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MALACOSTRACA

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Class MALACOSTRACA Latreille, 1806

[Diagnosis prepared by R. C. MOORE]

Crustaceans with carapace of widely varied form covering all or most of head and trunk regions, but vestigial in some. Head typically bearing paired compound eyes, commonly located at tips of movable stalks, rarely much reduced or lacking, with five pairs of appendages behind eyes, termed antennules (or first antennae), antennae (or second antennae), mandibles, maxillules, and maxillae. Trunk composed of well-differentiated thoracic and abdominal tagmata, former having eight somites and latter six (or uncommonly seven), all equipped with paired appendages except seventh abdominal somite, if present. Male genital apertures located on eighth thoracic somite (rarely on seventh) and female genital openings invariably on sixth thoracic somite.

Development usually with metamorphosis, although young seldom are hatched as nauplii. *L.Cam.-Rec.*

Despite exceptional diversity in form and size, malacostracans are joined together by more numerous morphological features in common than can be found in almost any other class of Crustacea. These include 1) the carapace enveloping the thoracic region, 2) movable paired stalked eyes, 3) biramous antennules, possessed by no other crustacean group, 4) flattened scalelike exopod on the antennae, 5) pairs of pereipods adapted for swimming, 6) generally elongate, ventrally flexed abdomen, and 7) commonly developed tail fan composed of uropods and the telson. These characters suggest that the Malacostraca are descendants of crustaceans of so-called caridoid facies, resembling the shrimps.

PHYLLOCARIDA

By W. D. IAN ROLFE

[Hunterian Museum, University of Glasgow] [Acknowledgments are expressed to H. B. WHITTINGTON, of Harvard University, to whom the author is specially indebted for help and guidance in preparing this chapter; also to H. K. BROOKS, of the University of Florida, and R. R. HESSLER and H. L. SANDERS, of the Woods Hole Oceanographic Institution, who contributed many ideas and suggestions in discussing Phyllocarida; and numerous museums which loaned specimens for study.]

[Chapter submitted April, 1961; revised 1962, 1963, 1964, 1965, 1966]

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INTRODUCTION

Phyllocarids are an important group of malacostracans distinguished by the bivalved nature of their carapace, in this re-

spect being reminiscent of less advanced crustacean assemblages such as the conchostracan branchiopods and the ostracodes. Unlike conchostracans and ostracodes, in which the entire body is enclosed by the two

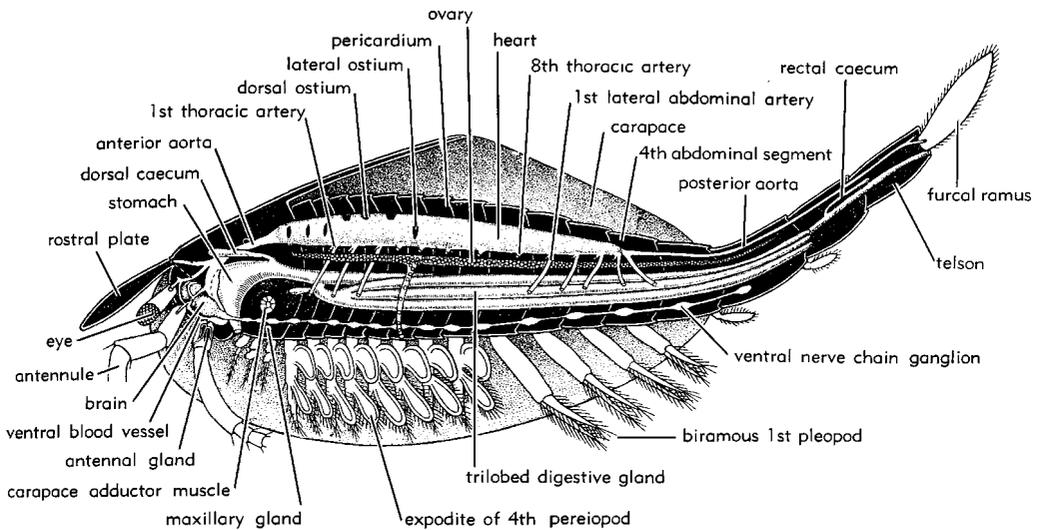


FIG. 120. Idealized figure of female *Nebalia bipes* (FABRICIUS), Rec., showing leptostracan morphology, $\times 12$ (68, after 271). (From H. G. Cannon, 1960, in Bronn's Klassen und Ordnungen des Tierreichs, v. 5, Abt. 1, Buch 4, Teil 1.)

valves, the carapace of phyllocarids covers only the anterior parts of the body, however, and phyllocarids are relatively much larger than the other groups mentioned. Also, at the front of the phyllocarid carapace is a movably articulated lanceolate rostral plate, which is a distinctive feature.

Appendages of the head, as observed in various genera of Phyllocarida, may project well in front of the carapace margin. In addition to pairs of antennules and antennae, stalked eyes are present and may be seen in side view of individuals. The thorax, which is mainly or entirely concealed by the covering valves, consists of eight short free segments. Commonly, their appendages (thoracopods) are well-developed limbs, long enough to reach beyond the lower margins of the carapace. The abdomen is exposed partly or entirely behind the carapace and consists of seven segments and a telson. In the living phyllocarids (Leptostraca) all except the pretelson segment bear appendages, but in only a few genera of fossil phyllocarids (Archaeostraca) are abdominal appendages known with certainty. The abdominal limbs are moderately short pleopods, adapted for swimming. Appendages of the telson are the two branches of a caudal furca, which are

movably articulated with the telson but unsegmented.

Phyllocarids are distributed from the Lower Cambrian to the Recent and they have wide occurrence geographically. They include the stock from which the higher Malacostraca arose, presumably during the Early Devonian.

MORPHOLOGY

The chief morphological features of Phyllocarida are shown in Figures 120 and 121 (see also Fig. 124).

SIZE

The largest leptostracan is *Nebaliopsis*, which reaches a length of about 4 cm.; the other Leptostraca are rarely longer than 12 mm. Many of the Archaeostraca, however, are very large; *Ceratiocaris ludensis* WOODWARD (U.Sil., Eng.) and *Schugurocaris? cornwallisensis damesi* (CHLUPÁČ) (U.Sil., Czech.) reach a length of 75 cm., other Silurian species of *Ceratiocaris* and *Heroldina rhenana* (BROILI) (L.Dev., Ger.) attaining a length of 60 cm. *C. pyriformis* RYABININ (U.Perm., Perm. region of USSR) and ROTHPLETZ's (1913) phyllocarid (U.Sil., Gotland) have carapace lengths of only 0.8

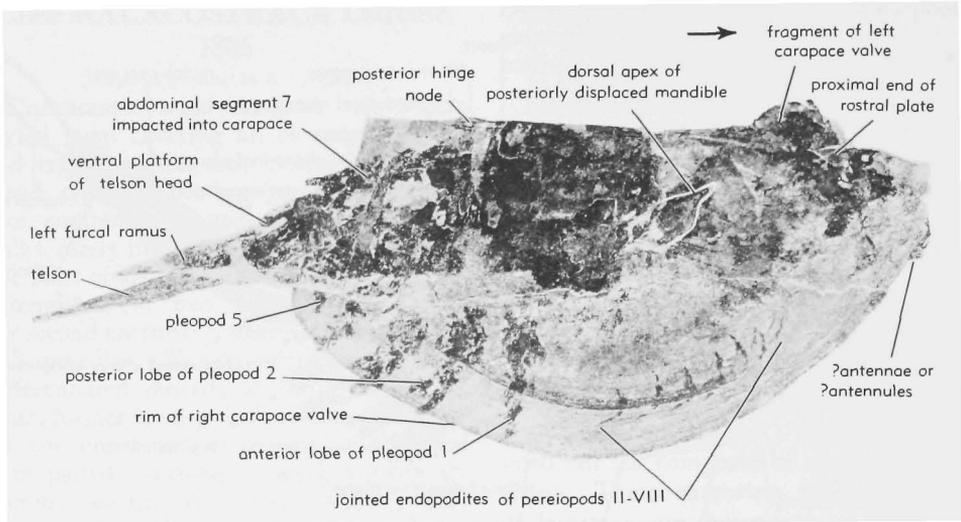


FIG. 121. *Ceratiocaris papilio* SALTER in MURCHISON, M.Sil., Scot.; showing limbs and morphological features of Archaeostraca Ceratiocarina, $\times 1.5$ (258).

mm. and 0.7 mm. respectively, but neither of these is an undoubted phyllocarid. Possibly the smallest genuine archaeostracan is *C. oklahomensis* (RUEDEMANN) (U.Sil., Okla.), which has a total length of only 8 mm.

INTEGUMENT AND PRESERVATION

In the Leptostraca the integument is thin and flexible, whitish, and transparent or semiopaque. Typical arthropod cuticular prisms, pore canals and gland-duct openings have been described from the cuticle of *Nebalia* by CLAUS (1888).

Many Paleozoic phyllocarids occur in concretions preserved as a substance that superficially appears to be colophane. This mineraloid has only been proved by analysis in the Middle Silurian *Ceratiocaris papilio*, however, where the dark brown colophane has been partially replaced within the thickness of the cuticle by calcite and dolomite (257). The cuticle of ca. 50 cm.-long specimens of *C. papilio* does not normally exceed 0.6 mm. in thickness, although it is locally thickened in such regions as the tips of the mandibular teeth. Microstructures recognized in the cuticle include moniliform and spiral ?pore canals up to 17μ in external diameter and up to 4,700 per sq. mm., laminae up to 7μ thick, "Balkenlagen," and prisms up to 270μ in diameter. In many

phyllocarids, the cuticle is penetrated by tubules attributable to aquatic thallophyte perforants.

Microstructure is probably detectable in many phyllocarids, and further study might enable the recognition of major stratifications needed to establish stages reached in the intermolt cycle. Prismatic structure has been detected in *Aristozoe*, *Caryocaris*, *Concavicaris*, *Dictyocaris*, *Echinocaris*, and *Montecaris*. Fossil phyllocarids, such as *Ceratiocaris*, probably had a flexible cuticle in life, although it is impossible to be certain of this in view of the ravages wrought by selective diagenesis. Others, such as *Aristozoe* and *Dithyrocaris paradoxides* (DE KONINCK), probably had a less flexible, possibly calcified cuticle. Phyllocarid cuticles show a great variety of surface sculpture, raised thick or thin anastomosing ridges or striae forming various patterns, scalelike elevated cusps, tubercles, and pits.

Phyllocarids probably formed part of the diet of contemporary predators, and GÜRICH has suggested that the fragmentary and crumpled nature of *Silesicaris* specimens indicates that they had passed through the gut of some predator (128).

CARAPACE

The carapace loosely envelops the thorax and part of the abdomen, except in *Sairo-*

GENUS	Rostral plate present	Carapace with hinge line	Carapace without hinge line	Median dorsal plate present	Anterior tubercle present	Number of thoracic segments	Number of abdominal segments	Telson present	Furca present	Cephalic appendages present	Mandible present	Thoracic appendages present	Abdominal appendages present	Intestinal infilling present
Aristozoe	-	●	-	-	-	+3	●	-	-	-	-	-	-	?Ord., Sil.-Dev.
Austriocaris	●	●	-	-	-	-	-	-	-	-	-	-	-	U.Trias.
Baituganocaris	?	●	-	-	-	?4	●	●	-	-	-	-	-	U.Dev.
Callizoe	-	●	-	-	●	-	-	-	-	-	-	-	-	L.Dev.
Canadaspis	●	●	-	-	-	?8	?7	??	●	-	●	-	●	M.Cam.
Caryocaris	?	●	-	-	-	-	?7	●	●	-	-	-	-	Ord.
Ceratiocaris	●	●	-	-	??	8	7	●	●	●	●	●	5	?Ord., ?Perm.
Concavicaris	●	●	-	-	-	-	-	●	●	-	-	-	-	Dev.-Penn.
Coreocaris	-	-	?	-	-	-	?4	●	?	?	-	-	-	L.Perm.
Dictyocaris	-	-	●	-	-	-	?8	-	-	-	-	-	-	Sil.-Dev.
Dithyrocaris	-	●	-	●	●	+7	7	●	●	-	●	-	-	Dev.-Penn.
Echinocaris	-	●	-	-	?	-	+6	●	●	-	●	-	-	? Dev.-Miss.
Eleutherocaris	-	●	-	-	-	-	-	●	●	-	-	-	-	U.Dev.
Elymocaris	●	●	-	●	●	-	+6	●	●	-	●	-	-	Dev.
Gonatocaris	?	●	-	-	●	-	+5	?	-	-	-	-	-	U.Sil.
Heroldina	●	●	-	-	-	-	+5	●	●	-	-	-	-	L.Dev.
Hymenocaris	-	-	●	-	-	-	?11	●	●	?	-	-	-	Cam.-Ord.
Montecaris	-	●	-	-	-	+4	7	●	●	-	●	-	-	Dev.
Nahecaris	●	-	●	●	?	?8	7	●	●	●	●	●	5	● L.Dev.
Odaraiia	-	?	-	-	-	-	+2	-	●	-	-	-	-	M.Cam.
Ohiocaris	-	●	-	●	-	-	+3	●	●	-	●	●	-	U.Dev.
Orozoe	-	●	-	-	-	-	-	-	-	-	-	-	-	Dev.
Pephricaris	-	●	-	-	-	+3	?6	●	●	-	●	-	-	U.Dev.
Ptychocaris	-	●	-	-	-	-	-	-	-	-	-	-	-	Dev.
Pygocaris	●	●	-	-	-	-	+3	●	-	-	-	-	-	?L.Dev.
Rhinocaris	●	●	-	●	●	-	+4	●	●	-	●	●	-	Dev.
Saccocaris	-	-	-	-	-	-	?3	?	?	-	-	-	-	Cam.-Ord.
Sairocaris	-	-	●	-	-	+3	7	●	●	-	●	-	-	● L.Carb.
Silesicaris	-	●	-	-	-	-	-	●	-	-	-	-	-	L.Dev.
Tropidocaris	●	●	-	●	●	-	+3	●	●	-	-	-	-	Dev.

FIG. 122. Morphological features observed in 30 phyllocarid genera (Rolfe, n).

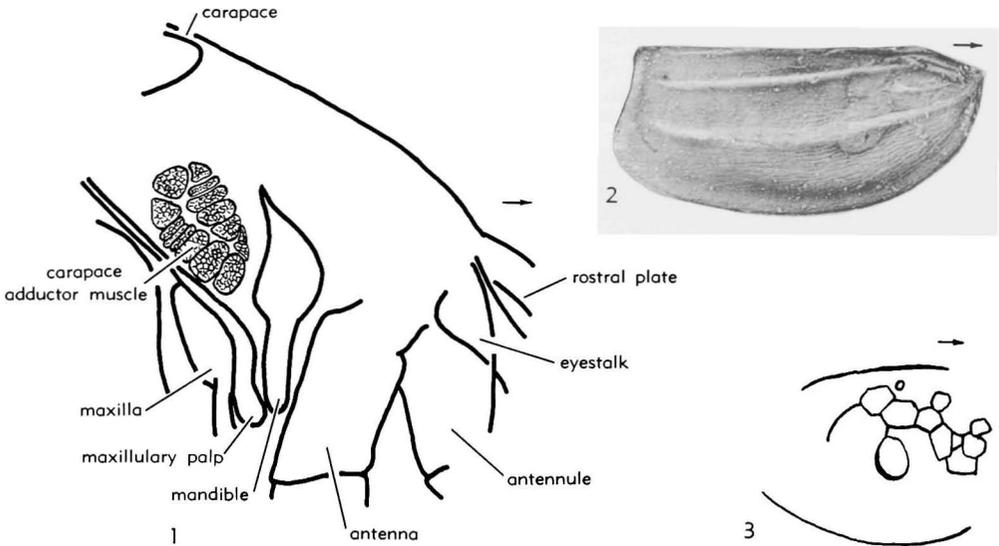


FIG. 123. Carapace muscle attachments in Phyllocarida; right lateral views.—1. Leptostracan *Nebalia bipes* (FABRICIUS), Rec., showing attachment of carapace adductor muscle, ca. $\times 50$ (366).—2. *Tropidocaris bicarinata* BEECHER, U.Dev., USA, showing anteromedian carapace adductor and cephalic limb muscle impressions between carinae, $\times 6$ (Rolfe, n).—3. *Ceratiocaris praecedens* CLARKE, U.Sil., USA; muscle scar on anterior tubercle, $\times 10$ (Rolfe, n).

caris where the posterior thoracic somites are exposed, as in many mysids. It may possess or lack a **hinge line** (Fig. 122), and in species of *Ceratiocaris* the hinge line is strengthened by three simple **hinge nodes** borne on the right valve (see Fig. 136). A large carapace must be more heavily sclerotized in order to maintain its shape and a zone must be left unsclerotized to permit hingement of the valves. In smaller, weakly sclerotized carapaces there is sufficient rigidity to maintain the shape and yet enough flexibility for movement without such a hinge line. In the Rhinocarina the valves are separated by a **median dorsal plate** extending back from the anterodorsal region. A double hinge structure is thus produced which may have permitted the valves to open out laterally.

In the Leptostraca the two valves of the carapace can be approximated by the **carapace adductor muscle**, derived from the maxillary somite. It is composed of a pair of lateral bundles of muscles united medially by a horizontal ligament, and is attached to the carapace anterolaterally (Fig. 123,1). Well-defined scars occur in *Canadaspis* and *Tropidocaris* (Fig. 123,2). The muscle scar seen above the carapace ad-

ductor scar presumably indicates the attachment of a cephalic limb dorsal muscle. Although carapace adductor muscle scars have been reported from many archaeostracans, few have been adequately demonstrated.

Pits left by individual muscle bundles have been observed on what CLARKE regarded as the "distinct eye node" of *Ceratiocaris praecedens* CLARKE (Fig. 123,3). This raises the question of whether such nodes may not be apodemes for the attachment of cephalic muscles to an otherwise probably flimsy carapace. BEECHER (1902) observed the apical invagination of these nodes in the Rhinocarididae and suggested that they might be attachment points for mandibular muscles. Other "optic nodes" described from fossil Phyllocarida are impressions through the carapace of the thickened dorsal apex of the mandible, or scars left by epiphytic organisms, such as discinid or craniid brachiopods. Others might be genuine eye tubercles, and would have value in generic or familial classification.

However, the tubercle may or may not be discernible in individuals of the same species of *Silesicaris* (128) and *Rhinocaris*, and is a variable character within these

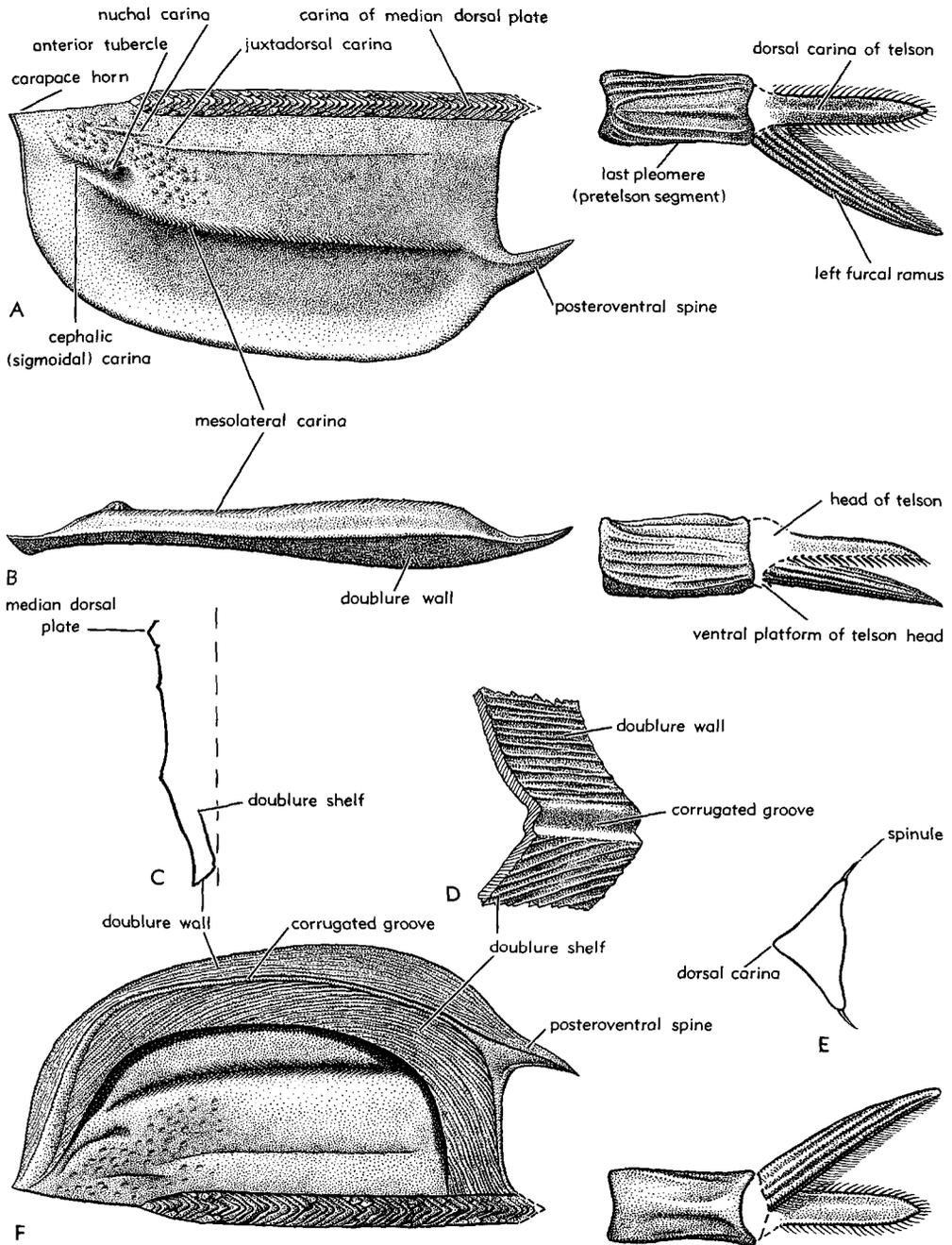


FIG. 124. *Dithyrocaris paradoxides* (ДЕКОНИЦК), L. Carb., Belg., showing morphological features of Archaeostraca Rhinocarina; only left side shown. The median dorsal plate is unknown in this species but one of *D. granulata* type has been interpolated. A. B. Dorsal and left lateral views, $\times 1$. C. Transverse section through middle of carapace, the broken line suggesting position of horizontal plane in relation to attitude of the valve during life, $\times 1$. D. Oblique view of slice of ventral doublure showing longitudinal striae of the wall and asymptotic striae of the shelf separated by corrugated groove, $\times 7$. E. Transverse section through middle of telson, $\times 4$. F. Ventral view, $\times 1$ (Rolfe, n).

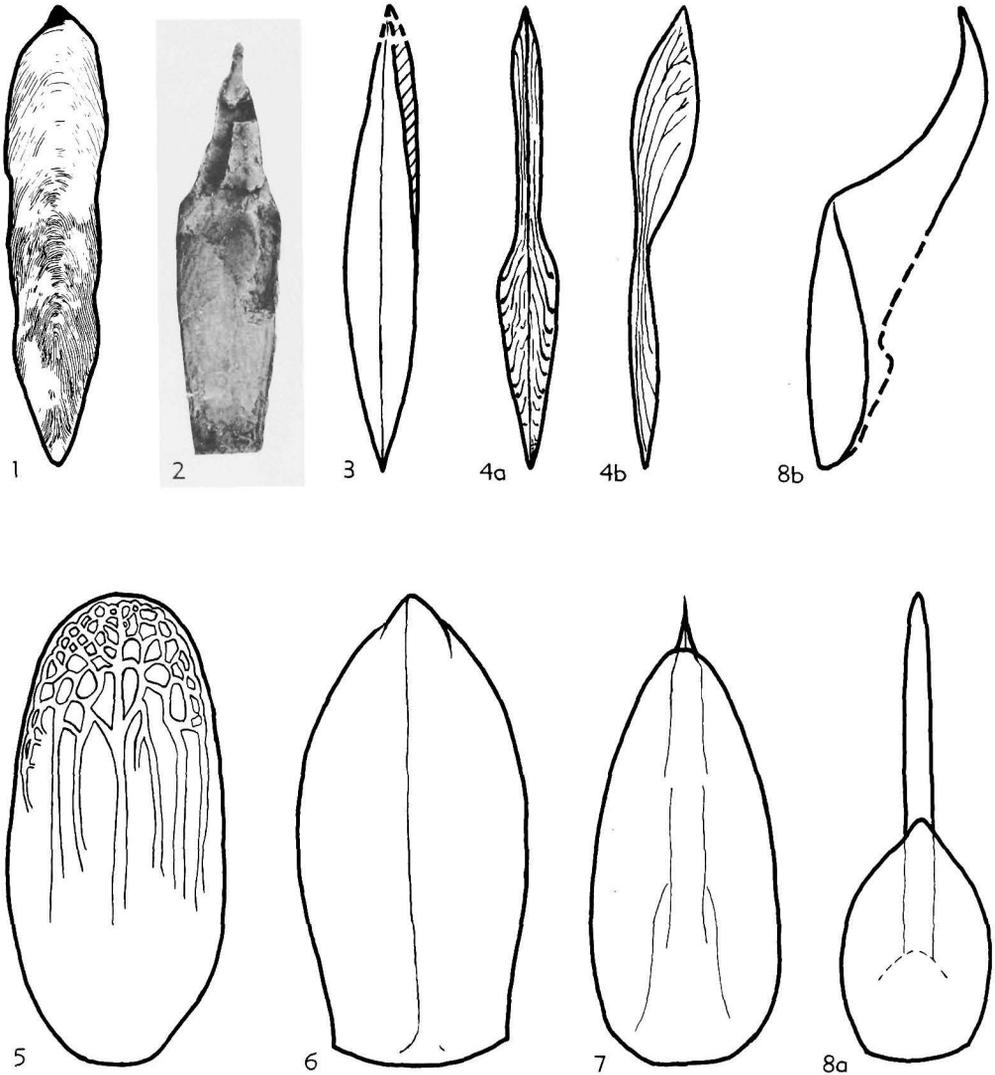


FIG. 125. Rostral plates of Phyllocarida; dorsal views, except where indicated, and oriented with anterior tip uppermost.—1. *Ceratiocaris papilio* SALTER in MURCHISON, M.Sil., Scot., $\times 3$ (258).—2. *Pygocaris schuberti* PERNER, ?L.Dev., Czech., $\times 5$ (Rolfe, n).—3. *Elymocaris siliqua* BEECHER, U.Dev., USA, right dors. lat., $\times 7.5$ (Rolfe, n).—4. *Rhinocaris columbina* CLARKE in HALL & CLARKE, M.Dev.-U.Dev., USA; 4a,b, dors., right lat., $\times 3.3$ (351, mod.).—5. *Nebalia geoffroyi* H. MILNE-EDWARDS, Rec., Medit.-E.Atl., showing median blood vessel and afferent network, $\times 60$ (352).—6. *Nebaliopsis typica* SARS, Rec., Atl.-Pac.-SW.Ind.O., $\times 20$ (382a, mod.).—7. *Paranebalia longipes* (WILLEMOS-SUHM), Rec., NW. Atl.-NW.Pac., $\times 75$ (377b).—8. *Nebaliella extrema* THIELE, Rec., Antarct.O.; 8a,b, dors., right lat., $\times 46$ (349, 382b).

genera. For this reason the significance previously accorded this polygenetic character is here minimized by synonymizing genera (e.g., *Emmelezoe*, *Limnocaris*) that are differentiated solely by the possession of such a structure (here termed **anterior tubercle**).

The carapace valves of Leptostraca are pervaded by a dense network of blood vessels and lacunae and, like the thoracopodal epipods and exopods, function as respiratory organs. Blood leaves the tubular heart anteriorly, flows through the network of each carapace valve and returns to the peri-

cardium opposite the last lateral ostium by a large posterdorsal afferent vessel. The well-marked branching ridges on the valves of *Carnarvonia* (see Fig. 149), *Rhinocaris*, and *Tropidocaris* (see Fig. 146) mark the position of internal grooves which possibly accommodated afferent blood vessels. These genera show a similar pattern of a posterior group of vessels converging into one main vessel which terminates anteriorly just dorsal from the carapace adductor muscle. This contrasts with the subvertical direction of the main blood vessel in the Ostracoda (HENNINGSMOEN, 1954, p. 55).

In the Aristozoidae and Echinocarididae the anterodorsal region of the carapace is inflated into lobes, which BEECHER attempted to correlate with subjacent cephalic appendages. Most of the lobes are situated too far dorsally to mark the position of such appendages, however.

A thickened rim is present along the free margin of most archaeostracan carapaces, in some forms separated from the main area of the valves by a marginal groove. This rim is distally reflected to form a **doublure**, in life connected with the cephalon by thin unsclerotized integument. The doublure is usually simple, but it may be elaborated into a proximal wall and a distal shelf in species of *Dithyrocaris* (Fig. 124). These marginal structures are commonly impressed through the outer integument of the carapace during diagenesis.

Anterodorsally, the carapace valve may terminate in a thickened **carapace horn**, which abuts against the thickened tip of the rostral plate in *Ceratiocaris*. In *Caryocaris maccoyi* (ETHERIDGE), the right and left carapace horns are produced into long slender processes, but they do not fuse together to form the eumalacostracan type of rostrum.

ROSTRAL PLATE

The carapace is produced anteriorly into a movable **rostral plate**. In the Archaeostraca the few rostral plates known (Fig. 122) are situated more dorsally than in Recent Leptostraca, where the rostral complex (68) is specialized for feeding. Figure 125 shows the variation in shape of phyllocarid rostral plates, which suggests that this

structure may be of use for future classification of the Archaeostraca.

EYES

Pedunculate compound eyes are present in Leptostraca, although the ommatidia have been lost in *Nebaliella* and *Nebalia typhlops*. Stalked eyes are known only from *Canadaspis* (see Fig. 149) and *Nahecaris*, but presumably most Archaeostraca had such eyes. The supposedly sessile eyes have been discussed above.

TRUNK

Two tagma can be distinguished in the trunk of Leptostraca and in several Archaeostraca (Fig. 122). These comprise a thorax of eight short segments, and an abdomen of eight longer segments, including the telson. Short pleurae may be present on the pleomeres of Leptostraca and Archaeostraca; large pleural spines are found in *Montecaris lehmanni* and *Pephricaris*.

In the Leptostraca, and also probably in the Hymenoststraca, the telson resembles the preceding pleomeres except that it bears a pair of posteroventral spines and the **furcal rami** at its distal end. In the Archaeostraca, however, the telson is produced dorsally between the furcal rami, which articulate proximally with the enlarged **telson head**. The furcal rami are commonly rodlike, but in *Nebaliopsis* and many Archaeostraca they are dorsoventrally flattened. In many Archaeostraca these expanded and densely setiferous rami formed with the flattened telson an efficient swimming structure analogous to the eumalacostracan tail fan (27). The archaeostracan telson head usually bears a **ventral platform** embracing the proximal part of the furca. In one species of *Schugurocaris*? (Fig. 126) the ventral surface of the telson head has a large area without cuticle, which probably was originally filled by the unsclerotized integument around the anus. The small median process just in front of this area (Fig. 126) is homologous with that in *Aristozoe regina* BARRANDE, which NOVÁK suggested controlled ventral flexure of the telson.

The spiniferous telson of the small *Ceratiocaris pusilla* MATTHEW is unusual in having been whiplike and flexible during life.

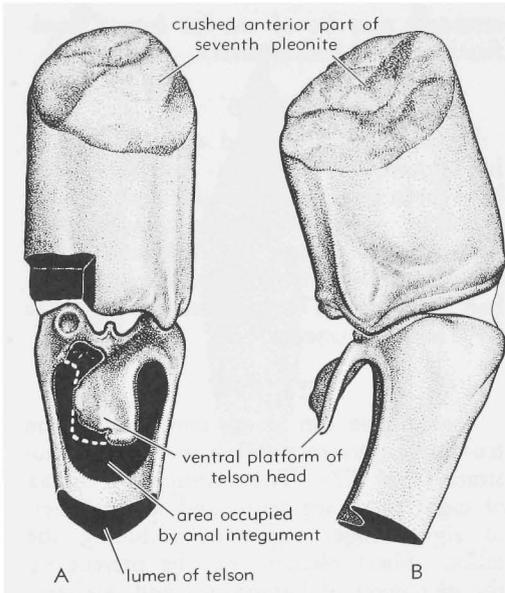


FIG. 126. Seventh pleonite (crushed anteriorly) and telson head of *Schugurocaris? cornwallisensis damesi* (CHLUPÁČ), U.Sil., Czech., showing articulation, ventral platform of telson head and space originally occupied by thin anal integument.—A. Ventral view, with right posteroventral process of pleonite cut away to show telson socket, $\times 1$.—B. Left lateral view, $\times 1$ (376b, mod.).

Dorsal spinules on the telson of *C. papilio* are set in thin-walled sockets (see Fig. 136), and were probably sensory.

APPENDAGES

The limbs of fossil Phyllocarida are poorly known, with the exception of the mandible, which has been recorded from numerous genera (Fig. 122). The following list tabulates the major records of such limbs with a brief description of each.

Fossil Phyllocarida Appendages

Canadaspis perfecta (WALCOTT), *M.Cam.*, B.C.; uniramous antenna, ?cephalic limbs, eight thoracopods composed of eight short segments with basal nonfilamentous ?epipod (WALCOTT, 1912; STØRMER, 1944).

Ceratiocaris telleri (WHITFIELD) and *C. monroei* WHITFIELD, *U.Sil.*, USA (Wis.); limb fragments (WHITFIELD, 1896).

Ceratiocaris papilio SALTER in MURCHISON, *M.Sil.*, Scot.; ?antennae, ?maxillipeds, seven slender thoracic endopods of at least four segments, five stouter pleopods (JONES & WOODWARD, 1888; ROLFE, 1962).

Coreocaris eishunensis KOBAYASHI, *L.Perm.*, S.Korea; ?antennae (KOBAYASHI, 1937).

Dithyrocaris sp., *L.Carb.*, N.Fr.; cephalic limb fragments (CARPENTIER, 1913).

Dithyrocaris? sp., *L.Carb.*, S.Fr.; thoracic branchiae (BÖHM, 1935).

Hymenocaris ornata SHERRARD, *L.Ord.*, S.E.Australia; ?antennae (SHERRARD, 1930).

Nahecaris stuerzi JAEKEL, *L.Dev.*, Ger.; antennae, eight thoracopods, five pleopods (BROILI, 1928, 1929).

Nahecaris balssi BROILI, *L.Dev.*, Ger.; antennae (BROILI, 1930).

Ohiocaris wycoffi ROLFE, *U.Dev.*, USA (Ohio); four thoracic ?endopods (ROLFE, 1962).

Rhinocaris? bipennis CLARKE, *U.Dev.*, USA (N.Y.); cephalic or thoracic limb fragments (CLARKE, 1898).

The archaeostracan mandible is well known only from *Ceratiocaris*, but that of other genera seems to have been identical. As can be seen in Fig. 127,2 the mandible is of generalized type, with a large inflated **mandible body** (corpus mandibulae) and a **gnathal lobe** set with paired incisor teeth and a simple molar process. In two species of *Ceratiocaris* the molar process is known to have a broad, laterally ridged surface for grinding (Fig. 127,1). The large **mandi-**

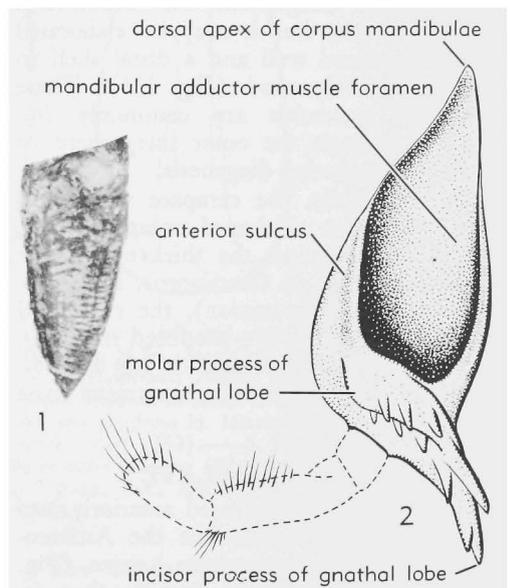


FIG. 127. Mandible of *Ceratiocaris*.—1. *C. monroei* WHITFIELD, *U.Sil.*, USA (Wis.), tooth base and ridged molar process of left mandible, $\times 6$ (258).—2. *C. papilio* SALTER in MURCHISON, *M.Sil.*, Scot., right mandible, mesial view, with palp of *Anaspides* type reconstr., $\times 6$ (Rolfe, n).

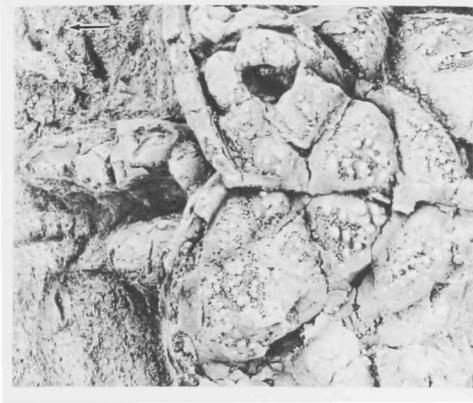


FIG. 128. *Echinocaris randallii?* BEECHER, L. MISS., USA (Pa.), three segmented ?mandibular palps at left, protruding from anterior of carapace valves, $\times 2.4$ (Rolfe, n). [According to K. E. CASTER, the right appendage was chelate when the specimen was originally collected by him.]

bular adductor muscle foramen for the transverse adductor muscle is rimmed by shallow anterior and posterior sulci marking internal ridges for attachment of dorsal muscles. BEECHER'S "manubrium" was simply a part of the corpus mandibulae preserved adjacent to this foramen. A palp has not been found in *Ceratiocaris*, although a small circular **palp foramen** is always present. A **palp** of at least three segments is present in *Echinocaris punctata* (HALL) and this was figured, although not recognized as such, by HALL & CLARKE (140, pl. 29, fig. 7). The stout, three-segmented appendages occasionally found protruding from the carapace of *Echinocaris* may be mandibular palps (Fig. 128).

No proof has been found that gastric teeth or ossicles are present in the Archaeostraca, although such teeth might be expected to occur. The structures referred to as such by previous authors are the heavily sclerotized, commonly abraded, gnathal lobes of the mandible, which are commonly all that remains after the thin-

ner corpus mandibulae has been broken off or crushed. The broader teeth illustrated by JONES & WOODWARD (160, pl. 26) are internal molds of the paired, thick-walled teeth, and not the surface of the cuticle.

The significance of the cephalic limbs of *Nahecaris* and the thoracopods of *Canadaspis* will be discussed under phylogeny, but it may be emphasized here that knowledge of the limb structure of these genera is inadequate for phylogenetic speculation.

Filamentous thoracic branchiae have been figured from *Dithyrocaris*; they are unknown in other Phyllocarida, however, and detailed study is required.

The least specialized leptostracan thoracopods are found in *Paranebalia*, and these contrast with the specialized thoracopods of *Nebalia*, which have large epipods and exopods (Fig. 129). The thoracopods are all similar, except in *Nebaliopsis*, where the first limb is modified to act as an interlimb space valve. In all Leptostraca except *Nebaliopsis*, the tip of each thoracic endopod of the breeding female carries long setae which curve inward to form the floor of a brood chamber in which the embryos develop.

Five pairs of lamellar pleopods occur in *Nahecaris* and probably also in *Ceratiocaris papilio*. In the Leptostraca six pairs of pleopods are present but only the first four are large and biramous, the posterior two being small and uniramous. The right and left limbs of the anterior four pairs are linked together by a small spined appendix interna at the base of the endopod to form powerful swimmerets.

SEXUAL DIMORPHISM

All Recent Leptostraca, except *Nebaliopsis*, show pronounced sexual dimorphism. Males also occur much more rarely than females. The carapace of the male is less deep than that of the female and the antennae are much longer (Fig. 130). In the male *Nebalia* the antennae may reach to the tips of the furca, whereas in the female they are shorter than the carapace. The furca of the male *Nebalia* is also longer than that of the female, the pleopods are larger and the antennules bear a greater number of sensory bristles.

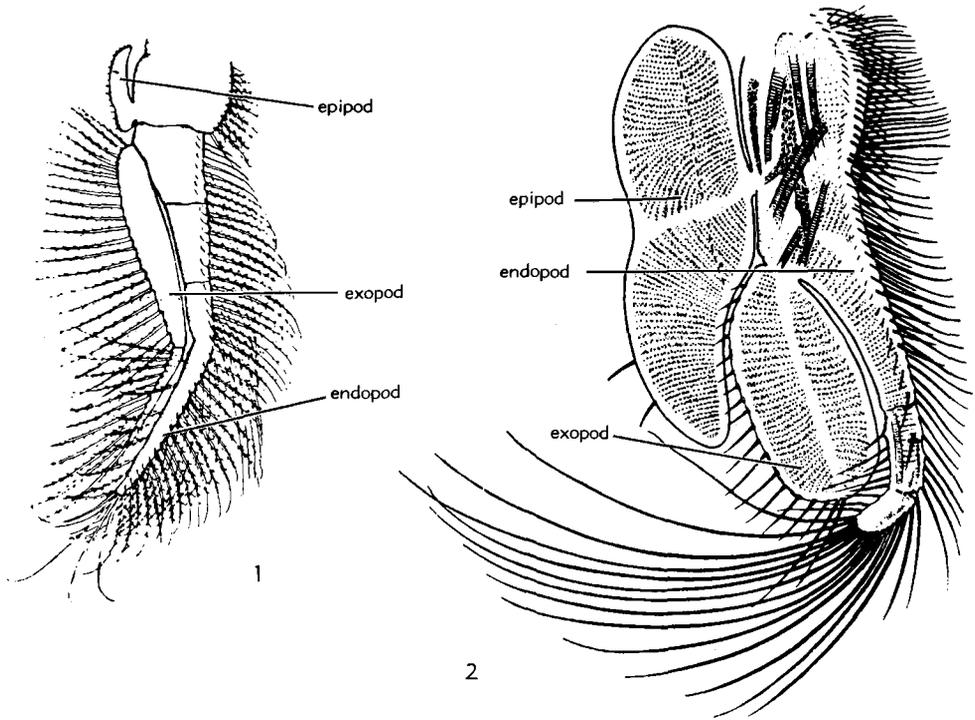


FIG. 129. Thoracopods of Recent Leptostraca showing little specialized and highly specialized conditions. —1. *Paranebalia longipes* (WILLEMOES-SUHM), fifth thoracopod of adult female, $\times 40$ (65, after 377b). —2. *Nebalia geoffroyi* H. MILNE-EDWARDS, first thoracopod of adult female, ca. $\times 25$ (68, after 352). (Fig. 129,1 from W. T. Calman in Lankester Treatise on Zoology, Pt. 7, Appendiculata, fasc. 3, A. & C. Black, Ltd., publishers, London; Fig. 129,2, from H. G. Cannon, 1960, in BRONN's Klassen und Ordnungen des Tierreichs, v. 5, Abt. 1, Buch 4, Teil 1.)

The antennules or antennae of the male may be modified in different genera, presumably to function as clasp ing organs. *Nebalia pugetensis* (CLARK) has an anteriorly curved, sickle-shaped region of the antenna consisting of about 30 segments, each segment bearing in front a spoon-shaped seta. In *Paranebalia* the antennular flagellum is transformed into a papillate cushion, and in *Nebaliopsis* the two terminal segments of the antenna are bent back to form a hook.

The ratio of carapace length to height has been used to differentiate species of *Ceratiocaris* and *Caryocaris*, although paleontologists since SALTER have been aware of the problem of sexual dimorphism. Scottish Silurian species of *Ceratiocaris* have been examined statistically but no significant difference in carapace shape was found between forms previously regarded as sexual dimorphs and distinct species. Variation

within one species of *Austriocaris* was attributed by GLAESSNER to sexual dimorphism.

PATHOLOGY

Fig. 131 shows a specimen of *Dithyrocaris* in which the mesolateral carina has been bowed out, presumably owing to a wound received during the soft-shell period of the molt cycle.

MISIDENTIFICATION

Fossil phyllocarids have commonly been misidentified, perhaps for the first time by LOUIS AGASSIZ, who in 1837 referred a species to his fish-spine genus *Onchus*. BARRANDE (1853) showed that this was neither *Onchus*, nor a eurypterid claw, as M'COY had suggested in 1849, but the telson and furcal ramus of a species of M'COY's own crustacean genus *Ceratiocaris*, previously known only from carapaces. Other instances

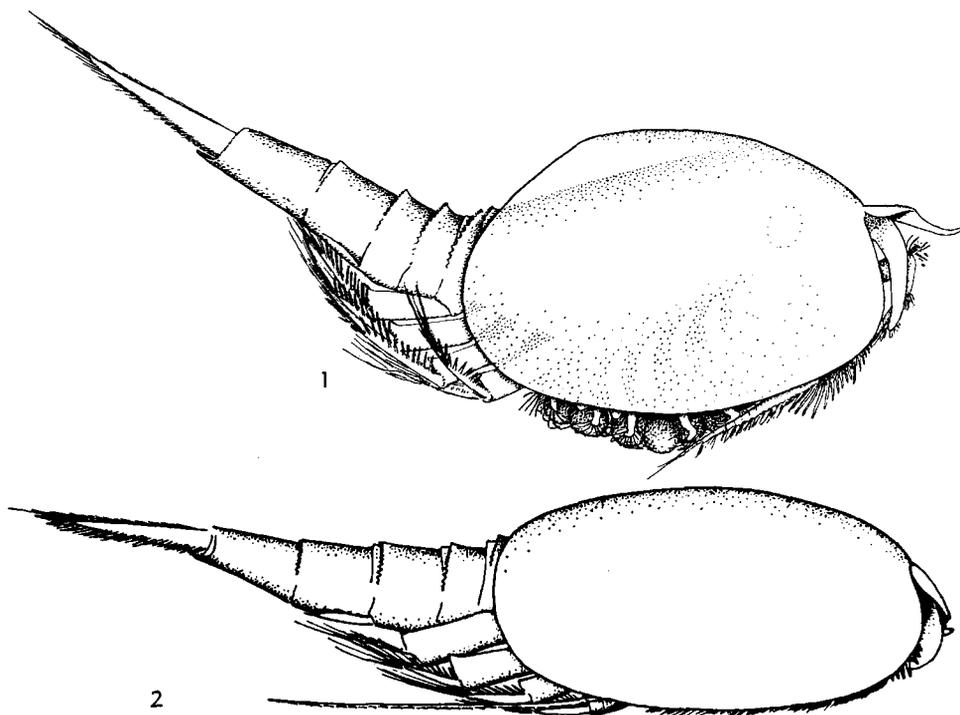


FIG. 130. Sexual dimorphism in *Nebaliella extrema* THIELE, Rec., right lateral view.—1. Female, $\times 10$ (349).—2. Male, ca. $\times 20$ (68) (Fig. 129, 2, from H. G. Cannon, 1960, in Bronn's Klassen und Ordnungen des Tierreichs, v. 5, Abt. 1, Buch 4, Teil 1).

of archaeostracan telsons and furcal rami being mistaken for fish spines are known, although they are quite distinct in general morphology and especially in microstructure.

Isolated archaeostracan carapaces may be difficult to distinguish from Bivalvia, and numerous carapaces now regarded as Ostracoda Archaeocopida are indistinguishable, except by their smaller size, from carapaces referred to the Phyllocarida. Whether such resemblances as that of the large *Pseudoarctolepis sharpi* to the ostracode *Pteroleperditia* are only due to convergence it is impossible to say. Convergent resemblances among crustacean carapaces are well known, as ROGER (1946) has pointed out, and carapaces should therefore not be referred to the Archaeostraca until the trunk tagma and furca are known. It is worth recalling that the Recent phyllocarid *Nebaliopsis* was first described as a gigantic ostracode, since only the carapace was brought up in the dredge.

Carapaces, telsons, and furcal rami of *Caryocaris* have been interpreted as graptolite rhabdosomes, floats, and "ovarian capsules," primarily on account of their occurrence in graptolite-rich shales.

Isolated archaeostracan mandibles are sometimes regarded as problematica, and CHLUPÁČ (73) has pointed out such an instance where gnathal lobes were described in a 1958 work on conodonts.

ONTOGENY

The eggs of all Leptostraca, except possibly in *Nebaliopsis*, are carried in the thoracopod brood chamber beneath the carapace. Development is embryonic and the young hatch as postlarvae. These postlarval or mancoid stages, as LINDER has termed them, differ from the adults in having a rudimentary 4th pleopod. CANNON has recently attributed a free-swimming, pelagic larva to *Nebaliopsis* (68), and suggested that the eggs of *Nebaliopsis* were laid

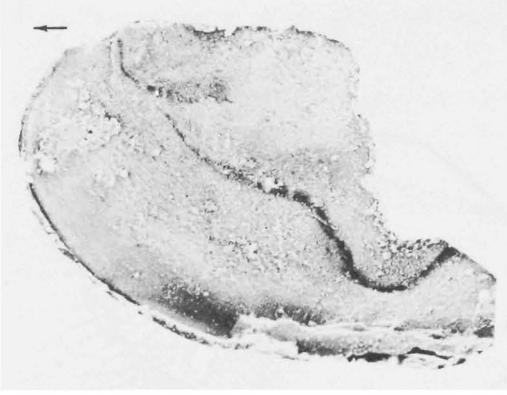


FIG. 131. Pathological right valve of *Dithyrocaris paradoxides* (DEKONINCK), L.Carb., Belg., rubber mold of fragment showing mesolateral carina bowed out in median region; (compare with normal valve shown in Fig. 124,A), $\times 3$ (Rolfe, n).

directly in the water. The presence of large antennae and yolk mass in the larva are, CANNON has suggested, adaptations for this planktonic existence.

HABITAT, DISTRIBUTION, AND HABITS

The only nonmarine form attributed to the Phyllocarida is the problematical *Coreocaris*. Other fossil genera are associated with undoubtedly marine faunas, or with primitive vertebrates and eurypterids. The second association is almost always enhanced by selective diagenesis of calcareous shells, with consequent enrichment of the preserved fauna in the noncalcified elements. No convincing evidence is found to indicate that the Archaeostraca were either fluvial (O'CONNELL) or "continental" (JUX, 162).

Fossil phyllocarids are generally rare, although they are locally abundant in the Middle Silurian laminated siltstones of Lesmahagow, South Scotland, the Upper Devonian of Cologne, Germany, and of Western Australia, the Viséan limestones of Visé, Belgium, and the Middle Pennsylvanian Mecca Shale of Indiana.

The wide distribution of the fossil *Caryocaris* and Recent *Nebaliopsis* is doubtless correlated with their large expanded furcal rami, which made sustained swimming possible. *Nebaliopsis* is bathypelagic and lives at depths down to 2,500 m., whereas

Caryocaris occurs in graptolitic shales and has been suggested to be planktonic. The remaining Leptostraca are bottom-dwellers and commonly live buried in the mud or under stones in shallow coastal waters, although species occur down to depths of 2,200 m. *Nebalia bipes* is extremely widespread, very resistant to unfavorable conditions, and thrives in water foul with decaying organic matter (65).

From studies of facies in Czechoslovakia and Eastern Europe, CHLUPÁČ (73) and KRESTOVNIKOV (168) have independently concluded that the thick-shelled forms *Aristozoe*, *Callizoe*, and *Orozoe* were benthonic and confined to shallow reef environments. Genera with a thinner cuticle, such as *Ceratiocaris*, they suggested were nektonic and planktonic and favored calmer, coastal lagoonal or neritic habitats. The Upper Permian *Nebalia? bentzi* inhabited shallow, coastal marine conditions, according to MALZAHN (186).

Although all Leptostraca are strong swimmers, only *Nebaliopsis* is adapted for a nektonic life. The other genera are highly adapted for burrowing in the mud, and such features as the plowshare-like rostral plate, the blind, curved eyestalks, and the extra segment in the antenna of *Nebaliella* have all been explained by CANNON as modifications to that end. *Nebalia* has an extremely efficient feeding mechanism for collecting the fine edible detritus from the mud, and this has been described in great detail by CANNON (1927). A feeding-respiratory current is sucked into a **filter chamber**, formed by the thoracopods and ventral body wall, by metachronal movements of the thoracopods. The current enters anteriorly, since the lamellar epipods and exopods act as valves preventing the lateral entry of water, while the amount entering is controlled by elevating or depressing the rostral plate. Food particles are filtered off by rows of setae on the endopodites and then combed from the filter setae and passed anteriorly to the mouth parts by other setae. The filtered current of water is then pumped laterally out of the chamber by the eighth thoracopods via the seventh interlimb space. When the filter chamber is blocked with eggs, the female utilizes food reserves stored in the fat-body.



FIG. 132. X-ray photograph of *Nahecaris stuertzi* JAEKEL, L.Dev., Ger., dors., showing mud-filling of intestine (light) through pyritized (dark) abdomen, $\times 0.75$ (Rolfé, n).

Nebaliopsis is specialized for feeding in quite a different way, as ROWETT has shown (1943, 1946). Although it possesses a filter chamber formed by the maxilla and first thoracopod, its main sustenance is probably derived from eggs floating in the water. These are sucked in and stored in the large midgut diverticulum and assimilated as required.

The alimentary canal of many fossil phyllocarids may be traced by the sediment

originally filling the gut (Fig. 132). This suggests that these genera were deposit-feeders, which probably, like CANNON's "ancestral *Nebalia*, would have fed simply on large pieces of detritus picked up directly by the mouth parts." The powerful archaeostracan mandible would be very suitable for dealing with large fragments.

BROILI (1928) has interpreted the antennae of *Nahecaris* as locomotory organs and suggested that the body limbs formed good swimmerets. The telson and furca were doubtless moved by powerful muscles situated in the elongated seventh abdominal segment, and BROILI has pointed out that the tail was probably used in swimming and steering. BEURLÉN (1930) has suggested that most Archaeostraca were benthonic and that the furcal spines were used in leaping forward.

Rhinocarididae, such as *Dithyrocaris*, may have had their carapace valves spread out laterally during life, suggesting a benthonic habit. This would imply considerable modification of the limbs and internal structures such as the carapace adductor muscle.

PHYLOGENY

The lack of detailed morphological data for most fossil phyllocarids, rightly emphasized by neontologists since CLAUS, has led to much speculation about their affinities. They have been compared with Notostraca, Conchostraca, Ostracoda, and free-living Cirripedia by FEDOROV and others, and with Eumalacostraca Euphausiacea by ROGER (256). Although some specimens may belong to some of these groups, no basis is seen for JUX's assertion (162) that all Archaeostraca should be referred to the Branchiopoda. The number and tagmosis of body segments and limbs, and the differentiation of the gnathal lobe of the mandible into incisor and molar processes, known from some of the Archaeostraca, leave no doubt that these are genuine Malacostraca. The large carapace, adductor muscle scar, rostral plate, and furca indicate their close relation to the Leptostraca.

Despite these complications, the Phyllocarida have long been recognized as the most primitive of malacostracans, the Paleozoic forms occupying various ecological

niches from which the later, higher Malacostraca were to displace them. Primitive features present in the Leptostraca according to SIEWING (271) are the rostral plate, eight free thoracomeres covered by a carapace but not fused with it, seven pleomeres, furca, both antennal and maxillary glands, heart extending from head into abdomen, lateral arteries segmentally arranged and consisting of visceral and limb components, gonads extending through whole body, and simple stomach and brain.

The presence of foliaceous thoracopods in *Nebalia* has classically been taken to indicate that the Leptostraca form a connecting link between the Branchiopoda and the Malacostraca. The absence of true endites from the thoracopods of *Nebalia*, together with the presence of more stenopodous thoracopods in *Paranebalia*, led CALMAN (65) to suggest that the phyllopodous form of the thoracopods might be secondary. CANNON has attacked the theory that the phyllopodium represents the archetypal crustacean limb and from a study of the feeding mechanism of *Nebalia* concluded that its foliaceous limbs are secondary adaptations for filter-feeding. Furthermore, the embryology of *Nebalia* was shown by MANTON (1934) to be eumalacostracan and not at all entomostracan.

Leptostracan specializations other than the lamellar thoracopods, according to SIEWING, are the carapace with adductor muscle, absence of posterior pleopods, presence of a scale on the antennule instead of a second flagellum, and absence of antennal exopod. The first two characters are present in Middle Cambrian forms and suggest that the Phyllocarida were already well differentiated from the ancestral malacostracan by that time.

The Middle Cambrian *Canadaspis* is poorly known and the supposedly trilobitan nature of the thoracopods has never been adequately demonstrated. The limbs can also be interpreted as endopods with a lamellar epipod but lacking an exopod. In the Upper Silurian-Lower Devonian, a great radiation from the Ordovician-Silurian ceratiocaridid stock gave rise to the Aristozoidae and Echinocarididae via *Callizoe* and *Ptychocarid*. It is possible that the Aristozoidae have reduced or lost the furca completely,

thereby indicating a major departure from the Ceratiocarina condition, as ČHLUPÁČ has pointed out. If this can be verified it would be of great interest as a reverse trend from that in the Leptostraca where the telson has been reduced. In the Middle Devonian the Rhinocarina were established from some line presumably within the Ceratiocarina. In terms of the number of genera, however, the Rhinocarina were less successful than the Ceratiocarina. The diminution in number of genera through the upper Paleozoic to only one genus in the Triassic suggests that the Archaeostraca were extinguished by the increase in number and diversity of the better adapted Eumalacostraca. Part of the post-Triassic lack of fossil Phyllocarida may be due to oversight. Little-known carapaces from the Mesozoic such as *Clausia* and *Protozoëa* are regarded as stomatopod larvae, but if found in Paleozoic strata they would be referred to the Phyllocarida.

The origin of the Leptostraca in or before the Late Permian is obscure; they were possibly derived from some basal stock within the Ceratiocarina or even the Hymenostrostraca. More probably, however, they diverged from the hypothetical cephalocarid-like ancestor (SANDERS, 1955, 1957, 1959) earlier than the other Phyllocarida. The long preperacarid geological history of the Phyllocarida does not support CANNON's suggestion (1927) that *Nebalia* "evolved from some primitive mysid-like malacostracan." It is likely that the reverse derivation occurred, the Phyllocarida representing the stock from which the eumalacostracan or caridoid type was eventually derived.

Following BROILI and BEURLEN, SIEWING (271, p. 153) has emphasized that the lack of a hinge line in the carapace, the biramous nature of the antennules, and the antennal exopod of *Nahecaris* are eumalacostracan features, and that *Nahecaris* can thus be regarded as a link between the Leptostraca and Eumalacostraca. However, BROILI's interpretation of the carapace structure is probably erroneous and *Nahecaris* is here reassigned to the Rhinocarina. The specialized rhinocaridid carapace structure prevents *Nahecaris* from being a simple "missing link" between the two groups. Furthermore, BROILI was not able to prove that the supposed exopod of the antenna did, in fact,

spring from the antennal protopod. Although this may be the case, the supposed exopod might belong to a more posterior cephalic appendage, and restudy is required. The biramous antennules do suggest an affinity with the Eumalacostraca and they contrast with the small antennular exopods of the Leptostraca, which may be secondary and due to relatively recent reduction, rather than being a primitive feature.

Several attempts have been made to relate other crustacean subclasses to the Phyllocarida. RUEDEMANN (1918) suggested that the sessile Cirripedia were derived from one of the Rhinocarina by a modification of the carapace to form compartments. This speculation, which recalls THOMPSON'S (1830) idea that *Nebalia* was the active larva of the sessile whale-barnacle *Coronula*, was shown by CALMAN (1919) to be based on superficial resemblances. BERNARD (1892), a proponent of the phyllopodan nature of the Phyllocarida, argued that "the extraordinary likeness of the shells of some of the early Ostracoda (e.g., *Leperditia*) to the shells of such phyllo-pods as *Ceratiocaris salteriana* makes a phyllo-podan origin for at least some of the Ostracoda very probable." Similarly, the genera now grouped under Ostracoda Archaeocopida were suggested by KUMMEROW in 1931 to bear the same relation to the Phyllocarida as the Decapoda Brachyura do to the Macrura. This suggestion was effectively formalized in RAYMOND'S 1935 classification of the Archaeostraca. Again, the similarity of the carapaces in these is probably only superficial and due to convergence. GLAESSNER (1928) suggested that the Cycloidea could be considered as benthonic Phyllocarida, the lack of a free abdomen perhaps paralleling the brachyuran trend of the Decapoda. Despite the work of HOPWOOD (1925) and others, the ventral morphology of the Cycloidea is still inadequately known and thus, as VAN STRAELEN & SCHMITZ (312) have pointed out, the systematic position of the group must remain uncertain.

CLASSIFICATION

The first phyllocarid found was described as *Cancer bipes* by FABRICIUS in 1780 and initially regarded as a malacostracan. From

the foliaceous nature of the thoracopods, MILNE-EDWARDS (1828) was led to suggest that this species was a branchiopod, and it was not until 1868 that *Nebalia* was shown to be a malacostracan (a "phyllopodiform decapod") by METCHNIKOV from its embryology and gastric mill. Meanwhile, several fossil phyllocarids had been described. SCOULER (1835) had described two Carboniferous phyllocarids and referred them to the Entomostraca Branchiopodes, the group to which LATREILLE had already in 1829 referred *Nebalia*.

The first direct comparison of a fossil form with *Nebalia* was not made until 1853, when SALTER described *Hymenocaris*. In 1879 PACKARD proposed that the fossil forms be united with the Nebaliidae to form a separate order of Crustacea, named Phyllocarida. CLAUS had already stressed (1872) that little was known of the fossil forms and their relationships, and in 1880 he reiterated this and, apparently unaware of PACKARD'S order, proposed the term Leptostraca for the Recent forms. In 1888 CLAUS firmly established the malacostracan nature of *Nebalia* and, emphasizing the supposed variability in number of body somites, separated the fossils as Archaeostraca. Subsequent use of the three names has been confused, despite BEURLIN'S clear summaries (29) of the history outlined above.

In the present treatment the old division of the Phyllocarida into Archaeostraca and Leptostraca is accepted with the addition of a new order, Hymenostocraca. The GROBBEN (1892) and CALMAN (1904) position of the Leptostraca is thus slightly emended, but the term will still be available to neontologists in its most usual connotation, namely for the Nebaliidae.

Ordinal classification is based essentially on the nature of the telson and furca. Such single-character classification is obviously unsatisfactory, but few other morphological features observable in fossil material are as conservative or reliable. Since 1880, when WHITFIELD published a table showing the "maximum number of naked segments known" in 13 fossil forms, undue emphasis has been laid on the supposed variation in number of body segments. As CALMAN (1913) pointed out, if this variation did

exist new orders would be required, and it would be difficult to regard them even as Malacostraca (271, p. 143). In fact, as Figure 122 shows, of 30 fossil phyllocarid genera tabulated, the number of abdominal somites (telson not included) is known with certainty in only five genera and the number of thoracic somites in only one, or possibly three. Significantly, the numbers of somites in these tagmata are respectively seven and eight, as in the Leptostraca. *Dithyrocaris*, for example, was reported by WHITFIELD to have one somite and by JONES & WOODARD (1898) to have three; but it was not until 1916 that CARPENTIER was able to prove the presence of seven abdominal somites and at least seven thoracic somites. The number of somites in other genera may be different but it has never been shown to be so.

Another character used in classification has been the nature of the carapace, whether with or without a hinge line. JONES & WOODWARD (1883-1899) and others, in reports on British Paleozoic Phyllocarida, divided the fossil forms into two major groups on this single character, although they proposed no formal names for divisions thus recognized. This character is often difficult to ascertain, and such a classification minimizes the significance of the median dorsal plate first recognized by HALL & CLARKE (140). The presence or absence of a simple hinge line is probably phylogenetically insignificant and functionally dependent on the size and degree of induration of the valves to be articulated.

The characters most used in generic and familial classification have been carapace shape and the nature of surface ornament. By analogy with other crustacean groups, however, these might be expected to be the most variable of characters. Recent Leptostraca are differentiated mainly by their limb structure, and if found fossil they would be separated into only two genera on the basis of carapace form, one comprising *Paranebalia-Nebalia-Nebaliella* and the other *Nebaliopsis*. Thus, *Montecaris* has convergently acquired the peculiar double structure, mesolateral ridge, and posteroventral spine of *Dithyrocaris paradoxides*, but, as known at present, it lacks the median dorsal plate, thereby excluding it from the

Rhinocarina. Further convergences are undoubtedly hidden by the present classification, but the lack of more conservative characters suggests that this problem will not be solved easily.

In the present systematic descriptions only genera which are known from several tagmata are classified, with the exception of genera such as *Austriocaris* where relationships seem clear. The others are listed and described subsequently. A tabulation of suprageneric divisions of the Phyllocarida with numbers of genera contained in each is given on page R113.

SYSTEMATIC DESCRIPTIONS

Subclass PHYLLOCARIDA Packard, 1879

[=Phyllocardia ETHERIDGE, 1892; Phyllostraca HENNIG, 1922; Phyllofarida RICHTER & RICHTER, 1927; Phillocarida REIN, 1936; Phyllocarida KRESTOVNIKOV, 1961; Phyllocardida HOWE, 1962, p. 162]

Malacostraca with large carapace of two valves, with or without hinge line along dorsal margin, connected by adductor muscle, produced anteriorly into movably articulated lanceolate rostral plate. Thorax of eight short, free somites; abdomen of seven somites and telson, seventh abdominal somite without appendages, telson bearing unsegmented, movably articulated furca. *L. Cam.-Rec.*

Order LEPTOSTRACA Claus, 1880

[=Leptocarida HAECKEL, 1889; Nebaliadae GROBEN, 1892; includes *Nebaliina* CLARKE in ZITTEL, 1900; *Nebaliacea* CALMAN, 1904]

Small to medium-sized, carapace without hinge line, telson not produced dorsally between furcal rami; outer ramus of antennule reduced to a scale; antenna without exopod. Gnathal lobe of mandible reduced or with only single row of teeth; six pairs of pleopods, anterior four pairs comprising biramous swimmerets with large protopod, posterior two pairs small and uniramous. *U. Perm.-Rec.*

Family NEBALIIDAE Baird, 1850

[*nom. correct.* SARS, 1887 (*pro* Nebaliidae BAIRD, 1850)]
[=Nebaliidae CLAUDIUS, 1880; *Nebalida* HAECKEL, 1896]

Characters of order. *U. Perm.-Rec.*

MALZAHN has described an eight-somite, 8 mm. long, furca-bearing abdomen from

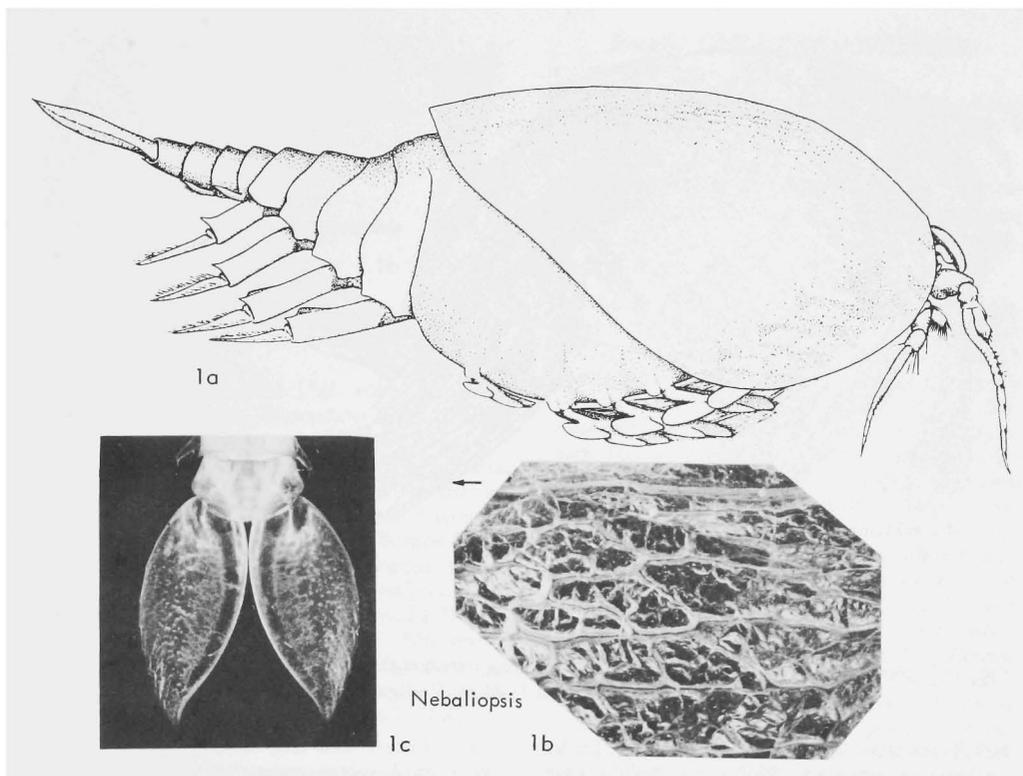


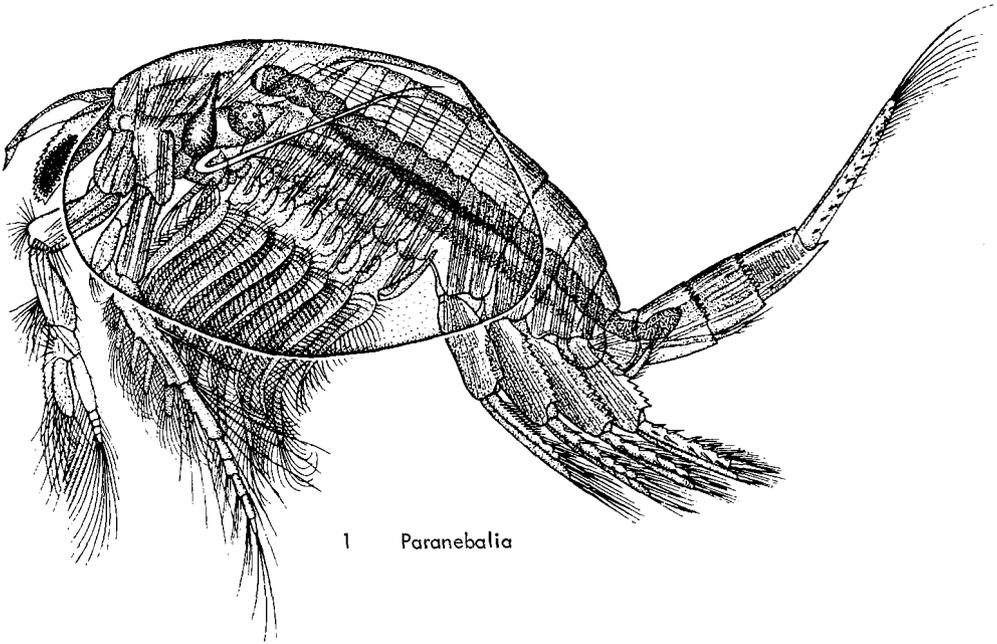
FIG. 133. Nebaliidae (p. R314).

the Upper Permian (Zechstein 1) of Germany as *Nebalia bentzi* (the carapace doubtfully referred to this species by MALZAHN, 186, is that of a young cumacean). The four most anterior somites bear large, two-segmented limbs, although they are not described as biramous. This specimen is probably a leptostracan, but it is impossible to refer it with certainty to any of the Recent genera, *Nebalia*, *Nebaliella*, or *Paranebalia*. Two generic names not listed below are *Pseudonebalia* and *Neonebalia*, quoted by KRESTOVNIKOV (1961). I have been able to find no other reference to these genera and it is presumed that they are *nomina nulla*.

Nebalia LEACH, 1814 [**N. herbstii* LEACH, 1814 (= **Cancer bipes* FABRICIUS, 1780; *Monoculus rostratus* MONTAGU, 1813; *Nebalia glabra*, *N. ciliata* LAMARCK, 1818; *N. montagui* THOMPSON, 1830); OD, M] [Although *N. herbstii* is type species of *Nebalia*, it is usually classed as a junior synonym of *Cancer bipes*. This misidentification of the type species needs to be referred to ICZN for decision by neontologists (Code, 1961, Art. 67, j, 70a)] [= *?Epinebalia* CLARK, 1932]. Carapace laterally compressed, valves

elliptical, posterodorsally truncate, smooth and translucent. Furcal rami rodlike, with rows of setae and spines. Eyestalk with basal scale; 4th segment of antennule without process; antennal peduncle of 3 segments; incisor process of mandible small and simple; maxillule with 2 endites and long setiferous palp; maxilla small, with 4 endites; 8 pairs of undifferentiated thoracopods concealed beneath carapace, each limb bearing large lamellar exopod and epipod. *Rec.*, cosmop.—FIG. 120. **N. bipes* (FABRICIUS), Atl.; ♀ idealized, $\times 12$ (68, after 271).—FIG. 129,2. *N. geoffroyi* H. MILNE-EDWARDS, Atl.; ♀ 1st thoracopod, *ca.* $\times 25$ (68, after 352). [= *Epinebalia* CLARKE, 1932 (type, *E. pugettensis*; OD).]

Nebaliella THIELE, 1904 [**N. antarctica*; OD]. Like *Nebalia* but with short row of setae inside posterior carapace margin; rostral plate with prominent ventral keel produced anteriorly into spine; eyestalk elongate, flat and crescentic, without ommatidia and lacking basal scale; 4th segment of antennule with tuft of bristles; antennar peduncle of 4 segments; incisor process of mandible large and with several teeth; thoracic limbs without epipods. *Rec.*, N. Atl.-S. Pac.-S. Ind. O.-Antarct. O.—FIG. 130, 1,2. *N. extrema* THIELE, Antarctic O.; 1, ♀, $\times 10$ (349); 2, ♂, $\times 20$ (68).



1 Paranebalia

FIG. 134. Nebaliidae (p. R314). (From H. G. Cannon, 1960, in Bronn's Klassen und Ordnungen des Tierreichs, v. 5, Abt. 1, Buch 4, Teil 1, Akad. Verlag. publ., by permission).

Nebaliopsis Sars, 1887 [**N. typica*; OD] [= *Nebaliopsis* KRESTOVNIKOV, 1961 (*nom. null.*)]. Carapace subtriangular, posteriorly acuminate, with median dorsal keel, transparent, and with large polygonal ornament of ridges; rostral plate short, triangular in cross section; thorax large, distensible; furcal rami flattened, leaflike, with serrate outer margins; eyes small, with few ommatidia, without basal scale; 4th segment of antennule produced distally into anteriorly denticulate, curved and pointed process; antennar peduncle of 4 segments; gnathal lobe of mandible reduced to simple knob; maxillule with vestigial palp; maxilla with greatly enlarged 1st endite; thoracopods reduced to lanceolate lobes; 1st limb with shorter protopod, longer endopod, and more setiferous epipod than succeeding limbs; 2nd to 4th pleopods with broad exopods. *Rec.*, Atl.-Pac.-SW. Ind.O.—FIG. 133, I. **N. typica*, W.Atl.; 1a, ♀, adult, right lat. view showing thorax distended by food in digestive sac, $\times 4.8$ (349); 1b, anterodorsal region of carapace showing median dorsal keel at top and network of ridges, $\times 4$ (Rolfe, n); 1c, dorsal view of posterior part of 7th abdominal somite showing tips of 6th pleopods, telson, and furca, $\times 3.8$ (Rolfe, n).

Paranebalia Claus, 1880 [**Nebalia longipes* WILLEMOES-SUHM, 1875; OD, M]. Like *Nebalia* but eyestalks elongate and denticulate, without basal scale; 4th segment of antennule produced distally into anteriorly serrate, pointed process; tips of thoracopods projecting well beyond ventral margin of carapace, their endopods and exopods elon-

gate, slender, with long setae on outer edge, epipods small, subtriangular. *Rec.*, NW.Atl.-NW.Pac.—FIG. 134, I. **P. longipes* (WILLEMOES-SUHM), W.Atl.; ♀, adult, left lat. view, $\times 22$ (68, after 377b).

Order HYMENOSTRACA Rolfe, new order

[=order *Hymenocarina* CLARKE in ZITTEL, 1900 (*nom. transl.* WALCOTT, 1912, p. 182, ex suborder *Hymenocarina* CLARKE in ZITTEL, 1900)]

Carapace without hinge line, last somite not elongate, telson ?not posteriorly produced, three pairs of caudal spines (?furcae) of unequal length. ?*L.Cam.*, *M.Cam.-L.Ord.*

The tentative erection of this new order is demanded by the peculiar character of the telson and furca. Such a single-character classification is unsatisfactory, but little better can be done in view of the present lack of information on more significant features.

Family HYMENOCARIDAE Haeckel, 1896

[*nom. correct.* ROLFE, herein (*pro* family *Hymenocarina* HAECKEL, 1896, *nom. imperf.*)] [= *Hymenocaridae* CLARKE in ZITTEL, 1900 (*nom. imperf.*)]

Characters of order. ?*L.Cam.*, *M.Cam.-L.Ord.*

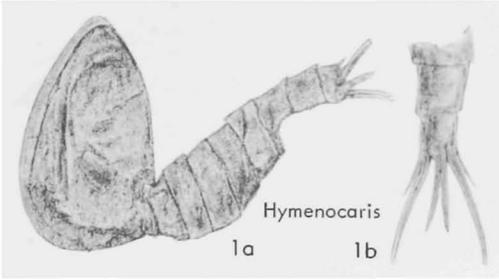


FIG. 135. Hymenocarididae (p. R315).

Hymenocaris SALTER, 1853 [**H. vermicauda*; OD, M] [= *Hymenocarys* BRINKMANN, 1954 (*nom. null.*)]. Carapace subovate, with posterior rim; surface smooth; telson similar to preceding somites; outer pair of caudal spines divergent, shortest; inner pair subparallel, of medium length; intermediate pair longest. [Middle Cambrian (Burgess Shale) species from Canada previously assigned to this genus now are assigned to *Canadaspis*.] ?*L. Cam.*, *M. Cam.-L. Ord.*, NW. Eu. (G. Brit.-?Swed.)-?N. Am. (Can.)-Australia-N. Z.—FIG. 135, 1. **H. vermicauda*, L. Ord., G. Brit. (Wales); 1a, left lat. view of distorted specimen, $\times 1$; 1b, ?dorsal view of somites, telson, and caudal spines, $\times 2$ (160).

Order ARCHAEOSTRACA Claus, 1888

[*nom. correct.* STROMER, 1909 (*pro* Archaeostraken CLAUSS, 1888)] [= Palaeocarida HAECKEL, 1889; Palaeocarides HAECKEL, 1896; Archaeocarida HENNIG, 1921; Archaeostraka RICHTER & RICHTER, 1927; Nahecarida BROILI, 1928; Palaeostracés LA-MEERE, 1933; Archeostrata STØRMER, 1935]

May be large, carapace with hinge line, seventh abdominal somite usually much longer than preceding ones, telson produced dorsally as median process between furcal rami; antennule biramous (known only in *Nahecaris*); antenna ?with flagellar exopod (supposedly in *Nahecaris*); gnathal lobe of mandible with large, paired teeth; ?five pairs of pleopods only. *L. Ord.-U. Trias.*

Suborder CERATIOCARINA Clarke in Zittel, 1900

[= Ceratiocarina RAYMOND, 1935; Ceatiocarina IVANOVA, 1960; Ceratiocarinae JUX, 1960; Ceratiocarida KRESTOVNIKOV, 1961]

Carapace with hinge line; rostral plate without longitudinal ridge, no median dorsal plate; eight short thoracic somites and seven longer abdominal somites where known (Fig. 122), pretelson somite usually elongated. *L. Ord.-U. Trias.*

Family CERATIOCARIDIDAE Salter, 1860

[*nom. correct.* ROLFE, 1961 (*pro* Ceratiocaridae SALTER, 1860)] [= Ceratiocaridae BEECHER, 1884; Ceratiocarida HAECKEL, 1896; Caryocaridae (*recte* Caryocarididae) CHAPMAN, 1903]

Carapace large, covering thoracic and anterior abdominal somites, lacking prominent nodes and ridges; furca long. *L. Ord.-L. Dev.*, ?*Carb.*, ?*U. Perm.*

Ceratiocaris M'COY, 1849 [ICZN, March, 1964, Op. 690] [**C. solenoides*; SD MILLER, 1889 (= *Cultellus rectus* M'COY, 1851, obj., *nom. nud.*)] [= *Leptocheles* M'COY, 1849 (type, *Pterygotius (Leptocheles) leptodactylus* M'COY, 1849; OD, M); *Leptonotus* BARRANDE, 1856 (*nom. nud.*); *Physocaris* SALTER, 1860 (type, *Ceratiocaris (Physocaris) vesica*; OD = *C. cassia* SALTER, 1860); *Phytocaris* ETHERIDGE, 1888 (*nom. null.*); *Astacoderma* HARLEY, 1861 (type, *A. subundulatum var. compositum*; SD ROLFE, herein); *Ceratiocaris* CLAUS, 1880 (*nom. null.*); *Caratiocaris* PACKARD, 1889 (*nom. null.*); *Ceratiocaris* HAECKEL, 1889 (*nom. null.*); *Cerathiocaris* SCALIA, 1922 (*nom. null.*); *Ceratiocaris* PÉNEAU, 1935 (*nom. null.*); *Ceratiocaris*, *Leratiocaris* PÉNEAU, 1946 (*nom. null.*); *Ceratioceras* KRESTOVNIKOV in ORLOV, 1960 (*nom. null.*); *Emmelezoe* ETHERIDGE, JONES & WOODWARD, 1886 (type, *Ceratiocaris elliptica* M'COY, 1849; SD GÜRICH, 1929); *Emmelezoe* LINDSTRÖM, 1895 (*nom. null.*); *Emmelezoe* CLARKE, 1902 (*nom. null.*); *Entomocaris* WHITFIELD, 1896 (*non* GÜRICH, 1929) (type, *E. telleri*; OD); ?*Calyptocaris* JONES & WOODWARD, 1898 (type, *Dithyrocaris? striata* WOODWARD & ETHERIDGE in GEIKIE, GEIKIE, PEACH, & ETHERIDGE, 1873; OD, M); *Limnocaris* CLARKE, 1902 (type, *Ceratiocaris (L.) praecedens*; OD, M); ?*Polystomurum* NOVOZHILOV, 1958 (type, *P. stoermeri*). Carapace elongate to subovate, with prominent anterior horn, posterior margin usually sinuous; right valve with or ?without 3 dorsal hinge nodes; rostral plate of medium length, only anterior indurated tip projecting free of valves; rostral plate and carapace with anastomosing, longitudinal striae. Body somites commonly encircled by posteroventrally inclined striae and anteriorly imbricating scale ornament; telson and furca rodlike, usually longitudinally grooved and bearing spinules, telson longer than furca; 8 thoracic appendages differentiated from ?5 abdominal appendages, poorly known. [*Emmelezoe* and *Limnocaris* are here synonymized since the presence or absence of the anterior tubercle or "eye spot" is at present unreliable for generic differentiation.] ?*L. Ord.*, *U. Ord.-L. Dev.*, ?*L. Carb.*, ?*U. Perm.*, cosmop.—FIG. 136, 1. *C. papilio* SALTER in MURCHISON, M. Sil., Scot.; right dorsolat. view (reconstr.), pleopods known to be present, but their structure unknown,

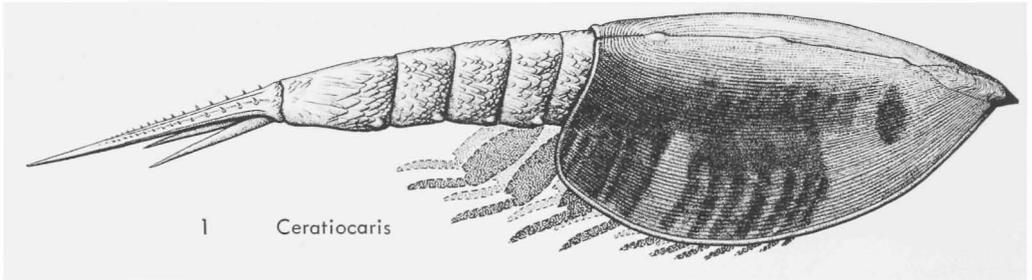


FIG. 136. Ceratiocarididae (p. R315).

hence pleopods of *Paranebalia* type are shown, $\times 1$ (258).

Caryocaris SALTER, 1863 [**C. wrightii*; OD] [= ?*Dawsonia* NICHOLSON, 1873 (type, *D. campanulata*; SD S. A. MILLER, 1889) (*non Dawsonia* HARTT in DAWSON, 1868; *nec* FRITSCH, 1879; *nec* CARPENTER in DALL, 1882); *Caryocaris* GURLEY, 1896 (*nom. null.*); ?*Rhinopterocaris* CHAPMAN, 1903 (type, *Lingulocaris mcoyi* ETHERIDGE, 1892; OD, M); *Rhinopteriocaris* KRESTOVNIKOV, 1961 (*nom. null.*); *Lamprocaris* NOVÁK in ŽELÍZKO, 1907 (*nom. nud.*); *Lamprocaris* ŽELÍZKO, 1919 (*fide* CHLUPÁČ) (type, *L. micans*; SD VAN STRAELLEN & SCHMITZ, 1934)]. Carapace elongate-subovate, posterior margin with (or ?without) fringe

of spines and spinules, anterodorsal carapace horn of each valve may be anteriorly produced; mid-ventral ridge may be present, subparallel to ventral margin but confluent with it antero- and posteroventrally; surface smooth, striate, or reticulate; telson and furca laterally expanded, leaflike; telson shorter than furca; external margins of furcal rami ?notched or serrate. [*Rhinopterocaris* may prove to be generically distinct, but the absence of posterior spinules and produced carapace horn from the type species and other species of *Caryocaris* may only be due to preservation. These structures are commonly not preserved in specimens of "*Rhinopterocaris*" and indeed were not noticed or figured by ETHERIDGE in his original description of the syntypes of the type species of *Rhinopterocaris*. Furthermore the significance of these characters at the generic level seems doubtful.] *L.Ord.-U.Ord.*, cosmop. [*U. Cam.* and *Sil.* records of this genus are based on generically indeterminate specimens.]—FIG. 137,1. **C. wrightii*, L. Ord., Eng. (Skiddaw, Cumberland), left lat., $\times 1.5$ (160).—FIG. 137,2. *C. maccoyi* (ETHERIDGE) [= *C. curvilata* GURLEY], L. Ord., USA (N.Y., N. Granville); LV lat., $\times 1.5$ (Rolfe, n).—FIG. 137,3. *C. monodon* (GURLEY), L. Ord., Can. (Que.); telson and furca, dors. (reconstr.), $\times 3$ (Rolfe, n).

Gonatocaris GÜRICH, 1929 [**Emmelezoë decora* CLARKE, 1902; OD]. Like *Ceratiocaris* but with carapace valves truncate anteriorly, coarsely ribbed

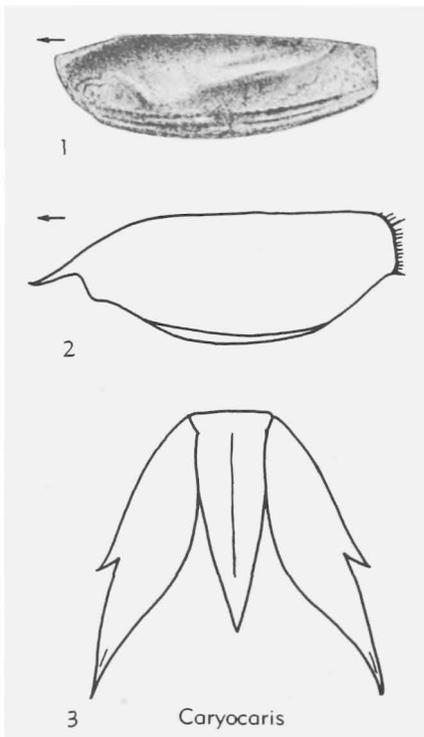


FIG. 137. Ceratiocarididae (p. R316).

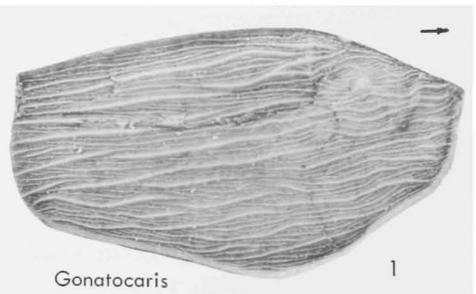
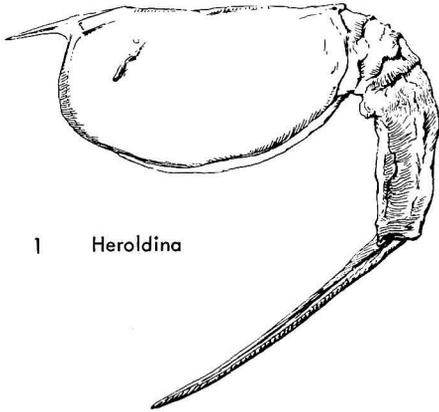


FIG. 138. Ceratiocarididae (p. R316).



1 Heroldina

FIG. 139. Ceratiocarididae (p. R317).

and with anterior tubercle. *U.Sil.*, N.Am.—FIG. 138, *I*. **G. decora* (CLARKE), Salina Gr. (Vernon Sh.), USA (N.Y.); RV (syntype) lat., $\times 4$ (Rolfe, n).

Heroldina BROILI, 1931 [*pro Heroldia* BROILI, 1929 (*non* VERHOEFF, 1926)] [**Mesothyra rhenana* BROILI, 1928; OD] [= *Allolepicthys* WHITLEY, 1940 (*pro Allolepis* HEINTZ, 1932, *non* JORDAN & HUBBS, 1925) (type, *A. longicornis*; OD)]. Like *Ceratiocaris* but carapace valves less acuminate anteriorly, larger rostral plate (length almost half that of carapace), projecting free from carapace anteriorly as triangular spine, and last abdominal somite very elongate. [CHLUPÁČ (1963) has suggested that this genus belongs to the Aristozoidae; although the last abdominal somite and telson indicate such an affinity, the carapace is unlike that of any aristozoid.] *L.Dev.*, W.Ger.—FIG. 139, *I*. **H. rhenana* (BROILI), Hunsrück Sh., Gemünden; left lat. view, $\times 0.25$ (346b).

Family AUSTRIOCARIDIDAE
Glaessner, 1931

[*nom. correct.* ROLFE, herein (*pro* Austriocarididae GLAESSNER, 1931)] [=Austriocaridae BROOKS & CASTER, 1956 (*nom. null.*)]

Carapace with excavate posterior margin and commonly a mesolateral or juxtadorsal ridge; rostral plate relatively short; posteroventral or posteromedian protuberances or internal impressions may represent carapace adductor muscle scars, suggesting that thorax projected free from carapace. *M.Dev.-U.Trias.*

Austriocaris GLAESSNER, 1931 [**A. carinata*; OD]. Carapace only known, posterior excavation arcuate or irregular, anterior margin concave or produced into small beak; posteroventral or ventromedian V-shaped furrow; surface smooth with mid-dorsal

granulations or posteroventral pits, or dorsoventrally striate. *U.Trias.*, W.Eu.(Austria).—FIG. 140, 2. **A. carinata*; RV with rostral plate, lat., $\times 0.6$ (111).

Concavicaris ROLFE, 1961 [*pro Colpocaris* MEEK, 1872 (*non* VON MEYER, 1862)] [**Ceratiocaris* (*Colpocaris*) *bradleyi* MEEK, 1872; SD S. A. MILLER, 1889]. Posterior excavation of carapace valves semicircular, anterior margin truncate or acuminate; may bear mesolateral ridge or bluntly serrate juxtadorsal ridge; surface ?smooth, reticulate or striate; doublure may be broad; telson shorter than furca, all smooth or longitudinally striate. *M.Dev.-M.Penn.*, Czech.-USA.-?E.Can.-Australia. —FIG. 140, 1a. *C. sinuata* (MEEK & WORTHEN), M.Penn., USA (Ill.); LV (holotype) lat., $\times 0.6$ (Rolfe, n).—FIG. 140, 1b. *C. rostellata* ROLFE, M.Penn., USA (Ill.); LV (holotype) lat., with anastomosing striae ornament shown diagrammatically, $\times 0.9$ (Rolfe, n).

Family ECHINOCARIDIDAE
Clarke in Zittel, 1900

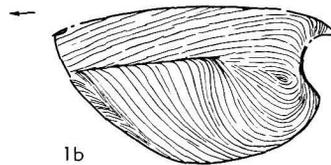
[*nom. correct.* CHLUPÁČ, 1963 (*pro* Echinocarididae CLARKE in ZITTEL, 1900)] [=Echinocaridae BOCK, 1946]

Carapace with hinge line, without anterior horn, with anterior swellings and lateral ridge. *L.Dev.-L.Miss.*

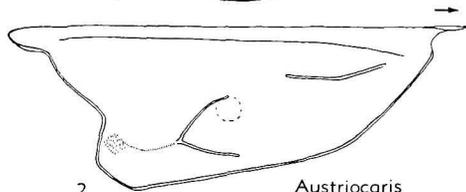


1a

Concavicaris



1b



2

Austriocaris

FIG. 140. Austriocarididae (p. R317).

Subfamily ECHINOCARIDINAE

Clarke in Zittel, 1900

[*nom. transl.* ROLFE, herein (*ex* Echinocaridae CLARKE in ZITTEL, 1900)]

Carapace subovate-subquadrate, anterodorsally rounded and without posteroventral spine; telson and furca thin, rodlike. *L. Dev.-L. Miss.*

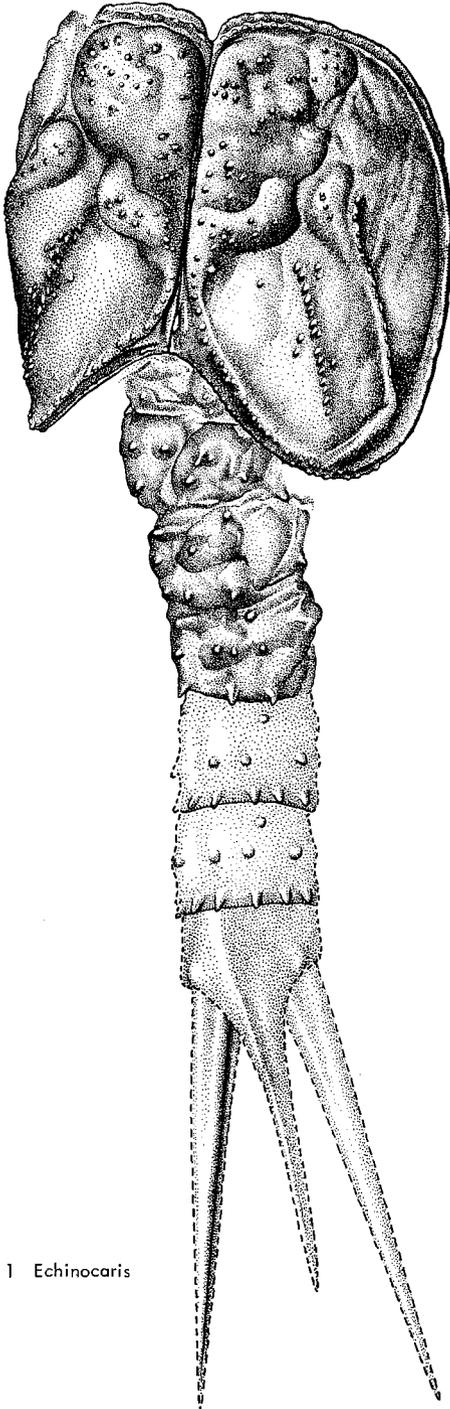
Echinocaris WHITFIELD, 1880 [**E. sublevis*; OD] [= *Echinocarys* BARROIS, 1891 (*nom. van.*)]. Carapace subovate-subelliptic, posterodorsally truncated, with prominent anterodorsal and mid-dorsal lobes; lateral ridge carinate, sigmoidal or sinuous; carapace and somites characteristically tuberculate or spinose; furca longer than telson, all slender, each furcal ramus grooved along inner side. *M. Dev.-L. Miss.*, cosmop.—FIG. 141, 1. *E. socialis* BEECHER, U. Dev. (Chemung), USA (Pa.); right dors. lat. (part reconstr.), $\times 4$ (Rolfe, n).—FIG. 142, 3. *E. punctata* (HALL), M. Dev. (Hamilton Gr.), USA (N.Y.); last 2 somites of abdomen, telson and furca; 3a, dors., showing clasping posterior spines, $\times 0.5$; 3b, vent., $\times 0.5$ (140).

Callizoe BARRANDE, 1872 [**C. bohémica*; OD, M] [= *Callizoe* BARRANDE in BIGSBY, 1868 (*nom. nud.*); *Calozoe* NICHOLSON & LYDEKKER, 1889 (*nom. null.*); *Calizoe* KRESTOVNIKOV, 1961 (*nom. null.*)]. Carapace like *Ptychocaris* but margin concave anteroventrally, anterior tubercle anteroventrally situated, lacks anteromedian pair of nodes and furrow, lateral ridge faint, not carinate; doublure wall concave; pitted ?hinge node developed at posterior end of hinge line. *L. Dev.*, Czech.—FIG. 142, 2. **C. bohémica*, U. Koněprusy Ls.; lat. view of LV (int. mold), $\times 3$ (Rolfe, n).

Ptychocaris NOVÁK, 1885 [**P. parvula*; SD VAN STRAELEN & SCHMITZ, 1934] [= *Ptychocaris* KRESTOVNIKOV, 1961 (*nom. null.*)]. Carapace elongate-subquadrate, with mid-anterior group of ?3 low nodes, anterodorsally situated prominent anterior tubercle, and posterior pair of large nodes (?carapace adductor and mandibular muscle attachments) bordered posteriorly and separated by furrows; lateral ridge prominent, carinate. *L. Dev.-M. Dev.*, Czech.-N. Can.—FIG. 142, 5. *P. simplex* NOVÁK, L. Dev. (Koněprusy Ls.), Czech.; lat. view of RV, $\times 1$ (77, after 370b).

Subfamily MONTECARIDINAE Rolfe, 1966

Carapace valves elongate-subquadrate, anterodorsally truncate, with anterodorsal grooves perpendicular to hinge line separating tuberculate areas; with carinate lateral ridge and posteroventral spine; telson and furca laterally expanded; telson with prominent, movable, lateral spines. ?*L. Dev.*, *M. Dev.-U. Dev.*



1 Echinocaris

FIG. 141. Echinocarididae (Echinocaridinae) (p. R318).

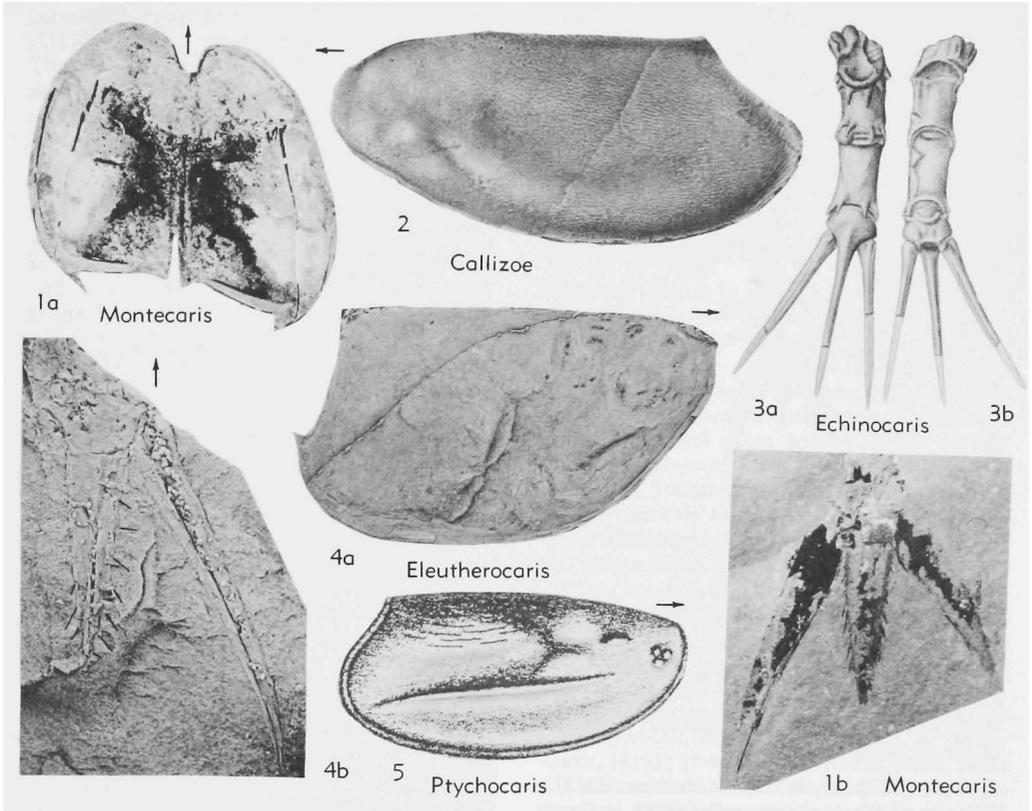


FIG. 142. Echinocarididae (Echinocaridinae) (2-3, 5), (Montecaridinae) (1, 4) (p. R318-R319).

Montecaris Jux, 1959 [**M. strunensis*; OD]. Anterodorsal grooves deep, 4 in number, 1st and 4th uniting ventrally; doublure broad; lateral ridge long, extending to posteroventral spine; small posterodorsal spine present; posterior margin of abdominal somites produced into spines; telson broad, equal in length to furca or shorter than it. ?*L.Dev.*, *M.Dev.-U.Dev.*, *C.Eu.*-?*W.Can.*-Australia. —FIG. 142,1. **M. strunensis* Jux, *U.Dev.* (Frasn.), Ger.; 1a, dorsal view of holotype, carapace valves spread out, $\times 0.5$; 1b, incomplete telson and furca, $\times 1$ (Rolfe, n).

Eleutherocaris CLARKE in ZITTEL, 1900 [**Echinocaris whitfieldi* CLARKE, 1885; SM CLARKE, 1902]. Like *Montecaris* but anterodorsal grooves of carapace shallow, lateral ridge short and restricted to anteroventral region, telson narrower; carapace with dorsal-ventral rows of anteriorly convex crescentic ridges or scales. *U.Dev.*, USA(N.Y.). —FIG. 142,4. **E. whitfieldi*, Naples Gr. (Hatch Hill), Naples; rubber molds of holotype; 4a, lat. view of LV, $\times 1.7$; 4b, telson and right furcal ramus, dorsal, ventral platform of telson head impressed through tergum, telson spines re-touched, $\times 1.7$ (Rolfe, n).

Family PEPHRICARIDIDAE Van Straelen, 1933

[*nom. correct.* ROLFE, herein (*pro* Pephricaridae VAN STRAELEN, 1933)]

Carapace valves semicircular, with prominent, posteriorly tapering, mid-dorsal-posteromedian fold; rim with long spines; last two abdominal somites with long spine on each side; telson shorter than curved furcal rami. *U.Dev.*

Pephricaris CLARKE, 1898 [**P. horripilata*; OD, M] [= *Pephrycaris* RUSCONI, 1950 (*nom. null.*)]. Characters of family. *U.Dev.*, USA(N.Y.). —FIG. 143,1. **P. horripilata*, Chemung, Alfred, Allegany Co.; dorsal view of lectotype showing anterodorsal "pits" due to erosion of mandible bodies, $\times 1.5$ (351b, mod.).

Family ARISTOZOIDAE Gürich, 1929

Carapace strongly convex, with dorsal-median nodes and large anterior horn but without lateral ridge; deep marginal groove

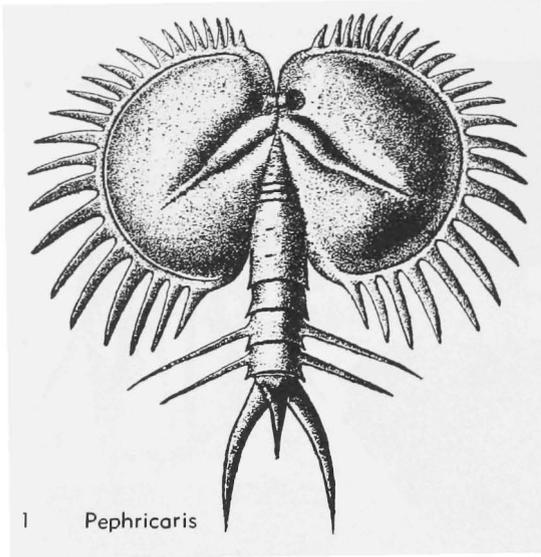


FIG. 143. Pephricarididae (p. R319).

demarcating broad rounded rim; last abdominal somite very elongate. [Furca unknown and possibly lacking. If this can be substantiated a new order would be indicated as CHLUPÁČ has suggested.] ?*M.Ord.*, *U.Sil.-M.Dev.*

Aristozoe BARRANDE, 1872 [**A. bisulcata*; SD S. A. MILLER, 1889] [= *Aristozoe* BARRANDE in BIGSBY, 1868 (*nom. nud.*); *Aristozoe* BARRANDE, 1872 (*nom. null.*); *Bactropus* BARRANDE, 1872 (type,

**B. longipes*; SD ROLFE, herein); *Bractropus* CANU, 1886 (*nom. null.*); ?*Phasganocaris* NOVÁK, 1886 (type, *Eurypterus pugio* BARRANDE, 1872; OD, M); *Phasganocaris* ROGER in PIVETEAU, 1953 (*nom. null.*)]. Carapace with relatively thick cuticle, subcircular-subelliptical, with rounded anterior horn, anterodorsal nodes separated by grooves, posterodorsal angle rounded; telson as in *Ceratiocaris*. [The two synonymized genera were described from last abdominal somites and a telson only, and were subsequently suggested by NOVÁK and GÜRICH to correspond with carapaces of *Aristozoe* spp.]. ?*M.Ord.*, *U.Sil.-M.Dev.*, Eu-Novaya Zemlya-?SE.Can.—FIG. 144, 1. *A. regina* BARRANDE, L.Dev.(U.Koněprusy Ls.), Czech.; 1a, left lat. view of carapace, $\times 0.8$; 1b, 7th abdominal somite and telson, $\times 0.8$ (370a). [= *Bactropus* BARRANDE in BIGSBY, 1868 (*nom. nud.*).]

Orozoe BARRANDE, 1872 [**O. mira*; OD, M]. Like *Aristozoe* but carapace subquadrate, rim anteroventrally and posteroventrally flattened and produced, with large, dorsoventrally flattened, posteriorly directed blunt spine on posteromedian area. *L.Dev.*, ?*M.Dev.*, Czech.-?Ger.—FIG. 145, 1. **O. mira*, L.Dev.(U.Koněprusy Ls.), Czech.; 1a,b, lat. and dorsal views of LV with spine restored, $\times 4$ (Rolfe, n).

Pygocaris PERNER, 1916 [**P. schuberti*; OD]. Like *Aristozoe* but with (?secondarily) thin cuticle, anterior horn acuminate, anterodorsal nodes not separated by grooves and may be only poorly developed, posterodorsal corner produced; rostral plate lanceolate, with 2 anterior constrictions. ?*L.Dev.*, Czech.—FIG. 145, 2. **P. schuberti*, Lochkov Ls., Kosoř; lat. view of LV (paralectotype), $\times 0.75$ (372).

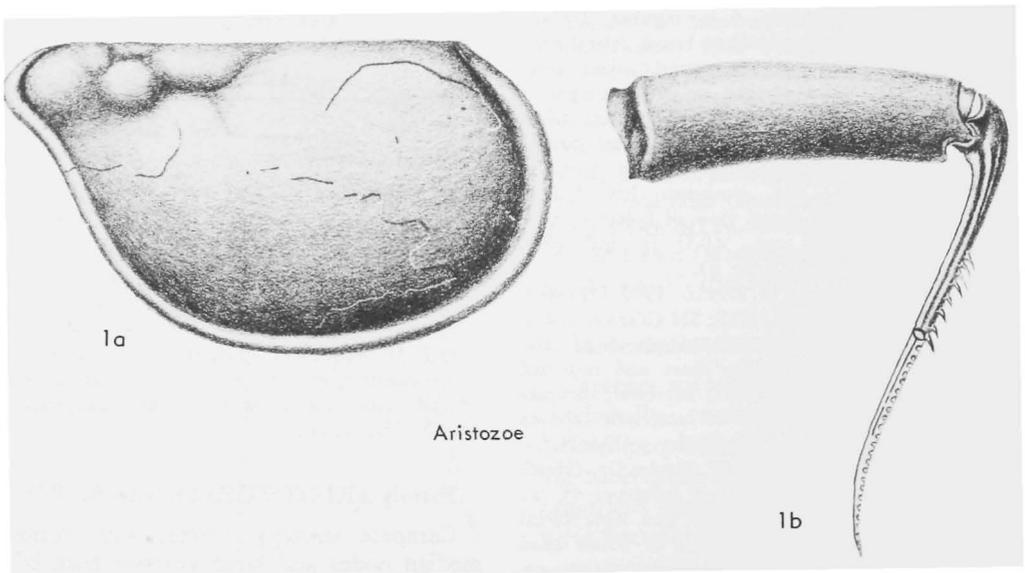


FIG. 144. Aristozoidae (p. R320).

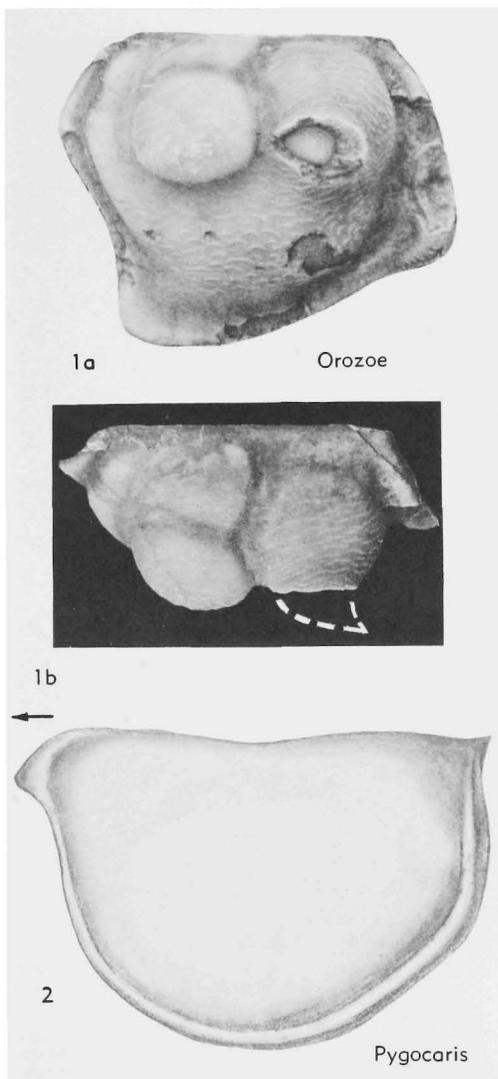


FIG. 145. Aristozoidae (p. R320).

Suborder RHINOCARINA
Clarke in Zittel, 1900

[=Nahecarina RICHTER, 1933; Rchinocarina IVANOVA, 1960]

Carapace with median dorsal plate separating valves behind rostral plate; last abdominal somite elongated. ?*Sil.*, *L.Dev.-M. Penn.*, ?*U. Perm.*

Family RHINOCARIDIDAE
Hall & Clarke, 1888

[*nom. correct.* ROLFE, 1962 (*pro* Rhinocaridae HALL & CLARKE, 1888)] [=Pinnacidae HALL & CLARKE, 1888; Pinnacidae CLARKE, 1893; Rhinocaridae CLELAND, 1903; Nahecaridae (*recte* Nahecarididae) BROILI, 1928; Reinocaridae

BROOKS & CASTER, 1956; Pseudodontichthyidae OBRUCHEV in ORLOV, 1964; includes Rhinocarinae (*recte* Rhinocaridinae) HALL & CLARKE, 1888 (*nom. transl.* KRESTOVNIKOV in ORLOV, 1960, *ex* Rhinocaridae HALL & CLARKE, 1888); Dithyrocarinae (*recte* Dithyrocaridinae) JONES & WOODWARD, 1899 (*nom. transl.* KRESTOVNIKOV in ORLOV, 1960, *ex* Dithyrocaridae JONES & WOODWARD, 1899); Rachuridae MILLER, 1889 (*nom. neg.*)]

Carapace valves elongate, subovate; median dorsal plate narrow and with chevron ornament; rostral plate and median dorsal plate slightly bent along median carina. ?*Sil.*, *L.Dev.-M. Penn.*, ?*U. Perm.*

Rhinocaris CLARKE in HALL & CLARKE, 1888 [**R. columbina*; SD S. A. MILLER, 1889] [=Phinocaris MATTHEW, 1888 (*nom. null.*); *Rhynocaris* CHERNYSHEV, 1938 (*nom. null.*)]. Posterior margin of carapace valves concave, with small to medium posteroventral and rarely posterodorsal spine; mesolateral carina faint or absent; anterior node may be present and from it branching furrows may radiate posteriorly; rostral plate projecting anteriorly from carapace, anterior half laterally compressed; somites encircled by posteroventrally inclined striae; telson subcircular in cross section, equal in length to furca or shorter than it. *M.Dev.-U.Dev.*, N.Am.—FIG. 146.4. **R. columbina*, USA(N.Y.); 4a,b, left lat. and dorsal views (reconstr.), $\times 0.7$ (351). [=Pseudodontichthys SKEELS, 1962 (type, *P. whitei*; OD)].

Dithyrocaris SCOULEUR in PORTLOCK, 1843 [*pro Argas* SCOULEUR, 1835 (*non* LATREILLE, 1795; *nec* OKEN, 1815)] [**Argas testudineus* SCOULEUR, 1835; SD ROEMER in BRONN & ROEMER, 1854] [=Argus GEINITZ, 1853 (*nom. null.*); *Arges* CLAUS, 1876 (*nom. null.*); *Anthropodontoides* BARKAS, 1871 (type, *A. bailesii*; OD, M); *Dithyrocarus* M'COY in GRIFFITH, 1842 (*nom. nud.*); *Ditryocharis* ROEMER, 1866 (*nom. null.*); *Dithyrocaris* MEEK & WORTHEN, 1873 (*nom. null.*); *Dythyrocaris* KAYSER, 1878 (*nom. null.*); *Dithyrocaris* BIGSBY, 1878 (*nom. null.*); *Dithyriocaris* HIND *et al.*, 1903 (*nom. null.*); *Dithyrocaris* BARROIS, 1891 (*nom. van.*); *Rhachura* SCUDDER, 1878 (type, *R. venosa*; OD, M); *Rachura* ZITTEL, 1885 (*nom. null.*); *Rhaehura* JONES & WOODWARD, 1899 (*nom. null.*); *Mesothyra* HALL in HALL & CLARKE, 1888, (type, *Dithyrocaris oceanii*; OD); *Mesothyris* RUEDEMANN, 1918 (*nom. null.*); *Chaenocaris* JONES & WOODWARD, 1898 (type, *Dithyrocaris tenuistriata* M'COY, 1844; SD ROLFE, *herein*)]. Like *Rhinocaris* but posterior margin of carapace valves straight or convex, with large posteroventral spine and usually with prominent mesolateral carina and anterodorsal granules; may bear up to 4 lateral carinae; doubleure usually broad, rim may have oblique, posteriorly imbricating ridges; somites ornamented as in *Rhinocaris* or with longitudinal carinae; telson subtriangular in cross section, shorter, equal in length to furca or longer than it; furcal rami flattened, commonly with deep longitudinal grooves. ?*Sil.*,

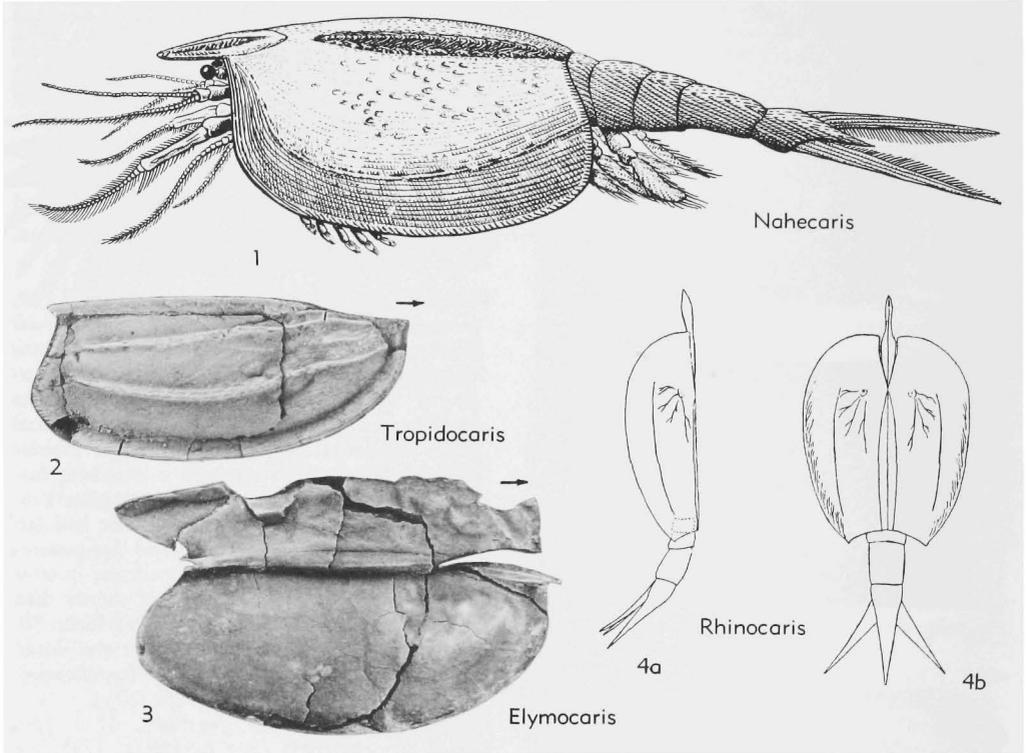


FIG. 146. Rhinocarididae (p. R321-R322).

?L.Dev., M.Dev.-M.Penn., ?U.Perm., Eu.-N.Am.-USSR-?Australia.—FIG. 147,1. **D. testudinea* (SCOULER), L.Carb., Scot.; dorsal view of holotype, $\times 2$ (Rolfe, n). [= *Chaenocartis* YANISHEVSKII, 1910 (*nom. null.*.)]

Elymocariss BEECHER, 1884 [**E. siliqua*; OD] [= *Elimocariss* KRESTOVNIKOV, 1961 (*nom. null.*.)]. Like *Rhinocaris* but carapace valves without posteroventral spine; no mesolateral carina, anterior tubercle present; rim with oblique, posteriorly imbricating ridges; rostral plate folded ventrally along 2 lateral, anteriorly converging carinae; telson with broad median ridge. M.Dev.-U.Dev., USA-?Can.—FIG. 146,3. **E. siliqua*, U.Dev. (Chemung), USA (Pa.); dorsal view of carapace showing median dorsal plate, rostral plate, and crushed LV, $\times 1.6$ (Rolfe, n).

Macrocariss S. A. MILLER, 1894 [**M. gorbyi*; OD]. Like *Rhinocaris* but carapace with short longitudinal ridges; no mesolateral carina. [Poorly known; ventral region of carapace and tailpiece unknown. Supposed body segments of MILLER's syntypes lack ornament of lectotype (Miller, 1894, fig. 43; Chicago Field Museum) and probably not crustacean; supposed "masticatory apparatus" is scolecodont.] L.Miss., USA (Ind.).

Nahecariss JAEKEL, 1921 [**N. stuertzi*; OD] [= *Nehecariss* GÜRICH, 1929 (*nom. null.*.)]. Like

Tropidocaris but with single lateral carina on each carapace valve. L.Dev., Ger.—FIG. 146,1. **N. stuertzi*; left dorsolateral view (reconstr.), $\times 0.7$ (Rolfe, n).

[BROILI maintained that the rostral plate of *Nahecariss* was completely fused with the carapace, but HENNIG and GÜRICH showed that it was free, at least in some specimens (which BROILI therefore asserted belonged to a different genus). Specimens in the Harvard Museum of Comparative Zoology show the rostral plate separated from the carapace laterally and probably posteriorly, though obscured by pyritization. A median dorsal plate is present, so that *Nahecariss* is certainly one of the *Rhinocarina*, as HENNIG and GÜRICH affirmed, but BROILI and RAYMOND denied. Thus no basis exists for BROILI's order *Nahecarina*, although, should the rostral plate definitely prove to be fused, the separate family might be resurrected.]

Tropidocaris BEECHER, 1884 [**T. bicarinata*; SD S. A. MILLER, 1889] [= *Tropocaris* JONES & WOODWARD, 1888 (*nom. null.*); *Tropidocaris* CLARKE, 1892 (*nom. null.*); *Tropidocaris*, *Tropidocaris*, *Trapidocaris* CHERNYSHV, 1938 (*nom. null.*); *Tropidocarinatus* STURGEON, HLAVIN, & KESLING, 1964 (*nom. null.*.)]. Like *Dithyrocariss* but with mesolateral carina extending to anterior border of carapace; rim broader and more convex; commonly lacks posteroventral spine. [The characters by which present genera of *Rhinocarididae* are differentiated are probably only of specific value and considerable revision is required.] ?M.Dev., U.Dev., Eu.-N.Am.—FIG. 146,2. **T. bicarinata*,

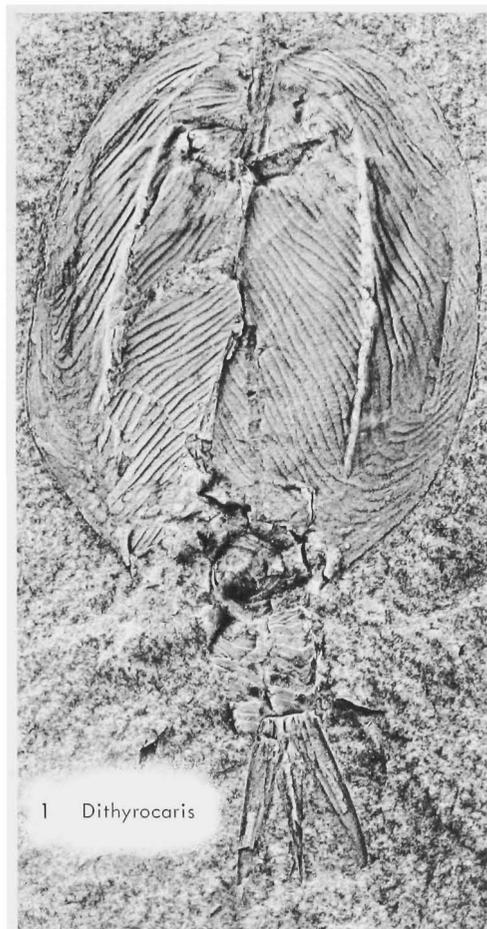


FIG. 147. Rhinocarididae (p. R321-R322).

U.Dev., USA(Pa.); lat. view of RV (lectotype), right half of median dorsal plate only preserved, showing adductor muscle impression and vascular ridges between lateral carinae, $\times 2$ (Rolfe, n).

Family OHIOCARIDIDAE Rolfe, 1962

Carapace valves subcircular, with anterodorsal-medioventral fold and marginal ridge dorsal from ventral margin; median dorsal plate broad, without median carina. *U.Dev.*

Ohiocaris ROLFE, 1962 [**O. wycoffi*; OD]. Characters of family. *U.Dev.*, USA(Ohio).—FIG. 148, 1. **O. wycoffi*, Chagrin Sh., Porter Creek (Cuyahoga Co.); dorsal view of holotype showing mandibles impressed through anterodorsal region of carapace valves; abdomen inverted relative to carapace, $\times 1$ (376a, mod.).

Phyllocarida Order and Family UNCERTAIN

Genera and families founded on isolated carapaces or tail pieces, or of family or order incertae sedis are described below. Some genera may not even be Phyllocarida, but they are too poorly known to be assigned with certainty to other groups.

Anomalocaris WHITEAVES, 1892 [*non* ORTMANN, 1893] [**A. canadensis*; OD] [= *Anomalocaris* WALCOTT, 1908 (*nom. null.*); *Anomalocaris* KRESTOVNIKOV, 1961 (*nom. null.*)]. Curved body of at least 14 subquadrate segments including telson, each segment with pair of ?ventral, elongate pointed, unsegmented appendages; dorsal and ventral processes on telson may represent ?furcae of *Hymenocaris* type. [Possibly the body of *Tuzoia*. Type of Anomalocaridae (*recte* Anomalocarididae) RAYMOND, 1935]. *L.Cam.-M.Cam.*, ?*U. Sil.*, N.Am.—FIG. 149,2. **A. canadensis*, M. Cam., Can.(B.C.); part of body, lat., $\times 0.5$ (Rolfe, n).

Baituganocaris KRESTOVNIKOV, 1961 [**B. tatarica*; OD]. Like *Montecaris*, but carapace without posteroventral spines and anterodorsal grooves. [Type of Baituganocarinae (*recte* Baituganocaridinae) KRESTOVNIKOV, 1961. Should this genus prove synonymous with *Montecaris*, as CHLUPÁČ has suggested, the subfamily Baituganocaridinae would have priority over Montecaridinae.] *U.Dev.*, E.Eu.-?Czech.—FIG. 149,3. **B. tatarica*, Shugurov Beds (Frasn.), Orenburg distr., E.Eu.; carapace displaced from abdomen (holotype), $\times 1.5$ (168).

Canadaspis NOVOZHILOV in ORLOV, 1960 [**Hymenocaris perfecta* WALCOTT, 1912; OD]. Carapace

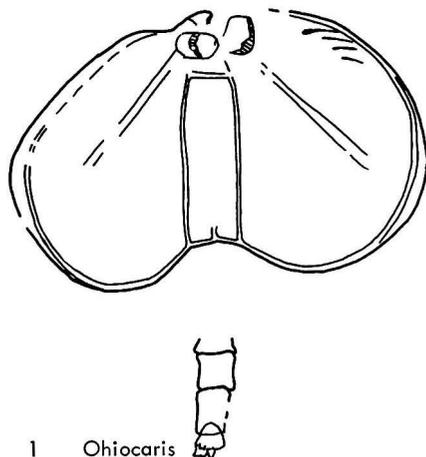


FIG. 148. Ohiocarididae (p. R323).

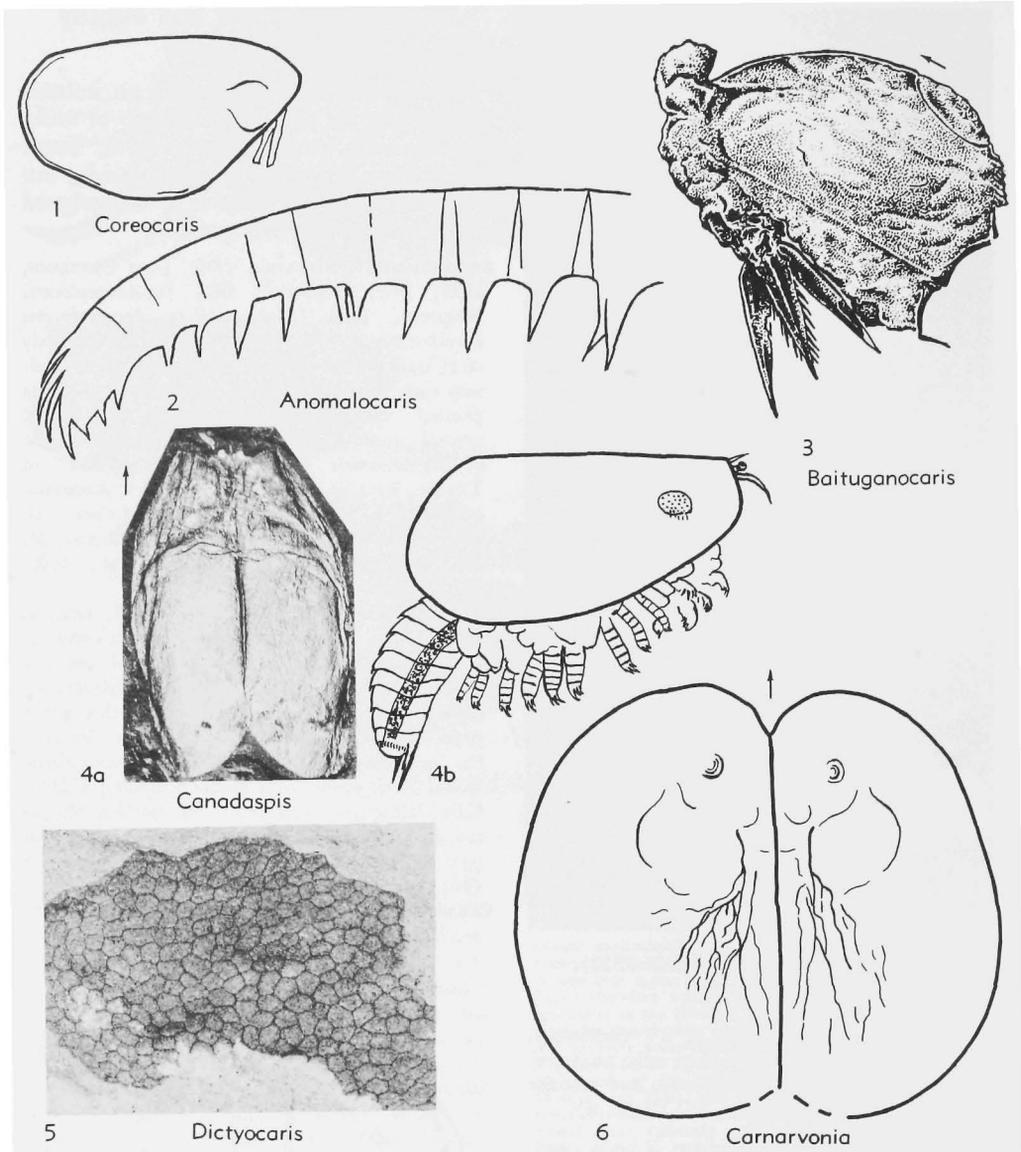


FIG. 149. Phyllocarida, Order and Family Uncertain (p. R323-R325).

with hinge line, valves subovate, each with large anteromedian adductor muscle scar; rostral plate small, eyes pedunculate; pleomeres of same length as thoracomeres, without pleopods; with posteroventral spines, especially well developed on ?pretelson somite and simulating furca; telson small, rounded, ?without furca; ?amandibulate; thoracopods of at least 8, short segments with 4 distal, anteriorly curved claws and large proximally attached lamella. [Type of order Canadaspidida and family Canadaspididae NOVOZHILOV in ORLOV, 1960.] *M. Cam.*, W. Can.—FIG. 149, 4. **C. per-*

jecta (WALCOTT), Burgess Sh., B.C.; 4a, dorsal view of carapace showing left ?antenna, eyes, and rostral plate, $\times 1.6$ (Rolfe, n); 4b, right lat. view of holotype (reconstr.) showing intestinal filling, $\times 1.7$ (Rolfe, n, after 384c).

Carnarvonja WALCOTT, 1912 [**C. venosa*; OD] [= *Caanarvonja* KRESTOVNIKOV, 1961 (*nom. null.*)]. Carapace with hinge line, valves subelliptical, with anterior tubercle; prominent ?vascular markings diverge posteriorly from main mid-dorsal, longitudinal trunk on each valve. *M. Cam.*, Can.—FIG. 149, 6. **C. venosa*, Burgess Sh.,

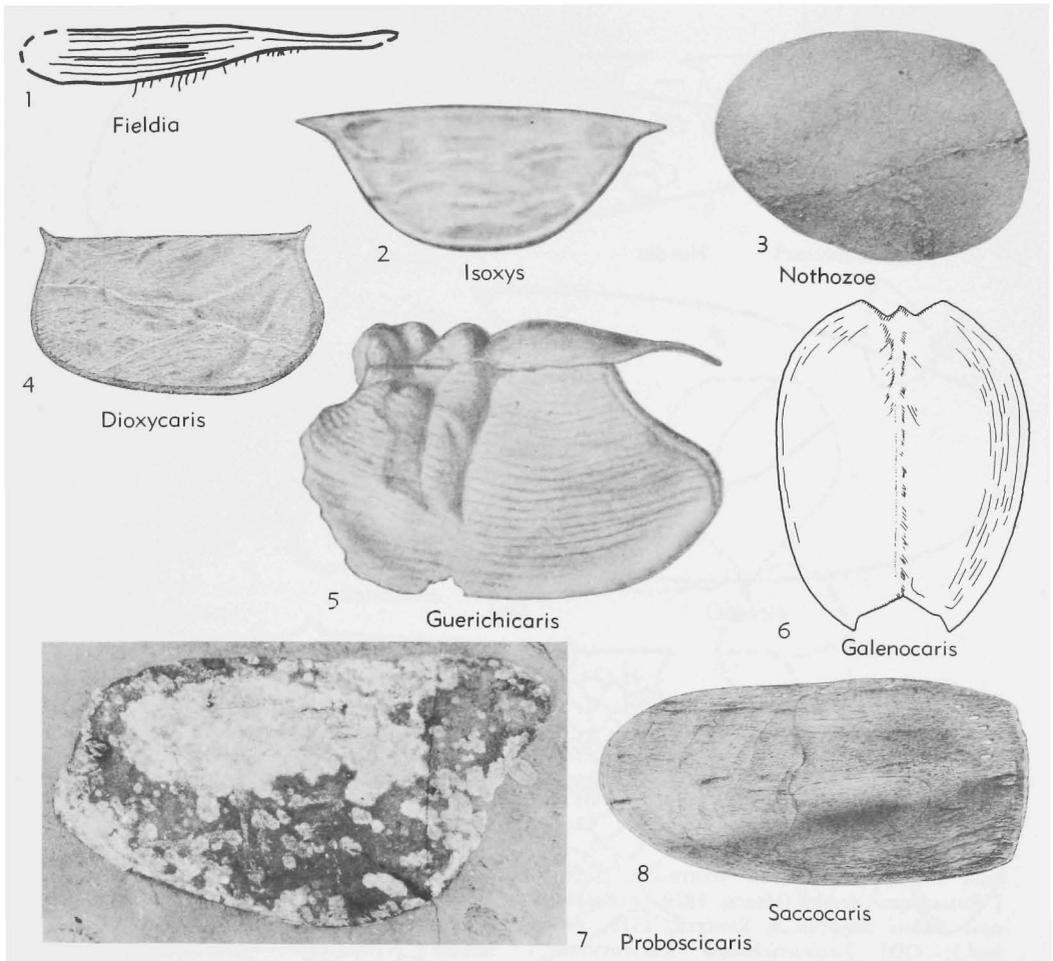


FIG. 150. Phyllocarida, Order and Family Uncertain (p. R325-R327).

B.C.; dorsal view of carapace (holotype) with valves spread out, $\times 0.6$ (Rolfe, n).

Coreocaris KOBAYASHI, 1937 [**C. eishunensis*; OD]. Carapace valves subovate, ?without hinge line. *L.Perm.*, S.Korea.—FIG. 149.1. **C. eishunensis*, Jido Ser.; right lat. view of carapace (holotype) showing ?cephalic appendages, $\times 4$ (Rolfe, n).

Dictyocaris SALTER, 1860 [**D. slimoni*; OD] [= *Dictyacris* HENDERSON, 1880 (*nom. null.*); *Didyocaris* VOGDES, 1889 (*nom. null.*); *Eohepatica* HEARD & JONES, 1931 (type, *E. dyfriensis*; OD, M); *Thallomia* HEARD & JONES, 1931 (*nom. van.*)]. Carapace without hinge line, valves subtriangular, with reticulation of grooves or ridges (probably indicating outlines of cuticular prisms). *M.Sil.-L.Dev.*, NW.Eu.-USA.—FIG. 149.5. **D. slimoni*, ?M.Sil., Scot.; carapace fragment showing reticulation, $\times 3$ (Rolfe, n).

Dioxyaris GÜRICH, 1929 [**Leperditia? argenta*

WALCOTT, 1886; OD] [= *Dyoxyaris* KRESTOVNIKOV, 1961 (*nom. null.*)]. Carapace ?with hinge line, valves subrectangular, anterodorsal and posterodorsal extremities produced obliquely into processes. *L.Cam.*, N.Am.—FIG. 150.4. **D. argenta* (WALCOTT), USA (Utah); lat. view of ?LV (holotype), $\times 0.7$ (384a).

Fieldia WALCOTT, 1912 [**F. lanceolata*; OD]. ?Carapace lanceolate, with at least 5 longitudinal furrows. *M.Cam.*, N.Am.—FIG. 150.1. **F. lanceolata*, Burgess Sh., Can.(B.C.); ?carapace lat., holotype, $\times 1.3$ (384c).

Galenocaris WELLS, 1944 [**G. campbelli*; OD, M]. Carapace ?without hinge line, valves elongate, with short posteroventral spine; anterodorsally and posteriorly truncate; short process between valves anteriorly. *U.Ord.*, N.Am.—FIG. 150.6. **G. campbelli*, Maquoketa Sh., USA (Ill.); dorsal view of carapace (holotype), $\times 2$ (385).

Guerichicaris VAN STRAELLEN, 1933 [*pro Entomo-*

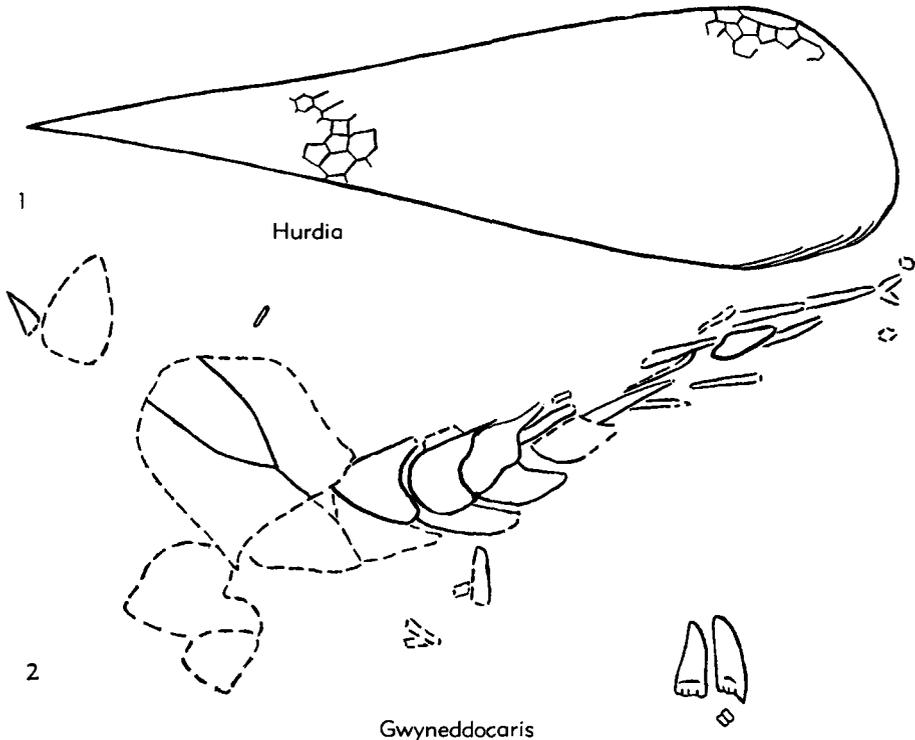


FIG. 151. Phyllocarida, Order and Family Uncertain (1); Discinocarina, Family Uncertain (2) (p. R325-R326).

caris GÜRICH, 1929 (non WHITFIELD, 1896)] [**Entomocaris dohmi* GÜRICH, 1929 (= *Entomocaris dohmi* RICHTER & RICHTER, 1918, *nom. nud.*); OD] [= *Guerichocaris* KRESTOVNIKOV, 1961 (*nom. null.*)]. Carapace with hinge line, valves subovate, anteriorly rounded, posterodorsally truncate; marginal rim narrow anteroventrally, broadening posteriorly; anterodorsal region of carapace with 3 deeply incised, oblique furrows separating 3 swellings; valves with coarse longitudinal striation. [Type of *Guerichicaris* (*recte* *Guerichicaris*) VAN STRAELLEN, 1933, of *Ceraticarina*.] *M.Dev.*, Ger.—FIG. 150,5. **G. dohmi* (GÜRICH), Couvin., Eifel; left posterodorsal view of carapace (paratype), $\times 3$ (128).

Hurdia WALCOTT, 1912 [**H. victoria*; OD]. ?Carapace triangular, commonly reticulate. *M.Cam.*, N. Am.—FIG. 151,1. **H. victoria*, Burgess Sh., Can.(B.C.); lat. view of small specimen showing reticulation, $\times 0.6$ (Rolfe, n).

Isoxys WALCOTT, 1890 [**I. chilhoweanus*; OD] [= *Isoxis*, *Isoxis*, KRESTOVNIKOV, 1961 (*nom. null.*)]. Carapace with convex hinge line, valves subelliptical; anterodorsal or mid-anterior and posterodorsal extremities of valves produced into sharp processes. [Type of *Isoxyidae* BROOKS & CASTER, 1956 (*nom. correct.* ROLFE, 1962, *pro*

Isoxyidae BROOKS & CASTER, 1956) including *Isoxys*, *Dioxyaris*, and *Tuzoia*, and thus junior synonym of *Tuzoiaidae* RAYMOND, 1935.] *L.Cam.-M.Cam.*, N.Am.-Spain.—FIG. 150,2. **I. chilhoweanus*, L.Cam., USA(Tenn.); lat. view of carapace (syntype), $\times 1.5$ (384b).

Lebesconteia JONES & WOODWARD, 1899 [*nom. correct.* ROLFE, herein (*ex Lebescontia* JONES & WOODWARD, 1899)] [**L. aenigmatica*; OD]. Carapace of ?*Dithyrocaris*, indeterminate. Other species may be *Bivalvia*. *U.Ord.*, *L.Carb.*, NW.Eu.

Mendocaris RUSCONI, 1950 [**M. australis*; OD, M]. Carapace with marginal excavation and anterior depression; poorly described and unfigured. *U. Cam.*, Argentina.

Nothozoe BARRANDE, 1872 [**N. pollens*; OD, M] [= *Nothozoe* BARRANDE in BIGSBY, 1868 (*nom. nud.*); *Nothozoe* ZITTEL, 1885 (*nom. null.*)]. Elliptical, subovate, or subcircular, smooth and gently arched molds of carapace valves. *L. Cam.-M.Ord.*, ?*L.Dev.*, W.Eu.-USA-?SW.China.—FIG. 150,3. **N. pollens*, M.Ord., Drabov Qtzt., Czech.; convex mold of ?LV of large specimen, $\times 0.6$ (Rolfe, n).

Odaraia WALCOTT, 1912 [**O. alata*; OD] [= *Odaria* FEDOTOV, 1925 (*nom. null.*); *Odaraia* ROGER in PIVETEAU, 1953 (*nom. null.*); *Odría*

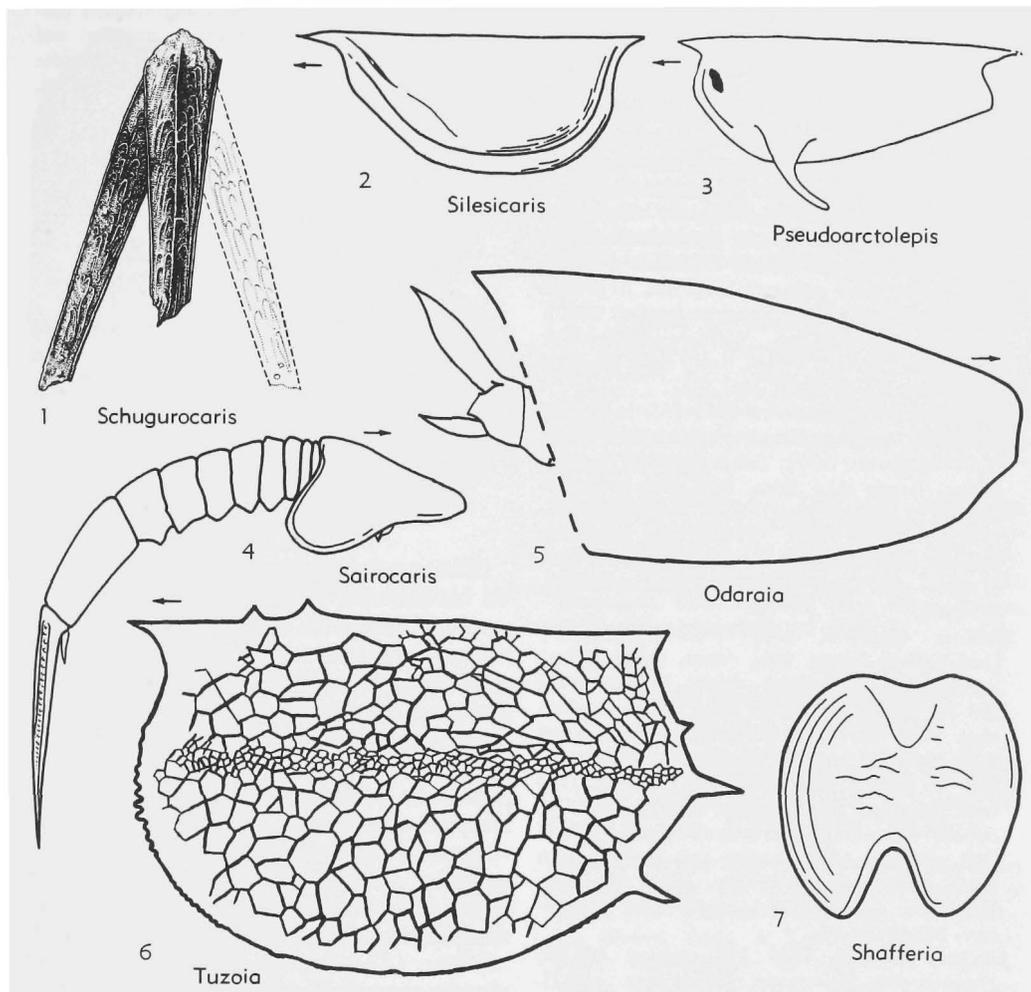


FIG. 152. Phyllocarida, Order and Family Uncertain (p. R326-R328).

KRESTOVNIKOV, 1961 (*nom. null.*), Carapace subtriangular, with oblique posterior truncation, furcal rami laterally expanded, lanceolate. *M.Cam.*, N.Am.—FIG. 152.5. **O. alata*, Burgess Sh., Can.(B.C.); lat. view of lectotype, $\times 0.5$ (Rolfe, n).

Proboscicaris ROLFE, 1962 [**P. agnosta*; OD]. Carapace valves subovate to subrectangular, with carapace horn anteriorly produced into spatulate beak. *M.Cam.*, N.Am.—FIG. 150.7. **P. agnosta*, Burgess Sh., Can.(B.C.); lat. view of RV (holotype), blotched with ?alga *Morania parasitica* WALCOTT, $\times 0.5$ (376a).

Pseudoarctolepis BROOKS & CASTER, 1956 [**P. sharpi*; OD]. Carapace elongate, with hinge line; anterodorsal and posterodorsal extremities of valves produced into processes, posterior margin concave; large, posteriorly curved, anteroventrally sit-

uated hollow spine and eroded area marking site of anterior tubercle on each valve. [Type of *Pseudoarctolepididae* BROOKS & CASTER, 1956 (*nom. correct.* ROLFE, 1962, *pro* *Pseudoarctolepididae* BROOKS & CASTER, 1956). This large form shows remarkable convergent resemblance to the ostracode *Pteroleperditia armata* (WALCOTT).] *M.Cam.*, N.Am.—FIG. 152.3. **P. sharpi*, Wheeler Sh., USA(Utah); lat. view of LV (reconstr.), $\times 0.7$ (58).

Saccocaris SALTER, 1873 [**Hymenocaris (Saccocaris) major*; M] [= *Saccocaris* SALTER, 1868 (*nom. oblit.*)]. Carapace ?without hinge line, valves subrectangular. *U.Cam.-L.Ord.*, G.Brit.-?Australia.—FIG. 150.8. **S. major* (SALTER), Wales; lat. view of LV (holotype), $\times 0.5$ (160).

Sairocaris ROLFE, 1963 [*pro Acanthocaris* PEACH, 1883 (*non* SIM, 1872)] [**Acanthocaris attenuata*

PEACH, 1883; SD VAN STRAELEN & SCHMITZ, 1934] [= *Acantocaris* KRESTOVNIKOV, 1961 (*nom. null.*)]. Carapace reduced, triangular, without hinge line, with or without mid-ventral excavation which may have allowed ventral exposure of gnathal lobes of mandibles; carapace smooth or ?longitudinally striate; abdomen and ?posterior thoracic somites not covered by carapace; telson as in *Ceratiocaris*, dorsal ridge may be tuberculate; furca reduced to short spines. [Emendation of the *Ceratiocarina* may be needed to include a family based on this genus without a hinge line. At present *Sairocaris* is too poorly known to warrant such a major change.] *L.Carb.*, W.Eu.—FIG. 152,4. *S. elongata* (PEACH), Visean, Scot.; right lat. view (reconstr.), $\times 1$ (Rolfe, n, after 371).

Schugurocaris KRESTOVNIKOV, 1961 [**S. magnifica*; OD] [= ?*Neurocaris* KRESTOVNIKOV, 1961 (type, *N. libelluliformis*; OD)]. Telson triangular in cross-section, longer than furca, both with ornament of cusps or oblique striae. *U.Dev.*, E.Eu.-Australia-?N.Can.—FIG. 152,1. **S. magnifica*, Shugurov Beds (Frasn.), Orenburg distr., E.Eu.; dorsal view of telson and furca (holotype) (part reconstr.), $\times 1$ (168).

Shafferia WALCOTT, 1917 [**S. cisina*; OD] [= *Schafferia* SHARP, 1901 (*nom. null.*) (WALCOTT'S original spelling should be conserved and not treated as a *lapsus* since Mount Schaffer, after which the fossil was named, is also (and more correctly) written Schaeffer. Confusion will then be avoided with *Schaefferia* ABSOLON, 1900 (*non* HOULBERT in OBERTHÜR, 1918)]. Like *Discinocarid* but shell thicker, bent along mid-line and with shallow indentation at end farthest from notch. *M.Cam.*, N.Am.—FIG. 152,7. **S. cisina*, Mt. Whyte F., Can.(B.C.); dorsal view of holotype, $\times 6$ (Rolfe, n).

Silesicaris GÜRICH, 1926 [**S. nasuta*; OD, M] [= *Silesiocaris* KOBAYASHI, 1937 (*nom. null.*)]. Outline of carapace valves like that of *Isoxys* but with well-defined marginal groove demarcating broad rounded rim and with deep, oblique antero-dorsal-mid-anterior furrow continued as fold which joins margin mid-ventrally; anterior tubercle sometimes detectable. *L.Cam.* (not *L.Dev.* as originally described), SW.Pol.—FIG. 152,2. **S. nasuta*, Bolków; lat. view of LV, $\times 2$ (128).

Trigonocarys BARROIS, 1891 [**T. lebescontei*; OD, M] [= *Trigonocaris* WILTSHIRE, WOODWARD & JONES, 1892 (*nom. van.*)]. Telson triangular, with 4 longitudinal, ventral ribs separated by furrows; furca shorter than telson, furcal rami laterally compressed, hourglass-shaped in cross section. *U. Ord.*, NW.Fr.

Tuzoia WALCOTT, 1912 [**T. retifera*; OD] [= *Puzoia* GÜRICH, 1929 (*nom. null.*); *Tuzoia* BROOKS & CASTER, 1956 (*nom. null.*)]. Carapace with hinge line, valves subelliptical, carapace horn slightly produced; usually reticulate; prominent lateral ridge carinate, with smaller reticulae than

on main area of valves; spines and spinules projecting from entire margin except anterior, and may occur on lateral ridge. [Type of Tuzoïidae RAYMOND, 1935 (=Isoxyidae BROOKS & CASTER, 1956.)] *L.Cam.-M.Cam.*, W.Can.-China.—FIG. 152,6. *T. burgessensis* RESSER, M.Cam. (Burgess Sh.), B.C.; lat. view of LV (paratype) (reconstr.), $\times 0.5$ (Rolfe, n).

NONPHYLLOCARID AND UNCERTAIN GENERA

In this section consideration is given to various nominal genera which have been improperly classed by authors as belonging to the Phyllocarida and to some which now are regarded as *incertae sedis*.

FORMS REFERRED TO DISCINOCARINA

The genera grouped by CLARKE (1900) in his suborder Discinocarina and referred to the Phyllocarida are of uncertain affinity. They have been compared and confused with graptolite "swim-bladders" and "gonangia," eurypterid metastomata, hyolithid opercula, polyalaphoran plates, bivalves, arthrodire dermal plates, and brachiopod carapaces. *Discinocarid gigantea*, which may be up to 18 cm. in diameter, has been suggested by analogy with *Oxlosia* to be a genuine acrotetid brachiopod. Some of these genera are known to be ammonoid anaptychi and have been synonymized with *Sidetes* (*Treatise*, p. L467-L468). Other genera are pre-Devonian and hence cannot be ammonoid aptychi, but RUEDEMANN'S (1916) suggestion that aptychi "would naturally also have existed in the Ordovician and Silurian cephalopods" has been largely overlooked. The sole crustacean feature of the remaining Discinocarina is the supposed "rostral plate," which shows little similarity to rostral plates of other fossil phyllocarids. Two cases of body segments associated with Discinocarina have been described, but these are both doubtful. It is tempting to suggest an analogy between the bivalved Peltocarididae and ammonoid diaptychi, and between the Discinocarididae and ammonoid anaptychi. Significantly, their stratigraphic range coincides with that of the michelinoceratid nautiloids. The isolated occurrence

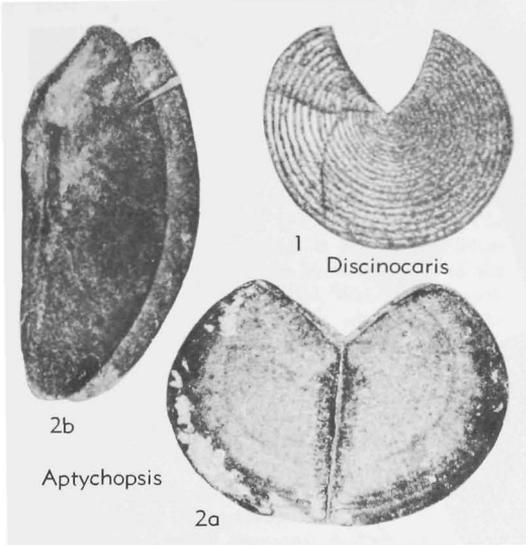


FIG. 153. Subclass Uncertain (Discinocarididae) (1); (Peltocarididae) (2) (p. R329).

of these shields may result from current sorting and selective diagenesis (KEYSERLING, 1846; CLARKE, 1902) in the same way as aptychi occur in aptychus beds.

No pre-Devonian Discinocarina have been found in nautiloid apertures, however, which makes difficult a ready acceptance of RUEDEMANN'S hypothesis. On the other hand, it seems worth recalling that, as DAMES (1884) and MATERN (1931) stressed, "only in exceptional cases do anaptychi and shells occur together."

Two groups of nominal genera previously classed as belonging to CLARKE'S order Discinocarina are included under this heading. One consists of forms which now are regarded as synonyms of *Sidetes*. The other contains genera *incertae sedis* which are not synonymized with *Sidetes*. Fossils included in this latter group are represented by circular to subcircular, ?originally conical, concentrically ridged, thin organic or carbonized films, with subtriangular plate filling a prominent notch. For reference purposes it is useful to retain the familial classification employed for them.

The genera here cited as synonyms of *Sidetes* are additional to those given in *Treatise Part L* (1957, p. L467-L468).

Sidetes GIEBEL, 1847, p. 821 [**S. striatus* GIEBEL, 1851; SM] [?= *Ellipsocaris* WOODWARD in DE-

WALQUE, 1880 (type, *E. dewalquei*; OD, M); *Spathiocaris* CLARKE, 1882 (type, *S. emersonii*; OD); *Spathiocaris* ETHERIDGE, WOODWARD & JONES, 1883 (*nom. null.*); *Spathiocaris* CAMPBELL, 1946 (*nom. null.*); *Ellipsocaris* BROOKS & CASTER, 1956 (*nom. null.*); *Spathiocaris*, *Spatiocaris*, *Spatchiocaris* KRESTOVNIKOV, 1961 (*nom. null.*); *Dipterocaris* CLARKE, 1883 (type, *D. pennaedaedali*; SD S. A. MILLER, 1889) (holotype of the type species is a *Spathiocaris* torn along its mid-line, as surmised by ETHERIDGE, WOODWARD & JONES, 1885)].

Family DISCINOCARIDAE
Etheridge, Woodward & Jones, 1885

[*nom. correct.* ROLFE, herein (pro family Discinocarida ETHERIDGE, WOODWARD & JONES, 1885, *nom. imperf.*)]
[=Discinocaridae HALL & CLARKE, 1888]

Without median suture line. *M.Ord.-U. Trias.*, ?*L.Jur.*

Discinocaris WOODWARD, 1866 [**D. browniana*; OD, M] [= *Aspidocaris* REUSS, 1867 (type, *A. trisica*; OD)]. Sides of notch straight. *M.Ord.-U. Trias.*, ?*L.Jur.*, W.Eu.-USA.—FIG. 153, 1. **D. browniana*, L.Sil. (Birkhill Sh.), Scot.; syntype, lacking triangular plate, $\times 2$ (386a).

Family PELTOCARIDIDAE
Clarke in Zittel, 1900

[*nom. correct.* ROLFE, herein (pro Peltocaridae CLARKE in ZITTEL, 1900)] [= *Peltocariden* HAECKEL, 1896 (vernacular)]

With median suture line. ?*L.Cam.-?M. Cam.*, ?*L.Ord.*, *U.Ord.-U.Sil.*, ?*U. Perm.*

Peltocaris SALTER, 1863 [**Dithyrocaris? aptychoides* SALTER, 1852; SD ETHERIDGE, WOODWARD & JONES, 1884] [= *Peltocharis* ETHERIDGE in GEIKIE, A., HORNE, SKAE, & ETHERIDGE, 1877 (*nom. null.*); =? *Culampaia* RUSCONI, 1949 (type, *C. ornata*; OD, M); *Culampia* ROGER in PIVETEAU, 1949 (*nom. null.*); *Peltoceras* KRESTOVNIKOV, 1961 (*nom. null.*)]. Notch semicircular, ?with nodes on valves at base of notch. ?*M.Cam.*, ?*L.Ord.*, *M. Sil.*, Eu.-?S.Am.

Aptychopsis BARRANDE, 1872 [**A. prima*; OD, M] [= *Aptychopsis* BARRANDE, 1870 (*nom. nud.*); *Aptychoides* BARRANDE, 1872 (obj.); *Aptichopsis* DUNCAN, WOODWARD & ETHERIDGE, 1872 (*nom. null.*); *Aptychopsis* WOODWARD, 1882 (*nom. null.*); *Aptychopsis* RUSCONI, 1949 (*nom. null.*)]. Like *Peltocaris* but sides of notch straight; valves without nodes. ?*L.Cam.*, ?*L.Ord.*, *U.Ord.-U.Sil.*, ?*U. Perm.*, Eu.-?E.Can.-?Australia.—FIG. 153, 2. **A. prima*, L.Sil.-M.Sil. (Liten Beds), Czech.; 2a, dors., $\times 3$; 2b, lat. with valves displaced, $\times 4$ (Rolfe, n).

GENERA UNCERTAIN

Anatifopsis BARRANDE, 1872 [**A. bohémica*; OD, p. 578] [= *Anatifopsis* BARRANDE in BIGSBY, 1868

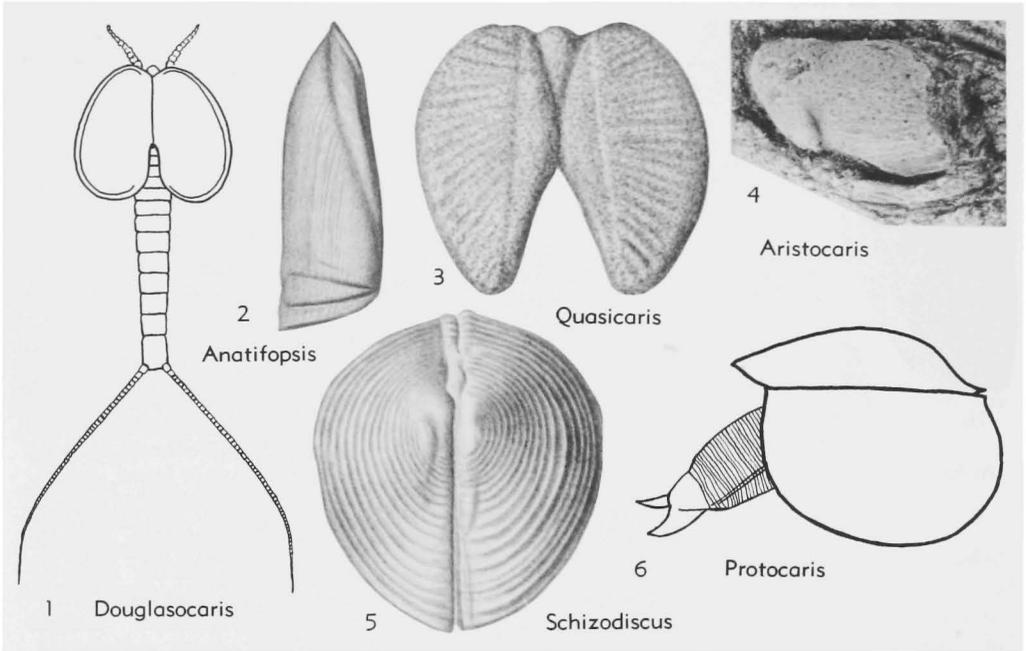


FIG. 154. Subclass Uncertain (Genera Uncertain) (p. R329-R331).

(*nom. nud.*). Thin-shelled ?Bivalvia; valves elongate, strongly convex, one end truncate, ?open in life; concentrically striate and with 2 vertical internal septa, diverging ventrally away from hinge line; may have platform developed along hinge line perpendicular to surface of valves. [Other species referred to this genus are polyplacophorans and dermal plates of *Cyathaspis*.] *L.Ord.-U.Ord.*, Eu.—FIG. 154.2. *A. prima*, *L.Ord.*, Czech., single valve, lat., $\times 2$ (343).

Aristocaris TOLMACHOV, 1926 [**A. incerta*] [= *Aristocaris* NEAVE, 1950 (*nom. null.*)]. ?Ostracode. *M.Dev.*, N.Can.—FIG. 154.4. **A. incerta*, Givet., Ellesmere I.; lat. (holotype), $\times 9$ (Rolfe, n).

Caridolites ETHERIDGE, WOODWARD & JONES, 1890 [**C. wilsoni*; OD, M] [= *Caridolites* NICHOLSON, 1873 (*nom. nud.*); *Cardiolites* CLARKE in ZITTEL, 1900 (*nom. null.*); *Cardiolites* KRESTOVNIKOV, 1961 (*nom. null.*)]. Based on supposed tracks of ?*Ceratiocaris*, possibly groove casts. *M.Sil.*, Scot.

Cryptozoe PACKARD, 1886 [**C. problematica*; OD] [= *Cryptozoe* POMPECKJ, 1912 (*nom. null.*); *Schopfia* JANSSEN, 1940]. [Dr. J. M. SCHOPF has isolated plant epidermis from the holotype (U.S. Natl. Mus. 38865) and suggests that this is a lycopod sporangium.] *M.Penn.*, USA (Ill., Mazon Creek).

Douglasocaris CASTER & BROOKS, 1956 [**D. collinsi*; OD]. Carapace with hinge line, valves subelliptical, smooth; ?9 abdominal somites, telson elongated but not produced and bearing pair of annulated

cerci; thoracic limbs biramous, nonfoliaceous, with 2- or 3-segmented protopod. ?Notostracan branchiopod. [Type of Douglasocaridae (*recte* Douglasocarididae) CASTER & BROOKS, 1956.] *L.Ord.*, N.Am.—FIG. 154.1. **D. collinsi*, "33 Formation," Douglas Dam, USA (Tenn.); dors. holotype (reconstr.), $\times 2$ (350, mod.).

Gwyneddocaris BOCK, 1946 [**G. parabolica*; OD]. *U.Trias.*, N.Am.—FIG. 151.2. **G. parabolica*, Lockatong F., USA (Pa.); dorsal view of holotype, $\times 4.8$ (Rolfe, n).

Dr. DONALD BAIRD recognized that the unique specimen of *Gwyneddocaris* comprises the mid-line scales and fin fulcra of a ganoid fish. He therefore obtained the independent opinion of Dr. HAROLD F. ROELLIG who agreed that "The specimen does represent the midline region of a fish. . . The 'univalved carapace' is probably scalation associated with the vent. I know of nothing quite like it along the dorsal midline. The 'thoracic somites' [Bock's numbers] 2,3,4,5,6 are midline scales. The 'spines' 20 and 21 are fulcra. The small size of these fulcra indicates that the fish is not *Semionotus* but probably *Catopterus*; fulcra of *Semionotus* are more robust. The tubercles illustrated in Bock's Fig. 5 as on the 'spines' are to be seen on the fulcra of both *Semionotus* and *Catopterus*."

Lingulocaris SALTER in RAMSAY, 1866 [**L. lingu-laeomes*; OD, M] [= *Mytilocaris* ETHERIDGE, 1888 (*nom. nud.*); *Lingulocaris* BARROIS, 1891 (*nom. van.*); *Lingulocaris* MARR, 1892 (*nom. null.*); *Modiolocaris* PEACH in JEHU & CAMPBELL, 1917 (type, *M. dakynsi*; OD, M)]. Thin bivalve shell with slight umbo, concentrically striate; ?ribeiroiid or Bivalvia. [Refers to type-species and *Modiolocaris* only. Other Lower Ordovician species referred to this genus are based on elongate carapaces resembling *Hymenocaris*. Further knowledge of

- these is needed before establishing a separate genus. The body segments shown on PEACH's restoration of *Modiolocaris* are imaginary; the holotype shows only a fracture plane.] *U.Cam.-L.Ord.*, G.Brit.
- Myocaris** SALTER, 1864 [**M. lustraria*; OD]. Ribeiroid. *L.Ord.-U.Ord.*, W.Eu.
- Pinnocaris** ETHERIDGE, 1878 [**P. lapworthi*; OD]. ?Ribeiroid or Bivalvia. *U.Ord.-U.Sil.*, Brit.
- Portalia** WALCOTT, 1918 [**P. mira*; OD]. The holotype of the type species is a ?sponge (MADSEN, 1957) and is overlain by a specimen of the ?actinarian *MacKenziea costalis* WALCOTT (according to WALCOTT, 1918; later identified as the worm *Miskoiia* by RESSER, 1931). STØRMER (1944, p. 101) has compared the specimens with *Protocaris*, interpreting the *MacKenziea* as a carapace, and has referred to the "papillae" of *Portalia* as arthropod appendages with "indications of gill-blades."
- Proracaris** BAILY, 1870 [**P. machenrici*; OD, M] [= *Protocaris* ETHERIDGE, WOODWARD & JONES, 1883 (*nom. null.*); *Proracaris* BAILY, 1875 (*nom. null.*); *Protocaris* JONES & WOODWARD, 1888 (*nom. null.*)]. Fragments of eurypterid according to ETHERIDGE, WOODWARD & JONES, 1890. *U.Dev.*, SE.Eire.
- Protocaris** WALCOTT, 1884 [non JONES & WOODWARD, 1888 (*nom. null.*)] [**P. marshi*; OD] [= *Protocaris* WOODWARD, 1895 (*nom. null.*)]. Carapace with hinge line, valves subelliptical. Large number (may exceed 45) of short body somites bearing lamellate appendages anteriorly. Telson not produced, furcal rami curved. ?Branchiopod. [Type of Protocaridae (*recte* Protocarididae) MILLER, 1889.] *L.Cam.-M.Cam.*, N. Am.—FIG. 154,6. *P. pretiosa* RESSER, M.Cam. (Burgess Sh.), Can.(B.C.); right lat. (holotype), $\times 0.7$ (Rolfe, n).
- Quasicaris** ROLFE, 1961 [pro *Pterocaris* BARRANDE, 1872 (non HELLER, 1862; nec CLAUS, 1876)] [**Pterocaris bohemia* BARRANDE, 1872; OD, M]. Like *Aptychopsis* but with posterior notch, thin radial striae and single longitudinal line on each ?valve. *M.Ord.*, Czech.—FIG. 154,3. **Q. bohemia* (BARRANDE), Drabov Qtzt., Mt. Drabov; internal mold, dors. (holotype), $\times 3$ (343).
- Salterina** JONES & WOODWARD, 1888 [**S. pholadiformis*; OD, M] (= *Dithyrocaris pholadomya* SALTER, 1863, *nom. nud.*; *D. pholadiformis* HUXLEY & ETHERIDGE, 1865, *nom. nud.*) [= *Salterella* JONES & WOODWARD, 1888 (non BILLINGS, 1861) (obj.), an offprint of the 1888 paper signed by T. R. JONES in the Harvard Museum of Comparative Zoology has the spelling corrected in JONES' handwriting.]. Fragment of large bivalve mollusk. *L.Carb.*, Eng.
- Schizodiscus** CLARKE in HALL & CLARKE, 1888 [non KITTL, 1891; nec KISHINOUE, 1902] [**S. capsa*; OD, M]. Carapace with hinge line, valves semicircular, with ridges concentric about mid-dorsal umbo. ?Conchostracan branchiopod. *M.Dev.*, N.Am.—FIG. 154,5. **S. capsa*, Hamilton Gr., USA(N.Y.); carapace valves spread out, dorsal (lectotype), $\times 3$ (140).
- Sinocaris** MANSUY, 1912 [**S. asiatica*; SD VAN STRAELEN & SCHMITZ, 1934]. Elongate valves with slight ventral excavation, posterior attenuation and prominent, longitudinal folds. ?Bivalvia. *Sil.*, SW. China.
- Strigocaris** VOGDES, 1889 [pro *Solenocaris* MEEK, 1872 (non YOUNG & YOUNG, 1868)] [**Ceratiocaris (Solenocaris) strigata* MEEK, 1872; OD, M] [= *Stringocaris* KOBAYASHI, 1937 (*nom. null.*)]. Two of the syntypes of the type species are Bivalvia, and the third is a fish bone, probably a coelacanth jugular plate. [*Strigocaris sanctiludovici* (WORTHEN) is possibly a phyllocarid carapace, but poorly preserved.] *L.Miss.*, USA.
- Trilobocaris** PŘIBYL, 1953 [**T. bohemia*; OD]. ?Carapace small, elongate, one valve convex, trilobed, the other flat, weakly bilobed. ?Ostracode or crinoid calyx plate (*vide* J. BOUŠKA and I. CHLUPLÁČ). *M.Dev.*, Czech.
- Xiphidiocaris** CLARKE in ZITTEL, 1900 [pro *Xiphocaris* ETHERIDGE, WOODWARD & JONES, 1886 (non MARTENS, 1872)] [**Ceratiocaris? ensis* SALTER, 1860; OD, M] [= *Xyphocaris* GÜRICH, 1929 (*nom. null.*)]. Telson of eurypterid *Carcinosoma*, according to RUEDEMANN. *M.Sil.-U.Sil.*, Eng., Australia.

EUMALACOSTRACA

By R. C. MOORE

Subclass EUMALACOSTRACA
Grobben, 1892

Malacostraca generally of shrimplike form distinguished from Phyllocarida by nonbivalve nature of carapace and lack of seventh abdominal somite, telson without unsegmented, movably articulated caudal furca. *M.Dev.-Rec.*

The Eumalacostraca include all malacostracans considered to be relatively advanced in divergent lines of evolution. They are divided into superorders designated as Eocarida, contained archaic forms, Syncarida, Peracarida, Eucarida, and Hoplocarida, of which the last four include most post-Paleozoic malacostracans.

EOCARIDA

By H. K. BROOKS

[University of Florida]

[Chapter submitted August, 1964]

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INTRODUCTION

Most of the Paleozoic eumalacostracan fossils with a carapace have a puzzling combination of morphological characteristics not consistent with the definition of any one of the Recent superorders. They are unique in that all have biramous thoracic appendages with a single joint in the protopod and there are furcal lobes and a median spine on the telson. However, structural trends toward the Mysidacea, Euphausiacea, and Decapoda are displayed. The superorder Eocarida was established (Brooks, 1962) for this archaic caridoid stock.

In older papers on eumalacostracan fossils from the Paleozoic, most authors classified shrimplike specimens as decapods. The single exception was HUXLEY (1857), who recognized some homologies between *Pygocephalus* and the Mysidacea. WOODWARD

(1907) figured and described a peracarid marsupium on *Pygocephalus*. In the following year PEACH (226) published a monographic study on the Upper Paleozoic Eumalacostraca from Scotland in which oöstegites were proved to exist also on *Tealliocaris*. He envisioned that a marsupium was present on all other contemporaneous caridoid genera. PEACH repeatedly compared morphological features of the fossils with those of the Recent Lophogastridae.

BROOKS (55) has demonstrated that a vertical classification of these caridoid Malacostraca consistent with established taxa for Recent Eumalacostraca is impossible. Their primitiveness and phylogenetic significance are best emphasized by recognition of the superorder Eocarida, fossils of which occur sporadically from Middle Devonian through the Permian.

MORPHOLOGY

Furcal lobes and a large median telson spine have been frequently figured on specimens of Paleozoic caridoid fossils. It was not until detailed morphological studies by BROOKS (55) that the significance of these and other archaic crustacean features were realized. It is possible that none of the known fossil eocarids are the direct ancestors of the extant Mysidacea, Euphausiacea, and Decapoda, but as a group they provide valuable morphological evidence bearing on malacostracan phylogeny.

Tagmosis of the body is into a **head**, **thorax**, **abdomen**, and a terminal **telson**. In the shrimplike members of the order Eocaridacea the abdomen is longer than the **cephalothorax** (Fig. 155,*A*), whereas in the prostrate eryonid and crablike Pygocephalomorpha (Fig. 155,*B*) they are subequal or the telson is reduced.

The **carapace** completely covers the head and thorax, but it is not fused with any of the postcephalic somites. The pygocephalomorphs all have the ventral margin of the carapace folded under and the **branchiostegal area** produced laterally, the lateral margins thus formed being keeled and usually serrate. The **lappets** of the carapace of the Eocaridacea fit closely against the pleura of the thoracic somites. However, in *Palaeopalaemon* an incipient double occurs near the ventral margins of the carapace.

Only one transverse sulcus is conspicuously developed on the carapace and this appears to be homologous with the **cervical groove** of decapods. In that the furrow bifurcates dorsally in *Palaeopalaemon*, it is possible that the posterior branch reaching the dorsum is equivalent to the "postcervical furrow" of GLAESSNER (118). There is no basis for derivation of a quadruple system of dorsal carapace sulci from a *Palaeopalaemon*-like animal, as BURKENROAD (62) has postulated.

Structure of the five pairs of cephalic appendages is believed to be comparable to that of the syncarids and mysidaceans. The **antennules** each consist of two multi-articulate **flagella** arising from a three-jointed **peduncle**. The **antennae** have a two-jointed protopod, the second of which ex-

tends as a **stipe** for the squamate exopod, the caridoid **scaphocerite**. The endopod consists of three joints and a long flagellum.

Little is known of the **mandible** except that in *Anthracaris* secondary articulation with the epistome is observed (Fig. 156,*B*), a feature found in Recent decapods and some stomatopods and mysidaceans. The two pairs of **maxillae** are unknown. The structures of *Tealliocaris* designated by PEACH (226) as mandibular palps and maxillae are incorrectly interpreted portions of thoracic appendages.

Each of the eight thoracic somites bears a pair of **perioopods**, which are biramous appendages. In all known fossils the appendages are distinct in possessing only one segment in the **protopod** (Fig. 156,*C*), as does the most primitive extant crustacean known, *Hutchinsoniella*. In all other eumalacostracans two or three segments occur in the protopod. The **endopods** have five segments, as do those of euphausiids and decapods. The **exopods** that have been observed have an unjointed stipe and a short flagellum (Fig. 156,*D*).

Nothing is known of the **branchiae** of eocarids; however, the branchiostegal development of the carapace of the pygocephalomorphs is suggestive of a **branchial chamber**. PEACH (226) reported podobranchiae on *Tealliocaris*, but re-examination of the specimens failed to confirm his interpretation.

Thoracic sexual features found on some eocarids are sternal processes, oostegites forming a brood pouch, and a seminal receptacle. **Gonopores** have not been observed, but it must be assumed they were associated with the base of the appendages of the sixth thoracic somite in females and the eighth thoracic somite in males. The function of **sternal processes** is unknown, but they are characteristic of mysidaceans and occur mid-ventrally on the sternites. It is only on *Tealliocaris* that low conical projections (Fig. 156,*E*), which may be homologous, are known to occur. PEACH (226) reported seeing oostegites on a variety of Paleozoic caridoid fossils, including the Palaeostomatopoda, but close scrutiny has proved their existence only on *Tealliocaris* and *Pygocephalus* (Fig. 156,*F,G*). In

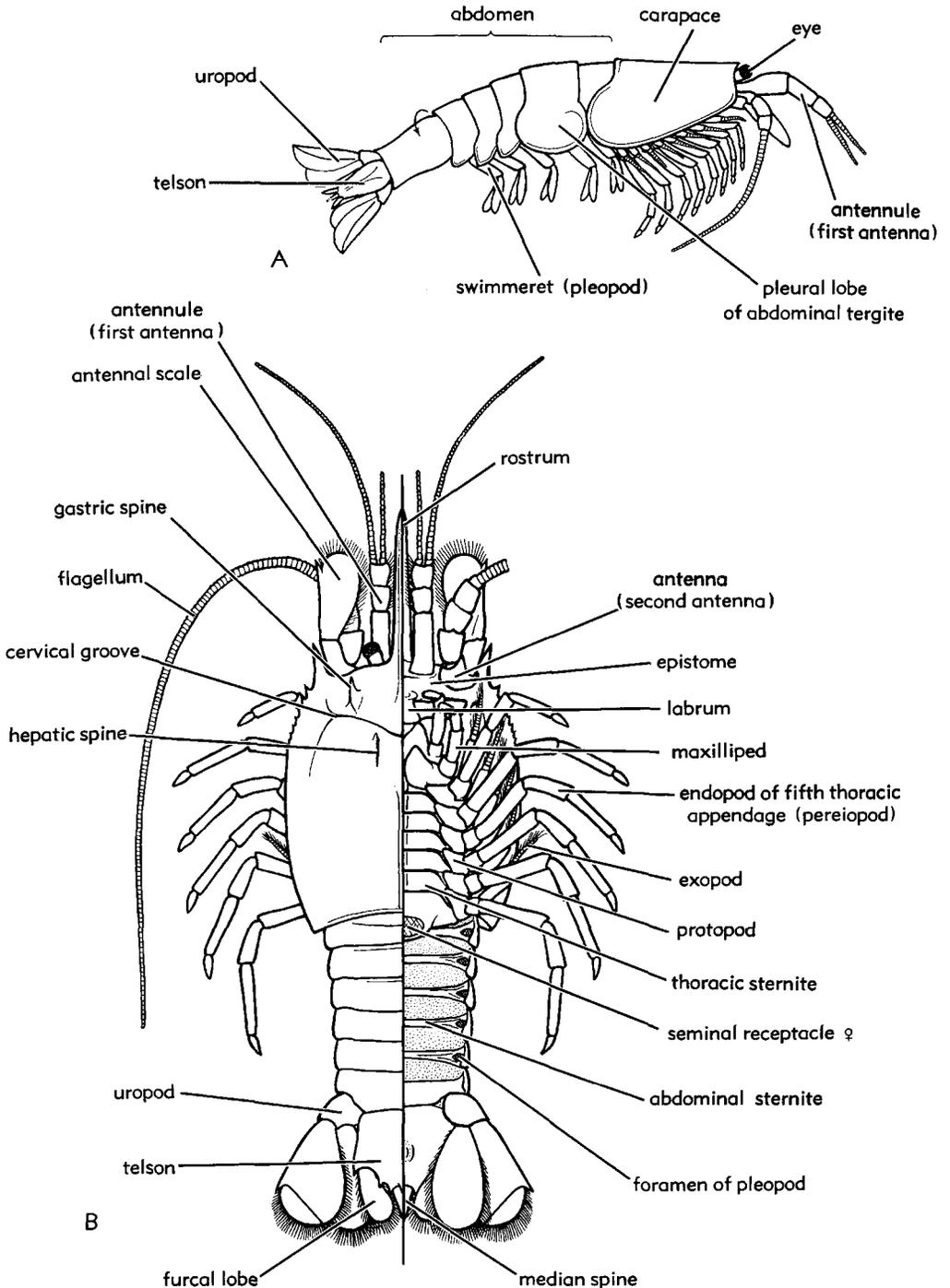


FIG. 155. Morphology of Eocarida.—A. *Crangopsis socialis* (SALTER), Eocaridacea, L.Carb., Scot.; $\times 4$.
 —B. *Anthracaris gracilis* (MEEK & WORTHEN), Pygocephalomorpha, Penn., USA (Ill.); $\times 2$ (55).

these fossils the **marsupium** occurs only on a few mature specimens, presumably the females, and is composed of large imbricating endites of the thoracic appendages.

The **seminal receptacle** occurs as a large medial pouch on the eighth thoracic sternite of *Pygocephalus* and *Anthracaris* (Fig. 156, C). Comparable but not homologous struc-

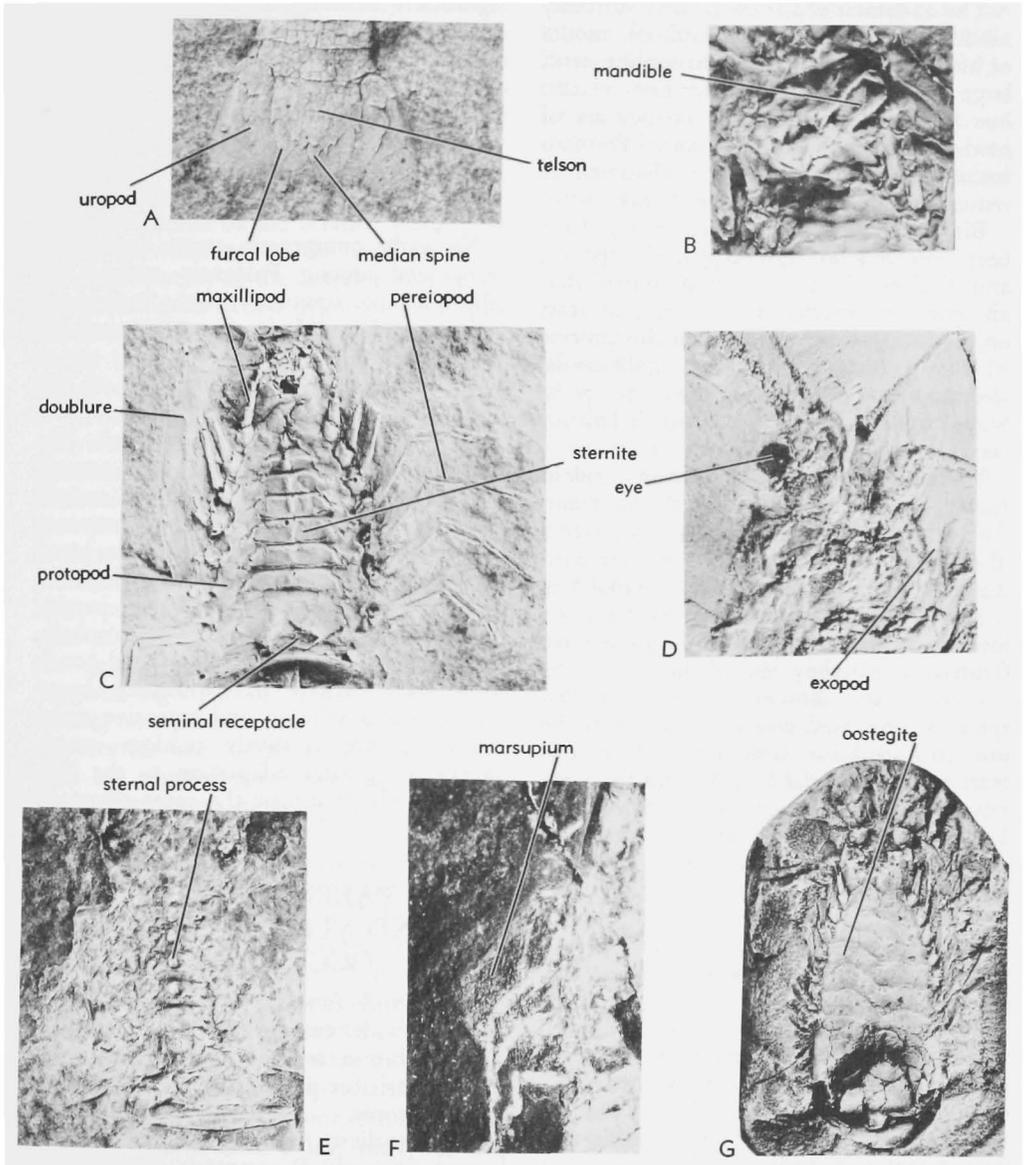


FIG. 156. Morphological features of Eocarida exemplified by photographs (all 55).—A. Caudal fan of *A. gracilis* showing uropods and telson with furcal lobes and median spine, $\times 3$.—B. *Anthracaris gracilis* (MEEK & WORTHEN), Penn., USA (Ill.), showing mandible with secondary epistome articulation, $\times 4$.—C. *A. gracilis*, showing sternal features of thorax and 1st 2 thoracic appendages modified as maxillipeds, also single joint of protopod of pereopods, $\times 4$.—D. *Mamayocaris jepseni* BROOKS, L.Perm., USA (Tex.), showing stalked compound eye and flagellate exopod of thoracic appendage, $\times 4$.—E. *Teallicaris loudonensis* PEACH, L.Carb., Scot., showing sternal processes, $\times 2$.—F. Marsupium of *T. loudonensis*, female, $\times 3$.—G. *Pygocephalus dubius* (MILNE-EDWARDS), U.Carb., Eng., showing marsupium composed of individual oostegites, $\times 3$.

tures are seen in some isopods, syncarids, and decapods. It is remarkable to find both a marsupium and a seminal receptacle on *Pygocephalus*.

The **abdomen** of the eocarids is variously modified for nektonic and benthonic modes of life. The six somites are shrimplike, with large **pleural lobes** in the order Eocaridacea, but in the Pygocephalomorpha they are of moderate development. In some Permian forms (e.g., *Notocaris*), the abdomen is reduced and flexed under the thorax.

Biramous **pleopods** (swimmerets) have been observed on *Anthracaris*, *Crangopsis*, and *Teallicaris*. It must be presumed that an appendix interna was present, at least on the more primitive forms, as this process of the endopod occurs on phyllocarids, stomatopods, euphausiids, and decapods. Sexual modification of the pleopods has not been observed.

Uropods are the most significant caridoid feature of these primitive eumalacostracans. The large, biramous spatulate appendages of the sixth abdominal somite combine with the platelike telson to form the **caudal fan**.

The **telson** of the eocarids has retained the crustacean **furca** (Fig. 156, *A*). In most Crustacea, including the phyllocarid malacostracans, this structure consists of two spinelike processes, whereas in eocarids the processes are lobate and contribute to formation of the caudal fan. A furca has been reported in larval stages of the Mysidacea, Euphausiacea, and Decapoda. However, ontogenetic evidence has been interpreted to indicate that the paired spines of adults are not homologous but are secondarily formed bristles. This may be correct, but true furca are retained on some extant syncarids.

The **median articulated spine** on the telson of the eocarids may not have a homologue in any extant Crustacea. Such a spine does occur on many Cambrian Pseudocrustacea. The Paleozoic phyllocarids and paleostomatopods have a median spine, but it is not articulated.

Internal anatomy of the eocarids can be inferred from the study of extant Crustacea. In the discussion of the phylogenetic relationships, some features will be discussed.

Small slitlike openings are present on the abdominal pleura of *Pygocephalus* and

Anthracophausia. The slits also occur on the telson. If they are openings of serial homologous glands of the archaic arthropod, then their presence on the telson is significant in indicating this to be a true somite. PEACH (226) has interpreted the opening on *Anthracophausia* as luminous organs. This is unlikely, considering the shallow coastal and estuarine water in which these animals lived.

ONTOGENY

No early ontogenetic stages have been recognized among Paleozoic eocarid fossils. The size frequency of the individuals in a normal sample is skewed toward the largest size.

The embryological development of this ancestral stock of the mysidaceans, euphausiids, and decapods can be inferred. The fact that all euphausiids and some penaeid decapods hatch as free-swimming nauplii prove that the Paleozoic eumalacostracans had retained their original crustacean larval stages. Secondary abbreviated development of the peracarids is correlated with incubation; thus only such Paleozoic pygocephalomorphs as possessed a similar brood pouch must have lacked free-swimming larval stages. Zoal eclosion and extensive metamorphism are relatively modern contrivances for greater adaptation to the benthonic mode of life by the more advanced decapods.

PALEOECOLOGY AND STRATIGRAPHIC OCCURRENCE

Form and function as interpreted by analogy with extant Crustacea and the stratigraphic occurrence of the fossils provides a basis for paleoecological conclusions and inferences.

The earliest eumalacostracan fossils known (*Eocaris*, *Devonocaris*, *Palaeopalaeomon*) all have shrimplike bodies. This supports the hypothesis that eumalacostracans arose from nekto-benthonic crustaceans. In fact, the antennal scale and the caudal fan are caridoid nektonic adaptations that distinguish this taxon. Suppression of the styliform furca and median spine corre-

lates with the development of the enlarged uropods and telson into a swimming structure. That the eocarids had not fully developed the retrograde evasion propulsion of the eucarids was suggested by BURKENROAD (62). He has correlated fusion of the carapace to the thoracic somites in eucarids with this habitus. The position of the intestine relatively low in the abdomen of *Anthracophausia* also was cited as evidence that the abdominal flexor muscles were not enlarged relative to the extensors.

The reduction of the relative size of the abdomen, widening of the cephalothorax, and modification of the anterior pereopods into maxillipeds in the pygocephalomorphs correlate with adaptation to a predominantly benthonic mode of life. The crab-like *Notocaris*, from the Permian of Africa, is the culmination of this adaptive trend.

Evidence relative to feeding habits of the Paleozoic Eumalacostraca is inconclusive. It should be noted that the typical crustacean jaw is a biting, triturating structure—in fact, Malacostraca are distinguished by possessing both molar and incisor mandibular processes. The presence of detrital casts of the intestine of some eocarid fossils (e.g., *Anthracophausia*, *Anthracaris*) suggests ingestion of clastic sediment in feeding on organic bottom detritus. None of the eocarids had chelate appendages. These facts are suggestive of scavenging to low-grade carnivorous modes of life.

Fossil eocarids occur sporadically in Paleozoic deposits, the conclusion being not that these Crustacea failed to thrive in the Paleozoic seas, but rather that their chitinous exoskeletons were destroyed under normal conditions of marine deposition (55, p. 261-262). Only *Palaeopalaemon*, with a calcareous reinforced exoskeleton, is found associated with a typical marine fauna. Most of the eocarid fossils occur in deposits indicative of coastal lagoons, estuaries, and swamps. As is true today, many of the coastal crustaceans probably were euryhaline and wandered into environments where catastrophic silting, hypersalinity, and stagnation enhanced the preservation of uncalcified chitinous remains. There is no positive evidence that any of the eocarids actually inhabited fresh water.

The known biostratigraphic range of the Eocarida is upper Middle Devonian to Permian. The Eocaridacea appear in the Devonian, reach their maximum development in the Mississippian, and are not known in deposits younger than Middle Pennsylvanian. Pygocephalomorphs originate in the Mississippian, occur with great frequency and diversity in Pennsylvanian dark shales and ironstone concretions, and last occur as highly specialized crablike forms in Permian strata.

PHYLOGENY

The rigid plan of tagmosis of the body and the consistency of position of the genital openings are indicative of a monophyletic origin of the subclass Malacostraca. The phyllocarids are the most primitive representatives of this natural group. Their remains occur in Cambrian to Recent deposits, whereas the caridoid Eumalacostraca first appear in the Devonian.

Ontogenetic, morphological, and stratigraphic evidence supports the theory of a phyllocarid ancestry for the Malacostraca, not the caridoid theory of CALMAN (65, p. 144). The presence of a seventh abdominal somite, a furca on the telson, occurrence of both antennal and maxillary glands, heart and gonads extending the length of the body, segmented arrangement of the lateral arteries, and the simple structure of the brain and stomach of the Recent *Nebalia* attest to their primitiveness (275, p. 88). That they are not on the direct line of descent for the Eumalacostraca is indicated by the possession of a rostral plate, carapace adductor muscle, and absence of the posterior abdominal appendages. Phyllocarids from the Cambrian already possessed these unique characteristics.

STEWING (275, p. 90) has proposed that *Nahecaris*, from the Devonian of Germany, is ancestral to the Eumalacostraca. The antennules of this phyllocarid does have two flagella, but the other eumalacostracan features reported by BROILI (54) do not exist. Thus, we must conclude that the archetype of the Malacostraca has not been discovered.

The first eumalacostracan fossils are also the most primitive caridoid Crustacea known, members of the order Eocaridacea.

These nekto-benthonic crustaceans have a relatively large abdomen, a caudal fan, scaphocerites, and undifferentiated biramous thoracopods. PEACH'S (226) report of oöstegites on *Crangopsis* has not been substantiated by critical restudy. The only morphological criteria that can be determined which prevent their being classified as Euphausiacea are the single joint of the thoracic protopod and absence of fusion of the thoracic somites with the carapace. Ontogenetic evidence bearing on the homology of the "furca" and median spine on the telson of Recent adult euphausiids is inconclusive.

Except for the single segment in the protopod of the thoracopods, furcal lobes, and median articulated spines on the telson of adults, and especially the absence of oöstegites, the eocarids are comparable to lophogastrid mysidaceans. The peracarid marsupium of the mysidaceans correlates with abbreviated ontogenetic development. Free nauplius stages are the original eumalacostracan mode of development, not incubation.

Syncarids have retained a remarkable number of primitive eumalacostracan characteristics; even furcal lobes are present on members of the Bathynellacea and Stygo-carididae. Absence of a carapace, presence of two segments in the thoracic protopod, and absence of a median articulated spine on the telson distinguish them from the Eocaridacea. The presence of a sperm receptacle on some extant syncarids is of no phylogenetic significance, as this structure is known to have evolved independently on different somites of various races of Malacostraca.

Comparison of the eocarids with the most primitive extant eumalacostracans, the euphausiaceans, lophogastrid mysidaceans, and syncarids, has emphasized the significance of the single segment in the thoracic protopod and the presence of furcal lobes and median spine on the telson. These are primitive crustacean features that have been lost or suppressed on extant forms. Loss of carapace, fusion of carapace with thorax, development of brood pouch, and other features mentioned above that are not present on the eocarids have been secondarily acquired by the different descendent races.

The Eocaridacea must be the ancestors of the modern Eumalacostraca, hoplocarids excepted.

The primitive skeletal morphology and internal anatomy of the Syncarida suggest that they were differentiated early in evolutionary history of the Eocaridacea. They first occur in Mississippian rocks. The taxonomic affinities of *Anthracocaris* (CALMAN, 1932) and *Acadiocaris* (BROOKS, 1962), of Mississippian age, which have a short carapace, are dependent on morphological details still unknown. We must accept the suggestion of CALMAN (66) that they are related to the Peracarida. They could be ancestral tanaidaceans, spelaeogriphaceans, or if they lack oöstegites, a stage in the evolution of the carapaceless syncarids.

Hoplocarid fossils first occur in the Mississippian. Their internal anatomy is indicative of early derivation from the malacostracan stock. Though they are caridoid, they are distinguished from the very beginning by possessing an articulated rostrum, subchelate thoracopods, and triramous antennules.

Admittedly, the superorder Eocarida represents several divergent stocks, the order Eocaridacea being the most primitive. *Palaeopalaemon* (U.Dev.-L.Miss.) is distinguished by a thorax that is only slightly shorter than the abdomen and by the presence of incipient branchiostegal development of the pleura of the carapace. It may have been from such a morphological type that the late Paleozoic Pygocephalomorpha evolved.

The pygocephalomorphs retained the primitive telson and unjointed thoracic protopod but show homeomorphic structural trends toward the decapods and mysidaceans. *Tealliocaris* has a brood pouch, sternal processes, and no seminal receptacle. These are mysidacean characteristics. On the other hand, *Anthracaris* lacks oöstegites, has a seminal receptacle, displays a secondary articulation between the mandible and epistome, and has endopods on the first three thoracopods that are incipiently adapted as decapod maxillipeds. The problems in classification are best exemplified by *Pygocephalus*, which not only has a peracarid marsupium but also the seminal receptacle of syncarids and decapods. All

of these Paleozoic genera have a laterally extended carapace and abdomen and cephalothorax of subequal length or a reduced abdomen. It is apparent that the pygocephalomorphs are the Paleozoic benthonic eumalacostracans. It is probable that the mysidacean and decapod characteristics cited are analogues and that the pygocephalomorphs are not ancestral to any extant Crustacea.

BURKENROAD (62) has presented a hypothetical argument that the Eucarida arose monophyletically from some unknown Paleozoic Malacostraca. The oldest decapod-like crustaceans are *Palaeopemphix* (GEMMELLARO, 1892), from the Permian of Sicily, *Antrimpos* (VAN STRAELEN, 1933), from the Permian of Madagascar, and *Protoclytiopsis* (BIRSHTEYN, 1958), from the Permian of Siberia. Probably these are not directly ancestral to the decapods. Morphological considerations that must be taken into account in deriving the eucarids from the eocarids are: (1) triple system of transverse carapace grooves on the older fossil decapods, (2) body gills of decapods, (3) carapace fused to thorax and enlarged abdominal flexor muscles of all eucarids, (4) development of an accessory process of the endopod of the second male pleopod to form the appendix masculina in euphausiaceans and decapods, (5) furca and median spine of the eocarids, and (6) the single segment in the protopod of the eocarids.

The triple system of transverse carapace grooves may be strictly a decapod feature that has independently evolved and need not be expected in the ancestral malacostracan stock. It is true that most of the earliest fossil decapods, including some species of *Palaeopemphix*, display this characteristic (118). Comparative morphology and embryology of extant decapods prove the primitiveness of the penaeids and carids, neither of which have the triple system. The nektonic euphausiaceans have retained the greatest number of eocarid characteristics and have only one transverse carapace groove.

The gills of the eocarids are unknown. Euphausiaceans have branchiae (podobranchiae) attached to the coxae of their appendages, whereas decapods have arthro-

branchiae, and pleurobranchiae in addition to podobranchiae. Arthrobranchiae originate ontogenetically on the proximal portion of the appendages and later change position to the basal articular membrane. The pleurobranchiae appear later and their place of origin is close to, if not actually on, the basal part of the embryonic appendages that have coalesced with the thorax. Thus, the development of the "body gills" of decapods can be correlated with increased body size, development of the branchial chamber, and especially the evolution of the efficient maxillary pump.

Fusion of the carapace with the thorax and the enlarged abdominal flexor muscles of both euphausiaceans and decapods has been attributed to the development of retrograde evasive propulsion (62). The caridoid caudal fan of all eumalacostracans is a swimming structure. Though it may have originally functioned principally for planing and steering, it is sometimes used by all nektonic forms, including the syncarid *Paranaspides*, for backward darting. Therefore, BURKENROAD's first criterion for monophyletic origin of the eucarids is of questionable significance.

The second and most relevant criterion suggested by BURKENROAD is the presence of an appendix masculina in both euphausiaceans and decapods. The development of copulatory structures from pleopods has evolved independently in male syncarids, stomatopods, eucarids, and even isopods. It is not altogether improbable that this copulatory structure of the euphausiaceans and decapods is a true analogy. Even BURKENROAD (62, p. 15) admits the modification of the first pleopod of the decapod as a spermatophore-handling organ is "not homologous with the Euphausiid [euphausiid] organ derived from a branch of the *appendix interna*, nor with the also independently-modified first endopods in various Reptant Decapods. . . ."

A furca and median spine on the telson are primitive crustacean characteristics. The furca is retained in the adults of eocarids, some extant adult syncarids and possibly the euphausiaceans. Embryologically these features are present throughout the Malacostraca. It is to be expected that these

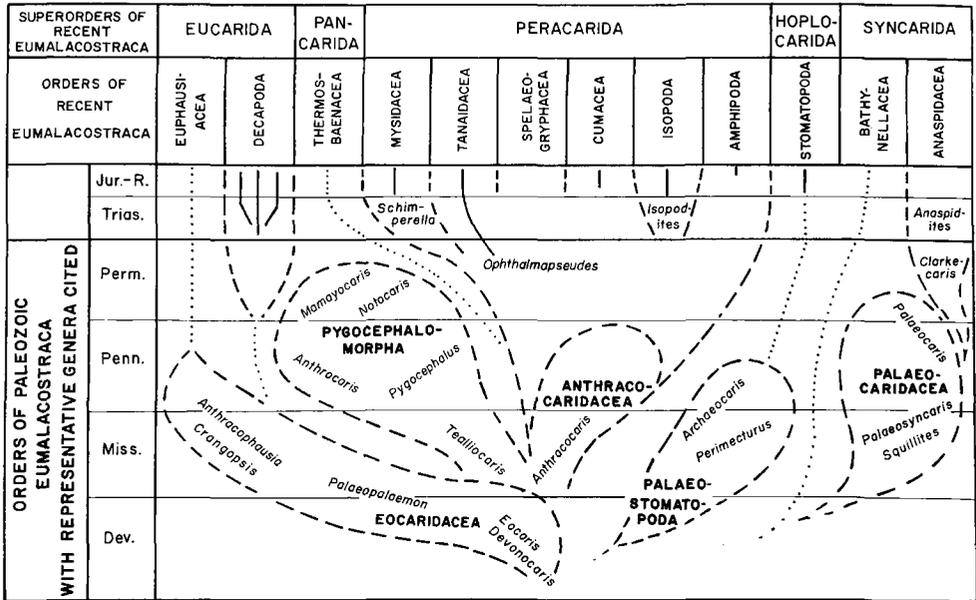


FIG. 157. Diagram showing inferred phylogenetic relationships of Paleozoic Eumalacostraca.

crustacean structures would be present on the Paleozoic ancestral eumalacostracan stock, the Eocarida.

Traditionally it has been assumed that the original crustaceans had three segments in the protopod of their appendages. The discovery of *Hutchinsoniella* (SANDERS, 1957) has cast doubt upon this theory. Again, the single segment of the eocarid protopod may be an archaic characteristic.

In summary, no valid objections are seen for considering the Paleozoic eocarids as ancestral to the Peracarida and Eucarida and for postulating that the euphausiaceans and decapods evolved their two common eucarid characteristics independently. The Syncarida and Hoplocarida are earlier derivatives (Fig. 157).

CLASSIFICATION

As indicated in foregoing discussion, a phylogenetic (vertical) classification consistent with the taxa established for Recent Eumalacostraca is impossible. Divergent evolution toward extant morphological types can be distinguished, but in the

pygocephalomorphs they are homeomorphic. Accordingly, the superorder Eocarida was established (55) for caridoid fossils which have a carapace not fused with the thorax, biramous thoracic appendages, a single segment in the protopod, and furcal lobes and a median articulated spine on the telson. Two orders, Eocaridacea and Pygocephalomorpha, are recognized.

Anthracomysis and *Palaemysis*, previously assigned to the Eocaridacea (55) on the basis of published descriptions, have been restudied. *Palaemysis* lacks statocysts in the uropods as portrayed by PEACH (226), and most fossils assigned here are abdomens and telsons of *Anthracophausia*. *Anthracomysis* (VAN STRAELEN, 1922) is the caudal fan of *Perimecturus fraiponti* VAN STRAELEN, a palaeostomatopod. *Gitocrangon granulata* RICHTER (1848) is a pseudofossil.

A revision of the European genera and species of eocarids is in progress. Many described species are synonyms and some have incorrect generic assignment. As previously suggested by BEURLEN (27, p. 126)

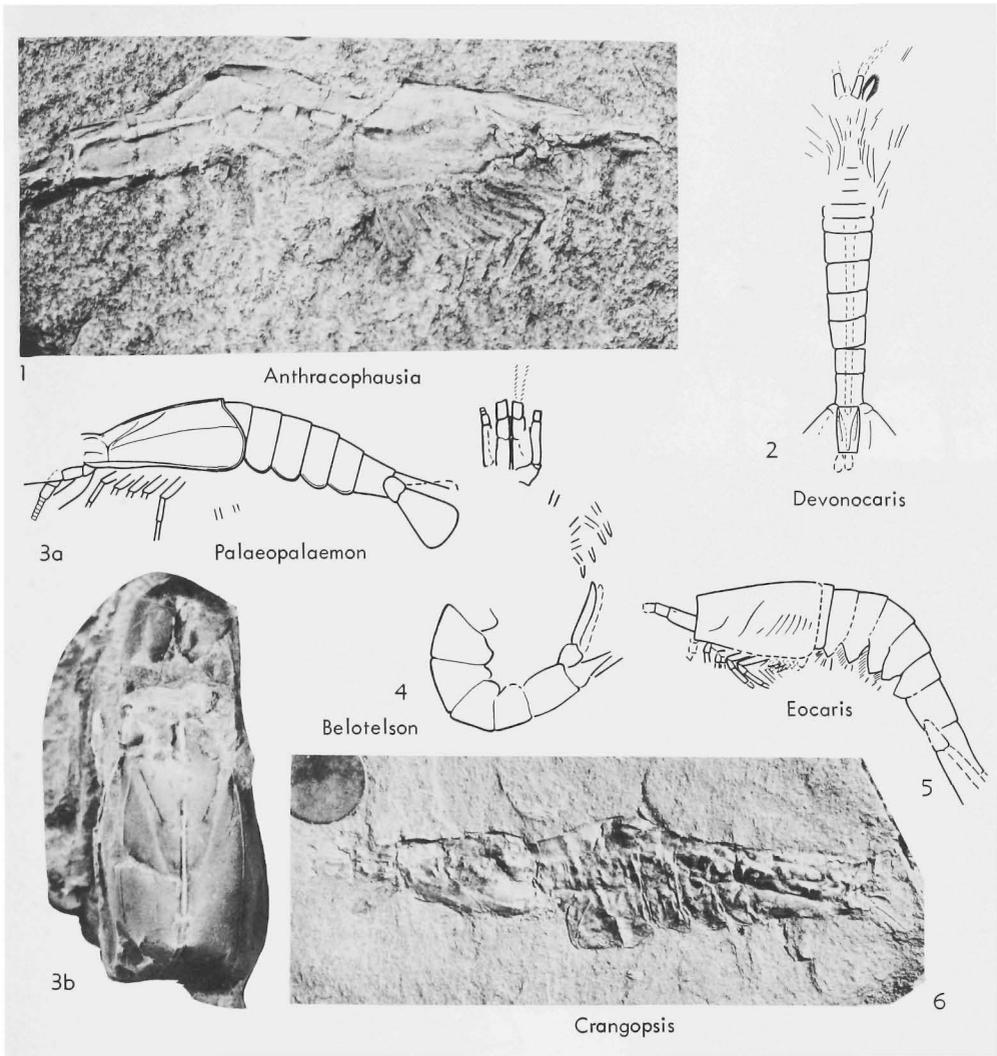


FIG. 158. Eocaridacea—Eocarididae (2,5); Palaeopalaemonidae (3); Anthracophausiidae (1,4,6) (p. R342-R343).

and GLAESSNER (117, p. 178), *Anthrapalaemon* is believed to be a synonym of *Pygocephalus*. Two or three new genera need to be proposed.

The Palaeostomatopoda (BROOKS, 1962), assigned tentatively to the superorder Eocarida, have now proved to be true hoplocarids. In addition to possession of subchelate thoracopods by *Perimecturus* and *Archaeocaris*, these genera have the distinctive triramous antennules of Recent Stomatopoda. PEACH (226) was mistaken in portraying a marsupium on these fossils.

A tabulation of suprageneric divisions of the Eocarida with numbers of genera contained in each is given on page R114.

SYSTEMATIC DESCRIPTIONS

Superorder EOCARIDA Brooks, 1962

Carapace with single transverse groove and not fused with thoracic tagmata; biramous thoracopods with single segment in

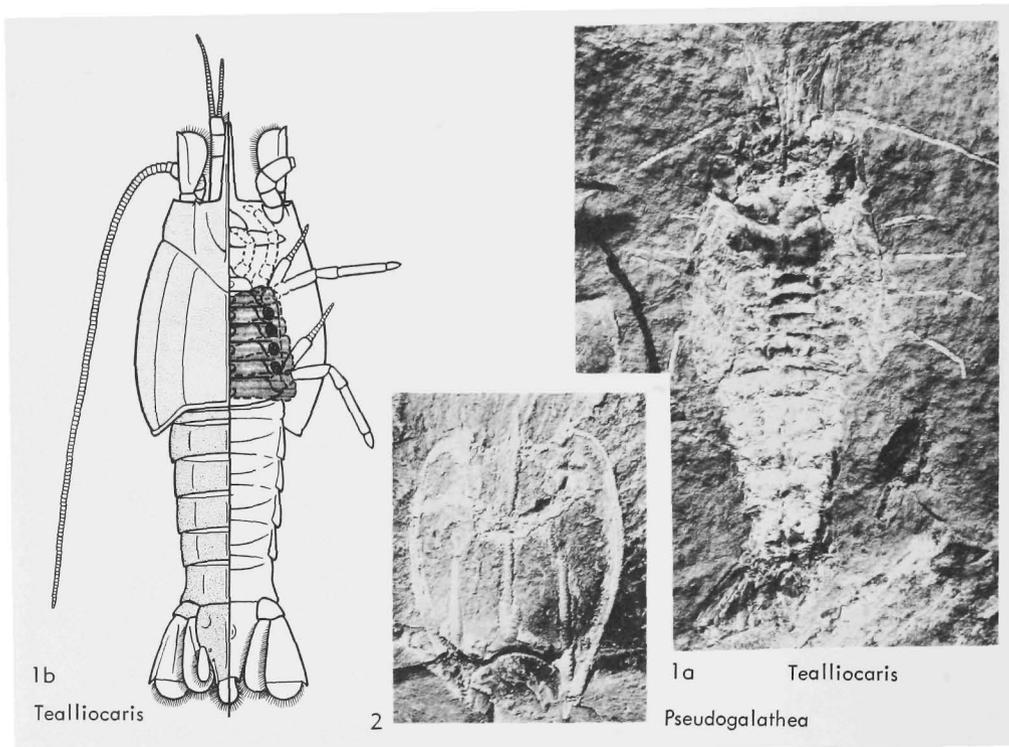


FIG. 159. Pygocephalomorpha (Mississippian)—Teallicarididae (p. R344).

protopod. Chief diagnostic characters are furcal lobes and median articulated spine on telson. *M.Dev.-Perm.*

Order EOCARIDACEA Brooks, 1962

Carapace relatively shorter than abdomen; pleura of carapace not produced laterally. *M.Dev.-Penn.*

Family EOCARIDIDAE Brooks, 1962

Transverse carapace grooves indistinct, not reaching dorsum; pleura of abdominal tergites large and pointed. *M.Dev.*

Eocaris BROOKS, 1962, p. 312 [**E. oervigi*; OD]. Presence of rostrum doubtful and ventral margin of carapace forming nearly right angle with straight anterior margin; carapace with 2 transverse grooves, neither reaching dorsum. *M.Dev.*, Eu. (Ger.).—FIG. 158,5. **E. oervigi*; $\times 1$ (55).

Devonocaris BROOKS, 1962, p. 308 [**Palaeocaris? cuylerensis* WELLS, 1957, p. 983; OD]. Thoracic somites relatively large, body of telson spade-shaped. *M.Dev.-U.Dev.*, N.Am.(N.Y.)-Eu.(Belg.).—FIG. 158,2. **D. cuylerensis* (WELLS), *M.Dev.*, N.Y.; $\times 3$ (55).

Family PALAEOPALAEEMONIDAE Brooks, 1962

Peduncle of antennules hypertrophied; carapace with well-developed cervical groove and incipient branchiostegal keel near ventral margin. *U.Dev.-L.Miss.*

Palaeopalaemon WHITFIELD, 1880, p. 41 [**P. newberryi*; OD]. Carapace with pair of longitudinal lateral carinae which become spines anterior to cephalic sulcus, rostrum probably present; pleural lobes of abdominal tergites rounded. *U.Dev.-L.Miss.*, N.Am.(Ohio-Ky.-Iowa).—FIG. 158,3. **P. newberryi*, *U.Dev.*, Ohio; 3a,b, $\times 1$, $\times 4$ (55).

Family ANTHRACOPHAUSIIDAE Brooks, 1962

Proximal segment of peduncle of antennules with recessed "eye socket"; rostrum prominent; carapace lacking ridges and spines but having large lappets. *Miss.-Penn.*

Anthracophausia PEACH, 1908, p. 61 [**A. dunsiana*; OD] [= *Palaemysis* PEACH, 1908 (type, *P. dunlopi*; OD)]. Rostrum keeled and falciform; pleural lobes of all abdominal tergites similar and pointed.

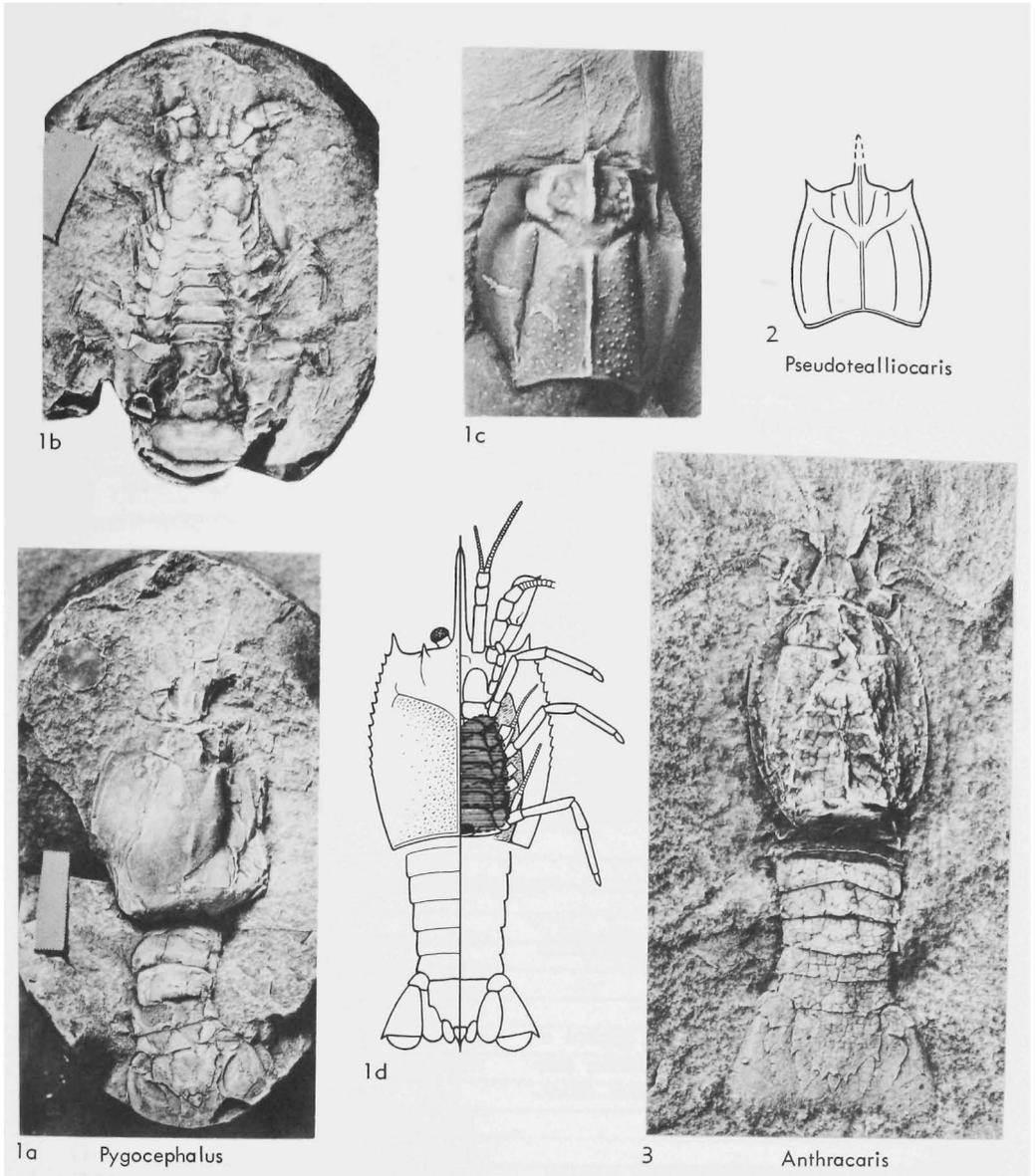


FIG. 160. Pygocephalomorpha (Pennsylvanian)—Pygocephalidae (p. R344-R345).

[Several species assigned to *Crangopsis* by PEACH (1908) belong to *Anthracophausia*. These include *C. couttsi*, *C. rhodesi*, *C. magna*, *C. robusta*, *C. minuta*, and *C. hastata*.] *Miss.-Penn.*, Eu.(Scot.-Eng.-?Fr.)-N.Am.(Ill.).—FIG. 158,1. *A. strongi* BROOKS, Penn., Ill.; $\times 3$ (55).

Belotelson PACKARD, 1886, p. 128 [**Acanthotelson? magister* PACKARD, 1886, p. 127; OD]. Spinelike telson and heavily chitinized bladlike outer margin of exopods of uropods characterize this in-

adequately known caridoid. *Penn.*, N.Am.(Ill.).—FIG. 158,4. **B. magister* (PACKARD); $\times 0.7$ (55).

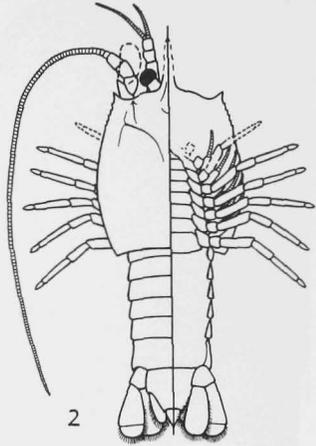
Crangopsis SALTER, 1863, p. 531 [**Uronectes socialis* SALTER, 1861, p. 394; OD]. Carapace thin, with faint suggestion of cervical groove; rostrum short, blunt; pleura of 2nd abdominal tergite large and rounded, overlapping those of both adjacent somites. *L.Carb.-U.Carb.*, Eu.(Scot.).—FIG. 158, 6. *C. eskdalensis* (PEACH), L.Carb.; $\times 2$ (55).



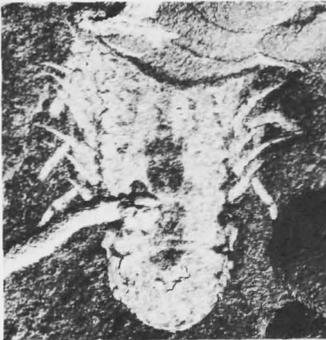
1a Paulocaris



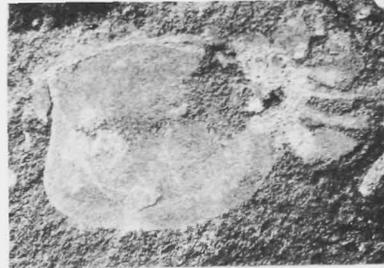
1b



2 Mamayocaris



3a Notocaris



3b

FIG. 161. Pygocephalomorpha (Permian)—Pygocephalidae (2); Notocarididae (1, 3) (p. R345).

Order PYGOCEPHALOMORPHA Beurlen, 1930

[emend. BROOKS, 1962]

Branchiostegal development in pleura of carapace; cephalothorax and abdomen subequal in length or abdomen reduced. *Miss.-Perm.*

Family TEALLIOCARIDIDAE Brooks, 1962

Carapace with prominent longitudinal carinae; anterolateral spines, if present, small; median process of telson lobate. *L. Carb.*

Teallicaris PEACH, 1908, p. 9 [**T. loudonensis*; OD]. Carapace lacking anterolateral spines but bearing sternal processes and oöstegites. *L. Carb.*, Eu.(Scot.-Fr.).—FIG. 159, 1. **T. loudonensis*, Scot.; 1a, b, dorsal view and reconstr., $\times 2$ (55). **Pseudogalathea** PEACH, 1882, p. 514 [**P. rotunda*;

OD]. Anterior and posterolateral angles of carapace produced, latter very prominent; carapace with median and 2 lateral longitudinal ridges and with heavy lateral thickening; abdomen and caudal fan relatively small. *L. Carb.*, Eu.(Scot.).—FIG. 159, 2. *P. macconochiei* (PEACH); $\times 3$ (55).

Family PYGOCEPHALIDAE Brooks, 1962

Carapace produced laterally with double, longitudinal carinae absent, but with prominent anterolateral spines; sternal processes lacking. *Miss.-Penn.*

Pygocephalus HUXLEY, 1857, p. 363 [**P. cooperi*; OD] [= *Anthrapalaemon* SALTER, 1861, p. 530 (type, *A. grossarti*; OD); *Palaeocarabus* SALTER, 1861, p. 530 (type, *Apus dubius* PRESTWICH, 1840); *Necroscilla* WOODWARD, 1879, p. 551 (type, *N. wilsoni*; OD); *Diplostylus* SALTER, 1863, p. 76 (type, *D. dawsoni*; OD)]. Hepatic spines absent from carapace; some female specimens bear-

ing oöstegites and seminal receptacle; telson narrowing backward in 2 abrupt steps, furcal lobes originating at last. *Penn.(U.Carb.)*, N.Am.(N.Scotia-Ohio).—FIG. 160,1. *P. dubius* (MILNE-EDWARDS), Eng.; 1a,b, dorsal and ventral views of specimens; 1c, dorsal view of carapace; 1d, reconstr.; all $\times 1.5$ (55). [= *Amphipeltis* SALTER, 1863.]

Anthracarid BROOKS, 1962, p. 173 [**Anthrupalae-mon gracilis* MEEK & WORTHEN, p. 50; OD]. Hepatic and gastric spines present on carapace, oöstegites never present, but large seminal receptacle on last thoracic sternite of mature females; base of telson broad; its width constricting abruptly at position of origin of furcal lobes. *Penn.*, N.Am.(Ill.).—FIG. 160,3. **A. gracilis* (MEEK & WORTHEN); dorsal view of complete specimen, $\times 3$ (55).

Pseudotealliocaris BROOKS, 1962, p. 199 [**Tealliocaris caudafimbriata* COPELAND, p. 44, 1957; ODI]. Carapace as wide as long, with large anterolateral spines, median keel, and 2 pairs of lateral carinae. *Penn.*, N.Am.(N.Scotia).—FIG. 160,2. **P. caudafimbriata* (COPELAND); dorsal view of carapace, $\times 1.3$ (55).

Mamayocaris BROOKS, 1962, p. 188 [**M. jepsemi*; OD]. Carapace lacking hepatic spines, dorsal carinae indistinct; body of telson subtriangular. *L.Perm.*, N.Am.(Tex.-S.Dak.).—FIG. 161,2. *M. jepsemi* BROOKS; dorsal view (reconstr.), $\times 2$ (55).

Family NOTOCARIDIDAE Brooks, 1962

Abdomen reduced and reflexed under thorax. *Perm.*

Notocaris BROOM, 1931, p. 572 [**Pygocephalus tapscottii* WOODS, p. 41, 1923; OD]. Carapace relatively long and narrow, without spines and dorsal keel. *Perm.*, S.Afr.—FIG. 161,3. **N. tapscottii* (WOODS); 3a, thorax with appendages and abdomen reflexed; 3b, lateral compression of cephalothorax, $\times 2$ (55).

Paulocaris CLARKE, 1920, p. 219 [**P. pachocoi*; OD] [= *Pygaspis* BEURLIN, 1934, p. 126 (type, *P. brasiliensis*; OD); *Liocaris* BEURLIN, 1931, p. 40 (type, *L. huenei*; OD)]. