associated with coleopteran elytra, a deformed conchostracan valve, and a new species of cockroach. Bed 3 itself is a gray to yellow-gray slaty clay containing gypsum. Whether the crustacean fauna is found in large wheel-shaped concretions or in the slaty clay is not clearly stated.

No branchiopod occurrences have been reported from the American Jurassic, although an interesting specimen from the Sundance beds (L.Jur.) of southwestern Wyoming was recently sent to me. It is poorly preserved, but seems to be closer to conchostracans in shell morphology and surface features than to any other group.

The Kazakhstan section mentioned above includes (in argillites) an insect-bearing bed below a crustacean horizon, together with carbonized material, plant fossils, and other organic remains. This lithic-biotic evidence may be taken, together with the Sundance material, as a provocative indication. American Jurassic deposits probably contain and would yield branchiopod faunas if workers undertook to search for them. In and above carbonized beds seem to be promising places in the light of the evidence from Kazakhstan.[1]

Family KETMENIIDAE Novozhilov, 1957

[=Paratriopsidae CHERNYSHEV, 1940, invalid name (25)]

Large flat shield, rounded, rectilinear or concave in front, with or without spines on margins. Elongated abdomen composed of three longitudinal divisions of movable somites, which have equal or nearly equal length; dorsal median part of somites separated from lateral parts by pairs of spines forming two longitudinal series; somites approximately 42, of which six are covered by shield and remainder project beyond shield. Telson of single angular, rounded or nearly rectangular somite, notched at its posterior margin, or with lateral margins curved in truncated ellipse (97). *L.Jur.(Lias.).*

Ketmenia CHERNYSHEV, 1940 [**K. schultzi*; OD]. Anterior margin of shield rectilinear or slightly recurved; posterior margin largely concave; spines developed on posterior lateral margins. Flattened, subtriangular bulge with equal sides on median portion of shield. Large, flat telson shaped like truncated ellipse, with spines on lateral margin and on posterior margins of dorsal and ventral surfaces (25). *L.Jur.(Lias.),* USSR(SE.Kazakh.).——FIG. 45,*5*. **K. schultzi,* Ketmen Mts.; *5a,* elongated abdomen and telson, ×2 (25, 97); *5b,* shield, ×1.25 (25, 97).

Almatium NOVOZHILOV, 1957 [**Ketmenia gusevi* CHERNYSHEV, 1940; OD]. Cephalothoracic shield more or less rounded, with concave posterior margin, all sides without spines; projecting ocular, rounded, anterior, with paired eyes adjoining. Appendages short, not projecting beyond limits of shield. Abdomen composed of 32 to 40 somites, with more or less long cerci (97). *L.Jur.(Lias.),* SE. Kazakh. (Ketmen Mts.)-NE. Kazakh. (Sajkan Mts.).——FIG. 45,*1*. **A. gusevi* (CHERNYSHEV), Ketmen Mts.; shield, ×0.8 (97).

Iliella CHERNYSHEV, 1940 [**I. spinosa*; OD]. Shield concave in front and rear, with spines along entire circumference; contour of shield in form of figure 8; raised mandibulars located in rear portion of shield; ocular tubercles, even and odd, in upper sector of shield (25). *L.Jur.(Lias.),* USSR(SE.Kazakh.).——FIG. 46,*2*. **I. spinosa,* Ketmen Mts.; shield, ×2 (25, 97).

Jeanrogerium NOVOZHILOV, 1959 [**J. sornayi*; OD]. Cephalothoracic shield oval, flattened, without spines on margins, or with short, small spines on posterior margin; appendages longer than cephalothoracic shield; 2 branches of somites projecting from cephalothorax. Somites of abdomen without spines on margin, at least in young individuals; number of somites 18+?15+8. Telson more or less rectangular, with long cerci (100). *L.Jur.(Lias.),* USSR(SE.Kazakh.).——FIG. 45,*3*. **J. sornayi,* Ketmen Mts.; complete individual (reconstr.), ×2 (100).

Kungeja NOVOZHILOV, 1957 [**K. tchakabaevi*; OD]. Shield helmet-shaped, with posterolateral growth diverging from sides; anterior margin rectilinear,

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[1] Since this was written *Cyzicus (Lioestheria)* sp. have been reported from the American Jurassic and Cretaceous.

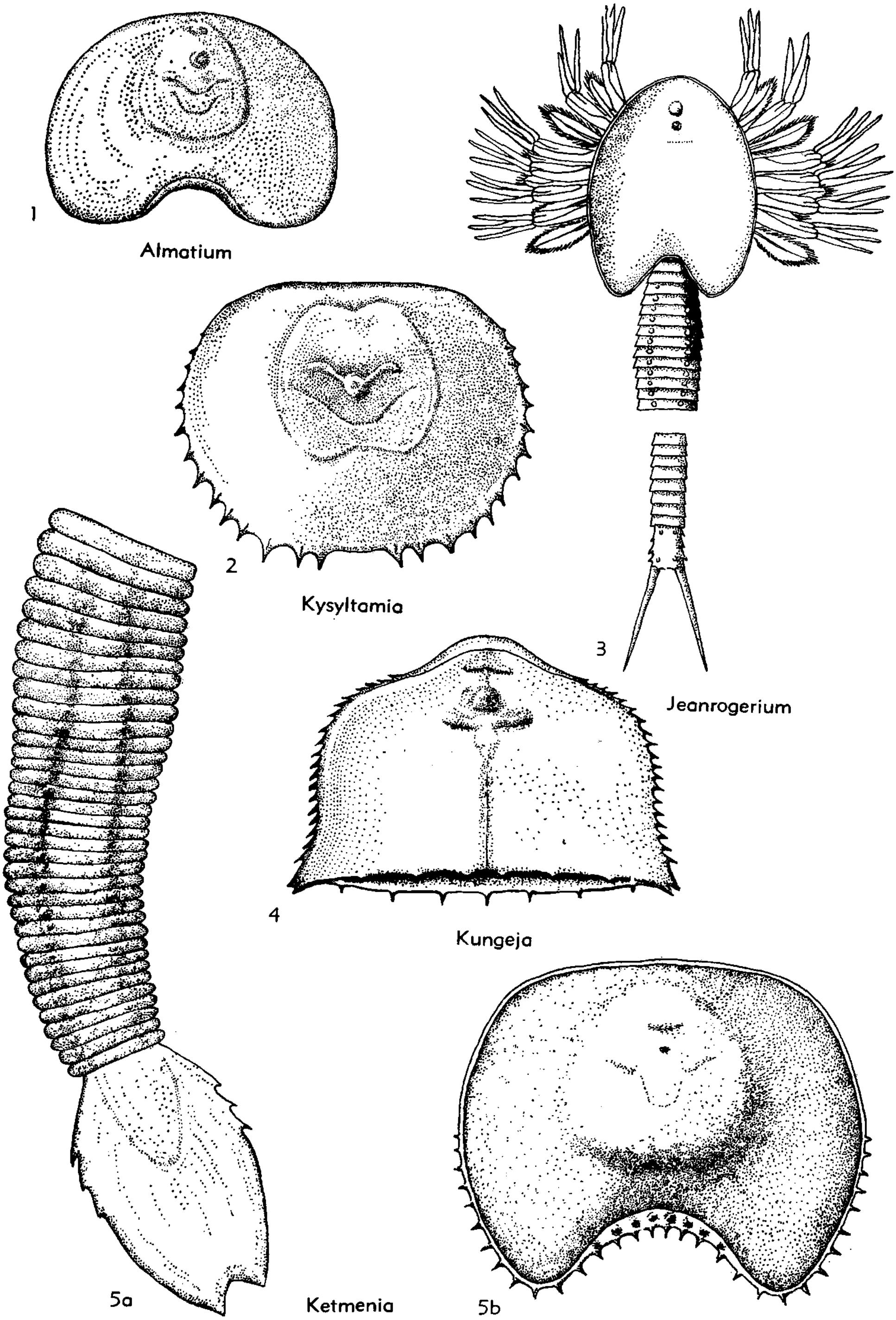

FIG. 45. Ketmeniidae (p. *R*138, *R*140).

limited by furrow or groove; spines on lateral and posterior margins; transverse equal ocular tubercles and rounded odd tubercle on rise of carapace; no flattened bulge in middle of shield (97). *L.Jur. (Lias.)*, USSR(SE.Kazakh.).——FIG. 45,*4*. **K. tchaḳabaevi*, Ketmen Mts.; shield, ×1.1 (97).

Kysyltamia NOVOZHILOV, 1957 [**K. tchiiliensis*; OD]. Shield irregularly oval, without concavity of posterior margin; lateral margin and posterior margins with spines. Unique ocular tubercle between mandibular rise (97). *L.Jur.(Lias.)*, USSR (SE.Kazakh.).——FIG. 45,*2*. **K. tchiiliensis*, Ketmen Mts.; shield, ×1.1 (97).

Panacanthocaris NOVOZHILOV, 1957 [**P. ḳetmenia*; OD]. Shield oval, with large shallow concavity on front margin, narrow on back margin, spines of different lengths on all perimeters but absent in posterior concavity; much of middle part of shield near anterior margin occupied by an ovate flattened bulge; odd ocular tubercles and raised mandibulars located in upper middle part of shield. Abdomen incompletely known. Telson large, divided into large winglike portions and bearing spines (97). *L.Jur.(Lias.)*, USSR(SE.Kazakh.).——FIG. 46,*1*. **P. ḳetmenia*, Ketmen Mts.; complete individual (reconstr.), ×1.1 (97).

Order ACERCOSTRACA
Lehmann, 1955

Dorsal carapace present; pair of sessile eyes; small antennae; 5 pairs of articulated thoracic appendages and numerous postgenital abdominal appendages. Like *Triops* but lacking postabdominal telson-furca development (66). *L.Dev.*

ANATOMY

LEHMANN's (1955) order Acercostraca closely resembles the notostracans, in general, and *Triops* in particular, in having a dorsal carapace, a pair of sessile eyes, small antennae, and about 50 pairs of appendages. Members of this assemblage lack the characteristic notostracan telson and furca, however (55).

X rays of fossil acercostracans have revealed the intestinal tract and anus, as well as some dorsal features of the carapace, such as the sessile eyes.

The Acercostraca, lacking telson and furca, have soft-part anatomy totally confined to the carapace. It is of interest that NOVOZHILOV's Kazacharthra also closely resemble the notostracans, differing from them in having fewer appendages and variable telson features. The Acercostraca apparently first appeared in Early Devonian time, whereas the oldest known representatives of the Kazacharthra occur in Lower Jurassic deposits.

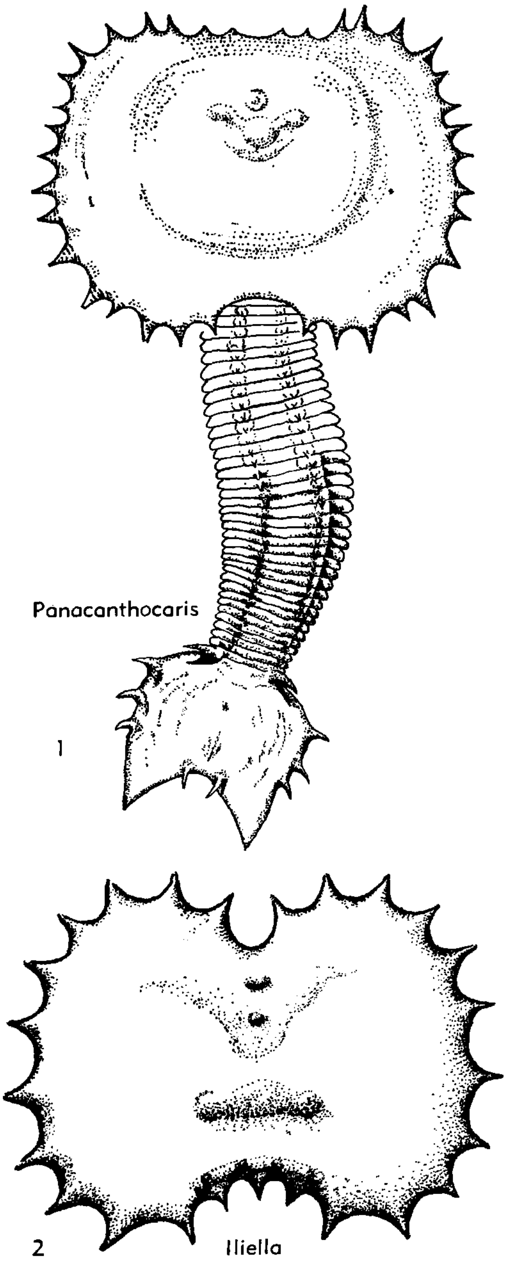

FIG. 46. Ketmeniidae (p. *R*138, *R*140).

INFERRED EVOLUTIONARY RELATIONSHIPS

Fossil notostracans are distributed from the Carboniferous to Permian and Triassic, in each of which systems *Triops* species are recorded. It thus appears that LEHMANN's order, derived from a still older type, may have given rise to the *Triops* line in Carboniferous time. An alternative possibility is that *Triops* descended from a pre-Carboniferous ancestral type and from this same ancestor, a side line branched off leading to the Acercostraca. The Kazacharthra then might be a Mesozoic offshoot of the *Triops* line.

The relative stability of living notostracan forms, classifiable in only two genera *(Triops, Lepidurus),* indicates that one branch of the *Triops* stock has been conservative in speciation from at least Carboniferous times onward.

Family VACHONISIIDAE Tasch, new family

Characters of order. *L.Dev.*

Vachonisia LEHMANN,[1] 1956, *nom. subst.* [*pro Vachonia* LEHMANN, August, 1955 (*non Vachonia* ABALOS, March, 1955)] [**Vachonia rogeri*; OD]. Shield broadly expanded, *Triops*-like, with median anterior notch and gently convex posterior margin, apparently covering entire body. Single pair of very small antennae; 5 pairs of thoracic appendages; about 50 pairs of postgenital abdominal appendages (66). *L.Dev.(U.Coblenz.),* Ger.——FIG. 47,*1*. **V. rogeri,* Hunsrück Shale; *1a,b,* ventral side, dorsal side shown by X-ray, ×9.4 (66).

Subclass DIPLOSTRACA Gerstaecker, 1866

[*nom. transl.* TASCH, herein (*ex* superorder Diplostraca BROOKS, 1959, *nom. transl. ex* subsection Diplostraca—of suborder Branchiopoda—GERSTAECKER, 1866, p. 1029)] [=Onchyura ERIKSSON, 1934] [*emend.* BROOKS, 1959, and TASCH, herein]

Bivalve carapace (single piece in cladocerans), laterally compressed, enclosing body and appendages, abdomen with end (together with postabdomen in cladocerans) bent ventrally forward. Antennules uniramous, small, tactile; antennae powerful swimming appendages. *L.Dev.-Rec.*

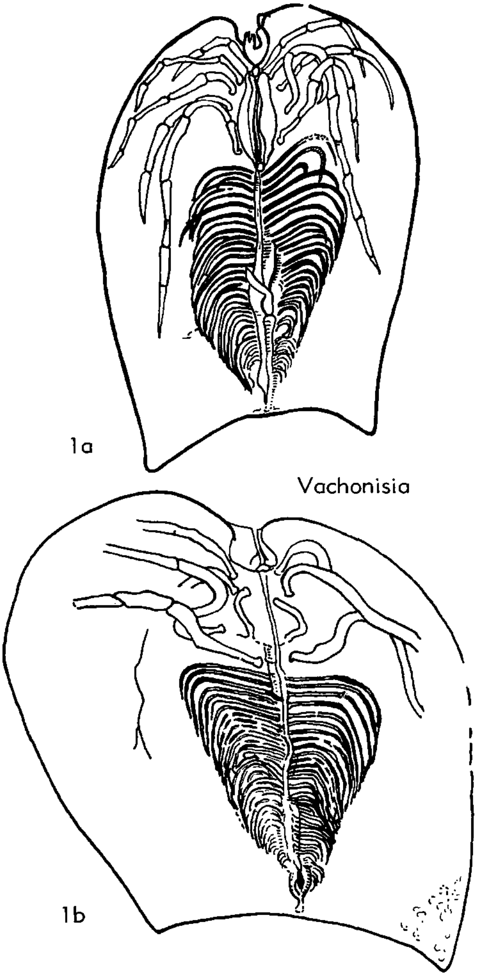

FIG. 47. Vachonisiidae (p. *R*141).

Order CONCHOSTRACA Sars, 1867[2]

[*nom. transl.* CALMAN, 1909 (*ex* suborder Conchostraca SARS, 1867)] [=tribe Holostraca GERSTAECKER, 1866; Phyllopoda conchiformia SIMON, 1866; Conchophylla STEBBING, 1902]

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[1] Paläont. Zeitschr., v. 30, p. 225, 1956.

[2] Completion of the conchostracan section of the Branchiopoda chapter was greatly expedited by two Sigma Xi research grants-in-aid. A Wichita State University research grant facilitated preparation of the plates.

RAYMOND's type material was studied at the Museum of Comparative Zoology at Harvard College. Types on deposit at the New York State Museum and the Geological Survey of Canada were loaned for study.

Messrs. E. S. BELT and W. BOCK and Drs. ADA SWINEFORD and E. G. WILLIAMS contributed material from the Upper Mississippian of Nova Scotia, Triassic of Pennsylvania, Permian of Kansas, and Pennsylvanian of Pennsylvania. Prof. Dr. ZDANEK SPINAR kindly sent representative specimens from the Carboniferous of Czechoslovakia. Data on South American conchostracans were graciously supplied by Prof. Dr. JOSUÉ CARMARGO MENDES.

Dr. M. T. COPELAND provided data on Canadian conchostracans and supplied excellent photographs and descriptions

Body enclosed within translucent bivalve shell, ending posteriorly in clawlike furca (with single exception); front of head produced downward, forming frontal process or rostrum; paired compound eyes sessile, more or less confluent; ocellus placed below compound eyes. Antennules short or long, variable from unjointed to multijointed; antennae natatory, biramous, much larger than antennules; trunk limbs (legs) variable, 10 to 32 pairs, of which 1 to 16 are postgenital; rami of caudal furca short, clawlike. Genital ducts opening on 11th segment; ova retained within shell, attached to 9th to 15th pair of legs. Young usually hatched in nauplius stage (120). *L.Dev.-Rec.*

ANATOMY

Conchostracans, or clam shrimps, have a short, laterally compressed body enclosed between two lateral valves that constitute the carapace. The head is located anteriorly, somewhat beyond the umbonal region, and bears sessile paired compound eyes and a well-developed ocellus. The front of the head is produced downward so as to form a rostral process or beak. Posteriorly, the telson is distinguished by two flattened, upwardly curved processes or claws. Two pairs of antennae are present, the antennules being small and simple, whereas the antennae are modified into powerful biramous swimming organs. During mating, males of *Cyzicus* (=*Isaura*) *cycladoides* have been observed (83) to use the antennae as aid in seizing the female carapace. I have noted multiple uses of these antennae in aquarium-reared conchostracans in my laboratory.

The antennae are employed as an aid in burrowing, as well as in escaping from bottom muds in which the clam shrimp has burrowed. They are also used to clamber up aquarium walls. When individuals rise nearly to water surface, anterior side up, the antennae are looped and act as a propellant. Sometimes they serve to aid in floating, when, in particular, clam shrimps graze on surface microplankton.

Trunk legs (swimming legs) vary from 10 to 32 pairs, of which from 1 to 16 are postgenital. Although phyllopod trunk appendages display a basic plan—that is, biramous, flat, translucent, lobed, and setose legs with a series of small lobes (endites) along the median margin—modifications of the plan occur in both male and female conchostracans. In males the initial one or two pairs of legs are hooked and prehensile. GRAVIER & MATHIAS (83) observed that during mating the male appears to use these robust hooks in maintaining steady attachment to the female (see Fig. 50,*1a,b*).

Repeated observations and experiments on aquarium populations during mating have convinced me that the mating attachment is not readily disturbed. The mating pair, with the male shell in a position perpendicular to the female shell, moved as a single unit when touched by a brush or when a passing individual clam shrimp collided with them. There also appears to be some competition for females. Individual males were seen on several occasions unsuccessfully attempting to seize copulating females with their prehensile legs. Such incidents cause the mating pair to migrate from the area.

In females, the elongated flabella, consisting of as many as three pairs of posterior legs, appears to serve the function of retaining eggs in position (85, 107).

CARAPACE

COMPOSITION

The composition of the carapace of *Limnadia lenticularis* may be taken as indicative of other conchostracan carapaces. SARS (122) found that it is composed of two distinct parts, an exterior chitinous coating that seems to consist of several layers, and an interior membranous lining that is continuous with the integument of the body. A similar composition has been reported for *Caenestheriella davidi* (58, p. 9). More recent researches on living clam shrimps have added further details (35).

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of recently collected specimens from Devonian rocks of the Canadian Arctic.

Other individuals who assisted with references, literature, specimens, or discussion and advice on pertinent problems include: Mme. SIMONE DEFRETIN, Mr. H. W. DRESSER, Dr. M. K. ELIAS, Mr. C. F. KILFOYLE, Prof. TEIICHI KOBAYASHI, Dr. S. A. LEVINSON, Dr. N. NOVOZHILOV, Dr. JEAN ROGER, Dr. C. J. STUBBLEFIELD, Dr. H. B. WHITTINGTON, and Dr. J. L. WILSON. Dr. K. E. CASTER communicated personal observations on conchostracan-xiphosuran associations on Brazilian coastal salt flats. Dr. G. FRYER generously supplied requested information on the habitat of living central African conchostracans. The late Dr. N. T. MATTOX helped me to decipher the taxonomy of *Cyzicus* and provided other valuable data on the ornamentation of living forms. Others who supplied data on and specimens of living conchostracans include Dr. LOUIS KORNICKER, Mr. BERNARD L. SHAFFER, and Dr. J. R. ZIMMERMAN.

A diverticule which separates the two cuticular layers of the valve is bounded by two epidermal layers, one above, and one below it. The surface ornament of conchostracan valves originates in the epidermal cells of the uppermost of these layers. Thus, certain adjacent epidermal cells give rise to fibers (cuticular prisms?) which either radiate in the corresponding cuticle or are sunk in the tissue itself. The latter fibers (prisms?) may unite and form a series of resistant pillars rooted in the external cuticle. Thus, a moderate relief is determined and its reflection on the exterior of the valve constitutes the valve ornamentation. Such pillars may be isolated, associated in a polygonal network, or appear as radial rows. In turn, they appear on the exterior of the valve as polygonal, reticulate, or radial. Punctate ornamentation may be accounted for by pore-canals penetrating cuticular fibers (prisms?).[1]

Sars (122) further noted that in *Limnadia* the two distinct carapace parts are connected by numerous cross bars. These, he found, were partially visible externally as small irregular opaque spots.

There can be little doubt, then, that surface ornamentation reflects epidermal-cell-generated fibers (prisms?) and their condition of merger or isolation, and the further condition of creation of relief on the inner side of the external cuticle. One wonders, since the same kind of fiber (prism?) enters into so many different types of ornamentation, whether the vagaries entering into determination of thickness of fiber bundles (prisms?) merits generic or familial taxonomic status. Insight leading to a plausible answer to this question is considered in discussion of "Ornamentation." Here it suffices to indicate that the epidermal cells can generate pore-penetrated fibers (prisms?) that yield punctate ornamentation and later in the same individual, fibers (prisms?) of radial type. This capacity for variable expression precludes fiber (prism?) arrangements themselves as more than secondarily useful taxonomic indicators.

I have studied six specimens of *Caenestheriella belfragei* from a large sample taken by a colleague from a pond near Liberal, Kansas. Thickness of valves in this sample measured along freshly broken edges varied from 0.06 to 0.08 mm. Individual layers, of which the exterior coating was composed, numbered six or seven, which indicates an average thickness of each layer ranging from 0.008 to 0.013 mm. While some variation may be expected in these figures for other genera and species, they are likely to be of the right magnitude.

In life, the corneous conchostracan carapace is never strongly calcified (83, p. 4).

The shells of living conchostracans are semitransparent to translucent and colored light amber, brown to brownish-red, or yellow. I have observed valves change to a deeper red-brown color prior to the animals' demise. This is due to changes in the color of the unoxygenated blood in the valve which in life serves a respiratory function.

GROWTH LINES

All above-mentioned species have carapaces with lines that reflect successive moltings. That is to say, during ecdysis, in addition to the casting off of a chitinous inner skeletal duplicature, a line of growth is added peripherally to each valve. Only the Lynceidae lack growth lines. In mature individuals of *Caenestheriella gynecia,* lines of growth are variable (15 to 26), with an average of about 20. In *Limnadia lenticularis* adults, growth lines are also variable (11 to 15, according to Sars; 5 to 16, according to Daday); in mature individuals of *Eulimnadia stoningtonensis,* 10 growth lines are reported. Because number of growth lines is important in studies of fossil conchostracans, variation found in living species of *Limnadia* is of interest (30, t. 8, p. 151-175). Growth lines vary from three in *L. nipponica* females, to 45 in *L. grobbeni* females. In the latter species males have ten fewer growth lines. Sexual difference in number of growth lines is well shown by *L. stanleyani,* in which males have ten growth lines and females 13 to as many as three times the maximum male number, even though the carapaces of both sexes are very similar in size.

It has been suggested (58, p. 42, 141) that for estherian conchostracans, low temperature retards carapace growth and is reflected in a smaller number of growth lines. Species reported from tundra regions are all small. In a temperate region, Mattox (86) found that living individuals of *Caenestheriella gynecia* collected during June of one year showed an average length of 10.6 mm. and 18 growth lines, whereas in July five years later similar individuals averaged 7.3 mm. in length and had 16 growth lines. This difference in growth rate was attributed to a greater precipitation in the earlier year, since more rainfall is reflected in larger or more permanent pools and increased food supply. It is helpful to keep factors of this sort in mind when studying fossil populations that show wide ranges in size and number of growth lines for the same overall shell size.

ORNAMENTATION

Living conchostracans, with few exceptions, display a variety of types of carapace sculpture. Kobayashi (58, fig. 1, table 1), based on data of Daday (30), classified these into some 20 types and noted that in a few forms female sculpture differs from that of males. He deduced a morphological series that may or may not correspond to any actual evolutionary or ontogenetic sequence but which is given here since it sums up the main

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[1] Cf. M. Novikoff, 1905, Zeitschr. wissensch. Zoöl., v. 78, p. 569-571, pl. 21, fig. 19, 26, 27, 31.

kinds of sculpture: (1) appearance of spots or striae, (2) enlargement of spots, (3) appearance and disappearance of grooves, (4) change of grooves from radial to dendritic, and (5) change of pattern from polygonal to reticulate.

As already noted for *Eulimnadia stoningtonensis,* the larval carapace is minutely punctate and this is retained in the adult. Various estherians studied by BAIRD (5) are reported to show minute raised clots or punctation on carapace interspaces. SARS (122, p. 119) noted that even in smooth and unornamented *Lynceus brachyurus,* under high magnification, the external lamella of the shells displays regularly rounded meshes or hollows.

NOVOZHILOV has founded his entire system of classification of fossil conchostracan valves (95, 98, 99) on fine shell sculpture of the type mentioned above. In so doing, he follows the lead of BAIRD, who originally tried to classify living clam shrimps on whether their valves were "dotted or punctate on the surface" or "longitudinally striated on their surface" (5). These efforts, based on living forms, have been rejected by all workers. No presently acceptable biological classification is based on valve sculpture. In fact, MATTOX (87) has eloquently spoken out against use of this feature for fossil clam-shrimp valves as well. He simply demonstrated that the same valve in numerous instances has both of BAIRD's types of sculpture. JONES (53) and others have shown—without addressing themselves to this particular debate but rather in the course of describing new material—that numerous species of the same genus may have as many as three different types of ornamentation. DEFRETIN (35) more recently has indicated that, while some species may be separable on the basis of shell sculpture, many are not, and thus classifications so predicated lead to blind alleys.

We may conclude that a wide spectrum of variation occurs in the above-noted valve-sculpture patterns within the same individual valve belonging to a given species, as well as within different species of the same genus. In brief, this characteristic cuts across specific, generic, and sexual lines. For conchostracan fossils, ornamentation can at best provide secondary evidence for distinguishing species and possibly subgenera. More rarely it may also serve in the same population to distinguish male and female shells. All evidence available is opposed to use of shell ornamentation for discriminating genera and families of fossil or living conchostracans.

ATTACHMENT OF CARAPACE TO BODY AND ORIENTATION

The mode of attachment of conchostracan shells to the body can be exemplified by living *Limnadia lenticularis.* SARS (122, p. 86, pl. 14) reported that the shell is attached to the body above by a narrow ligament, and a little below this, to each side by a strong adductor muscle, the insertion of which on the interior surface of each valve appears as a well-defined circular area in the foremost part of the valve. The ligamental attachment is anterodorsal and within the upper umbonal area. *Cyzicus morsei* shows a similar mode and location of shell attachment.

Fossil carapaces with subcentral beaks indicate that ligamental attachment of these forms was mediodorsal.

Dorsal and ventral sides, right and left valves, anterior and posterior locations on fossil conchostracan carapaces can readily be determined. Most often fossils cannot be removed from the bedding plane and orientation of the several valves must be achieved by inspection.

In exterior view, the umbo or umbonal beak occurs on the dorsal side. Since the conchostracan body is attached to the umbonal area on the interior, and behind the head region, the anterior location is always headward. If the umbonal region on a given valve is to the right, it is a right valve; if to the left, it is a left valve.

Both valves of fossil estherians in some occurrences are preserved on the same bedding plane. In such cases, direction and strength of bottom currents may be estimated by measuring the displacement and direction of displacement of the two valves along the dorsal margin (61, p. 5-6, fig. 2). Such displacement is generally negligible, owing to weakness of currents which might be expected from the nature of water bodies in which conchostracans are found.

Where fossil valves are found only with umbones and dorsal margins visible on a bedding plane, the individuals represented by such valves evidently died while burrowing in the bottom mud. Most conchostracan valves settle to the bottom and come to rest on their right or left sides, with the convex portion outward.

DIMORPHISM

The male and female shells of many conchostracans differ in shape. Thus, SPENCER & HALL (132) reported that female shells are narrower than those of males in species of *Limnadopsis.* KOBAYASHI & KUSUMI (61) measured carapaces of six genera *(Eulimnadia, Caenestheriella, Caenestheria, Leptestheria, Lynceus, Eocyzicus)* of living estherians on deposit at a hydrobiological station at Otsa, Japan, finding that the carapace outline commonly is different in male and female shells of the same species. In a sample of 15 male and 15 female carapaces of *Eocyzicus mongolianus* UENO plotted on a curve (61, fig. 9), I observed that a zone of overlap on the graph for length ranges from 10.7 mm. to 11.2 mm. In this zone, male and female carapaces were the same in size, whereas on either side of this zone only larger male shells are recorded, or in the opposite direction, only smaller female shells. As for height, the range in height of the male carapace falls within the broader range for females.

The interpretation given above differs from that of the cited authors who concluded that "the female is shorter than the male in *E. mongolianus*." Yet study of their graph suggests that dimorphism is expressed gradationally. This becomes an important consideration in dealing with fossil material, since dimorphism has been reported frequently (13, 58).

When considering dimorphism, it is useful to bear in mind the proportion of males to females found in natural populations of living conchostracans. SPANDL (131, fig. 10) indicated that for *Leptestheria dahalacensis* (RÜPPEL) males predominate in warm countries and constitute as much as 75 per cent of the population, whereas elsewhere males may constitute as little as 10 per cent of the population. JOLY (52) found 24 males in a population containing 30 individuals of *Isaura* (=*Cyzicus*) *cycladoides* in Toulouse, France, while other workers reported (83) three males for every female of this same species. In Breslau, Germany, SIEBORD (83) found in a population of 1,364 individuals almost 2.5 times the number of females compared with males of *Cyzicus tetracerus* (KRYNICKI) and SIMON (83) reported a marked predominance of males in populations of *Caenestheriella gubernatur* KLUNZINGER in Egypt.

MATTOX (86) has noted that in the genus *Caenestheriella* all American species are described on the basis of male and female specimens, though his new species from Ohio, *C. gynecia,* consisted only of female individuals.

INJURY AND REPAIR

Injury to the growing edge of conchostracan valves has been observed in living and fossil specimens (144). Successive growth lines posterior to the injured site curve upward to fill the gap in the valve created by the injury. New morphological structures may thus be formed in the process of healing the injury. Such structures have been observed and include a sinus or downwarp in the upcurve growth-line zone and one or more scallops on the peripheral margin between any two repaired zones on the same valve. This capacity for shell repair has continued unchanged from at least Permian (probably from Devonian) time to the present.

Individual valves with unique structures must be examined for injury-repair zones. Only when this kind of explanation of the unique feature has been excluded, can taxonomic recognition be made.

SOFT PARTS PRESERVED WITH FOSSIL VALVES

Very few instances of partial soft-part preservation of conchostracans have been recorded. Of these, only two (33, 158) have provided excellent anatomical data. The rarity of such finds is confirmed by my own experience in tracing conchostracan-bearing beds of the Wellington and Ninnescah Formations (Lower Permian) in the Kansas region. Although literally thousands of fossil clam shrimps have been collected from almost 1,000 feet of these deposits and from numerous zones, not one example was found where partial soft-part preservation could be seen.

WRIGHT's genus *Limnestheria* (158) was erected on soft-part anatomy found associated with valves. Her material included second antennae, mandible, trunk, telson, and appendages, from which she was able to show that the first pair of trunk limbs in males were modified as claspers. MATTOX (87), in reviewing her evidence, concluded that her interpretation of the appendages was erroneous in that two pairs of trunk limbs had been modified as claspers. This last factor affected classification of *Limnestheria*, and MATTOX proposed that it be placed in the Cyzicidae instead of Lynceidae. However, no cyzicids are known with valves bearing a large umbo surrounded by few growth lines, a condition that characterizes the valves of *Limnestheria.* The genus should be assigned to the Limnadiidae, in which family valves of this type are common. The fact that specialists such as WRIGHT and MATTOX differ in interpreting the appendages of *Limnestheria* indicates to me that any such interpretation in itself is inconclusive. MATTOX also noted that the antennae and telson are very similar to those of modern estheriids, denoting in his opinion a close relationship of the Carboniferous forms with living species.

