

PART Q
ARTHROPODA 3

CRUSTACEA
OSTRACODA

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CONTENTS

	PAGE
INTRODUCTION (R. C. Moore, H. W. Scott, P. C. Sylvester-Bradley)	Q2
MORPHOLOGY OF LIVING OSTRACODA (H. V. Howe, R. V. Kesling, H. W. Scott)	Q3
REPRODUCTION OF OSTRACODA (R. V. Kesling)	Q17
ONTOGENY OF OSTRACODA (R. V. Kesling)	Q19
SHELL MORPHOLOGY OF OSTRACODA (H. W. Scott)	Q21
DIMORPHISM OF OSTRACODA (H. W. Scott, John Wainwright)	Q37
ORIENTATION OF OSTRACODA SHELLS (H. W. Scott)	Q44
GLOSSARY OF MORPHOLOGICAL TERMS APPLIED TO OSTRACODA (R. C. Moore)	Q47
ECOLOGY OF OSTRACODE ASSEMBLAGES (R. H. Benson)	Q56
TECHNIQUES FOR PREPARATION AND STUDY OF FOSSIL OSTRACODES (I. G. Sohn)	Q64
IDENTIFICATION OF FOSSIL OSTRACODES IN THIN SECTION (S. A. Levinson)	Q70
CLASSIFICATION OF OSTRACODA (H. W. Scott)	Q74
SUMMARY OF CLASSIFICATION AND STRATIGRAPHIC DISTRIBUTION (R. C. Moore)	Q92
SYSTEMATIC DESCRIPTIONS (all authors)	Q99
SUPPLEMENT	Q422
INDEX	Q430

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INTRODUCTION

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The Ostracoda are small crustaceans living in marine, brackish and fresh water. They are characterized by having a bivalved shell hinged along the dorsal margin. Most species are of microscopic size (0.4 to 1.5 mm.), though some fresh-water forms are rather larger (up to 5 mm.), and macroscopic, free-swimming, marine forms (up to 30 mm.) are known, both fossil and Recent. The shell in most species is calcareous, and may be smooth or highly ornamented, but it does not possess growth lines (except rarely when early molts are retained outside later ones), as ecdysis is complete at each instar.

In the existing oceans, ostracodes¹ live from shore line out to depths of about 1,500 fathoms (2,800 m.) or more. They are also found in most nonmarine aquatic habitats, and one terrestrial species has been recorded, living in association with myriapods and isopods in the damp leaf mold of a tropical forest. Ostracodes are also known parasitic or commensal on other Crustacea, on Amphibia, and on fish. Most aquatic Ostracoda are benthonic in habitat, though many belonging to the order Myodocopida are free-swimming during at least part of the life cycle, as are several of the fresh-water Podocopida.

As fossils, they are abundantly represented in limestones, shales, and marls from Cambrian times onward and are in many places so abundant that they form rock coquinas. In the Upper Jurassic of England such a rock (Cypris Freestones, Lower Purbeckian) has been used as a building stone.

The first ostracodes to be named were described by the great Danish naturalist, O. F. MÜLLER, in 1776. Fossil representatives of the subclass were soon discovered, and by 1850 E. FORBES had already zoned the British Purbeck beds by means of Ostracoda. In 1866 G. O. SARS proposed subdivision of the Ostracoda into 4 groups classified as suborders (Myodocopa, Podocopa,

Platycopa, Cladocopa) on the basis of their appendages. This classification has stood the test of time and with minor changes is now universally adopted for Recent ostracodes. Certain Paleozoic groups do not fit the scheme well, however, and in 1953 a separate division (Paleocopa) was proposed by HENNINGSMOEN for their reception. Additional taxa are proposed herein, (Archaeocopida) for Cambrian forms with a flexible, partly calcified shell, thought to be ancestral to the other Ostracoda, and (Leperditicopida) for the distinctive, mostly large, thick-shelled Ordovician-to-Devonian forms included in the Leperditidae.

The foremost student of fossil Ostracoda during the latter half of the 19th century was the Englishman, T. RUPERT JONES. Thirty years after his death, in the 1920's, the greatly increased interest in micropaleontology that resulted from recognition of the value of fossil Ostracoda to explorations for oil led to a sudden revival of work on this group. ULRICH & BASSLER proposed a new classification of Paleozoic ostracodes in 1923, and since then an ever increasing volume of papers has testified to the importance of Ostracoda as indices of stratigraphic horizons. In 1933 C. I. ALEXANDER published an important paper on the finer shell structure of some post-Paleozoic ostracodes, and his work stimulated active research in details of shell morphology which previously had been overlooked. This has provided a firmer basis for taxonomic discrimination and has led to a great increase in the number of generic names proposed. The Ostracoda are now regarded as microfossils second only in importance to the Foraminifera as stratigraphic markers. At certain levels they have the advantage over Foraminifera of being more abundant and occurring in many environments of brackish- or fresh-water facies which are closed to Foraminifera.

Classification of the Arthropoda adopted in the *Treatise* is outlined in tabular form by STØRMER (*Treatise*, Part O, p. O15-O16, 1959). This recognizes division of the true arthropods (Euarthropoda) into four main

¹ Although the spelling "ostracod" is employed by most British and some American writers, the *Treatise* adopts "ostracode" because this word is derived from the Greek ὀστρακώδης (ostracōdes); Webster's New International Dictionary recognizes both spellings.—Editor.

groups (Trilobitomorpha, Chelicerata, Pycnogonida, and Mandibulata), which are ranked as subphyla. The Mandibulata comprises the classes Crustacea, Myriapoda, and Hexapoda. The subclass Ostracoda, described and illustrated in this volume, is not the most primitive or generalized major group of crustaceans but the most abundantly represented among fossils. It is convenient, therefore, to segregate the ostracodes in a separate volume, other crustacean assemblages and the remainder of mandibulates being assigned to *Treatise* Part R. Diagnosis of the subclass Ostracoda is given on page Q100.

Subphylum MANDIBULATA

Clairville, 1798

[*Emend.* from original application as major division of Insecta]

Euarthropods having mouthparts known as mandibles and 2 pairs of accessory feeding appendages called maxillae. Mandibles commonly modified to perform various feeding functions such as cutting, piercing, or sucking, but always present in some form during some stage of life. Either pair of

maxillae sometimes absent or vestigial. *Cam.-Rec.*

Class CRUSTACEA Pennant, 1777

Highly diverse, mostly aquatic mandibulates bearing 2 pairs of antennae. Body usually consisting of 3 main regions, head (or cephalon), thorax, and abdomen; head and thorax commonly fused forming cephalothorax. Body generally covered with hard chitinous carapace impregnated with calcium salts. Respiration by means of gills. Nauplius larva characteristic. *Cam.-Rec.*

ACKNOWLEDGMENTS

Special thanks are expressed to J. R. CORNELL and J. C. KRAFT for permission to use photographs of ostracode genera made by them in connection with doctoral dissertations submitted to the University of Minnesota. Also, assistance in the loaning of type specimens has been given by C. W. COLLINSON, Illinois Geological Survey; G. A. COOPER, U. S. National Museum; JOHN IMBRIE, Columbia University; M. B. MARPLE, Ohio State University; and N. D. NEWELL, American Museum of Natural History. This aid is gratefully acknowledged.

MORPHOLOGY OF LIVING OSTRACODA

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BODY SEGMENTATION AND APPENDAGES

The body of an ostracode is short, laterally compressed, and inclosed within a bivalved, calcareous carapace. The body shows no trace of segmentation, the boundary between head and thorax being represented merely by a slight constriction, but existence of ancestral segmentation is indicated by the nature and distribution of the appendages. A layer of soft tissue, the epidermis or hypodermis, hangs down on each side and secretes the shell.

The cephalic region of an ostracode is formed by a network of strong chitinous rods, which are connected by thin membranes of chitin. This framework includes the forehead and upper lip, fused together as a single structural unit. Attached to the framework are four pairs of appendages

named (in order backward) antennules, antennae, mandibles, and maxillae (Fig. 1). The posteroventral edge of the upper lip forms the anterior margin of the mouth. This rim is roughened or serrate but not toothed. The hypostome is the lower lip, which is located on the ventral side of the body, forming the posterior part of the mouth. It is a somewhat canoe-shaped movable structure with the anterior, open end forming the mouth rim. The maxillae lie parallel to its sides and the first thoracic legs are attached to its posterior points. Many species have two paired structures at the front of the hypostome, chitinous rake-shaped organs embedded in the tissue and soft setiferous paragnaths at the sides. Some ostracodes have a sensory structure (frontal organ) attached to the forehead.

The thoracic region contains various organs of the digestive and reproductive sys-

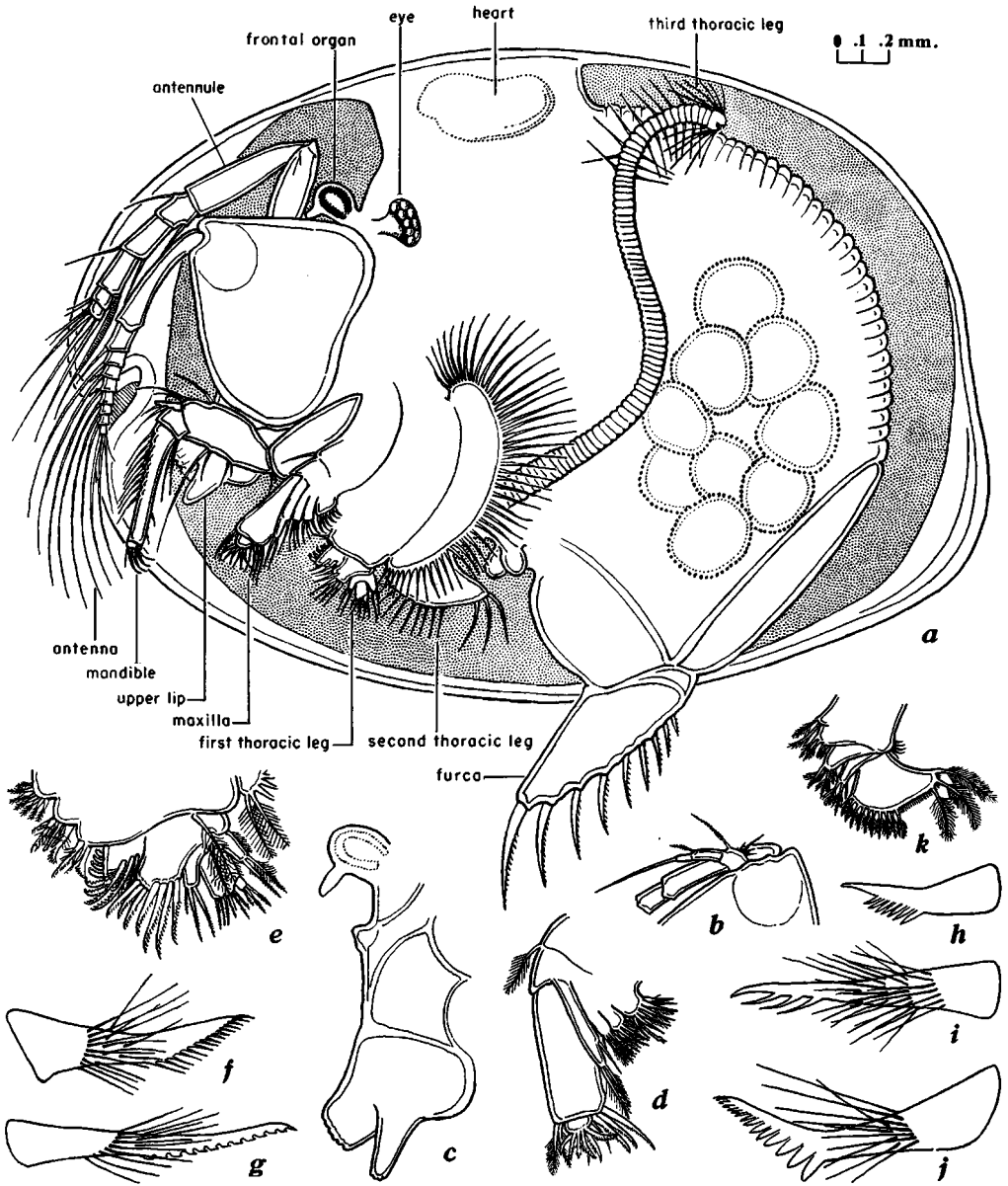


FIG. 1. Morphology of a representative myodocopid (myodocopine) ostracode, *Cypridina norvegica* BAIRD, Recent (Cypridinidae). *a*. Female with LV removed; eggs shown in one uterus at rear of body; genital lobes below base of 3rd thoracic leg.—*b*. Right antenna; inner face of endopodite and 1st podomere of exopodite.—*c*. Frontal organ and upper lip.—*d*. Left maxilla.—*e*. Left 1st thoracic leg; details of protopodite and endopodite.—*f-j*. Setae from protopodite of 1st thoracic leg.—*k*. Left 2nd thoracic leg. (Figs. *a*, *b*, *c*, and *k* to scale in upper right corner; from KESLING, after SARS and SKOGSBERG.)

tems, and bears one to three pairs of **thoracic legs**. An abdomen is wanting. In the great majority of ostracodes, a pair of **furcal rami** forms the posterior end of the body.

All arthropod appendages are composed of a number of segments called **podomeres**. The typical crustacean appendage is biramous, consisting of a single basal branch, (**protopod**) composed of two podomeres (**coxa, basis**). The basis bears two branches, an inner called the **endopod** and an outer called the **exopod**. Very few appendages of ostracodes have exactly this arrangement. Some have the coxa and basis fused to form a single podomere; some have an extra podomere (**precoxa**) in the protopod; some lack an exopod; some, in addition to both endopod and exopod, have excess lobes such as the **epipodial plate** on the outer surface or various **endites** directed inward from the protopod.

The antennules (or "first antennae" of many European workers) are uniramous, the exopod being lost; they are attached to the forehead. Typically each antennule is composed of eight podomeres, but through fusion a condition may be approached in which there are only five. The protopod, composed of one or two podomeres, is much larger than the remainder, and houses a nervous ganglion. The antennules of some species have a locomotor function (swimming, climbing, or digging), or they may be sensory, or serve as balancing organs. In the Myodocopida they are sexually dimorphic and in some species are used in copulation, the distal setae of the male being equipped with suctional structures (Fig. 2*b,c*); in the Halocyprididae (Fig. 3*b*) most of the setae of the male are longer than those of the female, and one is provided with a special sensory organ. In the Cladocopina they are used in swimming, being equipped with long natatory setae, which originate only on the small distal podomere (Fig. 4*a,c*). In the Platycopina the setae are strong and clawlike (Fig. 5*a*). In the Podocopina the antennules may bear long, feathered setae (Fig. 6) used for swimming or balancing, or they have clawlike spines that serve for digging or climbing (Fig. 7*a*).

The antennae ("second antennae" of some authors) are locomotor organs used for

swimming, walking, or climbing. They are biramous, although the exopod is much reduced in some forms. They are attached to the sides of the head near the junction of the forehead and upper lip, from which they curve forward and downward. The protopod is large, strong and movable, the two podomeres being fused or separate. In the Myodocopida (Figs. 1*a*, 3*a*) the exopod is long and bears long natatory setae, but the endopod is shorter (Fig. 1*b*) and in many species dimorphic and developed as a clasping organ in the male (Fig. 3*b*). In the Cladocopina (Fig. 4*d*) both exopod and endopod bear long, stiff setae to aid swimming. In both Myodocopida and Cladocopina the protopod is long, strong and undivided, but in the Platycopina the coxa forms a knee with the basis, and both endopod and exopod are well developed, broad, flattened, and equipped with stiff setae to aid in walking (Fig. 5*a*). In the Podocopina the exopod is much reduced in most forms (Figs. 6*a,b*; 8*a*); in the Cytheracea it is developed as a long, curved, hollow seta (Fig. 7*a*) serving as the duct for a powerful gland, and in some forms is dimorphic. The endopod in the Podocopina is leglike with four podomeres at most. Claws or natatory setae on the endopod are quite variously developed. Some are dimorphic, some sensory ("sense clubs"). Claws are developed on the terminal podomere.

The **mandibles** are situated at the sides of the mouth, and are very similar in all ostracodes. Each mandible consists of protopod, endopod, and exopod. The long coxa of the protopod is equipped at the ventral end with teeth which are used in mastication; those of the left and right mandibles meet in the center of the mouth. The basis and endopod together form the palp, which curves forward and downward; it is equipped with setae used for crawling and digging or for holding food fast and cutting off pieces (Fig. 1*a,4e*). In the Halocyprididae the proximoventral part of the basis is extended (Figs. 3*a,b*) and armed with cutting teeth. In the Platycopina the basis is long and provided with a comb of numerous long setae (Fig. 5*b*); a somewhat similar structure is found in the Darwinulidae of the Podocopina (Fig. 7*c*). In all forms the exopod is small and delicate, bearing a num-

ber of setae; in some species it functions as a **branchial plate**, accessory to that developed on the maxillae.

The maxillae work as supporting organs of the mandibles. They aid in carrying food to the mouth, in removing undesirable particles, and in creating water currents used in respiration and carrying in food particles in suspension. The maxillae lie at the sides of the hypostome, or, if a hypostome is ab-

sent, at the posteroventral sides of the head. The maxillae have a varied development in different groups of Ostracoda and the variations are regarded as important aids to taxonomy. The protopod in many species of all orders is equipped with two or three proximal endites bearing setae (Figs. 1*d*; 5*c*; 6*a,b*; 7*a*); in the Podocopina these endites are sometimes referred to as **masticatory processes**. In many forms the exopod is a

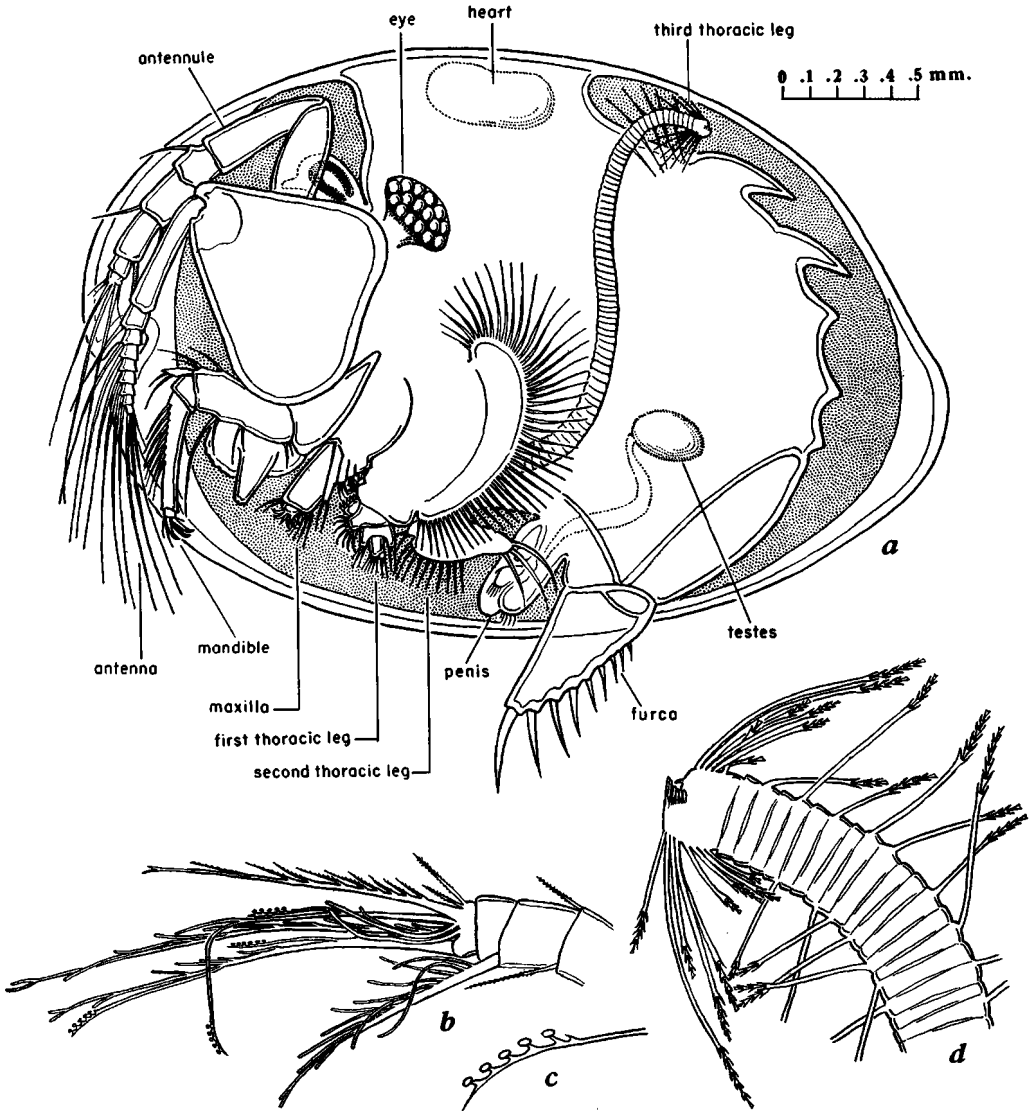


FIG. 2. Morphology of a representative myodocopid (myodocopine ostracode, *Cypridina norvegica* BAIRD, Recent (Cypridinidae). *a*. Male with LV removed; scale in upper right corner.—*b*. Distal end of male antennule.—*c*. Part of seta from male antennule showing sucktorial structures.—*d*. Distal end of right 3rd thoracic leg. (From KESLING, after SARS and SKOGSBERG.)

large vibratory plate equipped with a comb of long setae, commonly feathered (Fig. 5c; 6a; 7a; 8d). Some Mydocopida, however, lack an exopod or this element is much reduced (Fig. 1d), and in the Cladocopina it forms a palp of one or two podomeres with several distal setae directed medially (Fig. 4a,b). The endopod in most species forms a strong palp equipped with distal setae (Figs. 1d; 3a,b), but in the Podocopina it may be lacking. In the Platycopina the first

podomere bears a comb of numerous long setae (Fig. 5c).

Three pairs of thoracic appendages occur in the Mydocopida and Podocopina, two pairs in the Platycopina, and only a single pair in the Cladocopina.

The first thoracic legs are attached to the body at the junction of head and thorax. In some families they are highly modified as accessories to the jaw apparatus, consequently being referred to by some authors

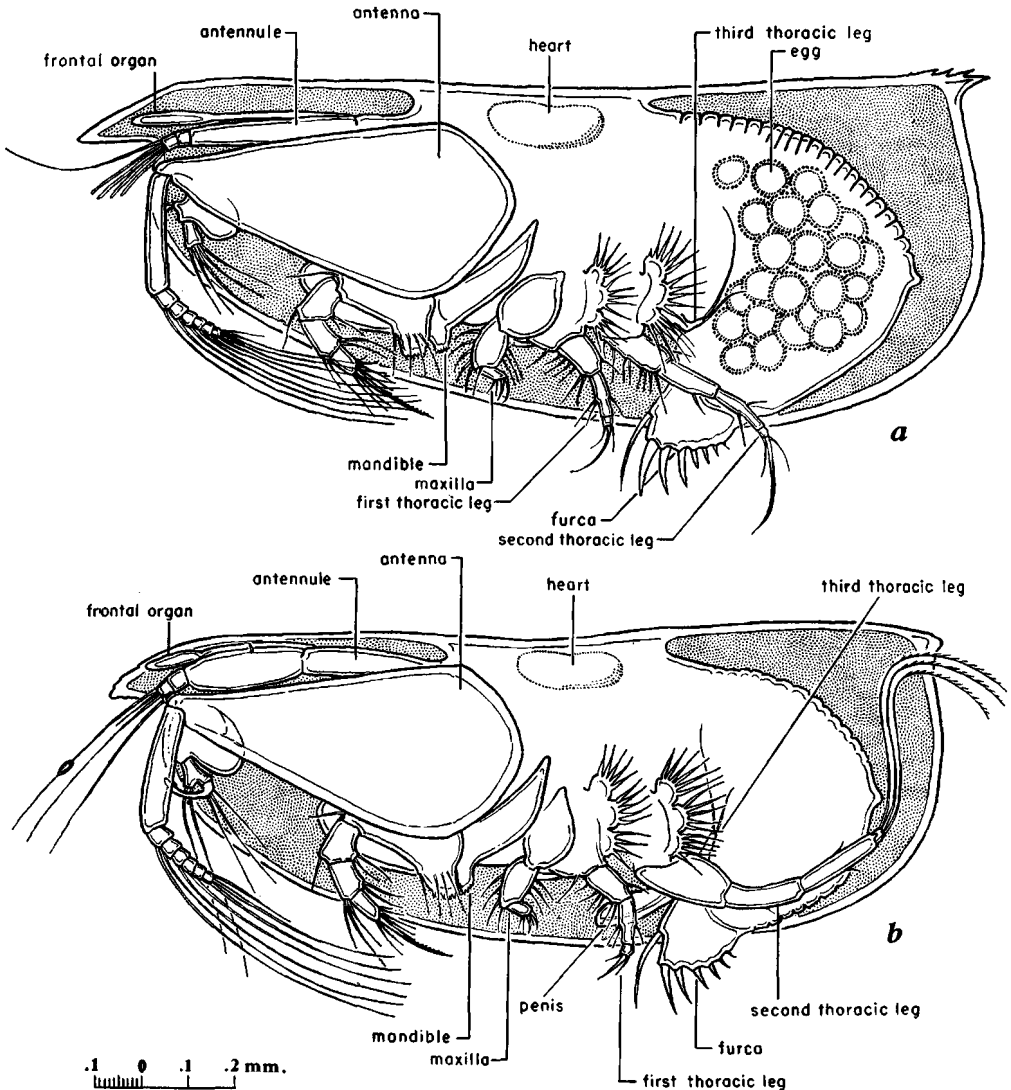


FIG. 3. Morphology of a representative mydocopid (mydocopine) ostracode, *Conchoecia elegans* Sars, Recent (Halocyprididae). a. Female with LV removed.—b. Male with LV removed. (Scale of both figures on lower left corner; from KESLING, after Sars.)

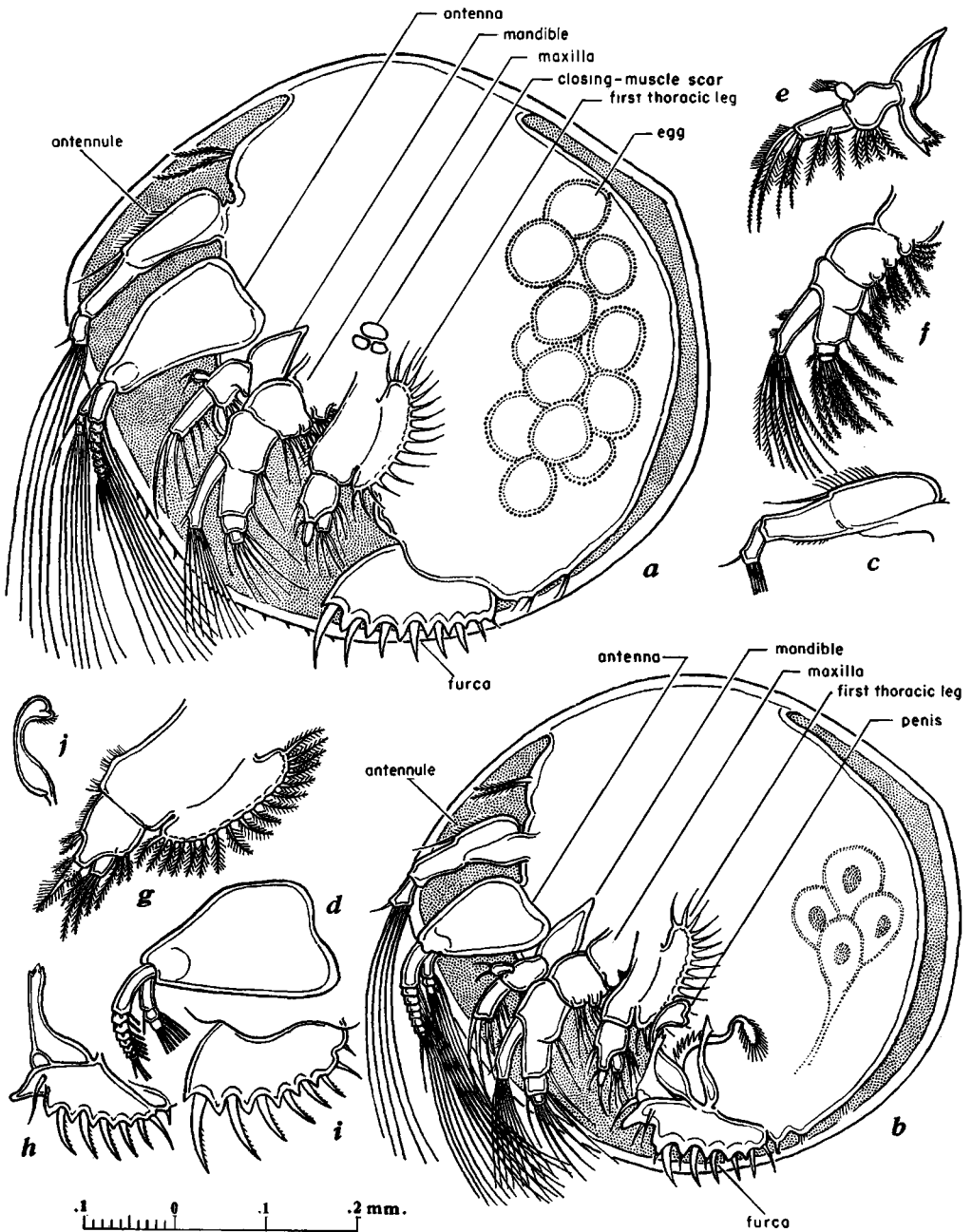


FIG. 4. Morphology of a representative myodocopid (cladocopine) ostracode, *Polycope orbicularis* Sars, Recent (Polycopidae). *a.* Female with LV removed.—*b.* Male with LV removed; testes shown in rear part of body.—*c.* Left antennule with distal setae broken.—*d.* Left antenna with setae broken on both exopodite (left) and endopodite (right).—*e.* Left mandible.—*f.* Left maxilla.—*g.* Left 1st thoracic leg.—*h.* Male left furca.—*i.* Female left furca.—*j.* Male penis. (All figures to scale in lower left corner; from KESLING, after SARS.)

as maxillipeds (or second maxillae). In other families they appear as unmodified leg structures, similar to the succeeding thoracic

legs. In some species the first thoracic legs are dimorphic, and the male legs not only differ from the female, but the left and right

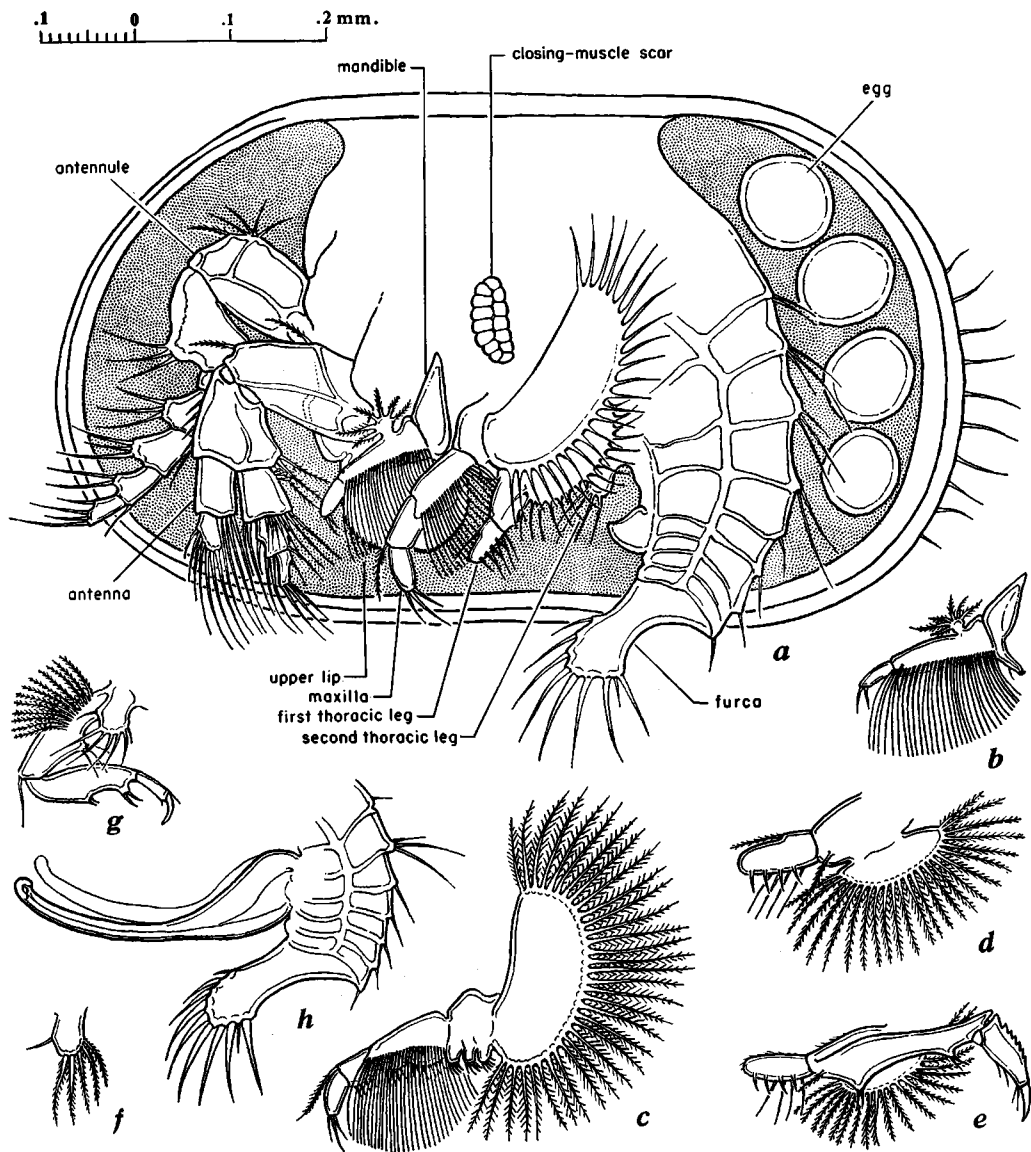


FIG. 5. Morphology of a representative podocopid (platicopine) ostracode, *Cytherella abyssorum* Sars, Recent (Cytherellidae). *a*. Female with LV removed; genital lobe shown above furca.—*b*. Left mandible.—*c*. Left maxilla.—*d*. Female left 1st thoracic leg.—*e*. Male left 1st thoracic leg.—*f*. Female left 2nd thoracic leg.—*g*. Male left 2nd thoracic leg.—*h*. Male furca and penis. (All figures to scale in upper left corner from KESLING, after Sars.)

legs of the pair also may differ from each other. In the Myodocopida the protopod is large, vertical and unjointed, and provided with anteroventral endites (Fig. 1*e*) with clawlike setae (Fig. 1*f-j*). The exopod takes the form of a large vibratory plate that probably aids respiration (Figs. 1*a*; 2*a*; 3*a,b*). The endopod is either composed of short

podomeres on the posteroventral edge of the basis (Cypridinidae, Fig. 1*e*) or is leglike and directed backward (Halocyprididae, Fig. 3*a*). In the Cladocopa this is the only thoracic leg. Its homology is somewhat controversial. The large basal segment bears a vibratory plate which by some is regarded as the exopod and homologous with the

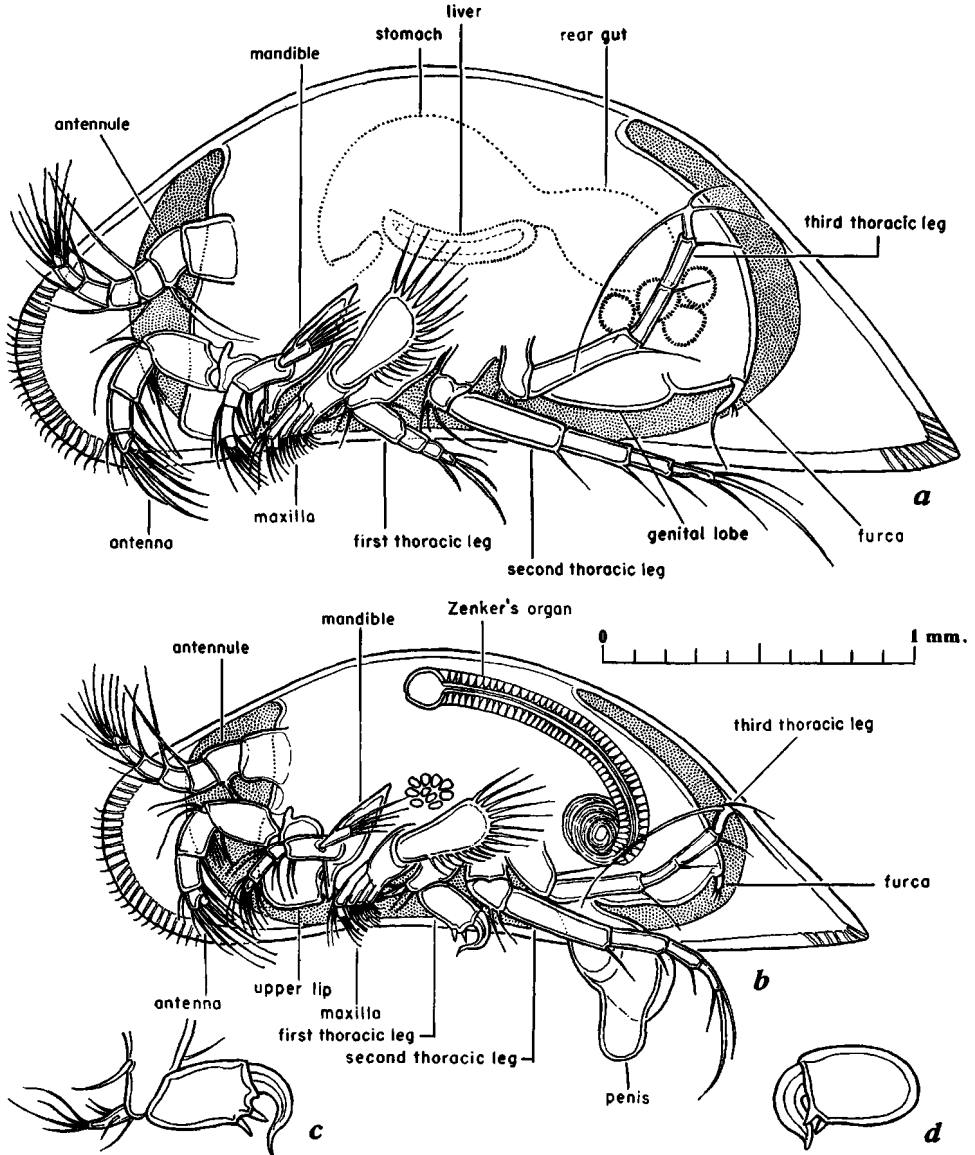


FIG. 6. Morphology of representative podocopid (podocopine) ostracode, *Macrocypris minna* (BAIRD), Recent (Macrocyprididae). *a*. Female with LV removed; 4 eggs shown in rear part of body.—*b*. Male with LV removed.—*c*. Male left 1st thoracic leg.—*d*. Palp of male right 1st thoracic leg. (Figs. *a* and *b* to scale at right; from KESLING, after SARS.)

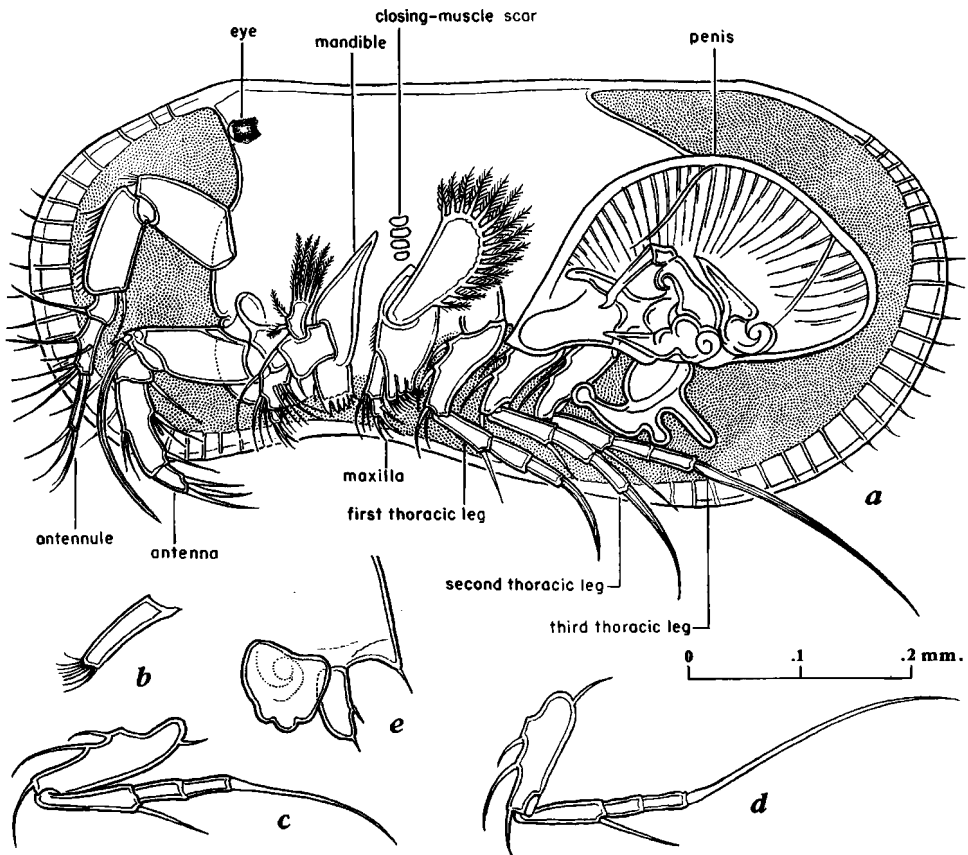


FIG. 7. Morphology of representative podocopid (podocopine) ostracode, *Limnocythere sanctipatricii* (BRADY & ROBERTSON), Recent (Limnocytheridae). *a.* Male with LV removed.—*b.* Male left brush-shaped organ.—*c.* Female left 3rd thoracic leg.—*d.* Male left 3rd thoracic leg.—*e.* Female furca and genital lobe. (All figures to scale at right; from KESLING, after SARRS.)

similar structure developed in the other orders and suborders; others regard it as an epidodial plate borne by the coxa (Fig. 4*a,b*). This basal segment bears a subtriangular podomere (?basis) to which are attached two setiferous lobes (?endopod and exopod). In the Platycopina the homology of the parts is likewise controversial. The appendage is dimorphic and in some species weakly developed or absent altogether in the females. That of males (Fig. 5*e*) bears a strong prehensile ramus of three podomeres directed backward (?endopod) used in copulation; this is absent in the female (Fig. 1*d*). In both sexes the basal protopod bears a vibratory plate with feathered setae (?epipod) and a distal lobe with a few short setae (?exopod). In the Podocopina this leg is variously developed and in many species is dimorphic. In the Cytheracea the

protopod ends in a masticatory process bearing setae (Fig. 9); the endopod is modified as a palp, composed commonly of a single podomere in the female, but in the male further modified to form a prehensile claw of one or two podomeres; the exopod forms a small branchial plate. In the Cytheracea this pair of legs is pediform and lacks the branchial plate; the legs are dimorphic in some species however (Fig. 7*a*). In the Bairdiidae (Figs. 10, 11) they are pediform but possess a branchial plate. In the Darwinulidae (Fig. 8*e*) both masticatory process and branchial plate are well developed but the endopod is pediform, as in the Cytheracea. In the Macrocyprididae there is no vibratory plate, the endopod in the female being subpediform, that of the male prehensile and asymmetric (Fig. 6*c,d*).

The second thoracic legs (not developed

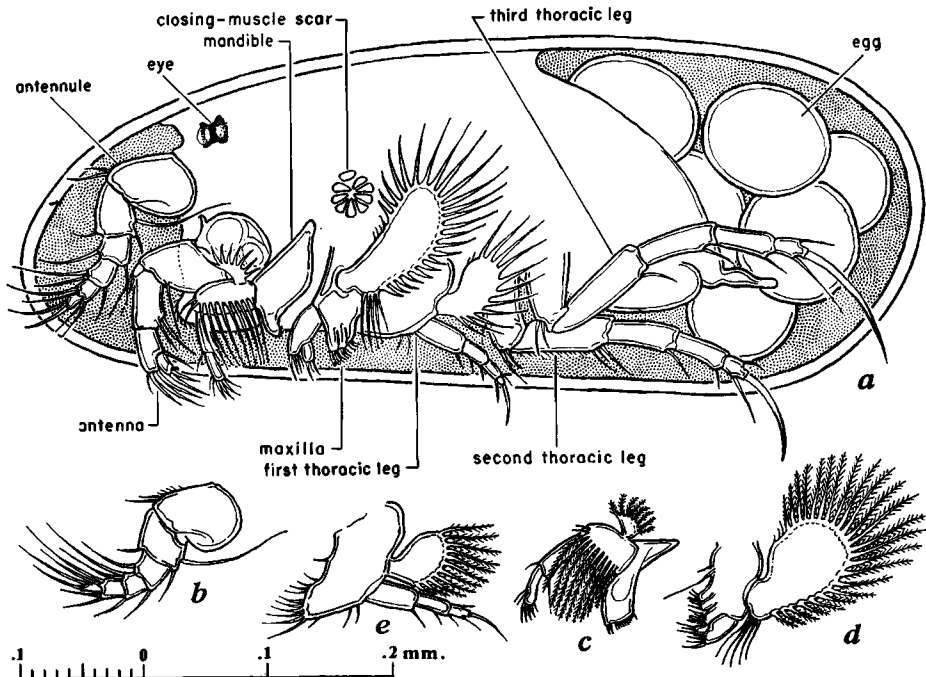


FIG. 8. Morphology of a representative podocopid (podocopine) ostracode, *Darwinula stevensoni* (BRADY & ROBERTSON), Recent (Darwinulidae). *a.* Female with LV removed.—*b.* Left antennule.—*c.* Left mandible.—*d.* Left maxilla from front.—*e.* Left 1st thoracic leg. (All figures to scale in lower left corner; from KESLING, after SARS.)

in the Cladocopina) closely resemble the first in the Halocyprididae, but in some species they are dimorphic (Fig. 3*a,b*). In the Cypridinidae (Fig. 1*k*) they take the form of a fixed lamelliform plate, never used in locomotion. In the Platycopina they are strongly dimorphic, that of the male (Fig. 5*g*) having an undivided protopod, an endopod of three backwardly directed podomeres, and a lamelliform exopod bearing setae. That of the female (Fig. 5*f*) is very small and consists of only the platelike exopod with setae. In the Podocopina this limb is uniramous and pediform, the protopod being strong and vertical and the endopod long and directed backward, with a strong terminal claw. In some species there is slight sexual dimorphism in the lengths of the podomeres and claws.

The third thoracic leg is developed only in the Mydocopida and the Podocopida. In the Cypridinidae this leg is long, mobile, vermiform and flexible, but lacks true joints (Figs. 1*a*; 2*a*). The distal end has long bristles with bell-shaped segments and a terminal comblike structure of setae (Fig. 2*d*).

This organ is used to clean the inside of the valves. In the Halocyprididae this limb is reduced to a small tapering stem of one or two podomeres and two setae (Fig. 3*a,b*). In some Podocopida this leg is also a cleaning organ of rather variable structure, upturned within the cavity of the shell and equipped with long cleaning setae (Fig. 6*a,b*), friction pads, a claw, and pincers, complete or in various combinations. In other Podocopida the limb is developed as a walking leg essentially similar to the two previous limbs (Fig. 7*a,c,d*; 8*a*); in some Cytheracea it is dimorphic in the proportions and lengths of podomeres and claws (Fig. 7*c,d*).

Male Cytheracea have paired brush-shaped organs (Fig. 7*b*) located in front of, between, or behind the thoracic legs. These are probably sexual sensory organs and not, as some suggest, rudiments of another pair of appendages.

The furcae ("furcal rami" of some authors) are appendage-like structures attached at the posterior end of the body. In the Mydocopida and Platycopina they con-

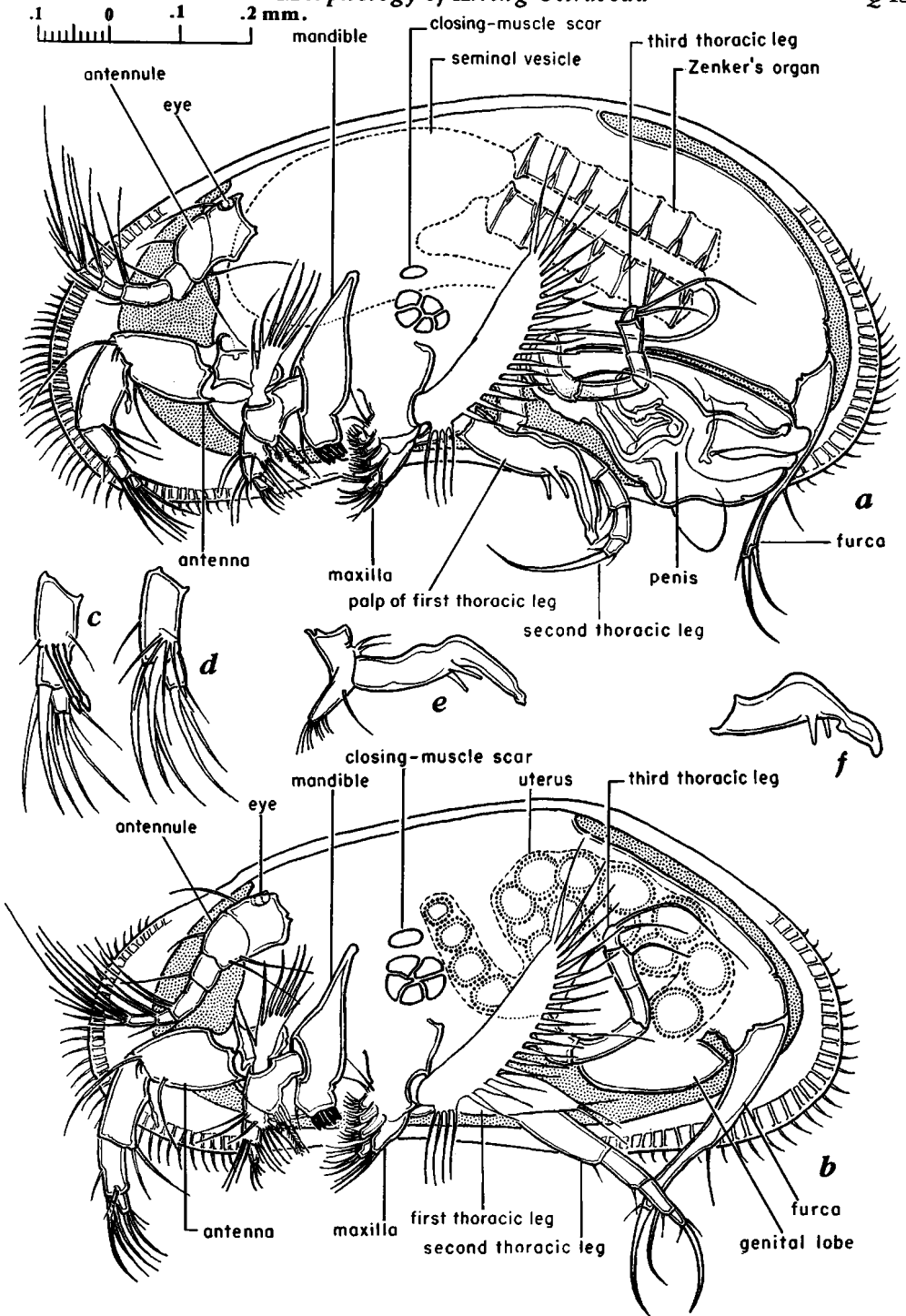


FIG. 9. Morphology of representative podocopid (podocopine) ostracode, *Candona suburbana* HOFF, Recent (Cyprididae). *a.* Male with LV removed; palp of maxilla turned backward to show "masticatory processes" or endites.—*b.* Female with LV removed.—*c.* Inner face of distal part of male right antenna, showing "male" setae.—*d.* Inner face of distal part of female right antenna.—*e.* Outer face of male left 1st thoracic leg.—*f.* Inner face of palp of male right 1st thoracic leg. (Figs. *a*, *b*, *e*, and *f* to scale in upper left corner, from KESLING.)

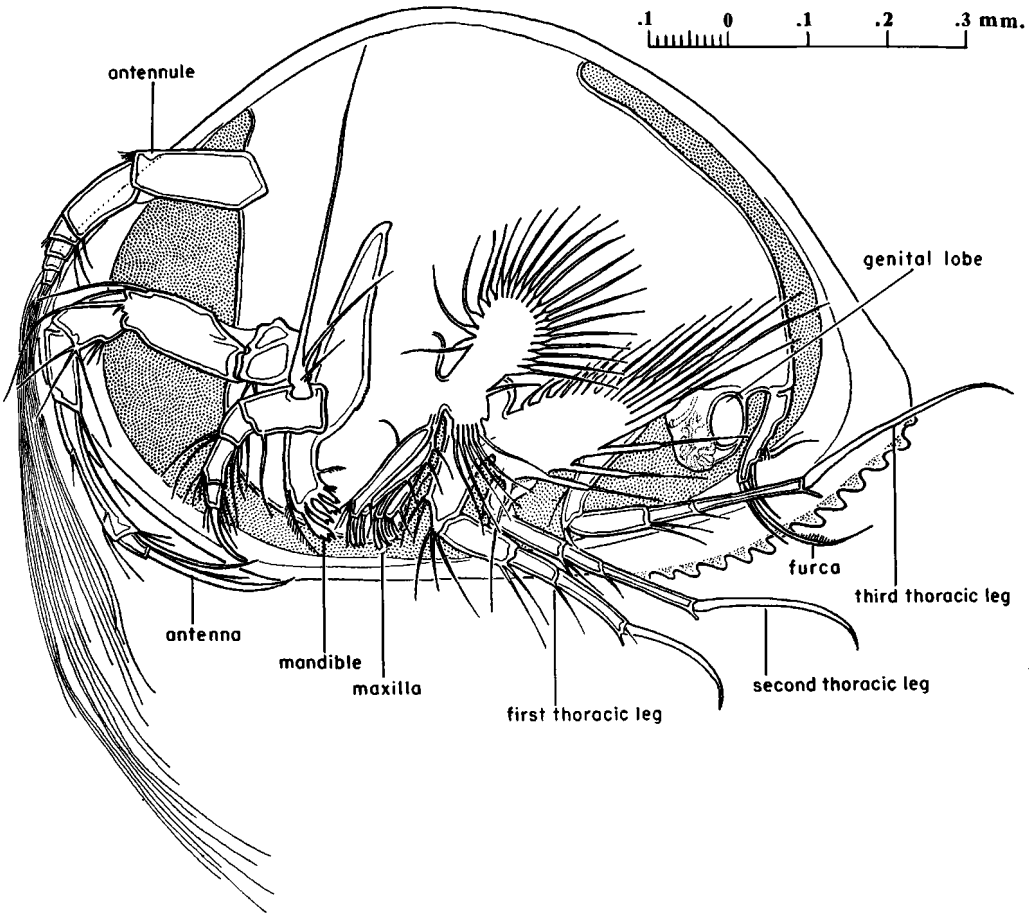


FIG. 10. Morphology of a representative podocopid (podocopine) ostracode, *Bairdia frequens* G. W. MÜLLER, Recent (Bairdiidae). Female with LV removed (compare with male in Fig. 11); note dimorphism in terminal claws of antenna and setae of exopod of 1st thoracic leg. (From KESLING, compiled from MÜLLER.)

sist of short, broad, lamelliform rami with several claws (Figs. 1a; 2a; 3a,b; 5a). In the Cladocopina they are similar but in some species are asymmetrical in the male, with the number of claws reduced in the left (Fig. 4h,i). In the Podocopina the furcae are extremely variable, and never lamelliform. In the Darwinulidae (Fig. 8a) they are lacking or represented by an unpaired reflexed process at the end of the thorax. In the Cytheracea they are dimorphic, in the female consisting of a small plate with two or more setae (Fig. 7e), in the males of most species fused with the penis (Fig. 7a). In the Bairdiidae they are small but well developed, variable, with at least three setae, of which one is long and strong (Figs. 10, 11). In the Macrocyprididae they are much

reduced and dimorphic (Figs. 6a,b). In the Cyprididae they are variable; in most genera, *Candona* for example, there is a long rodlike ramus and two powerful terminal claws and two setae (Fig. 12); this is reduced in *Cypridopsis* to a stumplike base and a long flagella-shaped terminal seta with or without basal spinule.

DIGESTIVE SYSTEM

The alimentary canal of ostracodes consists of the mouth, esophagus, stomach, and anus. Podocopidan Ostracoda have a short, narrow intestine and a voluminous rear gut between the stomach and anus. Some have livers at the sides of the stomach, which supply digestive fluids.

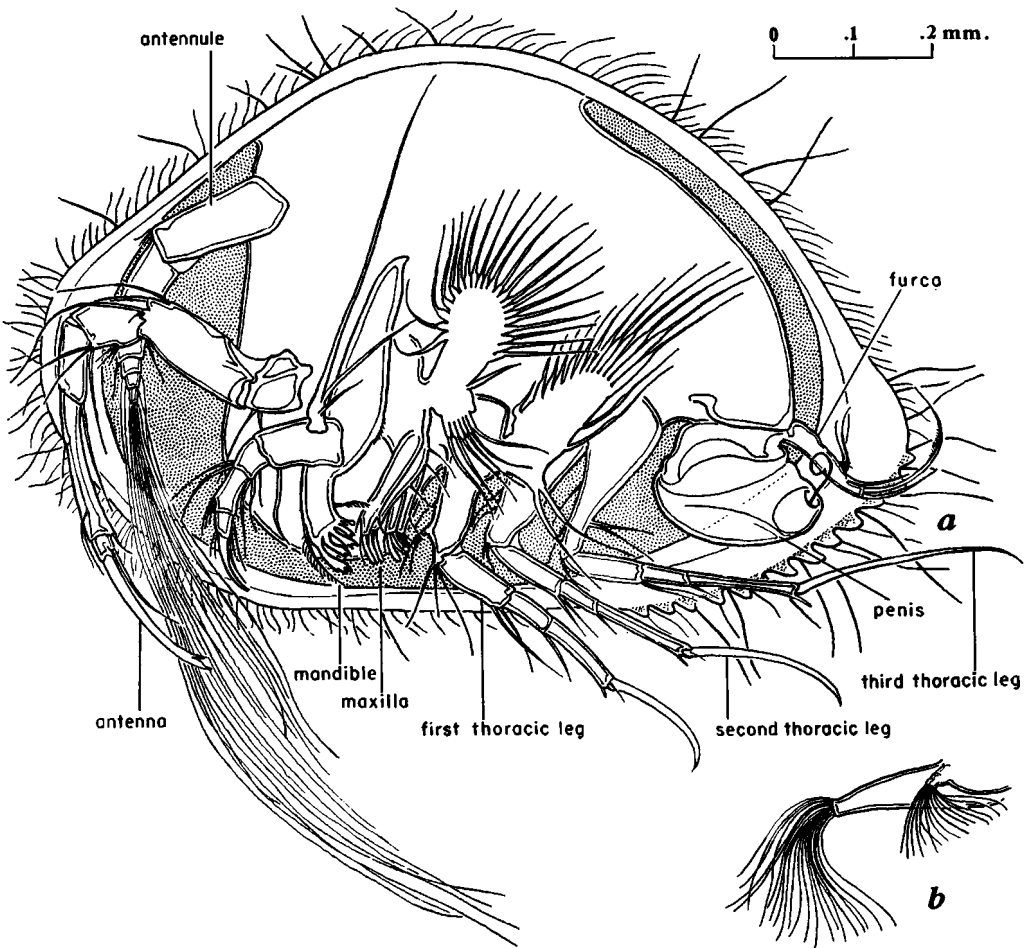


FIG. 11. Morphology of representative podocopid (podocopine) ostracode, *Bairdia frequens* G. W. MÜLLER, Recent (Bairdiidae). *a.* Male with LV removed; maxilla shown above its normal position and furca bent backward to show structures more clearly (at rest, exopod plate of maxilla lies outside that of 1st thoracic leg, and furcae lie between the penis).—*b.* Asymmetrical brush-shaped organs, which lie between bases of 2nd thoracic legs. (Both figures to scale in upper right corner; from KESLING, compiled from MÜLLER.)

GLANDULAR SYSTEM

The glandular system is not well understood in many families. The glands may be divided into secreting and excretory types, but glands of any sort have not been reported in some ostracodes. So-called "shell glands" (which have nothing to do with secreting of the shell) appear to be a combination of secreting and excretory glands. Other secreting glands are salivary (glands of the upper lip), livers (hepatopancreases), and those of the first thoracic legs. Certain marine ostracodes have glands in the upper lip that secrete light-producing substances. Some have glands that open at the borders

of the valves. In some genera, at least, there are excretory glands opening near the antennules and maxillae.

RESPIRATORY AND CIRCULATORY SYSTEMS

Respiration is accomplished through the body wall, by gills on the rear part of the body, by vibratory plates of certain appendages, or by combinations of these three. A distinct heart is found only in the Mydocopida (Figs. 1*a*; 2*a*; 3*a,b*).

NERVOUS SYSTEM

Primary divisions of the nervous system

are the cerebrum, the ventral chain of ganglia, and the circumesophageal ganglion. Lesser ganglia lie in most of the appendages.

The cerebrum lies in the forehead area, from which nerves extend to the eye, antennules, and antennae, and to the epidermis of the valves. Motor nerves extend from the circumesophageal ganglion to the an-

tennae and forehead area. The ventral chain sends nerves to most of the appendages from the mandibles posteriorly, including the furcae and ventral area.

The eye, when developed, is a complex structure, composed of one median and two lateral divisions. It is situated dorsal to the basal podomeres of the antennules. The lat-

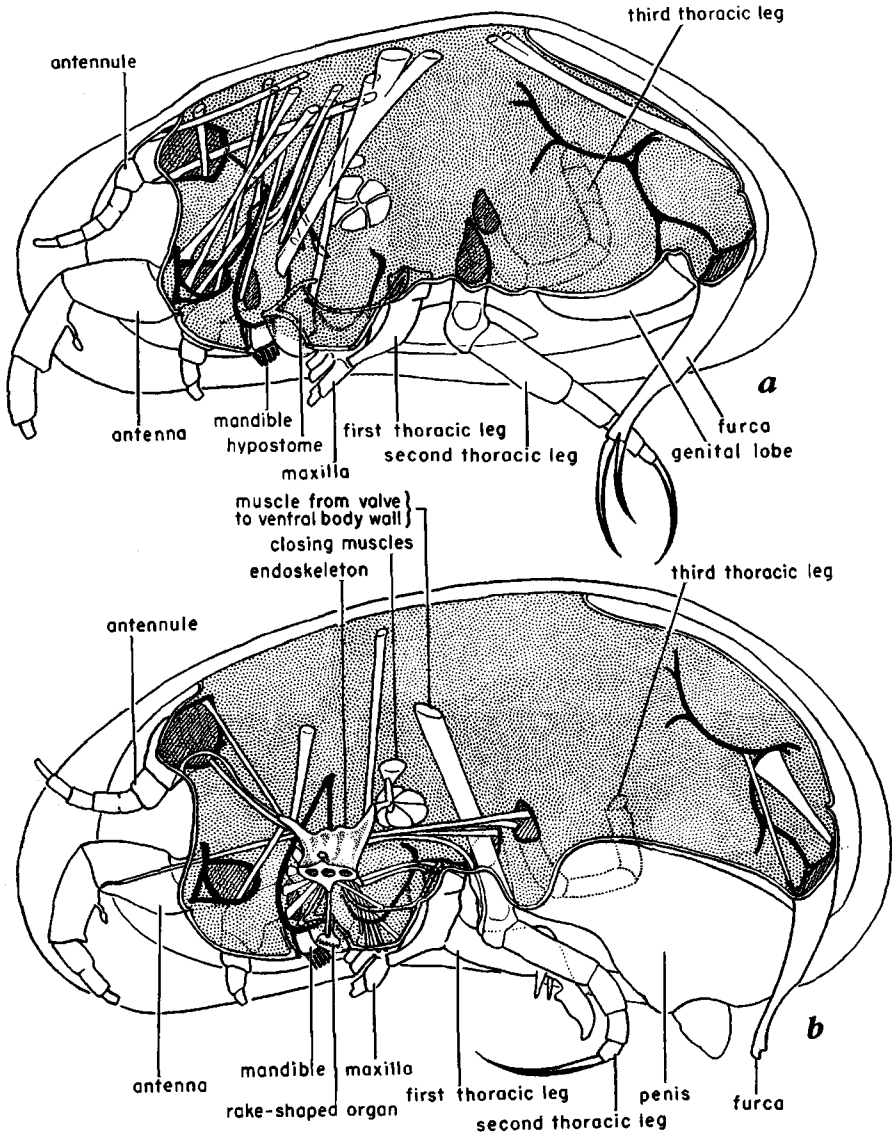


FIG. 12. Morphology of a representative podocopid (podocopine) ostracode, *Candona suburbana* HOFF, Recent (Cyprididae). *a*. Female with left half removed, showing muscles attached to dorsal part of valve and to appendages and rear part of body.—*b*. Male with left half removed, showing muscles from endoskeleton to appendages, rake-shaped organ, hypostome, closing muscles, and dorsal part of valve; muscles operating furca are attached to rear framework of body. Muscle from valve to ventral body wall is found only in males; it is contracted in copulation, unfolding the penis and swinging them out of the carapace.

eral divisions are reported to contain 10 to 15 cells and the median element 7 to 8. Many ostracodes have no eyes. In the Myodocopida (Cypridinidae) they are dimorphic, those of the male (Fig. 2a) being larger and with more lenses than those of the female (Fig. 1a). In the Podocopina (some Cytheracea) a glassy lenslike eye tubercle is observed in either valve at the anterior end of the hinge. An ocular sinus lies below the tubercle and serves to accommodate the eye. The frontal organ developed in some Ostracoda is believed to be sensory, but its use is not known certainly. Some authors believe that it is a kind of median eye.

MUSCULATURE

The body of an ostracode is provided with many muscles. Flexor and extensor muscles are well developed in all appendages. Separate muscles usually occur in each podomere so that each division is capable of independent action. The basal podomere of each cephalic appendage is attached to the inner dorsal area of the shell by flexor and extensor muscles (Fig. 12a). The bosses, at points of attachment, may be preserved in the fossil state.

Among the most important appendage muscles are those attaching the basal podomere of the mandibles to the shell. Several muscles extend from the mandible to the inner dorsal margin of the shell. Another set of mandible muscles is attached to the shell in an anteroventral position. They are attached slightly anterior and ventral to the closing muscles and serve as adjustor muscles. In most literature, the scars of the mandible-adjustor muscles have been erroneously included in the set of closing-muscle scars.

The adductors, or closing muscles, extend from valve to valve. Their distal ends are attached to the outer coating of the epidermis. In the calcareous portion of the shell, a raised boss is developed at the point of muscle attachment. This boss is the "muscle scar" referred to in fossil forms.

REPRODUCTION OF OSTRACODA

By R. V. KESLING

[University of Michigan]

PARTHENOGENESIS

Many species of fresh-water ostracodes lack males, as indicated both from observa-

The adductor muscle fibers connect near the middle of the body in a chitinous rod. From the chitinous rod to the inner margin of the valves they may extend as a closely packed set of fibers, as in *Cytherella*, or may diverge to form several isolated bosses, as in the Cytheracea.

When the adductor muscles relax, the valves are opened by an elastic ligament that lies along the dorsal margin. Contraction of the adductors, while closing the valves, creates tension on the ligament. Relaxation of the adductors releases the tension and the ligament contracts, thus opening the valves.

In the mid-area of the ostracode body is a chitinous framework known as the **endoskeleton** (Fig. 12b). It is suspended by muscles which extend to other body parts. Muscles connect the endoskeleton with most of the appendages, several glands, and the alimentary tract.

SEX ORGANS

The sex system is paired and, with few exceptions, the left half is not connected with the right. Gonads of Cypridinidae lie in the hypodermis, whereas those of other ostracodes are in the rear part of the body. The female system is made of ovaries, uteri, uterine openings, vaginae, and seminal receptacles. The seminal receptacles have adits and exits through the vaginae, and are not connected to the uteri inside the body. The male system includes the testes, vasa deferentia, and penes. Some genera have ejaculatory ducts or Zenker's organs, which pump sperm out through the penes (Fig. 6b). In some there are enlargements of the vasa deferentia that serve as seminal vesicles. Many species are parthenogenetic, but their females retain seminal receptacles. Of the syngamic species, a few have males with asymmetrical penes and many have dimorphic appendages. The penes in many Podocopina are extremely complicated (Fig. 7a) and accordingly some attempts have been made to use them in taxonomy, but the homology is imperfectly understood.

tions in nature and from cultures in aquaria. The females lay fertile eggs, which hatch out another generation of females.

Cyprinotus incongruens is parthenogenetic in one geographic range and syngamic in another. Furthermore, laboratory cultures of this species can be changed from syngamic to parthenogenetic by isolation of the females, and from parthenogenetic to syngamic by placing the females on a near-starvation diet. Such a reversal of reproductive processes does not occur in other species that have been investigated.

SYNGAMY

In species having males, the female lays fertile eggs only after copulation. The exact role of sperm in syngamic reproduction is questionable. The individual spermatozoa in many species are many times longer than the carapace, and absolutely, as well as relatively, larger than those of all other animals. LOWNDES, who studied the motility of ostracode spermatozoa, found that they advanced tail first and from this concluded that they were nonfunctional. If this is true, it does not explain why, in most syngamic species, impregnated and only impregnated female produce fertile eggs, nor why their eggs hatch out young individuals of both sexes.

COPULATION

Fresh-water species of ostracodes, which mature in about a month, live only a few months as adults. Although in some species young broods appear in the spring in great numbers and in others come forth in the summer, fresh-water ostracodes produce more than one or two generations per year. In each impregnated female, the seminal receptacles are distended with hundreds of spermatozoa, certainly more than enough to fertilize all eggs the animal could ever lay. Seemingly a single copulation is sufficient to impregnate a female for life.

Copulation has been observed in several Cyprididae, including *Candona fabaeformis*, *C. rostrata*, *Cypris marginata*, *Candonopsis kingsleii*, *Cyprinotus incongruens*, and *Notodromas monacha*. In all except the last-named species, the procedure is the same. The male spreads his valves apart, clambers onto the posterodorsal part of the carapace of the female, clasps the edges of the female valves with the palps of the first thoracic legs, unfolds and extends the ends of the paired penes, and inserts them into

the paired vaginae of the female. The female remains passive. The copulation is accomplished in minutes, and the accuracy of the male is attested by the fact that no female has ever been found to have spermatozoa in only one receptacle. ELOFSON recorded observations on the mating of many Cytheridae, including species of *Cythere*, *Leptocythere*, *Cythereis*, *Cytherura*, *Cytheropteron*, *Hirschmannia*, *Xestoleberis*, and *Paradoxostoma*. In these Cytheridae and in *Notodromas monacha*, the male approaches in a different way; the posteroventral edges of his valves are brought into contact with those of the female, so that the ventral sides of the two animals lie close together. No observations on the mating procedure of other families have been recorded.

Several marine species of Cypridinidae are known to have planktonic mating. One species, *Philomedes globosa*, is interesting because the adult male swims actively near the surface, whereas the adult female spends most of her life confined to the bottom, dragging her carapace through the mud. The adult females emerge from their final ecdysis with natatory setae; at certain times of the year, in the dark of night, flocks of females ascend over 100 fathoms from the bottom to copulate with the planktonic males. After mating, the females return to the bottom, shed their natatory setae by biting (or more properly "sawing") them off with the claws on the first thoracic legs, and by this self-mutilation lose for the rest of their lives the ability to soar upward from the mud. As for the males, they reach maturity with weak mouth parts, and probably die shortly after the nuptial swarming.

BROOD CARE

The Cyprididae, most Cytheridae, and presumably the Bairdiidae do not care for their young. After the eggs are laid (and in some species are attached to vegetation or bottom sediments), the female goes her way. Not all eggs are laid at one time, and broods of several stages may come from one mother.

The Darwinulidae, Cypridinidae, Halocyprididae, and Cytherellidae retain the eggs between the posterodorsal part of the body and the carapace. In many species, the young pass through more than one ecdysis before leaving the protection of the mother animal.

Nothing is known about the transfer of the eggs to the brood space, nor about the feeding of the young instars.

Eggs of most fresh-water ostracodes not only require no care, but can withstand desiccation for long periods of time. Sars

described from various parts of the world ostracode faunas which were raised from dried mud shipped to him. Eggs have been reported viable after drying for 30 years. Eggs of marine ostracodes are not known to survive any drying out whatsoever.

ONTOGENY OF OSTRACODA

By R. V. KESLING

[University of Michigan]

HATCHING AND MOLTING

An ostracode hatches from the double-walled eggs as a bivalved nauplius. The egg splits along the equatorial line, thus freeing the young ostracode. In none of the species investigated does the animal have in its first instar, or growth stage, as many appendages as are developed in the adult.

Like other crustaceans, the ostracode grows by ecdysis, molting the old hard parts and secreting new and larger ones. This externally discontinuous growth habit is very similar to hatching again, for the individual that emerges after ecdysis differs from the one that inhabited the old carapace. The molting process begins with splitting of the inner lamella from the outer side along the front edge; the chitin breaks open along the median plane of the body, and in sequence the appendages are meticulously withdrawn from their old chitinous armor; then the expansion of the hypodermis springs the animal free from the old carapace. During the relatively brief ecdysis, the animal increases to about twice its former volume, adds new appendages and organs, and alters the form and function of the old ones before secreting calcareous valves and a chitinous coat on the body and appendages.

NUMBER OF INSTARS

Unfortunately, few authors have studied the immature instars of species, being content with examination and classification of adults only. In two suborders (Cladocopina, Platycopina) the number of instars has not been established for any species.

Ostracodes belonging to the Cyprididae have nine instars, of which the last is the adult. Most of the Cytheracea also have nine instars, but three species of *Xestoleberis* have only eight. In the few species of

Cypridinidae that have been investigated six instars are observed and in the Halocyprididae there are seven instars. Much additional work is needed to understand the immature instars of nearly all ostracodes.

CHANGES IN ANIMAL

The ostracode adds new appendages in the young instars. Each appendage, except for those present in the nauplius when hatched, begins as a simple lobe, variously called an anlage, primordium, or incipient appendage. In successive instars, the anlage assumes the definitive form of the appendage, adding podomeres and claws or setae. New organs are added in the same way, and

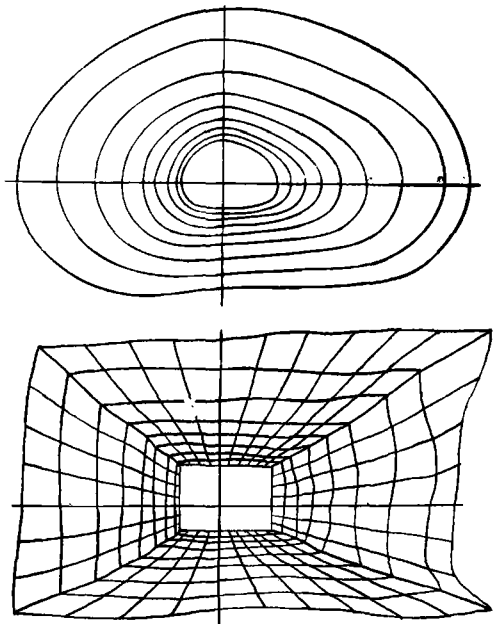


FIG. 13. Growth indicated by successive instars of *Cypridopsis vidua* (MÜLLER). a. Outlines of instars in lateral view successive, $\times 5$.—b. Plotted growth increments according to D'ARCY THOMPSON'S system of Cartesian coordinates (44).

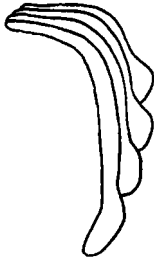


FIG. 14. Transverse section of adherent superposed instars of *Cryptophyllus obotoides* (ULRICH & BASSLER), M.Ord., $\times 10$ (49).

the animal becomes sexually mature only after the last ecdysis. In some species, however, there may be rare individuals which undergo further growth and ecdysis after sexual maturity is reached, for not uncommonly in a collection of a species rare individuals are found to be about double the volume of the majority.

The following chart summarizes the appearance of appendages in ontogeny, insofar as known. It is of particular interest that in all groups studied, the thoracic legs first reach their definitive form in the antepenultimate instar, regardless of the number of instars for the species. It seems that Cypridinidae hatch with the same stage of development as that achieved by the Cypridinidae after three moltings. The three species of *Xestoleberis* with nine instars begin the first growth stage with the appendages that other Cytheracea have in the second instar.

CHANGES IN CARAPACE

The carapaces of successive instars of a growing ostracode commonly differ not only in size, but in proportions, growth being allometric. The allometric index is slight, however, and varies during growth (Fig. 13). The shell of young instars is in all species thinner in proportion to its size than in the adult. The duplicature, in species in which it is developed, is narrower in the young instars, and the hinge more fragile. In species which have an advanced hinge in the adult (e.g., amphidont), earlier instars show a more primitive type (e.g., merodont). This ontogenetic succession

therefore parallels the presumed phylogenetic history and is considered to be an example of palingenesis. In species that are highly ornamented as adults, the ornamentation increases during ontogeny, both in the number of ornamental elements and in their relative size.

In a few genera (e.g., *Eridoconcha*, *Cryptophyllus*) some, but not all, of the early molts are retained outside the later ones, and become cemented to them (Fig. 14), thus reproducing growth lines of the same nature as those in the Conchostraca.

TIME REQUIRED FOR MATURITY

The Cypridinidae reach maturity in about three years. The Cyprididae develop in about 30 days, and Cytheracea in 40 days to three years, according to the species. In general, fresh-water species grow and mature much faster than marine. These figures are based on scanty information, since few species have been studied.

TABLE. Morphological Features of Ostracoda Occurring in Different Growth Stages

Taxon		Appendage												
Cypridacea	Cytheracea	<i>Xestoleberis</i> sp.	Cypridinidae	<i>Conchoecia</i> sp.	Antennule	Antenna	Mandible	Maxilla	First th. leg	Second th. leg	Third th. leg	Gonads	Genitalia	Furca
Instar number														
1	1	X	X	X	a
2	2	1	X	X	X	A	A
3	3	2	..	1	X	X	X	X	A
4	4	3	1	2	X	X	X	X	A	a	A
5	5	4	2	3	X	X	X	X	X	A	a	X
6	6	5	3	4	X	X	X	X	X	X	A	a	..	X
7	7	6	4	5	X	X	X	X	X	X	X	A	a	X
8	8	7	5	6	X	X	X	X	X	X	X	X	A	X
Adult						X	X	X	X	X	X	X	X	X

Explanation: X, structure present in definitive form; A, anlage always present; a, anlage present in some species, not in others; .., no trace of structure found.

SHELL MORPHOLOGY OF OSTRACODA

By H. W. SCOTT

[University of Illinois]

CONTENTS

	PAGE
GENERAL FEATURES OF CARAPACE	Q21
EXTERNAL FEATURES	Q21
Shape and size	Q21
Ventral area	Q23
Lateral surface	Q25
Dorsal area	Q28
INTERNAL FEATURES	Q28
Muscle scars	Q28
Hingement	Q31
REFERENCES	Q36

GENERAL FEATURES OF
CARAPACE

The ostracode carapace is bivalved, each valve being similar but not invariably a mirror image of the other. The two valves may be subequal or unequal in size. Inequality in size results in **overlap** of part of the free margin of the smaller valve by the larger, as in *Paraparchites* or *Kloedenella*, or in inclosure of the smaller valve by the larger all around the margin, as in *Cytherella*. A narrow edge of the free margin may be beveled in such a manner that the two valves fit without pronounced overlap, giving the appearance of equality as in *Amphisites*. Even in such shells, however, the beveled edge on one valve slightly overlaps the thin edge of the opposite valve. The two valves are articulated dorsally along the hinge and inclose the body of the ostracode.

The carapace is composed of two parts: (1) a hard layer of calcium carbonate, and (2) a soft layer, the epidermis. The hard shell substance is preserved in fossils and therefore represents the portion commonly studied by paleontologists. During life the hard shell is coated with a chitinous layer and the epidermis is enclosed in chitin. The outer chitinous layer can be recognized in some thin sections of fossils.

The hard shell layer is usually composed of two parts, the **outer lamella** and **duplitecture** (Fig. 15). The duplitecture, not definitely recognized in the archaeocopids, leperditicopids, and palaeocopids, extends along the free margin of the valve and is welded to the outer lamella. Both parts are composed of crystalline calcium carbonate; the long axis of the crystals is arranged at right angles to the shell surface. The calcium carbonate is precipitated by epidermal cells, though no special lime-secreting cells have been recognized. Because the ostracode sheds its hard shell in a series of molt stages, it is obvious that calcium carbonate precipitation is not continuous but is rhythmic. It is known that the ostracode can store an excess amount of calcium carbonate in its body and can create a new shell after molting in a calcium-free environment. The amount of calcium in the diet may control some shell features. Unusually thin or thick shells, bizarre ornamentation, or other aberrant features may be environmentally controlled.

EXTERNAL FEATURES

SHAPE AND SIZE

Ostracodes vary greatly in size. They commonly measure 0.7 or 0.8 mm. in length,

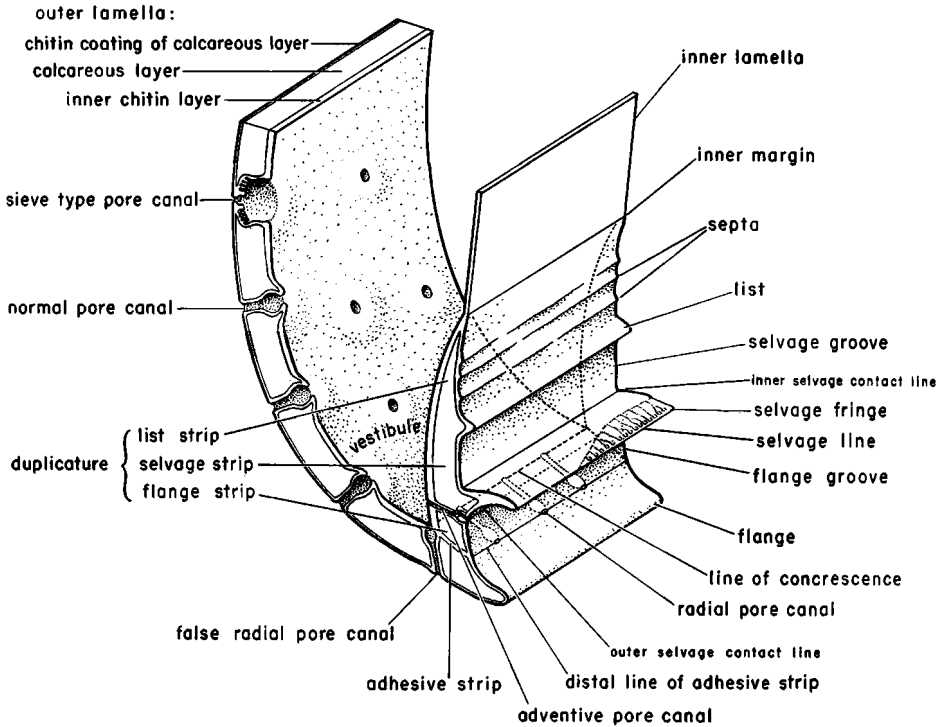


FIG. 15. Nomenclature of the duplicature and wall structure of a typical podocopid ostracode (44).

but some species may greatly exceed the average. For example, *Eoleperditia fabulites* commonly attains a length of 3 to 5 mm.

The outline or shape of an ostracode is one of the most important criteria in classification. Many families and genera may be identified by general outline of the carapace. Regardless of great variation in shape, most ostracode carapaces may be described as ovate, elliptical, or quadrate. The prefix "sub-" may be added to any of these terms to indicate deviations. Rarely ostracode carapaces are subrectangular, trapezoidal, or rounded in outline.

The dorsal edge of the carapace may be convex or straight, and the ventral margin convex, straight, or concave. The ends are usually rounded, but in some species they may be extended into elongate structures such as found in *Bairdia* and *Cytherura*. Rounding of the ends may be symmetrical (e.g., *Cytherella*) but they are more commonly dissimilarly rounded. The greatest extension of curvature of the ends may be either above or below mid-height.

The area adjacent to the hinge, as seen in

dorsal view, is referred to as the **dorsum** (Fig. 16). It may be broadly or narrowly arched, flat (with **dorsal plica** or marginal ridge), or concave. The terminations of the hinge may be marked by a change in outline. These changes represent the juncture between the dorsal border and ends of the carapace, referred to as the **cardinal corners**, which are very important in classifying shape of the carapace (Fig. 17). The cardinal corners range from acute (e.g., *Kirkbya*) to obtuse (e.g., *Oepikella*); usually they are obtuse and unequal.

The position of greatest height also controls outline. If the greatest height is in front of the mid-length, the carapace may be referred to as **preplete**, if posterior to the mid-length as **postplete**, and if at or near the mid-length as **amplete**.

When the greatest height is near one end of the carapace it produces what is known as **swing**. Preplete and postplete shells possess swing. Usually the posteroventral border swings forward, resulting in a narrow posterior half and a high anterior half (Fig. 18). Some exceptions to the forward direc-

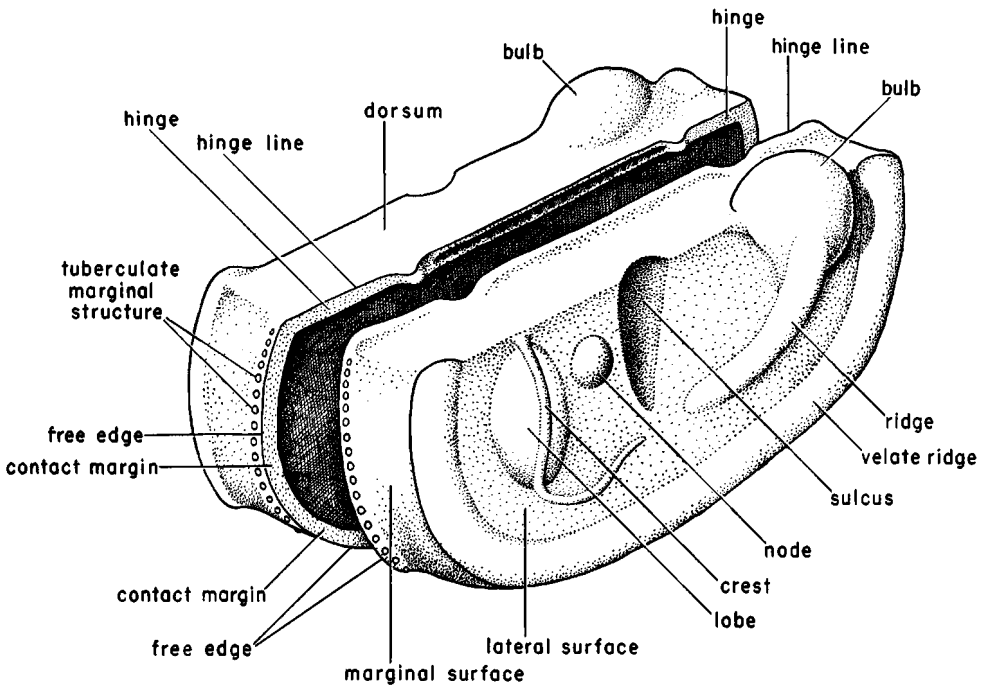


Fig. 16. Carapace nomenclature of a typical straight-backed ostracode (44).

tion of swing exist (e.g., *Leperditia* and a few other genera).

VENTRAL AREA

When the two valves of the carapace are opened they move outward around the **free edge** from the terminations of the hinge. The free edge extends around the anterior and posterior ends and along the ventral edge. The area adjacent to the ventral free edge, as seen from below, is the **venter**. Ventral structures, which may extend partly or entirely around the anterior and posterior ends, are referred to as **adventral**.

The closure of the carapace brings together a narrow portion of each valve. The area of contact is the **contact margin** (Fig. 16). The nature of contact is variable in detail but may be grouped into two types: (1) that in which one valve is distinctly larger than the other, the larger overlapping the smaller around all or a portion of the free edge (e.g., *Cytherella*, *Kloedenella*); and (2) that in which the valves are equal to subequal and overlap is wanting or slight (e.g., *Amphissites*).

The contact margin may be simple or complex. In the simplest type of closure a

single ridge, termed the **selvage**, extends along the free margin. If more than one ridge is present, the selvage is considered to comprise the principal ridge. When the valves are closed, the selvage fits into a groove in the opposite valve. In some ostracodes the proximal covering of the epidermis (*inner lamella*) is calcified to form the **duplicate** (Fig. 15). In such shells the contact margin is complex and the selvage constitutes the principal ridge. In the living animal the space between the inner and outer lamellae, called the **vestibule**, is filled by part of the epidermis. Proximal to the selvage may be a minor second ridge, termed the **list**. The two ridges are separated by a groove. Additional secondary ridges may be proximal to the list. Distal to the selvage is the **flange**, a ridge that commonly is a part of the outer instead of inner lamella. When both selvage and flange are present they are separated by the **flange groove**. The duplicate is attached to the outer lamella by an adhesive strip of chitin; the proximal line of contact is referred to as the **line of concrescence** (Fig. 15).

The ventral area may be simple and show only the contact of the valves along the free

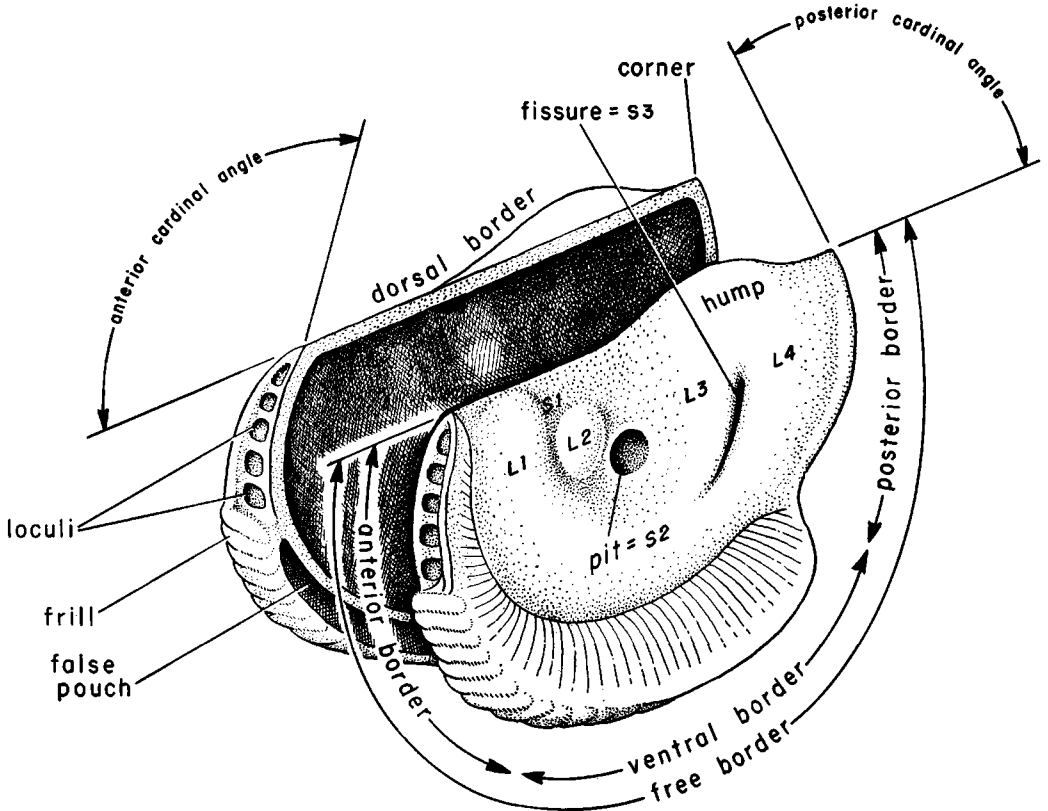


FIG. 17. Diagrammatic illustration showing some of the external features of a typical velate palaeocopid ostracode (44).

edge. The ventral area in many ostracodes, however, is modified by various ridges, frills, or flanges, which may be restricted to the venter or may extend to the cardinal corners. JAANUSSON (1957) groups such features into types designed as velate, histial, and carinal structures. Experience has shown that these terms cannot be applied in all cases without confusion. Distinction of the histium is especially troublesome. The typical velum is a ventral ridge, flange, or frill that may extend around part or all of the anterior and posterior ends. If it is considered as the primary or main ventral frill, as typified by hollinids and eurychilinids, then histium cannot be used for such velate structures. In many ostracode carapaces, secondary ridges occur in addition to the primary velate structure. KESLING & ROGERS (1957) refer to these secondary ridges in *Trepostella* as "extra" and "marginal or sub-marginal."

The morphological significance of the velum is not clear. In some carapaces it is related to dimorphism, but in others it does not seem to function as a dimorphic structure. Sections of *Beyrichia* show that the velum is a downfold lined with the inner chitin layer. Even in *Hollinella* where the two sides of the velum are in contact, a dark line representing the infolded inner chitin layer is preserved. Perhaps in such shells the frill is a true dimorphic velum, whereas the marginal rim in such a form as *Zygodolba* is a pseudovelum.

The term "carinal structure" was proposed by JAANUSSON (1957) for "different kinds of nondimorphic ornamental ridges situated lateroventrally and often occupying about the same position as the connecting lobe in quadrilobate valves." The term has been used to denote a kind of dimorphism, whereas it should refer only to prominent ornamental ribs on the lateral surface, not

including low costae or velate ribs or the histial ridge. Many species of *Amphissites* are ornamented with typical carinae. Lateral or lateroventral ribs may or may not be superimposed on a dimorphic lobe.

Ribs and ridges varying in number and complexity commonly are found on the lateral surface of ostracode valves. These ribs or costae may be coarse (e.g., *Glyptopleura*) or fine (e.g., *Graphiadactyllis*). A simple ridge may occur where the lateral surface meets the venter. In some carapaces it is difficult to distinguish between a marginal costa and velum. If the rib is on the lateral surface, it is more appropriately termed a **costa**, whereas if it occurs on the venter or extends ventrally from the contact of the lateral surface with the venter, it is either a velum or a velate structure.

The velum commonly is a wide frill-like structure extending lateroventrally from the free edge (Fig. 19). It may be a smooth bladeliike structure or its surface may be undulating, nodose, striate, or reticulate and its edge may be smooth, scalloped, or spinose. Velate structures are common in the Palaeocopida and previously have been applied only to this group, though velate-like structures occur in *Cythereis*, *Pterygocythereis*, *Kingmaina*, and other Mesozoic and Cenozoic genera.

LATERAL SURFACE

General features. The lateral surface of ostracode valves can be divided into posterior and anterior portions and into dorsal and ventral portions. For designation of specific points on the lateral surface, smaller subdivisions can be defined, as anteroventral, posteroventral, etc. (Fig. 18). The dividing line between anterior and posterior is placed at mid-length and between dorsal and ventral at mid-height. If the position of the adductor muscle scar is known, the surface in front of it is referred to as the pre-adductorial area and the posterior area as postadductorial.

Unfortunately, length and height are not always measured consistently, for such measurements vary according to methods of orienting the carapace. Students of the palaeocopids have oriented the carapace with the dorsal edge parallel to a horizontal line because in this group the hinge is fairly long and straight, producing a straight-

backed dorsum in lateral view (Figs. 16, 18). However, students of Cenozoic and Mesozoic ostracodes mostly have oriented them with the ventral edge or long axis parallel to a horizontal line. This procedure has been adopted because of the great variation in the shape of the hinge or dorsum in platycopine, myodocopine, podocopine, and cladocopine groups. Because these different methods of orientation are well entrenched in practice it seems best to continue them.

The lateral surface of ostracode valves may be smooth or highly ornamented by granules, pustules, striae, costae, pits, spines, or reticula. **Granules** may be closely packed or sparsely distributed over part or all of the surface (Fig. 19). If the raised protuberances are distinct and larger than granules they are described as **pustulae** or **papillae**. **Striae** are fine furrows separated by very minute ridges. In *Entomis* they cover the entire surface and are nearly parallel to each other. In *Glyptopleura* the ribs are coarser and are described as **costae**. The lateral surface of *Pyxiprimitia* and similar forms is marked by depressions in the shell called **pits**; they are not the openings of normal pore canals. Larger pits such as found in *Thlipsura* are not common; their function, if any, is unknown.

One of the most distinctive of all ornamental features of ostracode carapaces is a **reticulate** surface, found in many genera from Paleozoic to Recent. Reticula are represented by a network of intersecting bars that produce a lacy pattern. In some species the connecting bars are narrow and the depressions large, whereas in others the depressions are small and the surrounding barlike portions are relatively wide and flat. In the latter type there is a gradation between reticulate and punctate surfaces (Fig. 19). If the depressions are wider than the bars, the reticulate pattern is obvious but if the barlike divisions are wider than the depressions, the appearance is more that of a pitted or punctate surface. One of the most common faults in early classification was the separation of smooth specimens representing internal molds from fossils showing reticulate exterior surfaces.

The shell may be pierced by **normal pore** canals, which represent the passageway for hairs or setae (Fig. 15). The canals may be few or many, widely distributed, closely

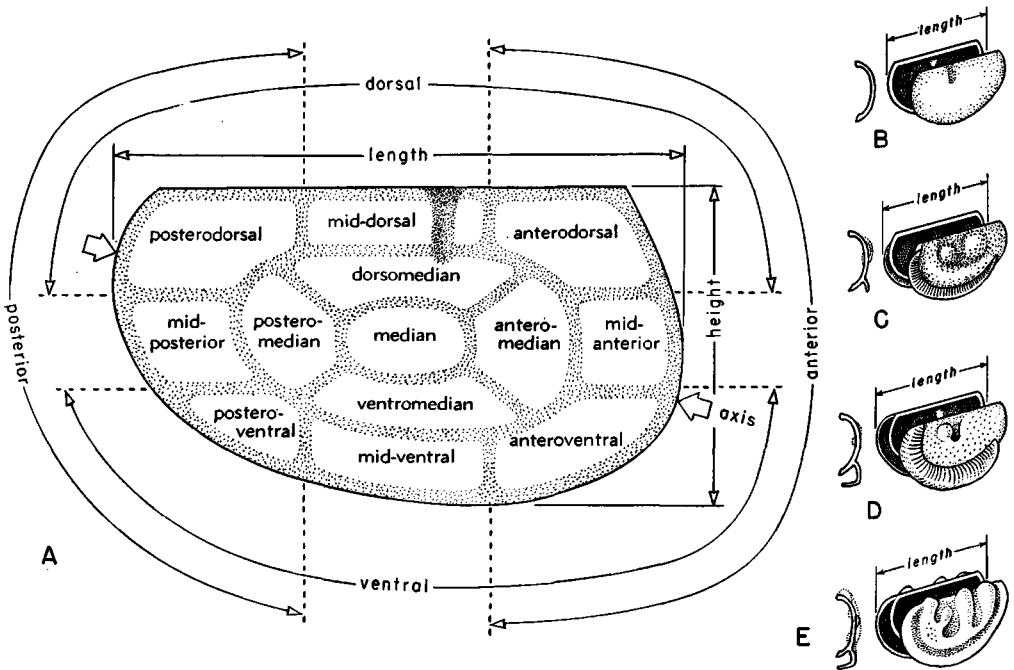


FIG. 18. Nomenclature of areas on the lateral surface and features relating to orientation and dimensions of typical straight-backed ostracodes. A. Diagram of RV. B-E, both valves and transverse sections of *Primitia*, *Hollinella*, *Piretella*, and *Tallinnella* (44).

packed, or entirely wanting. The projecting setae are sensitive to touch. In some ostracodes additional setae may extend through radial pore canals at the juncture of the duplicature with the outer lamella. Commonly they are concentrated at the anterior end but may extend along most of the free edge also.

Spines are distinctive features of many ostracode carapaces (Fig. 19). They are highly variable in number and size. Some are solid and ornamental, whereas others are hollow and apparently held some portion of the soft parts. Commonly but not invariably spines are located posteriorly. In *Pterygocythereis* and *Cytheropteron* the alate structure may extend backward into a spine in a posteroventral position; other spines may occur on both the posterior and anterior margins. In some genera (e.g., *Paracytheridea*) the caudal process in a posterodorsal position commonly is extended into a spine. Spines may develop along the dorsum (e.g., *Rakverella* and *Ctenonotella*, which may have several spines along the dorsal edge tilted slightly backward). *Dicranella* has two mid-dorsal spines and

Aechmina a single centrally placed dorsal spine; the lateral surface of *Cythereis* may bear many small spines, and spines are common on the edge of the velum in velate species.

Lobation and sulcation. Lobes and sulci are among the most distinctive features of many ostracode carapaces (Fig. 20). Early attempts to use them as a major basis of classification resulted in considerable confusion. Lobes represent elevations of the shell (domicilium) which are directly opposite internal depressions or troughs. This external lobation is a reflection of internal anatomy and therefore important. Unfortunately, the lobes cannot always be assigned to given internal organs. For convenience, lobes have been designated numerically from anterior to posterior parts of the valves, as L_1 , L_2 , L_3 , and L_4 . The presence of all lobes indicates a quadrilobate valve; a trilobate valve bears lobes designated as L_1 , L_2 , and L_3 ; a bilobate valve has only L_1 and L_2 .

Sulci are elongate depressions of the domicilium labeled S_1 , S_2 , and S_3 from front to back; valves may be unisulcate, bisulcate, or trisulcate (Fig. 20). Of the sulci S_2 is the

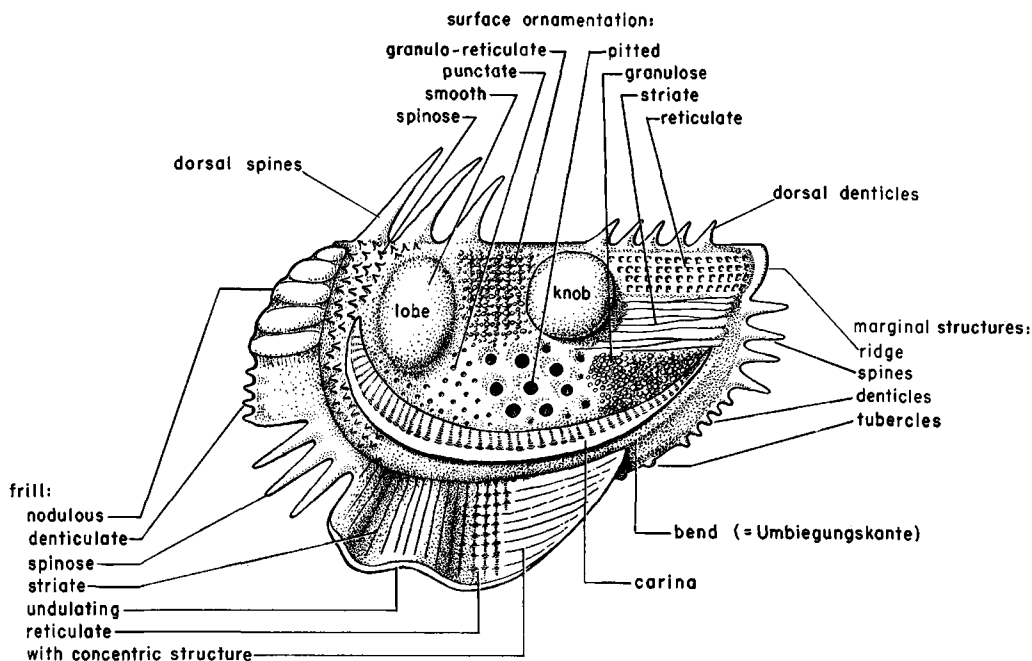


FIG. 19. Nomenclature of the lateral and marginal palaeocopid features of ostracode (composite) (44).

most significant because it marks the position of the adductor muscle. Sulci are expressed internally by corresponding elevations. Some shells possess elongate depressions which are not reflected internally; these may be referred to as furrows or fissures (Fig. 17). A typical sulcus opens dorsally and may open at both ends, whereas typical fissures do not open at either end and are contained within the shell.

In some forms all of the lobes merge ventrally into a ventral lobe. This is well illustrated in *Tetradella marchica*, a quadrilobate-trisulcate species in which L_1 and L_4 curve ventrally to form a long ventral lobe with L_2 and L_3 attached to it. A similar development is found in *Tallinnella dimorpha*.

The sulci S_1 and S_2 represent the points of attachment of muscles, S_2 denoting the position of the adductor muscle and S_1 the position of the muscles for one of the anterior appendages. S_2 is present in unisulcate species and S_1 and S_2 in bisulcate species. It has been observed that thick, short-hinged shells with a convex dorsum are seldom sulcate. S_2 has probably been developed due to the strain placed upon the carapace by the closing muscles. S_3 is com-

monly present in quadrilobate valves. The function of the lobes is not clear. In bilobate forms, where the two lobes are separated in part by S_2 , the lobes may not have had any special function and are only an indirect product of S_2 . The same may be true for some trilobate species wherein L_1 , L_2 , and L_3 are by-products of S_1 and S_2 . This is not an explanation for all lobation. Certain organs, such as the liver and stomach, may have occupied some lobes; the posterior lobe may have been occupied by reproductive organs.

Unisulcate *Eukloedenella*, bisulcate *Kloedenella*, and trisulcate *Dizygopleura* are all closely related genera. In such forms the differences in sulcation are of only generic importance. There is closer relationship among these genera with different degrees of sulcation than exists between such unisulcate genera as *Bolbina*, *Dilobella*, *Eukloedenella*, and *Plethobolbina*. It is common rather than exceptional that genera within a family show a variation in the number of sulci.

The number and character of sulci and lobes cannot be used generally for familial differentiation; they are aids to classification on all levels but are not by themselves gen-

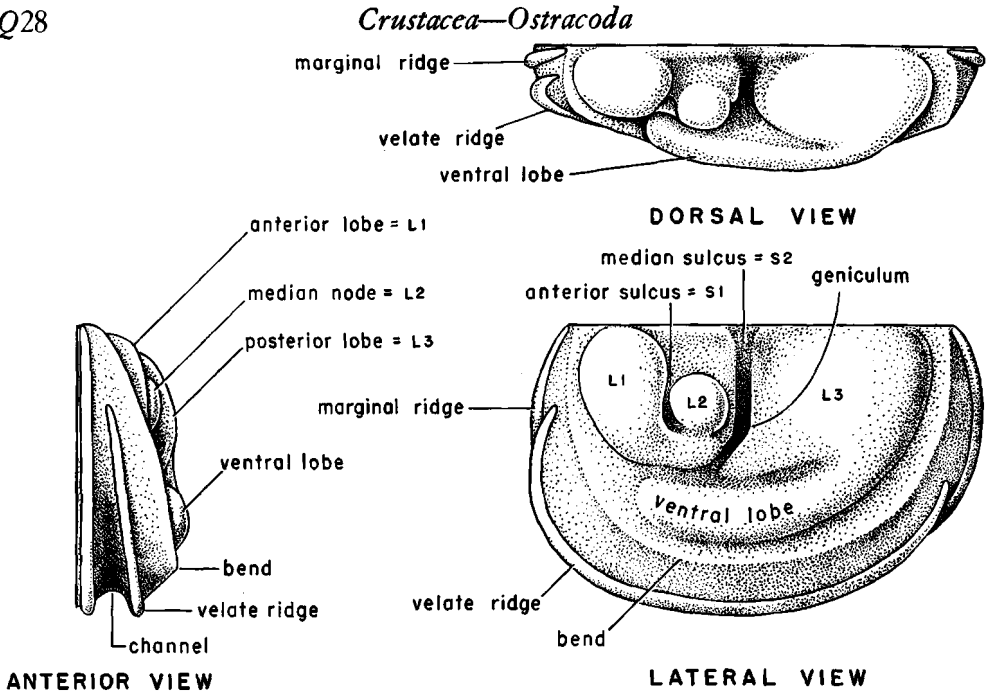


FIG. 20. Nomenclature of palaeocopid ostracode showing lobation, sulcation, and other features (LV) (44).

erally definitive in any category other than species. The number of sulci cannot be used solely for determining the affinities of genera. Phylogenetic lines based on sulcation have not been worked out, and much valuable information is expected to result from future studies of this subject. Classification based on lobation alone results in confusion.

DORSAL AREA

The general outline, nature of the hinge contact, form of lobation and sulcation, and presence of dorsal carinae are features that may be observed in dorsal view. Observation of the dorsum is essential to determine the position of greatest width of the ostracode carapace and character of the hinge line. The position of greatest width bears on dimorphism and orientation; the nature of the hinge bears on problems of classification and in some forms on orientation. The hinge line may be depressed in a channel (e.g., *Paraparchites*), comprise the highest, most dorsal edge of the carapace (e.g., *Welleria*), or be completely overlapped by the larger valve (e.g., *Cytherella*). The exterior terminations of the hinge fall into four general classes: (1) without cardinal angles and hinge contact not directly exposed (e.g.,

Cytherella, *Bairdia*); (2) with cardinal angles well developed, hinge line straight and uninterrupted by teeth or overlap, no channel (e.g., *Ctenobolbina*, *Primitia*); (3) with one end of hinge, usually anterior, interrupted by overlap of one valve, usually the larger, channeled or nonchanneled (e.g., *Eukloedenella*); and (4) with both ends of the hinge interrupted by toothlike structures of one valve fitting into socket-like notches in the other valve, channeled or nonchanneled (e.g., *Sansabella*, *Brachycythere*).

It should be pointed out that the internal characters of the hinge cannot be interpreted from the external characters and that hinge terminology can be used only when the internal features are known. However, the internal features of the hinge are known in only a few of the archaeocopids and palaeocopids; therefore, description of the carapace of such ostracodes specially calls for discussion of the external characters of the dorsum, including the hinge line.

INTERNAL FEATURES

MUSCLE SCARS

Muscle scars are very important shell features that commonly are preserved in Mesozoic and Cenozoic forms but less so in

Paleozoic ostracodes. Their value in classification and orientation has been neglected until recent years. Much is yet to be learned, but we know that orders and some superfamilies can be recognized on the basis of muscle patterns, as well as a few families and genera.

The presence of scars often has been overlooked because of the apparent opaqueness of the shell. However, coating the surface of many specimens with oil or water or converting calcareous specimens to fluorite may reveal excellently preserved scars. The use of stains and transmitted light also may aid in making muscle scars visible.

The best-known scars in Paleozoic ostracodes are found in the Leperditiiidae (Fig. 21, 1,2). In *Eoleperditia*, adductor, mandibular, antennal, and possibly stomach muscle-scars have been recognized. The large adductor scar is composed of as many as 100 small secondary scars. The over-all shape may be ovate (e.g., *Eoleperditia*) or chevron-shaped (e.g., *Herrmannina*). Muscle scars in many palaeocopids (Fig. 21,3,4) appear to be single circular structures about 100 microns in diameter. They are reflected exteriorly in several ways: as a "lucid spot," an unornamented, smooth circular spot, a raised, thickened area, or a pit; internally they may be marked by a circular depression or boss. In sulcate palaeocopids the adductor scar is most commonly opposite to the ventral and usually deepest part of S_2 . Internally, this point may be rough or raised, but does not form a distinct pattern of multiple scars.

Only a few scars of mydocopids have been recorded. They are represented by large clusters of many secondary scars, commonly grouped in a distinctive pattern (Fig. 21,8,13). The shape and number of the secondary scars and the over-all pattern may vary in different genera. Certainly, the long thin bars of *Entomoconchus* differ strikingly from the subround secondary scars of *Cylindroleberis* or the ovate scars of *Cyclasterope*.

The cladocopine mydocopids have a closely set triangular group of three subround secondary scars placed near mid-carapace (Fig. 21,9). They have not been reported often from fossils but are recorded from *Polycope*.

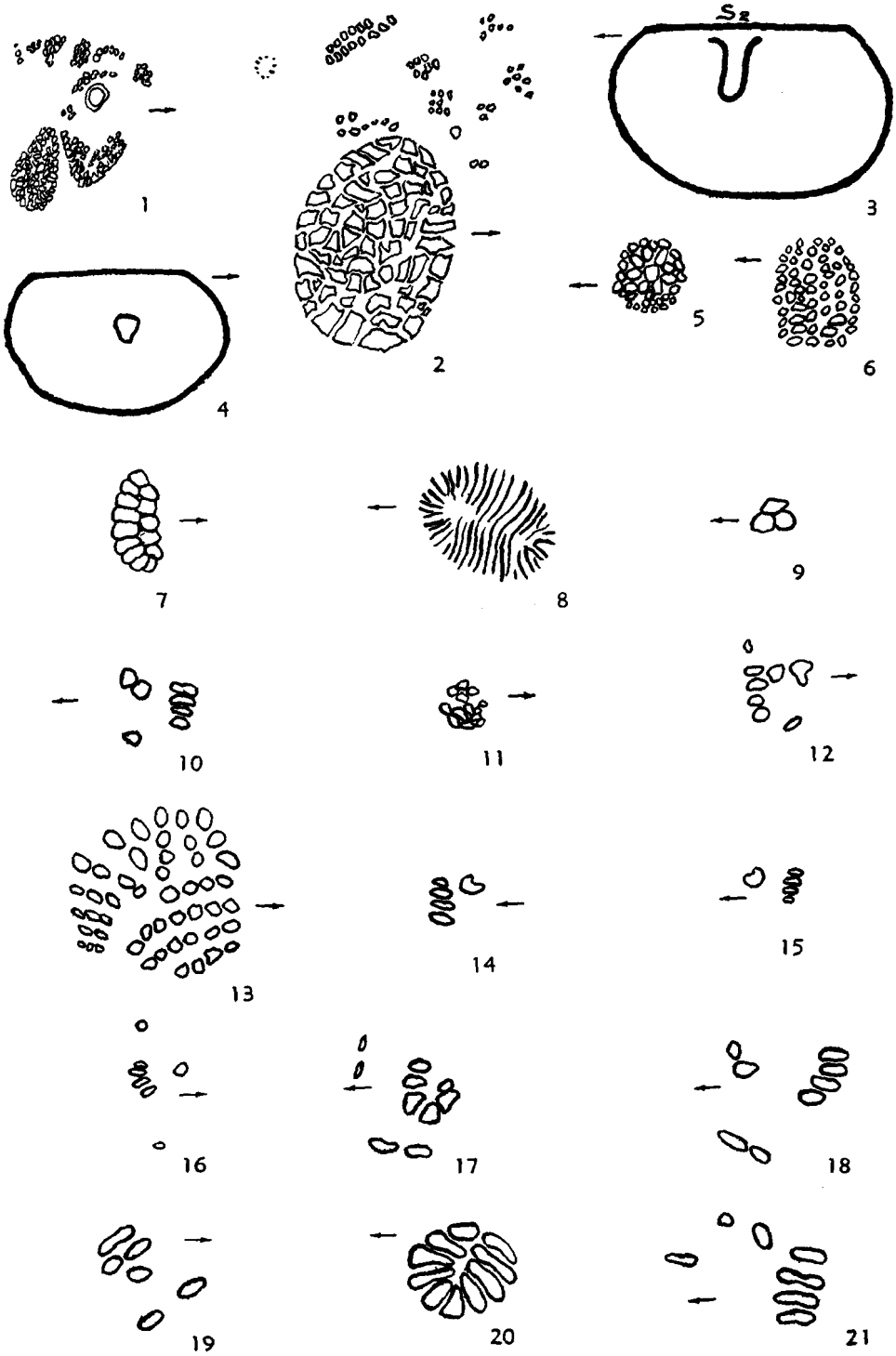
In the platycopines (Fig. 21,7) the adductor muscle scar is composed of a closely

spaced set of secondary scars arranged in a double row. The secondary scars are usually 10 to 14 in number. Their arrangement in a biserial manner is typical of the suborder.

Scars in some of the metacopine podocopids are well known, in others unknown. In *Cavellina* and *Healdia* (Fig. 21,5,6) the adductor muscle scar consists of a cluster of as many as 40 closely spaced secondary scars. TRIEBEL (1941, pl. 5, fig. 50) shows mandibular, antennal and adductor scars in *Cavellina*. The large number of secondary scars in *Cavellina* clearly shows that such a form cannot be classified with an ostracode like *Cytherella*, which has a small number of secondary scars, even though the outline of the carapaces is almost identical. Muscle scars have not been reported from some families of Metacopina and, therefore, the variation of scar pattern is unknown.

HOWE & LAURENCICH (1958) show how muscle scars differ among the superfamilies of the podocopids. In the Bairdiacea seven or more secondary scars are closely packed into a subcircular group, very closely packed in *Bythocypris*, loosely packed in *Bairdia*. In *Darwinula* (Fig. 21,20) they are arranged in a rosette of nine or ten elongate-ovate scars. Scars in the Cypridacea (Fig. 21, 17,19) are usually grouped into two sets, one large set of about six ovate scars of the adductor muscle and a second more anteroventral set of two discrete scars representing the mandibular muscles. In some valves antennal scars occur anterodorsally. None of the scars in the cypridids, which usually are visible through the translucent shell, are closely packed. Though not much work has been done on them it appears that the pattern is somewhat similar between such genera as *Candona* and *Cypria* and their value may be limited to family distinction. The Cytheracea (Fig. 21, 10,12, 14-16,18,21) have a typical set of four discrete ovate scars in a vertical row, flanked anteriorly by one or more isolated mandibular or antennal scars. The axis of the four adductor scars is usually inclined anteroventrally. A few genera can be identified by the pattern or shape of scars. Variation is produced by fusion, fission, or change in shape of either the adductor or mandibular scars.

Very little can be said about the development of the muscle-scar pattern. In the



Ordovician *Eoleperditia* the adductor muscle was extremely large, consisting of bundled muscle fibers that produced a broad scar with many closely packed secondary scars. In late Paleozoic *Healdia* and *Cavellina* the adductor muscle is marked on each valve by as many as 40 closely grouped secondary scars. This is in sharp contrast to most post-Paleozoic forms in which the secondary scars are few and commonly spaced well apart.

HINGEMENT

Hingement is one of the most important features for use in classifying Mesozoic and Cenozoic ostracodes. Hinge characters are not so well known among the palaeocopids but are used wherever possible. The following discussion is based in part on the reports of LEVINSON (1950), HOWE & LAURENCICH (1958) and SYLVESTER-BRADLEY (1956). Most of the definitions and examples are based on their work.

The two valves of an ostracode are articulated in a variety of ways along the dorsal margin. Types of hingement may be divided into four broad groups: (1) smooth contact without interlocking devices; (2) straight or curved, smooth or denticulate hinge bar (tongue or ridge or apical list) that fits into a corresponding smooth or denticulate groove (Fig. 22*A*); (3) straight or curved hinge bar and groove supplemented by cardinal teeth and sockets, which are smooth or partially to wholly crenulate (Fig. 22*B*); and (4) a peripheral lock in genera in which one valve is larger than the other, the edge (commonly the selvage) of the smaller valve fitting into a groove in the larger. These major types have been subdivided for the most part on the basis of modifications such as degree of denticulation of the bar or cardinal teeth.

The nature of hingement in the archaeocopids is unknown. In the leperditicopids several kinds of hingement have been recognized. In *Eoleperditia* hingement appears to be of adont type (Fig. 23,1), consisting of a simple bar and groove. In *Herrmannina*, however, well-preserved vertical bars and slots occur along the hinge in manner that characterizes the prionodont type (Fig. 23, 2). Thus, different types of hinges are recognized as occurring in one family (Leperditidae) as early as the Ordovician.

The adont hinge was common among the palaeocopids, although by no means the only type of hinge in this group (LEVINSON, 1950). Some leperditellids appear to have valves that meet smoothly along the hinge contact as though they were held together only by an elastic band. In many genera of the Kloedenellacea the hinge is adont but may be modified by one or more faint cardinal teeth, approaching the lophodont type (Fig. 23,3), characterized by simple anterior and posterior cardinal teeth in one valve that fit into corresponding sockets in the opposite valve. In the Glyptopleuridae the hingement is distinctly lophodont and in the Miltonellidae it is reported as amphidont (see below). Hingement among the palaeocopids is not sufficiently known to make possible discrimination of significant types of articulation common to various genera or families and determination of evolutionary trends in the nature of hingement.

WAINWRIGHT (1959) reports that the hingement of *Dizygopleura swartzi* and *Eukloedenella sinuata* is characterized by the presence of a hinge bar in the left valve and a corresponding groove in the right (adont). In *Eukloedenella* the hinge bar of the left valve is bounded ventrally along its entire length by a distinct groove that engages a well-defined ridge bordering the

(See facing page)

FIG. 21. Muscle scars of representative ostracodes.—LEPERDITICOPIDA: 1. *Herrmannia welleri*, L. Sil., $\times 8$. 2. *Eoleperditia fabulites*, M.Ord., $\times 11$.—PALAEOCOPIDA: 3. *Euprimites effusus*, M.Ord., $\times 37$. 4. *Tuaerenella carinata*, M.Ord., $\times 25$.—PODOCOPIDA (PODOCOPINA): 10. *Clithrocytheridea appendiculata*, Eoc., $\times 90$. 11. *Bythocypris arcuata*, Mio., $\times 60$. 12. *Cytheridea praesulcata*, Oligo., $\times 110$. 14. *Trachyleberis asperima echinata*, Oligo., $\times 75$. 15. *Krithe papillosa*, Mio., $\times 75$. 16. *Loxococoncha subtriangularis*, Oligo., $\times 115$. 17. *Candona neglecta*, Rec., $\times 165$. 18. *Pseudocythere caudata*, Rec., $\times 250$. 19. *Cypridopsis vidua*, Rec., $\times 93$. 20. *Darwinula stevensoni*, Rec., $\times 190$. 21. *Paradoxostoma variabile*, Rec., $\times 190$.—PODOCOPIDA (METACOPINA): 5. *Healdia leguminoidea*, Penn., $\times 250$. 6. *Cavellina*, Penn., $\times 180$.—PODOCOPIDA (PLATYCOPINA): 7. *Cytherella abyssorum*, Rec., $\times 160$.—MYDOCOPIDA (MYDOCOPINA): 8. *Entomocochus*. 13. *Cypridina homoedwardsiana*, Eoc., $\times 110$.—MYDOCOPIDA (CLADOCOPINA): 9. *Polycope orbicularis*, Rec. (1 after 75; 2, 5, 6 after 70; 3, 4 after 36; 7, 9 after 68; 8 after 366a; 10-16 after 42; 17-21 after 88.)

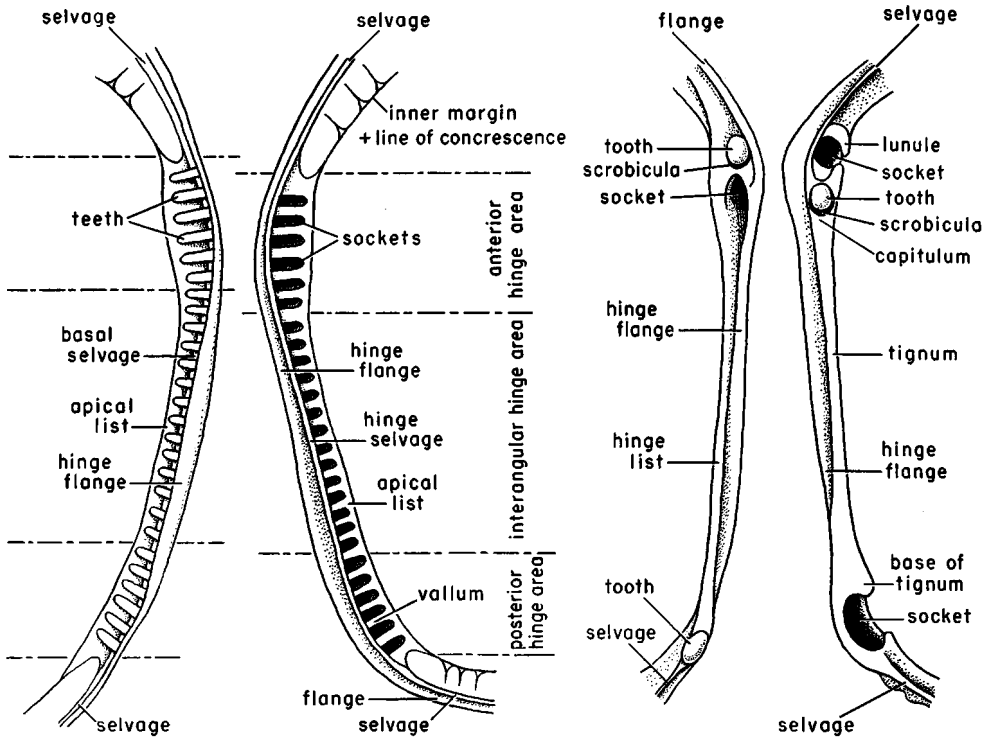


FIG. 22. Nomenclature of hinge elements of cytheracean ostracodes. A, B, *Cytheridea hungarica* ZALANYI, LV, RV (Cytherideidae); C, D, *Cythereis dentata* G. W. MÜLLER, LV, RV (Trachyleberididae) (44).

main hinge groove of the right valve. Such a groove is not present on the dorsal side of the main hinge element but a broad depression in the dorsum serves to accommodate the overhang of the right valve. In *Dizygopleura* the hinge bar of the left valve is not bounded either dorsally or ventrally by a supplementary groove; however, a depression of the dorsum serves to accommodate the overhanging right valve. The hinge bar shows no significant change in size throughout its length and no cardinal hinge teeth are present. As determined from the exposed hinge area of a right valve of *Kloedenella cornuta* no supplementary dentition occurs. The so-called anterior cardinal tooth of the kloedenellids is not part of the hinge-ment but merely a peculiar structure of the overlapping left valve in the region of the anterodorsal free margin; this structure is accommodated by a depression in the right valve. The hinge devices proper terminate immediately behind the "tooth." This structure is best developed in dizygopleurid species; it is less definitive but nevertheless

present in species of *Kloedenella* and *Eukloedenella*.

In both *Dizygopleura swartzii* and *Eukloedenella sinuata* the left valve overlaps the right valve around the entire free margin, in most pronounced manner antero- and posteroventrally (Fig. 24). Overhang of the dorsum of the right valve with respect to that of the left is seen in both species but it is better developed in *Dizygopleura*. This overlap is due to a dorsally directed thickening of the shell, particularly in the region of L_3 and the main sulcus of *Dizygopleura* and in corresponding positions of *Eukloedenella*.

The anterior "cardinal tooth" is a very distinctive feature formed by a thickening of the shell and lateral projection of the margin of the left valve in the region of S_1 and L_2 in quadrilobate and trilobate species and in a corresponding position in bilobate forms. In dorsal view this feature appears as a large, triangular toothlike structure extending from the left valve and overlapping the right valve. The dorsal over-

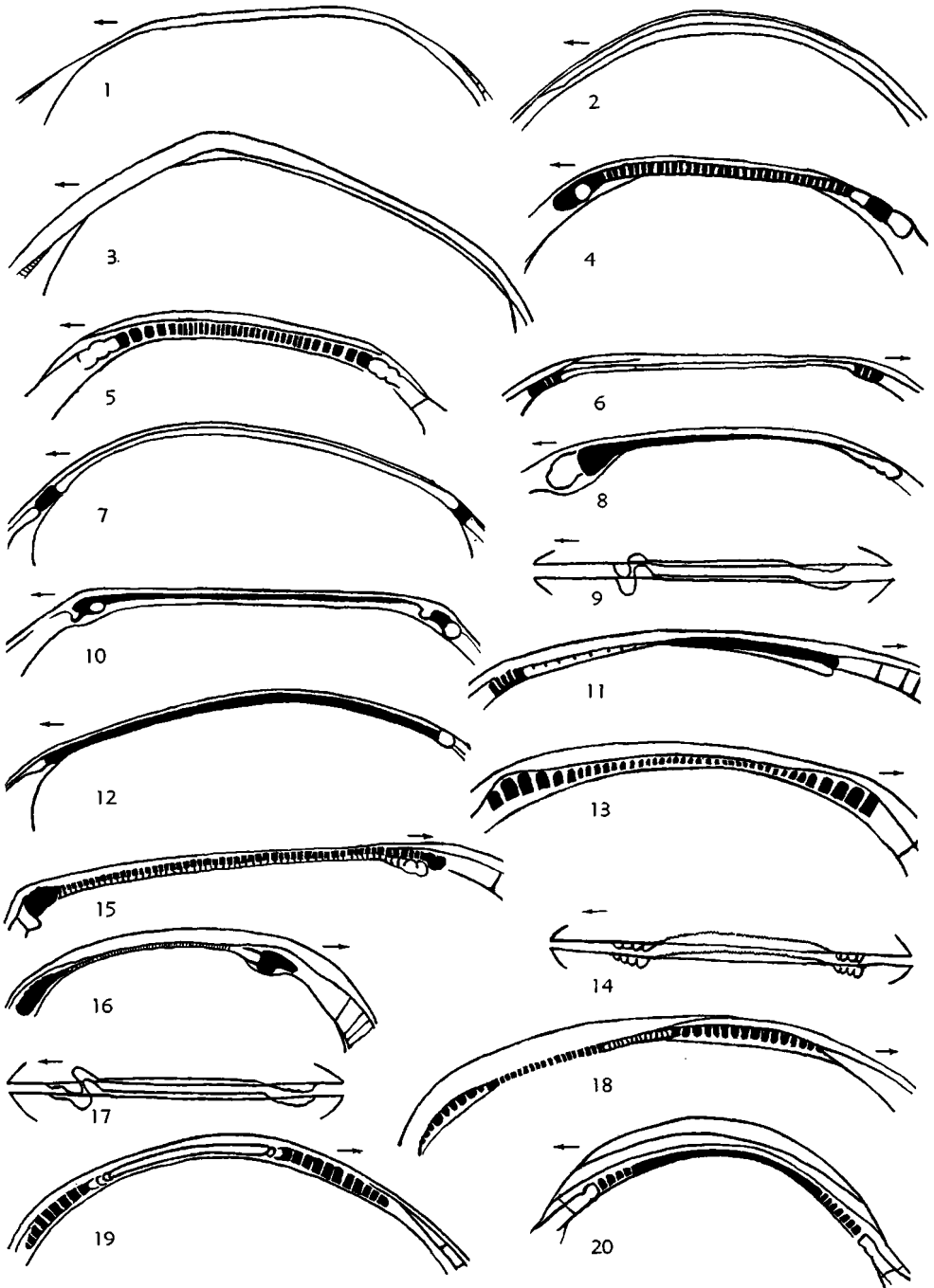


FIG. 23. Hinge structures characteristic of Podocopida (Podocopina).—1-3. CYPRIDACEA: 1, *Candona compressa* (Cyprididae), $\times 84$; 2, *Cypria ophthalmica* (Cyclocyprididae), $\times 130$; 3, *Cypridopsis aculeata* (Cyprididae), $\times 125$.—4-20. CYTHERACEA: 4, *Loxoconcha rhomboidea* (Loxoconchidae), $\times 133$; 5, *Cytheropteron latissimum* (Cytheruridae), $\times 123$; 6, *Cytherura gibba* (Cytheruridae), $\times 137$; 7, *Paradoxostoma normani* (Paradoxostomatidae), $\times 182$; 8-9, *Heterocythereis albomaculata* (Hemicytheridae), $\times 95$; 10, *Cytheromorpha fuscata* (Paradoxostomatidae), $\times 130$; 11, *Hemicytherideis elongata* (Cytherideidae), $\times 90$; 12, *Paradoxostoma variable* (Paradoxostomatidae), $\times 133$; 13-14, *Cythere lutea* (Cytheridae), $\times 137$; 15, *Leptocythere pellucida* (Leptocytheridae), $\times 137$; 16-17, *Hemicythere villosa* (Hemicytheridae), $\times 98$; 18, *Cyprideis torosa* (Cytherideidae), $\times 88$; 19, *Xestoleberis depressa* (Xestoleberididae), $\times 137$; 20, *Hemicytherura clathrata* (Cytheruridae), $\times 140$ (88).

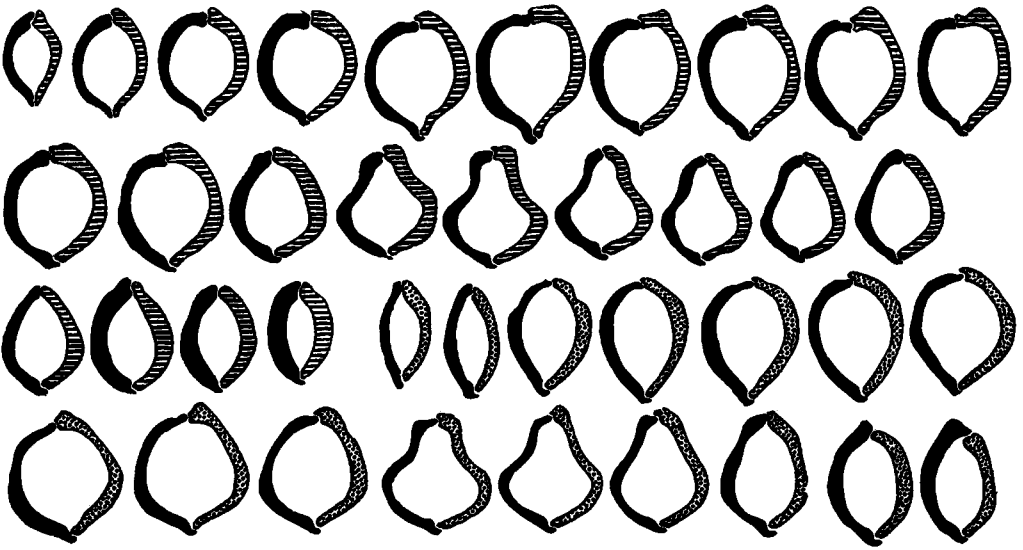


FIG. 24. Serial transverse sections of heteromorph carapaces belonging to Kloedenellocopina, left-to-right arrangement in each row indicating successive positions from rear toward front of carapace (camera lucida drawings). Sections in upper rows with left valve black and right valve ruled were drawn from a female of *Eukloedenella sinuata* ULRICH & BASSLER (M.Sil., Pa.), enlarged. Sections in lower rows with left valve black and right valve stippled were drawn from a female of *Dizygopleura swartzii* ULRICH & BASSLER (M.Sil., Pa.), enlarged (399).

hang of the right valve ends at the posterior margin of the tooth.

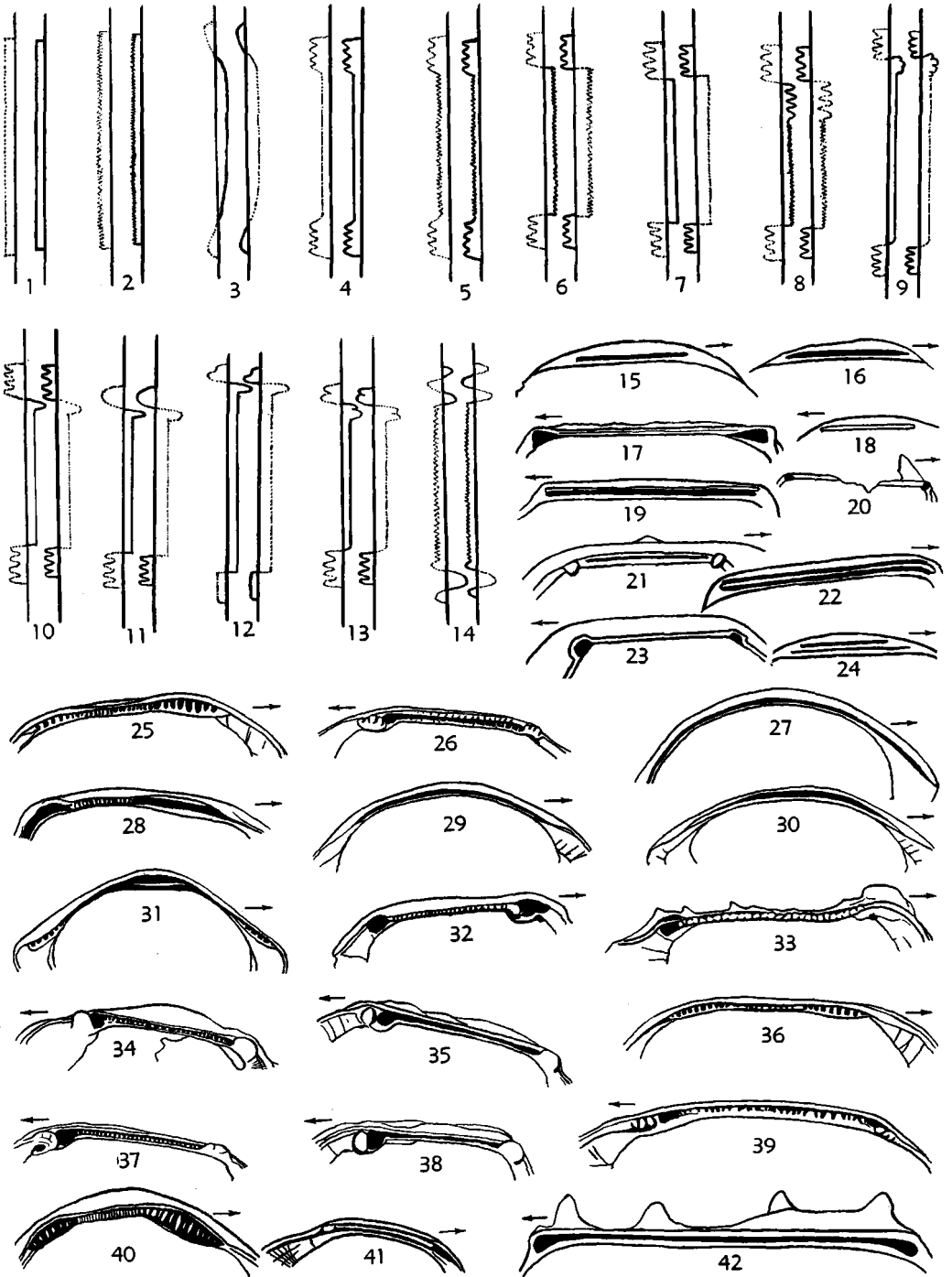
WAINWRIGHT also reports that in *Beyrichia moodeyi* and *Kloedenia normalis* the hinge element of the left valve consists of a bar extending the entire length of the hinge area without supplementary dentition or bounding grooves. The right valve is presumed to contain a corresponding groove. This agrees with the type of hinge structures reported by LEVINSON (1950, p. 66, fig. 1) for *Beyrichia fitti* and *B. jonesi*. The manner of articulation of the valves along the free margin could not be deter-

mined, since only single valves were available.

In *Drepanellina clarki*, according to WAINWRIGHT, the left valve contains a hinge bar with no supplementary hinge structures. This element is formed by the tapered dorsal edge of the valve. The right valve is presumed to contain the corresponding hinge groove. *Mastigobolbina typus* possesses a very narrow, shallow groove extending across the length of the hinge area of the left valve. This is presumed to have accommodated a fine ridge in the right valve.

(See facing page)

FIG. 25. Diagrammatic illustrations of ostracode hinge structures; 1-14, dorsal views of LV and RV; 15-42, interior views.—1. Adont.—2. Prionodont.—3. Lophodont.—4-7. Merodont types: 4, paleomerodont; 5, holomerodont; 6, antimerodont; 7, hemimerodont.—8. Entomodont.—9. Lobodont.—10-12. Amphidont types: 10, paramphidont; 11, hemiamphidont; 12, holamphidont.—13. Schizodont.—14. Gongylodont.—15. *Thlipsura furca*, $\times 40$.—16, 18. *Thlipsurella fossata*, $\times 24$.—17. *Ctenobolbina papillosa*, $\times 28$.—19. *Millerania cincinnatiensis*, $\times 52$.—20. *Ceratopsis chambersi*, $\times 13$.—21, 23. *Primitiopsis bassleri*, $\times 51$.—*Bonneprimites bonnemai*, $\times 40$.—24. *Eridoconcha rugosa*, $\times 57$.—25. *Haplocytheridea curvata*, $\times 60$.—26. *Paracytheridea brusselensis*, $\times 76$.—27. *Cypridina homoedwardsiana*, $\times 33$.—28. *Cyprideis apostolescui*, $\times 50$.—29. *Bythocypris cuisensis*, $\times 40$.—30. *Paracypris contracta*, $\times 40$.—31. *Bairdoppilata gliberti*, $\times 30$.—32. *Ruggieria micheliniana*, $\times 40$.—33. *Paracytheridea grignonensis*, $\times 76$.—34. *Cytheretta haimeana*, $\times 60$.—35. *Costa edwardsi*, $\times 50$.—36. *Cytheridea praesulcata*, $\times 13$.—37. *Bradleya cornueliana*, $\times 40$.—38. *Bradleya approximata*, $\times 40$.—39. *Boldella deldenensis*, $\times 89$.—40. *Haplocytheridea curta*, $\times 65$.—41. *Cuneocythere joveolata*, $\times 60$.—42. *Drepanella crasinoda*, $\times 27$. BEYRICHIOPINA are represented by 17, 20, 21, 23, 42; KLOEDENOCOPINA by 19, 22, 24; PODOCOPINA by 25, 26, 28-41; METACOPINA by 15, 16, 18, and MYDOCOPINA by 27 (1-14, after 34; 15-24, after 49; 25-39, 41, after 42; 40, after 7; 42, after SCOTT, n.)



The ventral edge of the left valve of *Drepanellina clarki* contains a groove—very distinct in the region of the dimorphic inflation—that accommodated a projection of the ventral edge of the right valve.

The **peripheral** type of hinge lock is found in the Cytherellidae and among some of the Paleozoic Cavellinidae and a modified form in the Bairdiidae. This type is well represented in the modern *Cytherella* and *Cytherelloidea*.

Merodont hingement (Fig. 25,4,7) consists of a bar terminated by crenulate teeth in one valve opposed to a groove and sockets in the opposite valve. Four varieties are known and all are believed to be a development of adont or prionodont structures. The **paleomerodont** variety of merodont hingement (Fig. 25,4), characterized by simple bar and crenulate cardinal projections, is found in *Schuleridea* from the Jurassic; the **holomerodont** type (Fig. 25,5), with crenulate bar and terminal cusps, is recognized in *Haplocytheridea*; a partial reversal of holomerodont called **antimerodont** (Fig. 25,6), in which the terminal projections and groove are crenulate, is found in *Clithrocytheridea*; and **hemimerodont** hingement (Fig. 25,7), similar to antimerodont except for smooth median elements, is seen in *Palaeocytheridea*. Varieties of merodont articulation are common in Mesozoic ostracodes. Whether or not it occurs in the Paleozoic is unknown, but clearly it seems to have been derived by modification of Paleozoic types of hingement; in what part of geologic time the modification occurred is not precisely determined.

In **entomodont** hingement (Fig. 25,8) four elements are distinguished: a median bar (and groove) with (1) a coarsely crenulate anterior element and (2) smooth or crenulate remaining portion and (3) anterior and (4) posterior crenulate teeth (and sockets). A variety in which the anterior

median element is lobate instead of crenulate is known as **lobodont** (Fig. 25,9). *Progonocythere* characterizes the former and *Acanthocythere* the latter.

Amphidont (heterodont of some authors) hingement (Fig. 25,10,12), characterized by a smooth tooth at the anterior end of the bar, is represented in the Cretaceous and becomes the most common type in the Tertiary. Its first reported appearance is in the Miltonellidae of the Permian. In the variety defined as **paramphidont** hingement (Fig. 25,10), as found in *Cythereis*, the median bar is crenulate or smooth, the anterior and posterior elements are notched or crenulate, and at the anterior end is also a smooth tooth or socket. In another variety called **hemiamphidont** (Fig. 25,11) the elements are like those of paramphidont hingement except that the posterior element is smooth or stepped, not crenulate (e.g., *Brachycythere*, *Alatacythere*). In a third variety, **holamphidont** (Fig. 25,12), the terminal elements are smooth or stepped and noncrenulate (e.g., *Amphicytherura*, *Trachyleberis*, *Pterygocythereis*).

The term **schizodont** (Fig. 25,13) has been applied to hingement observed in a small group having bifid anterior elements in both valves (e.g., *Paijenborchella*). This structure obviously is a minor modification of the amphidont type.

Loxoconcha has a rather complex hingement. Seen in lateral view, the hinge is somewhat convex, with the anterior element of one valve sharply downturned and the posteriormost element a knoblike tooth; in the opposite valve the reverse order of elements is found. This type has been referred to as **gongylodont** (Fig. 25,14).

Most of the named hingements may be found in the Cytheracea (Fig. 23,4,20). A highly varied set of hinge features are known to occur in the Cypridacea but they have not as yet been evaluated (Fig. 23,1,3).

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DIMORPHISM OF OSTRACODA

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CONTENTS

	PAGE
KLOEDENELLID DIMORPHISM	Q37
LOBATE DIMORPHISM	Q38
BEYRICHIID DIMORPHISM	Q39
VELATE DIMORPHISM	Q42
HISTIAL DIMORPHISM	Q42
REFERENCES	Q43

Syngamic and parthenogenetic methods of reproduction are known to occur in living ostracodes, somewhat rarely even within a single species that in part of its area of distribution may be syngamic and elsewhere parthenogenetic. Dimorphism in living or Mesozoic-Cenozoic ostracodes is not important in classification as it is among the Palaeocopida.

Dimorphic characters in the palaeocopids have been long recognized although much is yet to be learned about their morphology. Previous lack of adequate understanding often has resulted in misorientation of the carapace and confused classification. Various kinds of dimorphic structures have been described: (1) *kloedenellid* or *domiciliar*, characterized by slightly swollen to strongly inflated posterior portions of the carapace, as displayed in *Kloedenella* and many modern genera of the Podocopida; (2) *lobate*, distinguished by presence of a dimorphic lobe on the lateral surface in a lateroventral or anteroventral position, as found in *Zygobolbina* and *Bonnemaia*; (3) *beyrichiid*, marked by a strongly inflated portion of the domicilium that forms a pouch (crumina), as in *Beyrichia*, probably a spe-

cial type of velar development; (4) *velate*, including structures classed as (a) *simple velum*, straight to slightly convex, as in *Hollinella*, (b) *closed velum*, forming a false pouch (dolon), as in *Uhakiella*, (c) *locular*, with compartment-like divisions, as in *Abditoloculina* and *Tetradella*; and (5) *histial*, defined by a flangelike structure continuous with the ventral ridge connecting the lobes parallel to the free margin and protruding ventrally, as in *Sigmoopsis* and *Glossomorphites*.

The sex of an ostracode cannot readily be determined in all cases. Adult females of species exhibiting dimorphic structures can be recognized without difficulty, whereas the adult males of such species lack carapace structures trustworthy for distinguishing them from juvenile stages of both sexes. Accordingly, JAANUSSON (1956) has suggested that the adult females of dimorphic species be referred to as *heteromorphs* and the males and juveniles as *tecnomorphs*.

KLOEDENELLID DIMORPHISM

A common type of dimorphism seen both in the Kloedenellocopina and Recent ostracodes is characterized by inflation of the

posterior portion of the domicilium of the female. In the palaeocopid group such inflation is referred to as kloedenellid. Kloedenellid dimorphism is observed most readily in dorsal view. The males and pre-adult instars are usually elongate-ovate, with the greatest width medial, whereas the adult female carapace is wedge-shaped, with the greatest width in posterior position. This has been observed in many genera (e.g., *Kloedenella*, *Dizygopleura*, *Glyptopleura*, *Geisina*, *Sansabella*) and is believed to be present in all Kloedenellacea.

The posterodorsal inflation of the domicilium in kloedenellid heteromorphs is on the whole so similar to the genital inflations of certain living ostracodes that their homologous relationship can hardly be doubted. Fossil forms possessing such inflations were distinguished as females by VAN VEEN (1922) in *Kloedenella*, and by SWARTZ (1933) in *Kloedenella*, *Eukloedenella*, and *Dizygopleura*; these authors interpreted the dimorphic inflation as posterior in position, agreeing with now accepted orientation. However, ULRICH & BASSLER (1923a,b) did not recognize the presence of dimorphism in Middle Silurian Kloedenellidae and identified the wider end of the carapace as anterior, thereby assigning the domiciliar inflation to a forward location and the main sulcus to a posterior position.

Among Middle Silurian Kloedenellidae the species of *Dizygopleura* best illustrate relationships of the dimorphic swelling to other lobal features of the domicilium. In *D. swartzi*, a typical representative of the genus, the inflation is in the posterodorsal region of the carapace and merges anteriorly with L_4 so as partially to obscure the posterior margin of this lobe; in effect it is an annex to L_4 . TRIEBEL (1941, p. 356) points out that similar inflation in living ostracodes functions as a brood chamber, or that, in forms not offering protection for the young, it houses the enlarged oviduct. The exact function of the kloedenellid homologue is, of course, open to speculation.

In species of *Kloedenella* (e.g., *K. cornuta*) the dimorphic swelling tends to obscure the posterior border of the adjacent lobe L_3 . In both *Dizygopleura* and *Kloedenella* the dimorphic feature is well defined laterally and is quite apparent in dorsal aspect. In species of *Eukloedenella*, how-

ever, the inflation is not very distinct laterally, though easily recognized in dorsal view.

Unfortunately, inadequate attention has been paid to effects of kloedenellid dimorphism on shell features, and accordingly different dimorphs have been described as different species. Inflation or swelling of the posterior region of the carapace not only changes its shape in dorsal view but also causes the hinge channel to widen backward, in some species altering the degree of overlap from the posterocardinal point around the posterior end.

LOBATE DIMORPHISM

In some palaeocopids the anterior, anteroventral, or ventral portion of the carapace is raised into a distinct lobe. In some species this ventral lobe may be a part of the anterior (L_1) and ventral lobes. Transverse sections through these lobes (Fig. 26), show no evidence of a remnant partition such as always is found in *Beyrichia* (Fig. 27); only an external swelling of the domicilium and a corresponding internal deepening of the carapace is seen. A form of domiciliar dimorphism is indicated, differing from typical kloedenellid only both in its location and its lobate nature. In kloedenellid dimorphism the posterior portion of the carapace is swollen to produce a wedge-shaped general outline to the carapace, whereas in lobate dimorphism it is a portion of the anterior, anteroventral, or ventral area of the carapace that is inflated to produce a distinct lobe. This dimorphic lobe may be short or long, straight or curved, high or low, and smooth or ornamented. The lobe of *Zygo-bolbina* is a typical example of lobate dimorphism.

In members of the Zygo-bolbidae, dimorphism is characterized by anterior to anteroventral inflation of the domicilium; such an orientation of the dimorphic feature places S_2 anteriorly. These inflations are not homologous to the posterodorsal swelling of kloedenellids. In *Mastigobolbina typus* dimorphism is characterized by inflation of part of the domicilium anterior and anteroventral to L_2 (Fig. 26); in *Drepanelina clarki* the dimorphic feature is an enlargement of the ventral lobe (Fig. 26).

The zygo-bolbid mode of dimorphism was

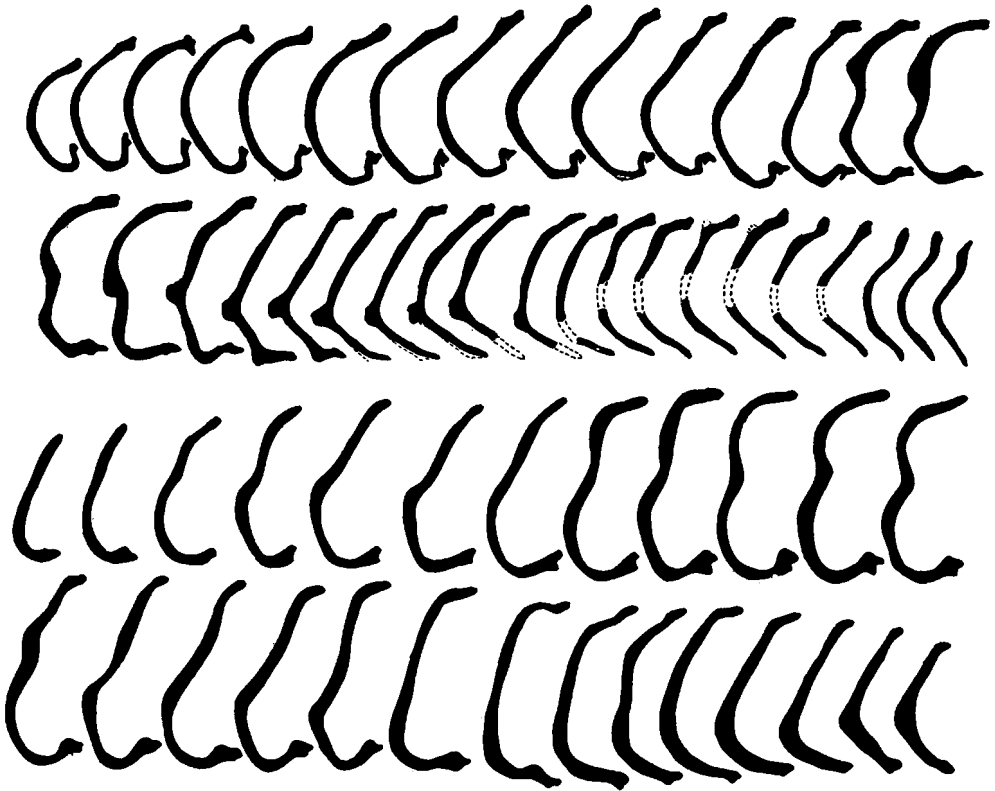


FIG. 26. Serial transverse sections of heteromorph left valves belonging to Beyrichicopina illustrating features of lobate dimorphism, left-to-right arrangement in each row indicating successive positions at approximate 100-micron intervals from rear toward front of valve. Upper two rows drawn from a specimen of *Mastigobolbina tyra* ULRICH & BASSLER (M.Sil., Pa.), enlarged. Lower two rows drawn from a specimen of *Drepanellina clarki* ULRICH & BASSLER (M.Sil., Pa.), enlarged (399).

apparently initiated during early Middle Silurian time (lower part of Rose Hill Formation) in the many species of *Zygobolba*, *Zygobolbina*, and *Zygosella* (ULRICH & BASSLER, 1923b, pl. 39-45); it continued through Rose Hill time in the genera *Bonnemaia* and *Mastigobolbina* and culminated in the genus *Drepanellina* of the Rochester Shale.

BEYRICHIID DIMORPHISM

Dimorphism in *Beyrichia*, distinguished as the beyrichiid type (Fig. 27), was recognized long ago by the presence of a large "pouchlike" structure. This was considered to mark the posterior end of the carapace and only recently has it been realized that the prominent swelling is anteroventral in the adult female.

The pouch of *Beyrichia* seems to be directly related to expansion of the velum.

This type of dimorphism has been called cruminal, to distinguish it from the external pouch formed as a velate structure in the Eurychiliniidae and Holliniidae.

RICHTER (1869) was first to recognize this type of dimorphism in several European species of *Beyrichia*, at the same time comparing the cruminae (small saclike projections) with the posterior swellings of the female of Recent *Cythere gibba*. ULRICH & BASSLER (1923a) suggested that cruminae were brood pouches in which eggs and larval forms could be protected. These authors (also KUMMEROW, 1931) interpreted the cruminae as belonging in a posterior position that would offer least resistance during movement of the animal through water and least impedance from obstacles encountered as the ostracode crawled along the bottom. BONNEMA (1930, 1932) placed the cruminae anteriorly, an orientation vigorously ob-

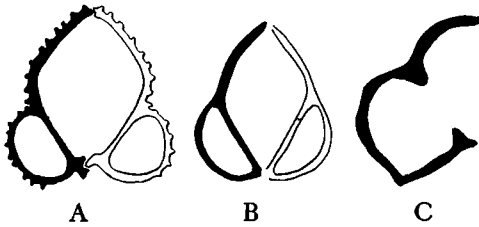


FIG. 27. Transverse sections of heteromorph carapaces and left valve belonging to Beyrichicopina, illustrating beyrichiid dimorphism.—A. *Hibbardia lacrimosa* (SWARTZ & ORIEL) (M.Dev., N.Y.), with complete inner partition in each valve (204).—B. *Phlyctiscapha rockportensis* KESLING (M.Dev., Mich.), with complete inner partition in each valve, enlarged (202).—C. *Beyrichia moodeyi* ULRICH & BASSLER (M.Sil., N.Y.), with incomplete inner partition enlarged (399).

jected to by KUMMEROW (1931). The currently accepted position of the cruminae is anterior to anteroventral, based on position of the adductor muscle scars.

The function of the cruminae has been the subject of much discussion among students of the Beyrichiidae. It has been suggested that this structure was used as a breeding room and should therefore occur posteriorly, a position in which eggs could most easily be transferred, by means of posterior appendages, from the region of the genitalia into the cruminae. However, the objection has been raised that currents produced by posterior natatory appendages would tend to flush the young out of the brood space. HESSLAND (1949), from a detailed study of the brood-pouch problem, reached judgment that the posterior location of the cruminae "would have been a serious hindrance during copulation or might even have made this process impossible." Such conclusions are based on observations made by ELOFSON (1941) on copulation in living ostracodes. HESSLAND (1949) points out that an anterior brood space would place the eggs and young in dangerous proximity to the oral appendages, and thus it is likely that they would suffer from indiscriminate eating habits of the adult animal.

SCHMIDT (1941) believed that cruminate specimens were males, and that the cruminae were used for storage of spermatozoa. TRIEBEL (1941) also suggested that the crumina was a male structure that served as a sperm vesicle. Conversely, it could be a structure of the female carapace into which

seminal fluids could be injected by the male animal during copulation, and subsequently utilized by the female when ovulation occurred. SCHMIDT (1941, p. 11) suggested that these chambers might be gas-filled cavities that could lend buoyancy to the carapace. The discovery by HESSLAND (1949, pl. 14, fig. 9) of larval carapaces in the cruminae of carapaces of *Beyrichia kloedeni* that were sectioned transversely, and similar observations by SPJELDNAES (1951) in *B. jonesi*, strongly suggest that the crumina was used as a brood chamber. In each of these reported occurrences, adventitious introductions of carapaces from without were not considered probable.

The possibility of transferring eggs from the region of the genitalia to anteroventral cruminae has been investigated by HESSLAND (1949).

Observation of lobate ostracodes in which orientation of the carapace is well established shows that the largest lobe of each valve (not to be confused with crumina) occurs posteriorly, and it is in this area that growth is most pronounced as the animal matures; we may therefore assume that the largest lobe of *Beyrichia moodeyi* occurs posteriorly and houses the genitalia. In the tecnomorphs of this species, the posterior lobe possesses an acuminate ventral extension that curves forward to its termination at a depression ventral to L_2 ; this depression occupies the same position as the crumina in heteromorphic valves. A slight inflation of the velum occurs subjacent to the extension of the posterior lobe. In the heteromorph, a similar extension of L_3 terminates at the posterodorsal margin of the crumina and is confluent with the subjacent inflation of the velum. This is indeed suggestive of a duct by means of which ova could be moved forward into the crumina by a bending of the abdomen.

The beyrichiid crumina has been judged by many workers to be an extension of the domicilium. KESLING & ROGERS (1957) conclude that ". . . the female brood pouch originated when a strongly convex part of the frill fused with the contact margin."

Transverse serial sections of *Beyrichia moodeyi* (Fig. 28) show that the crumina is not a swelling of the domicilium but a chamber within the velum formed by an inflation of the epidermal fold that produced

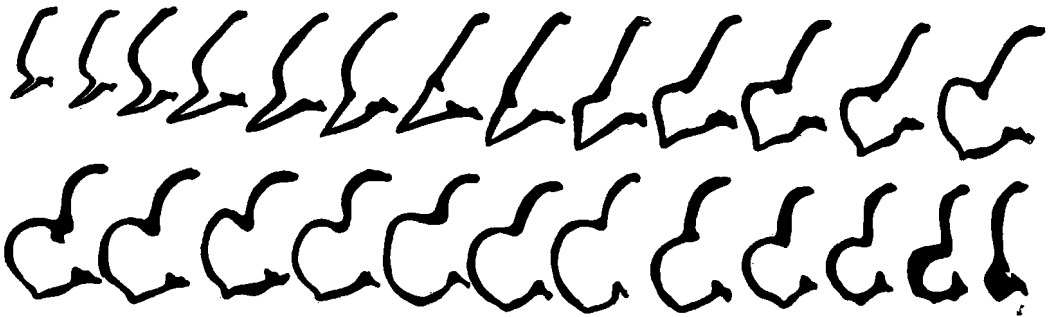


FIG. 28. Serial transverse sections of heteromorph left valve of *Beyrichia moodeyi* ULRICH & BASSLER (M. Sil., N.Y.) illustrating beyrichiid dimorphism; left-to-right arrangement in each row indicating successive positions at approximate 50-micron intervals from rear toward front of valve (two sections at left of top row hypothetical, showing coalescence of sides of velum), $\times 14$ (399).

the velum. In this species, the bulbous crumina is continuous with the narrow, elongate cavity within the velum. The latter extends backward, becoming narrower as the sides of the velum converge, and is presumed to be completely eliminated in the posteroventral region of the valve where the open cavity is reduced to a mere dark line—vestige of the epidermal fold—bisecting the velum. A reflection of the crest of the velum can be traced across the external, ventral surface of the crumina; the position of the crest is marked internally by a depression on the lower floor of the crumina.

KESLING (1957) notes that in some beyrichiid heteromorphs the velate structure is completely interrupted by the crumina, in others it encroaches onto the sides of the crumina, and in still others it extends across the entire crumina. He suggests that during phylogeny the velate structure could either have retreated from the crumina or gradually grown across it, but favors the second explanation because "the frill does not extend onto the pouch in Lower Silurian ostracodes. It likewise seems significant that the oldest known ostracodes having a frill across the brood pouch are from Upper Silurian rocks." Study of the Middle Silurian *Beyrichia moodeyi* shows that a diminution in relief of the crest of the velum along the ventral surface of the crumina parallels the development of the crumina, the crest being most reduced where the crumina attains maximum inflation. This is only a short step beyond the point at which the reflection of the velar crest did not extend across the entire crumina. Originally, according to KESLING (1957), the crumina developed

as a specialized section of the velum, and encroachment of the unspecialized velate structure onto and across the crumina evolved later. He gives excellent illustrations of the relationship of the velate structure to the crumina in several members of the Beyrichiidae.

The relationship between the crumina and the velate structure in species in which the latter is complete and extends along the proximoventral side of the crumina is not clear. In beyrichiids with broad velate structures the crumina is contained within the velum, as in *Beyrichia moodeyi*, and does not restrict the lobes to any great extent. *B. salteriana* possesses a reduced velate structure and the crumina has encroached upon the domicilium to restrict the lobes (KESLING, 1957); in this species, the velate structure appears to be interrupted by the crumina. A further reduction of the velate structure occurs in *Phlyctiscapha rockportensis*, in which the crumina merges externally with the domicilium and the much-reduced velate structure occurs proximoventral to the crumina paralleling the ventral free margin. Internally, however, the crumina is quite separate from the domicilium, a partition being present between parts of the two features.

The beyrichiid crumina, although in some shells possessing an external resemblance to the dimorphic swelling of members of the Zygodolbidae, is distinguished from the latter by its internal relationship with the domicilium. A survey of published transverse sections of beyrichiid heteromorphic carapaces shows a prevailing tendency toward separation of the cruminal cavity from

the domicilium, some being accentuated by the presence of a dividing wall (Fig. 27). Even where a partition is absent, the shell tends to be thickened and produced in a direction toward the contact margin of the valve in the area of the juncture between the domicilium and crumina; concurrently, the ventral marginal area of the valve is extended toward a union with this feature. On the other hand, no tendency toward separation of the domicilium and dimorphic inflation is observed in the Zygodolbidae. Further study of transverse serial sections of beyrichiid ostracodes is essential for proper understanding of structural relationships between the crumina and velate structure and determination of its phylogenetic significance.

VELATE DIMORPHISM

A fourth type of dimorphism is recognized in the development of certain velar adventral features. JAANUSSON (1957) has shown the relationship of the velum (frill) to dimorphism, but the problem has been complicated by introduction of the term "histium." We recognize the primary or main frill as developed in the Hollinidae as a velum. It may be associated with one or more secondary ribs in either a ventral or dorsal position; the secondary ribs may be continuous or broken into tubercles or spines. KESLING & ROGERS (1957) illustrate two subvelar ridges in *Treposeella lyoni* and *T. stellata*. The velum is not just an external ornamental feature comparable to a costa but is a structure believed to have been formed by a fold of the inner chitin layer. As such, it shows a dark line of chitin between the outer and inner walls. This has been observed in *Hollinella* and *Hibbardia*.

The velum may be expressed as a broad frill that commonly is incurved. When curved strongly inward the free edges of the velum may approach each other closely or actually touch so as to form a pouch (dolon). The position of the dolon, if present, varies from anterior, anteroventral, ventral, to posterior. The function of the velum and velar dolon has been variously interpreted but it is generally accepted as an expression of dimorphism. Velate structures may have served different purposes in different genera.

In many species of *Hollinella* a splendid

development of the velum is seen in the adult. In some species it is a frill that extends along the ventral and all or part of the anterior margin like sled runners; in others it is strongly convex and almost meets along a portion of the venter. A typical velar dolon is formed anteroventrally in the heteromorph of *Uhaqiella*. In the Primitiopsidae the dolon occupies a posterior position and in the Eurychilinidae a ventral position.

In a few genera a very distinctive type of dimorphic feature has the form of successive closely spaced compartments called loculi. The development of this peculiar structure has been well illustrated by KESLING (1958). It is here considered that loculi are modifications of the velum. The locular type of dimorphism is well developed in *Ctenolocolina* where a row of locular cups open ventrally from an anteroventral and ventral position. Some loculi, as pointed out by KESLING (personal communication), are developed outside the frill (abvelar) (e.g., *Tetradella*) and others inside the frill (advelar) (e.g., *Ctenolocolina*).

HISTIAL DIMORPHISM

The term histium has been applied loosely to a dimorphic structure which has been confused with velum. Extensive studies of this problem indicate that the term velum should be retained for the main frill and that histium should be restricted to such marginal structures as are found in *Sigmoopsis*. KESLING (personal communication) says: "Histium is a ridge or flange-like structure parallel to the free edge generally protruding ventrally and lateroventrally, which, as seen in lateral view, (1) is continuous with a ventral ridge connecting lobes (e.g., *Glossomorphites*), (2) lies in the position of a connecting ventral ridge or lobe with no sharply defined boundary separating it from the lobes (e.g., *Sigmoopsis*), or (3) continues downward from the lobate area with sharp line of demarcation (e.g., *Ogmoopsis*, *Aulacopsis*). The base of a histium is broad and flared at its junction with the rest of the valve, which in most genera lies at the bend of the valve between the lateral and marginal surfaces. Histium is not the equivalent of velum or velar ridge, which in nearly all hollinids (e.g., *Hollinella*) has a sharp line of junction with the rest of the lateral surface. If a ventral lobe

is present in the Hollinidae (e.g., *Hollinella*, *Hanaites*, *Abditoloculina*, *Falsipollex*), the velum or frill is below and distinctly set off from it. The broad structure around *Tetradella* is also a velum, and not continuous with the ventral connecting ridge. It is not certain that the ridge present in some sigmoopsids between the marginal ridge

and the histium is homologous to the velar structure in hollinids."

The primary character of a histium is that it is part of a ventral ridge connecting the lateral lobes or a ridge that continues ventrally from the lateral lobe. In this sense it does seem to characterize a distinct type of dimorphism.

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ORIENTATION OF OSTRACODE SHELLS

By H. W. SCOTT

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The question of which are anterior, posterior, dorsal, and ventral parts of fossil ostracode carapaces has been attacked in various ways by paleontologists. Of course, students of living ostracodes have not been concerned with such matters because the soft parts inside the carapace furnish definitive information. The problem of orientation has been most serious for those working with the palaeocopids, as evidenced by the fact that a given species has been oppositely oriented by workers who interpreted the same morphological feature as representing different functions. In fact, confusion has been so great that specimens of the same species have been oriented differently by the same worker.

ANTERIOR-POSTERIOR

The position of the brood pouch remained in doubt for a long time. At first it was considered to be invariably posterior, but later this was found to conflict with evidence furnished by other criteria. Seemingly the pouch in Beyrichiacea does not correspond to the dimorphic swelling in Kloedenellacea as indicated by the position of such features as major sulcus (S_2), adductor muscle scar, and "eye-spots," by the curvature of lobes or sulci, greatest width and height, narrowest and most extended ends, by size of the cardinal angles, and by the direction of spines. There has been no consistency in evaluation of these characters. Some have judged that dimorphic structures should be considered to outrank all other criteria in importance, but when the antero-ventral position of the brood pouch in Beyrichiacea came to be recognized most problems in orientation were resolved.

The adductor muscle scars now universally are recognized to have primary value in orientation. Muscle scars in the great majority of Recent ostracodes are located in front of the mid-length.

In addition to impressions on the carapace made by the adductor muscle, scars of the mandibular, antennular, and antennar muscles may be preserved. In some shells the adductor muscle scar occurs near mid-length of the valves, but usually most of the

muscle-scar pattern is anterior. In a few forms the scar may appear to be behind the mid-length, but if its position is compared to mid-length of the hinge it will be classifiable as anterior.

The position of the adductor muscle scar may be determined in several ways: (1) by direct observation of the scar on the interior or on molds and casts of the interior; (2) by looking through transparent valves; (3) by covering opaque shells with water or a clear oil so that the scar becomes visible through the shell; (4) by detecting one or more dark spots on the shell where the carapace is either thicker or thinner than average; (5) by noting the position of S_2 , which usually is associated with the adductor muscle; (6) by determining the position on the surface of an interruption of reticula, punctae, or other ornamental features; (7) by observing the central position of a radiate surface pattern of lines; (8) by determining the position of a pit, as in the Kirkbyidae; and (9) by marking the position of a raised smooth central boss. Any of these found to be placed distinctly or slightly away from the valve mid-length or hinge mid-length may indicate the position of the adductor muscle and thus aid in orientation.

The greatest height of the carapace commonly is anterior (Fig. 18). A striking exception to this rule is found in the Leperditicopida where the greatest height is definitely posterior. Large and excellently preserved muscle scars of the adductor muscle and muscles of anterior appendages are found abundantly in several genera of the order. They are located in the narrow anterior portion of the leperditicopids (Fig. 29). In some genera of palaeocopids, the greatest height is nearly medial, and in a few (e.g., some species of *Kloedenella* and *Eukloedenella*) variations within a given species may shift the position of greatest height from posterior to anterior, but in spite of exceptions the position of the greatest height is a valuable clue to orientation of ostracodes.

The greatest width of the carapace is usually in the posterior half, corresponding to position of the genital organs, but in some

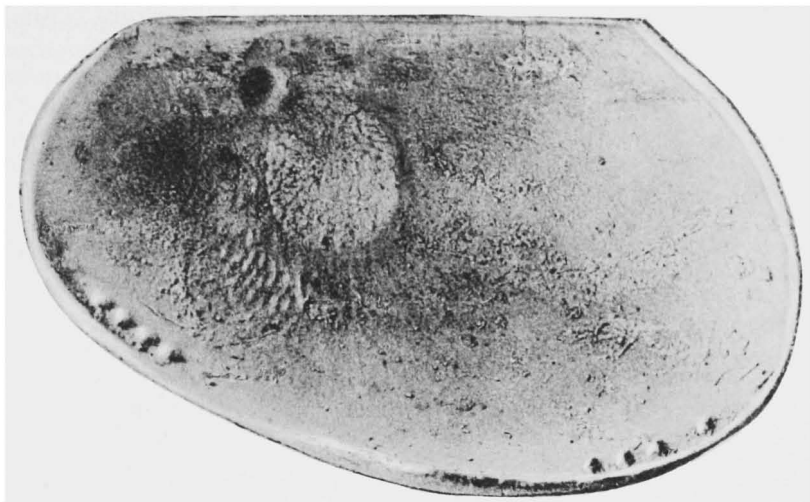


FIG. 29. **Eoleperditia fabulites* (CONRAD), M.Ord., USA (Ill.); RV int., showing eye spot, muscle scar, and tubercles along inner ventral margin (function of tubercles unknown but they may have acted as "door-stops" for smaller valve when valves were closed), $\times 10$ (70).

species it is medial or anterior. In forms having a kloedenellid type of dimorphism and in all modern dimorphic groups the greatest width is posterior in females and medial to posterior in tecnomorphs. In some palaeocopids consisting possibly of parthogenetic genera, the greatest width is medial, but careful measurements often will show that even in these the greatest width is slightly posterior. In the Healdiidae a furrow parallels the border of the widest end and is considered posterior. The Beyrichiacea are exceptional in that greatest width measured through the dimorphic structures is anterior. Greatest width of most ostracodes is in the end opposite to that possessing the greatest height and opposite to the end possessing the muscle scars. Exceptions are known but they do not lessen the value of greatest width as a criterion of orientation.

Dimorphic features, except in the Beyrichiidae and Zygobolbidae, are found in the posterior half of the carapace. They are important both for orientation and classification of many ostracodes ranging from Ordovician to Recent.

Some smooth ostracodes without sulci, lobes, or dimorphic structures may be difficult to orient, especially if the muscle scar is not discernible. In many shells, however, the cardinal angles differ, the more obtuse cardinal angle being usually anterior.

Though the problems of orientation have

been most varied among the palaeocopids, some difficulty has been experienced with other ostracodes. Semiround carapaces, such as those found among the Polycopidae and some Entomozoidae, may present special problems. Only a few of these are found as fossils. In the Mississippian *Discoidella* the reticulate pattern is a little off-center and the adductor scar is assumed to be off-center in the same direction. The hinge may be slightly closer to the anterior end. Some symmetrical fossil cypridids are difficult to orient, but commonly living representatives are available for comparison.

Detection of muscle scars in most Cytheracea is not difficult. Carapaces belonging to this group commonly are preserved in Mesozoic and Cenozoic sediments as single valves, so that the interiors may be examined in a translucent or transparent condition. Even closed valves may be oriented by the more acuminate posterior extremity (e.g., *Cythereis*), higher anterior end (e.g., *Cythereis*), or smoothly raised muscle swelling (e.g., *Cythereis dallasensis*). Generally, in the Podocopina the posterior end is more pointed than the anterior, and greatest height is in front of the mid-length.

Study of hingement aids orientation. LEVINSON (1950) found that the hinge, as a primary structural feature of the carapace, has more highly developed components at the anterior end.

In approximate order of importance for

orientation of fossil ostracodes the following criteria may be cited: (1) fossils with living representatives may be oriented accurately on the basis of observed internal morphology (e.g., *Bairdia*, *Cytherella*); (2) adductor muscle scars are anterior in position (e.g., *Healdia*, *Eoleperditia*, *Cythereis*); (3) in sulcate ostracodes S_2 marks position of adductor muscle scars and thus anterior position (e.g., Cytheridae, palaeocopids); (4) among dimorphic forms the posterior end is widest (e.g., *Kloedenella*) except carapaces exhibiting special types of dimorphism (e.g., *Beyrichia*, *Zygobolba*); (5) the anterior element of hinge structures usually is more complex than the posterior (e.g., *Kloedenella*); (6) in outline the posterior extremity of ostracode carapaces usually is more acuminate than the anterior (e.g., *Cythereis*, *Oligocythereis*); (7) ontogenetic development shows that the posterior half of the carapace is more acuminate than the anterior in instar stages (e.g., *Cytherella*); (8) among ornamental features it is observed that major spines are directed backward (e.g., *Cythereis*); and (9) the posterior portion of the hinge channel commonly is widest (e.g., *Kloedenella*).

In the past many new genera have been defined on the basis of "reversal of overlap" of the valves. Now it is known that reversal of overlap may occur within a population of a given species and therefore it cannot be used as a generic or specific character. Reversal has been reported in *Sansabella*, *Aurikirkkya*, and *Paraparchites*. Orientation should not be based on direction of overlap, but the direction of overlap must be determined after the orientation has been established by other criteria.

DORSAL-VENTRAL

To distinguish dorsal from ventral seemingly should be a simple matter of observation, but unfortunately, many published illustrations show the dorsal margin of ostracode carapaces in a ventral position. The problem is to determine the position of the hinge (dorsal) or the free margin (ventral). The question is readily resolved in single valves in which the hinge elements can be seen.

The long straight back of most leperditicopids and palaeocopids make recognition of the dorsum easily determined (Fig. 18).

In the straight-backed ostracodes of these groups the ventral margin is usually convex or rarely sinuate. (e.g., some kloedenellids).

The position of the hinge may be determined by the presence of hinge elements, often discernible exteriorly as well as interiorly, and in many genera by the presence of a hinge channel. Cardinal angles denote the terminal points of the hinge but are lacking in some shells. Eye spots, such as are developed excellently in *Cythereis*, denote anterior as well as dorsal position. Alate structures distinguish the ventral portion of a valve or carapace (e.g., *Brachycythere*, *Cytheropteron*). Radial pore canals and velate and histial structures are along the free margin (ventral). Short sulci are in the dorsal half of the carapace. If a sulcus is open at one end only, it opens dorsally.

The problem of dorsal-ventral orientation is most acute in such groups as the Darwinulacea, Cypridacea, Thlipsuracea, Quasillitacea, and the cytherellids-cavellinids. In some of these (e.g., *Cytherella*) hinge elements are not developed; in others the surface may be smooth and the outline may appear symmetrical. In such shells the dorsal margin is usually more convex than the ventral, or the ventral margin is straight to gently concave (e.g., *Darwinula*, *Cavellina*, *Healdia*, *Cypris*, *Candona*).

The criteria applicable to shape in outline of the carapace when viewed laterally vary from group to group. In the Beyrichi-copina the dorsal margin is straight and the free margin strongly to gently convex. In the Kloedenello-copina the dorsal margin is straight and the ventral convex to concave (sinuate). The dorsal outline of some Platycopina (e.g., *Cytherella*) is strongly convex and the ventral outline less convex, almost straight or slightly concave. However, in *Cytherelloidea* the dorsal margin varies from straight to gently concave or convex; the ventral margin is subparallel to the dorsal but is likely to be more concave.

Criteria other than outline, such as position of the pit, hinge elements, and costae, must be used in questionable forms. In the Metacopina great variation in outline is found; the Healdicea have strongly convex dorsal outlines when oriented with the ventral margin parallel to the horizontal, and gently convex to straight or gently concave ventral outlines; the Thlipsuracea have

dorsal outlines more convex than the ventral, but the ventral varies from gently convex to straight or gently concave; the Quasillitacea have a straight dorsal margin. When the straight dorsal margin of the Quasillitacea is oriented parallel to the horizontal, the ventral margin is usually broadly convex with an anterior swing or it is medially concave. The mid-ventral incurvature is similar to that found in the Podocopina.

A characteristic feature of the Podocopina is the medial concavity or incurvature of the ventral margin. This is sharply contrasted to the straight or convex dorsal outline.

ORIENTATION FOR ILLUSTRATION

The position of greatest height, magnitude of ventral swing, and line of greatest

length may vary according to the manner of orienting the specimen for illustrative purposes. The palaeocopids are oriented with the hinge parallel to a horizontal line. The hinge, fairly long and straight in most of the palaeocopids and archaeocopids, is used as the basic reference line; on the other hand, students of the podocopids usually orient specimens with a line through the greatest length parallel to the horizontal, though some are oriented with the venter parallel to the horizontal. Each method has been in use so long that continuation of common practice is recommended.

REFERENCE

Levinson, S. A.

- (1) 1950, *The hingement of Paleozoic Ostracoda and its bearing on orientation*: Jour. Paleont. v. 24, p. 63-75 (Tulsa).

GLOSSARY OF MORPHOLOGICAL TERMS APPLIED TO OSTRACODA

By R. C. MOORE

[University of Kansas]

[Relative importance of terms is indicated in accordance with the collective judgment of contributing authors, first rank by boldface capital letters, second rank by boldface small letters, and third rank (including some obsolete terms) by italic small letters. Annotation or remarks by some authors are given, inclosed by square brackets.]

accommodation groove. Furrow above median element of hinge for reception of dorsal edge of opposite valve when carapace is open.

adterior. Toward anterior extremity, forward.

ADDUCTOR MUSCLE SCAR. Impression on valve interior of muscle serving for closure of valves, generally located in front of mid-length.

adhesive strip. Thin chitinous layer between duplicature and outer lamella.

ADONT. Simple hinge of ridge-and-groove type, lacking teeth, with ridge or bar in one valve, which fits into groove along dorsal edge of other valve.

adplenate. Direction toward plenate end of carapace, referring to features in part of valve or carapace distinguished as plenate end.

adposterior. Toward posterior extremity, backward.

adventive pore canal. Tubule extending through duplicature.

adventral. Direction toward venter or location adjacent to venter.

ALA (pl., ALAE). Ventrally placed winglike lateral extension of valve, commonly directed backward (characteristic of some Cytheracea and Beyrichiacea).

alar process. Posteriorly attenuated ventrolateral ridge resembling but not associated with velate forms, common to more ornate cytherid ostracodes, particularly as development of one longi-

tudinal ridge of the reticulate system of ridges; usually precedes dorsolateral or mid-lateral ridges in evolution of highly ornate, reticulate cytherids.

ALATE EXTENSION. Any outward lateral extension in ventral half of valve, usually increasing in width backward and terminating abruptly, tending to have triangular shape (e.g., *Pterygocythereis*).

AMPHIDONT. Four-element hingement resembling entomodont and lobodont in general features, one valve having well-defined toothlike projections at extremities, separated by median furrow with deep smooth socket at anterior end, opposite valve with reverse arrangement of projections and depressions. [All descriptions of complicated hingements, such as variations of amphidont and merodont, should refer to tripartite division (posterior and anterior terminal elements and median element), for each element is modified *in toto* in merodont hinges or separately and differently in amphidont hinges. For example, in paramphidont hinges the anterior and posterior elements (teeth or sockets) are notched or crenulate, the median element (groove or bar) may be smooth or finely crenulate but modified at the anterior end adjacent to the anterior element to form a smooth tooth or socket (e.g., *Cythereis*). BENSON]

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- amplete.** With greatest height at or near mid-length of valve or carapace.
- ANTENNAL MUSCLE SCAR.** Impression on valve interior of attachment for muscle joined to antenna, located in front of adductor muscle scar, generally above and in some podocopids behind mandibular muscle scar.
- ANTERIOR.** Part of carapace in which antennules, antennae, and upper lip are located, front region.
- anterior area.** Part of either valve surface adjacent to front border (or margin), extending backward not farther than mid-length, divisible into anterodorsal, mid-anterior, and anteroventral areas.
- anterior cardinal angle.** Junction between anterior margin and hinge line.
- anterior corner.** Area immediately adjacent to anterior cardinal angle of either valve.
- anterior hinge area.** Front part of hinge in either valve.
- anterior horn.** Projection of anterior lobe above hinge line (e.g., *Ceratopsis*).
- ANTERIOR LOBE.** Rounded elevation adjacent to front of valve, best developed dorsally (commonly designated by symbol L_1).
- anterior longitudinal point.** Front extremity of longitudinal section of carapace where valves meet.
- ANTERIOR MARGIN (OR BORDER).** Front part of outline of either valve, forming part of free margin.
- ANTERIOR SULCUS.** Depression of valve surface extending adventrally from dorsum and located nearest to front (commonly designated by symbol S_1).
- ANTERIOR VIEW.** Appearance of carapace or valve as seen from front in line parallel to hinge line or axis.
- anterodorsal angle.** Generally obtuse angulation where relatively straight dorsal margin of valve meets rounded anterior margin (see anterior cardinal angle).
- anterodorsal area.** Surface of either valve adjacent to and including anterior corner.
- anteromedian area.** Front part of median surface of either valve intermediate between median and anterior areas.
- anteroventral area.** Front part of ventral surface of either valve.
- anteroventral depression.** Gently hollowed area between velate structure and median lobe in some beyrichiids, located anteroventrally.
- antimerodont.** Type of merodont hingement in which crenulate terminal projections of one valve (usually smaller) are separated by a crenulate furrow, with reverse arrangement of elevations and depressions in opposite valve (e.g., *Clithrocytheridea*).
- antiplenate.** Direction away from plenate end of carapace or valves, or referring to features in half of valves opposite plenate end.
- apical list.** Part of prionodont hinge on proximal side of teeth or sockets.
- area.** Somewhat arbitrarily delimited portion of valve surface as generally defined in lateral view; descriptive terms for individual areas include anterior, anteromedian, anterodorsal, anteroventral, dorsal, dorsomedian, median, mid-anterior, mid-dorsal, mid-posterior, mid-ventral, posterior, posteromedian, posterodorsal, posteroventral, ventral, and ventromedian.
- axis.** Straight line in sagittal plane connecting most widely separated edges of carapace or valve, invariably equal to or exceeding length.
- basal selvage.** Ridge between distal extremities of teeth in prionodont type of hingement.
- beak.** Anteroventral projection of free border of carapace (e.g., *Cypridea*); not equivalent to rostrum.
- beyrichiid dimorphism.** Sexual dimorphism characterized by development of anteroventral, ventral, or slightly posteroventral pouch-like structure (crumina) in valves of heteromorphs (presumed females), incompletely separated from domicilium by partition (e.g., *Beyrichia*, *Hibbardia*, *Phlyctiscapha*).
- bilamellar.** Double-walled part of free margin of some podocopid valves formed by welding of duplicature to outer lamella at expense of vestibule.
- bilobate.** Valves characterized by presence of only two rounded elevations (lobes) separated by a linear depression (sulcus) (e.g., *Dilobella*, *Parabolbina*); also may refer to two-lobed hinge teeth.
- bipartite interterminal furrow.** Double linear depression, typically crenulate, between extremities of hinge (e.g., *Loxococoncha*).
- bisulcate.** Valves characterized by presence of two linear depressions (sulci) separating three rounded elevations (lobes) (e.g., *Beyrichia*, *Kloedenia*).
- blood canals.** Branched grooves on interior of some valves inferred to mark position of blood vessels (e.g., *Leperditia*).
- border (or margin).** Periphery of carapace or valve as seen in lateral view.
- brood pouch.** Gently to strongly swollen portion of heteromorphous (presumed female) carapace, diverse in origin and actually unknown in function, located posteriorly (e.g., *Kloedenella*) or posteroventrally (e.g., *Hibbardia*), ventrally (e.g., *Trepostella*), or anteroventrally (e.g., *Beyrichia*, *Zygo-bolba*).
- bulb.** Very prominent spheroidal protuberance of valve, commonly in position of posterior lobe (L_3), that may extend above hinge line (e.g., *Falsipollex*).
- calcareous layer.** Relatively thick shell layer largely composed of calcium carbonate between outer and inner chitinous layers of carapace, commonly only part preserved in fossils.
- capitulum.** Wide prominence at anterior end of tignum in highly developed tooth-and-socket hingement.
- CARAPACE.** Protective covering of ostracode soft

- parts, including appendages, forming two nearly symmetrical valves joined together by hinge along dorsal margin; mostly hard and calcareous but soft and uncalcified in most Archaeocopida and many Myodocopida.
- cardinal angle.** Junction between hinge line and anterior or posterior free margin.
- cardinal corner.** Area immediately adjacent to cardinal angle.
- cardinal socket.** Major hollow at or near one or both extremities of hinge, for reception of tooth borne by opposite valve; may have smooth, bifid, or crenulate floor and may occur in either valve.
- cardinal tooth.** Major prominence at or near one or both extremities of hinge, fitting into socket of opposite valve; may have smooth, bifid, stepped, or crenulate summit and may occur in either valve.
- CARINA** (pl., **CARINAE**). In Palaeocopida, ridge or frill parallel to velate structure on its dorsal side, or compressed ridge appearing as forward-directed structure on anterior part of carapace (compare histium); in Podocopida, any well-defined, somewhat strongly projecting ridge on outer surface, as in many cytherids and cytherellids.
- carinal bend.** Rather sharp angulation (*Umbiegung-skante*) along distal edge of carina separating lateral and marginal surfaces of valve.
- carinal crest.** Attenuated projecting summit of carinal structure.
- carinal ridge.** Linear elevation with more or less rounded summit in adventral region connecting anterior lobe (L_1) and second posterior lobe (L_2) in some genera (e.g., *Tetradella*, *Tallinnella*, *Ogmoopsis*); compare histium.
- CAUDAL PROCESS.** Posterior projection of valve border generally above mid-height (e.g., *Loxococoncha*) or posteroventral and directed upward (e.g., *Cyprosina*).
- caudal siphon.** Posteroventral opening in valve borders (e.g., *Entomoconchus*) or produced as tubular structure (e.g., *Cyprosina*).
- channel.** Groove between valve margin and velate structure (e.g., *Ctenobolbina*, *Dicranella*), or depression of hinge line below dorsal margin.
- chevron muscle scar.** Inverted V-shaped muscle impression on interior of valves (e.g., *Leperditia*).
- CHITINOUS LAYER.** Thin waxy or transparent layer of chitin forming part of ostracode carapace, one covering outer side and another inner side of the calcareous shell layer.
- closed velum.** Ventrally incurved velate structures of right and left valves with distal edges meeting to inclose a false pouch (dolon) (e.g., *Uhakiella*).
- compound socket.** Depression in hinge line with bifid or crenulate floor (e.g., *Alatacythere*).
- connecting lobe.** Rounded linear elevation of valve surface confluent with 2 or more subvertically trending lobes (e.g., *Ceratopsis*, *Mastigobolbina*, *Tallinnella*).
- contact margin.** Edge part of valves exclusive of hinge, in contact when valves are closed, its distal limit comprising free edge.
- corner.** Area between front or rear part of dorsal border and anterior or posterior margin.
- COSTA** (pl., **COSTAE**). Rib on valve surface (e.g., *Glyptopleura*, *Cytherelloidea*).
- crenulate.** Notched by alternating small ridges and depressions, as in prionodont hingement.
- crest.** Small straight or curved ridge on valve surface (e.g., *Piretella*).
- CRUMINA** (pl., **CRUMINAE**). Saclike semiclosed space developed in ventral part of heteromorph domicilium (e.g., *Beyrichia kloedeni*).
- cruminal dimorphism.** Same as beyrichiid dimorphism.
- DENTICLE.** Small, delicate, spinelike projection differentiated according to location on carapace (e.g., dorsal, marginal); small toothlike projection of hinge element.
- DENTICULATE.** Bearing a series of small spine-like or toothlike projections.
- depression.** Broad gentle concavity on carapace surface without distinct limit.
- DIMORPHISM.** Development within a species of two shapes of adult carapaces, that of inferred females (heteromorphs) being moderately to strikingly differentiated from the form of adult inferred males (classed with juvenile stages of both sexes, which they resemble, as tecomorphs).
- DISTAL.** Direction outward from mid-region of ostracode body.
- distal line of adhesive strip.** Margin on outer side of junction of duplicature and outer lamella.
- distal zone of duplicature.** Part of duplicature between line of concrescence and distal line of adhesive strip.
- dolon.** Cavity (false pouch) formed by distally incurved parts of velate structure.
- DOMICILIAR DIMORPHISM.** Type of dimorphism marked by slightly to strongly swollen posterior portion of carapace in females (e.g., *Kloedenella*).
- DOMICILIUM.** Part of carapace exclusive of projecting velate structures.
- DORSAL.** Upper part of ostracode, when in normal position, comprising region that contains hinge, eyes, antennules, antennae, and stomach.
- dorsal area.** Part of valve surface adjacent to dorsal border, divisible into anterodorsal, mid-dorsal, and posterodorsal areas.
- dorsal denticle.** Small solid spinose projection on dorsal margin, chiefly different from dorsal spine only in small size.
- dorsal margin (or border).** Part of valve outline adjacent to hinge line, somewhat above or coinciding with it.
- dorsal plica.** Linear elevation of valve surface adjacent and parallel to dorsal margin.
- dorsal spine.** More or less prominent, solid or hollow pointed projection of valve on dorsal margin (e.g., *Ctenonotella*, *Rakverella*).

- DORSAL VIEW.** Appearance of carapace or valve as seen from above with line of sight in sagittal plane and normal to hinge line.
- dorsomedian area.** Part of valve surface intermediate between median and mid-dorsal areas.
- DORSUM.** More or less flattened area of carapace surface adjacent to hinge line and set off from lateral surface of valves.
- DUPLICATURE.** Part of border in which calcareous peripheral portion of inner lamella is in contact with outer lamella or separated from it by vestibule, generally narrow but in some genera (e.g., *Cytheretta*) considerably extended.
- EDGE.** Distal limit of valve periphery touching opposite valve when carapace is closed.
- entire** (velate structure). Frill or velate ridge extending from anterior to posterior cardinal angles.
- ENTOMODONT.** Type of four-element hingement corresponding to antimerodont or hemimerodont except for development of short anterior segment of median ridge as crenulate toothlike projection, remainder of median ridge being smooth or finely crenulate, opposite valve with reverse arrangement of elevations and depressions (e.g., *Progonocythere*); see note under amphidont.
- epiclinal.** Dorsum that projects above hinge line.
- extralobate area.** Part of valve surface not involved in lobation and sulcation.
- extralobate groove.** Linear depression along inner margin of extralobate area adjoining ventral lobe (e.g., *Eobeyrichia*).
- EYE TUBERCLE.** Polished transparent rounded protuberance in anterodorsal region of valve forming lens of eye (e.g., Cytheracea) or marking inferred position of eye (e.g., Leperditicopida).
- false pouch.** Chamber formed by distally incurved frills of some heteromorphs (equivalent to dolon) (e.g., *Piretella*, *Eurychilina*, *Tallinnella*); differs from true pouch in being developed outside of domicilium.
- false radial pore canal.** Tubule through outer lamella from line of concrescence but not penetrating chitin of adhesive strip.
- fissure.** Narrow steep-sided groove on valve surface subparallel to free margin (e.g., *Beyrichia kloedeni*).
- fissus.** Same as fissure.
- FLANGE.** Ridge along valve margin of some podocypids formed by projection of outer lamella as narrow brim.
- flange groove.** Surface of duplicature between selva and flange.
- flange strip.** Part of duplicature forming flange groove and in some genera the flange also.
- flexure.** Lateral offset of hinge line as seen in dorsal view.
- FREE EDGE.** Line of contact between closed valves except along hinge line; marks distal limit of contact margin and may lie inside free margin.
- FREE MARGIN (OR BORDER).** Anterior, ventral, and posterior parts of margin where valves are not held together by hingement.
- FRILL.** Wide velate structure that commonly extends beyond free edge of valves, mostly striate or septate radially (e.g., *Hollinella*, *Oepikium*, *Dibolbina*, *Chilobolbina*); commonly developed as double-walled outfold of shell.
- frontal rounding.** Curvature of carapace surface toward anterior valve margin as seen in longitudinal sections.
- frontal section.** Same as longitudinal section.
- furrow.** Shallow groove on valve surface.
- geniculum.** Abrupt lateral bend of sulcus.
- girdle socket.** Depression in hinge line with horse-shoe-shaped outline defining a small tooth, generally anterior.
- GONGYLODONT.** Type of hingement characterized by presence in one valve of finely crenulate median ridge between anterior rounded tooth bounded by sockets and posterior pair of rounded teeth separated by deep socket, opposite valve with reverse arrangement of elevations and depressions (e.g., *Loxocochna*).
- granuloreticulate.** Surface ornamentation of valves consisting of granules arranged in intersecting rows.
- granulose.** Surface ornamentation of valves consisting of more or less closely spaced minute protuberances, generally without distinct pattern, like grains of sandpaper.
- HEIGHT.** Maximum dimension of carapace or valve from dorsal to ventral margins measured perpendicularly to direction of length.
- hemiamphidont.** Type of amphidont hingement in which anterior toothlike projection of one valve is smooth or stepped (but not crenulate), whereas posterior projection is notched or crenulate, opposite valve with reverse arrangement of elevations and depressions (e.g., *Brachycythere*, *Alatocythere*); see note under amphidont.
- hemimerodont.** Type of merodont hingement in which one valve has crenulate ridges at extremities of hinge with smooth-floored furrow between, opposite valve with reverse arrangement of elevations and depressions; like antimerodont hingement except for smooth median furrow and opposing ridge (e.g., *Palaeocytheridea*).
- HETERODONT.** Hingement of valves effected by combination of tooth-and-socket and ridge-and-groove types, characterized by pointed or slightly crenulate teeth in one or both valves associated with ridge (hinge bar) in one valve and groove in other (e.g., Cytheridae).
- heteromorph.** Adult inferred female carapace in dimorphic genera (compare tecnomorph).
- HINGE.** Part of valves along or near dorsal margin serving for articulation.
- hinge area.** Surface involved in hingement of valves, commonly differentiated into anterior and posterior areas containing more complex elements

- and between these an interterminal area with simpler structures.
- hinge bar.** Smooth or finely crenulate ridge in interterminal hinge area of one valve, fitting into groove in opposite valve.
- hinge flange.** Structure of hinge corresponding to flange of contact margin and continuous with it in many species.
- hinge flange groove.** Furrow on distal side of hinge interterminal area corresponding to flange groove of contact margin and continuous with it in some species; termed accommodation groove in some Cytheracea because furrow serves to accommodate dorsal margin (hinge flange) of opposite valve when carapace is open.
- HINGE LINE.** Line along which valves articulate, seen when carapace is complete; it may coincide with dorsal margin or be depressed below it.
- hinge list.** Structure of hinge area corresponding to list of contact margin.
- hinge margin.** Part of dorsal border (or margin) of valves adjoining hinge.
- hinge selvage.** Structure of hinge area corresponding to selvage of contact margin and continuous with it in some species.
- hinge selvage groove.** Structure of hinge area corresponding to selvage groove of contact margin.
- HINGEMENT.** Collective term for structures comprising articulation of valves, classifiable in several types; same as hinge.
- histial dimorphism.** Type of dimorphism characterized by development of histium in heteromorphs.
- histium.** Adventral ridge or flange confluent with connecting lobe in some heteromorphs (e.g., *Sigmoopsis*, *Glossomorphites*), in quadrilobate valves forming ventrolaterally projected continuation of ventral end of connecting lobe and with same position in nonsulcate valves, commonly dimorphic.
- holamphidont.** Type of amphidont hingement in which both terminal toothlike projections of one valve are smooth or stepped (not crenulate) and separated by a long median furrow that may be smooth or finely crenulate, opposite valve with reversed arrangement of elevations and depressions (e.g., *Amphicytherura*, *Trachyleberis*, *Pterygocythereis*); see note under amphidont.
- holomerodont.** Type of merodont hingement in which crenulate toothlike ridges at extremities of hinge in one valve are separated by crenulate median ridge, opposite valve with depressions for reception of these elevations; like paleomerodont hingement except for finely crenulate nature of median ridge and furrow (e.g., *Haplocytheridea*).
- horn.** Dorsal part of lobe projecting more or less strongly above hinge line (e.g., *Beyrichia*, *Ceratopsis*).
- horseshoe-shaped ridge.** Prominent U-shaped elevation of valve surface bordering median sulcus (S₂) on anterior, ventral, and posterior sides in some genera (e.g., *Bolbibollia*, *Zygobollina*).
- hump.** Low but rather large dorsal inflation of valve surface projecting above hinge line.
- hypocline.** Dorsum inclined slightly downward-outward so that hinge line is not concealed in lateral view.
- inflation.** Large gently domed part of valve surface without distinct borders; sometimes used as synonym of width.
- INNER CHITINOUS LAYER.** Thin layer of transparent chitin secreted on inner side of calcareous shell layer.
- INNER LAMELLA.** Thin layer covering body in anterior, ventral, and posterior parts of carapace, chitinous except for calcified marginal parts forming duplicature; entirely distinct from inner chitinous layer on inside of outer lamella.
- INNER MARGIN (OF DUPLICATURE).** Proximal limit of duplicature.
- inner selvage contact line.** Proximal line between selvage and remainder of duplicature.
- inner surface.** Interior of carapace, in fossils comprising inner side of calcareous layer, which originally was covered by inner chitinous layer.
- INSTAR.** Ontogenetic stage comprising one of several successive forms assumed by animal between successive molts.
- interterminal hinge area.** Median part of hinge area generally bearing ridge-and-groove structures.
- KIRKBYAN PIT.** Central or subcentral steep-walled depression on valves of some palaeocopid genera, usually ovate and interrupting reticulate ornament (e.g., Kirkbyidae); inferred to mark location of adductor-muscle attachment.
- kloedenellid dimorphism.** Type of dimorphism characterized by inflated posteroventral part of domicilium in heteromorphs (e.g., *Kloedenella*); also termed domiciliar dimorphism.
- knob.** Prominent rounded protuberance of valve surface differentiated from surrounding area by distinct angulation (e.g., *Hollinella*).
- knurling.** Pointed projection of hinge line of one valve into that of opposite valve as seen in dorsal view.
- L₁, L₂, L₃, L₄.** Symbols respectively indicating lobes from front to rear parts of valve surface in many genera (e.g., *Tetradella*, *Ctenolocolina*, *Quadrijugator*).
- LATERAL SURFACE.** Flattened side of valve.
- LATERAL VIEW.** Appearance of carapace or valve as seen from side in direction normal to sagittal plane.
- left plenate.** Valve with plenate end at left as seen in lateral view.
- LEFT VALVE.** Half of carapace covering left side of ostracode (symbol, LV).
- LENGTH.** Maximum dimension of carapace or valve (a) in direction parallel to hinge line, according to customary procedure in measuring straight-backed ostracodes such as most palaeo-

- copid forms, or (b) in direction along axis drawn between farthest anterior and posterior extremities, applicable to curve-backed ostracodes such as many podocopid forms.
- LINE OF CONCRESCENCE.** Proximal line of junction of duplicature with outer lamella, coinciding with inner border of chitinous adhesive strip.
- lip.** Inward projection of duplicature.
- list.** Ridge on proximal side of selvage on contact margin, absent in many carapaces.
- list strip.** Part of duplicature on proximal side of list extending to inner margin, commonly bearing septa.
- lobate area.** Part of valve surface bearing lobes and associated sulci.
- lobate dimorphism.** Type of dimorphism characterized by inflation of lobe in posteroventral or lateroventral part of heteromorph carapace (e.g., *Zygobolbina*, *Bonnemaia*), without evidence of partition separating brood pouch from domicilium.
- lobate tooth.** Two-lobed hinge tooth.
- lobation.** Pattern of elevated portions of valve surface defined as lobes.
- LOBE.** Rounded major protuberance of valve surface, generally best developed in dorsal part of carapace; also used for part of hinge tooth (e.g., posterior tooth of *Quadracythere*).
- lobodont.** Type of hingement resembling entomodont except for rounded lobate nature of anterior toothlike projection of median ridge of one valve and rounded socket in opposite valve at anterior extremity of median furrow (e.g., *Acanthocythere*).
- loculus (pl., loculi).** Deep pitlike depression in ventral or anteroventral surface of some heteromorphs (e.g., *Tetrasacculus*, *Ctenoloculina*), formed by transverse processes joining velum with marginal ridge.
- longitudinal.** In direction of length.
- longitudinal rounding.** Lateral rounding of carapace or valve as seen in longitudinal sections.
- longitudinal section.** Any section of carapace or valve parallel to direction of length and in plane normal to sagittal plane.
- liphodont.** Type of three-element hingement consisting of short toothlike ridges at extremities of median groove in one valve (usually smaller) and reverse arrangement of elevations and depressions in opposite valve, all hinge elements smooth (e.g., *Eucythere*, *Cushmanidea*).
- lunule.** Crescentic concave or convex area at edge of a socket.
- MANDIBULAR MUSCLE SCAR.** Attachment mark on valve interior for muscle leading to mandibular appendage, typically distinguished by position in front of adductor muscle scars, generally below and may be in front of antennal muscle scar.
- MARGIN (OR BORDER).** Periphery of carapace or valve as seen in lateral view.
- marginal ridge (or rim).** Linear elevation of valve adjoining free edge.
- marginal structure.** Feature developed near free edge of valve and parallel to it but independent; may include marginal ridge, denticles, tubercles, spines.
- marginal surface.** Flattened area adjacent to free edge of valve and set off from lateral surface.
- median area.** Part of valve surface located nearest middle, approximately equidistant from dorsal and ventral borders and likewise from anterior and posterior borders.
- MEDIAN LOBE.** Lobe (L_2) next behind anterior lobe (L_1) and in front of median sulcus (S_2), weakly developed generally and entirely absent in some lobate carapaces.
- MEDIAN SULCUS.** Sulcus (S_2) next behind anterior sulcus (S_1) in bisulcate and trisulcate carapaces or only sulcus present in unisulcate forms; generally most prominent sulcus.
- MERODONT.** Type of three-element hingement characterized by crenulate toothlike projections at hinge extremities of one valve and long median ridge or furrow between, opposite valve with reverse arrangement of elevations and depressions; variations accompanied by development of accommodation groove above median element of larger valve include paleomerodont, holomerodont, antimerodont, and hemimerodont.
- mid-anterior area.** Middle part of anterior area, intermediate between anterodorsal and anteroventral areas.
- mid-dorsal area.** Middle part of dorsal area, intermediate between anterodorsal and posterodorsal areas.
- mid-posterior area.** Middle part of posterior area, intermediate between posterodorsal and posteroventral areas.
- mid-ventral area.** Middle part of ventral area, intermediate between anteroventral and posteroventral areas.
- MOLT.** Carapace cast off in molting (ecdysis); act of casting off shell.
- monolamellar.** Single shell thickness along free margin, in podocopids where junction of duplicature and outer lamella is simple turn-over.
- MUSCLE SCAR.** Mark on shell interior for attachment of muscle, generally distinguishable by localized differences in texture of surface, elevation, depression, or delimiting narrow groove, also discernible in many specimens by coating carapace with oil or water and by converting calcareous shell substance to fluorite.
- MUSCLE-SCAR PATTERN.** Arrangement of all muscle scars on valve interior.
- NODE.** Protuberance of intermediate size on valve surface (larger than tubercle, smaller than knob), clearly distinct from lobes.

- nonsulcate.** Valve surface evenly elevated, unilobate, lacking sulcus.
- NORMAL PORE CANAL.** Tubule piercing approximately at right angle almost any part of valve, commonly with enlarged proximal part lined with chitin; in living ostracodes carries hair (seta) that projects from surface.
- notch.** Sharp indentation of valve margin, in ostracodes with beak consisting of anterodorsally directed indentation behind beak.
- nuchal furrow.** Median sulcus in some Myodocopida (e.g., *Cypridella*).
- ocular sinus.** Hollow in shell substance beneath eye tubercle, communicating with valve interior and accommodating soft parts of eye.
- ocular tubercle.** Same as eye tubercle.
- OUTER CHITINOUS LAYER.** Thin covering of chitin over exterior of calcareous shell layer, which comprises first-formed part of shell after molting.
- OUTER LAMELLA.** Relatively thick mineralized shell layer inclosed between thin chitinous layers which conceals and protects soft parts of body and appendages.
- outer selvage contact line.** Distal line between selvage and remainder of duplicature.
- OUTLINE.** Boundary of carapace or valve as seen from any direction, but generally referring to side view, extending around all projections.
- overhang.** Same as overreach.
- OVERLAP.** Closure of valves in such manner that contact margin or selvage of one valve extends over that of other valve.
- overreach.** Projection in lateral view of one valve beyond the other along dorsum.
- paleomerodont.** Type of merodont hingement in which extremities of elongate median ridge are elevated as crenulate toothlike projections, opposite valve with reverse arrangement of elevations and depressions (e.g., *Schuleridea*).
- papilla** (pl., **papillae**). Small steep-sided prominences of nipple-like form on valve surface.
- papillose.** Surface covered with small steep-sided protuberances termed papillae.
- paramphidont.** Type of amphidont hingement in which both terminal toothlike projections of one valve are notched or crenulate and elongate median element comprises smooth or finely crenulate furrow that ends forward in smooth-floored deep socket, opposite valve with reverse arrangement of elevations and depressions (e.g., *Cythereis*); see note under amphidont.
- peripheral lock.** Closure of valves in inequivalved carapaces with sharp edges of smaller valve fitting in furrow along all or nearly all of larger valve margin (e.g., *Cythereella*, *Cytherelloidea*).
- PIT.** Relatively large, more or less circular deep hollow in valve surface.
- PITTED.** Surface of carapace marked by medium to relatively large steep-sided depressions.
- plenate end.** Convexly prominent wide part of carapace having swing.
- PORE.** Minute orifice on outer surface of valve which is opening of pore canal.
- PORE CANAL.** Minute tubular passageway extending through shell.
- postadductorial area.** Part of carapace or valve behind median sulcus (S_2).
- POSTERIOR.** Portion of carapace or valve covering sex organs and anus, direction opposite to anterior, backward.
- posterior area.** Surface of either valve adjacent to rear border and extending forward not farther than center.
- posterior cardinal angle.** Angle between posterior margin and hinge line.
- posterior corner.** Area immediately adjoining posterior cardinal angle.
- posterior frontal point.** Posterior point in a frontal (i.e., longitudinal) section, where the two valves meet.
- posterior hinge area.** Part of hinge area adjacent to posterior corner, generally containing complex elements.
- posterior horn.** Projection of posterior lobe above hinge line, in some carapaces (e.g., *Beyrichiidae*) inner and outer posterior horns.
- posterior lobe.** Rounded elevation of valve surface behind median sulcus (S_2), commonly developed chiefly in posterodorsal region and indicated by symbol L_3 ; in trilobate carapaces probably corresponds to L_3+L_4 of quadrilobate forms.
- posterior longitudinal point.** Posterior point in longitudinal section of carapace where two valves meet.
- posterior margin (or border).** Rear part of outline of carapace of either valve as seen in lateral view; forms part of free margin.
- posterior sulcus.** Groovelike depression behind posterior lobe (L_3), present only in quadrilobate carapaces, indicated by symbol S_3 .
- POSTERIOR VIEW.** Appearance of carapace or valve as seen from rear in direction parallel with hinge line or axis.
- posterodorsal area.** Surface of valve adjacent to and including posterior corner.
- posteromedian area.** Rear part of median surface of either valve, intermediate between tracts designated median and mid-posterior.
- postplete.** Greatest height behind mid-length of valve or carapace.
- POUCH.** More or less prominent swollen part of heteromorph carapace in ventral or anteroventral region (e.g., *Beyrichia*, *Apatobolbina*) or extending into posteroventral region, may be delimited by internal partitions in each valve into partly inclosed sacs (cruminae) (e.g., *Phlyctiscapha*).
- preadductorial area.** Part of domicilium in front of median sulcus (S_2).

- preplete.** Greatest height in front of mid-length of valve or carapace.
- primitiid sulcus.** So-called median sulcus in unisulcate forms, including juveniles of multisulcate genera.
- PRIONODONT.** Type of hingement resembling adont but distinguished by presence of crenulations along ridge and groove.
- PROXIMAL.** Direction inward toward middle part of ostracode body.
- proximal zone of duplicature.** Part of duplicature extending from inner margin to line of concrescence.
- psuedovelum.** Frill-like marginal or submarginal rim comprising single layer of shell, not compressed double-layered outfold of valve walls.
- PUNCTUM** (pl., **PUNCTA**). Small pitlike depression in valve surface.
- PUNCTATE.** Surface bearing many minute depressions resembling pin pricks.
- PUSTULA** (pl., **PUSTULAE**). Small protuberance on valve surface with pore at summit.
- QUADRILOBATE.** Valve distinguished by presence of four lobes.
- rabbeted.** Shell closure in which one valve bears recess for holding edge of opposite valve.
- RADIAL PORE CANAL.** Tubule extending through adhesive strip from inner to outer surface of duplicature.
- restricted (velate structure).** Velate ridge or frill confined to anterior and ventral parts of valve.
- RETICULATE.** Surface having a netlike pattern of small intersecting crests, striae, or rows of tubercles (e.g., *Amphissites*, *Hermanites*).
- RIDGE.** Elongate elevation of valve surface, commonly distinguished by location (e.g., ventral ridge), shape (e.g., horseshoe-shaped ridge, as in *Bolbibollia*, *Zygobolbina*; sickle-shaped ridge, as in *Drepanella*), or morphological significance (e.g., velate ridge, carina).
- ridge-and-groove hingement.** Articulation of valves characterized chiefly by ridge along hinge line of one valve fitting into groove of other (e.g., adont, prionodont).
- right plenate.** Valve with plenate end at right as seen in lateral view.
- RIGHT VALVE.** Half of carapace covering right side of ostracode, anterior margin at right as seen in lateral view (symbol, RV).
- rim.** Same as marginal ridge or rim.
- ROSTRAL INCISURE.** Gape below rostrum in front margin of valves for protrusion of antennae (e.g., *Cypridina*).
- ROSTRAL NOTCH.** Indentation of anterior margin of valves below rostrum, associated with opening termed rostral incisure.
- rostral sinus.** Same as rostral notch.
- ROSTRUM.** Anterior beaklike projection of valve margins overhanging an incisure or notch, generally at mid-height of valves or above (e.g., *Cypridina*).
- S₁, S₂, S₃.** Symbols respectively indicating sulci from front to rear parts of valve surface in many genera (e.g., *Tetradella*, *Quadrijugator*); S₁ and S₃ most commonly suppressed, S₂ being major sulcate structure and occurring alone in unisulcate genera (e.g., *Eurychilina*).
- SAGITTAL PLANE.** Plane bisecting ostracode longitudinally and dorsoventrally.
- SAGITTAL SECTION.** Any section of carapace or valve in or parallel to sagittal plane.
- scalloped.** With series of convex warps (e.g., frill of *Parabolbina*).
- SCHIZODONT.** Type of hingement resembling amphidont but having anterior tooth and socket of one valve both bifid, opposite valve with reverse arrangement of elevations and depressions (e.g., *Paijenborchella*).
- scrobicula.** Small groove at base of hinge tooth.
- second posterior lobe.** Rearmost lobe (L₄) in quadrilobate genera (e.g., *Tetradella*).
- SELVAGE.** Middle ridge of contact margin comprising principal ridge of duplicature and serving to seal valves when closed.
- selvage apophysis.** Thin lobelike overlapping projection of valve margin (mostly left) at position of podocopid incurvature of margin.
- selvage discontinuity.** Mid-ventral offset or gape in selvage at position of podocopid incurvature of margin (mostly in right valve) (e.g., many cytherids).
- selvage fringe.** Thin part of selvage reinforced structurally by slender ridges normal to selvage line.
- selvage groove.** Part of duplicature surface between selvage and list.
- selvage line.** Line formed by tapering edge of selvage.
- selvage strip.** Part of duplicature forming selvage and selvage groove.
- semisulcus.** Junction of lateral surface of valve with knob, bulb, node, or lobe, differing from sulcus in being bordered by a protuberance only on one side.
- septum.** Small ridge on list-strip part of duplicature.
- SHELL.** Calcareous and chitinous substance composing carapace.
- sickle-shaped ridge.** Narrow, strongly arcuate ridge on side of valve, shaped like sickle (e.g., *Drepanella*).
- sieve-type pore canal.** Wide normal pore canal partially closed by an internal apparently perforate plate.
- SIMPLE HINGEMENT.** Edge of one valve fitting against or under edge of other.
- simple velum.** Velate structure having simple flangelike form or forming ridge.
- SOCKET.** Well-defined hollow or pit in hinge area of one valve for reception of tooth in hinge of opposite valve.
- SPINE.** Solid or hollow, more or less elongate pro-

- jection from valve surface, with rounded or sharply pointed distal extremity.
- SPINOSE.** Valve surface or margin characterized by presence of somewhat numerous spines; also may refer to distal edge of frill.
- spur.** Flattened spinelike projection comprising modification of velate structure in tecnomorphs of some dimorphic genera (e.g., *Hollinella*, *Falsipollex*, *Ctenolocolina*).
- stria** (pl., **striae**). Minute furrow on surface of valve.
- striate.** Surface characterized by many subparallel striae, generally spaced closely; on frill commonly arranged normal to edge.
- submedian tubercle.** Prominent node or humplike development of anteromedian portion of valves in some podocopids (e.g., trachyleberids) commonly forming hub of convergent surface ornament; expressed as muscle-scar pit on interior of valves.
- subhial field.** Area between histium and free edge of valve.
- sulcation.** Pattern of linear depressed areas defined as sulci.
- SULCUS.** More or less prominent groove or trench on valve surface trending dorsoventrally and generally best developed in dorsal half of carapace; in some genera may be reduced to faint depression.
- SURFACE.** Exterior of valve or carapace, unless interior is specified.
- SURFACE ORNAMENT.** Relatively subordinate elevations, depressions, and varied sorts of markings on valve surface, mostly useful in taxonomy.
- swing.** Displacement of ventral part of valve or carapace in forward direction so as to produce a tapered appearance of posterior region associated with sloping, nearly straight posteroventral margin; direction reversed in some genera.
- taxodont.** Type of hingement; used by several authors for prionodont, merodont, antimerodont, etc.
- tecnomorph.** Specimen of dimorphic species other than adult inferred female (heteromorph); includes adult inferred males and juveniles of both sexes.
- THICKNESS.** Distance from outer to inner surface of valve (not same as width).
- tignum.** Long ridge or bar between large tooth and socket on hinge area of one valve.
- TOOTH.** Localized projection on hinge area fitting into socket of opposite valve, aiding articulation of valves.
- tooth-and-socket hingement.** Articulation effected by teeth on hinge area of one valve fitting sockets in opposite valve, considerably varied in form of teeth and sockets and to some extent in their placement.
- toothlet.** Minute tooth, generally in series.
- transverse rounding.** Curvature of valve or carapace in transverse section.
- transverse section.** Any section through carapace or valve in plane coinciding with line that represents width or parallel to this plane and normal also to sagittal plane; so-called vertical section intersecting sides approximately at right angles.
- TRILOBATE.** Valves having three lobes (L_1 , L_2 , L_3 , or L_3+L_4) and two sulci.
- TRISULCATE.** Valves having three sulci (S_1 S_2 S_3) and four lobes.
- TUBERCLE.** Low rounded prominence of intermediate size (larger than granule, smaller than knob) on valve surface, common along free margin.
- TUBERCULATE.** Surface ornament characterized by many tubercles.
- unilobate.** Valves with evenly elevated surface, without sulci (e.g., *Apatobolbina*).
- unisulcate.** Valves having a single sulcus (S_2), bilobate (e.g., *Dilobella*).
- vallum.** Part of hinge between two adjacent sockets (e.g., prionodont hingement).
- VALVE.** One of the two halves of carapace, hinged at upper (dorsal) edge, classed as left valve and right valve.
- velar dimorphism.** Type of dimorphism characterized by velate features or structures developed in association with the velum (e.g., *Hollinella*, *Uhaqiella*, *Abdiolocolina*).
- velate ridge.** Low, generally rounded ridge in position of velum, commonly serrate (typically found in juveniles of hollinellids).
- velate structure.** Any elongate ridge- or frill-like projection of carapace in position subparallel to valve margins, provided that if more than one such projection occurs on each valve, the velate structure is most adventral (compare carina, histium); typically developed as double-walled outfold of shell (*see* frill).
- velum.** Wide sail-like velate structure.
- ventral.** Lower part of ostracode in normal position, comprising region containing mouth, maxillae, and thoracic legs; also part of carapace or either valve covering this region.
- ventral area.** Surface of valve adjacent to ventral border, divisible into anteroventral, mid-ventral, and posteroventral areas.
- ventral lobe.** Rounded elevation (lobe) extending subparallel to ventral border and located generally near it (e.g., *Hollinella*); same as connecting lobe.
- ventral margin (or border).** Part of free margin of valve along ventral side.
- ventral ridge.** Like ventral lobe but more linear and sharply defined, commonly coalescent with subvertically trending lobes (e.g., *Tetradella*, *Sigmoopsis*) (same as histium).
- ventral selvaige furrow.** Elongate depression of external valve surface slightly distant from outer margin at position of podocopid incurvature of margin (e.g., *Campylocythere*).
- ventral view.** Appearance of carapace or valve seen from below in line of sagittal plane.

ventromedian area. Surface of valve intermediate between median and mid-ventral areas.
vestibule. Space between duplicature and outer lamella.
welded duplicature. Type of duplicature in valves having inner margin coincident with line of concrescence, forms without vestibule having wide

duplicature; adhesive strip continuous from its distal boundary to inner margin.
width. Greatest dimension of carapace or valve perpendicular to directions of length and height.
zygal ridge. Generally U-shaped ridge uniting ad-ventral parts of median and posterior lobes in some berychiids.

ECOLOGY OF OSTRACODE ASSEMBLAGES

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CONTENTS

	PAGE
FRESH-WATER OSTRACODES	Q56
BRACKISH-WATER OSTRACODES	Q57
MARINE OSTRACODES	Q58
Influence of physical and organic environmental factors on the distribution and form of marine ostracodes	Q60
Depth	Q60
Bottom sediment or substrate	Q61
Lithologic and micropaleontologic association	Q61
Salinity	Q61
Temperature	Q61
Redox potential and hydrogen-ion concentration	Q62
Plant dominance	Q62
Food and nutrients	Q62
Association with other animals	Q62
OSTRACODE BIOFACIES	Q62
OSTRACODE BIOGEOGRAPHY	Q63
REFERENCES	Q63

Ostracodes have become very successful inhabitants of every aquatic habitat. These microcrustaceans are found in sulphur springs, stagnant ponds, lakes, swamps, streams, brackish lagoons, estuaries, tide pools, salt marshes, epicontinental seas, and on the floor of ocean basins. As fossils they may occur in sediments deposited in all these environments, being particularly useful as paleoecological indicators of brackish and fresh-water sediments. In most ostracode-bearing sediment, carapaces or separated valves are present in sufficient quantity to be treated statistically. Assemblages of species and genera endemic to particular habitats can be established, and growth stages and ecologic variants can be identified from fossils.

The living animal is benthonic or pelagic, although pelagic ostracodes are rare as fossils. Most benthonic ostracodes crawl on and burrow in the bottom sediments, or crawl

and swim among aquatic plants. Some forms are thought to swim for short distances just above the bottom, but all ostracodes are ultimately dependent directly or indirectly on the nature of the bottom. Its prevailing benthonic habit therefore makes the ostracode intimately associated with the environment of deposition of the bottom sediments.

FRESH-WATER OSTRACODES

Ostracodes are found living in almost every pond, lake, spring, stream, or river at least part of the year. They inhabit temporarily filled drainage ditches and stagnant ponds in poorly drained fields, as well as permanent lakes where wave action may be varyingly strong.

The earliest known fresh-water ostracodes inhabited shallow ponds, coal-forming swamps, and sluggish streams of Early

Pennsylvanian time. They are found as fossils associated with the remains of fresh-water pelecypods, worms, and scales of fishes. The genera thus identified include *Cypridopsis* and *Candona*, which are represented by species now living.

Fresh-water ostracode assemblages have also been identified from Permian, Jurassic, and Tertiary strata. Many fresh-water species now living were present during the Pliocene.

Almost all Recent fresh-water ostracodes are smooth Cypridids, except for *Limnocythere*, which is a cytherid. They differ from most marine ostracodes in the relatively unornamented nature of their carapace. Some fresh-water marls and limestones are almost entirely composed of the smooth valves of such ostracodes. Judging from the number of fossil species represented in a typical example of these deposits, a reconstructed living assemblage seems to denote many habitats. Actually, however, such a deposit commonly represents only a few habitats that occur in and on the bottom and among the grasses. One species may occupy a certain ecologic niche during only part of the year and after the laying of eggs by the females, the adults die. The same niche may then be occupied by a second and even a third species within a year, depending chiefly on mildness or harshness of the winter. Most fresh-water ostracodes produce several broods of young in a season but may be present in a given habitat only a few months. Large fossil populations are the result. As each individual molts some seven to nine times, a very large number of carapaces and separated valves can accumulate in the sediment in a short time.

HOFF (5) found that most fresh-water species live in (1) temporary still waters, including ponds and ditches; (2) temporary running waters, such as intermittent streams; (3) permanent still waters ranging from small ponds to large lakes; and (4) permanent running waters. Some species may be present in all four environments but are more successful in one than in the others.

Zonation and subdivision are present within any one of these habitats. The nature of the sediment encourages or excludes burrowers. Fine, organic-rich muds are more heavily populated by burrowers, such as

Candona and *Chlamydotheca*, than are coarse sands. Gyttja and other organic oozes are devoid of ostracodes, presumably because of their lack of oxygen. The euphotic zone allows attached plants to grow, and with them a prolific fauna of swimming and crawling ostracodes develops. *Cypridopsis* is found in swarms around the roots of floating vegetation. Fossil ostracodes are seldom found in river sand deposits because of the poor opportunity for preservation and the instability of the sediment.

Changes in temperature with changing latitude are reflected in the presence or absence of warm- and cold-water ostracode species. Also some species are known to be syngamic in one part of their temperature range and parthenogenetic in another.

The stomach contents of various fresh-water ostracodes have been examined and found to contain traces of diatoms, protozoans, bacteria, and algae. Most ostracodes are scavengers; some may be predators; only one (*Entocythere*) is known to be parasitic.

Variations in acidity and alkalinity of the water in which ostracodes live are expressed more by the presence or absence of intolerant species than by thinning or thickening of the carapace. For example, *Candona* is intolerant of acid waters. Slightly alkaline stagnant ponds are likely to contain very prolific ostracode faunas. Ostracodal limestone may be found forming in this alkaline environment.

BRACKISH-WATER OSTRACODES

The ecologic flexibility of ostracodes is well demonstrated by the presence of large populations belonging to endemic assemblages in brackish-water estuaries and lagoons. Few invertebrates possess sufficient tolerance to withstand the wide variations in salinity that characterize this environment; fewer still are represented in the fossil record. Ostracodes are the most abundant microfossils present in brackish-water sediments, and they contribute significantly to the volume of sediments in some brackish lagoons. Accompanying a decline in the number and importance of marine Foraminifera with decreasing salinity, ostracodes show progressive increase. This relationship between two important

microfossil groups provides an important method for the recognition of ancient shorelines.

The earliest indications of brackish-water ostracodes are discovered in Silurian rocks of the Central Appalachians. Because of the absence of modern forms until the Jurassic, brackish-water assemblages of older strata are identified mainly by association with sedimentary features and apparent paleogeographic position. The Bathonian strata of France contain the first brackish-water faunas with ostracode species belonging to presently living families. In Purbeckian and Wealdian sediments of Britain, a complete transition from fresh-water to brackish to marine assemblages is preserved. The Pascagoula clay (Miocene) of Mississippi contains a brackish-water assemblage that is generically similar to those living today. Species of the genera *Cyprideis*, *Cytheridea*, *Haplocytheridea*, *Cytherura*, and *Loxiconcha* typically are present in Recent assemblages.

Where a gradient in salinity exists from fresh-water to marine, the ostracode fauna is divisible into four intergrading biofacies. The limnic or fresh-water ostracodes are scarce in waters more saline than 2 ‰. The brackish-water biofacies contains a population that is most abundant in waters having about 10 ‰ salinity. However, this biofacies is sometimes represented by two adjacent and transitional faunas, an oligohaline (0.2-2 ‰) assemblage and a more saline brachyhaline (mesohaline, 2-17 ‰) assemblage. Marine ostracodes seldom survive to reproduce in waters with less than 17 ‰ salinity.

Brackish-water ostracodes are found sometimes in hypersaline lagoons (Fig. 30). The tolerance of ostracodes usually associated with estuaries and brackish lagoons for great changes in salinity allows them to live in lagoons too saline for most normal marine ostracodes. In Florida Bay, where waters are periodically saline in excess of 55 ‰, species of *Haplocytheridea*, *Loxiconcha*, and *Cyprideis* produce large populations. Most evaporite-bearing strata do not contain ostracodes, although an assemblage interpreted to represent a hypersaline environment has been found in the Devonian of Russia.

The genus *Cyprideis*, a typical brackish-

water ostracode, inhabits waters of all degrees of salinity from fresh to marine. Species of this genus have both smooth and nodose forms of the same instar stages present in the same population in different individuals, but the number of nodose dimorphs increases in proportion to the smooth dimorphs as salinity increases. Ornate ostracodes increase in abundance throughout the entire ostracode population as the conditions of normal marine environment are approached. Extraction of salts for the development of a heavier and more complicated carapace may require less energy in waters with a higher concentration of calcium.

MARINE OSTRACODES

Geological evidence indicates that the marine environment was first to be inhabited by ostracodes and it is represented by the greatest diversity of forms throughout the fossil record. Most marine ostracodes possess complicated exoskeletons that in some way reflect the surrounding marine, benthonic habitat. Carboniferous species of *Cypridina* and a few other fossil pelagic ostracodes have been described, but most fossil marine ostracodes were crawlers, burrowers, and near-bottom swimmers.

The geographic and environmental distribution of Recent marine ostracodes is still very incompletely known. Information about their ecology is restricted to just a few well-studied areas. G. S. BRADY (2, 3) described the ostracode faunas from seas surrounding the British Isles and those contained in collections acquired by the Challenger Expedition (1873-76). Most of the genera described in his reports no longer include the variety of species he assigned to them. G. O. SARS (11) described many species from the North Atlantic near Norway and Greenland, along with some data on their environment. The first exhaustive ecologic study of the ostracodes of a marine area was undertaken by G. W. MÜLLER (9) in 1894 on the Bay of Naples fauna. In the 1930's, REMANE (10) included ostracodes in his general ecologic studies of the North Sea and Baltic areas. ELOFSON (4) in 1941 published on the ecology of the Skagerak marine ostracode fauna with additional information concerning North Atlantic coastal

forms. More recently KRUIT (7) has described the ostracode fauna of the Rhone Delta and surrounding bays. HORNIBROOK (6) has studied the recent faunas of New Zealand and found some living palaeocopid species. BENSON (1) published the first ecologic study primarily devoted to marine

ostracodes from North America in reporting on the fauna of Todos Santos Bay, Baja California (Fig. 30).

Interpretation of the paleoecology of Paleozoic marine ostracodes is entirely the product of (1) comparison of their carapace structures with those of living forms whose

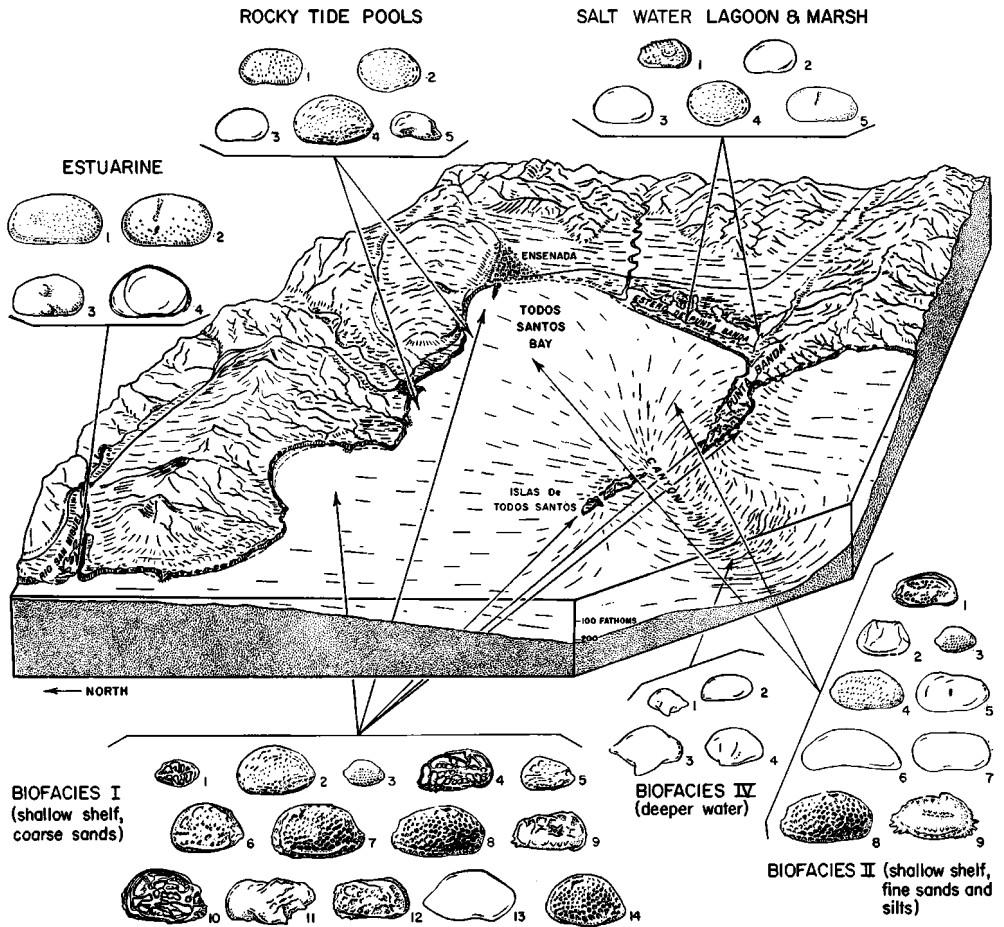


FIG. 30. Distribution of the various ostracode biofacies in the Todos Santos Bay Region, Baja California, Mexico, and their major constituents. Species found in the individual biofacies are listed below.

BIOFACIES I. (1) *Hemicytherura* sp. cf. *H. clathrata*; (2) *Brachycythere lincolnensis*; (3) *Cytherura bajacala*; (4) *Bradleya diegoensis*; (5) *Quadracythere regalia* (molt); (6) *Hemicythere jollaensis*; (7) *Quadracythere regalia* (adult); (8) *Hemicythere californiensis*; (9) *Bradleya pennata*; (10) *Bradleya aurita*; (11) *Paracytheridea granti*; (12) *Cythereis glauca*; (13) *Bairdia* sp. aff. *B. verdesensis*; (14) *Brachycythere driveri*.

BIOFACIES II. (1) *Brachycythere* sp.; (2) *Palmenella carida*; (3) *Cytherura bajacala*; (4) *Leguminocythereis corrugata*; (5) *Cytherura* sp. cf. *C. gibba*; (6) *Paracypris pacifica*; (7) *Cytherella banda*; (8) *Hemicythere californiensis*; (9) *Pterygocythereis semitranslucens*.

BIOFACIES IV. (1,3) *Cytheropteron pacificum*; (2) *Bythocypris actites*; (4) *Cytheropteron newportense*.

SALT-WATER LAGOON AND MARSH. (1) *Puriana pacifica*; (2,3) *Xestoleberis aurantia*; (4) *Loxoconcha lenticulata*; (5) *Cyprideis (Goerlichia) castus*.

ROCKY TIDE POOLS. (1) *Haplocytheridea maia*; (2) *Loxoconcha lenticulata*; (3) *Xestoleberis aurantia*; (4) *Brachycythere lincolnensis*; (5) *Caudites fragilis*.

ESTUARINE. (1) *Cyprideis (Goerlichia) miguelensis*; (2) *Cyprideis (Goerlichia) stewarti*, (3) *Cyprideis (Goerlichia) sp.*; (4) *Cypridopsis vidua*.

morphology is otherwise quite different, (2) speculation on the function of extinct structural features of the carapace, (3) examination of associations with a few long-range ostracodes like *Bairdia* which are living today, and lastly, (4) association with other marine fossil organisms. Some study has been devoted to the association of ostracodes with various lithologic types of sedimentary rocks.

One can see, therefore, that knowledge of the ecology of marine ostracodes is still in its early stages, partly because Recent forms living in deeper waters are relatively inaccessible and that paleoecology suffers from the lack of knowledge about the habits and environmental requirements of extinct species.

INFLUENCE OF PHYSICAL AND ORGANIC ENVIRONMENTAL FACTORS ON THE DISTRIBUTION AND FORM OF MARINE OSTRACODES

Assuming that environment is the principal agent of natural selection and the catalyst for the evolution of the many varied shapes and structures found in ostracode exoskeletons, there should be correlation between some of these structures and the environmental factors to which they are exposed.

The shapes of the appendages of living ostracodes reflect their use for swimming, crawling, or burrowing. The swimmers have long natatory setae that form fanlike oars with the antennules. The antennae have less well-developed natatory setae for the same purpose. The burrowers have no natatory setae; instead, the antennae and antennules of these ostracodes are shaped for digging. The anterior appendages of the crawlers are very similar but are modified more for grasping.

The shape and ornament or lack of ornament of the carapace also reflects the environment. The shape, weight, thickness, and rigidity of the valves, and the hinge-ment correspond to the type of substrate of the burrower and crawler or currents that affect the swimmer. The carapace of swimmers generally is smooth, high in proportion to length, with thin light-weight valves and simple hinges. These swimming forms need to move about freely, unimpeded by a massive exoskeleton.

Crawlers, which occasionally swim short distances, are not true swimmers. Some never leave the bottom and wander over the surface of various sediments. Most of these forms are highly ornamented and possess thick, strong valves with flat venters. Some venters are extended laterally into keels, alae, or vela for support on soft oozes. Species inhabiting areas with coarser sediments tend to be reticulate or spinose, the spines encasing setae that extend the sensory apparatus of the ostracode outward so as to feel interstices among the sand grains. Further development of the surface of the carapace into a reticulate system of ribs strengthens the valves against impact in an environment of shifting sands. Possibly this coarse shell also makes them a little less digestible by their natural enemies; however, small fish avoid eating even the thin-shelled ostracodes.

The carapaces of most burrowers, which live in soft sediments, are smooth like those of swimmers but they are much more elongate. Burrowers that inhabit the interstices of coarse-grained substrates, relatively few in number, are very small, short, and usually possess robust carapaces.

Many of the physical and organic environmental factors that affect an ostracode are not expressed in the morphology of individuals so much as in distribution of populations. In the light of present knowledge, it is difficult, for example, to tell what morphologic feature allows or compels *Echinocythereis dasyderma* BRADY to live in waters 12,000 feet deep and to explain why *Puriana rugipunctata* (HOWE) lives in or on shallow calcareous sediments. It is true that these ostracodes are very different in appearance but what selective factor has placed them in their respective habitats is not now evident from examination of their shapes or ornament.

The following environmental factors are important in determination of the ranges and locations of certain living marine ostracode species and assemblages.

DEPTH

Benthonic ostracodes live on the floor of modern seas and oceans at all depths, but they are most abundant in shallow seas of shelf areas. Bathymetric pressure seems to exert little or no effect on ostracodes, but

other factors such as fading light, diminishing plant life, stability and change in composition of the bottom sediment do affect the benthonic ostracode. These factors affect the fresh-water ostracode living in deeper lakes, as well as marine ostracodes. *Echinochytthereis* and *Cytheropteron* are two deep-water ostracode genera in present oceans, but these genera contain shallow-water species. *Hemicythere*, *Xestoleberis* and *Cythere* (s. s.) are typical tide-pool genera, but are occasionally found in shelf sediments. Intermediate between the deep-water genera and those adapted for life in tide pools are the normal marine shallow-shelf forms that are represented by many species in late Mesozoic and Cenozoic sediments. These genera are influenced considerably by the nature of the bottom sediment.

BOTTOM SEDIMENT OR SUBSTRATE

The texture and stability of the sediment composing the substrate exerts a strong influence on marine ostracodes, just as it does on fresh-water forms. Even the plant dwellers are indirectly affected by the plant's preference for a particular substrate. Smooth-shelled forms are predominant in fine-grained muds, the rougher more ornate ostracodes being found in coarser, or more calcareous sediments. Such terms as *endopelose* (silt and clay burrowers), *endopsammon* (sand burrowers), *epipelose* (silt and clay surface wanderers), and *epipsammon* (sand-surface crawlers) have been suggested by REMANE (10) and ELOFSON (4) for ostracode assemblages typical of certain bottom sediments, emphasizing the control of the substrate over the character of the associated assemblage.

LITHOLOGIC AND MICROPALAEONTOLOGIC ASSOCIATION

Most workers on fossil ostracodes collect their specimens from calcareous shales and sands, particularly the shale partings in limestone sequences. Even Recent marine ostracodes are most abundant in sediments that will become limestones, calcareous shales, or calcareous sands. However, the ease with which sediments can be broken down by washing influences the reported productivity of a given stratigraphic unit as much as does the actual abundance of a fauna. Therefore, not much reliance can be placed on the reported lack or relative lack

of ostracode faunas in limestones and siliceous shales.

Ostracodes are rarest in euxinic black shales and fine muds, evaporites, and well-sorted sands. Pyritized ostracodes have been reported from black shales, but they are more likely to be found in transition beds above and below such strata. Ostracode faunas have been described from both red and green shales. The influence of redox potential will be discussed below.

SALINITY

Except in lagoons and estuaries where the marine water becomes brackish because of continental run-off, and in confined shallow basins where evaporation is dominant, variations in salinity of open marine waters are not sufficiently large to influence marine ostracodes appreciably.

Few marine species and genera are successful inhabitants in waters with less than about 17 ‰ salinity, and then only for short periods during heavy rains in tide pools, salt-water lagoons, and marshes.

The ability of normal marine ostracodes to live in salinities greater than 55 ‰ has not been studied. The ostracodes of Florida Bay, which has salinities up to 55 ‰, compose a special assemblage of tolerant marine species and euryhaline brackish-water species.

TEMPERATURE

Changes in the temperature of the sea northward and southward along the coasts of continents, along the edges of off-shore water masses, and during seasonal heating of shallow waters are reflected in the geographic distribution of vegetatively stenothermal species and time of reproduction during the year of the reproductively stenothermal species.

In warm tropical waters more species are present than in colder waters, but the total number of individuals in either area is dependent on the productivity of that area. Cold-water faunas are distinct from warm-water faunas. For example, the shallow neritic faunas of Norway and northern Scotland contain species different from those found in comparable faunas of southern Ireland and the Bay of Biscay. Possibly or probably as result of contemporary temperature differences, the Miocene ostracode faunas of Florida contain many species that are ab-

sent in the Miocene faunas of Virginia and Maryland.

Depth zonation, using the predominance of certain ostracode species along given isotherms, has not been attempted to the extent that it has with the foraminifers of the Pliocene and Recent of California. Some ostracodes are restricted to the 2°C. isotherm in the abyssal depths of the ocean, but this fauna is poorly known.

REDOX POTENTIAL AND HYDROGEN-ION CONCENTRATION

Minor variations in the acidity, alkalinity, and oxygen content that normally are found in marine environments have little or no determinable influence on the number or kind of ostracodes that may be present in a given area. The pH seldom falls into the acid range except below the sediment-water interface. It is not known whether burrowing ostracodes are restricted to nonacid sediments or whether they would not burrow in carbon-rich oozes devoid of oxygen.

Few ostracodes are found in euxinic environments or in black shales. Little is known about the minimum oxygen requirements of living marine ostracodes, and few places in present oceans are available for this kind of study. Fossil ostracodes are found in red and green shales and are sometimes associated with glauconitic sands.

PLANT DOMINANCE

Marine salt-marsh grasses such as the turtle grass (*Thalassia*) of Florida and the Gulf Coast and the eel grass (*Zostera*) of the Pacific Coast offer protection for ostracode populations. These ostracodes are absent in the intervening bare spots. A filigreed coralline alga growing in a tide pool can teem with species of *Xestoleberis* and *Cythere*, whereas a neighboring different type of alga may be associated with numerous individuals of species of *Loxoconcha* or *Hemicythere*. Ostracodes living on or near green algae commonly are different from those of brown algae.

FOOD AND NUTRIENTS

Most of the discrete particles found in the stomachs of marine ostracodes are too small to identify except by color.

The level of the phosphate and nitrate content of the water is reflected in the rise and fall of the ostracode population. Areas

of upwelling, such as off the Pacific coast of Baja California, are luxuriant in all life and the general ostracode population is large. Warm waters, low in nutrient content, are correspondingly low in ostracode population except near the mouths of rivers draining mature limestone, and phosphate-rich inland areas. The faunas off the mouths of rivers in Florida are richer than surrounding areas of the sea floor.

ASSOCIATION WITH OTHER ANIMALS

Ostracodes live in association with most invertebrates that are now found preserved as fossils. They are found in the brachiopod-trilobite-bryozoan assemblages of the lower Paleozoic and are found in most of the normal marine benthonic faunas through and including the mollusk-foraminifer faunas of today. KUMMEROW (8) notes that ostracodes appear and disappear abruptly in the stratigraphic record as though occurring in pockets on the sea floor. They are associated with many "dwarfed" faunas, but are not themselves dwarfed. In sediments where conodonts are plentiful, ostracodes are rare, but they are found together in the transition zones between their respective preferred habitats. In sediments where calcareous foraminifers are abundant, ostracodes are not. Ostracodes are almost invariably absent in *Globigerina* ooze. The exchange in abundance between marine foraminifers and brackish ostracodes might be used to indicate marine transgression and regression. Brackish-water ostracodes and oysters lived in the same brackish-water habitat during the Cretaceous.

OSTRACODE BIOFACIES

Many assemblages of ostracode species have been described as characteristic of particular stratigraphic facies of Recent sedimentary environments. It is not possible to do more than list some of these assemblages or facies, as each worker has developed his own classification.

Fresh-water assemblages. Temporary still-water (pond), temporary running water, permanent still-water (lake), permanent running water (river), and prodelta.

Brackish-water assemblages and biofacies. Oligohaline, mesohaline, brachyhaline, polyhaline, marginal bay, midbay, lower bay, and estuarine.

Marine assemblages and biofacies. Salt-water lagoon, salt-tidal flats, salt-marsh channel, subtidal channel, bay mouth, open bay, open gulf, sandy bottom (epipsammon and endopsammon), mud-bottom (epipelos and endopelos), tide pool (supralittoral), abyssal, deep water, shallow water, etc.

OSTRACODE BIOGEOGRAPHY

Marine, fresh-water, and brackish Recent and Cenozoic ostracode faunas have been described from many parts of the world. A similarity exists between some of these that justifies their placement in some of the conventional biogeographic realms. Although the local migrations of some European and American faunas have been described or implied to explain the recurrence of forms at various stratigraphic levels or affinities with forms from other areas of equal age, little study has been devoted to establish the geographic extent of the various ostracode species. The following provinces or realms have known ostracode faunas, and on cursory examination appear to contain faunas more related to those in the same realm than to those of other realms.

Marine. Celtic (Britain and North Sea), Boreal (Norway, Greenland, and North Atlantic), Lusitanian (Mediterranean), Transatlantic (North America, east Coast), Caribbean (Trinidad, Gulf of Mexico, southern Florida), Californian, Japonic, Novo Zealandic.

The Indo-Pacific, West African, Patagonian, Peruvian, and Panamanian ostracode faunas are poorly known.

Fresh-water. Holarctic, Neotropical, Ethiopian and Australian. The Oriental ostracodes are largely undescribed.

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TECHNIQUES FOR PREPARATION AND STUDY OF FOSSIL OSTRACODES

By I. G. SOHN

[United States Geological Survey]

CONTENTS

	PAGE
RELEASE OF FOSSILS FROM MATRIX	Q64
Boiling in water	Q65
Special treatment	Q65
CLEANING	Q66
Washing	Q66
Drying	Q66
CONCENTRATION	Q66
Sieving	Q66
Heavy-liquid separation	Q67
Picking	Q67
PREPARATION OF INDIVIDUAL SPECIMENS	Q67
MOUNTING SPECIMENS	Q68
STUDY WITH REFLECTED LIGHT	Q68
Ammonium chloride coating	Q68
Magnesium oxide coating	Q68
Staining	Q69
Silver nitrate coating	Q69
STUDY WITH TRANSMITTED LIGHT	Q69
Liquid immersion technique	Q69
Canada balsam technique	Q69
Hydrofluoric acid technique	Q69
STUDY WITH POLISHED AND THIN SECTIONS	Q69
REFERENCES	Q69

This outline of methods for extracting microfossils from sediments is based on the techniques of preparing sedimentary rocks for the extraction of ostracodes in the micropaleontological laboratory of the U. S. Geological Survey, Washington, D. C. The same methods are applicable to preparation of other microfossils, and most have been described previously. The purpose of this outline is to give a step-by-step description of methods that can be used with a minimum of equipment. Additional information is available in TRIEBEL (1958), POKORNÝ (1958), WITWICKA, BIELECKA, STYK, & SZTEJN (1958), and JEKHOVSKY (1959).

The "preparation" of sediments for extraction of microfossils may be said to have three goals: (1) release of fossils from the enclosing matrix; (2) cleaning of fossils from adhering matrix so that morphologic characters can be observed; and (3) con-

centration of the fossils by reducing the volume of material to be examined.

A—RELEASE OF FOSSILS FROM MATRIX

The first step in undertaking work on fossil ostracodes is to remove them from the sedimentary matrix in which they occur. Methods for accomplishing this vary considerably because of differences in the nature of the fossil-bearing sedimentary materials and in some samples because of the mode of preservation of the fossils. Generally the methods of disaggregation used in preparing ostracodes for study yield specimens in bulk, but occasionally effort must be directed to individual fossils found embedded in hard rock. Attention here will be given to methods of separating the ostracodes from enclosing sediment; this will be

followed by description of procedures for cleaning and concentrating the fossils.

(1) BOILING IN WATER

Most soft sediments break down by boiling them in water to which one or two tablespoons of soda ash are added. Stir occasionally in order to prevent burning of the pot. Sediments that have interstitial water do not break down as readily as those that are dry; consequently it is good practice to air-dry collections prior to boiling. An empirical test for disaggregation by boiling is to bite off a small piece of sediment—if it disintegrates in the mouth, the sediment will break down more or less readily by boiling in water. Add a tablespoon of salt to bentonitic sediments in order to inhibit swelling.

(2) SPECIAL TREATMENT

Sediments that will not break down by boiling in water are treated by using hydrogen peroxide, gasoline or sodium acetate, freezing and thawing, and, as a last resort, by mechanical crushing.

(a) HYDROGEN PEROXIDE AND GASOLINE METHOD

Dry the sample, cover it in a saucepan with 15 per cent hydrogen peroxide, and let it soak from two to 24 hours. Most samples will break down. Add water and boil. Some calcareous fossils are corroded by the hydrogen peroxide, and consequently its use is limited.

The storing of hydrogen peroxide in concentrations of more than 15 per cent is a potential fire hazard. The recommendations of manufacturers and distributors as to storage and handling should be followed.

Dry the sample, cover it in a saucepan with commercial gasoline (which is stored in a metal container), and soak from 15 minutes to one hour. Filter gasoline back into container, add two tablespoons of soda ash, cover the sample with water and boil. Varsol, which is not as flammable as gasoline, and also less expensive, may be substituted for gasoline.

(b) SODIUM ACETATE METHOD

Rocks are comminuted in nature by freezing and thawing. The force exerted by the formation of ice crystals in pores breaks the rock. This is accomplished in the laboratory

by use of sodium acetate. Break the dry specimens to about 1 cubic inch, place in a beaker or crucible, and cover with sodium acetate. Add 4 or 5 drops of water, cover the beaker, and place on low heat. The sodium acetate will melt and soak into the pores of the rock. Remove from heat and cool by placing in a pan of water. The sodium acetate will crystallize and rupture the specimens. Add a few drops of water and repeat the process. It will be noted that the first crystallization weakens the rock so that it will subsequently break down more readily. Continued melting and solidifying will not only disintegrate the rock, but also will break up the fossils; consequently, it is best to decant the melted solution of sodium acetate into a second beaker to which are transferred the larger pieces of rocks, and repeat the process.

The sodium acetate that remains with the broken sediment will be dissolved when the sediment is boiled and washed.

Occasionally the force of crystallization will break the glass beaker, but if the pan of cooling water is clean, the uncontaminated sediment can be recovered. Crystallization is accelerated by adding a few grains of sodium acetate to act as nuclei for the crystals.

(c) FREEZING AND THAWING

Results comparable to those yielded by the sodium-acetate method can be obtained by the slower method of freezing in a refrigerator and thawing. The broken sediment should be removed after each thawing to prevent breaking of the fossils, and the sediment then may be boiled.

(d) MECHANICAL CRUSHING

This process of disaggregation consists of applying a crushing rather than breaking force to the rock fragments, generally by means of an electrically driven laboratory crusher. The same results can be obtained with an iron mortar and pestle, or by placing small chunks of rock in a canvas bag and applying a crushing force by use of a wood mallet or the handle of a hammer. Boiling samples prepared in this way serves no purpose, and so the next step is washing, as described in B.

(e) SOLUTION OF MATRIX IN ACID

Silicified fossils can be removed from

limestone by dissolving the matrix with hydrochloric acid. Certain fossils are more successfully removed by use of acetic acid, or the more expensive but quicker-acting formic acid.

Wash the rock to remove all adhering mud, break into chunks, and place in glass vessel. Cover with water and add sufficient acid to start bubbling. Periodically decant, add water and acid. Neutralize the mud residue by adding soda ash and then proceed with washing.

Calcareous and chitinous fossils in a siliceous matrix can be removed with hydrofluoric acid. This method is usually avoided because of the corrosive nature of H_2F ; procedures are described in handbooks on pollens and spores.

B—CLEANING

The most generally useful method of cleaning ostracodes after they have been freed from a sedimentary matrix is by washing in clear water and drying. This is adapted especially for preparation of bulk samples.

(1) WASHING

The broken sediment and fossils are washed through a battery of sieves. This operation reduces the volume two ways; unbroken pieces of rock and larger fossils are separated from the microfossiliferous fraction, and finer material is removed. The sieves used in washing tend to become clogged, however, because (a) fine sediment lodges in holes of the mesh, and (b) commonly too much material is put in the sieve.

For convenience in washing, two kinds of sieves (A,B) are used. Sieve A is 10 inches in diameter and 5 inches deep, with 200-mesh copper screen reinforced on the bottom by 16-mesh copper screen; a 1-inch sleeve below the screen protects the mesh and prevents contamination from the bottom. The edge of this sleeve is perforated by 0.25-inch semicircular holes 2.5 inches apart. These holes permit the water to flow out from beneath the screen. Sieve B is 9 inches in diameter and 5 inches deep, with a 16-mesh copper screen. This sieve fits into sieve A, serving to catch particles larger than most microfossils. Three copper angles are soldered on the outside of sieve B 1.5

inches below the top in order to keep the bottom of this sieve well above the screen of sieve A, and three legs 0.5 inch long on the bottom of the sieve protect the screen. The mesh is attached on the inside of the sieves by smooth solder for ease of cleaning.

Standard sieves of 16- and 100- or finer mesh can be used. For Foraminifera a 200-mesh screen is necessary. Tilt the standard sieves by propping one end with a spoon handle or piece of wood in order to permit the water to escape from beneath the screen.

The sample is washed with a hose attached to a double-feed swivel faucet. If the fine sediment clogs the screen, the end of the hose is pinched in order to increase the velocity of the water and held close to the screen; this invariably breaks the seal and the fine sediments can be washed out. Washing is continued until the water escaping from the screen is clear.

(2) DRYING

The washed sediment can be dried either in the sieve, if the sieve is not needed for a second sample, or transferred to paper towels or newspapers for drying. Spread several thicknesses of papers and turn the sieve over on the paper; most of the wet sediment will fall out. With the hose, wash the remaining sediment to the center of the screen and drop gently face down on the paper. The remaining sediment will bounce off the screen. Repeat if necessary. Fold the paper over several times, insert an identifying label, and set aside to dry. Remove any large fossils from the plus 16 fraction, which can be discarded, dried in the same manner as the minus 16 fraction and stored, or subjected to other methods of disintegration.

C—CONCENTRATION

Concentration of fossils is accomplished by dividing the sample into various fractions according to particle size, by use (where suitable) of specific gravity separations, and by hand-picking of specimens, generally under a low-power microscope.

(1) SIEVING

The dried sample is conveniently separated into size-determined parts by use of different screens. The minus 16 plus 200-mesh sediment is dry-sieved through a

series of 40-, 60-, 80-, and 100-mesh screens, or 150-mesh if very small fossils are found.

In order to avoid contamination the sieves are dipped for a few minutes in an aqueous solution of methylene blue, after each use. Any specimens (except pyritized fossils) in the mesh are then colored blue, being then easily recognized as contaminants should they become incorporated in subsequently sieved samples (Beckmann, 1959). An alcohol solution of methylene blue dries faster than a water solution.

(2) HEAVY-LIQUID SEPARATION

Many types of microfossils can be concentrated by use of heavy liquids, and various techniques for accomplishing this are described. Ostracodes do not usually lend themselves to such treatment and must be hand-picked under a binocular microscope.

(3) PICKING

Samples obtained from the 40- and 60-mesh screens are conveniently picked under low power, whereas those from smaller screen sizes require medium power.

Various picking trays have been described. The simplest is a flat-bottomed black-painted tray with 0.15-inch or higher sides that is open on one end. Horizontal and vertical lines desirably are painted or grooved on the picking surface. The distance between the lines should correspond approximately to the field of view seen through the microscope. Scatter an evenly distributed layer of prepared sediment on the tray so that each particle can be seen. By moving the tray back and forth under the microscope every grain can be examined and the fossils picked out.

For lifting the fossils and transporting them to a hollowed slide or other receptacle, it is best to use a 00 sable or camel-hair brush. Dip the brush in water and pass it over the back of the other hand while the handle is rolled between the fingers. This removes excess water and makes a point on the tip of the brush. The wet brush will pick up particles when they are touched and drop them in a microslide when the brush with an adhering particle is swept over the bottom of the slide. Some workers wet the brush with saliva; from the standpoint of the worker, this is not advisable

because the brush may become contaminated with harmful substances such as dyes and carbolic or other acid used to inhibit bacterial growth in the glue—not to mention that specimens adhering to the brush may be swallowed. Always examine the brush under the microscope before dipping in water in order to insure that specimens inadvertently picked up by the brush are not dropped into the water.

D—PREPARATION OF INDIVIDUAL SPECIMENS

Many ostracodes are so fragile that they are destroyed by boiling; other specimens have ornaments that break when crushed from hard rocks. These have to be handled on an individual basis. Slabs of rock may be broken along bedding planes and the surface examined with a microscope. Each specimen is stained with malachite green in alcohol. This serves two purposes; it helps locate the specimen on the slab and shows where the matrix is breaking. A groove is scraped around the specimen far enough from it to insure against accidental breaking. From the groove a cut below the specimen can be made so as to allow its removal. Use sharp needles, a vibratool or a dental drill.

Although the various methods of disaggregating sediments and subsequent washing commonly result in clean specimens, matrix sometimes adheres to the outside of specimens or fills the inside of valves. This extraneous material needs to be removed in order to observe shell structures. Such cleaning may be done manually, chemically, or by mechanical methods.

For manual cleaning the specimen on a slide is covered with a drop of water and the matrix removed with a sharp needle. The drop of water, in addition to possibly softening the matrix, prevents the specimen from popping out of the slide when touched with the needle. A chewed wood toothpick makes an excellent stiff-bristled microscopic broom to sweep out matrix from a valve. When sharpened, the toothpick can be used instead of a needle on fragile specimens.

For cleaning of specimens chemically, matrix can be removed from individual carapaces or valves by soaking in hydrogen peroxide in a concave glass slide, observing progress of reaction with a microscope. A

toothpick may be used to sweep away the matrix. Hydrofluoric acid will remove siliceous matrix from calcareous specimens and at the same time render the specimens translucent (SOHN, 1956). The valves of hollow carapaces are sometimes dissociated by the gas pressure that is generated in this process.

Mechanical methods of cleaning also may be employed. Experiments with the use of ultrasonic vibrations have proved successful in cleaning individual ostracode specimens, but if incipient fractures are present, the specimens tend to break in this process. Ultrasonic treatment is based on high-frequency acoustical waves that are transmitted to water or other liquids by means of electrostrictive or magnetostrictive devices called transducers. The transducers are designed for various industrial uses, either as integral parts of stainless steel tanks or as units immersible in existing tanks. A generator transmits the ultrasonic energy to the transducer. This process is very good for disaggregating some groups of fossils such as diatoms and foraminifers, although not usable generally for recovery and cleaning of ostracodes because of tendency toward breakage.

For ease in ultrasonic treatment of individual specimens, the following procedure is recommended. The fossils are covered with about 0.25-inch of water in a beaker that is about 0.5-inch in diameter. This beaker is placed in a larger beaker to which water is added in such amount that the small beaker does not float and tip over. The larger beaker then is placed in the transducer tank in which the depth of water is controlled to prevent floating and tipping of the large beaker. About one minute of ultrasonic treatment is sufficient to clean most specimens.

E—MOUNTING SPECIMENS

It is customary to glue ostracode specimens to micropaleontological slides, and for this purpose all types of glue, including Duco cements, have been used. Most glues and Duco cement may in time contract upon hardening and thus rupture some specimens. Experience has shown that a dilute solution of gum tragacanth, to which a few drops of phenol or oil of cinnamon are added in order to prevent the develop-

ment of molds, is admirably suited for the purpose of mounting small fossils. The specimens are easily unglued by use of a wet brush. Should it be necessary to remove all traces of the gum tragacanth from a specimen, it may be immersed in alcohol; then the gum tragacanth forms a milky cohesive gel-like substance that can be teased away easily with a needle.

F—STUDY WITH REFLECTED LIGHT

Ostracodes usually are examined with reflected light. Finer details are better seen when the specimen is either coated or stained. For best results in photography specimens should be coated. TRIEBEL (1958) describes methods of preparing specimens for photography.

(1) AMMONIUM CHLORIDE COATING

BASSLER & KELLETT (1934, p. 9, fig. 2) describe an apparatus whereby a thin film of ammonium chloride sublimate is deposited on the specimen through the combination of fumes of concentrated hydrochloric acid and ammonia. This method is not satisfactory for microscopic specimens because of large grain-size of the sublimate commonly caused by high humidity. HESSLAND (1949, p. 115) describes a method which is an improvement on that reported by BRANSON & MEHL (1933, p. 17), and by COOPER (1935, p. 357), for obtaining a fine-grained deposit of ammonium chloride sublimate. A simplification of HESSLAND's method is to use glass tubing of 2- or 3-mm. inside diameter about 4 inches long. One end is drawn out to form a fine nozzle, and ammonium chloride powder is inserted through the other end. The wider end is then sealed with plastic wood or plaster of paris. When the tube is heated, a jet of ammonium chloride is released through the nozzle. The vapor can then be directed over the specimen and a fine-grained sublimate is deposited on the specimen. A vial prepared in this manner has been in use by me for several years.

(2) MAGNESIUM OXIDE COATING

A small piece of magnesium ribbon held by forceps when ignited will serve to white-coat a specimen that is passed over the magnesium oxide fumes. This method is

advantageous in that the film remains on the specimen until it is washed off. The light emitted by burning magnesium can be injurious to eyesight and therefore care should be taken not to look directly at the light.

(3) STAINING

Any kind of stain causes fine detail to stand out on specimens and for this purpose almost all sorts of ink and food-coloring preparations can be used (Artusy & Artusy, 1956). Malachite green (HENBEST, 1931, p. 358) dissolved in alcohol has proved to be most suitable for staining ostracodes because of rapidity with which it dries. This stain can be removed by washing with alcohol.

(4) SILVER NITRATE COATING

LEVINSON (1951) has described a technique for depositing a metallic film of silver nitrate on ostracodes. For such treatment a clean specimen is heated for about three seconds, allowed to cool to room temperature, and then painted with 5 per cent silver nitrate solution. After 15 seconds the excess is drawn off with filter paper and the specimen is reheated over a bunsen flame for one minute. The resulting metallic film is permanent, but has the disadvantage of obscuring pore-canals and muscle scars.

G—STUDY WITH TRANSMITTED LIGHT

The muscle scars, pore canals, and duplication structures of ostracodes are best observed in transmitted light, and methods of making the valves translucent have been devised. The same methods can be used to observe certain structures with reflected light.

(1) LIQUID IMMERSION TECHNIQUE

In some instances water is adequate to observe the structures with transmitted light but usually glycerin or an immersion oil is used. WAGNER (1957, p. 17) soaked ostracode specimens for several hours in castor oil in order to make them translucent.

(2) CANADA BALSAM TECHNIQUE

Specimens mounted in Canada balsam will show structures by transmitted light that are otherwise not seen.

(3) HYDROFLUORIC ACID TECHNIQUE

Calcareous specimens can be converted to fluorite by use of hydrofluoric acid (SOHN, 1956). Fluorite is more translucent in water or glycerin than calcite, and many specimens that do not show any shell structure in the calcitic state, will exhibit muscle scars and marginal structures when converted to fluorite.

H—STUDY WITH POLISHED AND THIN SECTIONS

Overlap, certain types of hingements, and duplicatures of ostracodes can be observed by use of polished surfaces and thin sections. The specimen is mounted on a glass slide in Canada balsam, bioplastic, or other suitable medium and ground in the same manner as thin sections of rocks. When the desired point on the specimen is reached, the specimen is turned over on the slide and the other side then is ground to make a thin section.

It is possible to reconstruct the structure of a complete ostracode carapace by means of a series of polished surfaces (KESLING & SOHN, 1958, p. 518) records of which can readily be made photographically and by aid of camera lucida. When Canada balsam is used, the specimen is oriented with a toothpick or a warm needle. It is easier to observe wall structures if the specimen is stained prior to mounting in the cement. The stain sometimes penetrates the shell material so that the inside border of the shell can be seen.

SYLVESTER-BRADLEY (1941, p. 6) has used the following method on large specimens with thin shells, obtaining excellent results. First he made a drawing of the specimen to be studied. The specimen was then broken with a needle, and the lines of fracture recorded on the drawing. Each fragment was then mounted on its edge with a gum tragacanth smear, and examined.

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IDENTIFICATION OF FOSSIL OSTRACODES IN THIN SECTION

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CRITERIA USED FOR IDENTIFICATION

Research has revealed that various genera and species of ostracode fossils can be identified in thin section. This is possible because of variability in such characteristics as shell layering, shell thickness, overlapping of the edges of the carapace, the position and nature of ridges, frills and spines on the surface of the valves, and shell structures reflected by the deep vertical groove or trench in the valves, referred to as the sulcus.

PROCEDURES FOR PREPARATION OF THIN SECTIONS

Two methods are used in the sectioning

of free specimens for the study of shell characteristics of known species. The method discussed first is used for most Paleozoic and Mesozoic species; the second method is used for fragile Paleozoic and Mesozoic forms and for all Cenozoic forms.

(1) In the first method, a small quantity of thermoplastic (such as Lakeside) is heated on a clean, oil-free frosted glass slide to just above the temperature at which it becomes fluid. As quickly as possible, the slide is placed under a binocular microscope (magnification about 30×) and the specimen is introduced into the thermoplastic. The thermoplastic will harden in approximately 30 seconds but will probably remain fluid for a sufficient length of time for the

specimen to be oriented in any desired position. However, a fine needle heated over a flame may be used to keep the thermoplastic fluid; the needle also is a satisfactory tool for orienting the specimen in the desired position. The slide is then ground by hand, using a figure eight motion, on carborundum paper (e.g., No. 400-A Tufbak, Behr-Manning) until the desired position on the specimen is reached. A smooth surface is obtained on the thermoplastic by adding a few drops of mineral oil on the carborundum paper. Suction cups (such as are obtainable from toy darts or arrows) of the same diameter as the slide afford an easy method for holding the slide against the carborundum paper. The specimen can be examined periodically from the reverse side of the slide to see progress of the grinding.

The slide is then washed in carbon tetrachloride to remove all adhering mineral oil. The thermoplastic is next melted in the vicinity of the specimen by using the heated needle (if the entire slide is heated the thermoplastic tends to run to edges of the slide). With the heated needle the specimen is oriented so that its flat side (that portion of the specimen previously ground down) is flush against the slide. Only slight pressure is needed to assure close contact between the specimen and the slide. The slide is again ground on No. 400-A carborundum paper and mineral oil until clear structures are obtained; then it is again washed with carbon tetrachloride.

The specimen may be stained by using a few drops of Heeger's solution (made by acidifying a solution of potassium ferricyanide with hydrochloric acid). The solution should be allowed to remain on the specimen for not more than 10 seconds; the slide then must be thoroughly washed with water. If the specimen is stained it must be covered the same day.

For covering the specimen the procedure is as follows. In a small evaporating dish, 5 drops of castolite hardener (catalyst) is mixed with 15 ml. of castolite (plastic). This is sufficient to cover approximately 10 slides. Two drops of this mixture are put directly on the specimen and a clean, oil-free cover glass is placed directly over the mixture. The cover glass must be firmly pressed against the slide to remove the air bubbles and excess mixture.

After all slides of a batch have been covered, the slides are placed approximately 7 inches from an infra-red heat lamp for 30 to 45 minutes and then allowed to set for 15 minutes. A single-edged razor blade is used to remove excess castolite from the slide. The slides are next washed in a mixture of 2 parts acetone to 1 part carbon tetrachloride. As a final step the slide is washed with a detergent soap. With a little practice approximately 30 specimens can be sectioned and covered during a normal eight-hour day.

(2) As noted above, the second method is used primarily for fragile Paleozoic and Mesozoic and all Cenozoic forms. In a large evaporating dish mix 12 drops or 1 ml. of castolite hardener with 25 ml. of castolite. Immediately pour the mixture into a plastic ice cube tray containing a dozen 1.5 cm. (approximately 0.5-inch) cells. If a 0.25-inch slit is made in the walls of each individual cell, it will facilitate the removal of the castolite cubes. Each cell should be filled approximately half full. When the tray is placed 7 inches from an infra-red heat lamp for 3 minutes at a temperature of 63°C., the mixture quickly hardens. Overheating causes the castolite to crack. The specimen is immediately placed on the top surface of the hardened castolite and oriented in the desired position. The castolite is sufficiently tacky to retain the specimen in a fixed position. Another mixture of castolite and castolite hardener is prepared and poured into the cells, filling them. If a double batch is originally made, the portion to be used at this time will have jelled and may be difficult to pour.

The tray is next placed back under the heat lamp for 3 minutes and then the material should set for 12 hours for complete hardening. After the heat-lamp treatment it is possible to pop the cubes from the tray to place them again under the lamp for an additional minute. This speeds the hardening process.

Using a diamond lap, the cube is slowly ground on one plane until the specimen is encountered. The cube is then ground by hand to the desired position, using No. 400-A carborundum paper and mineral oil, after which the slide is washed in carbon tetrachloride. A small amount of Lakeside thermoplastic is placed on a frosted slide and

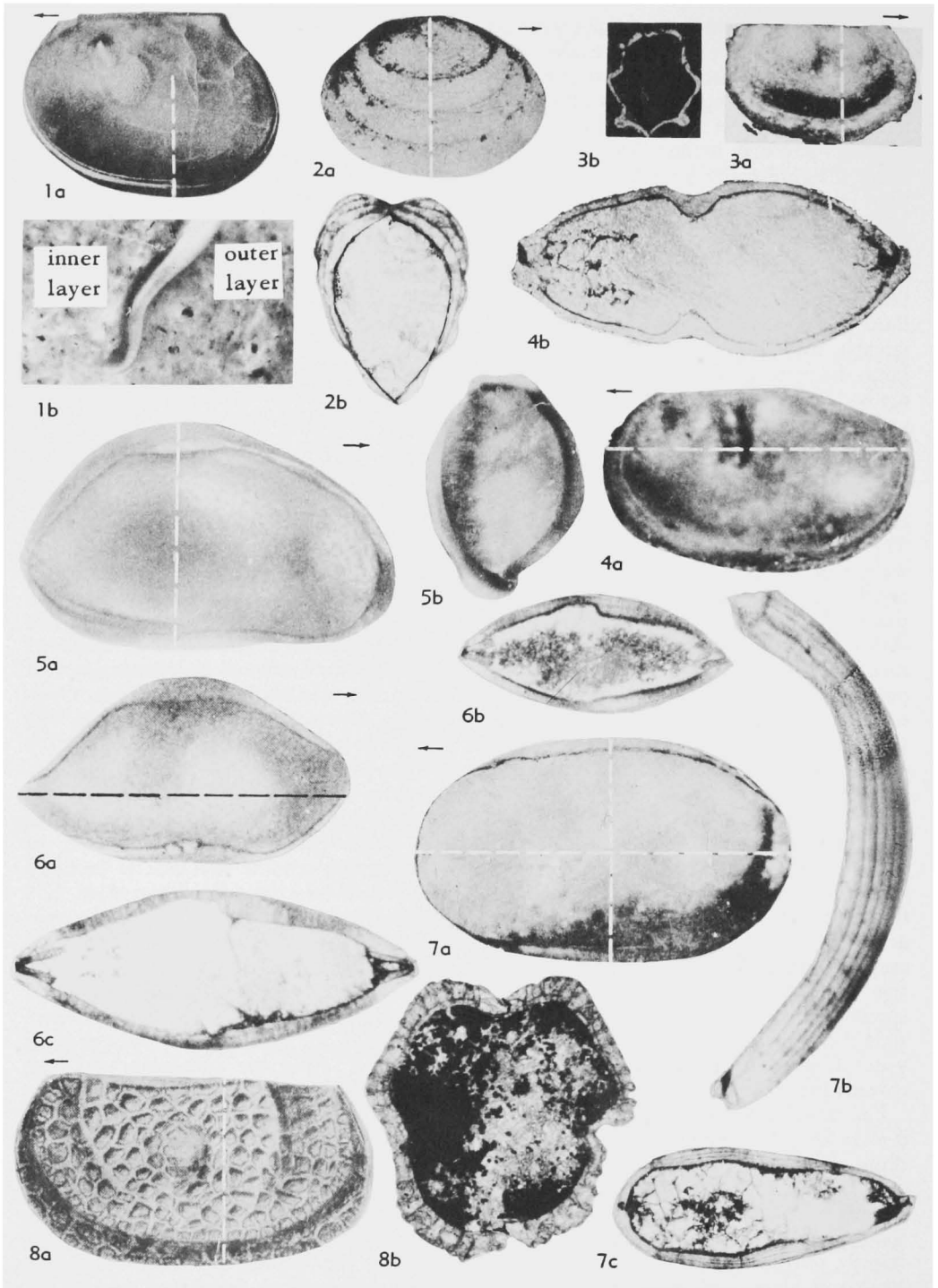


FIG. 31. Representative features shown by ostracode thin sections (lines on views of carapaces indicate location of sections illustrated).—1. *Isochilina*; 1a, LV lat., $\times 2$; 1b, part of section, $\times 13$.—2. *Cryptophyllus*; 2a, R lat., $\times 38$; 2b, transv. sec., $\times 50$.—3. *Eridoconcha*; 3a,b, R lat., transv. sec., $\times 45$.—4. *Limnoprimitia*; 4a, L lat., $\times 35$; 4b, long. sec., $\times 47$.—5. *Bairdiacypris*; 5a, R lat., $\times 21$; 5b, transv. sec., $\times 19$.—6. *Bairdia*; 6a, R lat., $\times 36$; 6b,c, long. secs., $\times 33$, $\times 46$.—7. *Cavellina*; 7a, L lat., $\times 48$; 7b, transv. sec. LV, $\times 115$; 7c, long. sec., $\times 37$.—8. *Amphissites*; 8a, L lat., $\times 50$; 8b, transv. sec., $\times 75$ (Levinson, n).

melted and the ground side of the cube is pressed firmly against the slide. The cube is again ground on the diamond lap until the desired thickness is nearly approached. Final grinding is done on carborundum paper with mineral oil. The slide is washed with carbon tetrachloride, stained, and covered as described above.

A phase-contrast microscope with a polaroid filter has proved to be the most satisfactory instrument for examining ostracode thin sections.

EXAMPLES OF THIN SECTION IDENTIFICATION

Observations have shown that members of the family Leperditidae (L.Ord.-M.Dev.) have a single primary shell layer comprising the external expression of the valve and a secondary layer internal to the primary layer, usually restricted to the dorsal and ventral portions of the carapace (Fig. 31,1). As some genera and species which are members of this family show minor variations in the basic shell structure, this type of shell layering can be used to recognize forms with a limited stratigraphic range.

The genera *Eridoconcha* (U.Ord.) and *Cryptophyllus* (M.Ord.-U.Jur.) and some species of *Amphissites* (M.Dev.-M.Perm.) possess a many-layered shell formed by the incomplete molting of the valves, with the newly formed shell cemented to one or more older shells (Fig. 31,2). Species of *Cryptophyllus* are considered to be important subsurface markers of the Bromide, Tulip Creek, and Oil Creek formations of the Simpson Group (M.Ord.) in Texas and the Mid-Continent area, and species of this genus can be readily identified in thin section.

The genus *Cavellina*, a smooth-shelled ostracode (?Sil., M.Dev.-Penn., ?Perm.) has been found to possess from 4 to 9 layers of shell material with the total thickness of the layers approximately the same as the shell thickness of other ostracode genera (Fig. 31,7). Preliminary studies suggest that the number of layers may have stratigraphic significance.

Species of six genera of the family Kirkbyidae have been sectioned and all show a two-layered shell structure. In these forms (Fig. 31,8) the inner layer contains the pore

canals and is knoblike in cross section, with intermediate areas filled by the outer layer. In some specimens the inner layer is laminated and the outer layer is prismatic, as in the shell structure of Gastropoda and Pelecypoda. It is believed that in the ostracodes either of these layers may dominate or be developed to the exclusion of the other, which offers an additional criterion for identification of one-layered forms.

In the majority of ostracodes, one valve is larger than the other, edges of the larger valve overlapping the smaller. Some forms overlap only along the venter, whereas others may have the overlap restricted to one of the free margins or dorsum. Variations in the amount and nature of overlap are quite conspicuous in thin sections and can be used to identify many forms (Fig. 31,5).

As seen in thin sections, major ridges and frills appear as if the shell has been folded to form these features (Fig. 31,3). In addition, the shell is indented at the inner surface where folding occurs, and a darkened area bisecting this extension of the shell is commonly developed. These criteria and observation as to length and width of the extension, as seen in thin sections, permit the identification of such features.

In a number of genera, the position of the sulcus is reflected, in thin section, by a pronounced thickening of the shell where this feature occurs (Fig. 31,4). Thus, identification of this character is permitted, providing an important criterion for the separation of Paleozoic forms.

The genus *Bairdia* is a smooth-shelled ostracode frequently encountered in rocks from Middle Silurian to Recent age. Longitudinal sections of *Bairdia* are distinctive, for an inner extension of shell is observed at either the anterior or posterior margin or at both margins (Fig. 31,6); in different species the extensions range from very thin and elongate to short and stubby. Sections of some species of *Bairdia* show an abrupt thinning of the shell from mid-length to the posterior extremity. Such variations suggest that thin sections of species of this genus (abundant in Mississippian to Permian beds) may be readily used for age determinations.

CLASSIFICATION OF OSTRACODA

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CONTENTS

	PAGE
INTRODUCTION	Q74
Early work	Q74
DEVELOPMENT OF OSTRACODE CLASSIFICATION	Q75
CLASSIFICATION ADOPTED IN TREATISE	Q78
General discussion	Q78
Order Archaeocopida	Q81
Order Leperditicopida	Q81
Order Palaeocopida	Q81
Suborder Beyrichicopina	Q83
Suborder Kloedenellocopina	Q85
Order Podocopida	Q86
Suborder Podocopina	Q86
Suborder Metacopina	Q88
Suborder Platycopina	Q89
Order Mydocopida	Q90
Suborder Mydocopina	Q90
Suborder Cladocopina	Q91
Summary of characters	Q91
REFERENCES	Q91

INTRODUCTION

Taxonomy of the ostracodes has undergone major changes in recent years. Early authors classified the Palaeocopida primarily on the basis of sulcation, lobation, and ornamentation. Dimorphic features were mostly disregarded in distinguishing family-group taxa and only occasionally used at the generic level. While confusion existed in classification of the palaeocopid ostracodes, students of other groups, mostly Mesozoic and Cenozoic podocopids, were making progress in taxonomy by using muscle-scar patterns and hinge structures. In this manner they were able to relate many fossil genera to their living relatives.

EARLY WORK

The oldest published figures of an ostracode known to me are found in a paper by GODEHEU DE RIVILLE (1760); they represent a Recent form. A few years later, O. F. MÜLLER (1772) gave illustrations of other

living species, indicating that they differed from insects and stating that shortly he intended to describe them as representatives of a new genus. Such a paper appeared (MÜLLER, 1776) containing definition of the new genus *Cypris*, to which ten described species were referred. Later, he (MÜLLER, 1785) added details to observations on *Cypris* and introduced another new genus, *Cythere*. All this work was based on modern ostracodes.

The date when the first fossil ostracode was recognized is not known certainly, but among oldest publications concerned with such fossils is one by DESMAREST (1813). This is cited by SOWERBY (1825), who described and figured *Cypris faba* from Tertiary deposits of France on the basis of DESMAREST'S work.

The first known observation of a Paleozoic ostracode seems to have been made by DALMAN (1826) when he described a fossil named *Battus*, classified by him with the

Trilobita. In 1834 KLÖDEN published description of a new species of ostracode as *Battus tuberculatus* (now assigned to the genus *Beyrichia*); *Battus* is not available for the fossils described by DALMAN and KLÖDEN because it had been used (1777) for lepidopteran insects. The oldest acceptable name for a Paleozoic ostracode is *Entomoconchus* M'COY, 1839. Publication of this genus was followed (M'COY, 1844) by the introduction of *Bairdia* and (M'COY, 1846) *Beyrichia*. The latter is the oldest generic name applied to a palaeocopid ostracode.

DEVELOPMENT OF OSTRACODE CLASSIFICATION

As somewhat incomplete background for discussion of the classification of fossil and living ostracodes adopted in this *Treatise*, it is desirable to take account at least briefly of selected main contributions by previous workers.

A monograph by G. O. SARS (1866) represents the earliest basic work devoted to major classification of the Ostracoda. In this publication he introduced four new groups designated as suborders (ostracodes as a whole being defined as an order) and two new families. SARS' classification, based almost entirely on Recent genera, is summarized as follows. No Paleozoic fossils were included by him.

Classification of Ostracoda by Sars, 1866

Suborder **PODOCOPA**, nov.

Family Cypridae Baird, 1845 [*recte* Cyprididae]

Family Cytheridae Baird, 1850

Suborder **MYDOCOPA**, nov.

Family Cypridinidae Baird, 1850 [*recte* Cypridinidae]

Family Conchoeciidae, nov. [=Halocyprididae Dana, 1853]

Suborder **CLADOCOPA**, nov.

Family Polycopidae, nov.

Suborder **PLATYCOPA**, nov.

Family Cytherellidae, nov.

The first comprehensive effort to deal with classification of Paleozoic ostracodes is recorded in E. O. ULRICH'S (1894) report on Ordovician Ostracoda from the upper Mississippi Valley region of the United States. No suborders were recognized, 13 families (of which three were new) being arranged simply as divisions of ostracodes as a whole. An outline of the classification given by ULRICH follows.

Classification of Lower Paleozoic Ostracoda by Ulrich, 1894

Order **OSTRACODA**

Family Leperditiiidae Jones, 1856

Family Beyrichiidae Matthew, 1886

Family Barychilidae, nov.

Family Entomidae Jones, 1873 [=Entomozoidae Pribyl, 1951]

Family Cypridinidae Baird, 1850

Family Entomoconchidae Brady, 1868

Family Polycopidae Sars, 1866

Family Cytherellidae Sars, 1866

Family Cytheridae Baird, 1850

Family Thlipsuridae, nov.

Family Cypridae Baird, 1845 [*recte* Cyprididae]

Family Beecherellidae, nov.

Family Darwinulidae Brady & Norman, 1889

In a report by FREDERICK CHAPMAN (1901) on Silurian fossils from Gotland, a partial classification of ostracodes is given by T. R. JONES, as follows.

Classification of Silurian Ostracoda by Jones, 1901

Order **OSTRACODA**

Section **PODOCOPA** Sars, 1866

Family Leperditiiidae, Jones, 1856

Subfamily Aparchitinae, nov.

Subfamily Beyrichiinae, nov. [*recte* Matthew, 1886]

Family Cytheridae Baird, 1850

Section **CYPRIDIDA**, nov.

Family Cyprididae Baird, 1845

Family Bairdiidae Sars, 1888

Section **PLATYCOPA** Sars, 1866

Family Cytherellidae Sars, 1866 [*recte* Jur.-Rec.]

A milestone in classificatory study of Paleozoic ostracodes is represented by a contribution to the Silurian volume of the Maryland Geological Survey by ULRICH & BASSLER (1923). The Silurian formations of the middle Appalachian Mountains region are rich in well-preserved ostracodes that are very useful for zonal subdivision of the strata. These fossils furnish the main basis for recognition of numerous new genera and several families and subfamilies. The classification given in this report is summarized as follows.

Classification of Paleozoic Ostracoda by Ulrich & Bassler, 1923

Order **OSTRACODA**

Family Leperditiiidae Jones, 1856

Family Aparchitidae, nov. [*recte* Jones, 1901]

Superfamily Beyrichiacea [Matthew, 1886]

- Family Beyrichiidae Jones [*recte* Matthew, 1886]
 Family Primitiidae, nov.
 Subfamily Eurychilinae, nov.
 Family Zygobolbidae, nov.
 Subfamily Zygobolbinae, nov.
 Subfamily Drepanellinae, nov.
 Family Kloedenellidae, nov.
 Family Kirkbyidae Ulrich & Bassler, 1906
 Superfamily Cypridacea, nov. [*recte* Baird, 1845]
 Family Thlipsuridae Jones [*recte* Ulrich, 1894]
 Family Beecherellidae Ulrich, 1894
 Family Bairdiidae, nov. [*recte* Sars, 1888]
 Family Cypridae Zenker [*recte* Baird, 1845]
 Family Cytherellidae Sars, 1866
 Family Entomidae Jones, 1873 [=Entomozoidae Pribyl, 1951]
 Family Cypridinidae Sars [*recte* Baird, 1850]
 Family Entomoconchidae Ulrich [*recte* Brady, 1868]
 Family Polycopidae Sars, 1866
 Family Darwinulidae Jones [*recte* Brady & Norman, 1889]
 Family Barychilinidae Ulrich, 1894
 Superfamily Cytheracea, nov. [*recte* Baird, 1850]
 Family Cytheridae Zenker [*recte* Baird, 1850]

In 1934 a comprehensive catalogue of then-known Paleozoic ostracodes was undertaken by R. S. BASSLER and BETTY KELLETT. This represents a considerable expansion of knowledge that is expressed in recognition of a notably enlarged number of families. Three superfamilies are distinguished but no subordinal category or categories. The arrangement of Paleozoic Ostracoda given in this report is as follows.

Classification of Paleozoic Ostracoda by Bassler & Kellett, 1934

- Superfamily Leperditacea, nov. [*recte* Leperditacea Jones, 1856]
 Family Leperditidae Jones, 1856
 Family Leperditellidae Ulrich & Bassler, 1906
 Superfamily Beyrichiacea Ulrich & Bassler, 1923 [*recte* Matthew, 1886]
 Family Beyrichiidae Jones [*recte* Matthew, 1886]
 Family Primitiidae Ulrich & Bassler, 1923
 Subfamily Primitiinae, nov. [*recte* Ulrich & Bassler, 1923]
 Subfamily Eurychilinae Ulrich & Bassler, 1923
 Family Zygobolbidae Ulrich & Bassler, 1923
 Subfamily Zygobolbinae Ulrich & Bassler, 1923
 Subfamily Kloedeninae Ulrich & Bassler, 1923 [*recte* Kloedeniinae]
 Subfamily Drepanellinae Ulrich & Bassler, 1923
 Family Kloedenellidae Ulrich & Bassler, 1923
 Family Kirkbyidae Ulrich & Bassler, 1906
 Family Glyptopleuridae Girty, 1910
 Family Youngiellidae Kellett, 1933

- Superfamily Cypridacea Ulrich & Bassler, 1923 [*recte* Baird, 1845]
 Family Cypridae Zenker [*recte* Cyprididae Baird, 1845]
 Family Thlipsuridae Jones [*recte* Ulrich, 1894]
 Family Beecherellidae Ulrich, 1894
 Family Bairdiidae Lienenklaus [*recte* Sars, 1888]
 Family Cytherellidae Sars, 1866
 Family Entomidae Jones, 1873 [=Entomozoidae Pribyl, 1951]
 Family Cypridinidae Sars, 1866
 Family Entomoconchidae Jones, Kirkby, & Brady [*recte* Jones, 1868]
 Family Barychilinidae Ulrich, 1894

For many years F. M. SWARTZ, of Pennsylvania State University, has been working intensively on stratigraphy and paleontology of middle Paleozoic formations of the Appalachian region. Independently, and associated with others, he has published several important papers concerned mainly with descriptions of ostracodes collected from Silurian and Devonian strata of this region. One of his papers (SWARTZ, 1936) contains an outline of ostracode classification that is worthy of notice. It is incomplete in that various groups are omitted from consideration.

Classification of Middle Paleozoic Ostracoda by Swartz, 1936

- Superfamily Beyrichiacea [*recte* Beyrichiacea Matthew, 1886]
 Division family Beyrichiidae
 Family Beyrichiidae, Ulrich, 1894 [*recte* Matthew, 1886]
 Family Zygobolbidae Ulrich & Bassler, 1923
 Division family Primitiidae
 Family Primitiidae, Ulrich, 1923
 Family Hollinidae, nov.
 Family Tetradellidae, nov.
 Family Drepanellidae, nov. [*recte* Ulrich & Bassler, 1923]
 Family Acronotellidae, nov.
 Family ?Primitiopsidae, nov.
 Family ?Aechminidae (Leperditacea?), nov.
 Division family Kloedenellidae
 Family Kloedenellidae Ulrich & Bassler, 1923
 Family ?Glyptopleuridae Girty, 1910
 Division family Kirkbyacea
 Family Kirkbyidae Ulrich & Bassler, 1906
 Family Youngiellidae Kellett, 1933
 [Division not indicated]
 Family Leperditellidae Ulrich & Bassler, 1906
 Family Beecherellidae Ulrich, 1894
 Family Bairdiidae Sars, 1888
 Family Cytherellidae Sars, 1866

Until the time of its publication, the most

comprehensive effort to treat the classification of Paleozoic ostracodes was reported in a paper by GUNNAR HENNINGSMOEN (1953) devoted to known straight-hinged forms. In the arrangement of family groups, both superfamilies and suborders were distinguished. A summary of HENNINGSMOEN'S classification is as follows.

Classification of Paleozoic Straight-hinged Ostracoda by Henningsmoen, 1953

Suborder PALEOCOPIA, nov.

Superfamily Beyrichiacea Ulrich & Bassler, 1923
[recte Matthew, 1886]

Family Sigmoopsiidae, nov. [recte Sigmoopsidae]

Subfamily Sigmoopsiinae, nov. [recte Sigmoopsinae]

Subfamily Glossopsiinae, nov. [=Quadrijugatoridae Kesling & Hussey, 1953]

Family Tetradellidae Swartz, 1936

Subfamily Tetradellinae Swartz, 1936 (incl. Dilobellinae)

?Subfamily Piretellinae Öpik, 1937

Subfamily Bassleratiinae Schmidt, 1941 (incl. Ctenentominae)

Family Primitiidae Ulrich & Bassler, 1923

Family Eurychilinidae Ulrich & Bassler, 1923

Subfamily Eurychilinae Ulrich & Bassler, 1923

?Subfamily Euprimitiinae Hessland, 1949
[=Eurychilinidae Ulrich & Bassler, 1923]

?Subfamily Primitiopsiinae Swartz, 1936
[recte Primitiopsinae]

Family Aparchitidae Jones, 1901

Family Drepanellidae Ulrich & Bassler, 1923

Subfamily Drepanellinae Ulrich & Bassler, 1923

?Subfamily Bolliinae Bouček, 1936 (incl. Ulrichiinae Schmidt, 1941)

?Subfamily Aechmininae Bouček, 1936

?Family Acronotellidae Swartz, 1936

Family Beyrichiidae Jones, 1894 [recte Matthew, 1886]

Subfamily Beyrichiinae Jones, 1894 (incl. Kloedeninae Ulrich & Bassler, 1923
[recte Matthew, 1886])

Subfamily Zygobolbinae Ulrich & Bassler, 1923

Family Hollinidae Swartz, 1936

Family Kloedenellidae Ulrich & Bassler, 1908

Subfamily Kloedenellinae Ulrich & Bassler, 1908

Subfamily Beyrichiopsiinae, nov. [recte Beyrichiopsinae]

Subfamily Glyptopleurinae Girty, 1910

Family Kirkbyidae Ulrich & Bassler, 1906
(incl. Amphissitinae Cooper, 1941)

?Family Youngiellidae Kellett, 1933

?Family Miltonellidae Sohn, 1950

?Family Alanellidae Bouček, 1936

Superfamily Leperditacea Bassler & Kellett, 1934

[recte Leperditiaea Jones, 1856]

Family Leperditidae Jones, 1856

Subfamily Leperditinae Jones, 1856

Subfamily Isochilininae Swartz, 1949

?Family Leperditellidae Ulrich & Bassler, 1906

Subfamily Leperditellinae Ulrich & Bassler, 1906

?Subfamily Conchoprimitiinae, nov.

?Subfamily Eridoconchinae, nov.

Suborder PODOCOPA Sars, 1866

Family Quasillitidae Coryell & Malkin, 1936
(incl. Graphiodactylidae Kellett, 1936)

Subfamily Quasillitinae Coryell & Malkin, 1936

Subfamily Ropolonellinae Coryell & Malkin, 1936

The first all-inclusive effort to classify Recent and fossil ostracodes is contained in a textbook on micropaleontology prepared by VLADIMIR POKORNÝ (1958). This is especially noteworthy because of recognition given to the importance of muscle-scar patterns, hinge structures, characters of the duplicature, and dimorphic features as guides in classification. Notice of POKORNÝ'S separation of the Leperditia from Palaeocopida, inclusion of platycopines and podocopines in the Podocopida, and assignment of cladocopines with myodocopines in the Myodocopida is important. The arrangement of suprageneric taxa adopted by POKORNÝ differs in various ways from that accepted in the *Treatise* but approaches it in many ways. An outline of POKORNÝ'S classification follows.

Classification of Recent and Fossil Ostracoda by Pokorný, 1958

Subclass OSTRACODA Latreille, 1806

Order LEPERDITIIDA Pokorný, 1953

Family Leperditidae Jones, 1856

Subfamily Leperditinae Jones, 1856

Subfamily Isochilininae Swartz, 1949

Order BEYRICHIDA Pokorný, 1953

Family Beyrichiidae Matthew, 1886

Subfamily Beyrichiinae Matthew, 1886

Subfamily Zygobolbinae Ulrich & Bassler, 1923

Subfamily Treposellinae Henningsmoen, 1954

Family Tetradellidae Swartz, 1936

Subfamily Tetradellinae Swartz, 1936

Subfamily Sigmoopsidinae Henningsmoen, 1953 [recte Sigmoopsinae]

Subfamily Quadrijugatorinae Kesling & Hussey, 1953

- Subfamily Piretellinae Öpik, 1937
- Subfamily Bassleratiinae Schmidt, 1941
- Family Eurychilinidae Ulrich & Bassler, 1923
 - Subfamily Eurychiliniinae Ulrich & Bassler, 1923
 - Subfamily Euprimitiinae Hessland, 1949 [=*Lepeditellidae* Ulrich & Bassler, 1906]
- Family Pribylitidae, nov.
- Family Aparchitidae Jones, 1901
- Family Acronotellidae Swartz, 1936
- Family Primitiopsidae Swartz, 1936 [*recte* Primitiopsidae]
- Family Drepanellidae Ulrich & Bassler, 1923
 - Subfamily Drepanellinae Ulrich & Bassler, 1923
 - Subfamily Aechmininae Bouček, 1936
- Family Hollinidae Swartz, 1936
- Family Neodrepanellidae Zaspelova, 1952 [=Drepanellidae]
- Family Kirkbyidae Ulrich & Bassler, 1906
- Family Punciidae Hornibrook, 1949
- Familiae incertae ordinis
- Family Alanellidae Bouček, 1936 [=Beecherellidae]
- Family Lepeditellidae Ulrich & Bassler, 1906
 - Subfamily Lepeditellinae Ulrich & Bassler, 1906
 - Subfamily Eridoconchinae Henningsmoen, 1953
- Family Conchoprimitiidae Henningsmoen, 1953
- Family Kloedenellidae Ulrich & Bassler, 1908
- Order *PODOCOPIDA* Pokorný, 1953 [*recte* Sars, 1866]
- Suborder *PLATYCOPA* Sars, 1866
 - Family Cytherellidae Sars, 1866
 - Subfamily Cytherellinae Sars, 1866
 - Subfamily Cavellininae Egorov, 1960
 - Family Healdiidae Harlton, 1933
 - Family Thlipsuridae Ulrich, 1894
 - Family Barychilinidae Ulrich, 1894
 - Family Beecherellidae Ulrich, 1894
- Suborder *PODOCOPA* Sars, 1866
 - Family Macrocyprididae G. W. Müller, 1912
 - Family Bairdiidae Sars, 1888
 - Family Cyprididae Baird, 1845
 - Subfamily Pontocypridinae G. W. Müller, 1894
 - Subfamily Ilyocypridinae Kaufmann, 1900
 - Subfamily Paracypridinae Sars, 1923
 - Subfamily Candoninae Kaufmann, 1900
 - Subfamily Cyclocypridinae Kaufmann, 1900
 - Subfamily Cypridinae Baird, 1845
 - Tribe Cypridini Baird, 1845
 - Tribe Erpetocypridini Kaufmann, 1900
 - Tribe Notodromadini Kaufmann, 1900
 - Tribe Cyprinotini Bronstein, 1947
 - Tribe Cypridopsini Kaufmann, 1900
 - Subfamily Cyprideinae Martin, 1940

- Family Cytheridae Baird, 1950
 - Subfamily Limnocytherinae Sars, 1925
 - Subfamily Cytherideinae Sars, 1925
 - Subfamily Cytherinae Baird, 1850
 - Subfamily Eucytherinae Puri, 1953
 - Subfamily Cytherettinae Triebel, 1952
 - Subfamily Cytherurinae G. W. Müller, 1894
 - Subfamily Loxoconchinae Sars, 1926
 - Subfamily Bythocytherinae Sars, 1926
 - Subfamily Xestoleberidinae Sars, 1928
 - Subfamily Microcytherinae Klie, 1938
 - Subfamily Psammocytherinae Klie, 1938
 - Subfamily Paradoxostomatinae Brady & Norman, 1889
- Family Darwinulidae Brady & Norman, 1889
- Order *MYODOCOPA* Pokorný, 1953 [*recte* Sars, 1866]
- Suborder *MYODOCOPA* Sars, 1866
 - Family Cypridinidae Baird, 1850
 - Subfamily Cypridininae Baird, 1850
 - Subfamily Philomedinae G. W. Müller, 1912
 - Family Entomoconchidae Brady, 1868
 - Family Halocyprididae Dana, 1853
 - Subfamily Halocypridinae Dana, 1853
 - Subfamily Thaumatoocypridinae G. W. Müller, 1906
 - Family Entomozoidae Přibyl, 1951
 - Subfamily Entomozoinae Přibyl, 1951
 - Subfamily Bouciinae Přibyl, 1951
 - Family Bolbozoidae Bouček, 1936
- Suborder *CLADOCOPA* Sars, 1866
 - Family Polycopidae Sars, 1866

CLASSIFICATION ADOPTED IN TREATISE

GENERAL DISCUSSION

Up to the present a satisfactory basis for classification of all Ostracoda has not been found. No single morphological feature can be used to define orders, superfamilies, and families. Criteria used for separating the families of one superfamily may be entirely different from those used in another superfamily. Similarly, distinction of genera within a family is often schematic and inconsistent. On the other hand, some genera and families possess such striking shell characters that they are readily recognizable and traceable throughout long expanses of time. For example, the shape of the carapace of *Bairdia* is a very diagnostic feature that has persisted at least from late Paleozoic to Recent.

The most primitive orders—Archaeocopida, Lepediticopida, and Palaeocopida—

have no living representatives (possibly except in Punciidae) and therefore must be distinguished by differences in the shell. The thin carapace of the archaeocopids distinguishes them from the leperditicopids. The thick shells and large compound muscle scars serve to separate the leperditicopids from all other orders. The palaeocopids are differentiated from the two more primitive orders first by their small, fairly simple muscle scars, and secondly by the presence of one or more such features as lobation, sulcation, strong ornamentation, and dimorphic structures. None of the three primitive orders possess a duplicature.

The Podocopida are represented by many living species. This order was first defined by zoologists on the basis of the soft parts. Only in recent years have the shell features been carefully described, most of this work being done by paleontologists. In the podocopids the type of hingement, muscle-scar pattern, and outline of the carapace are used for classification. The Cypridacea are ovate to elongate-ovate in outline, with a convex dorsum, and an incurvature along the medial portion of the venter. They are readily separated from the Cytheracea by lack of a highly ornamented surface. Also, the Cytheracea, with few exceptions, have strongly developed hinge elements and distinct muscle scars.

Various criteria are used to divide ostracodes into superfamilies. In the palaeocopids, dimorphic structures are of primary importance. Secondarily, the presence or absence of sulci and lobes, the general outline of the valves, in conjunction with major ornamentation and the presence or absence of a velum, may be used. Of these, the kind of dimorphic structure present is the most important and is used for all dimorphic forms. The well-developed S_2 or pit, the strongly asymmetrical valves and kloedenellid dimorphism distinguish the Kloedenellacea; a smooth carapace, channeled hinge, and asymmetrical valves are characteristics of the Paraparchitacea; anteroventral or ventral cruminal dimorphism separates the Beyrichiacea from the nondimorphic Drepanellacea; a dimorphic velate structure sets representatives of the Hollinacea apart from the nondimorphic Drepanellacea; the carapace outline of Youngiellacea separates the group from all others; and the reticulate

pattern, combined with presence of a median pit, distinguishes the Kirkbyacea.

Superfamilies among the mydocopids are determined for the most part by the presence and nature of the rostrum.

Among the podocopids, superfamilies are based mostly on differences in hingement, muscle-scar patterns, and to some extent on outline. The undifferentiated hinge and convex back of the cytherellids readily separate them from the cytherids, which have a complex hinge and convex or straight back. The large number of closely spaced muscle scars and the elongate form of the Darwinulacea are unique to this group. The simple hinge and carapace shape of the Bairdiacea combine to make these features of major importance in classification. Characterization of the Cypridacea is difficult, but this group may be separated from others by ovate outline, convex back, incurved mid-venter, simple hingement, lack of major sulci or lobes, and generally unadorned surface.

Family differentiation is based on various major features depending on the order within which the family falls. In the Leperditicopida, the two families are distinguished by the symmetry of the carapaces; the leperditiids have asymmetrical valves, the larger overlapping the smaller around the free margin, whereas the isochilinids have subequal valves.

Families within the palaeocopids are distinguished by differences in such morphological features as variation in dimorphic structures, differences in ornamentation (e.g., reticulate or costate surfaces), degree of sulcation and lobation, and variation in outline.

In the Kloedenellacea, Glyptopleuridae are costate, whereas the Sansabellidae are noncostate. The strongly obtuse anterior cardinal angle of the Kloedenellidae separates this family from other members of the superfamily. In some families adventral dimorphic structures are used for distinction. The velate structures of Hollinidae differentiate them from histial dimorphic features of the Sigmooopsidae. Other families may be separated on differences in outline of the carapace or hingement.

Among the podocopids, families commonly are defined to a considerable extent by variations in hingement and muscle-scar

patterns. Major differences in outline and ornamentation may be helpful but are likely to be confusing. Hingement and muscle scars are by far the most important, and lack of knowledge of these factors often makes classification insecure.

Ostracode genera are interpreted rather narrowly. This practice has resulted in the creation of many monospecific genera and has given rise to a few monogeneric families. Such features as reversal of valve overlap around the free margin is still evaluated differently by various workers; some consider it to lack even specific value, whereas others assign it generic value. *Sansabella* may be found in Late Mississippian sediments, in a single sample, with specimens identical in all respects except for reversal of overlap. This is equally true for *Paraparchites*.

Distinction of genera is based, for the most part, on major shell features, but not commonly on ornamentation. Hinge characters, muscle-scar patterns, outline, lobation and sulcation, and adventral structures are most important. Though outline of the carapace in different genera is often found to be similar, other characters may be quite unlike. The outline is usually constant within a genus but may vary slightly, especially as modified by dimorphism or as represented by instar stages. Hinge characters are specially significant in delineating post-Paleozoic genera. The carapaces of many genera of the Cytheracea have similar outlines and are separated from one another primarily on the basis of hinge characters. Such forms as *Archicythereis*, *Cythereis*, and *Oligocythereis* look somewhat alike externally but hinge structures differ greatly. In post-Paleozoic ostracodes the valves often are found separated from each other, and therefore hinge details may be observed. This is seldom true in palaeocopids and thus hingement is not an important aid to classification in this group; more information is constantly being gathered and in time it is hoped that the hingement of all families will be known.

Muscle-scar patterns are very important for classification of ostracodes at the generic level. They have primary value among the platycopines, metacopines, and podocopines. Adductor and mandibular scars are diagnostic of many genera of these sub-

orders. They are not well enough known among the palaeocopids to have significance in generic classification.

Lobation and sulcation aid generic classification but must be used with caution. Similar sulcation may be found in wholly unrelated genera and dissimilar sulcation may occur in very closely related forms. Sulci and lobes are more important in the Hollinacea, Beyrichiacea, and Kloedenellacea than in any other groups. The number of sulci and lobes usually remains constant in each genus but it may vary within a family.

Specific differentiation between ostracodes is based on differences in ornamentation, modification of outline, and the size and shape of various structural features such as alae, sulci, pore canals, and lobes. However, all of these characters may vary from instar to instar and between the sexes; therefore, caution must be used in evaluating the significance of any observed variation. KESLING (1954) has discussed in detail factors affecting speciation.

Observation of instars indicates that ornamentation becomes more complex with advancing age of the ostracode. Increase in complexity has been observed in many genera; *Glyptopleura*, *Amphissites*, *Beyrichia*, *Cythereis*, *Amphizona*, *Eridocconcha*, *Loxocconcha*, and others show this tendency. The number of costae, size of reticulations, number or size of spines, and numerous other ornamental features may vary in an ontogenetic series. That the younger instars are simpler is known to be true, but as usual, some exceptions have been observed and others may be discovered. In at least one species of *Healdia*, a pair of posterior spines is considerably reduced in the adult, whereas they are long and prominent features of the instars.

The question of degree of individual variation among ostracodes has not been fully explored. It has been reported in a few cases, but it is sometimes difficult or impossible to determine whether the observed variation is natural or due to the nature of preservation. In some species the thin outer layer may be reticulate and the next layer smooth or differently ornamented. In the Kirkbyidae it is not uncommon to find shells in which one portion of the valve differs from another in ornamentation, yet

examination of many specimens may show that the observed variation is a matter of preservation rather than natural variation. Differences between individuals are usually observed in reticulate, granulose, papillose, or punctate species.

Dependence on molds and casts of the carapace interior for creation of new species has led to many unnecessary complications. Of course, exterior features of ornamentation cannot possibly be preserved in such fossils. Features of hingement also are lost; sulci and nodes may be more subdued, and external adventral features of dimorphism and overlap may be completely missing. Steinkerns may yield important supplemental information, but they are seldom by themselves an adequate basis for erection of new species.

Sexual dimorphism has been recognized in many ostracodes, both fossil and living. In some, the valves strikingly reflect dimorphism, for the inferred females may be posteriorly inflated (*Kloedenella*), or have velate frills (*Hollinella*), or develop large adventral pouches (*Beyrichia*), or postero-dorsal inflation (*Cypris*), whereas the inferred males may possess none of these features and appear relatively simple and unornamented. Lack of recognition of dimorphism is a factor that always must be considered in ostracode studies. It can best be understood by studying populations from a single zone, and best of all by examination of a population from a single bedding plane.

ORDER ARCHAEOCOPIDA

The order Archaeocopida has been erected to include a group of Cambrian and ?Early Ordovician ostracodes. The zoological affinities of the group are not certain, but they appear to be most closely related to the Ostracoda, having many features in common with the palaeocopids.

The carapace of the archaeocopids is only slightly calcified. Its high chitin content makes it more or less flexible and therefore commonly strongly wrinkled. The hinge is long and straight. An eye tubercle is usually prominent in all families except the Indianidae. The four currently recognized families are separated on the basis of outline of carapace, presence or absence of puncta, folds, and eye tubercles.

Though archaeocopids have been reported from Early Ordovician strata, they are essentially Cambrian organisms. They have been described from North America and Europe and were probably widely distributed in Cambrian seas. Relations of the Archaeocopida to other ostracodes are indicated diagrammatically in Figure 32.

ORDER LEPERDITICOPIDA

The Leperditicopida were a very successful Ordovician-Devonian group. Many specimens have been found with well-preserved internal markings on the carapace. They are characteristically straight-backed and possess a compound muscle scar composed of many small units. The shell is usually thick and has one or more secondary layers both dorsally and ventrally. The large muscle-scar pattern and secondary shell layers are not observed in any other ostracodes. These features are so striking that their true relationship to other groups is unknown. The leperditiids appear in the Ordovician as highly differentiated ostracodes, and in so far as known, no other group developed from them. The order has a wide geographic range, being common in Europe and North America. Its stratigraphic range is limited to the Ordovician-Devonian part of the column, most representatives occurring in Ordovician and Silurian deposits. Inferred relations to other ostracode orders are illustrated diagrammatically in Figure 32.

ORDER PALAEOCOPIDA

The Palaeocopida are a group of Paleozoic ostracodes (other than Punciidae) possessing characters that clearly distinguish them from more recent genera. Chief among these are the nature of muscle scars, dimorphic structures, marginal extensions, and the dorsal surface.

A review of the diagnoses of palaeocopid families shows that they have not been differentiated on any single carapace feature. Some families are set apart from others on one or more of the following criteria: shape or outline of the carapace, costation, reticulation, sulcation, smoothness, and various types of dimorphism. Of these features dimorphism is by far the most important. Genera within families are separated for the most part on degree of lobation, sulca-

tion, adventral structural developments, and major ornamental features. Hinge characters, when known, may be used to define genera and possibly families. Muscle-scar patterns are of value, but are seldom preserved in the palaeocopids. Some members of this assemblage show no evidence of

dimorphism and may have reproduced parthenogenetically.

The inferred relations of palaeocopids to other ostracode orders are indicated in Figure 32 and those of superfamilies are shown in Figure 33; both diagrams indicate known stratigraphic distribution of these taxa.

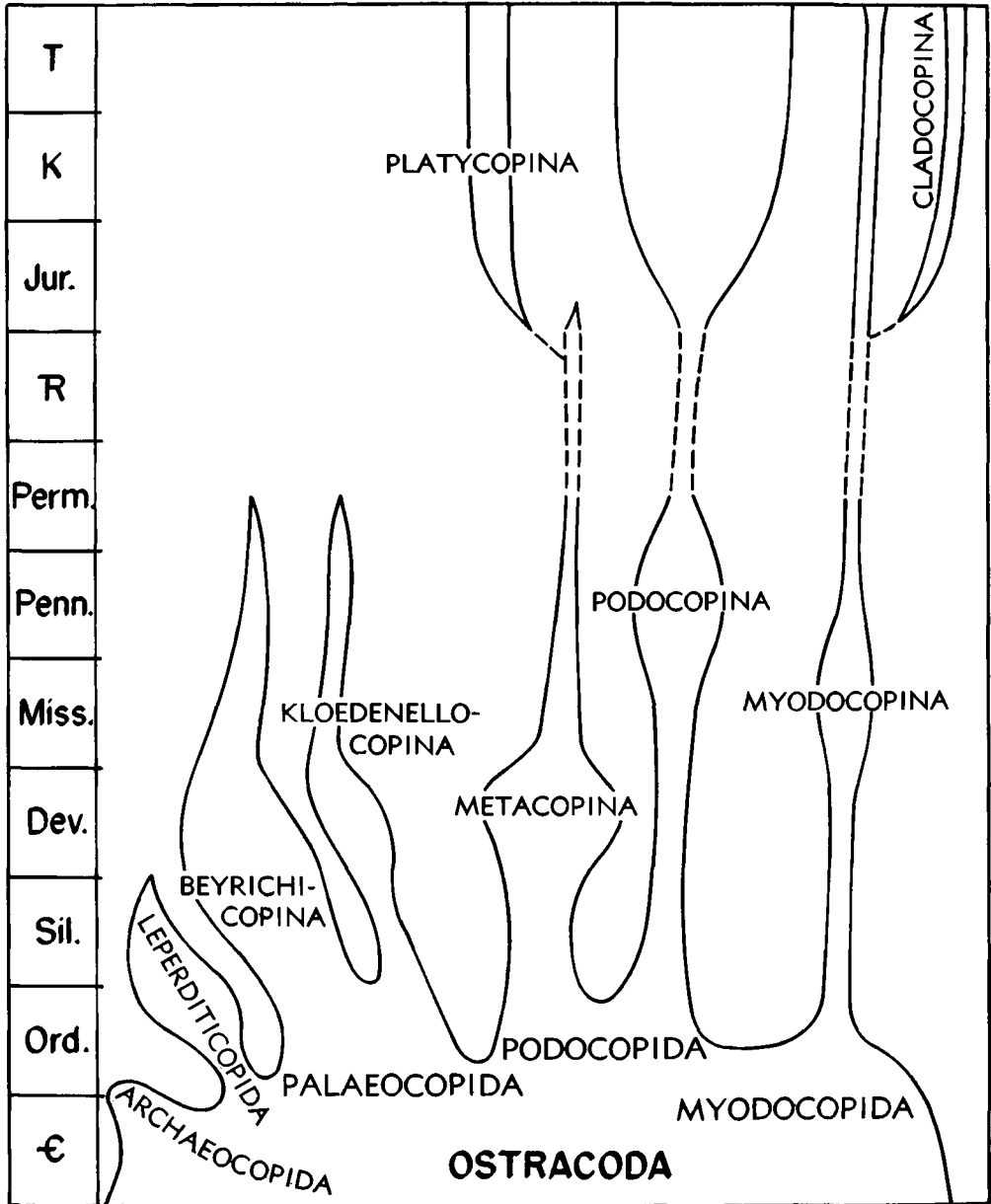


FIG. 32. Diagram representing stratigraphic distribution and inferred relationships of ostracode orders and suborders (Scott & Sylvester-Bradley, n).

a ventral margin that is straight to gently concave or convex. The development of the concave ventral edge in many adult podocopids appears to represent an advanced trait, the growth of which is recognizable in ontogeny of the individual.

Another aspect of shape is the "forward swing" of most Beyrichiina. The ventral margin is convex, with the greatest degree of truncation posterior. This produces a carapace in which the anterior half is higher than the posterior half, resulting in a "forward ventral swing" which is in contrast to the "posterior swing" of the Leperditidae.

The straight back and convex venter with forward swing are present in the Early Ordovician ostracodes, contemporaneous with the convex back and concave venter of the podocopids and the backward swing of the leperditids.

The Beyrichiacea are among the most abundant and striking of early Paleozoic palaeocopids. The anteroventral to ventral dimorphic pouch, which is an enlargement of the carapace wall, is the distinguishing feature. This swelling is not formed by a frill of the eurychilid type but is a development of the carapace wall. It is recognized only in the Beyrichiidae and Zygobolbidae. For this reason these two families are separated from the nondimorphic Drepanellacea. The family Beyrichiidae ranges from the nonsulcate *Apatobolbina* with its dimorphic lobe, through the bilobed *Bolbiprimitia*, to the strongly lobate and sulcate *Beyrichia*. Most of the Beyrichiacea are reticulate but a few are unornamented. Hingement, so far as known, is by means of primitive bar and groove. The superfamily ranges from Ordovician to Devonian but had its most striking development in the Silurian.

The Drepanellacea are separated from Hollinacea because they are nondimorphic, and as such, lack the marginal structures so characteristic of the latter group. The margin of most Drepanellacea is raised as a thick rim. This structure is represented by a relatively narrow, flat, marginal, smooth rim, sometimes referred to as a velum but more appropriately called a pseudovelum. It extends only slightly below the ventral surface and shows no evidence of being associated with dimorphism. No marginal rim or velate structure is present in the

Aechminidae or Richinidae. Rare reports of such occurrences need checking. Most Drepanellacea are ornamented with reticula or nodes, or both. The group seems to be related to the dimorphic Hollinacea. The most peculiar family is the Aechminidae, in which the large dorsal spine makes them appear wholly unrelated to other Drepanellacea. However, if the two nodes of *Ulrichia* were reduced to one, a form not greatly unlike *Aechmina* would be produced. Perhaps *Aechminaria*, with one large and one small node next to an intervening sulcus, is an intermediate stage between *Ulrichia* and *Aechmina*.

The Hollinacea are a major group of palaeocopids represented from Ordovician to Permian (Fig. 33). They are all ornamented in some fashion. Lobation, sulcation, and nodes are common structural features. The valves are subequal in size. Dimorphism in the form of a velate structure is present, the velum being modified in various ways as a dimorphic organ; in some, loculi are developed along the velum, either outside (e.g., *Tetradella*) or inside (e.g., *Ctenolocolina*). Dimorphic structures commonly result in carapaces that are strikingly dissimilar in the two sexes. Loculate and nonloculate discrete lobes or merged lobes may be merely marks of dimorphism.

The Kirkbyacea contain a group of very distinctive reticulate palaeocopids which are among the most highly ornamented of Paleozoic genera. Reticula occur in all and costae and nodes are common to many. The kirkbyan pit, which characterizes the entire assemblage, is represented by a break in the reticulate pattern, that probably defines the position of the adductor muscle scar. Hingement of the Kirkbyacea resembles that found in the Kloedenellacea, suggesting a possible relationship of these superfamilies, both of which may be related to the earlier Leperditellacea. The Kirkbyacea are abundant from Devonian to Permian, probably attaining a climax in Late Mississippian. Reported Silurian occurrences have not been confirmed.

The Oepikellacea are a small group of early Paleozoic ostracodes. Some doubt exists as to their true nature, because the type of *Aparchites* has not been restudied and its true characters are not fully known. Present information indicates that the

Aparchitidae and Pribylitidae are nondimorphic. However, the Oepikellidae have a well-developed velar dolon and perhaps should be placed with the Hollinacea. The tecnomorphic valves look very much like *Aparchites*, and the family is provisionally included in the Oepikellacea. The velum is a prominent feature in the heteromorphs of Oepikellidae, but in the Aparchitidae and Pribylitidae the velum is absent or weakly developed as a row of spines or a faint ridge parallel to the free edge. Solutions to problems of classification must await further study of *Aparchites* and related genera.

The Primitiopsacea represent a small assemblage of Middle Ordovician to Middle Devonian ostracodes. In the posterior part of the carapace they developed velar dimorphism characterized by open or closed dolonal flanges; if closed, an extradomiciliar chamber is produced. Two genera are known, one from Sweden and one from North America.

The Youngiellacea include a group of small subrectangular nondimorphic ostracodes with a prionodont hingement. The surface varies from smooth to reticulate or costate. The superfamily is not known to be closely related to any other palaeocopid. Minute size of the carapace, prionodont hingement, and elongate shape separate it from all other groups. *Moorites* has a general resemblance to *Cytherelloidea* in outline and ornamentation but hingement differs. It may be that affinities of the group are closer to the Platycopina than the Palaeocopida but the Youngiellacea are tentatively assigned to the latter. They are known only from Mississippian and Pennsylvanian formations.

SUBORDER KLOEDENELLOCOPINA

POKORNÝ (1958) recognized that the kloedenellids differ greatly from the beyrichiids and recorded them as *incertae ordinis*. He included in this listing *Paraparchites* and related genera. Also considered to be uncertain in ordinal assignment were the Leperditellidae and Conchoprimitiidae. Undoubtedly these groups differ greatly from other ostracodes and where to classify them has been a vexing problem, because all do not seem to have features in common that would allow placing them in a single group.

The Kloedenellacea are a large group of palaeocopids containing several important families and many genera. They are subrhomboidal to subrectangular in outline and have asymmetrical valves. One valve strongly overlaps around all or a portion of the free margin of the smaller valve. Most genera have a sharply defined S_2 , though in a few species the sulcus may be weak or represented by a pit. In the genus *Dizygopleura* three sulci are present. The surface of the valves ranges from smooth to highly ornamented. Ornamentation is primarily of two types—reticulate, as in *Geisina*, and costate, as in *Glyptopleura*. Rarely are spines present. Hingement is fairly well known and consists of hinge tongue-and-groove in all genera and in some forms a connecting link between cardinal teeth and sockets. Dimorphism is represented by a swelling of the posterior portion of the carapace and is referred to as kloedenellid in type. The dimorphic swelling is not always readily recognized.

The Kloedenellacea are represented in the Silurian by several genera, among them *Kloedenella* and *Dizygopleura*. The origin of the group is not certainly known but possibly the lobation and sulcation of *Dizygopleura* are closely related to those of the zygobolbids. This may be more apparent than real, because the types of dimorphism are strikingly different. By Mississippian time the superfamily had developed several important branches—costate glyptopleurids, smooth sansabellids, reticulate miltonellids, and others.

The Kloedenellacea and Paraparchitacea have some features in common and are placed here in the new suborder Kloedenellocopina (Fig. 33). The straight back and unequal valves are common to all. The larger valve overreaches and overlaps all or a portion of the free margin of the smaller valve. The hinge is straight, producing for the most part well-defined cardinal corners (e.g., *Sansabella*), but some carapaces are rounded at one or both ends (e.g., *Paraparchites*). The ventral margin is usually convex but exceptions are found in *Kloedenella*, where the ventral edge may vary from distinctly concave to straight or gently convex.

Many kloedenellocopine forms are sulcate, ranging from unisulcate to trisulcate; some

are smooth and nonsulcate. None are typically lobate or nodose, as is so characteristic of the Beyrichicopina. S_2 is usually represented as a prominent sulcus or by a pit. In *Sansabella* a faint sulcus or pit may be present, but in some species no evidence of either may be seen. In *Glyptopleura*, S_2 is often partially obliterated by longitudinal costae.

Dimorphism is recognizable in the Kloedenellacea by swelling of the posterior portion of the female carapace. Velate, histial, or lobate dimorphism such as occurs in the Beyrichicopina is lacking. Dimorphism in the Paraparchitacea has not been conclusively shown or disproved. Adult specimens show that the greatest width commonly is medial, but in some the greatest width is behind the mid-length. These may be dimorphs. If so, the type of dimorphism is close to that found in the Kloedenellacea.

The Leperditellacea constitute one of the most difficult of all ostracode groups to classify. It includes in part the old Primitiidae, which constituted a classificatory wastebasket into which many diverse forms were previously dumped. Recent examination of the type of *Leperditella* by LEVINSON shows that it is closely related to *Primitia*, the only difference being a poorly defined S_2 in *Leperditella*. This discovery has clarified many problems in the classification of the primitiids and leperditellids. The superfamily contains what often has been thought of as the true primitiids. They are nonvelate, straight-hinged, unisulcate ostracodes. The sulcus S_2 may be sharply or broadly outlined. The valves are unequal and dimorphism has been reported in only one genus. Little is known about the hinge, but it is believed to be simple (adont) without cardinal teeth or sockets. The surface is smooth, punctate, or reticulate. Spines are present in *Parahealdia*. The group appears early in the Ordovician and becomes important in Middle and Late Ordovician. Its numbers are reduced in the Silurian and Devonian, and only one genus, *Coryellina* (Penn.-Perm.), is recognized in the late Paleozoic. Inclusion of the Leperditellacea in the Kloedenellocopina is not wholly satisfactory. This superfamily, in common with the kloedenellids, has a straight hinge, unequal valves with overlap around the free margin, and a definite S_2 . It differs in lack-

ing kloedenellid dimorphism and in having a more convex ventral outline. The hinges may differ, but more study is needed on this subject.

Members of the Paraparchitacea are here considered to be related to the Kloedenellidae but distinct from them because of being nonsulcate, possessing a shorter hinge, and being unornamented, except for a few species that bear one or two spines (Fig. 33). The valves are asymmetrical, the larger strongly overlapping the smaller around the free margin, as in other Kloedenellacea. However, dimorphism has not been recognized. The generally smooth, nonsulcate surface, nonvelate margin, channeled hinge, and strong overlap distinguish the group. They developed in the Middle Devonian, possibly as a parthenogenetic offshoot from the dimorphic Kloedenellidae. They attained their greatest abundance in the Mississippian.

ORDER PODOCOPIDA

SARS (1866) erected the Podocopa on the basis of locomotor appendages to include families named Cypridae [recte Cyprididae] and Cytheridae. Later, SARS (1888) added the Bairdiidae and BRADY & NORMAN (1889) added the Darwinulidae and Paradoxostomatidae. SARS had observed that an antenna (second antenna of European usage) was modified as a walking structure, rather than a swimming organ. Therefore, all living podocopids are anatomically related in possessing antennae modified for use as ambulatory organs. Because these appendages are not adapted for fossilization, paleontologists must rely on preserved hard parts for classification. Fortunately, the Podocopida possess carapace features that distinguish them from other orders. All have calcified shells with well- to poorly-developed inner calcareous lamellae. Furthermore, they have a muscle-scar pattern consisting for the most part of a few secondary scars that usually are well preserved in fossil specimens. Inferred relationships of the podocopids to other ostracode orders are shown diagrammatically in Figure 32; subdivisions of the Podocopida and their stratigraphic occurrence are illustrated in Figure 34.

SUBORDER PODOCOPINA

The Podocopina are represented in early

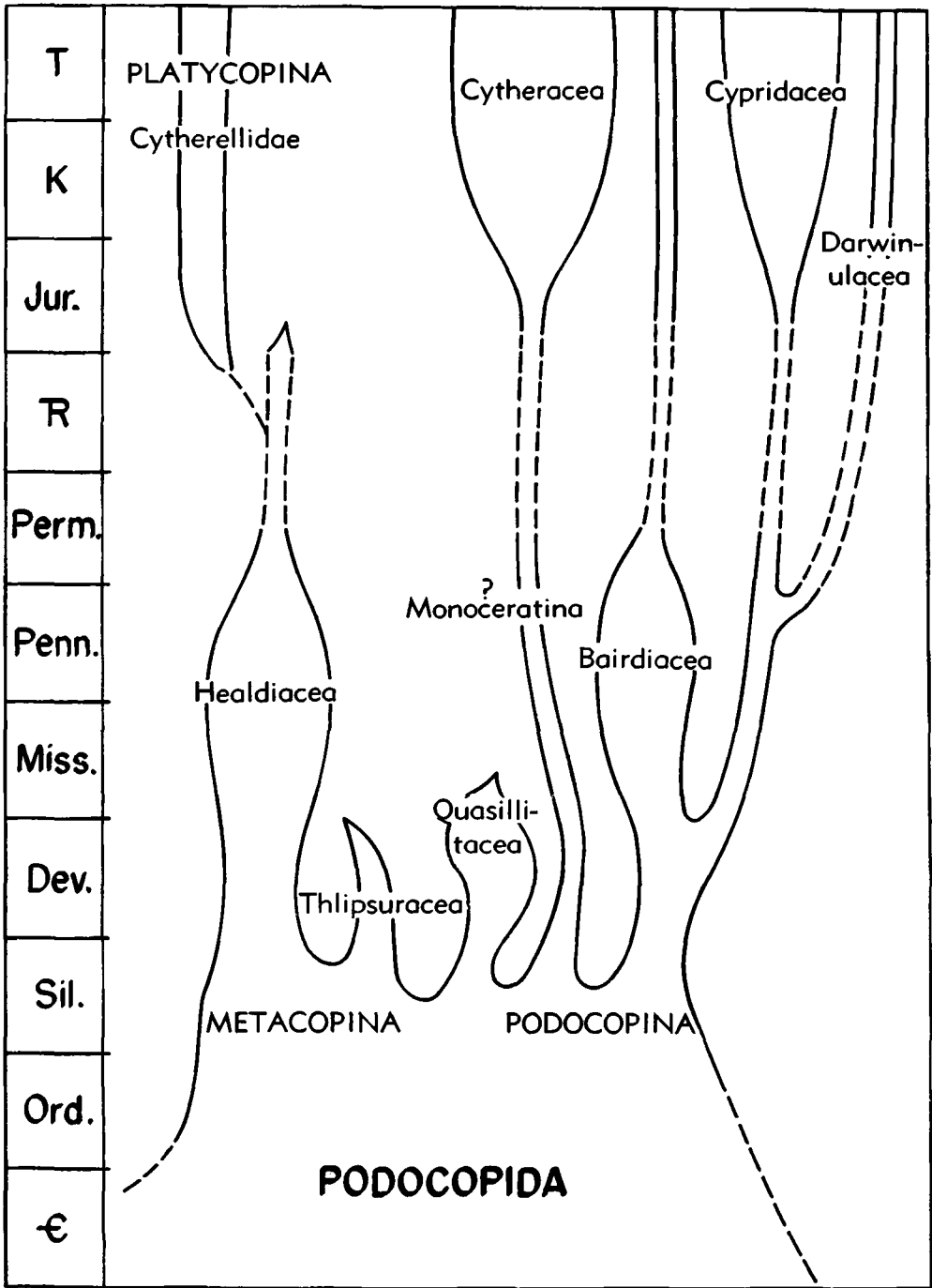


FIG. 34. Diagram representing stratigraphic distribution and inferred relationships of podocopid suborders and superfamilies (Scott & Sylvester-Bradley, n).

Paleozoic deposits by the Bairdiacea. The ancestral stock of the Bairdiacea is unknown, but the occurrence of a well-developed duplicature in forms as old as Silurian is interesting. Possibly sections of pre-Silurian fossils may show an earlier development of this important structural feature. The superfamily ranges from Ordovician to Recent. Throughout this time very little change in morphology of the group is observed. Shape, hingement, muscle-scar pattern, and wide duplicature remained more or less constant, but the number of muscle scars decreased slightly.

The Cypridacea probably developed from the bairdiid stock in early Paleozoic time. They became a very successful group and have invaded a great variety of habitats, including marine, brackish-, and fresh-water. They are a very difficult group for the paleontologist to classify because of their general lack of distinguishing external characteristics. Outline, minor features of the hinge and free margin, and muscle scars are the most usable criteria. The inner lamella is typically developed in cypridids from late Paleozoic to Recent. Whether or not this structure is present in forms described from the early and middle Paleozoic remains questionable; only further work can clarify this important point.

The Darwinulacea are a small, monotypical group without known close relatives. Their elongate-ovate shell with radially arranged muscle scars is typical of the assemblage. They are fresh-water ostracodes that may have been derived from some late Paleozoic cypridid stock.

The Cytheracea are one of the largest groups of ostracodes. Though most genera are represented by living species, classification of the superfamily has not been wholly satisfactory. The most important features of the carapace for purposes of classification are the hinge and muscle scars. Secondly, outline and such features as ornamentation and alae are of some aid. The mid-ventral incurvature of the valve margin is one of the most characteristic features of the Podocopina. A similar incurvature occurs in the thlipsurids, quasillitids, and a few of the kloedenellids, however. The Cytheracea show great range in form and ornamentation. Classification of the group is based largely on differences in dentition, supple-

mented by muscle scars. These criteria admittedly are rather weak and no uniformity of opinion exists in evaluating them when applied at family and subfamily levels.

The origin of the Cytheracea is not clear. Seemingly, the group was derived in late Paleozoic time from *Monoceratina*-like forms or from quasillitids. The shape, incurved ventral margin, primitive inner lamella, and tripartite hinge of the quasillitids suggest possible relationship with the Cytheracea. The shape and stratigraphic occurrence of *Monoceratina*, however, suggest that this genus may be a connecting link between the Palaeocopida, on one hand, and cytherids, on the other (Fig. 34). The true relationship is unknown at present.

SUBORDER METACOPINA

One of the most important problems in classification of the ostracodes has concerned disposition of the cavellinids, healdiids, quasillitids, and thlipsurids. The morphology of these groups shows certain characters that are transitional between those typical of the Platycopina and Podocopina.

The Healdiidae differ from other Healdiacea in two important respects: (1) the hinge contact is posterodorsal when the long axis of the carapace is oriented horizontally, and (2) the smooth lateral surface is interrupted posteriorly by a marginal rim, or one or two spines, or both rim and spines. Dimorphism has been recognized by differences in outline of the dimorphs and greater posterior thickness of the inferred females, but criteria for separating the dimorphs needs further study. The stock is primarily of late Paleozoic age, one genus (*Hungarella*) has been reported from the Lower Jurassic.

The Quasillitidae possess many characteristics reminiscent of the Beyrichicopina and Podocopina. The muscle scar of *Euglyphella*, *Quasillites*, *Bufina*, and others of the group is represented by a circular boss. On some specimens numerous small secondary scars within the circular spot have been recognized. Though some spots commonly are bald, the absence of secondary scars is probably due to lack of preservation. The complex scars are comparable in general form to the scars found in healdiids; the simple round scars are not unlike those of the palaeocopids, but in no specimen are

they cytherid. The terminal ribs and spines of *Quasillites*, *Bufina*, and *Parabufina* are very similar to those of the healdiids and the outline of the carapace in the latter two genera is comparable to the form of *Healdia*. In features of outline, ornamentation, and muscle scars the quasillitids may be compared with the healdiids.

Hingement is not known for all of the quasillitids. Described hinges vary from those represented by arcuate sockets at ends of the hinge in one valve (with corresponding teeth in the opposite valve) to those in which the anterior socket is divided into numerous minute depressions that received crenulations of the corresponding tooth; the sockets and teeth are connected by a tongue and groove. This type of hingement is not known to occur in the healdiids but is similar, though not identical, to some found in the Cytheracea. In outline and form *Euglyphella* is rather similar to some of the Trachyleberididae but hingement and muscle-scar patterns differ.

The evidence points strongly toward a close relationship between the Healdiidae and Quasillitidae, and they are here included in a new suborder named Metacopina. The relationship of the healdiids and quasillitids indicates that the two groups are near the main stem from which the Podocopina developed. The presence of a calcified primitive inner lamella in some forms and complex hinge in most is considered important enough to warrant placing the group in the Podocopida, but difference of the muscle-scar pattern from that seen in the Podocopina serves to distinguish the Metacopina.

Calcareous inner lamellae are absent or poorly developed in the Thlipsuridae. The outline of the carapace in this family is ovate, the valves are unequal (LV overlapping RV on free margin), and the ends are rounded. The thlipsurids seem to be closely related to the healdiids in outline, and the left valve overreaches the right. There is a very close relationship between the Healdiidae and Cavellinidae in muscle-scar patterns. It seems rather clear that the Thlipsuridae, Healdiidae, and Quasillitidae are closely related and they are here included in the Metacopina.

The Krausellidae and Pachydomellidae are small, poorly known Paleozoic families.

Shell characteristics indicate that they belong to the Metacopina.

SUBORDER PLATYCOPINA

SARS (1866) established the Platycopa to include the family Cytherellidae. Members of this family, as now defined, are restricted to Mesozoic-Cenozoic sediments. Many have been described from the Paleozoic, but they are considered to belong to the Cavellinidae.

The platycopines are composed of only one family, the Cytherellidae. The cytherellids are very closely related to the cavellinids and some workers would prefer to include the latter with the platycopines; however, there is a major difference in the muscle-scar patterns of the two groups. The muscle scar in the cavellinids is composed of many units, whereas the scar in the cytherellids is made up of only a few units. In outline and in shape the cytherellids and cavellinids are almost identical, and there is no doubt in the minds of most workers that the two groups are very closely related. They are so closely related that at one time *Cavellina* was thought to be a synonym of *Cytherella*. However, the muscle-scar pattern of *Cavellina* is similar to that found in *Healdia* and it seems more desirable to give a high priority to muscle-scar patterns in classification than it does to shape. By including the cavellinids in the metacopines we are bringing together a group of ostracodes with a common muscle-scar pattern and excluding the cytherellids because of a difference in this pattern.

Though the Cytherellidae are retained as the only family representing the Platycopina, it is believed that they developed directly from the Cavellinidae (Fig. 34). In the development of the cytherellids they retained the cavellinid shape for the most part, but were subjected to a reduction in the number of units and the shape of the muscle scar. As presently conceived, all Paleozoic forms previously referred to *Cytherella* belong to the Cavellinidae. The reduction in the number of muscle-scar units from the cavellinids to the cytherellids must have taken place for the most part in early Triassic time.

The cytherellids show dimorphism by inflation of the posterior portion of the female carapace.

ORDER MYODOCOPIDA

The presence of a well-developed rostral incisure and rostrum characterizes ostracodes assigned to the order Myodocopida. This assemblage is very unequally divided into an Ordovician-to-Recent suborder named Myodocopina, which contains numerous families, and a Recent suborder designated Cladocopina, which contains only a single family (Fig. 32).

SUBORDER MYODOCOPINA

The Myodocopina, which include many Paleozoic genera, range from small to large in size of the carapace, some attaining a length of 30 mm. One of the most characteristic features is the presence of a rostrum and rostral notch along the front margin in many, but not all of them. In some Pennsylvanian species of *Cypridinella* the inner surface of the carapace is modified by a complex design of ridges arranged in a diamond-shaped pattern. Externally, the valves are mostly smooth but may be

marked by a swelling just above the center. Some genera developed a nuchal furrow, a feature most often found in genera having a poorly developed rostrum.

The Myodocopina can be divided into two groups, one in which the rostral incisure is well developed (superfamilies Cypridinacea and Halocypridacea) and another in which this incisure is not well developed (superfamilies Entomozoacea, Entomoconchacea, and Thaumatoocypridacea). This grouping is rather artificial, because genera without a rostral incisure may be more closely related to some incisure-bearing forms than they are to each other. Some workers believe that the Entomozoacea are ancestral to the Thaumatoocypridacea but evidence is inconclusive. The Entomozoacea and Entomoconchacea are not certainly classifiable as myodocopids.

The Entomozoacea are large myodocopids with a nuchal furrow but no rostrum. The nuchal furrow is used in orientation, anterior direction being considered to lie on

TABLE. Characters of Ostracode Orders and Suborders

Order	ARCHAEO-	LEPERDITI-	PALAEOCOPIDA		PODOCOPIDA			MYODOCOPIDA	
	COPIDA	COPIDA	BEYRICHOCOPINA	KLOEDENELLOCOPINA	PODOCOPINA	METACOPINA	PLATYCOPINA	MYODOCOPINA	CLADOCOPINA
Suborder									
<i>Valve Size</i>	Subequal to unequal	Subequal to unequal	Equal to subequal	Unequal	Unequal to subequal	Unequal	Unequal	Equal to subequal	Equal to subequal
<i>Duplicature</i>	Absent	Absent	Absent	Absent	Present	Absent or poorly developed	Absent	Present	Present
<i>Dimorphic Structures</i>	None	None	None or various (a)	None or posterior swelling	None or posterior swelling	None or posterior swelling	None or posterior swelling	None or relative convexity	None or relative convexity
<i>Dorsal Margin</i>	Straight	Straight	Straight	Convex to straight	Convex to straight	Convex to straight or angled	Convex	Convex to straight or sinuate	Convex
<i>Ventral Margin</i>	Convex	Convex	Convex	Convex or rarely sinuate	Sinuate to convex	Convex to sinuate	Convex to straight or sinuate	Convex	Convex
<i>Muscle Scars</i>	Unknown	Very large, compound	Circular spots or unknown	Circular spots or unknown	Few discrete scars	Circular group (b)	Cluster of 8-14 biserial scars	Complex set of scars or unknown	Mostly median cluster of 3 scars
<i>Major Lateral Features</i>	Smooth, punctate or ridged	Mostly smooth	Sulcate, nodose, lobate, costate, reticulate	Sulcate to smooth, costate, reticulate	Smooth to reticulate, costate, alate, spinose, nodose, or sulcate	Smooth to reticulate, posterior spines or deep fissures	Smooth to costate	Costate to smooth	Reticulate punctate

(a) May include velate, pseudovelate, loculate, histial, lobate, structures associated with posteroventral, ventral, or anteroventral swellings.

(b) Composed of several to many individual scars.

its concave side. The superfamily is restricted to the Paleozoic.

The Entomoconchacea are large forms similar to the Entomozoacea but with a posterior siphon. They range from Devonian to Carboniferous but are nowhere abundant.

The Thaumatozoidacea are represented by a single rare genus (*Thaumatozoides*) which contains several Jurassic species and one living form.

The Cypridinacea are the most abundant myodocopids. They are characterized by a rostrum overhanging an anterior incisure, and a caudal siphon or nuchal furrow may be present. In the Sarsiellidae the rostrum may be absent, being usually found in males but lacking in females. Extreme forms of dimorphism exist. Members of this superfamily have been reported from the Ordovician. They have been identified certainly from the Silurian, are most abundant in the Carboniferous, and many genera, especially those in the Cypridinidae, Sarsiellidae, and Cylindroleberididae, are found in modern seas.

SUBORDER CLADOCOPINA

The Cladocopina contain a small group of ostracodes with a subcircular outline and three closely spaced muscle scars. Only one family, Polycopidae, is included in the suborder. Of its three genera, *Polycope*, *Polycopsis*, and *Parapolycope*, the last two are known only from modern seas.

SUMMARY OF CHARACTERS

The more or less diagnostic morphological characters of the orders and suborders of ostracodes recognized in the *Treatise* are summarized in the table on p. Q90.

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SUMMARY OF CLASSIFICATION AND STRATIGRAPHIC DISTRIBUTION

By **R. C. MOORE**

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The tabular outline of classification that follows is accompanied by statement of the reported stratigraphic range of each taxon and by numbers indicating the count of recognized genera and subgenera in each. Where only a single number is given, this refers to genera, but if two numbers appear, the first indicates genera and the second subgenera (e.g., "5; 2" denotes 5 genera and 2 subgenera, the latter figure being exclusive of nominotypical subgenera). Also, the outline affords a useful means of explicit statement of the authorship of systematic descriptions or diagnoses, except that contributions of material on individual genera are recorded only in the text. The several authors are indicated by code letters listed as follows.

Authorship of Systematic Descriptions

BENSON, R. H.	BN
BERDAN, J. M.	BE
BOLD, W. A. VAN DEN	BO
HANAI, TETSURO	HA
HESSLAND, IVAR	HE
HOWE, H. V.	HO
KESLING, R. V.	KE
LEVINSON, S. A.	LE
MOORE, R. C.	MO
REYMENT, R. A.	RE
SCOTT, H. W.	SC
SHAVER, R. H.	SH
SOHN, I. G.	SO
STOVER, L. E.	ST
SWAIN, F. M.	SW
SYLVESTER-BRADLEY, P. C.	SY

The stratigraphic distribution of orders, suborders, superfamilies, and families of Ostracoda recognized in the *Treatise* is indicated graphically in Figure 35. Taxa of

differing rank are segregated and plotted in the order of their first known appearance in the geologic record. Numerals associated with names on the diagram are keyed to the following list of suprageneric divisions so that cross references are made easily. For example, the family Hollinidae, which appears on part 2 of Figure 35 is numbered 67 (at left of the name) and accompanied (at right) by the numeral 22, because this family has position 22 in the tabular summary of "Suprageneric Divisions of Ostracoda." Oppositely, working from the systematically arranged list of taxa, if one wishes to find the position of Hollinidae on the stratigraphic distribution diagram, the italic numeral 67 refers him to the proper place on the figure.

Genera are similarly plotted in other diagrams distributed through parts of the text devoted to systematic descriptions. These are identified conveniently by reference to the alphabetically arranged list of families given with the explanation of Figure 35. It is hoped that the compilation of data in these ways will be found useful for various purposes.

Suprageneric Divisions of Ostracoda

[The bracketed index numbers at the left margin of the tabular outline are for cross reference to and from the stratigraphic-distribution diagram (Fig. 35), numbers in roman type corresponding to those that follow names of taxa in the diagram and those in italic type corresponding to those that precede these names in the diagram.]

	Ostracoda (<i>subclass</i>) (896; 15). <i>L.Cam.-Rec.</i> (SY)
[1-1]	Archaeocopida (<i>order</i>) (12). <i>L.Cam.-M.Cam., ?U.Cam.-?L.Ord.</i> (SY)
[2-37]	Bradoriidae (2). <i>L.Cam.-M.Cam.</i> (SY)

- [3-39] Beyrichonidae (4). *L.Cam.-M.Cam., ?U.Cam.-?L.Ord.* (SY)
- [4-36] Hipponicharionidae (3). *L.Cam.* (SY)
- [5-38] Indianidae (3). *L.Cam.-M.Cam.* (SY)
- [6-2] Leperditicopida (order) (15). *?U.Cam., L.Ord.-U.Dev.* (SC)
- [7-40] Leperditidae (10). *?U.Cam., L.Ord.-U.Dev.* (SC)
- [8-45] Isochilinidae (5). *L.Ord.-M.Dev.* (SC)
- [9-3] Palaeocopida (order) (261; 2). *L.Ord.-M.Perm., ?Rec.* (SC)
- [10-4] Beyrichicopina (suborder) (191; 2). *L.Ord.-M.Perm., ?Rec.* (SC)
- [11-21] Beyrichiacea (superfamily) (31; 2). *M.Ord.-L.Perm.* (LE)
- [12-66] Beyrichiidae (25). *M.Ord.-U.Dev., ?L.Carb.-?L.Perm.* (LE-BE-MO)
- [13-63] Zygobolbidae (5; 2). *?M.Ord.-?L.Sil., M.Sil., ?Dev.* (BE)
- Family Uncertain (1). *L.Sil.* (SC)
- [14-22] Drepanellacea (superfamily) (35). *M.Ord.-M.Perm.* (SC)
- [15-61] Drepanellidae (6). *M.Ord.-U.Dev.* (SC)
- [16-85] Aechminellidae (7). *L.Dev.-M.Perm.* (SO)
- [17-64] Aechminidae (6). *M.Ord.-M.Miss.* (LE)
- [18-59] Bolliidae (9). *M.Ord.-M.Dev.* (SC)
- [19-74] Kirkbyellidae (1). *M.Sil.-M.Penn., ?U.Penn.* (SO)
- [20-62] Richinidae (4). *M.Ord.-U.Dev.* (SC)
- Family Uncertain (2). *M.Ord.-U.Ord.* (SC)
- [21-14] Hollinacea (superfamily) (80). *L.Ord.-M.Perm.* (SC-MO)
- [22-67] Hollinidae (19). *M.Ord.-M.Perm.* (KE)
- [23-54] Bassleratiidae (6). *?L.Ord., M.Ord.* (LE)
- [24-58] Chilobolbinidae (2). *M.Ord.-M.Sil., ?U.Sil.* (LE)
- [25-43] ?Eurychilinidae (10). *L.Ord.-U.Dev.* (LE-MO)
- [26-42] Piretellidae (8). *L.Ord.-U.Ord.* (HE)
- [27-41] Quadrijugatoridae (13). *L.Ord.-U.Ord.* (KE)
- [28-44] Sigmoidopsidae (16). *L.Ord.-U.Ord., ?L.Sil.-?U.Sil.* (KE-HE)
- [29-57] Tetradellidae (3). *M.Ord.-L.Sil.* (SC-KE)
- [30-56] Tvaerenellidae (2). *L.Ord.-U.Ord.* (HE)
- Family Uncertain (1). *M.Ord.* (SC)
- [31-29] Kirkbyacea (superfamily) (22). *?L.Dev., M.Dev.-M.Perm.* (SO)
- [32-105] Kirkbyidae (4). *L.Miss.-M.Perm.* (SO)
- [33-95] Amphissitidae (3). *M.Dev.-M.Perm.* (SO)
- [34-93] Arcyzonidae (5). *M.Dev.* (KE)
- [35-109] Cardiniferellidae (1). *U.Miss.* (SO)
- [36-104] Kellettinidae (3). *?L.Miss., M.Miss.-M.Perm.* (SO)
- [37-87] ?Placideidae (3). *L.Dev.-M.Perm.* (SO)
- [38-98] ?Scrobiculidae (3). *?M.Dev., L.Carb.(Miss.)-M.Perm.* (SO)
- [39-20] Oepikellacea (superfamily) (9). *L.Ord.-M.Penn.* (HE)
- [40-55] Oepikellidae (1). *M.Ord.-U.Ord.* (HE)
- [41-65] Aparchitidae (5). *L.Ord.-M.Penn.* (HE)
- [42-76] Pribyltitidae (3). *U.Sil.-M.Dev.* (HE)
- [43-25] Primitiopsacea (superfamily) (7). *M.Ord.-M.Dev.* (HE)
- [44-70] Primitiopsidae (7). *M.Ord.-M.Dev.* (HE)
- Primitiopsinae (5). *M.Ord.-M.Dev.* (HE)
- Leiocyaminae (2). *M.Sil.-U.Sil.* (HE)
- [45-31] Youngiellacea (superfamily) (4). *?U.Dev., L.Miss.-U.Penn.* (SO)
- [46-99] Youngiellidae (3). *L.Miss.-U.Penn.* (SO)
- Family Uncertain (1). *U.Dev.* (SO)
- [47-35] Punciacea (superfamily) (2). *Rec.* (SY)
- [48-142] Punciidae (2). *Rec.* (SY)
- Superfamily and Family Uncertain (1). *Ord.* (BE-SC)
- [49-5] Kloedenellocopina (suborder) (51). *L.Ord.-U.Jur.* (SC)
- [50-24] Kloedenellacea (superfamily) (27). *?U.Ord., L.Sil.-M.Perm.* (SO)
- [51-69] Kloedenellidae (5). *?U.Ord., L.Sil.-U.Penn., ?L.Perm.-?M.Perm.* (SO)
- [52-96] Geisinidae (4). *M.Dev.-M.Perm.* (SO)
- [53-97] Glyptopleuridae (3). *?M.Dev., M.Miss.-M.Perm.* (SC)
- [54-100] Beyrichiopsidae (7). *U.Dev.-M.Perm.* (SO)
- [55-101] Lichviniidae (4). *U.Dev.-M.Perm.* (SO)
- [56-107] ?Miltonellidae (3). *?U.Miss., M.Perm.* (SO)
- [57-108] Sansabellidae (1). *M.Miss.-M.Penn.* (SO)
- [58-16] Leperditellacea (superfamily) (19). *L.Ord.-U.Jur.* (LE-MO)
- [59-50] Leperditellidae (19). *L.Ord.-U.Jur.* (LE-MO)

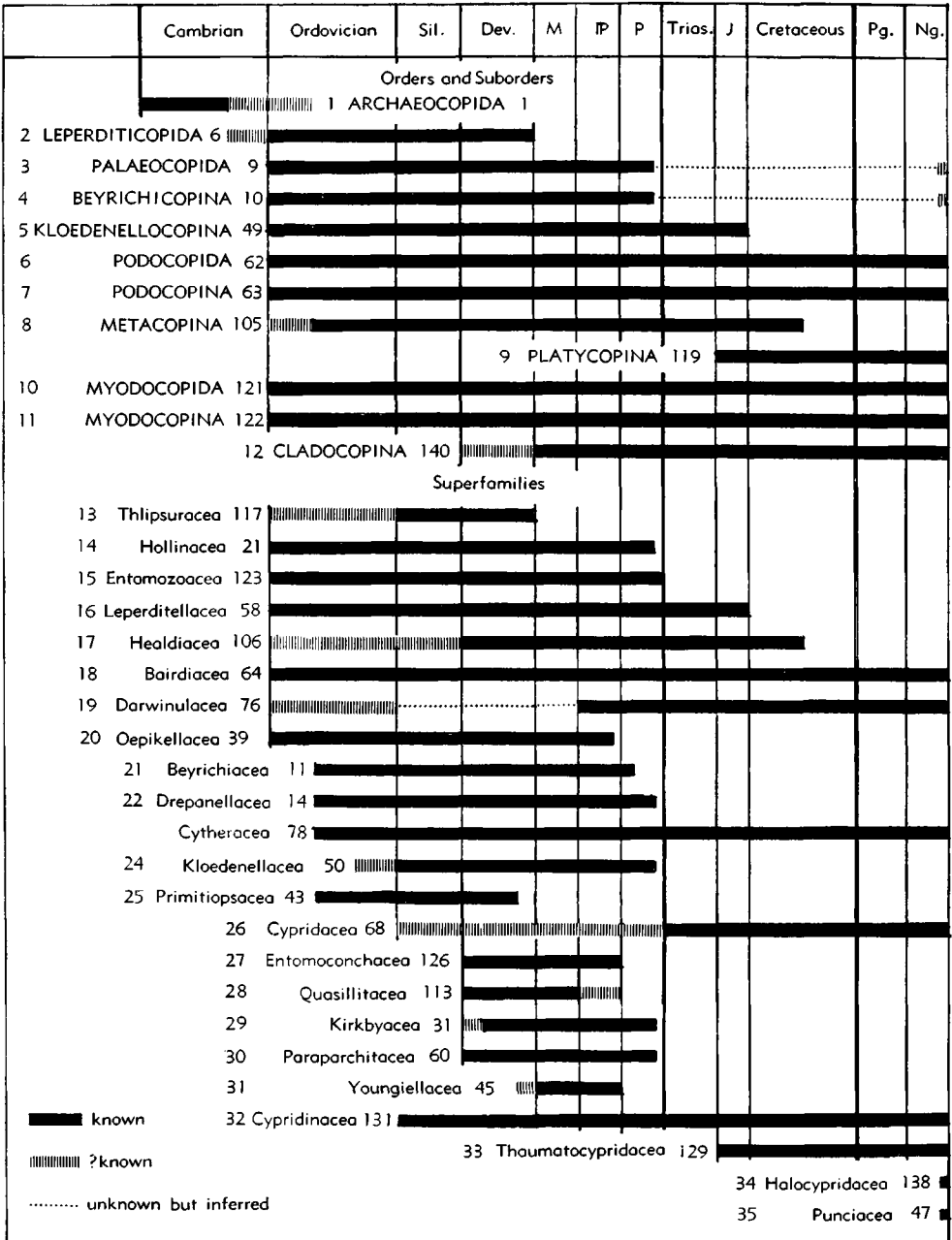


FIG. 35. Stratigraphic distribution of suprageneric ostracode taxa, geologic periods plotted according to relative time values (Moore, n). The numbers following the names of taxa indicate systematic placement as given in the preceding tabular outline of ostracode classification. Also, an alphabetical list of families is accompanied by index numbers referring to the serially arranged numbers that precede the names of taxa on the diagram; this facilitates location of any selected family as plotted with respect to stratigraphic occurrence.

Ostracode Families with Index Numbers

[Figures cited with families show stratigraphic distribution of component genera]

Acronotellidae—68 (Fig. 184)
 Aechminellidae—85 (Fig. 57)

Aechminidae—4 (Fig. 57)
 Amphissitidae—95 (Fig. 94)

Aparchitidae—65 (Fig. 105)
 Arcyzonidae—93 (Fig. 94)

	Cambrian	Ordovician	Sil.	Dev.	M.	P.	P.	Trias.	J.	Cretaceous	Pg.	Ng.
	36	37	38	39								
	36	37	38	39								
	36	37	38	39								
	36	37	38	39								
40	Leperditidae 7											
41	Quadrijugatoridae 27											
42	Piretellidae 26											
43	Eurychilinae 25											
44	Sigmoopsidae 28											
45	Isochilinae 8											
46	Pachydomellidae 112											
47	Thlipsuridae 118											
48	Entomozoidae 124											
49	Bairdiocyprididae 108											
50	Leperditellidae 59											
51	Bairdiidae 65											
52	Darwinulidae 77											
53	Macrocyprididae 67											
54	Bassleratiidae 23											
55	Oepikellidae 40											
56	Tvaerenellidae 30											
57	Tetradellidae 29											
58	Chilobolbinidae 24											
59	Bolliidae 18											
60	Krausellidae 111											
61	Drepanellidae 15											
62	Richinidae 20											
63	Zygobolbidae 13											
64	Aechminidae 17											
65	Aparchitidae 41											
66	Beyrichiidae 12											
67	Hollinidae 22											
68	Acronotellidae 80											
69	Kloedenellidae 51											
70	Primitiopsidae 44											
71	Bolbozoidae 125											
72	Cavellinidae 110											
73	Paracyprididae 74											
74	Kirkbyellidae 19											
75	Beecherellidae 66											
76	Pribylitidae 42											
77	Berounellidae 81											
78	Buregiidae 142											
79	Cyprosinidae 128											
80	Ropolonellidae 116											
81	Bufinidae 115											
82	Cypridinellidae 135											
83	Entomoconchidae 127											
84	Quasillitidae 114											
85	Aechminellidae 16											
86	Paraparchitidae 61											
87	Placideidae 37											

FIG. 35 (Continued).

Bairdiidae—51 (Fig. 138)
 Bairdiocyprididae—49 (Fig. 278)
 Barychilinidae—94 (Fig. 278)
 Bassleratiidae—54 (Fig. 65)
 Beecherellidae—75 (Fig. 138)
 Beyrichiopsidae—100 (Fig. 117)
 Berounellidae—77
 Beyrichiidae—66 (Fig. 47)
 Beyrichonidae—39 (Fig. 36)
 Bolbozoidae—71 (Fig. 311)
 Bollidae—59 (Fig. 57)
 Brachycytheridae—119 (Fig. 184)
 Bradoriidae—37 (Fig. 36)
 Bufnidae—81 (Fig. 296)
 Buregiidae—78
 Bythocytheridae—89 (Fig. 184)
 Cardiniferellidae—109 (Fig. 94)
 Cavellinidae—72 (Fig. 278)
 Chilobolbinidae—58 (Fig. 65)
 Cycloocyprididae—125 (Fig. 147)
 Cylindroleberididae—137
 Cyprellidae—102 (Fig. 311)
 Cyprididae—113 (Fig. 147)
 Cypridinellidae—106 (Fig. 311)
 Cypridinidae—113 (Fig. 311)
 Cyprosinidae—79 (Fig. 311)
 Cytherellidae—120 (Fig. 308)
 Cytherettidae—131 (Fig. 184)
 Cytheridae—121 (Fig. 184)
 Cytherideidae—112 (Fig. 184)
 Cytherissinellidae—117
 Cytheruridae—126 (Fig. 184)
 Darwinulidae—52
 Drepanellidae—61 (Fig. 57)
 Entocytheridae—138
 Entomoconchidae—83 (Fig. 311)
 Entomozoidae—48 (Fig. 311)
 Eucandonidae—114 (Fig. 147)
 Eurychilinidae—43 (Fig. 65)
 Geisinidae—96 (Fig. 117)
 Glyptopleuridae—97 (Fig. 117)
 Halocyprididae—139
 Healdiidae—88 (Fig. 278)
 Hemicytheridae—134 (Fig. 184)
 Hipponicharionidae—36 (Fig. 36)

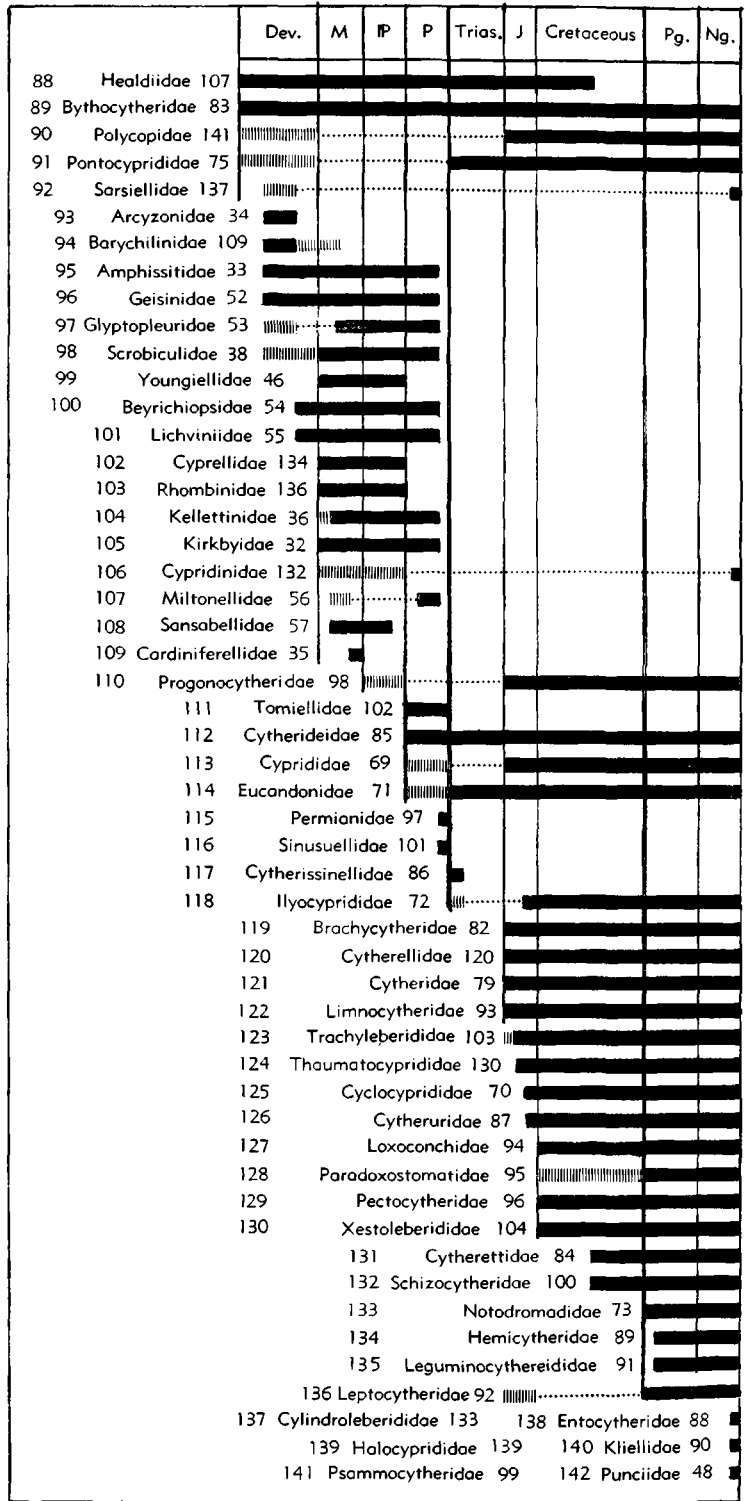


FIG. 35 (Continued).

[60-30]	Paraparchitacea (<i>superfamily</i>) (5). <i>L.Dev.-M.Perm.</i> (SC)		Ilyocypridinae (6). ? <i>Trias.</i> , <i>U.</i> <i>Jur.-Rec.</i> (SW)
[61-86]	Paraparchitidae (5). <i>L.Dev.-M.</i> <i>Perm.</i> (SC)		Cyprideinae (2;6). <i>Trias.-L.Cret.</i> (SW)
	Suborder, Superfamily, and Family Uncertain (19). <i>M.Ord.-Penn.</i>	[73-133]	Notodromadidae (3). <i>Paleoc.-Rec.</i> (SW)
[62-6]	Podocopida (<i>order</i>) (530;11). <i>L.Ord.-</i> <i>Rec.</i> (SY)	[74-73]	Paracyprididae (6). ? <i>Sil.</i> , <i>Jur.-Rec.</i> (SW)
[63-7]	Podocopina (<i>suborder</i>) (444;9). <i>L.</i> <i>Ord.-Rec.</i> (SY-SW-HO)	[75-91]	Pontocyprididae (7). ? <i>Dev.</i> , <i>Trias.-</i> <i>Rec.</i> (SW)
[64-18]	Bairdiacea (<i>superfamily</i>) (21). <i>L.</i> <i>Ord.-Rec.</i> (SH)		Family Uncertain (12). <i>M.Ord.-U.</i> <i>Jur.</i> (SW)
[65-51]	Bairdiidae (14). <i>L.Ord.-Rec.</i> (SH)	[76-19]	Darwinulacea (<i>superfamily</i>) (2). ? <i>Ord.</i> , <i>Penn.-Rec.</i> (SW)
[66-75]	Beecherellidae (3). <i>U.Sil.-M.Dev.</i> (BE)	[77-52]	Darwinulidae (2). ? <i>Ord.</i> , <i>Penn.-</i> <i>Rec.</i> (SW)
[67-53]	Macrocyprididae (2). ? <i>L.Ord.-</i> ? <i>Mio.</i> , <i>Plio.-Rec.</i> (SY)	[78-23]	Cytheracea (<i>superfamily</i>) (281;2). <i>M.Ord.-Rec.</i> (HO)
	Family Uncertain (2). ? <i>L.Dev.</i> , <i>U.</i> <i>Miss.</i> , <i>U.Cret.</i> (SH-SO-BE)	[79-121]	Cytheridae (6). <i>L.Jur.-Rec.</i> (HO)
[68-26]	Cypridacea (<i>superfamily</i>) (140;7). ? <i>Sil.-?Perm.</i> <i>Trias.-Rec.</i> (SW)	[80-68]	Acronotellidae (2). <i>U.Ord.-U.Sil.</i> (KE)
[69-113]	Cyprididae (74;1). ? <i>Perm.</i> , <i>L.Jur.-</i> <i>Rec.</i> (SW)	[81-77]	Berounellidae (2). <i>U.Sil.-L.Dev.</i> , <i>L.Carb</i> (SO-BE)
	Cypridinae (58;1). <i>L.Jur.-Rec.</i> (SW)	[82-119]	Brachycytheridae (15). <i>L.Jur.-Rec.</i> (HO)
	Cypridopsinae (6). ? <i>Perm.</i> , <i>U.</i> <i>Cret.-Rec.</i> (SW)	[83-89]	Bythocytheridae (8). <i>L.Dev.-Rec.</i> (SY-KE)
	Disopontocypridinae (4). <i>Oligo.-</i> <i>Rec.</i> (SW)	[84-131]	Cytherettidae (5). <i>U.Cret.-Rec.</i> (HO)
	Candoninae (6). <i>Tert.-Rec.</i> (SW)	[85-112]	Cytherideidae (42). <i>Perm.-Rec.</i> (HO)
[70-125]	Cyclocyprididae (5). <i>U.Jur.-Rec.</i> (SW)		Cytherideinae (23). <i>Perm.-Rec.</i> (HO)
[71-114]	Eucandonidae (25). ? <i>Perm.</i> , <i>L.</i> <i>Trias.-Rec.</i> (SW)		Cuneocytherinae (4). <i>L.Jur.-Mio.</i> (HO)
[72-118]	Ilyocyprididae (8;6). <i>Trias.-Rec.</i> (SW)		Eucytherinae (4). <i>Jur.-Rec.</i> (HO)

FIG. 35 (Continued).

Hollinidae—67 (Fig. 65)	Oepikellidae—55 (Fig. 105)	Rhombinidae—103 (Fig. 311)
Ilyocyprididae—118 (Fig. 147)	Pachydromellidae—46 (Fig. 278)	Richinidae—62 (Fig. 57)
Indianidae—38 (Fig. 36)	Paracyprididae—73 (Fig. 147)	Ropolonellidae—80 (Fig. 296)
Isochilinidae—45 (Fig. 41)	Paradoxostomatidae—128 (Fig. 184)	Sansabellidae—108 (Fig. 117)
Kellettinidae—104 (Fig. 94)	Paraparchitidae—86 (Fig. 131)	Sarsiellidae—92 (Fig. 311)
Kirkbyellidae—74 (Fig. 57)	Pectocytheridae—129 (Fig. 184)	Schizocytheridae—132 (Fig. 184)
Kirkbyidae—105 (Fig. 94)	Permianidae—115	Scrobiculidae—98 (Fig. 94)
Kliellidae—140	Piretellidae—42 (Fig. 65)	Sigmoopsidae—44 (Fig. 65)
Kloedenellidae—69 (Fig. 117)	Placideidae—87 (Fig. 94)	Sinusuellidae—116
Krausellidae—60 (Fig. 278)	Polvcopidae—90 (Fig. 311)	Tetradellidae—57 (Fig. 65)
Leguminocythereidae—135 (Fig. 184)	Pontocyprididae—91 (Fig. 147)	Thaumatoocyprididae—124 (Fig. 311)
Leperditellidae—50 (Fig. 131)	Pribylitidae—76 (Fig. 105)	Thlipsuridae—47 (Fig. 296)
Leperditiidae—40 (Fig. 41)	Primitiopsidae—70 (Fig. 111)	Tomiellidae—111
Leptocytheridae—136 (Fig. 184)	Progonocytheridae—110 (Fig. 184)	Trachyleberididae—123 (Fig. 184)
Lichviniidae—101 (Fig. 117)	Psammocytheridae—141	Tvaerenellidae—56 (Fig. 65)
Limnocytheridae—122 (Fig. 184)	Punciidae—142	Xestoleberididae—130 (Fig. 184)
Loxoconchidae—127 (Fig. 184)	Quadrijugatoridae—41 (Fig. 65)	Youngiellidae—99 (Fig. 105)
Macrocyprididae—53 (Fig. 138)	Quasiliitidae—84 (Fig. 296)	Zygobolbidae—63 (Fig. 47)
Miltonellidae—107 (Fig. 117)		
Notodromadidae—133 (Fig. 147)		

- Krithinae (3). *U.Cret.-Rec.* (HO) [111-60]
 Neocytherideidinae (8). *L.Jur.-Rec.* (HO) [112-46]
 [86-117] Cytherissinellidae (2). *L.Trias.* (BO-RE) [113-28]
 [87-126] Cytheruridae (18). *U.Jur.-Rec.* (RE) [114-84]
 [88-138] Entocytheridae (2;2). *Rec.* (HO) [115-81]
 [89-134] Hemicytheridae (14). *Eoc.-Rec.* (HO) [116-80]
 [90-140] Kliellidae (2). *Rec.* (HO)
 [91-135] Leguminocythereididae (5). *Eoc.-Rec.* (HO)
 [92-136] Leptocytheridae (4). *?Jur., Tert.-Rec.* (HO) [117-13]
 [93-122] Limnocytheridae (12). *L.Jur.-Rec.* (HO) [118-47]
 [94-127] Loxoconchidae (6). *Cret.-Rec.* (HO) [119-9]
 [95-128] Paradoxostomatidae (11). *?Cret., Eoc.-Rec.* (HO-SY) [120-112]
 Paradoxostomatinae (7). *?Cret., Eoc.-Rec.* (HO-SY)
 Microcytherinae (1). *Mio.-Rec.* (HO-SY)
 Cytheromatinae (3). *Oligo.-Rec.* (HO-SY) [121-10]
 [96-129] Pectocytheridae (4). *L.Cret.-Rec.* (HA) [122-11]
 [97-115] Permianidae (1). *U.Perm.* (BO-RE) [123-15]
 [98-110] Progonocytheridae (20). *?Penn., L.Jur.-Rec.* (HO) [124-48]
 Protocytherinae (10). *Jur.-Cret.* (HO)
 Protocytherinae (10). *?Penn., L.Jur.-Cret.* (HO)
 [99-141] Psammocytheridae (1). *Rec.* (HO)
 [100-132] Schizocytheridae (5). *U.Cret.-Rec.* (HO) [125-71]
 [101-116] Sinusuellidae (1). *U.Perm.* (BO)
 [102-111] Tomiellidae (5). *Perm.* (BO-HO) [126-27]
 [103-123] Trachyleberididae (33). *?L.Jur., M.Jur.-Rec.* (SY) [127-83]
 [104-130] Xestoleberididae (4). *L.Cret.-Rec.* (HO)
 Family Uncertain (51). *M.Ord.-Rec.* (HO-RE-BO)
 [105-8] Metacopina (*suborder*) (71). *?L.Ord., M.Ord.-L.Cret.* (SY) [128-79]
 [106-17] Healdiacea (*superfamily*) (41). *?Ord.-?Sil., Dev.-L.Cret.* (SH) [129-33]
 [107-88] Healdiidae (9). *L.Dev.-L.Cret.* (SH) [130-124]
 [109-49] Bairdiocyprididae (12). *?Ord., Sil.-Perm., ?Jur.* (SH) [131-32]
 [109-94] ?Barychilinidae (4). *M.Dev., ?L.Miss.* (KE) [132-106]
 [110-72] ?Cavellinidae (10). *?L.Sil.-?U.Sil., L.Dev.-U.Penn., ?L.Perm.-?U.Perm.* (BN)
 Krausellidae (3). *M.Ord.-M.Dev.* (BE)
 Pachydomellidae (3). *?L.Ord.-?U.Ord., L.Sil.-U.Dev.* (BE-SO)
 Quasillitacea (*superfamily*) (15). *L.Dev.-U.Miss., ?L.Penn.-?U.Penn.* (SC)
 Quasillitidae (7). *L.Dev.-U.Miss., ?L.Penn.-?U.Penn.* (SO-ST)
 Bufinidae (4). *L.Dev.-U.Dev., ?L.Miss.-?U.Penn.* (SO-ST)
 Ropolonellidae (3). *L.Dev.-U.Dev.* (SO)
 Family Uncertain (1). *M.Dev.*
 Thlipsuracea (*superfamily*) (15). *?L.Ord.-?U.Ord., L.Sil.-U.Dev.* (SC)
 Thlipsuridae (15). *?L.Ord.-?U.Ord., L.Sil.-U.Dev.* (KE)
 Platycopina (*suborder*) (3;2). *L.Jur.-Rec.* (SC-SY)
 Cytherellidae (3;2). *L.Jur.-Rec.* (RE)
 Suborder and Order Uncertain (12). *M.Ord.-Rec.*
 Myodocopida (*order*) (57;2). *L.Ord.-Rec.* (SY)
 Myodocopina (*suborder*) (53;2). *L.Ord.-Rec.* (SY)
 Entomozoacea (*superfamily*) (15). *L.Ord.-U.Perm.* (SY)
 Entomozoidae (14). *Ord.-U.Perm.* (SY)
 Entomozoinae (9). *Ord.-U.Perm.* (SY)
 Bouciinae (1). *U.Sil.* (SY)
 Richteriniinae (4). *L.Dev.-U.Dev.* (SY)
 Bolbozoidae (1). *L.Sil.-U.Dev.* (SY)
 Entomoconchacea (*superfamily*) (5). *L.Dev.-U.Carb.* (SY)
 Entomoconchidae (4). *Dev.-Carb.* (SY)
 Entomoconchinae (2). *Dev.-Carb.* (SY)
 Oncotechmoninae (2). *M.Dev.* (SY)
 Cyprosinidae (1). *L.Dev.-U.Dev.* (SY)
 Thaumatoocypridacea (*superfamily*) (1). *M.Jur.-Rec.* (SY)
 Thaumatoocyprididae (1). *M.Jur.-Rec.* (SY)
 Cypridinacea (*superfamily*) (27;2). *Sil.-Rec.* (SY)
 Cypridinidae (13;1). *?Carb., Rec.* (SY)
 Cypridininae (8;1). *?L.Carb.-?U.Carb., Rec.* (SY)

	Philomedinae (5). ? <i>L.Carb.</i> -? <i>U.Carb.</i> , <i>Rec.</i> (SY)	[138-34]	Halocypridacea (<i>superfamily</i>) (5). <i>Rec.</i> (SY)
[133-137]	Cylindroleberididae (3;1). <i>Rec.</i> (SY)	[139-139]	Halocyprididae (5). <i>Rec.</i> (SY)
[134-102]	Cyprellidae (1). <i>L.Carb.</i> - <i>U.Carb.</i> (SY)	[140-12]	Cladocopina (<i>suborder</i>) (4). ? <i>L.Dev.</i> -? <i>U.Dev.</i> , <i>L.Miss.</i> - <i>Rec.</i> (SY)
[135-82]	Cypridinellidae (4). <i>L.Dev.</i> - <i>U.Carb.</i> (SY)	[141-90]	Polycopidae (3). ? <i>L.Dev.</i> -? <i>U.Dev.</i> , <i>L.Jur.</i> - <i>Rec.</i> (SY)
[136-103]	Rhombinidae (2). <i>L.Carb.</i> - <i>U.Carb.</i> (SY)		Family Uncertain (1). <i>Miss.</i>
[137-92]	Sarsiellidae (3). ? <i>M.Dev.</i> , <i>Rec.</i> (SY)	[142-78]	Order and Suborder Uncertain (21). <i>Dev.</i>
	Family Uncertain (1). <i>L.Sil.</i> - <i>U.Sil.</i>		Buregiidae (1). <i>Dev.</i> (SH)
			Family Uncertain (20). <i>L.Ord.</i> - <i>Mio.</i>
			Nomina Dubia (78)

SYSTEMATIC DESCRIPTIONS

By R. H. BENSON, J. M. BERDAN, W. A. VAN DEN BOLD, TETSURO HANAI, IVAR HESSLAND, H. V. HOWE, R. V. KESLING, S. A. LEVINSON, R. A. REYMENT, R. C. MOORE, H. W. SCOTT, R. H. SHAVER, I. G. SOHN, L E. STOVER, F. M. SWAIN, and P. C. SYLVESTER-BRADLEY

CONTENTS

	PAGE
SUBCLASS OSTRACODA Latreille, 1806	Q100
ORDER ARCHAEOCOPIDA Sylvester-Bradley, n. order	Q100
ORDER LEPERDITICOPIDA Scott, n. order	Q103
ORDER PALAEOCOPIDA Henningsmoen, 1953	Q110
Suborder Beyrichicopina Scott, n. suborder	Q111
Superfamily Beyrichiacea Matthew, 1886	Q112
Superfamily Drepanellacea Ulrich & Bassler, 1923	Q123
Superfamily Hollinacea Swartz, 1936	Q133
Superfamily Kirkbyacea Ulrich & Bassler, 1906	Q163
Superfamily Oepikellacea Jaanusson, 1957	Q168
Superfamily Primitiopsacea Swartz, 1936	Q171
?Superfamily Youngiellacea Kellett, 1933	Q173
?Superfamily Punciacea Hornibrook, 1949	Q175
Superfamily and Family Uncertain	Q175
Suborder Kloedenellocopina Scott, n. suborder	Q175
Superfamily Kloedenellacea Ulrich & Bassler, 1908	Q176
?Superfamily Leperditellacea Ulrich & Bassler, 1906	Q186
Superfamily Paraparchitacea Scott, 1959	Q190
Suborder and Family Uncertain	Q193
ORDER PODOCOPIDA Müller, 1894	Q196
Suborder Podocopina Sars, 1866	Q196
Superfamily Bairdiacea Sars, 1888	Q201
Superfamily Cypridacea Baird, 1845	Q208
Superfamily Darwinulacea Brady & Norman, 1889	Q253
Superfamily Cytheracea Baird, 1850	Q254