DECHASEAUX (33) studied the soft-parts preserved in valves of *"Estheria"* (=*Cornia*) *cebennsis,* observing mandibles, fragments of the biramous antenna, impression of the ocellus and interior of the digestive tube, and the caudal furca. Some strings of eggs were also found fossilized with the valves. As compared with modern estheriids, she concluded that the Carboniferous specimen had larger and fewer eggs, a characteristic head profile, more or less elongate appendages, shorter antennae, and a longer caudal furca. She further observed that the eggs of Triassic clam shrimps are smaller and more numerous in given individuals, attributing this change to natural selection.

The examples cited make it obvious that those rarely fossilized soft parts of clam shrimps provide an insight into anatomical similarities with living forms and show significant differences too. Unfortunately, the rarity itself prevents paleontologists working with fossil clam shrimps from relating their material directly to living forms described on the basis of soft-part anatomy.

Modification and specialization of appendages appears to have been achieved in the conchostracans by Carboniferous time. Since the fossil record of this group at present extends back to the Devonian, we can surmise that many of the evolutionary trends inferred from fossil valves in younger beds date back at least to Devonian time.[1]

ONTOGENY

GENERAL FEATURES

Several studies on the life cycles of living conchostracans are available (Sars, 122; Berry, 9; Mattox, 86; and others). The reported investigations deal with three distinct genera, *Limnadia, Eulimnadia,* and *Caenestheriella.* A resumé of essential findings is helpful to paleontologists in understanding the probable rate and mode of growth of the animals represented by fossil conchostracan carapaces.

The body length at time of hatching of the nauplii is 0.25 mm. for *Limnadia lenticularis* and 0.37 mm. for *Caenestheriella gynecia.* Comparative figures are lacking for *Eulimnadia stoningtonensis*, although we know that the end of the first 24 hours it attains a body length of 0.75 mm. At hatching, no shell is discernible in any of these species.

In *Limnadia,* the earliest rudiments of a shell and the first appearance of the six foremost legs—all encased in larval skin—occur at a body length of 0.65 mm. At 96 hours after hatching, *Caenestheriella gynecia* has a body length of 1.1 mm. and a shell of 1.5 mm. in length. *Eulimnadia stoningtonensis* starts to develop its carapace on the third day. The carapace is minutely punctate, suggesting that punctation of the adult carapace, at least in some genera, is a larval characteristic.

CONCHOSTRACAN EGGS

An excellent literature is now available on experimental studies of conchostracan eggs. Studies make clear that conchostracan eggs when kept dry, moist, or frozen, can hatch and all at approximately the same time (85). Kelley (57) noted a variation in number of eggs produced by females according to age of individuals. He also observed that once egg production begins, as few as 15 to 20 eggs may be shed at each ecdysis. Mattox & Velardo (1950) reported that for *Caenestheriella gynecia,* the egg masses were attached to the exopodite of the tenth swimming appendage in groups of 35 to 120. During ecdysis, the cuticle (or skeleton) is cast off and with it the attached egg masses. Kelley found that if feeding conditions are satisfactory, ecdysis occurs every second or third day but diminishes toward the end of life.

These experimental data are of interest to paleontologists since fossil clam shrimp eggs have been reported (33, 53, 58). It also has important bearing on such items as population density, number of generations per season, temperature of the water, and other related factors pertaining to clam-shrimp-bearing beds in the rock column. In turn, these sorts of data can help in elucidating paleoecology.

My study of the eggs of *Cyzicus mexicanus* was directed toward obtaining details of special interest to a paleontologist. Since conchostracan eggs, when fossilized, are found in association with clam-shrimp valves, it is useful to know how, in the living condition, these eggs are placed in the valves. Egg masses were found to lie below the dorsal margin behind the umbo in a tilelike pavement of white-brownish spheres about 0.1 mm. in diameter. They were separated by a darker mucoid-type matrix so that no two eggs were in contact.

A count of four layers of eggs in a rectangle 3.3 mm. long by 3 mm. wide was recorded for each valve. A few eggs were observed that stretched in a stringlike arrangement beyond the roughly rectangular or ovate egg mass. Under high power, the eggs were found to have a thin, fibrous, translucent pellicle or outer sheath and an inner dense yolk. Measurements of several eggs yielded an average diameter of 0.13 mm.

ECOLOGY AND PALEOECOLOGY

A chief habitat of living conchostracans is small, temporary, alkaline, inland ponds. These are generally no larger than an acre

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[1] Cf. P. Tasch, 1963, *Evolution of the Branchiopoda:* Harvard Univ., Museum Comp. Zoology, Spec. Publ. 1963, Chapter XI.

in extent (107) and mostly much smaller. Flood-plain pools (Missouri River, for example), roadside ditches, puddles in cultivated fields, and almost any shallow depression filled with water are more often than not likely to have a brood of conchostracans (144, 146, 147). They have also been reported from spring water (102), along margins of certain large lakes (e.g., Africa) and on coastal salt flats (e.g., Brazil).

The pH of waters inhabited by clam shrimps ranges from 7 to 9.

Some living species are known from both fresh and brackish water *(les eaux saumâtres)* environments. These include *Cyzicus (=Isaura) cycladoides* JOLY, *Cyzicus (=Isaura) jonesi* (BAIRD), *Lynceus rotundus* THIELE, and *Leptestheria vieligera* THIELE (83, p. 8).

Conchostracans are found in temporary pools at all altitudes and are cosmopolitan in distribution. The latter fact can be explained by the properties of the resting egg, which can withstand long desiccation of the pools so as subsequently to become dispersed by wind or water. This, in turn, can explain the world-wide distribution of fossil estheriid conchostracans.

According to PENNAK (107, p. 338), with rare exceptions, a pond never contains more than one species of a particular genus at a time. Collections from some 500 ponds in Kansas and Oklahoma by one of my colleagues revealed the presence of only a single conchostracan species *(Cyzicus mexicanus)*. This contrasts with fossil occurrences of distinct species of the same genus obtained from the same horizon (and hence presumably in life, occupants of the same water body or closely adjacent water bodies). A possible explanation, if we grant that lumping might reduce the number of distinguished fossil species, could be that in succeeding years a given pond of the geologic past was inhabited by different species. The increment of sediment during a geologically negligible period of time would be undetectable in the rock record, so that different species would occur apparently on the same time plane though actually having existed in different years.

In this regard, it should be stressed that several living conchostracan genera commonly occur side by side in the same pool, as in Australia (132, p. 458), in which species of *Limnadopsis, Lynceus,* and *Cyzicus* occur together. Fossil leaiid and estheriid valves are not uncommon on the same bedding plane in both Pennsylvanian and Permian beds sampled by me and others. Several distinct genera bearing spines on the initial (or larval) valve were found together on the same bedding planes in the Wellington Formation of Kansas (142). Also, different phyllopod orders are not uncommon in the same body of water. GAUTHIER (83, p. 11), for example, has reported the notostracan *Triops* (=*Apus*), the anostracan *Streptocephalus,* and the conchostracan *Leptestheria,* in the same Algerian pond.

A variety of nonmarine and marine forms are found in association with conchostracan fossils. These include *Unio, Anodonta, Trigonia, Gervillia, Spirorbis, Anthracomya, Lingula,* and *Limulus*. An association with ammonoids has also been reported (98, p. 57). Estheriid valves have been found in coelocanth coprolites or in beds containing coelocanth remains. They have been reported in typical marine strata bearing trilobites and in association with insects and plants. The fossil notostracan *Triops* has been found in the same beds as *Cyzicus* and *Leaia*.

My study of Wellington deposits (Lower Permian) in Kansas and Oklahoma has revealed that faunal and floral associates included xiphosurans, ostracodes, eurypterids (143, 146, 147), numerous insect orders (including many extinct orders) (147), fresh- and brackish-water mollusks (clams and snails), fish, and a considerable number of plant fossils in some places, largely consisting of carbonized wood, seed coats, leaves, and charophytes. Fishes are represented in some deposits by teeth attached to jaws, scales, and fragments of other parts. Segmented worms are represented by burrows. A microflora of pollen and spores has also been found (147).[1]

It may be observed that test tubes placed in some modern ponds bearing clam shrimps have yielded samples of copepods, cladocerans, numerous protozoans, and algae, as well as numerous water beetles and insect larvae. Some or all of these are present before, during, or after the occupancy of clam shrimps. The most abundant large crustacean in most modern ponds sampled by the writer and colleagues is the crayfish. Snails and more infrequently clams are prominent faunal associates of living clam shrimps.

Association with marine forms has led one investigator (58, p. 52) to speculate as to whether estherians did not originally

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[1] Other palynomorphs and protists have since been reported and include hystrichosphaerids and dinoflagellates (Tasch, P., 1962, Internatl. Palynology Conf., Tucson, Ariz., abstracts).

live in a shallow sea. Several other explanations that eliminate need to postulate a unique event might explain such occurrences: (1) existence of temporary pools close to ancient fluctuating shore lines or lagoons and invasion of the sea over such

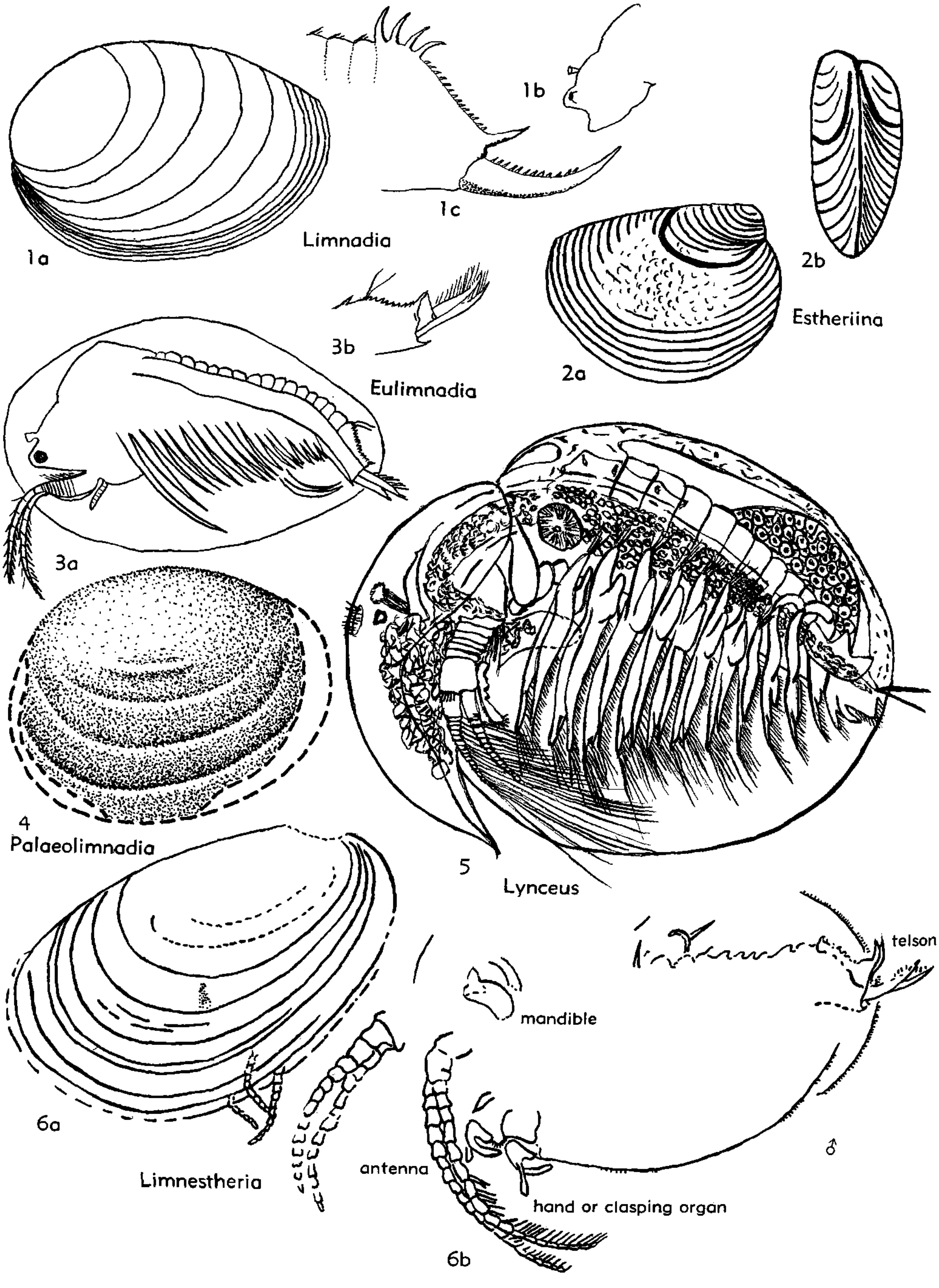

FIG. 48. Lynceidae *(5)*; Limnadiidae (Limnadiinae) *(1,3)*, (Estheriininae) *(2,4,6)* (p. *R*149-*R*150).

an area, mixing the faunas, and (2) dispersal of estheriid eggs to near-shore marine or estuarine area.

The close proximity of shales and marls containing fossil estheriids to fossiliferous marine beds or beds bearing casts of salt crystals favors the first explanation, whereas the second is supported by extensive distribution of estheriids. A third possibility could be torrential flooding that covered pools so as to form a widespread sheet of water which then ran off to the sea, mingling the faunas. Flooding of modern rivers definitely accounts for the distribution of some living clam-shrimp species (57).

As noted above, living conchostracans can withstand brackish water and it is in zones of brackish-water deposits that the mixture of the fresh-water and marine forms in question probably occurred. A good fossil example is the genus *Limnestheria* of the Kilkenny Coal Measures of Ireland. Here, the almost black carbonaceous shales containing the conchostracan fauna grade downward into the so-called "fleck-rock" which grades laterally eastward into marine (goniatite) shales. An ancient delta is suggested by these relationships and the conchostracan fauna is thought to have lived in an estuarine environment (158).[1]

Suborder LAEVISCAUDATA Linder, 1945

[=*nom. transl.* TASCH, herein (*ex* "tribe" Laeviscaudata LINDER, 1945)]

Shell more or less globular, without umbones, with very few lines of growth or lacking them; connection between 2 halves in groove; terminal claws rudimentary without dorsolateral spines (70). *L.Cret.-Rec.*

Family LYNCEIDAE Stebbing, 1902 (1896)

[Lynceidae STEBBING, 1902 (March), based on *Lynceus* LINNÉ, 1785, having "won general acceptance, is to be maintained in the interests of stability" (Zool. Code, 1961, Art. 40,a), cited with its own author and date, but it "takes the date of the rejected name of which it is to be considered the senior synonym" (Art. 40,b), thus replacing Limnetidae SARS, 1896, based on *Limnetis* LOVÉN, 1846] [=superfamily Lynceoidea STEBBING, 1902 (*nom. transl.* NOVOZHILOV, 1960); Lynceidae SAYCE, 1902 (August), p. 257; Paleolynceiinae TASCH, 1956 (*nom. nud.*)].

Valves lacking growth lines; head not entirely covered by carapace. Antennules 2-segmented; only the first pair of postcephalic limbs prehensile in males. *L.Cret.-Rec.*

Lynceus O. F. MÜLLER, 1785 [**L. brachyurus*; OD] [=*Limnetis* LOVÉN, 1846 (75)]. Head beak-shaped in profile; rostrum broad in male, pointed in female; flagella of antennae 16-segmented; claw of claspers regularly and smoothly curved, sickle-shaped. *L.Cret.-Rec.,* N.Am.(Can.-USA)-Eu.-Asia.——FIG. 48,*5*. **L. brachyurus,* USA(Ill.); ♀ left valve cut away to show head, trunk, appendages, egg masses, ×25 (107). [Fossil species: *L. stschukini* CHERNYSHEV, 1940, =*Paleolynceus* TASCH, 1956 *(nom. nud.), L.Cret.,* USSR(Transbaikal) (25).]

Suborder SPINICAUDATA Linder, 1945

[*nom. transl.* TASCH, herein (*ex* "tribe" Spinicaudata LINDER, 1945)]

Laterally compressed, with or without umbones and with many lines of growth; connection between halves elevated; telson with dorsolateral spines and with large terminal claws (70). *L.Dev.-Rec.*

Superfamily LIMNADIOIDEA Baird, 1849

[*nom. transl.* TASCH, herein (*ex* Limnadiadae BAIRD, 1849)]

Valves characterized by prominent umbo. *Carb.-Rec.*

The carapaces of several genera of the Limnadioidea exhibit well-marked curvature of the posterior margin near the dorsal line, thus producing a distinctive outline. Branchiopod bivalves of this type are designated as **limnadiiformes.** Such recurvature is observed in some other superfamilies (e.g., Leaioidea, Vertexioidea) of the Spinicaudata and may result in a spinous projection above the dorsal margin of the carapace (e.g., *Keratestheria,* Ipsiloniidae).

Family LIMNADIIDAE Baird, 1849

[*nom. correct.* TASCH, herein (*pro* Limnadiadae BAIRD, 1849, p. 86, *nom. imperf.*, Zool. Code, 1961, Art. 29)] [=Limniadiidae BURMEISTER, 1843, *(nom. null.)*]

Carapace broadly oval, compressed, with variable number of concentric growth lines around prominent umbo, mid-dorsal surface of head bearing pedunculate, pyriform frontal organ. *Carb.-Rec.*

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[1] Present evidence suggests transition from an original marine to a fresh water environment during the Carboniferous. With regard to conchostracans several such events, occurring in pulses, may have taken place at different times (cf. P. TASCH, 1963 (Harvard Univ., Museum Comp. Zoology, Spec. Publ. chapter XI).

Subfamily LIMNADIINAE Baird, 1849

[*nom. transl.* TASCH, herein (*ex* Limnadiadae BAIRD, 1849, *nom. imperf.*)]

Characterized by distinctive frontal organ. *Rec.*

Limnadia BRONGNIART, 1820 [**Monoculus lenticularis* LINNÉ, 1761; OD]. Shell broad, ovate; antennules shorter than scape of antennae, flagella of antennae with 12 to 14 segments; 22 pairs of legs. *Rec.*, cosmop.——FIG. 48,*1*. **L. lenticularis* (LINNÉ); Mass. (Woods Hole); *1a*, left valve, enlarged; *1b*, pyriform frontal organ on dorsal surface of head, ×4 (87); *1c*, telson and cercopods, enlarged (129).

Eulimnadia PACKARD, 1874 [**E. agassizii*; OD]. Carapace narrow, ovate; growth lines ranging from 1 to 12; conspicuous ventral spine on telson at base of terminal spines (cercopods); 18 pairs of legs; antennules variable in length, flagella of antennae with 9 segments. *Rec.*, USA-W.Indies-Mexico.——FIG. 48,*3*. **E. agassizii*, USA (Mass.); *3a*, left valve cut away to show soft-part anatomy, ×6; *3b*, telson, enlarged (102).

Subfamily ESTHERIININAE Kobayashi, 1954

[=Estheriinidae KOBAYASHI, 1954 (*nom. transl.* NOVOZHILOV, 1957, *ex* Estheriininae KOBAYASHI, 1954); Paleolimnadiinae TASCH, 1956]

Valves with large prominent umbo resembling living *Limnadia*. Presence and morphology of frontal organ. unknown. *Carb.-L.Cret.*

Estheriina JONES, 1897 [**E. bresiliensis*; OD] [=*Sinoestheria* CHANG, 1957]. Valves more convex for limited area in umbonal region (neanic stages) than lower down in ventral region; growth lines sharp and widely spaced on convex portion but more numerous and closer together on flat marginal area. *L.Cret.(Bahian)*, Brazil.——FIG. 48,*2*. **E. bresiliensis*; *2a*, right valve, ×6; *2b*, ventral view, ×5 (54).

Bilimnadia NOVOZHILOV, 1957 [**Estheria anabarensis* (NOVOZHILOV), 1946; OD] [Inadequately documented; doubtful]. *M.Trias.*, SW.Asia.

Leptolimnadia NOVOZHILOV, 1954 [**L. rhombiformis*; OD]. [Inadequately documented; doubtful.] *L.Cret.*, NE.Asia(Sib.-Mongolia).

?**Limnestheria** WRIGHT, 1920 [**L. ardra*; OD]. Carapace oval, punctate, about 10 growth lines surrounding large, smooth, umbonal area. Antennae, trunk limbs, telson of estherian type; first one (158) or two (87) pairs of trunk limbs modified as claspers in males. *Carb.(Kilkenny Coal Measures)*, Eire.——FIG. 48,*6*. **L. ardra*, Ardra; *6a*, right valve, ×7; *6b*, male with modified hooked appendages, ×10 (158).

Notocrypta NOVOZHILOV, 1954 [**N. altissima*; OD] [Inadequately documented; doubtful]. *U.Cret.*, NE.Asia(Mongolia).

Palaeolimnadia RAYMOND, 1946 [**Estheria wianamattensis* MITCHELL, 1927; OD] [=*Paleolimnadia* TASCH, 1956]. Relatively long oval carapace, large smooth umbonal region, and few growth lines. *Trias.(Wianamatta Series)*, Australia (New S. Wales).——FIG. 48,.*4* **P. wianamattensis* (MITCHELL); left valve, ×21 (111).

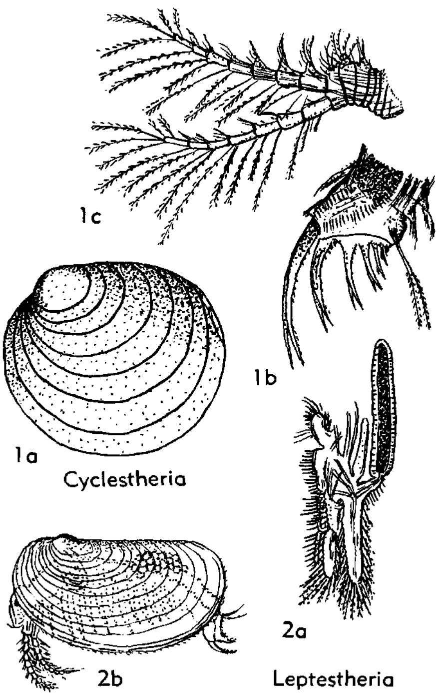


FIG. 49. Cyclestheriidae *(1)*; Leptestheriidae *(2)* (p. *R*150-*R*151).

Pseudolimnadia NOVOZHILOV, 1954 [**P. remota*; OD]. [Inadequately documented; doubtful]. *L. Cret.*, NE.Asia(Sib.-Mongolia).

Trigonlimnadia NOVOZHILOV, 1954 [**T. trigonoides*; OD]. [Inadequately documented; doubtful.] *L.Cret.*, NE.Asia(Mongolia).

Family CYCLESTHERIIDAE Sars, 1899

Shell subspherical, with distinct umbonal region. Head strongly compressed anteriorly; surrounded by thin crest, rounded in front. Eyes united in single organ removed from anterior edge of head. Antennules simple cylindrical, neither articulate nor lobular; antennae stout with upper branch and part of scape bearing strong recurved spines; 16 pairs of legs with only first pair prehensile in males. *Rec.*

Cyclestheria SARS, 1887 [**Estheria hislopi* BAIRD, 1859; OD]. Characters of family. Caudal plate with dorsal spines strongly developed (121). *Rec.*, Australia-India-E.Afr.-Brazil?.——FIG. 49,*1*. **C.*

hislopi (BAIRD), India; *1a*, left valve, enl.; *1b*, caudal plate from right side, enl.; *1c*, right antenna from inner side, enl. (121).

Family LEPTESTHERIIDAE Daday, 1923

Rostrum at anteroventral extremity armed with conspicuous spine. *Rec.*

Leptestheria SARS, 1898 [**L. siliqua*; OD]. Shell much compressed, oblong, umbones very small. Upper lappets of exopodites on 10th and 11th pairs of branchial legs in female transformed to thick, sausage-shaped appendages for support of egg-mass (124). *Rec.*, Eu.-N.Am.-S.Am.-Afr.——FIG. 49,*2*. **L. siliqua*, S.Afr.(Capetown); *2a*, legs of 10th pair showing peculiarly transformed upper lappet of expodite, enlarged; *2b*, egg-bearing female, ×12 (124).

Superfamily CYZICOIDEA Stebbing, 1910

[*nom. transl.* NOVOZHILOV, 1958 (*ex* Cyzicidae STEBBING, 1910)]

Lacking serrate dorsal margin or radial ribs on valves, or large umbonal area. *L. Dev.-Rec.*

Family CYZICIDAE Stebbing, 1910

[=*emend.* BARNARD, 1929] [=Estheriidae SARS, 1900; Caenestheriellidae DADAY, 1913; Lioestheriidae RAYMOND, 1946; Isauridae BOCK, 1953; Bairdestheriidae NOVOZHILOV, 1954; Eocyzicinae (subfamily) *nom. transl.* NOVOZHILOV, 1954 (*ex Eocyzicus* DADAY, 1915); Aquilonoglyptidae NOVOZHILOV, 1958; Kontikiidae NOVOZHILOV, 1958]

Rostrum apex without spine. Shell thin, pellucid, laterally compressed, outline variable from ovate and elliptical to subrectangular, with numerous growth lines. Ornamentation distinct and variable, ranging from polygonal pattern in interspaces to longitudinal striae that may anastomose. *L.Dev.-Rec.*

Cyzicus AUDOUIN, 1837 [**Limnadia tetracera* KRYNICKI, 1830, p. 176; OD]. Rostrum of male broadly spatulate in profile; rostrum of female terminating acutely; flagella of antennae with 16 to 22 segments (2). *L.Dev.-Rec.*, cosmop.

C. (Cyzicus) [=*Estheria* RUEPPELL, 1837 (*non* ROBINEAU-DESVOIDY, 1930); *Isaura* JOLY, 1841, (p. 1068).] Rostrum and segmentation of flagella of antennae as in genus. *Rec.*, cosmop.——FIG. 50,*1a,b*. *C. (C.) cycladoides* (JOLY), Eu.(Fr.); *1a*, mating pair, ×4 (83); *1b*, right valve with appendages, ×3 (52).——FIG. 50,*1c*. **C. (C.) tetracera* (KRYNICKI), USSR; telson and cercopods, enl. (129).——FIG. 50,*1d*. *C. (C.) mexicanus* (CLAUS), USA; section through entire animal (front part of thorax), enl. (102).

C. (Euestheria) DEPÉRET & MAZERAN, 1912 [**Posidonia minuta* VON ZEITEN, 1833, p. 453; SD RAYMOND, 1946, p. 238] [=*Estheria (Euestheria)* DEPÉRET & MAZERAN, 1912; *Palaeestheria* DADAY, 1915; *Estherites* KOBAYASHI & HUZITA, 1941; *Bairdestheria* RAYMOND, 1946; *Estheriellites, Howellisaura* BOCK, 1953; *Indoestheria, Palaeoorthothemos, Paleoleptestheria, Pseudoasmussia, Rossoestheria, Trigonestheria, Trigononorassaia* NOVOZHILOV, 1954; *Concherisma* NOVOZHILOV, 1956; *Aquilonoglypta* NOVOZHILOV, 1958; *Sphaerorthothemos* NOVOZHILOV, 1960]. Carapace generally ovate but with wide variation in shape, size, and ornamentation. Characterized by pattern of minute polygons in spaces between growth lines. *L.Dev.-U.Cret.*, cosmop. (36).——FIG. 50,*4*. **C. (E.) minuta* (VON ZEITEN), U.Trias., G.Brit.; *4a*, left valve, ×5; *4b*, detail of polygonal ornamentation, ×45 (111).

C. (Lioestheria) DEPÉRET & MAZERAN, 1912 [**Estheria (Lioestheria) lallyensis* DEPÉRET & MAZERAN, 1912, p. 167; OD] [=*Estheria (Lioestheria)* DEPÉRET & MAZERAN, 1912; *Estheria (Diaplexa), Estheria (Diaphora), Estheria (Polygrapta)* NOVOZHILOV, 1946; *Pseudestheria, Lioestheria* (DEPÉRET & MAZERAN), 1912; *Bairdestheria* RAYMOND, 1946; *Liograpta, Brachygrapta, Rhombograpta, Pseudopolygrapta* NOVOZHILOV, 1954; *Sphaerograpta* NOVOZHILOV, 1958]. Carapace variable in size and shape, though generally ovate; numerous extremely close-set, irregular, and fine concentric growth lines; intervales with fine sculpture, dominantly punctate and granulate—latter commonly expressed as hachure-type markings (longitudinal striae); polygonal mosaic sculpture of *C. (Euestheria)* completely absent, irregular, or feebly expressed. *L.Dev.-L.Cret.*, cosmop. (36).——FIG. 50,*6a*. *C. (L.) raaschi* (RAYMOND), Perm.(Leonard.), USA(Okla.); numerous costellae with narrow, minutely punctate, intervales between them, ×12 (111).——FIG. 50,*6b,c*. *C. (L.) sibirica* (NOVOZHILOV), Perm.(Tartar.), USSR(Lower Toungouska River); *6b*, right valve, ×8; *6c*, detail, long. striae, ×64 (98).

Caenestheria DADAY, 1913 [**Estheria sarsii* SAYCE, 1902; SD TASCH, herein (based on first named nominal species in Hungarian edition, 1913)]. Occipital angle (notch) of head is brief in both sexes, more or less broadly rounded. *Rec.*, cosmop.——FIG. 50,*2*. **C. sarsii* (SAYCE), Australia; *2a*, right valve, male; *2b*, male, head, enl. (30).

Caenestheriella DADAY, 1913 [**C. variabilis*; SD RAYMOND, 1946, p. 225] [=*Opsipolygrapta* NOVOZHILOV, 1954]. Rostrum extended, compressed, and acutely terminated in both sexes, and with conspicuous, deeply cleft occipital notch. *Rec.*,

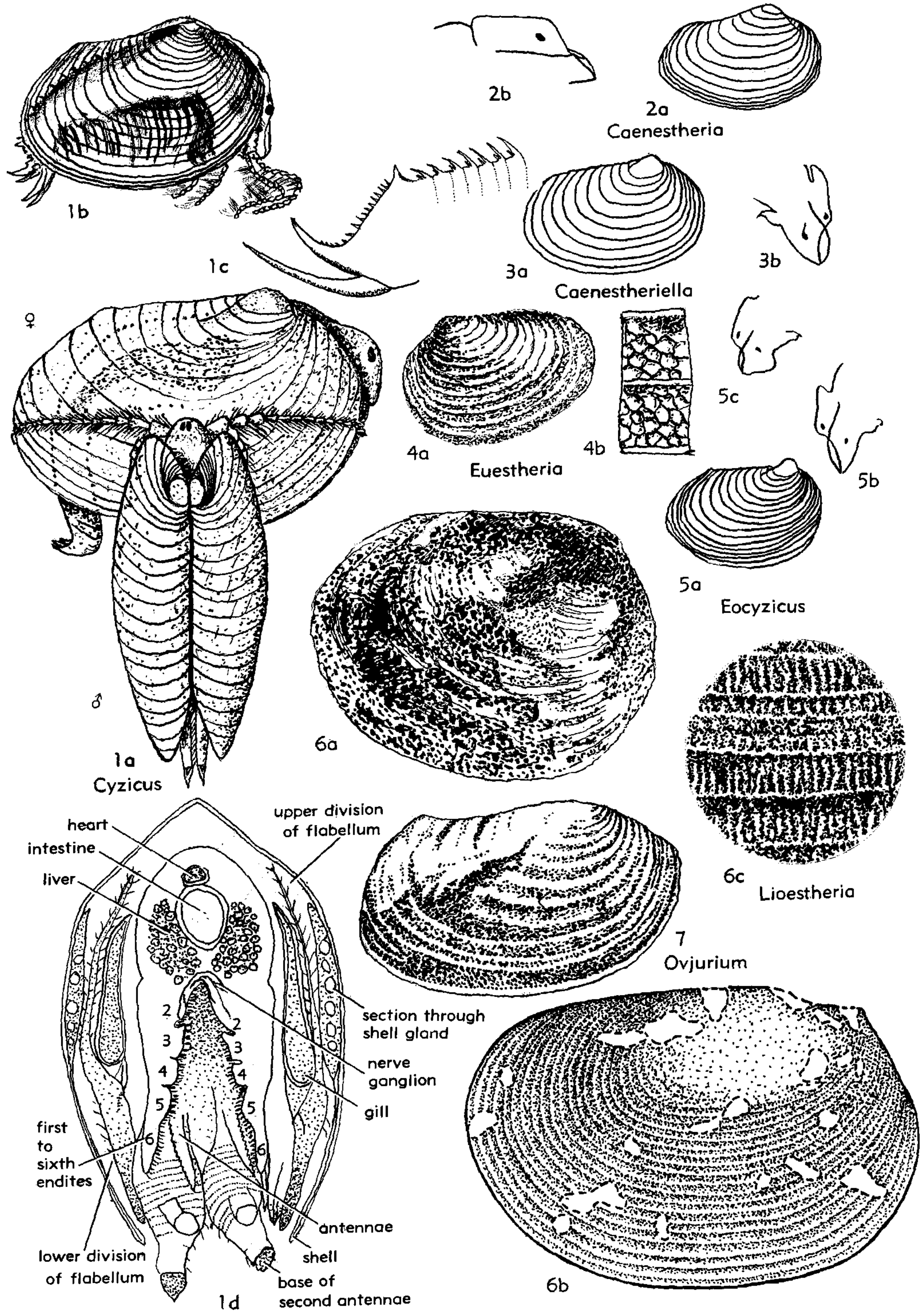


Fig. 50. Cyzicidae (p. *R*151, *R*153).

cosmop.——FIG. 50,*3*. **C. variabilis,* Hung.; *3a,* male, right valve; *3b,* female, head showing rostrum and occipital notch, enl. (30, 31).

Eocyzicus DADAY, 1913 [**Estheria digueti* JULES RICHARD, 1895, p. 103; SD TASCH, herein (based on first-named nominal species in Hungarian edition, 1913)]. Rostrum of female terminating acutely but male rostrum spatuliform in side view; occipital notch shallow and rounded. *Rec.,* N.Am.-Australia - India - E. Afr. - ?Brazil.——FIG. 50,*5*. **Eocyzicus digueti* (RICHARD), USA(Calif.); *5a,* male or female valve; enlarged; *5b,* female rostrum; *5c,* male rostrum, enl. (30).

Kontikia NOVOZHILOV, 1958 [**Estheria wianamattensis* MITCHELL, 1926; OD]. [Inadequately documented; doubtful.] *U.Trias.,* Australia.

Ovjurium NOVOZHILOV & VARENTSOV, 1956 (p. 672) [**O. ubsanuri*; OD]. Characterized by elongate valves with parallel anterior and posterior margins; length of valves equal to height; irregular alveolar ornamentation. *M.Dev.(Givet.),* DANSSR(Tuva).——FIG. 50,*7*. **O. ubsanuri,* Touva; right valve, ×9 (165).

Ragozinia NOVOZHILOV, 1958 [**Estheria evenkensis* LYUTKEVICH, 1938 (=*R. leonidi* NOVOZHILOV, 1958; OD]. [Inadequately documented; doubtful.]

Rossokontikia NOVOZHILOV, 1958 [**R. tikhomirovi*; OD]. [Inadequately documented; doubtful.] *U. Dev.(Frasn.),* USSR(Povolzhya).

Sedovia NOVOZHILOV, 1958 [**S. fecunda*; OD]. [*Inadequately documented; doubtful.] *M.Trias. (Anis.),* ArcticO.(Laptevykh Sea).

Sinokontikia NOVOZHILOV, 1958 [**S. youngi*; OD]. [Inadequately documented; doubtful.] *M.Trias. (Anis.),* S. China.

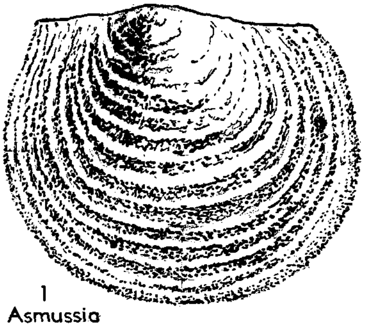
Tigjanium NOVOZHILOV, 1958 [**T. dorofeevi*; OD]. [Inadequately documented; doubtful.] *M.Trias. (Anis.),* ArcticO.(Laptevykh Sea).

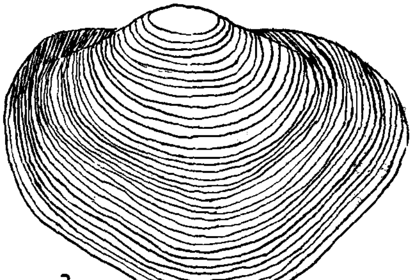
Turfanograpta NOVOZHILOV, 1958 [**T. chowmincheni*; OD]. Longitudinal striae in intervals and short, curved spines about 0.05 mm. apart on ventral margin of each interval. [Similar spines in some living conchostracans are more closely spaced.] *L.Cret.(Tougoulouk Ser.),* W.China(Sin-Kiang, Tourfan Basin).——FIG. 51,*3*. **T. chowmincheni*; *3a,* left valve, ×10; *3b,* detail showing curved spines, ×120 (99).

Ubsanuria NOVOZHILOV & VARENTSOV, 1956 [**Trigonestheria kyzylensis* NOVOZHILOV, 1954; OD]. [Inadequately documented; doubtful.] *M.Dev. (Givet.),* USSR(Tuvinsk).

Ujgurokontikia NOVOZHILOV, 1958 [**U. chaoi;* OD]. [Inadequately documented; doubtful.] *U.Jur.,* S. China.

Vilegenia NOVOZHILOV, 1953 [**D. tuberculata* NOVOZHILOV, 1946; OD]. [Inadequately documented; doubtful.] *M.Trias.(Anis.),* ArcticO. (Laptevykh Sea).


1
Asmussia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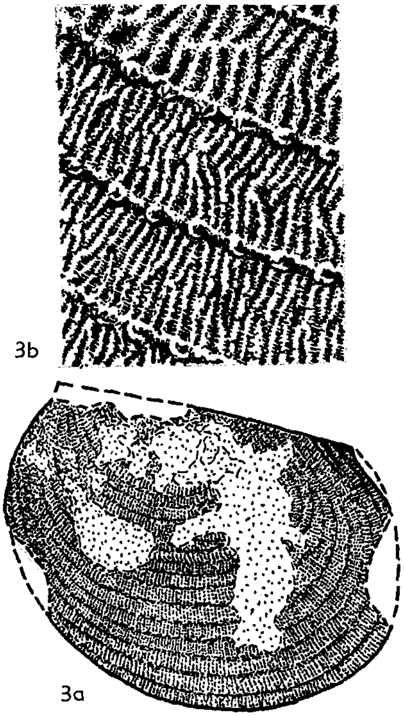
Beligum



Turfanograpta

FIG. 51. Cyzicidae *(3)*; Asmussiidae (Asmussiinae) *(1,2)* (p. R153-R154).

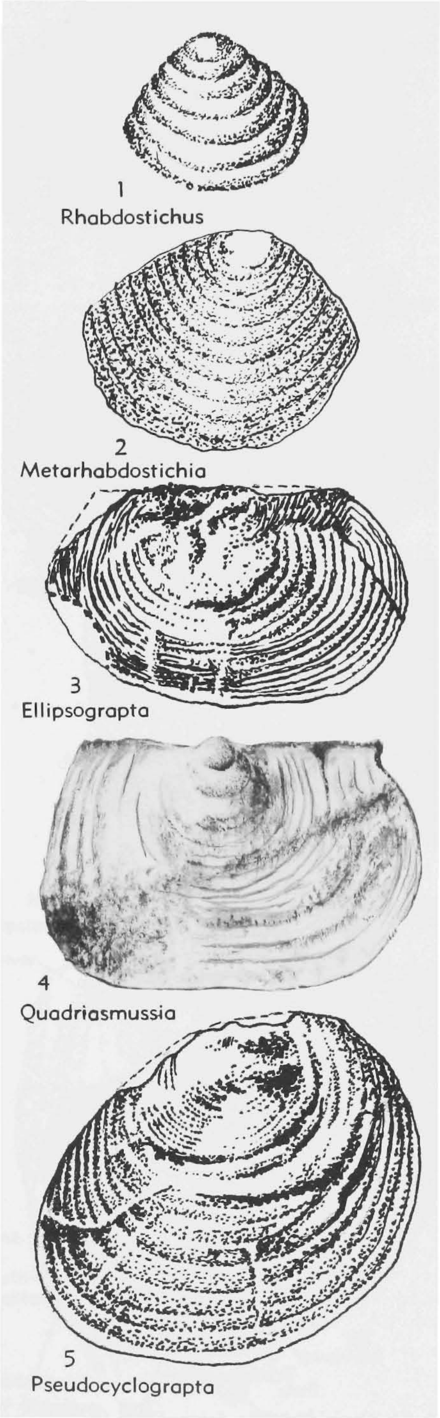


FIG. 52. Asmussiidae (Asmussiinae) (p. *R*154-*R*155).

Family ASMUSSIIDAE Kobayashi, 1954

[*nom. transl.* NOVOZHILOV, 1958 (*ex* Asmussiinae KOBAYASHI, 1954] [Rhabdostichidae RUSCONI, 1946; Cyclestherioidinae KOBAYASHI, 1954; Asmussidae TASCH, 1956 (syn. homonym); Glyptoasmussiidae NOVOZHILOV, 1957]

All members of family characterized by generally straight hinge line; carapace shape and beak position variable; ornamentation ranging from hachure-type to alveolar. *L. Dev.-U.Cret.*

Subfamily ASMUSSIINAE Kobayashi, 1954

[=*emend.* TASCH, herein] [=Asmussiinae NOVOZHILOV, 1954 (synhomonym); Loxomegaglyptinae NOVOZHILOV, 1958]

Subcentral beaks generally rising slightly above dorsal margin; carapace outline varying from subovate to subcircular or subquadrate. *L.Dev.-U.Cret.*

Asmussia PACHT, 1849 [**A. membranacea*; OD] [=*Posidonomya* PACHT, 1852 (*non* BRONN, 1834); *Estheria* JONES, 1856 (*non* ROBINEAU-DESVOIDY, 1830; *nec* RUEPPEL, 1837); *Erisopsis, Orthothemos* RAYMOND, 1946; *Loxomicroglypta* NOVOZHILOV & VARENTSOV, 1946; *Cyclograpta* NOVOZHILOV, 1954; *Levenḳia* NOVOZHILOV, 1955; *Glyptoasmussia* NOVOZHILOV & VARENTSOV, 1956; *Loxopolygrapta, Loxomegaglypta* NOVOZHILOV, 1958]. Carapace subovate, hinge line straight, beak subcentral, number of concentric growth lines variable, ranging from 13 to 30 or more; interspaces bearing reticulate pattern. *L.Dev.-U.Cret.*, Eu. (G. Brit.-USSR)-Asia(China)-N. Am.(USA). ——FIG. 51,*1*. **A. membranacea,* Dev., Livonia; left valve, ×12 (53).

Beligum NOVOZHILOV, 1958 [**B. doroshḳoi*; OD]. Irregularly subovate valves showing dual curvature, that is, of both anterior and posterior ventral portions; beak median, umbo rising above dorsal margin. *U.Dev.(Frasn.)*, USSR(Khakassie, Bereck River).——FIG. 51,*2*. **B. doroshḳoi*; left valve, ×7 (98).

Ellipsograpta CHANG, 1957 [**E. elliptica*; OD]. Carapace elliptical, dorsal margin straight; both anterior and posterior margins well rounded; umbo subcentral; ornament of hachure-type or of small radially aligned tubercles. *M.Cret.* or *U.Cret.*, China(NW.Heilungkiang).——FIG. 52,*3*. **E. elliptica*, Nenkiang Sh.; left valve, ×10 (23).

Metarhabdostichia NOVOZHILOV, 1958 [**M. tverdoḳlebovi* (=*Estheria meta* NOVOZHILOV, 1946); OD]. Like *Rhabdostichus* but with valves 10 to 15 times larger. *L.Trias.*, USSR(Tigrian River, Sea of Laptev).——FIG. 52,*2*. **M. tverdoḳlebovi*; right valve, ×10 (98).

Pseudocyclograpta CHANG, 1957 [**P. convexa*; OD]. Carapace subcircular, with straight or slightly arched dorsal margin and central or subcentral umbo, chiefly characterized by swollen umbonal region, bearing more numerous growth lines than rest of valve; ornament of hachure type. *M.Cret.*

or *U.Cret.,* China(Nengkiang).——Fig. 52,*5*. **P. convexa,* Nenkiang Sh.; right valve, ×9 (23).

Quadriasmussia Kobayashi, 1954 (*emend.* Tasch, 1955) [**Estheria hercynica* Kummerow, 1939; OD]. Carapace subquadrate, expanded ventrally, hinge line straight; prominent convex umbonal area (neanic stage) tapering to subrounded beak, whole area resembling complete valve of *Rhabdostichus pulex* in number of growth lines, shape and size; adult portion of valve gently undulating to flat. *L.Carb.(Culm),* Eu.(Ger.).——Fig. 52,*4*. **Q. hercynica* (Kummerow), Harz Mtns.; left valve, ×12 (62).

Rhabdostichus Raymond, 1946 (*emend.* Tasch, 1955) [**Estheria pulex* Clarke, 1882; OD] [=*Estheria* Clarke, 1882 (*non* Robineau-Desvoidy, 1830; *nec* Rueppell, 1837; *nec* Jones, 1856); *Cyclestherioides* Raymond, 1946; *Brachysteria* Novozhilov, 1954; *Ausmussiella* Novozhilov, 1955; *Cyclotunguzites* Novozhilov, 1958]. Carapace subovate to subcircular, with rounded subcentral umbonal beak and few, relatively widely spaced concentric growth lines. [One or more species of this genus (e.g., *R. pulex*) may represent the neanic stage of other members of the family, as suggested by unusually small size and general characteristics.] *L.Dev.-M.Cret.,* N.Am.(USA)-S.Am.-USSR.——Fig. 52,*1*. **R. pulex* (Clarke), M.Dev.(Hamilton), USA(N.Y.); left valve, ×48 (26).

Ulugkemia Novozhilov, 1955 [**Estheria(?) sinuata* Lyutkevich, 1929; OD] [=*Rhodendorfium* Novozhilov, 1955; *Tshuvashium* Novozhilov, 1958]. Carapace with concavity at anterior, posterior or ventral margins of valves; ornamentation finely alveolar. *M.Dev.(U.Givet.),* N.Asia(USSR).——Fig. 53,*3*. *U. sinuata* (Lyutkevich), Sib.; left valve, ×6 (78).

Wetlugites Novozhilov, 1958 [**W. pronus*; OD]. Lower portion of valve semiovate, upper portion trapezoidal; dorsal margin straight; initial valve with berry-shaped projection above dorsal margin which is anteroterminal in position; ornament alveolar. *L.Trias.,* USSR(Viatka Valley).——Fig. 53,*5*. **W. pronus,* right valve, ×15 (98).

Subfamily TORGALYKIINAE Tasch, 1961

Beaks terminal or nearly terminal, not rising above dorsal margin; valve shape variable. *Dev.-U.Jur.*

Torgalykia Novozhilov, 1955 [**T. ovjurensis*; OD]. Valves rounded, irregular; beak terminal. *Dev.,* USSR(Touva Region).——Fig. 53,*4*. **T. ovjurensis,* Torgalyk River; left valve, ×6 (164).

Eremograpta Novozhilov, 1958 [**Cyclograpta (s.s.) insperata* Novozhilov, 1954; OD]. Shape of valves in form of pouch or almost rounded. *U.Jur.,* E.Asia(Mongolia).——Fig. 53,*1*. **E. insperata* (Novozhilov); left valve, ×2 (95).

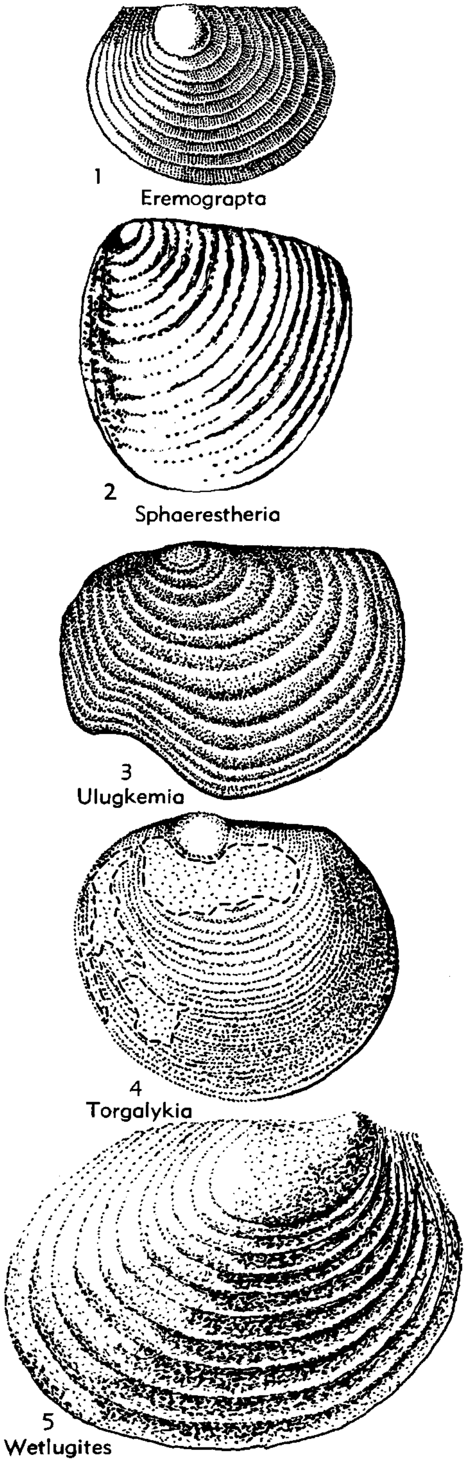


Fig. 53. Asmussiidae (Asmussiinae) *(3,5)*, (Torgalykiinae) *(1,2,4)* (p. *R*155-*R*156).

Estheridium Novozhilov, 1958 [**E. parvum*; OD]. [Inadequately documented; doubtful.] *U.Perm. (Tatar.),* Sib.(Lower Tunguska).

Sphaerestheria Novozhilov, 1954 [**Estheria koreana* Ozawa & Watanabe, 1923; OD]. Distinguished by roundly trigonal configuration of valves; ornament unknown. *U.Trias.(Rhaet.)-L. Jur.(Lias.),* Korea (Kyonguito).——Fig. 53,2. **S. koreana* (Ozawa & Watanabe); left valve, ×6 (166).

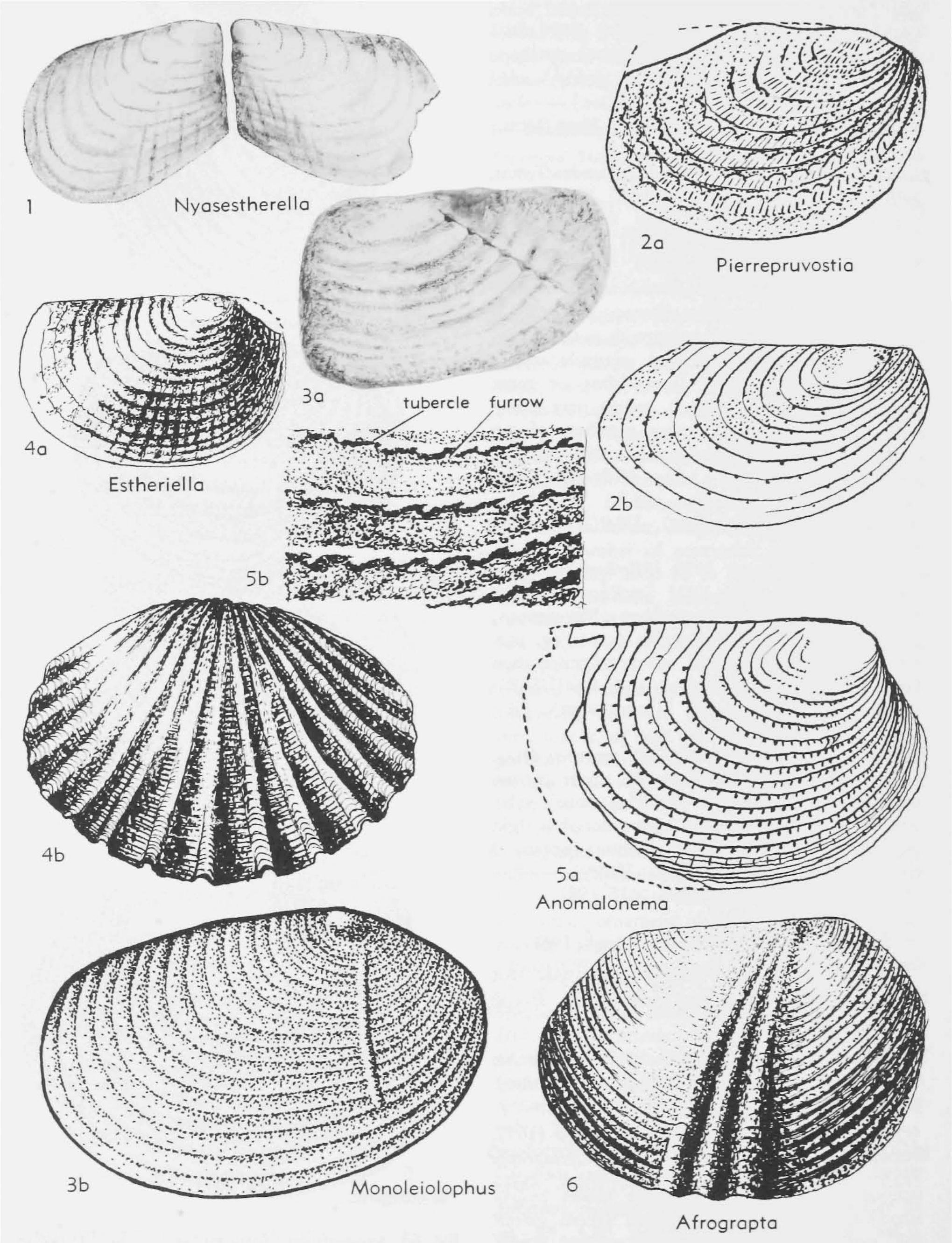


Fig. 54. Estheriellidae (Estheriellinae) *(1,2,4,5),* (Monoleiolophinae) *(3,6)* (p. *R*157).

Taimyrites Novozhilov, 1958 [**T. strachovi*; OD]. [Inadequately documented; doubtful.] *L.Trias.,* Sib.(Taimyr).

Superfamily ESTHERIELLOIDEA Kobayashi, 1954

[=*nom. transl.* Tasch, herein (*ex* Estheriellidae Kobayashi, 1954)]

Valves bearing variable number of interrupted or continuous radial costae that do not cross umbo. *U.Carb.-L.Cret.*

Family ESTHERIELLIDAE Kobayashi, 1954

[*non* Estheriellidae Kobayashi, 1953, 58, p. 138, *lapsus calami?*] [=Afrograptidae Novozhilov, 1958 (99); Teixeiriinae Novozhilov, 1958]

Carapace bearing variable number of radial costae which, in general, become obsolete near umbo. *U.Carb.-L.Cret.*

Subfamily ESTHERIELLINAE Kobayashi, 1954

[*nom. transl.* Tasch, herein (*ex* Estheriellidae Kobayashi, 1954] [=Anomalonematinae Novozhilov, 1958]

Carapace bearing five or more costae. *U. Carb.-L.Cret.*

Estheriella Weiss, 1875 [**Posidonomya nodocostata* Giebel, 1857 (=*Estheriella costata* Weiss, 1875; OD] [=*Congestheriella, Mesoleaia* Kobayashi, 1954: *Pteriograpta* Novozhilov, 1954: *Tancrediella, Pseudoestheriella* Novozhilov, 1956; *Angolestheriella, Camerunograpta* Novozhilov, 1958]. Carapace suboval to subelliptical, with several (usually 7 to 12) nodose radiating costae, weak on anterior and posterior sides. *L.Trias.(Bunter),* Ger. (Sachsen); *L.Cret.(Weald.),* W.Afr.——Fig. 54, *4a.* **E. nodocostata* (Giebel), Durrenberg; right valve, ×10 (53).——Fig. 54,*4b. E. camerouni* Defretin, L.Cret., N.Cameroun; valve showing details of radiating costae, ×75 (35).

Anomalonema Raymond, 1946 [**Estheriella reumauxi* Pruvost, 1911; OD]. Valves with or without posterodorsal recurvature but always characterized by interrupted radial costae. *U.Carb. (Penn.),* Eu.-N.Am.

A. (Anomalonema). Valves with posterodorsal recurvature, beak terminal; individual growth lines presenting scalloped appearance of low relief on ventral side owing to numerous small tubercles that represent interrupted very fine costae; in anteroventral region crowding of growth lines leads to visual illusion of continuous costae (109). *U.Carb.(Westphal.),* Eu.(NE. Fr.)-G.Brit.(Kent-Lancashire coal fields, *Anthraconauta phillipsi-tenuis* Zone).——Fig. 54,*5.* **A. (A.) reumauxi* (Pruvost), Fr.; *5a,* right valve, ×9 (109); *5b,* detail of ornament, ×35 (110).

A. (Pierrepruvostia). [**Pierrepruvostia defretinae* Novozhilov, 1958; OD] [=*Estheriella reumauxi* Pruvost, 1919, fig. 34, *non* 35; *Anomalonema (Pierrepruvostia) defretinae* Tasch, 1960]. Lacking posterodorsal recurvature; beak not terminal; subovate; otherwise like *A. (A.) reumauxi* (109). *U.Carb.(Penn.),* Eu.(NE.Fr.)-N.Am.(NE.USA). ——Fig. 54,*2a.* **A. (P.) defretinae* (Novozhilov); right valve, ×10 (110).——Fig. 54,*2b. A. (P.) williamsi* Tasch, Alleghen., USA(Pa.); right valve, ×7 (140).

Nyasestheriella Kobayashi, 1954 (*emend.* Tasch, 1955) [**Estheriella nyasana* Newton, 1910; OD]. Carapace extremely small, obliquely subquadrate, with anterior margin straight, truncated, umbones anteroterminal, 12 equidistant concentric lines crossed by numerous obscure radial riblets (costae); fine pits and granules covering thin test. *Permo-Carb.(Karoo),* Nyasaland.——Fig. 54,*1.* **N. nyasana* (Newton), Nrana; paired valves, ×30 (93).

Subfamily MONOLEIOLOPHINAE Novozhilov, 1954

[=Karagandiinae Tasch, 1961] [=*emend.* Tasch, 1961]

Carapace with one to four radial costae. *Penn.-L.Cret.*

Monoleiolophus Raymond, 1946 (*emend.* Tasch, 1955) [**Monoleiolophus unicostatus* Raymond, 1946 (*non* Reed, 1929) (=*M. conemaughensis* Kobayashi, 1954); OD] [=*Monoleaia* Miroschnichenko, 1956; *Monoleiopholus* Tasch, 1956 (*nom. null.*)]. Carapace with single posterior nodose costa which reaches posterior ventral margin but fades anteriorly and does not reach beak. *Penn.(Conemaugh),* USA(Pa.).——Fig. 54,*3a.* **M. unicostatus*; left valve, ×7.5 (111).——Fig. 54,*3b. M. karagandica* (Miroschnichenko), U. Carb.(U.Namur.), USSR(Karaganda Basin); left valve, ×14 (91).

Afrograpta Novozhilov, 1958 (99) [**Estheriella (Dadaydedeesia) tricostata* Defretin, 1953; OD]. Carapace with 3 radial ribs in medial sector. *L. Cret.(Wealden),* Afr.——Fig. 54,*6.* **A. tricostata* (Defretin), N.Cameroun, right valve, ×7.5 (35).

Superfamily LEAIOIDEA Raymond, 1946

[*nom. transl.* Novozhilov, 1958 (*ex* Leaiadidae Raymond, 1946)]

Valves bearing up to five radial ribs that cross umbo. *M.Dev.-L.Cret.*

Family LEAIIDAE Raymond, 1946

[*nom. correct.* Novozhilov, 1958 (*pro* Leaiadidae Raymond, 1946, p. 280)] [=Hemicycloleaiinae, Cycloleaiidae, Lioleaiinae Novozhilov, 1952; Amphikoilidae Novozhilov, 1953; Praeleaiinae, Igorvarentsoviinae, Rostroleaiinae Novozhilov, 1956]

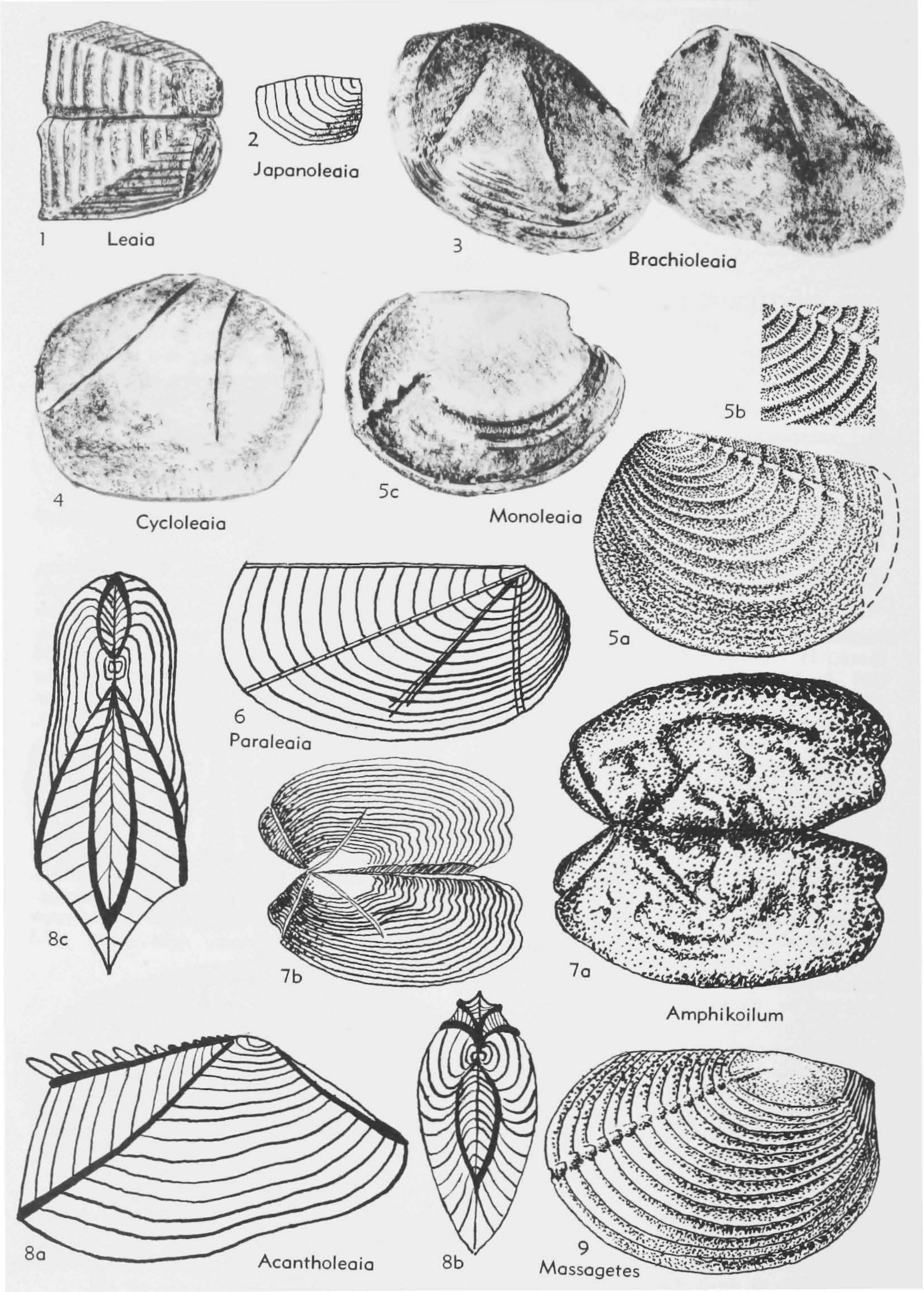


FIG. 55. Leaiidae (p. R159).

Carapace with one or more (up to 5) radial ribs, carinae or flat, diagonal edges which diverge from umbo and have concave areas between them; carina may be nodose. *M.Dev.-L.Cret.*

Leaia Jones, 1862 [**Cypricardia leidyi* Lea, 1855, p. 341; OD] [=*Hemicycloleaia* Raymond, 1946; *Dolicholeaia, Leaianella, Kaltanleaia, Gonioleaia, Lioleaia* Novozhilov, 1952; *Mimoleaia, Australoleaia, Siberoleaia* Novozhilov, 1954; *Eoleaia* Kobayashi, 1954; *Igorvarentsovia, Falsirostria, Granirostria, Brachiorrhynchia, Tataroleaia* Novozhilov, 1956]. Carapace outline variable from quadrate to semicircular; valves bearing 2 radial hollow ribs, indistinct in some species, and 3rd rib may be present where dorsal margin thickens, *Miss.(L.Carb.)-U.Perm.,* cosmop.——Fig. 55,*1*. **L. leidyi* (Lea), Miss.(Chester.), USA(Pa.); paired valves, ×5 (53).

Acantholeaia Almeida, 1950 [**A. regoi*; OD]. Carapace suboval; valves tricarinate, with series of spines which issue obliquely from subdorsal carina at points where growth lines intersect carina and diminish in size toward umbonal region; median sector very wide. *U.Perm.,* S.Am.(Brazil).——Fig. 55,*8*. **A. regoi,* Estrada Nova Gr., São Paulo; *8a,* right valve, lateral view; *8b,c,* both valves, anterior and dorsal views, all ×15 (1).

Amphikoilum Novozhilov, 1953 [**A. ermakorum*; OD]. Bicarinate, undulant valves with elevated anterior carina that proceeds from just below or at dorsal margin, crosses umbo, and reaches anterior sector of ventral margin; another thinner, posterior carina in groove proceeds at acute angle from anterior carina, ending high above ventral margin at about 9th growth line; anterior cavity in front of anterior carina, posterior cavity also present, both carinae confined to anterior third of valves. *L.Carb.(Dinant.),* USSR(Kemerovovskaya Oblast, E. of Novosibirsk).——Fig. 55,*7*. **A. ermakorum,* Ostrog Series, Barzasski Region; *7a,* both valves, ×14; *7b,* carapace (reconstr.), ×11 (96).

Brachioleaia Novozhilov, 1952 [**Leaia quadriradiata* Mitchell, 1925; OD] [=*Quadrileaia* Kobayashi, 1954]. Carapace outline suboval to subsemicircular; valves with 2 typical leaian radials and 2 additional, unequal, weak, short marginal radials located anteriorly and posteriorly near margin. *U.Perm.,* Australia(NewS.Wales).——Fig. 55, *3*. **B. quadriradiata* (Mitchell); two right valves, ×10 (92).

Cycloleaia Novozhilov, 1952 [**Leaia discoidea* Mitchell, 1925; OD] [=*Symmetroleaia* Novozhilov, 1952; *Discoleaia* Kobayashi, 1954 (obj.); *Kargalia* Novozhilov, 1956]. Shape discoidal; valves with two unequal radial ribs originating from blunt umbo, far apart distally. *L.Perm.-U.Perm.,* Australia (New S. Wales)-Eurasia (Urals).——Fig. 55,*4*. **C. discoidea* (Mitchell), New S. Wales; right valve, ×6 (92).

Japanoleaia Novozhilov, 1952 [**Estheria rectangula* Yokahama, 1894; OD] [=*Pseudoleaia* Kobayashi, 1953]. Carapace subquadrate; valves with two flat diagonal edges that (expressed as carinae or radial ribs in other members of family) proceed from umbo, one to posteroventral angle and other to middle part of ventral margin. *L.Cret.(Neocom.),* Japan.——Fig. 55,*2*. **J. rectangula* (Yokahama), Yuasa; right valve, ×5 (159).

Massagetes Novozhilov, 1954 [**M. karagandensis*; OD]. Valves subovate, characterized by thin anterior carina that proceeds from lower portion of umbo and terminates at about 9th growth line and by thickened posterior carina that proceeds higher up on umbo and forms acute angle with anterior carina, posterior carina extending to ventral margin. *U.Carb.(Stephan., Tentek Series),* SW.Asia(Kazakhstan).——Fig. 55,*9*. **M. karagandensis,* Karagand Dist.; right valve, ×13 (96).

Monoleaia Tasch, 1956 [**Leaia unicostata* Reed, 1929; OD] [=*Jaxartus* Novozhilov, 1954; *Inkus* Novozhilov, 1956; *Monoleaia* Miroschnichenko, 1956 (jr. homonym?, month of publication uncertain)]. Carapace subovate, valves with single imbricate or nodose radial extending from umbo to rounded posterior ventral margin. *U.Carb.-U. Perm.,* SW. Asia (Kazakhstan)-S. Am. (Brazil).——Fig. 55,*5a,b*. **M. unicostata* (Reed), U.Perm., Brazil; *5a,* left valve, ×9; *5b,* detail of ornamentation, ×9 (112).——Fig. 55,*5c*. *M. monocarinata* (Lyutkevich), 1956 [=*Leaia monocarinata* Lyutkevich, 1941], U.Perm.(Tartarian), USSR; right valve, ×20 (80).

Paraleaia Raymond, 1946 [**P. klieveri* (=*Leaia leidyi* var. *klieveri* Goldenberg, 1873); OD] [=*Troisleaia* Miroschnichenko, 1956; *Teiichium* Novozhilov, 1956]. Narrow and short radial groove, furrow *(Furche)* or accessory radial in wide median section between 2 typical leaian radials. *U.Carb.(Stephan.),* Eu.(W.Ger.).——Fig. 55,*6*. **P. klieveri,* right valve, ×10 (49).

Praeleaia Lyutkevich, 1929 [**P. quadricarinata*; OD] [=*Lioleaiina* Novozhilov, 1952; *Metaleaia* Kobayashi, 1953]. Carapace elongate-oval; valves bearing four or five radials that fan out from umbo; no radial or dorsal margin. *M.Dev.,* Eu. (Est.); *L.Trias.,* USSR(Sib.).——Fig. 56,*1a*. **P. quadricarinata,* M.Dev., confluence of Ruia and Pliusa Rivers; left valve, ×4 (78).——Fig. 56, *1b*. *P. triasiana* Chernyshev, L.Trias., Kuznetsk Basin; right valve, ×8 (24).

Pteroleaia Copeland, 1962 [**P. canadensis*; OD]. Multiribbed, rostrate carapace with dorsal marginal rib or keel around which growth lines are recurved sinuously. *M.Dev.-U.Dev.,* Canad. Arctic.——Fig. 56,*2*. **P. canadensis,* Can.(Melville Is.); left valve, 4-ribbed specimen, ×4 (29).

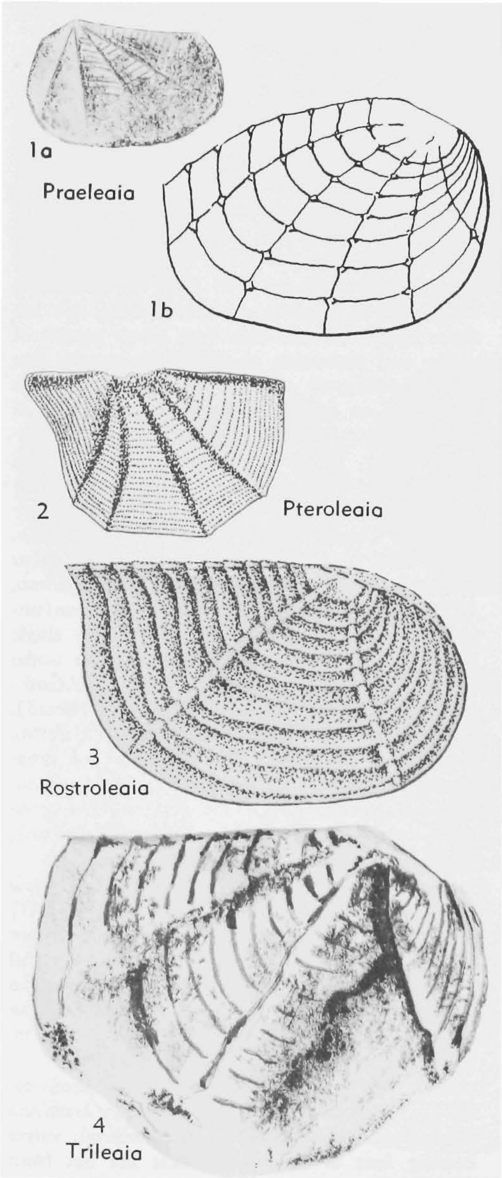


FIG. 56. Leaiidae (p. *R*159-*R*160).

Rostroleaia NOVOZHILOV, 1952 [**R. martynovae*; OD]. Elongated pod-shaped valves bearing 2 carinae; posterodorsal sector limnadiiform, this feature being expressed in some species by sharply pointed termination of dorsal margin. *U.Perm. (Kazan.)*, USSR(Urals).——FIG. 56,*3*. **R. martynovae*, Nikolaevsk Gorge; right valve, ×8 (96).

Trileaia KOBAYASHI, 1954 [**Leaia belmontensis* MITCHELL, 1925; OD]. Carapace outline semicircular to subelliptical; valves with three distinct carinae in addition to thickened straight dorsal margin. *U.Perm.*, Australia(NewS.Wales).——FIG. 56,*4*. **T. belmontensis* (MITCHELL); right valve, ×11 (92).

Superfamily VERTEXIOIDEA Kobayashi, 1954

[*nom. transl.* TASCH, herein (*ex* Vertexiinae KOBAYASHI, 1954] [=Limnadiopseoidea NOVOZHILOV, 1958 (superfam.) (name not based on first-published family-group taxon included in superfamily)]

Carapace with posterior or anteroposterior recurvature of growth lines, or growth lines ending in one or several spinous apophyses, with or without spine or tubercle on initial valve or may bear single rib; also, may be characterized only by single rib and posterodorsal recurvature of growth lines. *L. Carb.-Rec.*

Family VERTEXIIDAE Kobayashi, 1954

[*nom. transl.* NOVOZHILOV, 1958 (*ex* Vertexiinae KOBAYASHI, 1954)]

Carapace bearing spine or tubercle on each larval valve; serrated margin also occurs where extremities of zones of growth do not all terminate at dorsal margin, and extremities then may be expressed as spinous apophyses. Ornament variable, from irregular alveoli to punctate. *L.Carb.-U. Trias.*

Vertexia LYUTKEVICH, 1941 [**V. tauricornis*; OD]. Carapace subovate, beak (of larval valve) developed as hollow spine with broad base; spinous apophyses terminate extremities of growth bands; last apophysis a broad-based spine. Sculpture punctate. *U.Perm.(Tatar.)*, Eu.(USSR).——FIG. 57,*1*. **V. tauricornis*, Fileyskoe beds, N.Dvina Valley; *1a*, lat. view, ×21; *1b*, lat. view with two spines, ×10; *1c*, umbonal view, ×11 (80).

Cornia LYUTKEVICH, 1937 [**C. papillaria* LYUTKEVICH, 1937, p. 63; OD, *non C. melliculum* LYUTKEVICH, 1937, p. 64 (*nom. nud.*, incorrectly designated as genotype); *non C. melliculum* LYUTKEVICH, 1941, p. 36, not "one of the originally included nominal species"—ICZN Code (1961) Art. 69,a] [=*Pemphicyclus* RAYMOND, 1946]. Valve shape varying from subovate to subrectangular, beak position subcentral to anterior; small spine or tubercle rising from center of initial valve; sculpture punctate. *U.Carb.(Westphal.)-U. Perm. (Tatar.)*, USSR (Sib.)-N. Am. (USA).——FIG. 58,*1a*. *C. papillaria*, U.Perm.(Tatar.), Kuznetsk Basin; two valves, ×17 (79).——FIG. 58, *1b*. *C. laminata* (RAYMOND), L.Perm.(Leonard.), USA(Kans.-Okla.); right valve, ×24 (142).

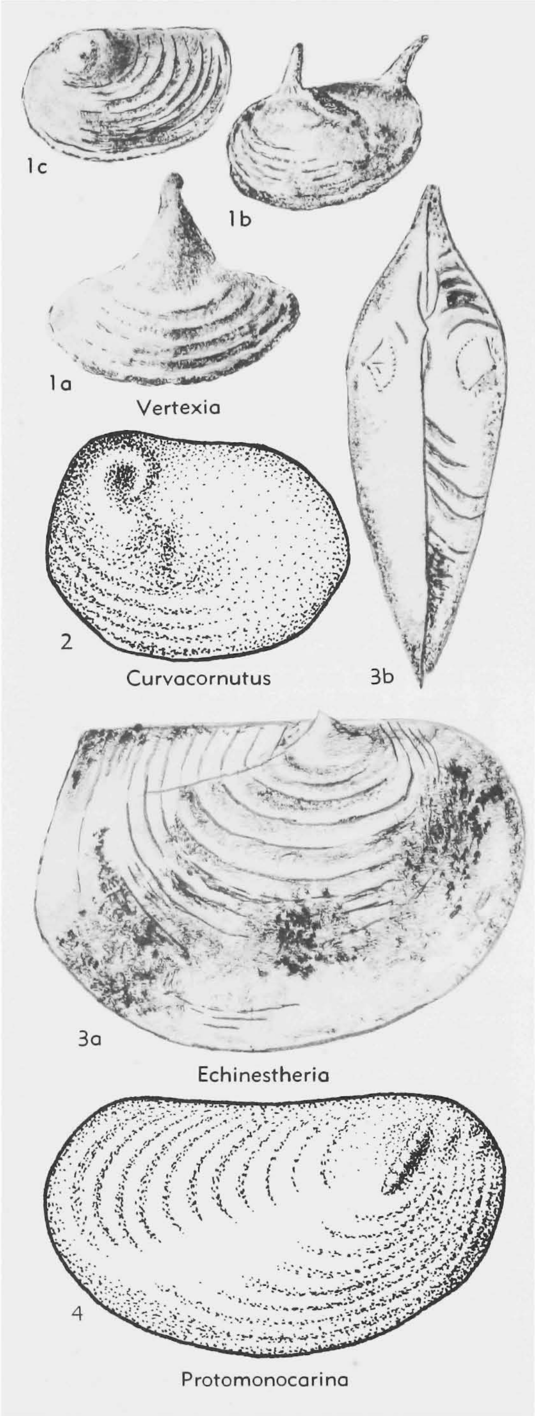


FIG. 57. Vertexiidae (p. *R*160-*R*161).

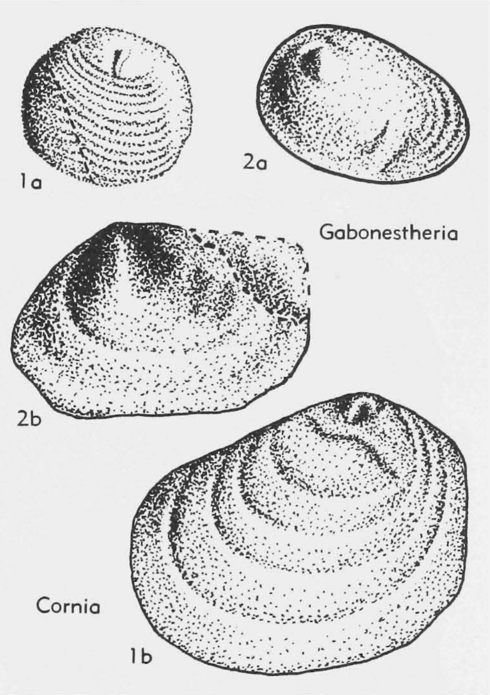


FIG. 58. Vertexiidae (p. *R*160-*R*161).

Curvacornutus TASCH, 1961 [**C. prima;* OD]. Subovate valves bearing looped or markedly curved spine on each initial valve; umbo situated in anterodorsal sector of valve. *L.Perm.,* N.Am. (USA).——FIG. 57,*2*. **C. prima,* Leonard, USA (Kans.); left valve, ×15 (142).

Echinestheria MARLIÈRE, 1950 [**Estheria (Echinestheria) marimbensis*; OD]. Carapace cycladiform, with straight dorsal margin; submedian beak (in larval shell) expressed as large conical spine with broad base. Ornament of interspaces finely reticulate. *U.Trias.,* Port.-W.Afr.——FIG. 57,*3*. **E. marimbensis* (MARLIÈRE), Cassanje F., Angola; *3a,b,* right valve, dorsal view, ×15 (82).

Gabonestheria NOVOZHILOV, 1958 [**Estheria (Pemphicyclus) gabonensis* MARLIÈRE, 1950; OD] [=*Estheria (Pemphicyclus)* MARLIÈRE, 1950]. Large, robust spine on initial shell situated in anterodorsal sector of valve; sculpture finely reticulate. *L.Perm.,* W.Afr.-N.Am.(USA).——FIG. 58, *2a*. **G. gabonensis* (MARLIÈRE), Fr.Equat.Afr. (Gabon); left valve, ×16 (82).——FIG. 58,*2b*. *G. dickinsoni* TASCH, 1960, Leonard, USA(Kans.); left valve, ×19 (142).

Protomonocarina TASCH, 1962 [**P. kechii;* OD]. Subovate valve bearing embryonic rib of five beadlike segments. *L.Perm.,* N.Am.(USA).——FIG. 57,*4*. **P. kechii,* Leonard, USA(Kans.); right valve, ×18 (145).

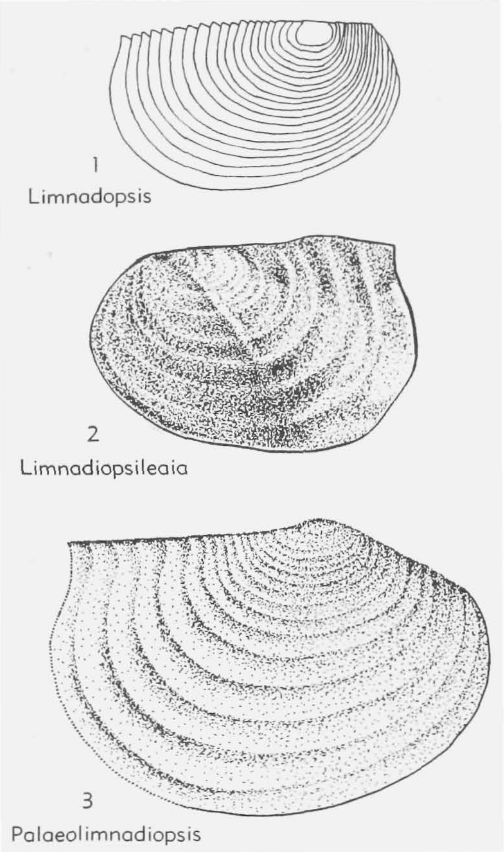


FIG. 59. Limnadopsidae (p. R162).

Family LIMNADOPSIDAE[1] Tasch, new family

[=Limnadiopseidae Novozhilov, 1958 (*recte* Limnadiopsidae) (name based on *Limnadiopsis* Daday, 1925, *nom. neg.*)]

Posterodorsal margin recurved, dorsal margin varying from subdued serrate (hence, almost straight) to markedly serrate, with spinous apophyses at end of growth bands. Soft parts unknown in fossilized state. *L.Carb.-Rec.*

Limnadopsis Spencer & Hall, 1896 [**L. brunneus*; SD Raymond, 1946 (p. 269)] [=*Limnadiopsis* Daday, 1925, p. 177 *(nom. null.)*; *Limnadiopsium, Limnadiopseites* Novozhilov, 1958]. Carapace ovate to subovate, compressed, narrower in male than female; union between halves of carapace extending along whole length of dorsal line and rising into much-compressed spined keel (strongly to moderately serrate condition); lines of growth continued on dorsal keel into backwardly directed spines, posterior edges of which are formed by lines of growth, spines decreasing in size from behind forward; beaks well marked. Antennules much smaller than antennae, 26 to 32 pairs of feet. Haft organ present. *Rec., C.Australia* (N.W.Terr.).——Fig. 59,*1*. **L. brunneus,* Port Darwin; right valve, ×4.9 (132).

Belgolimnadiopsis Novozhilov, 1958 [**Estheria (Euestheria) stockmansi* Mallieux, 1939]. [Inadequately documented; doubtful.] *L.Dev.,* Eu. (Belg.).

Limnadiopsileaia Tasch, 1962 [**L. noblensis*; OD]. Valves resembling *Palaeolimnadiopis* but bearing single anterior rib. *L.Perm.(Leonard.),* N.Am. (USA).——Fig. 59,*2*. **L. noblensis,* Wellington F., USA(Okla.); left valve, ×3.2 (145).

Palaeolimnadiopsis Raymond, 1946 (*emend.* Tasch, 1960) [**P. carpenteri*; OD] [=*Macrolimnadiopsis* Beurlen, 1954; *Paleolimnadiopsis* Tasch, 1956 *(nom. null.)*]. Well-defined terminal beak rising above straight dorsal margin (subdued serrate); growth lines closely spaced and numerous on beak, fewer and more widely spaced on rest of valve. *L.Carb.-Cret.,* N.Am.(USA)-S.Am.-Eu.-(USSR).——Fig. 59,*3*. **P. carpenteri,* L.Perm. (Leonard.), USA(Okla.); right valve, ×2.4 (111).

Rossolimnadiopsis Novozhilov, 1958 [**Rossolimnadiopsis marlieri*; OD]. [Inadequately documented; doubtful.] *U.Perm.(Kazan.),* USSR (Vladimirskaya Oblast).

Family PEMPHILIMNADIOPSIDAE Tasch, 1961

Carapace bearing a tubercle-type spine on initial valve and posterior recurvature of growth lines in adult portions of valves. *Penn.*

Pemphilimnadiopsis Tasch, 1961 [**Estheria ortoni* Clarke, 1900; OD]. Initial valve with nodelike hollow spine, last few growth lines recurved near dorsal margin; relatively large umbo on generally small valve. Resembles *Cornia* but differs in having posterior recurvature. *Penn.,* USA (Ohio).——Fig. 60,*1*. **P. ortoni* (Clarke), Conemaugh, Carollton; left valve, ×11.3 (141).

Family IPSILONIIDAE Novozhilov, 1958

[*emend.* Tasch, herein] [=Keratestheridae Novozhilov, 1958]

Carapace variable in shape, dorsal margin terminating in aliform apophyses formed by

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[1] Note to R. C. Moore from Professor L. W. Grensted at request of W. E. China, ICZN: "The generic ending *-opsis* makes it genitive ὄχεως, *opseos,* and this (as the accent shows) is treated as a dissyllable. The stem therefore is not *-opse* (or Ionic, *-opsi*) but *-ops*. Poeciliopsinae and Macropsidae are therefore quite correct."

incurvature of anterior or posterior extremities of growth lines, or both of these. Ornament alveolar. *Dev.-L.Cret.*

Ipsilonia Novozhilov, 1953 [**I. auriculata*; OD]. Both ends of dorsal margin winged, valves having form of Greek small letter epsilon. *Dev.*, Eu. (USSR).——Fig. 60,*3*. **I. auriculata*, Koura Region (N. of Caucasus Mtns.); right valve, ×8.1 (98).

Aculestheria Cardosa, 1963 [**A. novojilovi* Cardosa, 1963; OD]. Like *Ipsilonia* but valves broader from anterior to posterior and less elongate dorsal to ventral; apophyses subequal, posterior one being more pronounced. *L.Cret.(Wealden)*, Bahia Series, Brazil.

Keratestheria Chernyshev, 1948 [**K. rugosa*; OD]. Slight incurvature anteriorly below dorsal margin; incurvature of last few growth lines posteriorly forming spine-type projections above dorsal margin with apex directed away from umbonal area. *M.Jur.*, USSR(Sib.).——Fig. 60,*2*. **K. rugosa*, Chitinskaya Oblast (E. of Lake Baikal); right valve, ×4 (161).

Sajania Novozhilov, 1958 [**Ipsilonia kashtagensis* Novozhilov & Varentsov, ?unpubl.); *Sajania kashtagensis* Novozhilov, 1958, p. 110, fig. 17 (98)]. [Inadequately documented; doubtful.] *M. Dev.*, USSR(Sib.), Tuvinskaya Aut. Oblast (SW. of Lake Baikal).

REJECTED GENERIC NAMES

Bileaia Kobayashi, 1954 (127), *nom. dub.*

Palermisca Novozhilov, 1956 (128), jr. subj. syn. of *Dadaydeesia.*

Dadaydeesia Raymond, 1946 (104), pelecypod.

Estheriopsis Rusconi, 1947, probably pelecypod.

Teixeirium Novozhilov, 1958, probably pelecypod.

Fernandoalmeidium Novozhilov, 1958, *nom. dub.*

Innocentium Novozhilov, 1957, inadequately documented.

Eoasmussia Soot-Ryen, 1960, probably pelecypod.[1]

REJECTED SUBFAMILY NAMES

Fernandoalmeidiinae Novozhilov, 1958 (see *Fernandoalmeidium*).

Teixeiriinae Novozhilov, 1958 (see *Teixeirium*).

Order CLADOCERA Latreille, 1829

[=suborder Cladocera Sars, 1865] [*nom. transl.* Calman, 1909 (*ex* Cladocera Latreille, 1829)]

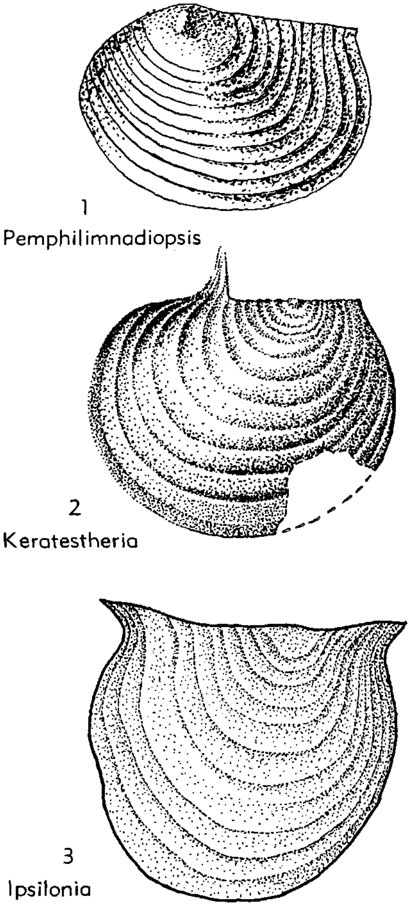

Fig. 60. Pemphilimnadiopsidae *(1)*; Ipsiloniidae *(2,3)* (p. *R*162-*R*163).

[Dr. J. L. Brooks of the Osborn Zoological Laboratory, Yale University, kindly provided, in advance of publication, the first few pages of his chapter on taxonomy of the Cladocera for a revised edition of Ward & Whipple's "Fresh Water Biology." In addition, he provided some valuable references to the literature and technical advice on specific questions. Dr. J. G. Mackin, of the Department of Oceanography, Texas Agricultural and Mechanical College, kindly aided with references to the literature. Dr. F. M. Swain, of the University of Minnesota, confirmed his find of calcified cladoceran fossils. Dr. D. G. Frey, of Indiana University, generously provided some of his publications on cladocerans and discussed with me various aspects of known cladoceran subfossils. Illustrations for this chapter were financed by a Wichita State University Research Grant.]

Carapace univalved, generally enclosing body but leaving head free, reduced in some forms and serving only as a brood sac; paired eyes sessile, coalesced. Antennae biramous (with single exception), natatory; trunk limbs four to six pairs, none of which are postgenital; furcal rami clawlike. De-

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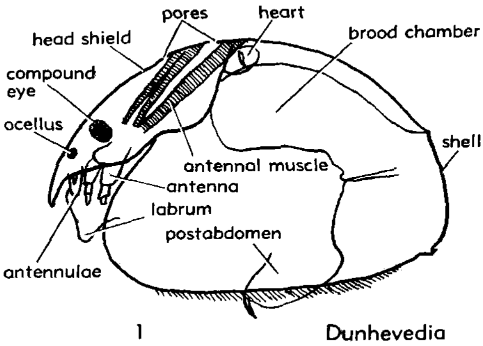
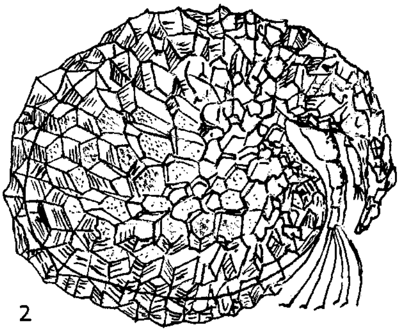
[1] If any conchostracans are found in Ord.-Sil. strata, they are likely to be marine. Soot-Ryen's figured material (Norsk Geol. Tidss., 1960, Bd. 40, pl. 1, fig. 4), however, is closer to a pelecypod-type of organization and lacks definitive conchostracan characters. Homeomorphy between pelecypods and conchostracans is not uncommon. An alleged, but unnamed, Silurian conchostracan genus (Adamazak, 1961, Acta Paleont. Polonica, VI(1): 29-104, pl. 7) is a likely homeomorph of ostracodes in the suborder Eridoconcha.



Dunhevedia



Chydorus

Fig. 61. Anatomical features of cladocerans.——*1. Dunhevedia crassa,* lateral view showing head pores and other anatomy, enlarged (42).——*2. Chydorus faviformis,* male, shell covered with deep polygonal cells, enlarged (42).

velopment embryonic, rarely with metamorphosis. *Oligo.-Rec.*

ANATOMY

The Cladocera, or water fleas, have a body composed of a few somites, exhibiting only obscure segmentation. The head is free of the apparently bivalved shell that covers the body and limbs. Actually, the carapace is a single piece, its point of juncture with the body being marked by a cervical sinus or notch (21, 107). The front of the head is produced downward to form a beaklike rostral process, as in conchostracans. Adult cladocerans possess only four head appendages (antennules, antennae, mandibles, maxillules), but embryos have distinct rudimentary maxillae also. In adults of most other fresh-water crustaceans, however, maxillae are well developed (107).

Frey (42) observed that head pores apparently occur in all Cladocera, at least during embryonic growth or in early instars. He described two series of minute head pores on or near the mid-line of species belonging to genera of the Chydoridae. The number and symmetry of such pores, he noted, were indicators of relationships at generic and suprageneric levels, and thus he was able to employ this known but little used structural feature of the shield to distinguish subfossils from the Schleinsee and Wallensen (41, Table 1) in Germany, as well as exuvia of Recent forms (Fig. 61,*1*).

The antennules perform a sensory function, although in males of some species they serve as clasping organs for holding the female. They are usually very small, unsegmented, and attached to the rear of the rostral process. In contrast, the antennae are large biramous swimming appendages, as in conchostracans. Like the head from which they rise, they are free of the shell and are the chief organs of locomotion.

The mouth parts of the head consist of mandibles and maxillules. The mandibles are formed of single sclerotized pieces, the opposite faces of which are toothed and ridged to form a grinding surface for food. The maxillules, located just behind the mandibles, are small pointed appendages that bear curved setae. These structures serve as a pair of "hands" to pass food to the grinding surface of the mandibles (21). The head also bears large compound-lensed eyes that operate by three muscles on each side. They are capable of rotation.

Trunk appendages are usually five in number. They are leaflike in form, bearing numerous hairs and long setae. The structure of the feet differs in different families but serves the general function of creating water currents through the valves for respiratory and nutritional ends. Modifications for other functions can be seen in the Daphniidae and other families. Here the first pair of feet are prehensile. The hooks and spines serve to anchor the cladocerans to weeds, among which they live, or are used for prehension of food, such as algae. In the genus *Leptodora* the foliaceous character of the limbs is lost, for they are modified to serve in seizing and holding prey (21).

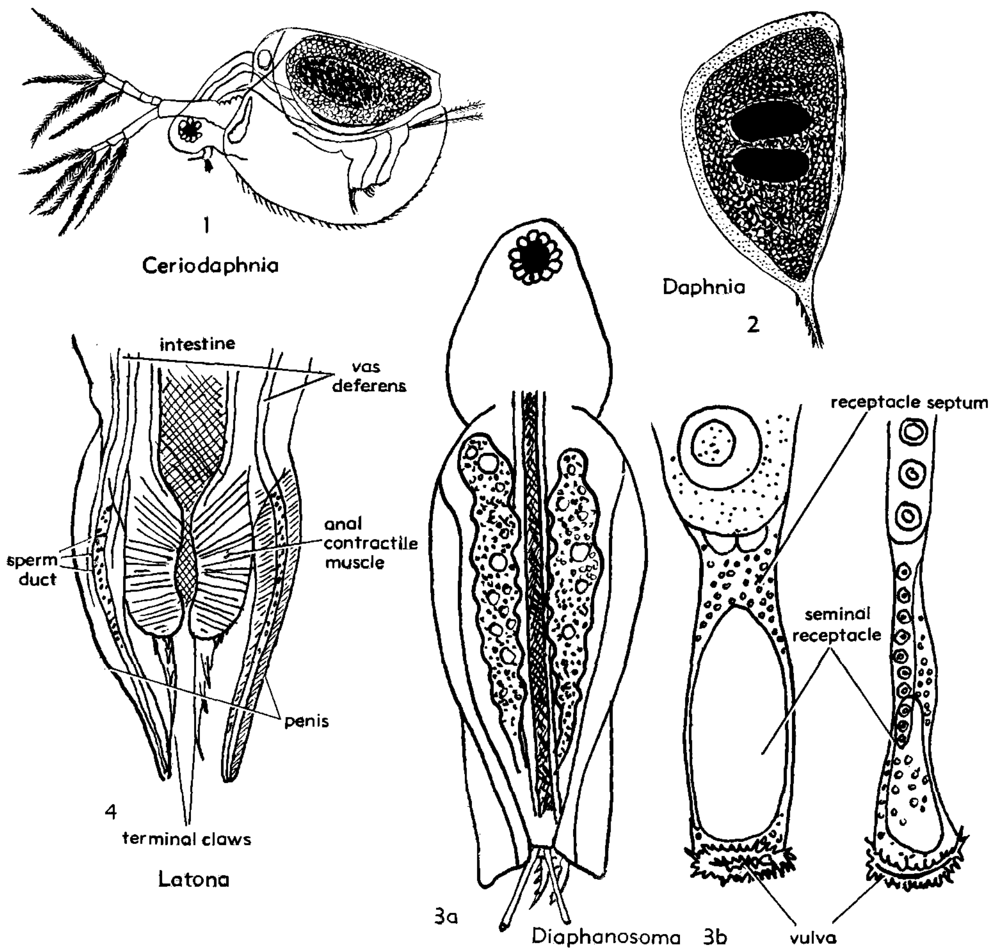


FIG. 62. Anatomical features of cladocerans.——*1. Ceriodaphnia megops,* adult female with ephippial eggs, ×42 (150).——*2. Daphnia pulex,* a separated ephippium containing eggs, enlarged (12).——*3. Diaphanosoma brachyurus*; *3a,* showing disposition of ovaries; *3b,* two views of the posterior part of the ovary, enl. (105).——*4. Latona setifera,* male genitalia, enl. (105).

CARAPACE

FORM AND STRUCTURE

For paleontologists the shell of cladocerans holds chief interest because it is commonly preserved wholly or partially in postglacial deposits. Furthermore, it bears close analogies to the conchostracan carapace, particularly in ornament. Although the cladoceran shell comprises a single piece, as previously noted, it is bent along the back in a manner that gives a bivalved appearance. In side view, different cladoceran shells are variable in shape, ranging from nearly square to oval and subcircular.

Forms like *Daphnia* have a single posterior dorsal spine that prolongs the junction of the carapace halves (12, fig. 1064, p. 695). In *Scapholeberis* a spine projects from the junction of straight posterior and ventral margins (12, fig. 1076, p. 699). The shell is actually a duplicature of the skin and has a very delicate inner layer and a tougher outer wall.

A remarkable adaptation of the shell is seen in the Chydoridae and Daphniidae (12, p. 357, 684) (Fig. 62,*1*,*2*). After the fertilized egg enters the brood chamber, the walls thicken and darken to form an ephippium. During molting in species of

Daphniidae, the semielliptical portion of the dorsal region of each half of the carapace (ephippium) separates from the rest, whereas in the Chydoridae this part does not separate and the eggs remain enclosed in the carapace.

PENNAK (107, p. 357) has observed that the separated ephippia (Fig.62,*2*) may sink to the bottom or float on the surface. Where they do not sink, the ephippia may be blown ashore and accumulate in diminutive windrows. One might anticipate future finds of such windrows in the fossil record.

The ephippial development is apparently an adaptation to withstand drying and freezing conditions. Especially in small ponds, drying up during summer months is common. The ephippia and their contained eggs can withstand such adverse conditions. When the basins fill again in early autumn, ephippial eggs give rise to parthenogenetic females.

GROSCHOPF (47, p. 32) has reported fossil ephippia of *Daphnia* in addition to other cladoceran remains, in samples from borings through postglacial lake deposits. SCOURFIELD (128) also found fossil ephippia belonging to *Bosmina* and several species of *Alona* in postglacial sediments. FREY (41) found numerous ephippia in lake deposits (Wallensen) of Germany.

ORNAMENTATION

Shell markings, or ornament, in cladocerans are quite varied. In *Ceriodaphnia acanthina* the carapace is strongly reticulated (12, fig. 1080, 1081) and reveal, under high power, a series of irregular polygons with short spinules emerging at points of contact of any two polygon sides (see Fig. 62, *1*). *Streblocerus pygmaeus* also has a reticulated carapace. The reticulations of this form, however, make scalelike ridges, which give the dorsal margin a serrate appearance. Many other genera exhibit reticulation, but the most remarkable development of this condition is to be found in the carapace of certain species of *Chydorus*, in which the shell is covered by very distinctive deep polygonal cells (Fig. 61,*2*) (see Fig. 64,*6c*).

Numerous genera have carapaces bearing longitudinal striations. These generally run from front to back in an almost parallel series of straight or arcuate lines (12, figs. 1119, 1127, 1130). Some species, like *Chydorus piger*, have oblique striae on the lower portion of the shell, whereas the dorsal anterior part lacks striae and is smooth. Many reticulated shells may also bear fine striae (12, figs. 1143, 1165), as in *Alonella excisa*. Still others may have both longitudinal and oblique striae, as in *Pleuroxus truncatus*. Forms like *Euryalona occidentalis* (12, fig. 1124) bear a series of obscure concentric lines that parallel the ventral margin.

ONTOGENY

During growth, cladocerans undergo molting, although this is variously expressed in different genera and species. *Moina macrocopa* has two juvenile instars, whereas species of *Daphnia* vary from three *(D. longispina)* to as many as five *(D. pulex)*. The next later instar represents the adolescent stage, occurring between the last juvenile and first adult stages. Adult cladocerans shed successive instars. These are more variable in number than the juvenile instars, so that *D. pulex* has 18 to 25 and *D. longispina* 10 to 19.

Accompanying final development of each adult instar, the young are released from the brood chamber to the outside (107). BIRGE (12, p. 681) observed that no free-swimming larval forms are known among cladocerans. It should be noted, however, that *Leptodora* is an exception to the general rule. Upon release from the brood chamber, the young are well grown, hatching out in a form closely resembling that of their parents. This event is followed by molting in most genera, i.e., casting off the old skin. Exceptions are found in *Ilyocryptus* and *Monospilus* (12, figs. 1110, 1168). In these genera a new and larger shell appears beneath the old one, which is not cast off. Next follows an observable increase in size and release of a new clutch of eggs to the brood chamber. In still other cladocerans, such as *Polyphemus* and *Leptodora*, the shell is reduced to an egg case.

REPRODUCTION

Reproduction may be sexual or asexual (parthenogenetic). According to BIRGE (12), species that live in open waters of lakes reproduce chiefly by asexual means. Males of any species are rarely seen and are invariably outnumbered by females.

DIMORPHISM

Dimorphism is expressed in the smaller size of males, which, however, have larger antennules and modified abdomens. Their first feet commonly bear a stout hook for clasping females during copulation (21, 107).

CYCLOMORPHOSIS

A problem such as occurs in study of species of the genus *Daphnia* might well confuse paleontologists. Finding fossil forms of radically variant morphology, one would generally conclude that distinct species should be erected to embrace each morphological type. Yet, cyclomorphosis, or seasonal changes in morphology, is found to alter drastically the appearance of individuals belonging to a single given species of *Daphnia*. Thus, the normal round head of the species in winter becomes a bizarre helmet by midsummer, and reversion to the "normal" head type begins in early autumn (107, fig. 226, p. 360; 118, pl. 21, fig. 223). Cyclomorphic changes also involve variations in size of the eye and posterior spine length (107). The cause or causes of this phenomenon are still baffling. Coker and others suggest that the more prominent helmet-type heads are produced by high temperatures. Genetic factors and turbulent conditions are also credited with a causative role (107).

Specialists on living cladocerans generally recognize that *Daphnia pulex* and *D. longispina* are two highly variable species. The endless numbers of intergrades representing these two species can be accounted for by cyclomorphosis and are not regarded as meriting separate nomenclatural designations.

ECOLOGY

HABITAT

Cladocerans live in fresh to brackish and slightly alkaline waters of all types (12, 107). They are found associated with the marginal vegetation of rivers, in the weedy margins of lakes and swamps, in shallow, silty, and muddy ponds, in both permanent pools and temporary rain-water pools. Some species are common in the shallow ditches of rice paddies (150).

A few marine genera are known; for example, Uéno has reported the genus *Penilia* from the Pacific Coast of Japan. American and South American marine genera include *Evadne* and *Podon* (14, 107). In addition, a few species are restricted to or frequently found in acid or bog waters. *Acantholeberis curvirostris* is abundant in sphagnum bogs of Maine, Wisconsin, and Louisiana. *Streblocerus serricaudatus*, found in weedy pools and lake margins in North America, occurs in weedy bog ponds in the Kyoto region of Japan.

Although various species most frequently live among weeds and feed on algae, bottom-dwellers are known. The latter include *Ilyocryptus* and *Monospilus*. The former lives in mud (12).

SALINITY, pH, TEMPERATURE

Most cladocerans are found in waters with a pH range of 6.5 to 8.5. Very few species are limited in distribution by temperature (105). Most species are eurythermal (107).

The amount of calcium and magnesium in solution plays an important role in the life of some cladocerans. *Holopedium* is apparently confined to calcium-poor waters. Magnesium appears to inhibit reproduction in various species of *Daphnia* (107).

PREDATORS AND FOOD

Cladocerans, together with copepods, play an important role in the food chain of waters which they inhabit. Insect larvae consume cladocerans and in turn are eaten by larger fishes. Certain fish feed directly on cladocerans. In Japan some species of *Moina*, *Daphnia*, and other genera are known as "mijinko," used by pisciculturists as food for goldfish fry (150).

Birge has pointed out that cladocerans have definite food preferences (12). Diatoms, for example, are preferred to blue-green algae. Some forms of algae are favored over others. Both of these are generally plentiful in the ecological niches that cladocerans fill.

FAUNAL AND FLORAL ASSOCIATES

Frey (41) lists the following microfossil associates found with fossil cladocerans in a German glacial lake: Protozoa rhizopods *(Assulina, Nebella)*; Porifera *(Spongilla*, spicules, gemmules); Turbellaria *(Gyratrix, Otomesostoma, Dendrocoelum, Polycelis, Planaria)*; Bryozoa *(Plumatella, Cristatella*, statoblasts); Oligochaeta (cocoons); Ostracoda; Tendipedidae (midges); Hydrocarina *(Notaspis)*; water mites.

In test tubes planted in a Sedgwick County (Kansas) pond, I have found cladocerans, copepods, insect larvae, and varied protozoans. Blue-green algae, diatoms and other flora, as well as various fishes, have been reported in modern cladoceran-stocked ponds.

STRATIGRAPHICAL AND BIOLOGICAL VALUE

SUBFOSSIL GROUPS

Published references to subfossil (Recent) cladocerans are few. Investigations generally have not been directed primarily to search for cladocerans but rather to determining the nature of animal and plant remains contained in successive layers of lake deposits. Essentially, work has been restricted to that done by limnologists. Recently, SWAIN, a geologist, made an extensive limnological study, giving emphasis to types of data which have greatest interest to geology (135). MESSIATZEV and associates have studied the bottom sediments of three very large lakes near Moscow (90) and have figured species of cladocerans found buried in them (e.g., *Bosmina, Alona, Pleuroxus, Chydorus, Graptoleberis, Acroperus, Alonella, Peracantha, Eurycercus, Sida, ?Daphnia*).

LUNDQUIST (76) has reported *Lynceus* (= *Alona*) and other *Cladocerenschale* from postglacial bottom deposits. In similar deposits of the Grossen Plöner Sees, Ostholstein, GROSCHOPF (47), whose primary concern was a pollen analysis of the bottom sediments, found ephippia of *Daphnia* sp. Shells, antennae, mandibles, and other remains of *Daphnia, Bosmina,* and other cladocerans have been found in deep cores of pelagic "gyttja." CONGER (28), primarily interested in diatoms occurring in sediments of Crystal Lake, Wisconsin, merely mentioned crustacean remains also obtained, presumably cladocerans.

An excellent description of "fossil species" of cladocerans was published by AUSTIN in a study of Connecticut lake sediments (3). This reports the occurrence of *Bosmina* remains, postabdomens of *Leydigia,* carapaces of *Chydorus,* and abdomens of *Eurycercus.*

SCOURFIELD (128) has studied cores of bottom deposits of Lake Windermere, England. The cores consisted mainly of dark brown organic deposits resting on pink laminated glacial clay. Overlying the organic deposit was a semiliquid ooze that was not considered to be part of the core. Cladoceran remains were generally empty valves and head shields, detached abdomens, mandibles, claws, setae, etc. Most common were remains of the planktonic genus *Bosmina.* Three other planktonic genera included *Daphnia, Bythotrephes,* and *Leptodora.* All other forms belonged to the littoral Chydoridae, including *Eurycercus, Camptocercus, Alonopsis, Graptoleberis, Alona, Rhynchotalona, Alonella, Paracantha, Chydorus,* and *Anchistrophus.*

FREY (41, table 4) has listed species and subspecies of Chydoridae in seven major studies of European lake sediments. In addition to work by MESSIATZEV (90) and SCOURFIELD (128), already mentioned, papers by ROSSOLIMO (114), ZEMP (160), and FREY (40, 41) are cited. Still other reports on subfossil cladocerans include publications by POULSEN (Denmark) (108), BREHM, KRASSKE, and KREGER (Austria) (16). FREY (41) has culled data from the works of five other investigators: TIDELSKI (Germany), NIPKOW (Switzerland), GAMS (Austria), SCOURFIELD (Ponder's End, England), and DEEVEY (New Zealand). Noticeably absent from the literature are reports on subfossil cladocerans from Canada, Central and South America, Africa, Australia, and Asia.

A recent study of lake deposits in Minnesota has indicated that cores from Burnside Lake, at a depth up to 5 inches below the bottom, consist of "silty clay, abundant pollen, diatoms, cladocerans" (135, p. 621). In the coarse fractions of copropel from Prior and Minnetonka Lakes, some 18 percent of the fraction consist of sclerotized exoskeletons of arthropods, mainly cladocerans. Also it was noted that cladocerans, along with planktonic diatoms and testate protozoans, are abundant in the upper parts of the cores. Cladocerans are not very common in the lower parts of the cores. It will be valuable to have all cladoceran fragments from such samples identified, as in various studies mentioned above.

All cladocerans reported in the abovementioned studies are subfossils, being found preserved but not fossilized, sclerotized[1] but not calcified. Faunas preserved

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[1] A. G. RICHARDS (1951, *The integument of arthropods,* Univ. Minnesota Press, p. 48) indicates that the body wall of *Daphnia* and *Leptodora* gives a positive test for chitin. Where such evidence exists, we may speak of "chitinous" rather than "sclerotized."

in postglacial deposits make it obvious that the depositional and faunal history of such lakes can be unraveled by coring at several stations along a traverse (41, figs. 1, 2). Since all subfossil genera and species have living representatives in the waters of present-day lakes, important biological data can be derived. Thus, Scourfield (128) has indicated that morphologically the species of *Bosmina* in cores studied by him, when compared to species now living in lake waters, "probably does point to a less evolved condition." More systematic work in such directions can provide valuable data on cladoceran, and hence on branchiopod, evolution.

From the point of view of geology and paleontology, students of the Pleistocene, especially, may derive new data relating to glacial lakes and postglacial sedimentation, climatic changes, and the like through systematic study of cladocerans and related forms found in cores. Cladocerans can be of value as stratigraphic markers for correlating equivalent horizons of lake deposits both within a region and in neighboring or distantly separated regions. This will probably be found true when, instead of generalized reports that merely record the presence of remains found in cores, generic and specific identifications of the material are given.

Some genera of cladocerans have been reported from marine environments (14, 107, 150) and it is altogether possible that certain Recent and older lagoonal or other sediments may contain remains of these or related genera.

Frey (41) has pointed out two assumptions used by him in identifying fossil cladocerans from a late glacial lake (Wallensen, northern Germany). First, he assumed "no major shift in the zoogeography of the Cladocera, aside from a northward readjustment with the retreat of the glaciers and the amelioration of climate." Second, he assumed that no extensive morphological changes had occurred in cladoceran species during the last 11,000 years or so. On this basis, he found it possible to make seemingly useful comparisons of subfossil cladocerans with species occurring in Europe at the present time.

POPULATION STUDIES

Brooks (18) has discussed an interesting difference in the reproductive biology of *Daphnia middendorfiana,* pointing out that high-latitude populations produce viable resting eggs in the absence of males, whereas low-latitude populations produce males and require that resting eggs be fertilized. This last is thought to be the "more primitive" condition. Brooks surmised that the expansion of this species from low latitudes to the Arctic of North America, Greenland, and Siberia probably occurred in relatively recent times. He further commented on the "nearly identical appearance" of *D. middendorfiana* populations wherever they occur. Thus, the difference in reproductive biology lacks morphological analogues and since it is a "secondary condition" may be regarded as a "temporary clone" not justifying nomenclatural recognition (88).

The chief differences discernible in cladoceran populations may be regarded as minor variations (geographic clines). On the other hand, present evidence indicates that major variation in cladoceran populations probably dates back to the older Tertiary. It is hoped that future fossil finds will document this speculation.

GEOLOGIC OCCURRENCE AND ORIGIN

Brooks (18) has suggested that forms such as *Daphnia retrocurva* and *D. dubis,* inhabitants of large deep glacial lakes, originated "sometime during the Pleistocene." His suggestion is based on present geographical and ecological distribution, coupled with morphological distinctness of observed forms. On the other hand, *D. laevis,* a southern species inhabiting shallow pools, and *D. parvula,* inhabiting small lakes, denote a "relatively old" origination. This thesis is sustained, according to Brooks, by the fact that *D. laevis* is morphologically similar to species restricted to Africa south of the Sahara, whereas *D. parvula,* widely distributed in South America and North America, is judged to be older than *D. retrocurva.*

Frey (41) has observed that the mentioned seven major studies of cladocerans collected from European glacial lake sediments include, among other families, 43 species and subspecies of central European chydorids listed by Wagler. Brooks (18) thought that *Daphnia thorata* may have lived in extinct glacial lakes such as Lakes Lahontan and Bonneville, as well as in contemporary lakes of the time, judging from their present distribution.

Noting the "close similarity between the structures of adult Cladocera and larvae of certain conchostracans" [*Cyclestheria* (121)], Brooks (17, 19) was persuaded that "the Cladocera are (or may be) neotenic (paedomorphic) derivatives of some early conchostracan." As already discussed, Permian collections from the Kansas-Oklahoma region or other parts of the world have not yet yielded any cladoceran remains. My experiments with living cladocerans allowed freshly caught specimens to dry on pond muds. Even after thorough desiccation, the general morphology of the carapace could be deciphered. Hence, in ancient lacustrine sediments also, one could expect that, in some instances in Permian fresh-water sediments, cladocerans would have been found by now, if present. While tracing Leonardian conchostracan-bearing beds in Kansas and Oklahoma, I have hunted thoroughly for cladoceran remains in the sediments. None were found. We may thus, at present, place cladoceran origination in the Mesozoic or possibly early Cenozoic time. [As noted subsequently, Miocene cladocerans have been discovered.]

Evidence for the missing link at the point of conchostracan-cladoceran separation should be sought in fluvatile and lacustrine sediments of Upper Cretaceous-pre-Oligocene age. Association with post-Cretaceous or younger fossil clam shrimps is one possibility. Another may be found in organic shales of Mesozoic-Tertiary age. Living *Cyclestheria hislopi* (Baird) is the most likely candidate for the type transitional conchostracan. Postulates such as this have been made for various ancestral and transitional types among fossil vertebrates. These types were sought for and occasionally field search has been rewarded. It is time for invertebrate paleontologists to pursue such germinal suppositions. The possibility is very real that fossilized cladoceran remains, impressions, and the like, may be found in Tertiary lacustrine or near-shore marine sediments.[1]

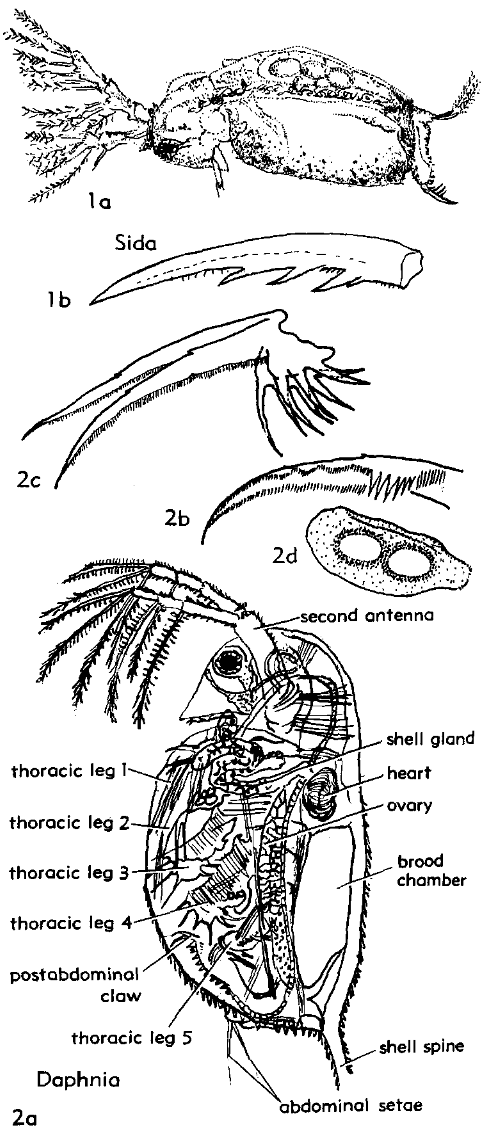

Fig. 63. Sididae *(1)*; Daphniidae *(2)* (p. R171).

Suborder EUCLADOCERA Eriksson, 1934

Body and legs enclosed in small univalved carapace (less than 6 mm. in length) bent along back and appearing bivalved, legs usually flattened branchial appendages (17, 19). *Oligo.-Rec.*

Superfamily SIDOIDEA G. O. Sars, 1888

[*nom. transl.* Brooks, 1959 (*ex* Sididae G. O. Sars, 1888)]
[="tribe" Ctenopoda Sars, 1865]

Six pairs of legs, all foliaceous and all similar except last (19). *Rec.*

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[1] After this had been written, it was gratifying to learn that Dr. F. M. Swain (oral communication) has collected calcified cladoceran ephippia from Miocene lacustrine sediments in Nevada. Subsequently two important preliminary reports have become available: (1) D. G. Frey, 1960, "Cladocera from the Eemian Interglacial of Denmark," Paleont. Soc. program (Denver), abstract, p. 100, recording 25 species of chydorids; and (2) K. A. Dickinson & F. M. Swain, 1961, "Ostracoda and Cladocera of the Late Tertiary Humboldt Formation, Northeastern Nevada," Soc. Econ. Paleont. Mineral. program (Denver) abstract, p. 91, recording three calcified ephippia assigned to a new genus, *Daphnia*, n.sp., and *D.* sp., which were illustrated and described in the oral presentation of the paper.

Family SIDIDAE G. O. Sars, 1888

Carapace of usual eucladoceran type, without gelatinous mantle; feet entirely covered by shell. Antennae biramous in female, rami flattened, dorsal ones with numerous setae, both lateral and terminal. *Rec.*

Sida Strauss, 1820 [**Daphnia crystallina* O. F. Müller, 1785; OD]. Dorsal ramus of antennae 3-jointed; rostrum pointed; shell elongate with rounded ends. *Rec.*, Eu.(Eng.-USSR)-N.Am.——Fig. 63,*1*. **S. crystallina* (Müller); *1a*, entire individual (USA), lat. view, ×12 (12); *1b*, subfossil (USSR, Moscow, postabdominal claw, enl. (90). [Other subfossils are known from USA (Conn.) (3).]

Superfamily DAPHNIOIDEA Strauss, 1820

[*nom. transl.* Tasch, herein (*ex* Daphnides Strauss, 1820, *nom. imperf.*)] [="tribe" Anomopoda Sars, 1865; superfamily Chydoroidea Stebbing, 1902 (*nom. transl.* Brooks, 1959 (*ex* Chydoridae Stebbing, 1902)]

Legs five or six pairs, first and second pairs more or less prehensile, with cylindrical joints, others foliaceous (19). *Oligo.-Rec.*

Family DAPHNIIDAE Strauss, 1820

[*nom. correct.* Tasch, herein (*pro* Daphnides Strauss, 1820, *nom. imperf.*) Zool. Code (1961), Art. II,e,iii] [=Daphniades Baird, 1850; Daphnidae F. Leydig, 1860 (*nom. imperf.*)]

Body oval, head rounded, dorsal ramus of antenna three-segmented; ventral ramus four-segmented; postabdomen distinctly set off from body, usually compressed and bearing anal spines; claws invariably denticulate; may be pectinate; typical ephippium formed. *Oligo.-Rec.*

Daphnia O. F. Müller, 1785 [**Monoculus pulex* De Geer, 1778; OD]. Carapace with sharp caudal spine extending from upper posterior angle, no cervical sinus; surface with polygonal usually rhomboid markings (12). *Oligo.-Rec.*, cosmop.——Fig. 63,*2a,b*. **D. pulex* (De Geer), *Rec.*, USA; *2a*,♀, configuration of valve and gross anatomy, enl. (12); *2b*, subfossil (Conn.), *D. pulex*-type claw, enl. (41). [Other subfossils are known from Ger.(Schleinsee, Grossen Plöner Sees, 41, 47) and USSR(Moscow, 90).]——Fig. 63,*2c*. *D. longispina* (Müller); subfossil from Aus.(Längsee), *D. longispina*-type claw and postabdominal teeth, enl. (41). [Other subfossils are known from Switz.(Zürichsee, 41), USSR(lakes near Moscow), Eng.(Lake Windermere), fossils from Mio. lake deposits (Humboldt F.) of NE. Nevada.]——Fig. 63,*2d*. *D. fossilis* Heyden, Oligo.(Braunkohle), W.Ger.; fossil ephippia bearing two ephippial eggs (0.2-0.4 mm. diameter), enl. (170b). [*See* also Fig. 62,*2*.]

Family CHYDORIDAE Stebbing, 1902

Fornices extended and covering antennules in whole or part, and uniting with rostrum to form beak that projects in front of antennules (19). *Rec.*

Subfamily CHYDORINAE Stebbing, 1902

Anus on dorsal side of postabdomen with postanal portion bearing denticles; no hepatic caeca. Two summer eggs and ephippial egg. Male with strong hook on first legs (19). *Rec.*

Chydorus Leach, 1843 [**Lynceus sphaericus* O. F. Müller; OD]. Postabdomen ordinarily short, with prominent preanal angle; shape spherical or ovate; rostrum long and acute (19). *Rec.*, cosmop.——Fig. 64,*6a,b*. **C. sphaericus* (Müller), cosmop.; *6a*, entire individual, lat. view, ×120 (12); *6b*, subfossil from Ger.(Wallensen); shell fragment, enl. (41). [Other subfossils are known from Eng. (Arctic bed at Ponder's End, Lake Windermere, 41, 128), USSR (small lakes and bogs near Moscow, 90, 114), Switz. (Wauwiler See, 160), Denm. (Naestved, 108), Aus. (Schwarzsee, Langsee, 16, 40).]——Fig. 64,*6c*. *C. faviformis* Birge, subfossil from USA(Conn.); carapace, ×90 (3).——Fig. 64,*6d*. *C. piger* Sars, USA (Maine); carapace, ×100 (12). [Subfossils are known from Eng. (Lake Windermere, 128), USSR (lakes and bogs near Moscow, 90), Switz. (Wauwiler See, 160), Ger. (Wallensen, 41).]——Fig. 64,*6e*. *C. globosus* Baird, USA; carapace, enl. (12). [Subfossils are known from USSR (Moscow, 90).] [*See* also Fig. 61,*2*.]

Acroperus Baird, 1843 [**A. harpae*; OD]. Crest on head and back, carapace subquadrate, obliquely striated, inferoposteal angle rounded or acute, usually with teeth, postabdomen broad, without marginal denticules (19). *Rec.*, Eu.(Eng.-USSR)-N.Am.——Fig. 64,*3*. **A. harpae*, USA; *3a*, entire individual, lat. view, ×20 (12); *3b,c*, subfossil from Ger.(Wallensen), showing shell and posterior ventral angle, both enl. (41). [Other subfossils are known from Eng. (Arctic bed at Ponder's End, 41), USSR (small lakes and bogs near Moscow, 90), Switz. (Wauwiler See, 160), Aus. (Schwarzsee, Längsee, 16, 40).]

Alona Baird, 1843 [**Lynceus quadrangularis* O. F. Müller, 1785; OD]. Shell subquadrate, surface with longitudinal striae (19). *Rec.*, cosmop.——Fig. 64,*1a,b*. **A. quadrangularis* (Müller); *1a*, postabdomen from USA, enlarged (12); *1b*, subfossil from USSR(Moscow), postabdomen, enl. (90). [Other subfossils are known from USSR (lakes and bogs near Moscow, 114), N.Ger. (small morainal basins and Wallensen brown coal pit, 41), USA(Conn., Linsley Pond, 3), Switz. (Wauwiler See, 160), Aus. (Längsee, 40).].——Fig. 64,*1c*. *A. guttata* Sars; postabdomen from USA, enl. (12). [Subfossils are known from Eng. (Lake Windermere, 128), USSR (lakes and bogs near Moscow, 114), Switz. (Wauwiler See, 160), Aus. (Schwarzsee, Längsee, 16, 40), Ger. (Wallensen, 41).]——Fig. 64,*1d*. *A. affinis* (Leydig); subfossil, from USA(Conn.), postabdomen and claw, ×100 (3). [Other subfossils are known from Eng. (Lake Windermere, 127), Denm. (Naestved,

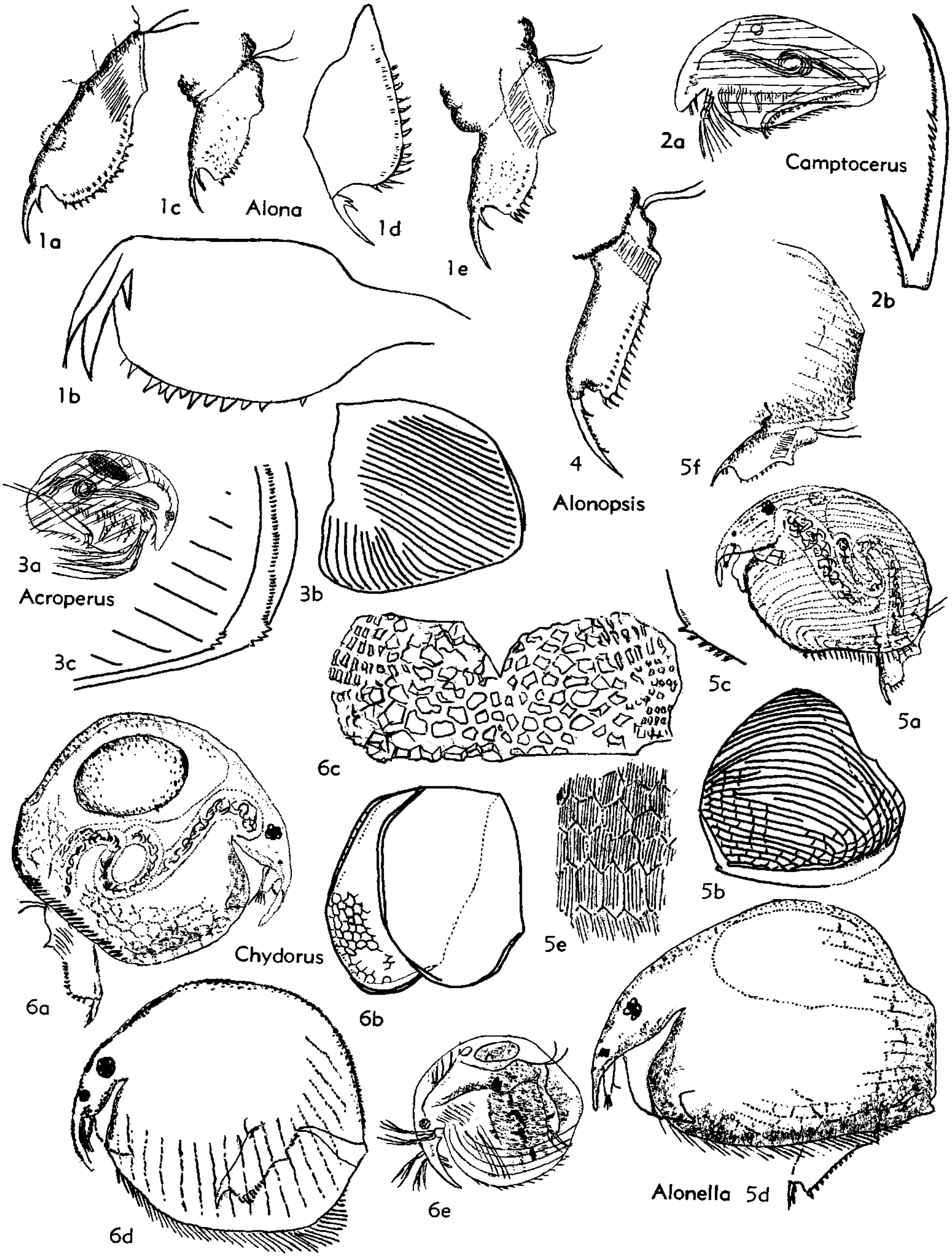

Fig. 64. Chydoridae (Chydorinae) (p. *R*171-*R*173).

108), Aus. (Schwarzsee, Längsee, 16, 40), Ger. (Wallensen, 41).]——Fig. 64,*1e*. *A. costata* Sars; postabdomen from USA, enl. (12). [Subfossils are known from Eng. (Lake Windermere, 128.]

Alonella Sars, 1862 [**A. pygmaea*; OD]. Postabdomen large, preanal angle ordinarily prominent (12). *Rec.*, cosmop.——Fig. 64,*5a-c*. *A. nana* (Baird); *5a*, subfossil from Eng. (Lake Windermere) entire individual, lat. view, ×150 (128); *5b,c*, subfossil from Ger. (Wallensen); shell and posteroventral angle, both enl. (41). [Other subfossils are known from Aus. (Längsee, 40), USSR (small lakes and bogs near Moscow, 90, 114).] ——Fig. 64,*5d,e*. *A. excisa* (Fischer); *5d*, entire individual from USA, lat. view, ×150; *5e*, detail of valve markings, enl. (12). [Subfossils are known from USSR (small lakes near Moscow, 90), Eng. (Lake Windermere, 128), Aus. (Schwarzsee, Längsee, 16, 40), N.Z. (Pyramid Lake, 41).]——Fig. 64,*5f*. *A. exigua* (Lilljeborg); specimen from USA, post. part of shell and postabdomen, ×50 (12). [Subfossils are known from Eng. (Lake Windermere, 128), Aus. (Längsee, 40), Ger. (Wallensen, 41).]

Alonopsis Sars, 1862 [**Alona elongata* Sars, 1861; OD]. Carapace not tumid, postabdomen broad (12). *Rec.*, Eu.(Eng.-USSR)-N.Am.——Fig. 64, *4*. **A. elongata* (Sars); specimen from USA, postabdomen, ×120 (12). [Subfossils are known from USSR (lakes and bogs near Moscow, 106), Switz. (Wauwiler See, 160), Eng. (Lake Windermere, 128), Ger. (Wallensen, Up. Alleröd, 41), Aus. (Längsee, 40).]

Anchistrophus Sars, 1862 [**A. emarginatus*; OD]. Carapace with conspicuous projection on anterventral margin (12). *Rec.*, Eu.-N.Am. Subfossils are known from Eng. (Lake Windermere, 128).

Camptocerus Baird, 1843 [**Lynceus macrourus* O. F. Müller, 1785; OD]. Ovoid shape; crest on head or back; carapace with angles rounded and small teeth at inferoposteal angle; surface longitudinally striated (12). *Rec.*, Eu.-N.Am.-Australia. ——Fig. 64,*2a*. **C. macrourus* (Müller); entire individual from USA, lat. view, ×50 (12). ——Fig. 64,*2b*. *C. rectirostris* Schoedler; subfossil from Ger. (Wallensen), female claw, enl. (41). [Other subfossils are known from Eng. (Lake Windermere, 128), USSR (small lakes near Moscow, 90), Switz. (Wauwiler See, 160), Denm. (Naestved, 108), Aus. (Längsee, 40).]

Graptoleberis Sars, 1863 [**Lynceus testudinaria* Fischer, 1848; OD]. Rostrum broad, semicircular, posterior margin of carapace with 2 strong teeth at inferoposteal angle; shell and head with conspicuous reticulation (12). *Rec.*, Eu.-N.Am.-S. Am.——Fig. 65,*5*. **G. testudinaria* (Fischer); *5a*, entire individual from USA, lat. view, ×100 (12); *5b*, subfossil from USSR (Moscow); portion of carapace, enl. (90). [Other subfossils are known from Switz. (Wauwiler See, 160), Eng. (Lake Windermere, 128); Aust. (Längsee, 40), Ger. (Wallensen, 41).]

Leydigia Kurz, 1874 [**Lynceus quadrangularis* Leydig, 1860; OD]. Postabdomen with numerous clusters of large spines; carapace without markings. *Rec.*, Eu.-N.Am.——Fig. 65,*4a*. **L. quadrangularis* (Leydig); postabdomen of specimen from USA, ×100 (12).——Fig. 65,*4b*. *L. acantheroides* (Fischer); entire individual from USA (La.) showing longitudinally striated carapace, ×80 (12).

Percantha Baird, 1843 [**Lynceus truncata* O. F. Müller, 1785; OD]. Oval carapace with lower extremity slightly curved backward and like upper extremity of anterior margin beset with strong hooked spines (12). *Rec.*, Eu.(Eng.-USSR)-N.Am. (Can.)-C.Asia.——Fig. 65,*1*. **P. truncata* (Müller); *1a*, entire individual from Eng., lat. view, enl. (4); *1b*, subfossil from Ger. (Wallensen), caudal margin of shell, enlarged (41). [Other subfossils are known from USSR (Moscow, near small lakes and bogs, 90, 114), Switz. (Wauwiler See, 160), Aus. (Längsee, 40).]

Pleuroxus Baird, 1843 [**Lynceus trigonellus* O. F. Müller, 1785; OD]. Inferoposteal angle with 2 or 3 small teeth, commonly minute or may be absent; dorsal margin of postabdomen slightly convex, broader behind anus, apex rounded; 14 to 16 marginal denticles (12). *Rec.*, Eu.(Eng.-USSR)-N.Am.-S.Am.-C.Asia.——Fig. 65,*2*. **P. trigonellus* (Müller); *2a*, entire individual from USA, lat. view enl. (12); *2b,c*, subfossil from Ger. (Wallensen), postabdomen, shell, enl. (41).

Rhynchotalona Norman, 1903 [**Alona falcata* Sars, 1861; OD]. Postabdomen stout, thick, bent at anus, truncate at apex, with two to four stout marginal denticles near apex and lateral series of very fine spinules in continuous row almost to anus (12). *Rec.*, Eu.(Eng.-USSR)-Afr.-N.Am.——Fig. 65,*3*. **R. falcata* (Sars); entire individual from USA, lat. view, ×100 (12). [Subfossils are known from Eng. (Lake Windermere, 128).]

Subfamily EURYCERCINAE Kurz, 1874

Anus terminal; two hepatic caeca (63). *Rec.*

Eurycercus Baird, 1843 [**Lynceus lamellatus* O. F. Müller, 1785; OD]. [*non Eurycercus* Blyth, 1844; *nec* Busch, 1851]. Postabdomen very large, flattened, quadrangular, dorsal margin with more than 100 sawlike teeth; claws on spiniferous projection with 2 basal spines, and denticulate (12). *Rec.*, Eu.(Eng.-USSR)-N.Am.——Fig. 65,*6*. **E. lamellatus* (Müller); *6a*, entire individual from USA, lat. view, ×17; *6b*, postabdomen, ×50 (12). [Subfossils are known from USSR (lakes and bogs near Moscow, 90, 114), N.Ger. (small ground moraine basins, 41), USA(Conn., 3); Switz. (Wauwiler See, 160), Denm. (Naestved, 108); Ger. (Wallensen, 41), Aus. (Längsee, 40).]

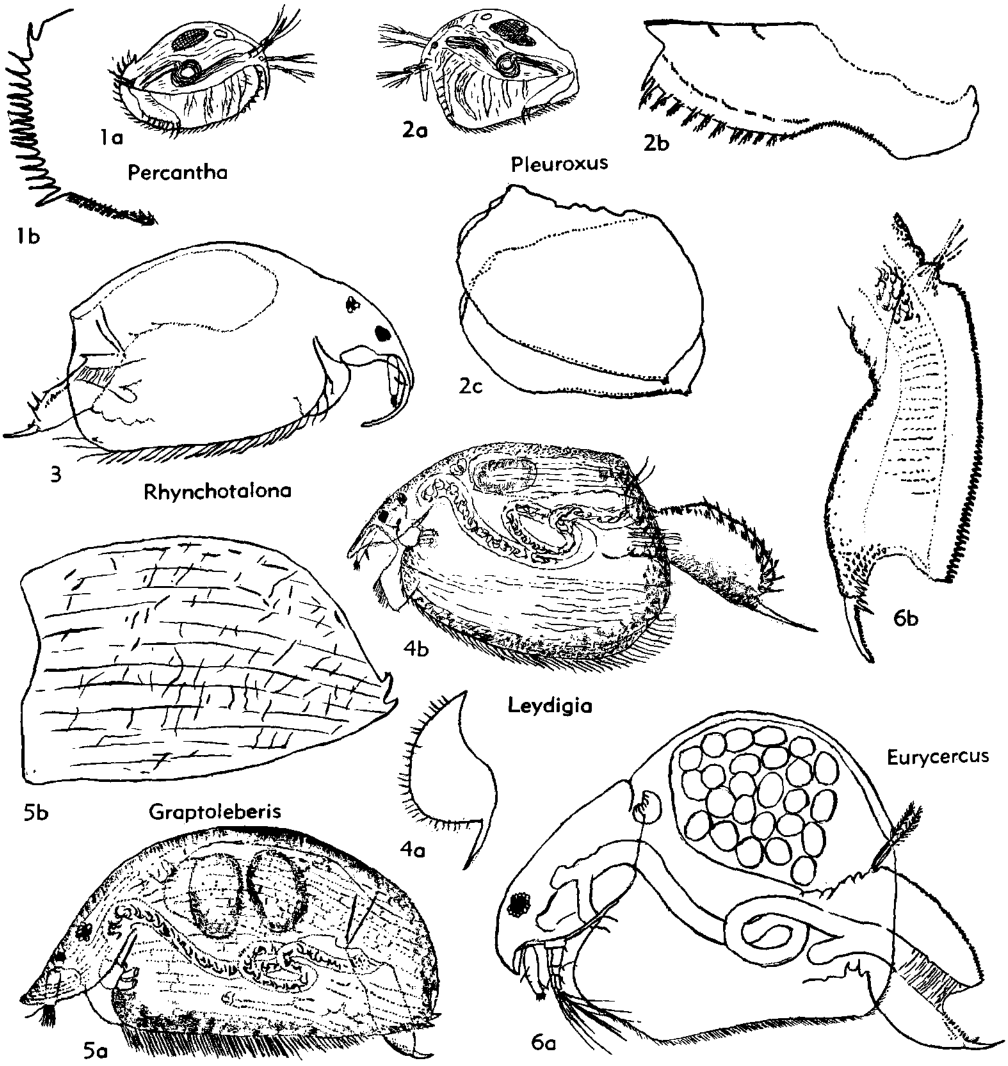

Fig. 65. Chydoridae (Chydorinae) *(1-5)*, (Eurycercinae) *(6)* (p. *R*173).

Family BOSMINIDAE Sars, 1863

Carapace small, rarely greater than 0.5 mm.; six pairs of legs; body short, high, commonly oval or round; carapace covering entire body. *Rec.*

Bosmina Baird, 1845 [**Lynceus longirostris* O. F. Müller, 1785; OD]. Antennules of female approximately parallel to each other, curving backward, fixed to head; carapace thin, inferoposteal angle with spine (=*mucro*); postabdomen subquadrate; claws set in cylindrical process; female with short, blunt rostrum, smaller than male (12). *Rec.*, Eu.-Asia M.-Afr.-N. Am.-S. Am.——Fig. 66, *4a,b*. **B. longirostris* (Müller); *4a*, entire individual, lat. view, ×100; *4b*, postabdomen, enl. (12). [Subfossils are known from USSR (small lakes and bogs near Moscow, 90, 114), Ger. (Wallensen, 41), Switz. (Wauwiler See, 160), Aus. (Schwarzee, Längsee, 16, 40).]——Fig. 66,*4c*. *B. longirostris cornuta* Jurine; subfossil from USSR (Moscow), mucrones of shell, enl. (90). [Other subfossils are known from Switz. (Wauwiler See, 160).]——Fig. 66,*4d,e*. *B. longispina* Leydig; *4d*, subfossil from USA (Conn.), claws, enl.; *4e*, claws of living form, USA, enl. (12).——Fig. 66,*4f,g*. *B. coregoni* Baird; *4f*, subfossil from Aus. (Längsee), claws, enl. (40); *4g*, subfossil from USA (Conn.),

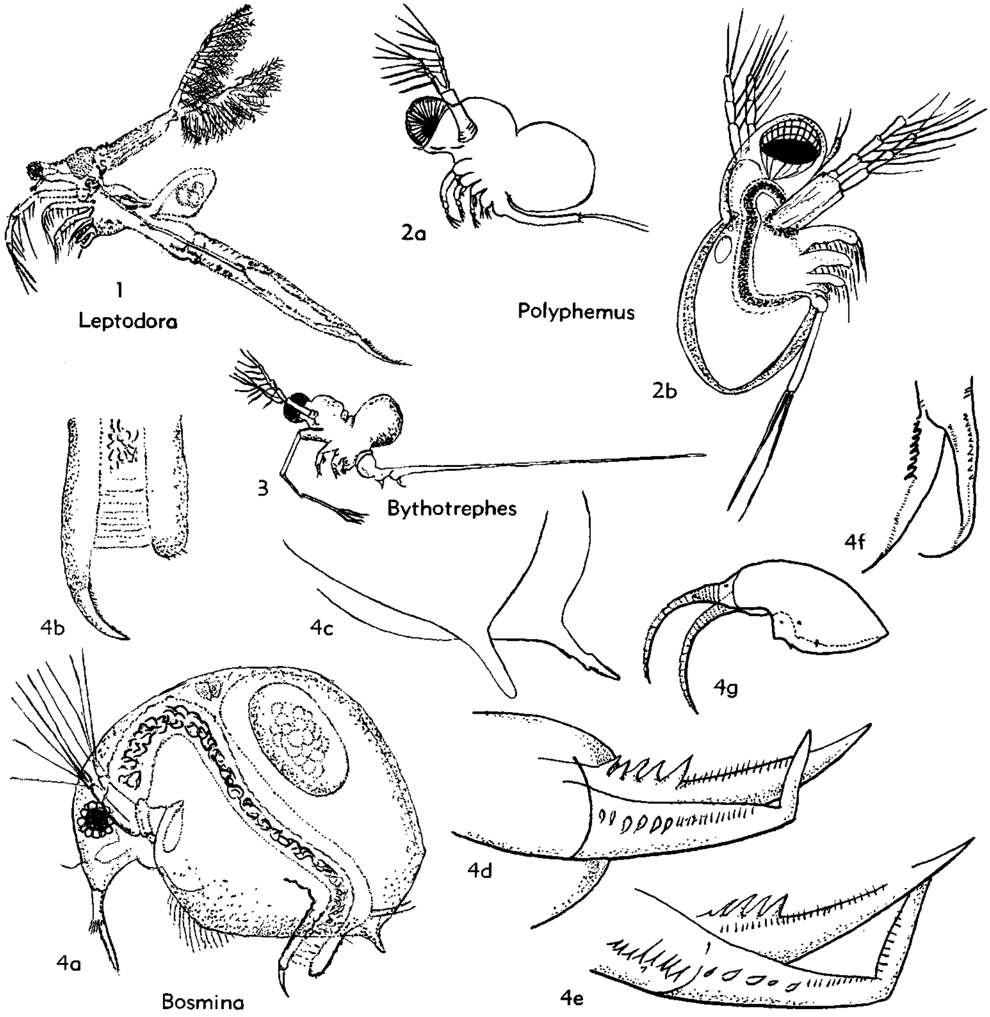

FIG. 66. Bosminidae *(4);* Polyphemidae *(2,3);* Leptodoridae *(1)* (p. *R*174-*R*176).

head shield and rostrum, enl. (3). [Other subfossils are known from USSR (small lakes and bogs near Moscow, 90, 114), Aus. (Lunzer Untersee, Lünnersee, 41). In addition, subfossils from Eng. (Lake Windermere) and USSR (Moscow) are assigned to *B. obtusirostris* SARS.]

Superfamily POLYPHEMOIDEA Baird, 1845

[*nom. transl.* BROOKS, 1959 (*ex* Polyphemidae BAIRD, 1845)] [=tribe Onchyopoda SARS, 1865]

Four pairs of jointed appendages with subcylindrical joints (19). *Rec.*

Family POLYPHEMIDAE Baird, 1845

Carapace not enclosing legs and abdomen, being converted into large globular brood sac (12). *Rec.*

Polyphemus O. F. MÜLLER, 1785 [**Monoculus pediculus* LINNÉ, 1761; SD]. Four pairs of legs not covered by shell; shell only extends to brood pouch. Head separated from thorax through a long notch. Setae of the root (base) of swimming antennae, pinnate. Postabdomen drawn out backward in cylindrical process. *Rec.*, cosmop.——FIG. 66,*2a*. *P.* sp., showing carapace (dorsal posterior bulge) modified to serve as brood sac, enl.

(12).——Fig. 66,*2b*. **P. pediculus* (Linné), Eng.; entire individual, enl. (4).

Bythotrephes Leydig, 1860 [**B. longimanus*; OD]. Body resembling that of *Polyphemus*; huge eye in front of head; brood sac not overhanging caudal process as in *Polyphemus*, hence better defined; extreme elongation of slender caudal process is a distinctive character (12). *Rec.*, Eu.——Fig. 66,*3*. **B. longimanus*; entire individual, lat. view, enl. (167). [Subfossils are known from Eng. (Lake Windermere), mandibles, detached terminal seta of first pair of legs (128) (cf. *Polyphemus*, Fig. 66,*2a*).]

Suborder HAPLOPODA Sars, 1865

Largest of cladocerans (to 18 mm.) with carapace reduced to small brood sac. Legs not flattened but with cylindrical joints; without branchial appendages (19). *Rec.*

Family LEPTODORIDAE Lilljeborg, 1900

Head elongated, slender, eye filling its anterior end; body with four somites, first part bearing six legs and dorsal brood sac (i.e., shell reduced to an egg case); abdomen with three somites, ending in two short claws; mandibles long, slender, pointed, with three spines near apex (19, 67). *Rec.*

Leptodora Lilljeborg, 1900 [**Polyphemus kindtii* Focke, 1844; OD]. Characters of family. [Brooks (17) has observed that "in some ways *Leptodora* is more like an aberrant conchostracan than a derivative of the Eucladocera."]. *Rec.*, Eu.-N.Am.-C.Asia.——Fig. 66,*1*. **L. kindtii* (Focke); entire individual from USA showing appendages and carapace reduced to egg case, ×3 (12). [Subfossils are known from Eng. (Lake Windermere), consisting of characteristic mandibles (128).]

Subclass SARSOSTRACA Tasch, new subclass

Body elongate, lacking carapace, with 11 to 19 pairs of trunk limbs which are either typically branchiopod or modified, and ending posteriorly in single or double furcae; furcal rami unsegmented. *L.Dev.-Rec.*

Order ANOSTRACA Sars, 1867[1]

[*nom. transl.* Calman, 1909 (*ex* suborder Anostraca Sars, 1867)] [=Phyllopoda Latreille, 1802; tribe Gymnota Gerstaecker, 1866; Phyllopoda pisciformis E. Simon, 1886; suborder Phyllopoda anostraca Sars, 1867; tribe Gymnophylla Stebbing, 1902]

Body elongate, without carapace, ending posteriorly in caudal furca; posterior somites without legs (apodous); paired compound eyes pedunculate, small median sessile ocellus in front. Antennules short and slender; antennae large and prehensile in males, reduced in females; trunk limbs (swimming legs) 11 to 19 pairs, none postgenital; rami of caudal furca unsegmented. Genital ducts opening on first two apodous segments which are more or less fused; paired eversible penes in male; ova retained in ovisac formed of united oviducts; young hatched in metanauplius state (21). *L.Dev.-Rec.*

ANATOMY

The Anostraca, or fairy shrimps, lack a shell, as indicated by the name of the order, and have an elongate body composed of distinct somites. The head bears stalked compound eyes, antennules, and antennae. The antennae of males are greatly enlarged and specialized for clasping females during copulation (Fig. 67,*1a,b*).

The thoracic somites bear 11 to 19 pairs of swimming legs. The four to nine abdominal somites are limbless (Fig. 67,*2*), the anterior two being coalesced to form the genital somite. The most posterior somite is the telson, which bears two terminal, platelike, plumose cercopods (caudal rami, furcal rami) (21, 69).

Some interesting variations from the general pattern are observed within the anostracans. The American genus *Thamnocephalus*, for example, is reminiscent of the notostracan *Lepidurus* in that the telson is produced as a thin plate above the anal opening (supra-anal plate in *Lepidurus*) (102).

Each thoracic somite bears a pair of very similar foliaceous appendages (exclusive of the less-developed last pair). These are biramous, lobed, and setose. The functions of food-gathering, movement, and respiration are served by these versatile appendages. The components of each appendage include (1) one or two pre-epipodites which

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[1] Technical advice and literature were provided by Prof. R. W. Dexter, of Kent State University (Ohio), and Prof. J. E. Lynch, College of Fisheries, University of Washington. Dr. A. R. Palmer, of the U. S. Geological Survey, kindly provided photographs of his Mojave Desert anostracans and literature concerning them. Illustrations for this chapter were financed by a Wichita State University Research Award.

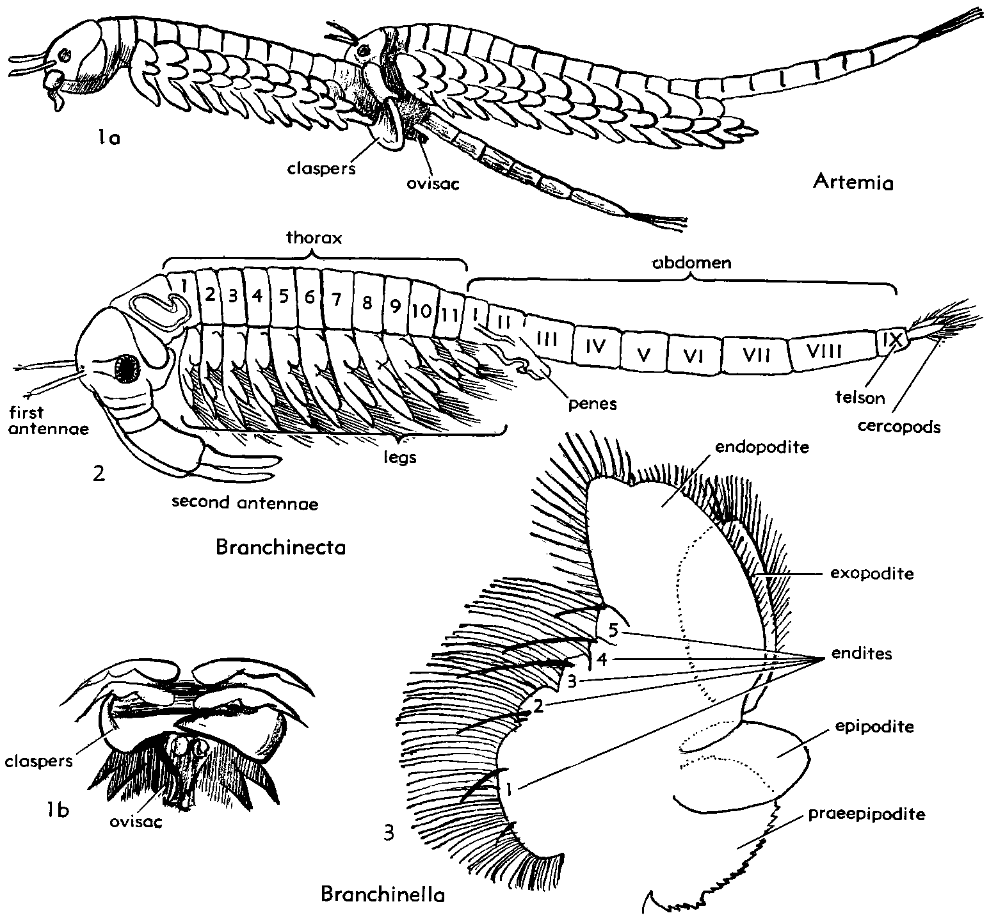

Fig. 67. Morphological characteristics of anostracans.——*1. Artemia salina,* Great Salt Lake; *1a,* a pair of swimming individuals, male clasping mate with claspers in front of ovisac, ×6 (102); *1b,* detail of *1a,* view from beneath of male claspers and ovisac, ×30 (102).——*2. Branchinecta paludosa,* male, terminology after Linder (69).——*3. Branchinella compacta,* male, eighth leg from the front, anterior setae sharply marked; terminology after Linder, ×15 (69).

exhibit variable fusion (lateral view); (2) a spineless epipodite at the base, and an exopodite and an endopodite distally; and (3) along the medial margin, five setae and filament-bearing endites (37) (Fig. 67,*3*).

The sexes are separate (Fig. 67,*1a*; 68,*3a*). Eggs are retained in the uterine portion of the oviduct of females (21), the young being hatched in the metanauplius stage. Parthenogenesis is also known (e.g., *Artemia*) (83). Where both sexes are represented, females outnumber males as much as two to one. Males of *Artemia,* for example, are commonly completely absent from communities of parthenogenetic females (83, p. 37-39). Dexter (37) has observed that males are "not as uncommon as is generally believed" and may outnumber females in a given population.

Although anostracans lack a carapace, they possess a tissue system that Calman (21) considered almost equivalent to an endoskeleton. A marked development of structures to which muscles can be attached includes trabeculae and plates of connective tissue. The external cuticle, by contrast, is almost membranous.[1]

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[1] A. G. Richards (1951, p. 48) indicates that the body wall of *Artemia* gives a positive test for chitin. *See* footnote 1, p. *R*000).

Among living anostracans, anatomical features of taxonomic value are (1) unique characteristics of the antennae at the species level; (2) frontal appendage between the antennae; (3) position and structure of the two penes of males at the familial level (37).

ECOLOGY

SALINITY AND pH

Anostracans generally live in small, temporary, alkaline water pools (83). Dexter (37) has noted that the most usual habitat is in rain pools and temporary ponds formed from melting snow and ice.

One anostracan species *(Branchinecta shantzi)* is known from Alpine lakes (37). The brine shrimp *(Artemia salina,* Fig. 67,*1a*), is an exception to the general rule, since it inhabits inland saline water bodies such as the Great Salt Lake (102). Recently, Lynch (77) described a new anostracan species *(Branchinecta campestris)* found associated with *Artemia salina* in several ponds in Grant County, Washington. He noted that the new species was adapted to life in water "of so high a content of dissolved salts that only *Artemia salina* can develop abundantly in the same habitat." Other anostracans display this salinity tolerance also. For example, laboratory experiments indicate that although adults of *Branchipus stagnalis* rapidly succumb in sea water, they can survive a half month in water containing 1 to 5 grams of NaCl per liter (83, p. 9). Thus, we may conclude that certain anostracans can become adapted to an inland or a marine coastal, brackish-water environment. No marine species of Anostraca are presently known, however.

Small quantities of ammonium salts were found necessary for normal growth of *Branchipus stagnalis,* and this species, as well as *Chirocephalus diaphanus,* were able to live in waters containing up to 0.5 gram per liter of gypsum. This indicates that organic decay in bottom sediments or small amounts of evaporites in solution are not inimical to anostracan survival.

Experiments with *Artemia* eggs (Tasch, 1954, unpublished) have shown that small quantities of phosphates, ferric oxides, and ferrous oxides added to brine solutions inhibited normal hatching. The egg cases were observed to break and the yolk to extrude but no hatching occurred as in normal brine solutions.

Different anostracan species can withstand differing ranges of pH: *Chirocephalus* (6.4 to 7.8), *Branchipus* (7.2 to 7.6), *Streptocephalus* (7.4 to 7.6), although the usual range reported is between 7 and 7.5.

TEMPERATURE

Anostracan genera and species vary in their temperature tolerance. A species of *Branchinecta* from the Antarctic was collected under a layer of ice. Laboratory experiments show that *Branchipus stagnalis* can withstand a range of 17° to 41° C. even when the temperature varies rapidly (83). The most favorable temperature reported is between 15° and 20° C. *Branchipus* becomes inert at 0° C.

FAUNAL ASSOCIATES AND PREDATORS

Three of the branchiopod orders may occur together in the same pool. The anostracan genus *Thamnocephalus* was reported to have occurred in the same Ellis County (Kansas) pool in which the notostracan *Triops longicaudatus* and the conchostracans *Leptestheria compleximanus* and *Cyzicus mexicanus* were also found (102). Species of *Triops* are almost always found with the anostracan *Branchipus stagnalis* in certain localities, and *Lepidurus* species almost always occur with *Chirocephalus diaphanus* and conchostracan young.

Since natural predators of anostracans include frog tadpoles, salamanders, ostracodes *(Cypris, Cyclocypris),* and various insect larvae, one might anticipate that future finds will be made in the fossil record of such predator-prey assemblages. A recent fossil discovery discussed below is an augury of others to come. Mathias observed an egg of *Chirocephalus* that had passed through the digestive tube of a frog and voided in its feces, yet developed into a normal nauplius (83, p. 78).

FOOD

The food of anostracans is mainly plankton. Included in their diet, as reported by several observers, are: infusoria, rotifers, diatoms, and algae (83).

REGENERATION

A remarkable crustacean attribute is the capacity to regenerate torn or lost appendages and body parts. Anostracans such as *Artemia salina* show this capacity to a marked degree, although it should be noted that only 1 or 2 per cent of injured individuals show partial or total regeneration (83, p. 70). Experiments indicate that *Artemia* will show more rapid regeneration in saline water than in fresh water. Other anostracans have demonstrated this regenerative capacity. *Chirocephalus diaphanus,* for example, regenerated severed furca in three or four days.

GEOLOGIC OCCURRENCE

Although the fossil record of anostracans seems to be sparse, published discoveries are of great interest. The Eocene

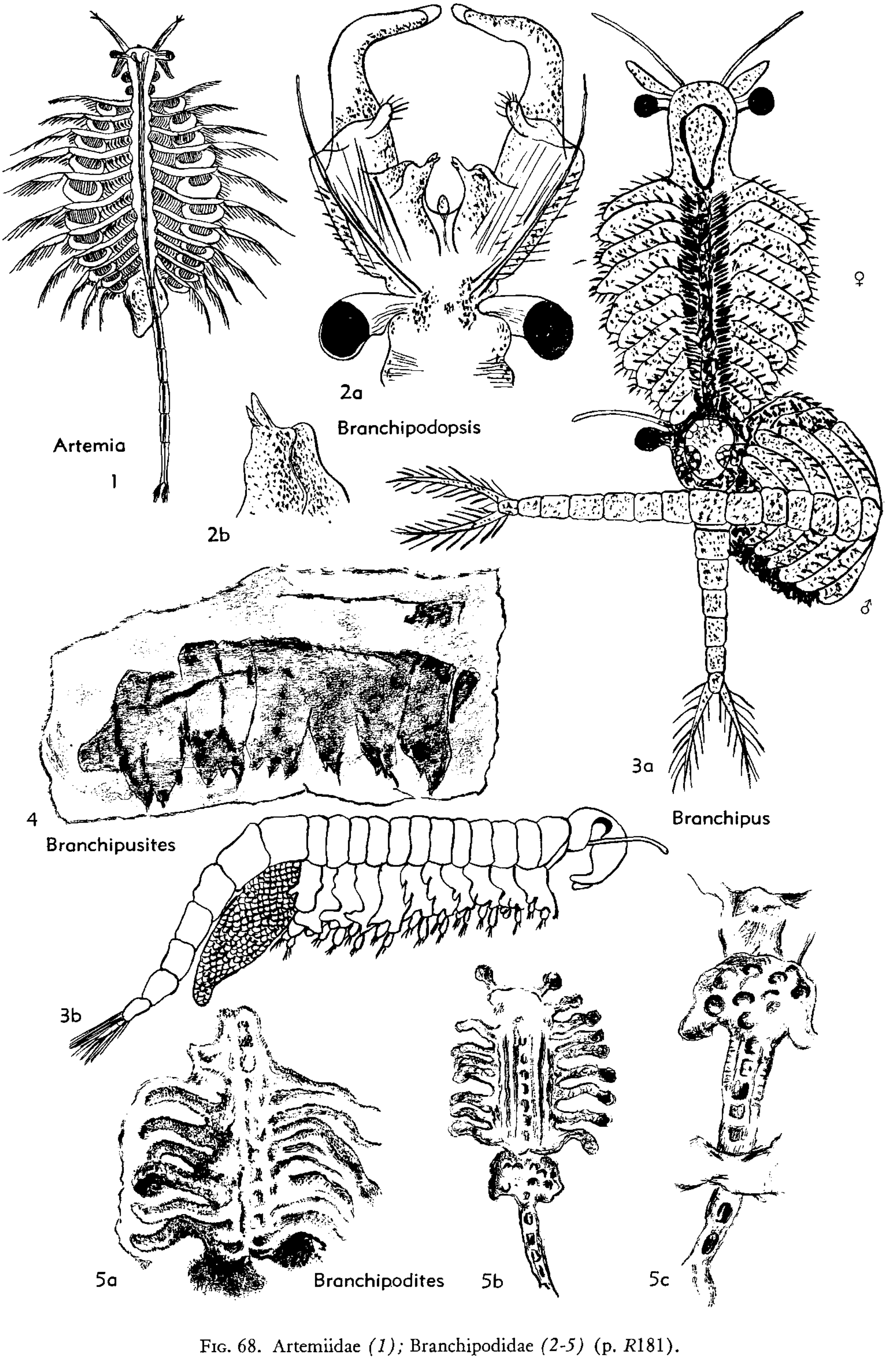

FIG. 68. Artemiidae *(1)*; Branchipodidae *(2-5)* (p. *R*181).

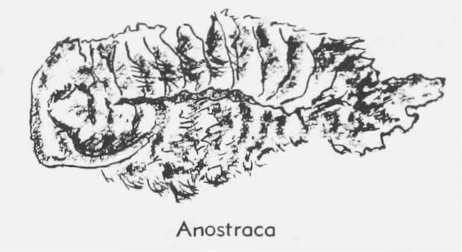

FIG. 69. Fossil anostracan from ?middle Miocene lake deposits in Mojave Desert, California, ×? (170c).

fresh-water argillaceous limestone from the Isle of Wight has yielded, in association with plant remains and an insect fauna, an undoubted *Branchipus*-like anostracan (*Branchipodites*, Fig. 68,5). The plant remains included palm leaves *(Flabellaria)*, seeds of a water lily *(Nelumbium)*, leaves of rushes, and remains of other aquatic plants. The insect fauna included representatives of the orders Coleoptera, Hymenoptera, Lepidoptera, Diptera, Neuroptera, Orthoptera, and Hemiptera, and the class Arachnida. Of the neuropterids, caddis flies were represented by the well-known genus, *Phryganea* (156). Experiments performed by MATHIAS showed definitely that larval *Phryganea* preys on anostracans (83). It is not surprising, then, to find such a predator-prey association in the fossil record.

In 1954 another remarkable arthropod fauna represented by silicified fossils has been reported in calcareous nodules of lacustrine deposits of ?middle Miocene age in the Mojave Desert, California (103, 104). The nodules were associated with borate beds (cf. discussion on evaporites above) and occurred in brown, paper-thin shales, laminated siltstones, and thin limestone beds. A large part (35 percent) of the fauna consisted of fairy shrimps (Fig. 69). The insect fauna was represented by the orders Ephemerida (mayfly nymphs), Odonata (dragonfly nymphs), Thysanoptera (thrips), Hemiptera (true bugs), Coleoptera (beetle larvae), Diptera (midge larvae, pupae, and adults), and the class Arachnida (cf. Isle of Wight Eocene insect fauna).

Since genital organs were not found to be preserved in the Mojave Desert silicified fossil anostracans (released from the nodules by formic acid treatment), no assignment of the 150 specimens has been made. The best specimen in the collection was preserved in an undetermined organic material—all the rest were silicified (A. R. Palmer, 1956, personal communication). One may observe that the insect fauna here too, may include anostracan predators. Among the 150 specimens of the Mojave Desert anostracans, the overall body length was found to be 4 to 5 mm. Parts preserved and recognizable in the head region included antennae, mandibles, maxillules, and maxillae. Typical anostracan legs were also observed (Fig. 69) (104).

The oldest yet-discovered fossil anostracan is *Gilsonicaris*, from the Lower Devonian of Germany (151). Its elongate segmented body and the cephalon bear closest affinities to the anostracans. VAN STRAELEN concluded that it is very close to *Branchipodites vectensis* in all characters except the larger number of trunk segments in *Gilsonicaris*. VAN STRAELEN assigned the genus to a new family, Gilsonicaridae (*recte* Gilsonicarididae). This family is here included in systematic descriptions for completeness, but it should be realized that anostracan assignments at the familial level have little meaning in the absence of preserved genitalia.

Other fossils considered to represent anostracans are doubtful. GOLDENBERG found a *Branchipus*-like impression with only swimming legs and portions of the trunk preserved in Stephanian deposits of West Germany (45). The same deposits yielded a variety of arthropod crustaceans and estheriid conchostracans. WOODWARD found an anostracan-like fossil *(Rochdalia)* in the middle Coal Measures of England (157).

The recent discovery of Miocene cladocerans, noted previously, indicates the probable existence of branchiopod faunas yet to be found in Tertiary nonmarine beds. Anostracan fossils should be sought in any Tertiary formation yielding insect fossils, since likelihood of an insect predator-anostracan prey association exists.

The presence of the brine shrimp *Artemia salina* in Aftonian interglacial deposits (Pleistocene) of the Great Salt Lake is indicated by fecal pellets found in a recently obtained core (at Saltair). The oldest initial occurrence of these shrimps in the Salt Lake area is about 600,000 years before the present, as estimated by me from published core-log data (39). One may anticipate future discovery of fossil brine shrimps in interglacial sediments at different localities. It is likely that they would be preserved as impressions.

Family ARTEMIIDAE Grochowski, 1896

Thoracic somites 11; penes proceeding ventrally close to each other, rigid and apical parts without spines, no sharply defined vesiculae seminales. Single pre-epipodite on each leg; rami of caudal furca variably fused with last abdominal somite or freely movable; ovisac subglobular or cylindrical. Head of males without frontal process; antennae of males biarticulate, not fused or only slightly so at base (46, 69). *Pleist.-Rec.*

Artemia LEACH, 1819 [**Cancer salina* LINNÉ, 1758; OD]. Postgenital region with eight somites; distal segment of male clasping antennae compressed and blade-shaped. *Rec.*, cosmop.——FIG. 68,*1*. **A. salina* (LINNÉ), USA(Conn.); ventral view, ×6.5 (102). [*See* also Fig. 67,*1*.]

Family BRANCHIPODIDAE Simon, 1886

[=restricted DADAY, 1910 (30); *emend.* LINDER, 1941 (69)]

Like *Artemiidae* in number of somites and genital organs except that apical parts of penes bear several spines. Basal segments of antennae in males coalescing medially in so-called clypeus (Fig. 68,*2b*) (69, 129). *?U.Carb., ?Eoc., Rec.*

Branchipus SHÄFFER, 1776 [**Cancer stagnalis* LINNÉ, 1758; OD]. Penis without basal process; apical segment or copulatory part of penis elongate, cylindrical, and on both lateral sides serrate-denticulate; ovisac short, oval-shaped, sharply rounded at posterior apex, forming prominent tubercle above in middle. *Rec.*, Eu.-Asia-Afr.——FIG. 68,*3*. **B. stagnalis* (LINNÉ); *3a*, copulating pair (Fr.), enl. (83); *3b*, female (Ger.), lat. view showing ovisac, ×16 (45).

Branchipodopsis G. O. SARS, 1898 [**B. hodgsoni*; OD]. Digitiform, short, plainly sensory outgrowth from distal parts of clypeus (69, 123). *Rec.*, Asia-Afr. (arid regions).——FIG. 68,*2*. **B. hodgsoni*, S.Afr.; *2a*, head of male, dorsal view, enl.; *2b*, lat. dorsal view of clypeus, enl. (30).

?**Branchipodites** WOODWARD, 1877 [**B. vectensis*; OD]. Males with large clasping antennae, females with small antennae and egg pouches; female trunk with 8 pairs of legs; abdominal somites narrow, elongated. Eyes stalked. *Eoc.*, Eng.——FIG. 68,*5*. **B. vectensis*, Bemdridge Ls. (freshwater), Isle of Wight; *5a*, thorax and paired legs, ×11; *5b*, female with egg pouch, eight pairs of legs, and stalked eyes, ×14; *5c*, ventral view of egg-pouch containing eggs, and abdominal somites, ×19 (156).

?**Branchipusites** GOLDENBERG, 1873 [**B. anthracinus*; OD]. Preserved eight trunk somites with lateral appendages that resemble lamellar branchial feet of *Branchipus*. *U.Carb.(Stephan.)*, W.Ger.——FIG. 68,*4*. **B. anthracinus*, Saarbrücken; lat. view showing *Branchipus*-type lamellar branchial feet and eight thoracic somites, ×15 (45). [*See Arthropleura*, p. R617.]

Family BRANCHINECTIDAE Daday, 1910

Thoracic somites 11; penes proceeding ventrolaterally to laterally, widely separated from each other; male antennae not fused basally and terminal segment not laminate (30, 69). *Rec.*, Eu.-Asia-N.Am.-S.Am.

Branchinecta VERRILL, 1869 [**Branchipus paludosus* O. F. MÜLLER, 1788 (=*B. arctica, B. groenlandica* VERRILL, 1869); OD]. Basal segment of male clasping antennae serrate on inner margin (30, 152). *Rec.*, N.Am.(Alaska-Can.-Greenl.)-N. Eu.——FIG. 70,*1*. **B. paludosa* (MÜLLER), N. Greenl.; *1a,b*, ♂ and ♀, lat. views, ×5 (102). [*See* also Fig. 67,*2*.]

Family CHIROCEPHALIDAE Daday, 1910

Thoracic somites 11; penes proceeding ventrally close to each other, sharply defined and mostly with large seminal vesicles. Each leg with two pre-epipodites or only one with deep incision on its edges; male antennae two-segmented, quite separate from each other; basal segment seldom without all outgrowths; frontal appendages missing (30, 69). *Rec*

Chirocephalus PRÉVOST, 1803 [**C. diaphanus* (=*Cancer stagnalis* SHAW, 1791; *Branchipus diaphanus* MILNE-EDWARDS, 1840; *Chirocephalus stagnalis* (SHAW) DADAY, 1910); OD]. Characters of family (30). *Rec.*, Eu.-Afr.-Asia.——FIG. 70,*2*. **C. diaphanus*, Eng.; female, ovisac containing eggs, enl. (15).

Eubranchipus VERRILL, 1870 [**Branchipus vernalis* VERRILL, 1869; OD]. Antennal appendages nearly bilaterally symmetrical with slightly obtuse apex (37, 153). *Rec.*, N.Am.——FIG. 70,*3*. **E. vernalis* (VERRILL), USA(New England); ♂, lat. view, ×3.5 (102).

Family POLYARTEMIIDAE Simon, 1886

Thoracic somites 17 to 19; sharply marked off seminal vesicles absent and penes proceeding ventrally close to one another with

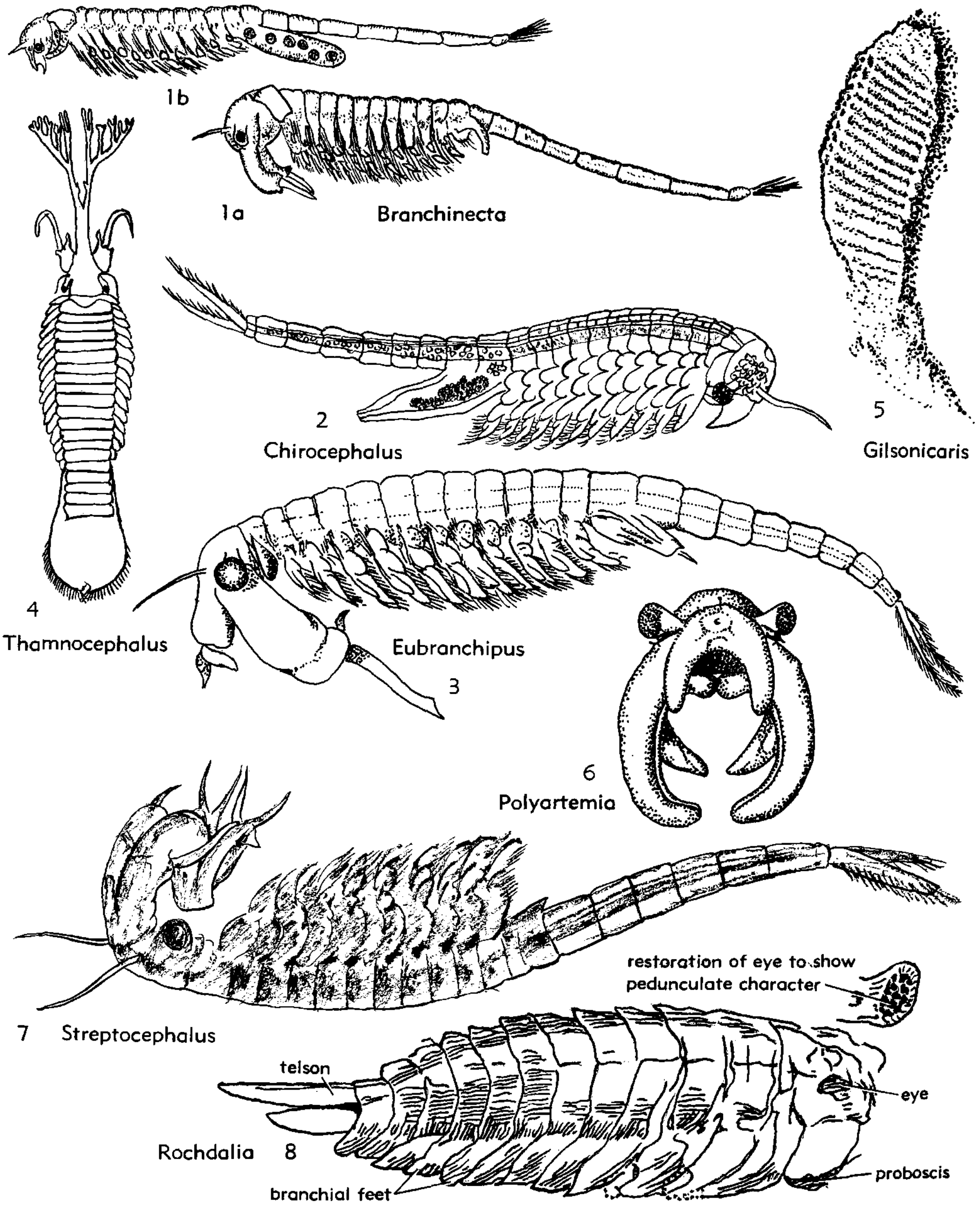

FIG. 70. Branchinectidae *(1)*; Chirocephalidae *(2,3)*; Polyartemiidae *(6)*; Streptocephalidae *(7)*; Thamnocephalidae *(4)*; Gilsonicarididae *(5)*; Family Uncertain *(8)* (p. *R*181-*R*183).

rigid basal parts, which bear two faint median warts (69, 129). *Rec.*

Polyartemia Fischer, 1851 [**P. forcipata*; OD]. Thoracic segments 19. *Rec.*, Eu.-Asia.——Fig. 70,*6*. **P. forcipata,* Arctic; head, enl. (168).

Family STREPTOCEPHALIDAE
Daday, 1910

Thoracic somites 11; penes proceeding ventrally close to each other, lacking sharply defined seminal vesicles; one pre-epipodite on each leg; basal parts of penes soft and flexible; antennae of males with "hand" (Fig. 71) (30). *Rec.*

Streptocephalus Baird, 1852 [**S. similis*; OD]. Characters of family (6). *Rec.*, cosmop.——Fig. 70,*7*. **S. similis,* Santo Domingo, W.Indies; ♂, lat. view, ×8 (6).

Family THAMNOCEPHALIDAE
Simon, 1886

[=*emend.* Linder, 1941]

Like Streptocephalidae in number of thoracic somites and nature of male genital organs (except for upward loop of vas deferens in first genital somite and retractibility of whole penes); differs in that antennae of males lack "hand"; cercopods densely and uniformly setose along margin, generally thin and slender, rarely broadly leaflike and partly running along sides of abdomen (69, 129). *Rec.*

Thamnocephalus Packard, 1879 [**T. platyurus*; OD]. *Rec.*, N.Am.——Fig. 70,*4*. **T. platyurus,* USA(Kans.); ♂, dorsal view, ×1 (102).

Family GILSONICARIDIDAE
Van Straelen, 1943

[*nom. correct.* Tasch, herein (*pro* Gilsonicaridae Van Straelen, 1943)]

Trunk segments 18. *L.Dev.*

Gilsonicaris Van Straelen, 1943 [**G. rhenanus*; OD]. Elongate, regularly segmented body without carapace; 18 trunk somites, of which 11 bear appendages; somites subequal in length, diminishing in size posteriorly; cephalon wider than long and equal in length to first three thoracic somites, divided by longitudinal groove. [Very close to *Branchipodites vectensis* but with many more segments.] *L.Dev.(Hunsrück.)*, Ger.——Fig. 70, *5*. **G. rhenana,* Bundenbach; ventral view of thorax and abdomen, ×3 (151).

Family UNCERTAIN

Rochdalia Woodward, 1913 [**R. parkeri*; OD]. Head rounded, expanded downward in beaklike proboscis; eyes pedunculate; 11 thoracic somites ending in pointed telson; four somites behind head largest, all somites with recurved lobelike swimming feet. *U.Carb.(M.Coal Measures)*, Eng.——Fig. 70,*8*. **R. parkeri* Rochdale; carapace, oblique dorsal view, ×3 (157).

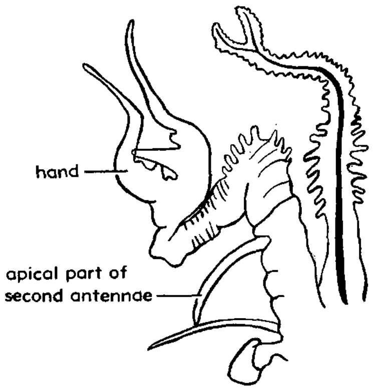

Fig. 71. *Streptocephalus proboscideus,* male, enl. (69).

Rolfe (1967, Palaeontology, v. 10, no. 2, p. 307-313) has presented evidence indicating that *Rochdalia,* heretofore thought to be an anostracan, is indistinguishable from a Carboniferous insect nymph of the family Breyeriidae, order Palaeodictyoptera. It is also possible, as has been suggested previously by authors and reiterated by Rolfe, that such presumed anostracan fossils as *Gilsonicaris* and *Branchipusites* may prove to be a myriapod and a trilobitomorph *Arthropleura,* respectively.

Order LIPOSTRACA Scourfield, 1926

Carapace lacking. Antennae biramous, natatory; trunk limbs about 11 pairs in two series, first three pairs foliaceous and lobed, posterior eight pairs biramous; furcal rami unsegmented, styliform, preceded by another smaller pair of styliform appendages in terminal somite (127). *M.Dev.*

ANATOMY

The Lipostraca, known only from fossils, are elongated branchiopods. Even so, a fully grown adult reaches a maximum of 3 mm. in length. A bivalved shell or dorsal shield is absent. While the head lacks stalked eyes, it has mouth parts, antennules, and antennae. The antennules are very distinctive, being three-jointed. The essential features, found in the larval forms of other branchiopods, are retained in the antennae.

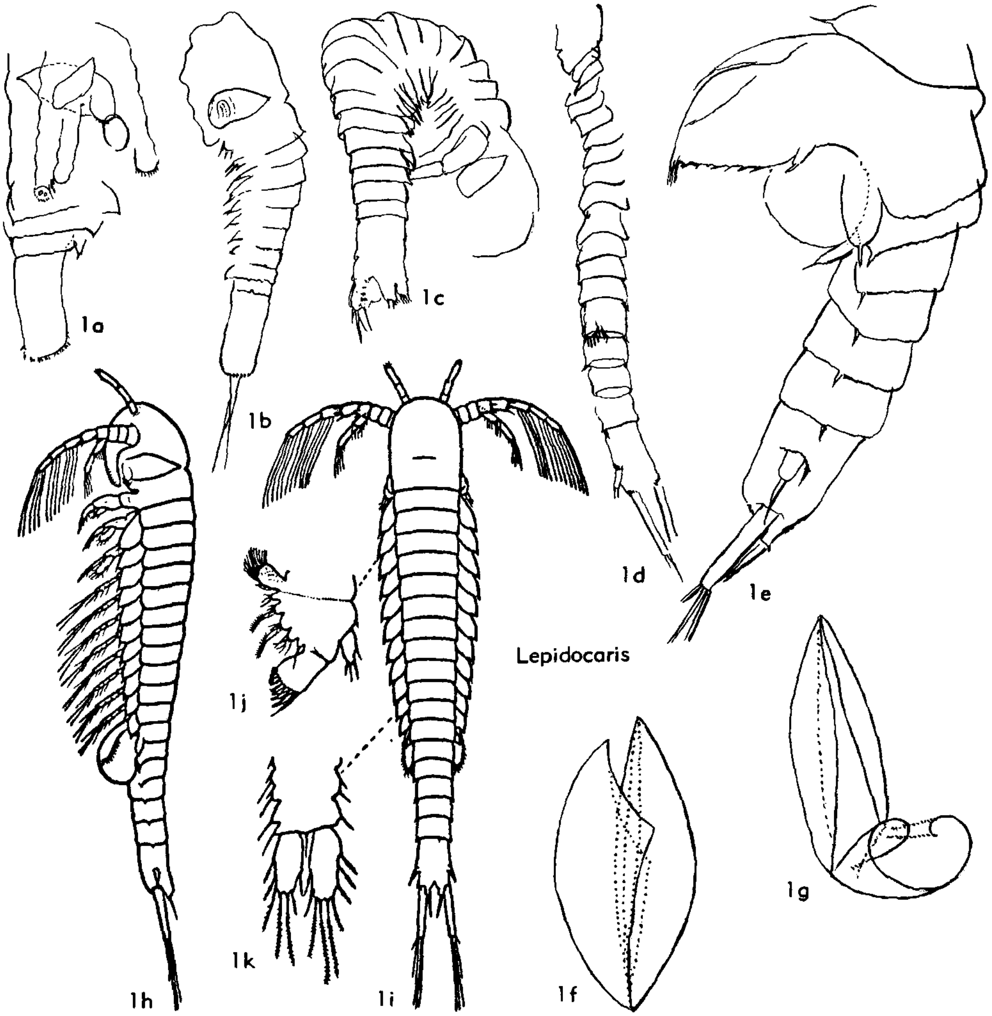

FIG. 72. Lepidocarididae (p. R185).

In adults of both sexes, these are large, biramous, swimming organs. In adult males, the pair of powerful clasping organs arise just behind the mandibles and are developed from the maxillules. In this feature they differ importantly from the anostracans, in which the antennae have been modified to give rise to this organ.

It is especially the 11 pairs of trunk limbs that make lipostracans "somewhat peculiar" branchiopods. Two sharply separate series can be distinguished, the first including the front three pairs. Even these, though of usual branchiopod type (i.e., foliaceous), are modified, for their terminal parts are modified quite uniquely to serve as scraping and rasping organs. The second series of trunk appendages includes the 4th to 11th pairs of limbs, which differ from equivalent pairs in all other branchiopods in having the form of biramous copepod-like swimming feet.

Adult females bear an egg pouch and its cover, which may have developed from modified trunk limbs. In adult males the last two pairs of appendages are modified somewhat from the preceding copepod-type swimming feet.

Finally, the distinctive character of the caudal segment should be noted. It terminates in two short knobs (primary furcae), from the center of which two long articulated processes project backward (secondary furcae). These double furcae are one of several unique lipostracan features.

GEOLOGIC OCCURRENCE

Lipostracans have so far been found only in the Rhynie Chert, Devonian Old Red, of Scotland. The chert is semitransparent rock, so that a drop of oil on the surface of flakes or thin sections brings out astonishingly minute structural details of lipostracans contained in the chert.

Although microscopic in size, the Lipostraca are abundantly represented by both sexes in various stages of growth from minute larvae with only four somites to fully grown adults (Fig. 72,*1*). There has never been any doubt that SCOURFIELD's evidence was adequate to establish a new order. No other trace of pondlife was found with the lipostracans. However, from the same chert beds, arachnids and plant fossils have been described. SCOURFIELD was impressed by the primitive characters seen in lipostracans (such as the biramous II antennae) combined with greater specialization than is found in living anostracans (127). He also noted the absence of associated pondlife. Making these two observations led him to infer that the environment into which lipostracans fitted must have been "very peculiar." As a result, he favored the postulate that the water in which the Rhynie Chert was deposited may have been hot and highly charged with silica.

TASCH (137), from a review of all published evidence concerning the Rhynie Chert biota concluded that "the fifteen points of difference which SCOURFIELD found between lipostracans and anostracans cannot be attributed to the Rhynie thermal environment." Further, "all mutational effects leading to the appearance of the new crustacean order Lipostraca should be referred to specific variations that occurred outside the Rhynie area."

Family LEPIDOCARIDIDAE
Scourfield, 1926

Characters of order. *M.Dev.*

Lepidocaris SCOURFIELD, 1926 [**L. rhyniensis*; OD]. Characters of order. *M.Dev.(Rhynie Chert, Middle Old Red Sandstone),* Scot.——FIG. 72,*1*. **L. rhyniensis*; *1a,* young with four somites, ×2.40; *1b,* young with 10 somites, ×150; *1c,* half-grown individual, ×130; *1d,* adult, with 19 somites, ×150; *1e,* female adult (note egg pouch marked by dotted arc), ×130; *1f,g,* ?egg cases, ×210 (127); *1h,i,* lat. and dorsal views of adult female (reconstr. by Scourfield, 127), ×25; *1j,k,* appendages of trunk, enl. (169).

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MYSTACOCARIDA

By Robert R. Hessler
[Woods Hole Oceanographic Institution]

[Submitted December, 1961]

GENERAL FEATURES

The mystococarids are very minute crustaceans, fully developed adults having a length of only 0.5 mm. Their elongate body (Fig. 73,*A*) is divided into cephalon, maxilliped segment, and thoraco-abdomen.

The cephalon is about one-third the length of the body and bears antennules (first antennae), antennae (second antennae), mandibles, maxillules (first maxillae), and maxillae (second maxillae) (Fig. 73). The anterior end of the cephalon is marked off from the remainder by a deep constriction and is characterized by a pair of anterolateral indentations and a single anteromedial indentation. This anterior division of the head carries the antennules and, dorsally, paired simple eyes (ocelli) (Fig. 73,*B*). Ventrally, a very long labrum extends posteriorly past the end of the cephalon to the region of the maxilliped somite (Fig. 73,*A*).

Functionally the maxilliped is a cephalic limb (Fig. 73,*G*), although the maxilliped somite is not fused to the cephalic complex. However, because of the nature of the musculature, movement of the maxilliped somite with the first thoracic somite is freer than with the cephalon.

Following the maxilliped somite are four thoracomeres bearing reduced limbs. In all other respects these thoracic somites do not differ from the five which follow them, and functionally the two groups of somites cannot be considered as separate tagma. Dahl (1) has labeled the nine somites, plus the telson, as the thoraco-abdomen. A caudal furca occurs at the end of the telson (Fig. 73,*A*).

Pairs of toothed irregular furrows (Fig. 73,*B*) are found dorsolaterally on the posterior end of the cephalon and on the maxilliped somite. Homologous to these are a pair of regular dorsoventral furrows, also toothed, located laterally on each of the thoracoabdominal somites except the telson. The function of these furrows is not known.

APPENDAGES

The antennules are uniramous and consist of eight segments. Each segment carries setae, usually distributed in an irregular, distal crown. This rather inflexible appendage is directed strongly forward and is probably primarily sensory in function.

The antennae (Fig. 73,*C*) are biramous. A fringe of conspicuous setae runs down the ventral edge of the nine-segmented exopod, with setal length increasing distally. The endopod has four segments which bear a few stiff medioventral setae. Subdivision of the protopod is unclear.

The mandibles (Fig. 73,*D*) are strikingly like the antennae. The exopod has seven or eight segments, of which the basal ones never bear setae. The three- or four-segmented endopod carries setae on the medial edge of all its segments. A masticatory process projects from the protopod medially under the labrum. Both the mandibles and antennae function in feeding, as well as locomotion.

The uniramous maxillule (Fig. 73,*E*) consists of a four-segmented endopod and a protopod of uncertain subdivision. It bears large, stout setae which are particularly concentrated on the distal segment, where they aid locomotion, and on the basal two segments, where they are used in feeding.

The maxillae (Fig. 73,*F*) are like the maxillules in form, segmentation, and general setation, but their protopodial segments are even more richly supplied with trophic setae.

In *Derocheilocaris typicus* Pennak & Zinn, and *D. remanei* Delamare Deboutteville & Chappuis, the maxilliped is a biram-

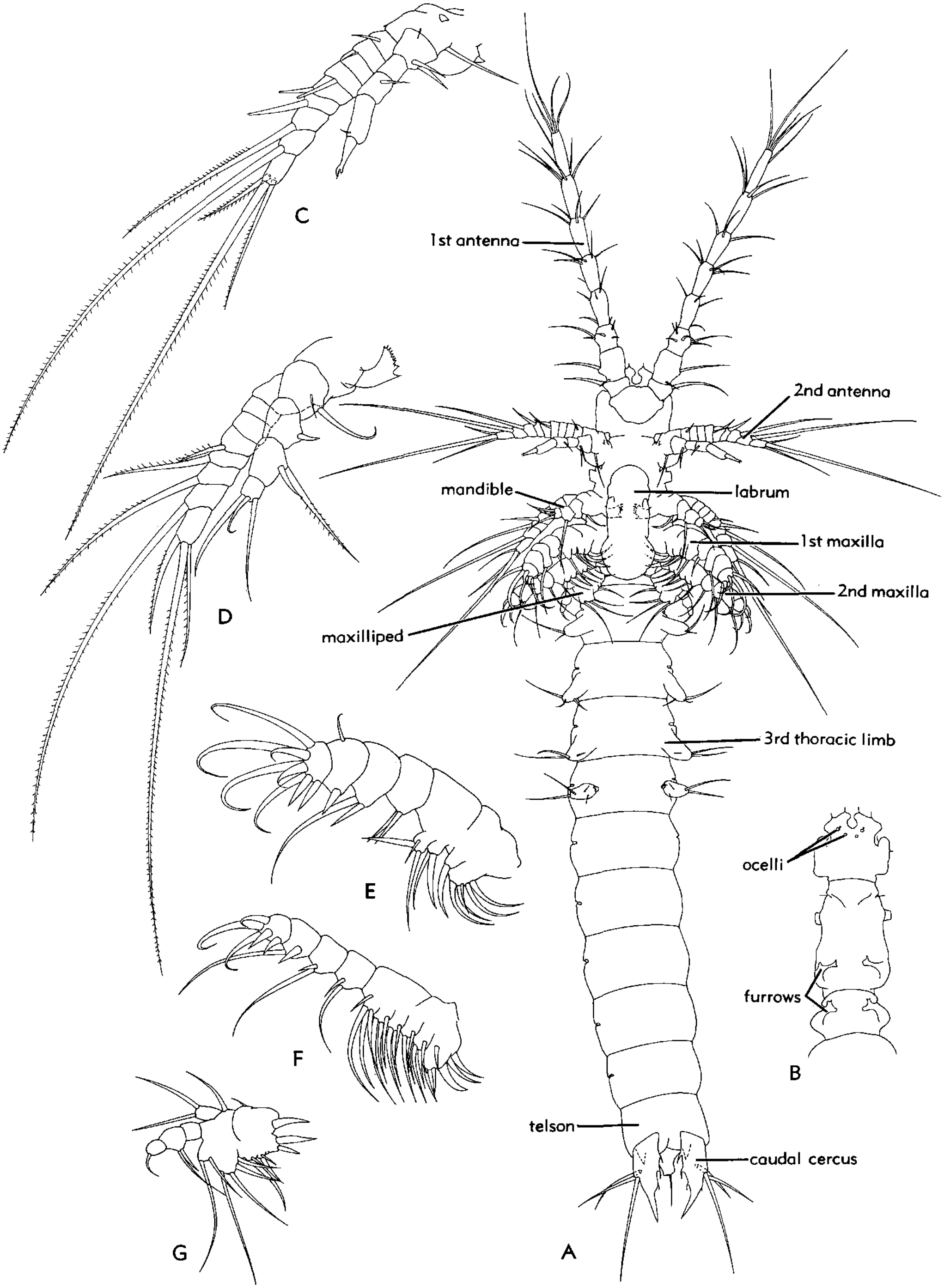

FIG. 73. Morphology of typical adult mystacocarid, *Derocheilocaris typicus* PENNAK & ZINN.——*A*. Complete specimen, ventral view.——*B*. Cephalon and maxilliped somite, dorsal view.——*C*. Antenna.——*D*. Mandible.——*E*. Maxillule.——*F*. Maxilla.——*G*. Maxilliped (*A,B,* ×250; *C-G,* ×500) (Hessler, n).

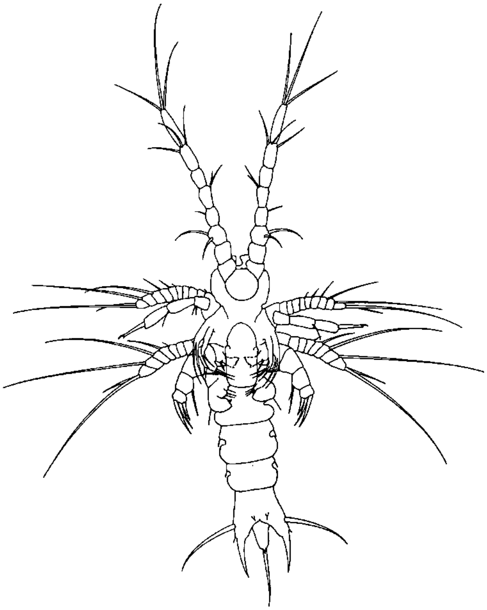

FIG. 74. Stage one metanaupliar larva of *Derocheilocaris typicus* PENNAK & ZINN, ventral view, ×250. At this stage, only antennules, antennae, mandibles, and rudimentary maxillules are present (Hessler, n).

ous limb with a foliaceous protopod (Fig. 73,*G*) (2-4, 6). The endopod has three segments, whereas the exopod is unjointed. In *D. galvarini* DAHL, both endopod and exopod are absent. This limb probably functions only in feeding.

The much-reduced, unjointed limbs of the first four thoracoabdominal somites are nearly immobile. The third pair of limbs bears the genital pore in both sexes and the fourth limb of the male is modified for copulation.

Stout, claw-like caudal rami are used for grooming and to give purchase as the animal moves forward.

DEVELOPMENT

The development of the Mystacocarida is gradual, beginning with a nauplius (Fig. 74) or metanauplius having four postcephalic somites. Limbs and somites appear gradually. There are no metamorphic changes in limb morphology except the eventual loss of the naupliar process of the antennae and mandibles.

MODE OF LIFE

Both larva and adult are totally benthonic, living in the interstitial spaces between sand grains. Their elongate body form is typical of arthropods living in this habitat. Mystacocarids are best known from intertidal beaches, but they occur in subtidal sand as well.

AFFINITIES

The Mystacocarida are thought to be related to the Copepoda, as suggested by the similar tagmosis of the two classes, and by the similarity of the cephalic limbs. Yet it is clear that mystacocarids are more primitive than copepods, for they possess features which unite them to other classes as well. The musculature of the antennules is like that of the cephalocarids and larval branchiopods. The nerve cord is a simple ladder resembling that of the branchiopods, but is even similar to that of the cephalocarids. The cephalic limbs, although like those of the copepods, are most easily related to the cephalocarid condition. Indeed, the mystacocarid mandible, because of its unreduced condition in adults and close similarity to the antenna, is even more primitive than that of cephalocarids. Finally, although the maxillipeds functionally are cephalic appendages, the somite bearing them is free and appears to be only now in the process of cephalization.

DISTRIBUTION

The Mystacocarida are an unusually conservative group. Not only do all the species closely resemble each other, but individual species have extremely wide geographic ranges (4, 6). *Derocheilocaris typicus* extends from Massachusetts to Florida and lives in microenvironments varying from subarctic at one end of this range to tropical at the other. *D. remanei* extends from the Atlantic coast of France, into the Mediterranean, down the coast of Africa, and around the Cape of Good Hope into the Indian Ocean as far as Durban. These extensive ranges exist in spite of the fact that both adults and larvae are entirely infaunal, with the result that gene flow must be very limited.

Class MYSTACOCARIDA Pennak & Zinn, 1943

Body divided into cephalon, maxilliped somite, and thoracoabdomen of ten somites (including telson). Antennules uniramous. Antennae and mandibles similar, biramous; fewer segments on endopods than on multiarticulate exopods. Maxillules and maxillae similar, uniramous, multisegmented; maxillipeds either lacking rami or bearing reduced exopods and endopods. Thoracic limbs reduced. Caudal cerci present. Nerve cord ladder-like, with short commissures. Labrum large. Total size of adult about 0.5 mm. *Rec.*

Since the class is monogeneric, it is not possible to characterize separately the class, order, family, and genus.

Order MYSTACOCARIDIDA Pennak & Zinn, 1943

[*nom. correct.* HESSLER, herein (*pro* order Mystacocarida PENNAK & ZINN, 1943)]

Characters of class. *Rec.*

Family DEROCHEILOCARIDIDAE Pennak & Zinn, 1943

[*nom. correct.* HESSLER, herein (*pro* Derocheilocaridae PENNAK & ZINN, 1943)]

Characters of order. *Rec.*

Derocheilocaris PENNAK & ZINN, 1943, p. 4 [**D. typicus*; OD]. Characters of family. *Rec.*, N.Am.-S.Am.-SW.Eu.-Medit.-Afr.——FIG. 73, 74. **D. typicus*, N.Am.(Atl. Coast); 73,*A-G*, adult, showing morphological features, 73,*A,B*, ×250, 73, *C-G*, ×500; 74, early naupliar larva, ×250 (Hessler, n).

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OSTRACODA

By RAYMOND C. MOORE

The bivalved crustaceans termed ostracodes are represented by nearly 1,000 described genera which range in age distribution from Cambrian to Recent. They include innumerable species known only as fossils and countless collected individual specimens are referred to them. As a group their paleontological importance merits special attention. Accordingly, they have been assigned a *Treatise* volume (Part Q, 442 p., 1961) that removes them from a place in taxonomic sequence of the divisions of Crustacea described and illustrated in the present volume.

The following outline of main divisions of the Ostracoda is given, changed from that published in Part Q by elevating the rank of the assemblage to class, matching others such as Branchiopoda, Cirripedia, Malacostraca, and by omission of superfamilies.

Main Divisions of Ostracoda

- Class OSTRACODA Latreille, 1806
  - Order ARCHAEOCOPIDA Sylvester-Bradley, 1961
  - Order LEPERDITICOPIDA Scott, 1961
  - Order PALAEOCOPIDA Henningsmoen, 1953
    - Suborder BEYRICHICOPINA Scott, 1961
    - Suborder KLOEDENELLOCOPINA Scott, 1961
  - Order PODOCOPIDA Sars, 1866
    - Suborder PODOCOPINA Sars, 1866
    - Suborder METACOPINA Sylvester-Bradley, 1961
    - Suborder PLATYCOPINA Sars, 1866
  - Order MYODOCOPIDA Sars, 1866
    - Suborder MYODOCOPINA Sars, 1866
    - Suborder CLADOCOPINA Sars, 1866

EUTHYCARCINOIDEA

By Raymond C. Moore
[University of Kansas]

INTRODUCTION

Euthycarcinoids are a distinctive group of arthropods which combine some characteristics of merostomes and diplopods with features that are judged to indicate proper placement of them among the Crustacea. They are known only as Lower Triassic fossils from northern Alsace and Moselle in the Saar region and from the Middle Triassic of Australia. The first ones discovered were three rather poorly preserved specimens which Handlirsch (1914) described. He made reconstructions that prove to be erroneous in various ways and interpreted the fossils to be archaic copepods. He named the species *Euthycarcinus kessleri* and because it fitted no recognized group of copepods, erected for it a new order termed Archicopepoda. Not until a half century later has significant information been obtained, so that meanwhile archicopepods have remained as a puzzling, little-understood group, supposedly related to the copepods. An exceptionally fine contribution to knowledge of these fossils recently has been published by Gall & Grauvogel (1964), based on more than 100 specimens, most of which are beautifully preserved. Plates accompanying the descriptions given by these authors adequately document important revisions of Handlirsch's work both in respect to morphology and to interpretation of relationships. They reject the order Archicopepoda as a misnomer and introduce in its place the new name Euthycarcinoidea, with proposal that it should be applied to an independent subclass of the Crustacea.

MORPHOLOGY

Euthycarcinoids have a moderately slender elongate body which is divisible into three tagmata defined as head, thorax, and abdomen (Fig. 75). The length of observed specimens ranges from 5 to 65 mm., with an average of approximately 40 mm.; maximum width of the body is 12 mm. The head is not divided into somites, though attached appendages indicate its derivation by fusion of antecedent anterior somites. Annexed to the head is the first thoracic somite, with appendages functioning as maxillipeds inferred to belong with the buccal complex. The thorax contains 11 somites in addition to the first one, each provided with pairs of uniramous appendages. The abdomen includes five somites and an elongate telson.

The head is semicircular in outline, with evenly rounded front and sides and rectilinear posterior edge, except for small genal spines at the posterolateral angles. The dorsal side, which is gently convex, bears medium-sized sessile eyes, elliptical in outline, close to the lateral margins slightly in front of mid-length. The ventral side, presumably nearly flat, shows a small rostral plate medially in front. Behind this plate is a pair of mandibles and the buccal complex; antennules and a pair of antennae are attached in anterolateral locations. The exoskeletal covering is chitinous, somewhat thickened along the dorsal posterior edge and at the genal angles.

The thoracic somites are protected dorsally and to some extent laterally by five chitinous tergites, each of which is strengthened by a median crest that forms part of a longitudinal ridge running from the head to the telson. The tergites are weakly convex and trapezoidal in outline, with anterior portions projecting beneath neighbors and posterior borders thickened and provided with small spines. The second thoracic somite, bearing one pair of thoracopods, corresponds to the first tergite; the third to fifth somites with three pairs of thoracopods are covered by the second tergite; two additional groups of three somites and six pairs

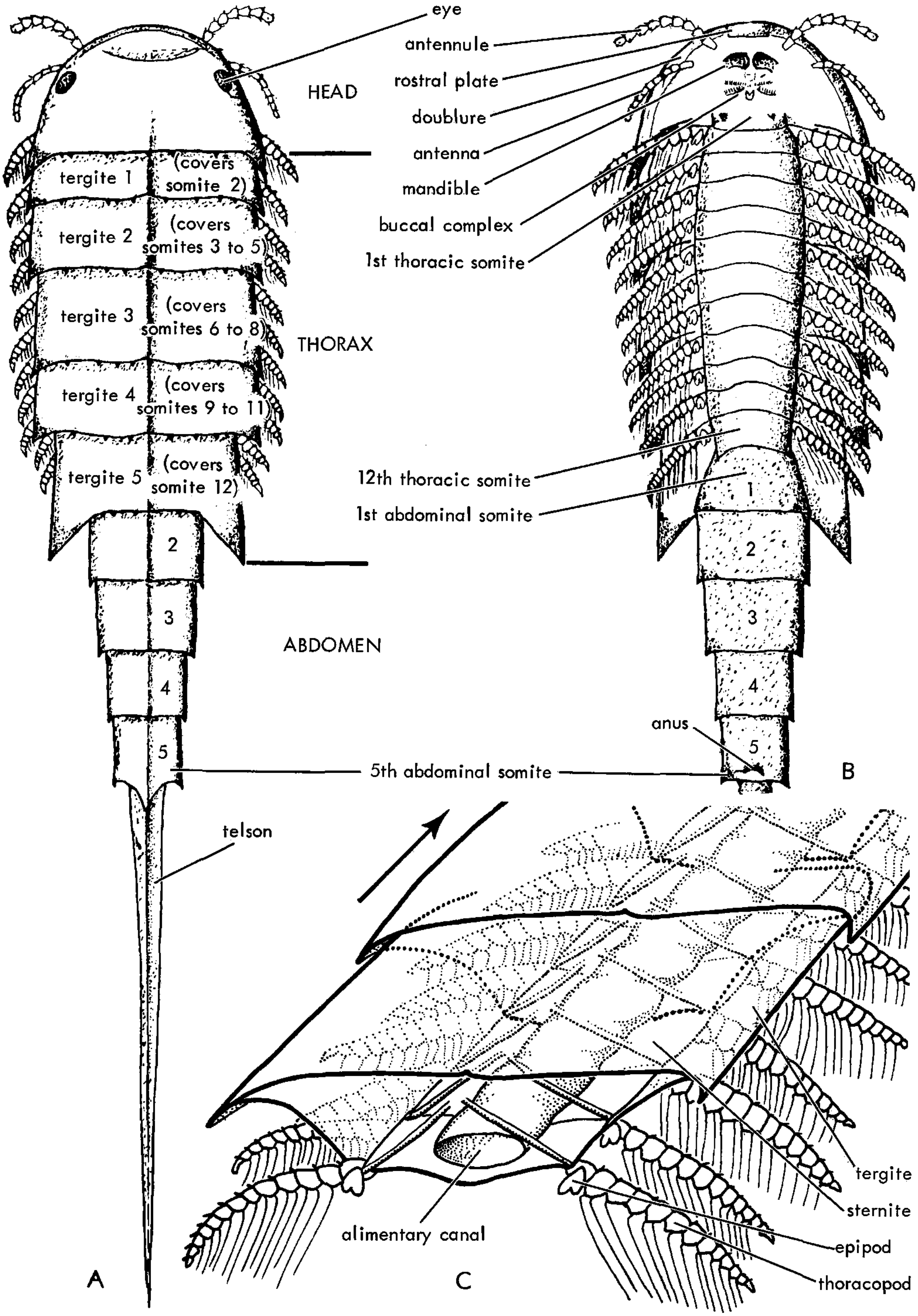

Fig. 75. Morphological features of *Euthycarcinus kessleri* (Handlirsch), L.Trias., France.——A,B. Dorsal and ventral views (reconstr.), ×3.——*C.* Oblique view of mid-portion of thorax with exoskeleton treated as though transparent (arrow points to front of animal), *ca.* ×6 (all mod. from Gall & Grauvogel, 1964).

of thoracopods match the third and fourth tergites; and the last thoracic somite (12th) with one pair of appendages underlies the fifth tergite. Thus, 11 limbs are present on each side of the thorax (Fig. 75,*1*,*2*). The anterior thoracopods are largest and the posterior ones smallest. Each contains 12 or 13 similar segments, the proximal one being identified as a coxa and bearing a small epipod. Posterior sides of the limbs are lined by rows of long setae, providing adaptation for swimming.

In the Middle Triassic euthycarcinoids named *Synaustrus* (3) multiple thoracic somites correspond to tergites *2*, *3*, and *4*, as in *Euthycarcinus*, but only two somites (instead of three) belong with tergite *2* (Fig. 75A). Riek reported two somites associated with tergite *5*, but one of these is abdominal and therefore structure of this region is exactly similar to that of *Euthycarcinus*.

The abdominal somites have subcylindrical sheaths of chitin and are limbless. Four of these skeletal units are visible on the dorsal side but five are seen on the ventral side, for the anterior abdominal somite is concealed by the fifth thoracic tergite. The anus is located on the ventral side of the fifth abdominal somite just in front of the base of the telson. The telson of *Euthycarcinus* resembles the large caudal spike of *Limulus;* it is an elongate rigid structure strengthened by its dorsal keel.

The chief endoskeletal structures of the euthycarcinoids are slender arched struts with outer extremities adjoining bases of the limbs but inner positions somewhat variable (Fig. 75,*3*). They extend above the digestive canal and probably furnished support for it. This canal, identified in fossils by a filling of fine sediment, extends from the head to the terminal somite of the abdomen. Except for minor swellings in each somite, it is featureless.

Several pairs of brownish spots in the cephalic region are inferred to mark attachment places for muscles, chiefly for buccal appendages. Paired elliptical imprints along the axis of the body are interpretable as insertion spots for longitudinal ventral muscles; in the abdominal region the spots are accented by small ferruginous deposits.

ONTOGENY

Some specimens of *Euthycarcinus* have been found with almost perfectly preserved brood sacs, adjacent to which indeterminable remains of small arthropods may occur, seemingly just emerged from eggs. The most diminutive yet-observed individual belonging to the species is a specimen 5 mm. in length. At this stage of growth the head, thorax, and abdomen with telson are already well developed and multi-articulated appendages have appeared.

Comparative examination of specimens of *Euthycarcinus* ranging in length from 5 to 35 mm. indicates that in the course of growth size increase of the thorax is much more rapid than enlargement of the head and that the thorax progressively becomes more slender. No changes in the number of thoracic somites during ontogeny are reported. Abdominal somites become elongated during growth.

The eyes of juvenile individuals are centrally located on the head and during growth of the animal migrate laterally to their near-marginal position in adults.

Molting was facilitated by a splitting apart of the exoskeleton along a line of dehiscence near the front and side margins of the head. Numerous fossils, distinguished by delicacy of cuticle and lack of coloration, are interpreted to represent exuviae—the cast-off exoskeletons of molted individuals.

ECOLOGY

Euthycarcinoids are judged to have been adapted to burrowing in the soft bottom sediments of shallow fresh-water ponds and swampy areas, although undoubtedly they could swim. Evidently they were mud-eaters, as indicated by the fine-sediment filling of alimentary tracts in fossils and by the nature of the buccal apparatus, ill-suited for tearing and chewing large food chunks.

Class EUTHYCARCINOIDEA Gall & Grauvogel, 1964

[*nom. transl.* Moore, herein (*ex* subclass Euthycarcinoidea Gall & Grauvogel, 1964, p. 17)]

Moderately slender elongate body divisible into head, thorax, and abdomen; head bearing pair of sessile eyes near lateral margins and incorporating anterior thoracic somite, antennules and antennae attached to underside of head, which also contains mouth parts; thoracic somites (11 in addition to that joined with head) covered by articulated exoskeleton consisting of five tergites and bearing 11 pairs of multisegmented uniramous thoracopods, each provided with long setae along posterior margins; abdomen with five subcylindrical somites, limbless, but with long styliform telson. *L.Trias.-M.Trias.*

Order EUTHYCARCINIDA
Gall & Grauvogel, 1964

[*nom. transl. et correct.* Moore, herein (*ex* subclass Euthycarcinoidea Gall & Grauvogel, 1964, p. 17)]

Characters of class. *L.Trias.-M.Trias.*

Family EUTHYCARCINIDAE
Moore, new family

Characters of order and class. *L.Trias.-M. Trias.*

Euthycarcinus Handlirsch, 1914, p. 5 [**E. kessleri*; OD, M]. Characters of family. *L.Trias.(Upper Bundsandstein),* France(Alsace-Moselle).——Fig. 75,*1-3*. **E. kessleri*; *1,2,* dorsal and ventral aspects of entire specimen (reconstr.), ×3 (Gall & Grauvogel, 1964); *3,* oblique schematic view of mid-thoracic region, exoskeleton treated as though transparent, anterior direction indicated by arrow, *ca.* ×70 (mod. from Gall & Grauvogel, 1964).

Synaustrus Riek, 1964 [**S. brookvalensis;* OD]. Closely similar to *Euthycarcinus* in morphological features and size, differing only in having one less thoracic somite corresponding to the 2nd tergite. *M.Trias.,* Australia.——Fig. 75A. **S. brookvalensis,* Hawkesbury Series, New South Wales; dorsal view of holotype (reconstr.), ×2 (Riek, 1964).

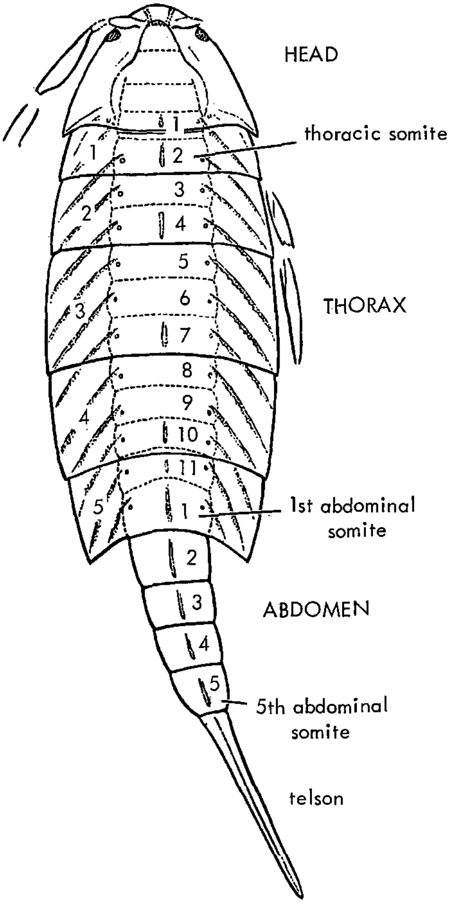

Fig. 75A. Euthycarcinidae (p. *R*199).

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COPEPODA

By A. R. Palmer
[United States Geological Survey, Washington, D.C.]

[Chapter submitted January, 1962; revised July, 1965]

INTRODUCTION

Copepods are small crustaceans, rarely exceeding 5 mm. in length, that are found in nearly all aquatic environments. Both free-living and parasitic forms exist within the group. Only free-living forms have been found as fossils.

The bodies of free-living copepods are typically elongate, distinctly segmented, and commonly subcylindrical in shape. A prominent movable articulation at about the mid-length of the body furnishes a natural basis for differentiating fore and rear divisions **(prosome, urosome)** (Fig. 76,*A*). The prosome includes the head region with its paired appendages, covered dorsally and laterally by a cephalic carapace, and four or five thoracic segments that bear biramous jointed legs with setae that aid in swimming. The urosome includes one or two thoracic somites with appendages, four to six abdominal somites without appendages, and a terminal pair of setose caudal rami.

CLASSIFICATION

The conventional classification of copepods is that of Sars (1901-03) (3) in which three orders of free-living forms and four orders of mainly parasitic or commensal forms were recognized, as follows:

Main Divisions of Copepoda Recognized by Sars (1901-03)

Free-living orders	Commensal or parasitic orders
Calanoida	Caligoida
Harpacticoida	Monstrilloida
Cyclopoida	Notodelphyoida
	Lernaeopoida

Lang (1948) (1) has proposed an alternative classification based on his arguments that Sars' classification places in widely separated orders more or less closely related free-living and parasitic forms. This classification, which stresses morphologic relationships rather than adaptive characteristics, reduces the copepods to four groups that he calls suborders, as follows:

Main Divisions of Copepoda Recognized by Lang (1948)

Progymnoplea (equivalent to part of Calanoida)
Gymnoplea (equivalent to part of Calanoida)
Propodoplea (for one family of Sars' Harpacticoida)
Podoplea (includes all copepods not assigned to other suborders, these being divided among revised groups named Harpacticoida and Cyclopoida)

All known fossil copepods are harpacticoids or cyclopoids in either classification. They are assigned here to the orders Cyclopoida and Harpacticoida following the conventional classification of Sars.

Although body form is sufficient for differentiation of the Cyclopoida and Harpacticoida, precise identification of specimens below the ordinal level requires knowledge of morphologic details of the appendages that are rarely well preserved in fossils. Therefore, meaningful determination of species may be difficult or impossible.

ECOLOGY AND PALEOECOLOGY

Recent copepods are found in nearly all aquatic environments. The majority of the calanoid and cyclopoid species comprise a significant part of the plankton assemblages in marine and fresh standing waters and are a major food for fish. The harpacticoid species are mostly benthonic and have been reported from unusual environments, including interstitial waters of beach sands and damp forest moss. Some cyyclopoid and harpacticoid species may form cysts or cocoons for survival during anaerobic periods

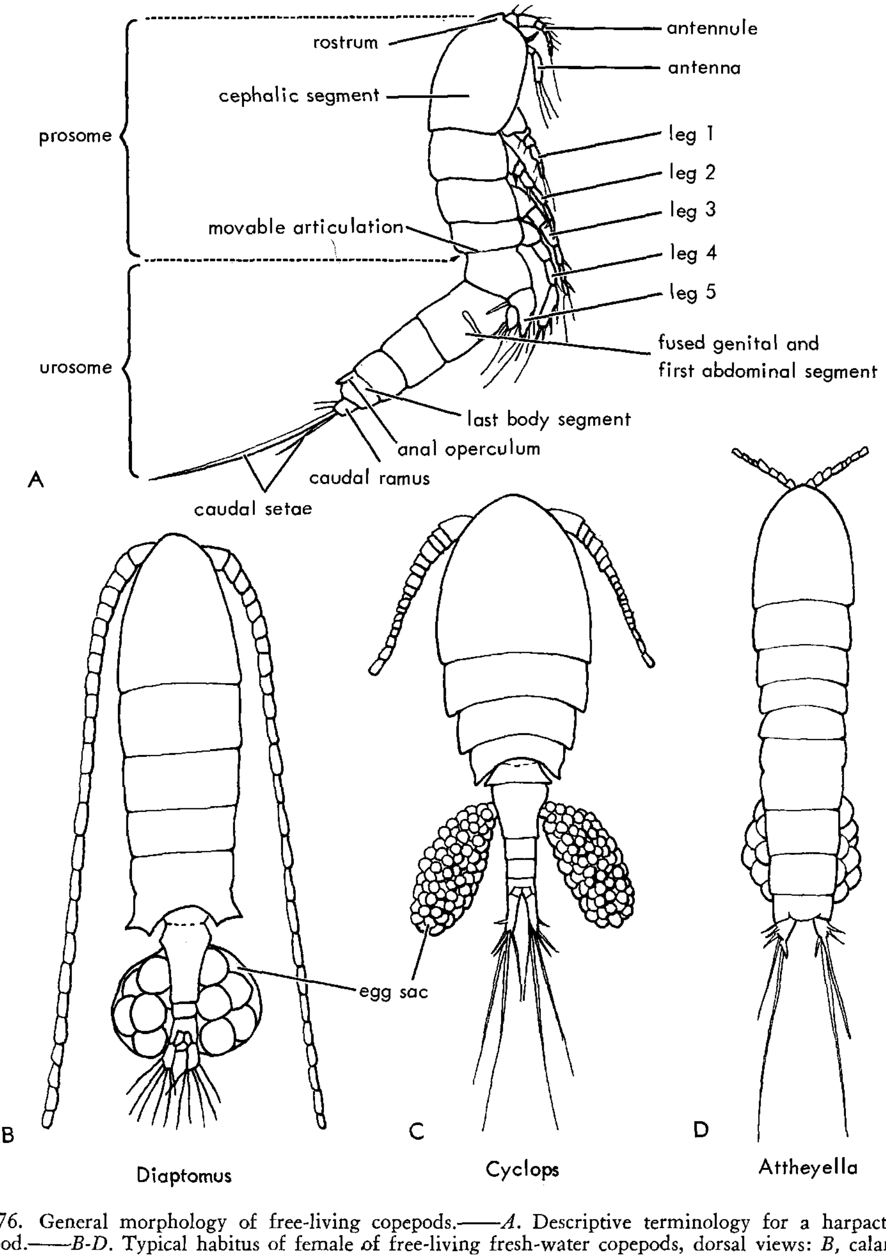

FIG. 76. General morphology of free-living copepods.——*A*. Descriptive terminology for a harpacticoid copepod.——*B-D*. Typical habitus of female of free-living fresh-water copepods, dorsal views: *B*, calanoid; *C*, cyclopoid; *D*, harpacticoid. (From Ward and Whipple, Fresh-water Biology; Fig. *A* slightly modified.)

in lacustrine environments. Cyclopoid cysts are also resistant to desiccation.

Fossil copepods have been found both in North and South America only in lake deposits associated with boron minerals.

Class COPEPODA
H. Milne-Edwards, 1840

Elongate body composed of more or less fused cylindrical chitinous segments which

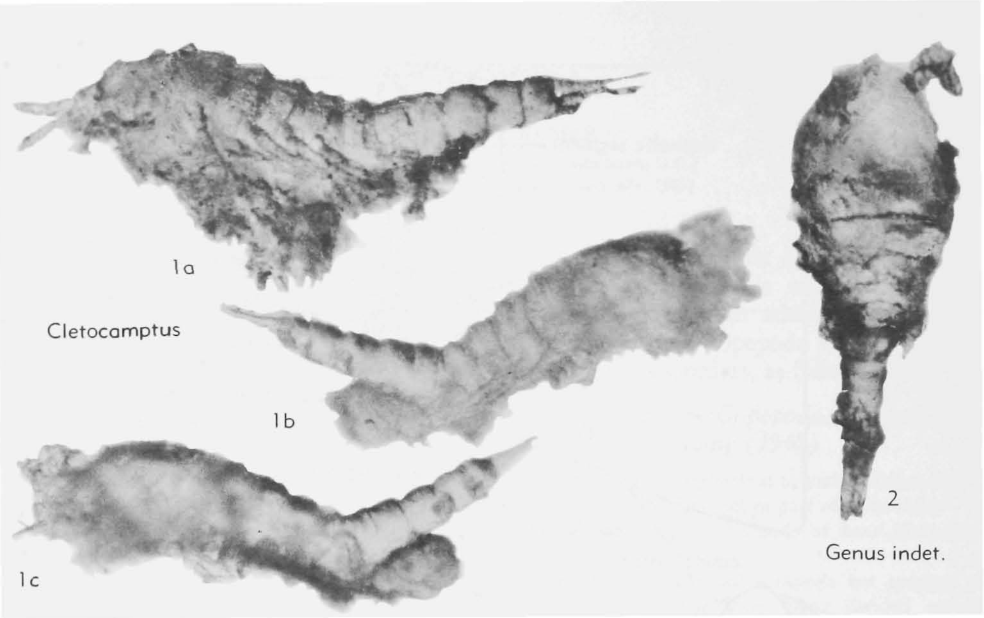

FIG. 77. Cyclopoida *(2);* Harpacticoida (Cletodidae) *(1)* (p. *R*202).

are divided at prominent movable articulation into prosome (in front) and urosome (in rear); prosome including four or five thoracic somites which bear biramous swimming legs and cephalic somite which bears pairs of antennules, antennae, mandibles, maxillules, maxillae, and maxillipeds; urosome including one or two thoracic somites and five to seven limbless abdominal somites, terminal one bearing pair of caudal rami. Body form substantially modified in parasitic groups. *Mio.-Rec.*

Order CALANOIDA Sars, 1903

Prosome distinctly broader than urosome, movable articulation separating them placed between thoracic somites 6 and 7; antennules long (Fig. 76,*B*). *Rec.*

Order CYCLOPOIDA Sars, 1903

Prosome distinctly broader than urosome, movable articulation located between thoracic somites 5 and 6; antennules short (Fig. 76,*C*). *Mio.-Rec.*

Genus undet., Mio., USA(Calif.).——FIG.77,*2*. Genus and species undet., Mojave Desert; dorsal view of body, ×90 (2).

Order HARPACTICOIDA Sars, 1903

Prosome only slightly broader than urosome, movable articulation located between thoracic somites 5 and 6; antennules short (Fig. 76,*A,D*). *Mio.,* N.Am.; *Pleist.,* S.Am. (Arg.); *Rec.*

Family CLETODIDAE T. Scott, 1904

Maxillipeds composed of two, less frequently three segments, ultimate one terminating in movable claw. First leg of swimming type, without claws or clawlike setae on ultimate segment of exopod. Body normal, not markedly elongate; body somites distinct, wider distally than proximally. Antennules reduced; antennal appendage with single segment. Endopods of second to fourth legs usually with reduced number of segments; endopods of male as in female, or endopods of third leg modified. *Mio.-Rec.*

Cletocamptus SCHMANKEVITSCH, 1875 [**C. retrogressus*; ?OD]. Antennules 6-segmented; 5th leg single-segmented in both sexes. *Mio.-Rec.,* N.Am. ——FIG. 77,*1*. *C.* sp., Mio., Mojave Desert lake beds, USA(Calif.); *1a,* left lat. view of female, ×90; *1b,c,* right and left lat. views of female, showing eggs below thorax, ×90 (2).

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BRANCHIURA

By Robert R. Hessler
[Woods Hole Oceanographic Institution]

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INTRODUCTION

The Branchiura comprise one of the most highly specialized and closely circumscribed of all classes of Crustacea. The members of this group are ectoparasites of fishes (although some have been found occasionally on amphibians as well) both in fresh and salt water. Unlike most parasites, they swim quite well and are completely capable of leaving their host. Many of the characteristics of the class obviously are adaptations for this ectoparasitic mode of life.

MORPHOLOGY

The strongly dorsoventrally flattened body is divided into cephalon, thorax, and abdomen (Fig. 78). The lateral portions of the cephalic shield project a variable distance posteriorly as a pair of rounded lobes or alae. A single naupliar eye is located dorsally, while paired compound eyes occur ventrally.

The cephalon carries the usual five pairs of cephalic limbs. The proximal two segments of the uniramous, four-segmented antennules are heavily developed, the second segment bearing a large, posteriorly directed hook. The basal segments of the uniramous, four-segmented antennae are also strongly developed and likewise fitted with a hook. The mouth is located at the tip of a piercing proboscis, while the mandibles are tiny, bladelike jaws at sides of the mouth. When not in use the proboscis folds back into a mid-ventral groove. Anterior to the proboscis is a delicate preoral spine, with which a poison gland is associated.

The maxillules are uniramous. In *Dolops* Audouin, 1837, they are normally developed and bear distal claws, but in the other three described genera they are modified to form paired, stalked sucking discs. The six-segmented uniramous maxillae are characterized by generally having numerous large and small, posteriorly directed spines on their ventral surface. The ventral surface of the cephalon may also be studded with small spines of the same sort. All of these spines serve to prevent the animal from slipping backward on its host.

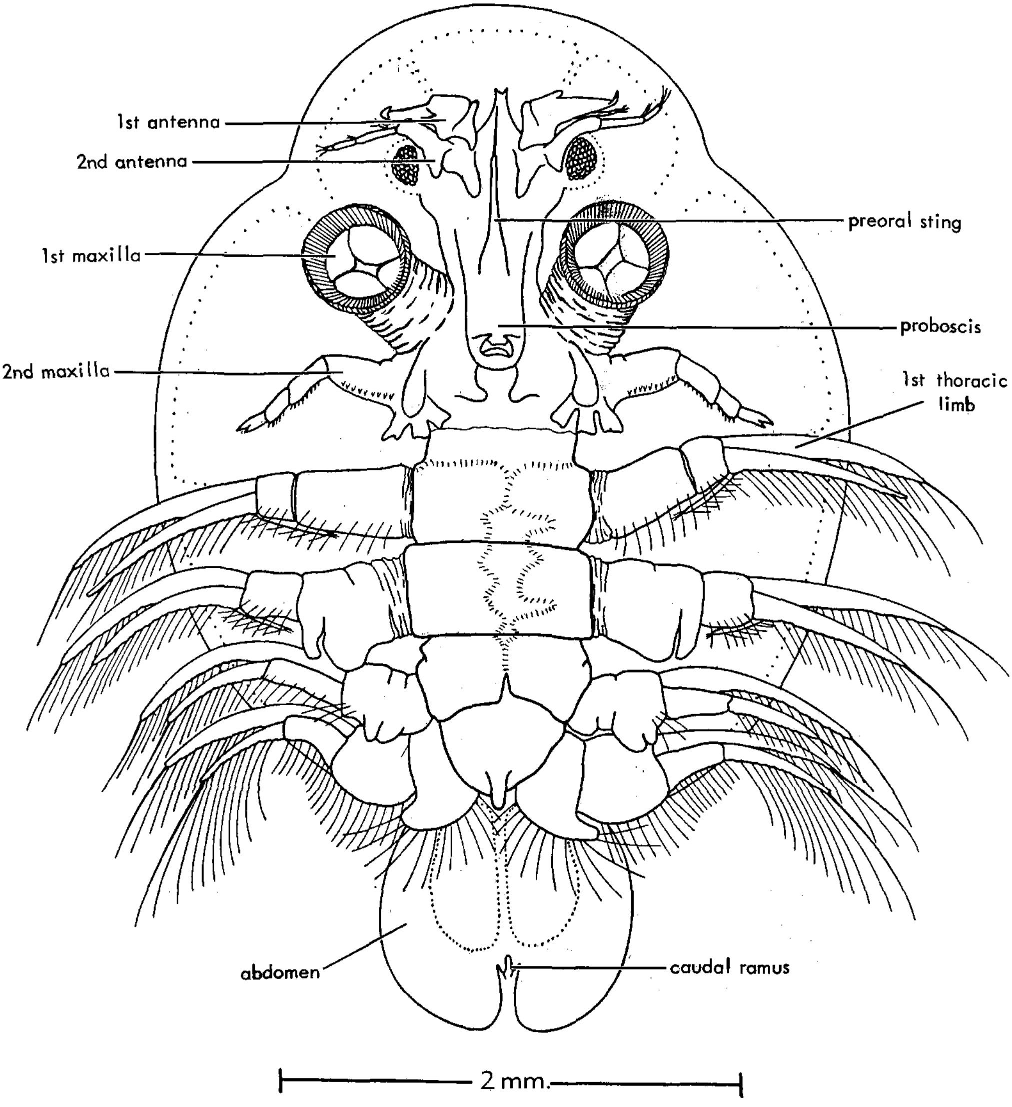

FIG. 78. *Argulus laticauda* SMITH, ventral view of adult male, ×58 (6).

Four thoracic somites occur, of which the first is partially fused to the cephalon. Each thoracic limb extends strongly laterally and serves as a swimming appendage. It has a three-segmented protopod and two rami which are fringed with natatory setae. The unjointed exopod is larger than the endopod and on the first two thoracic limbs has a flabellum which is reflected medially. The endopod may consist of one to three segments. In the male the basal segments of the last three thoracic limbs are modified for copulation.

The abdomen is undivided (although the nervous system indicates that it may consist of two fused somites) and bifurcates posteriorly. A pair of minute caudal rami are present.

DEVELOPMENT

In many species the first free-living stage is a metanauplius (FIG. 79) (5). The mandibles and antennules, in contrast to those of adults, are natatory, much as nauplii of other classes, and no sucker is present on the maxillules.

With later development the antennae are reduced to their adult form. The distal segments of the mandibles are lost, while the basal portion develops into the sides of the proboscis. In *Argulus, Chonopeltis,* and *Dipteropeltis,* the basal portion of the maxillules develops into a sucker. At the same time, thoracic limbs develop.

In other species, the young hatch at a far more mature stage of development.

AFFINITIES

The Branchiura have long been classed under the Copepoda, particularly because of their similarity to the Siphonostoma (6). In conjunction with this determination it was thought that the maxillules were minute processes on the tip of the proboscis, and that the two pairs of subsequent limbs were maxillae and maxillipeds. However, MARTIN (2) has shown that the proboscis is primarily a derivative of the basal portion of the larval mandible and that it does not bear minute maxillules. The last two pairs of cephalic limbs are, then, maxillules and maxillae. Thus, the tagmosis of the Branchiura is basically different from that of the Copepoda and warrants independent status of the group.

Class BRANCHIURA Thorell, 1864

Body dorsoventrally flattened with five pairs of cephalic appendages; mouth on suctorial proboscis which is formed largely from mandibular components; thoracic somites four, first being partially fused to cephalon; thoracic limbs biramous, natatory; abdomen undivided, with caudal rami. [Ectoparasites on fishes.] *Rec.*

The Carboniferous family Cyclidae PACKARD, 1885, containing the genera *Cyclus* DE KONINCK, 1842, and *Halicyne* VON MAYER, 1844, were included by HOPWOOD (1925) in the Branchiura. The resemblance of members of this family to living branchiurans is superficial, however. The cyclids differ from the branchiurans in several basic ways. The mouth is not modified for piercing and the antennae are normally developed, not modified for hooking into the host. The presence of a pair of maxillules modified as suckers is highly conjectural. Finally, the cyclids have too many thoracic limbs and therefore are considered to be unrelated to the Branchiura.

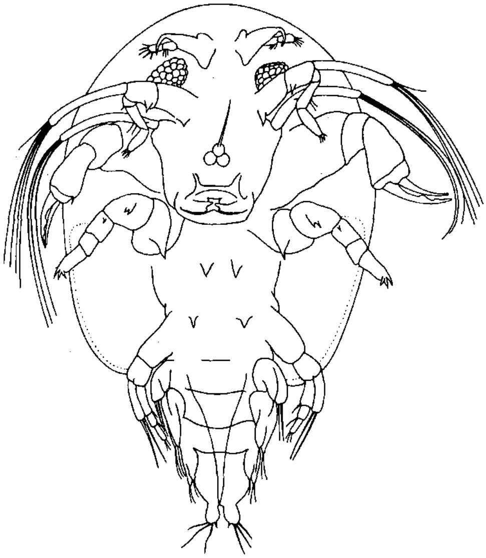

FIG. 79. *Argulus japonicus* THIELE, ventral view of stage-one metanaupliar larva, ×80 (5).

Order ARGULOIDA Wilson, 1932

Characters of class. *Rec.*

Family ARGULIDAE Leach, 1819

Characters of class. *Rec.*

Argulus MÜLLER, 1785, p. 121 [**Monoculus foliaceus* LINNÉ, 1758; SD JURINE, 1806, p. 433] [=*Binoculus* GEOFFROY-ST. HILAIRE, 1732; *Ozolus* LATREILLE, 1802; *Agenor* RISSO, 1826; *Huargulus* YÜ, 1939]. Antennules present; maxillules developed as suckers. Rec., cosmop.——FIG. 78. *A. laticauda* SMITH, N.Am.; adult, showing morphological features, ×25 (6).——FIG. 79. *A. japonicus* THIELE, Japan; nauplius, ×80 (5).

Dolops AUDOUIN, 1837, p. 13 [**D. lacordarei*; OD] [=*Gyropeltis* HELLER, 1857]. Maxillules normally developed, not modified as suckers; preoral sting absent. *Rec.,* S.Am.-C.Am.-Afr.

Chonopeltis THIELE, 1901, p. 46 [**C. inermis*; OD]. Antennules and preoral sting absent; maxillules developed as suckers. *Rec.*, Afr.

Dipteropeltis Calman, 1912, p. 766 [**D. hirundo*; OD] [=*Talaus* Moreira, 1913; *Moreiriella* Mella Leitão, 1914]. Antennules and antennae minute, imperfectly segmented, maxillules developed as suckers; preoral sting reduced; alae greatly elongate. *Rec.*, S.Am.

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CIRRIPEDIA

By William A. Newman,[1] Victor A. Zullo[2] and T. H. Withers[3]

[[1]Scripps Institution of Oceanography, La Jolla, California; [2]Department of Geology, California Academy of Sciences, San Francisco, California; [3]formerly of the Department of Geology, British Museum (Natural History), London (deceased)][4]

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[4] A *Treatise* chapter on the Cirripedia Thoracica was prepared (1953) by T. H. Withers. Following his death, this manuscript was revised and enlarged by Newman and Zullo. They also added sections on methods, anatomy of soft parts, life histories and evolution of the Thoracica, and sections on systematics of the remaining orders (Apoda, Ascothoracica, Acrothoracica and Rhizocephala), thus forming an integrated treatment of the entire class. The completed typescript and illustrations were received in December, 1967.—Editor.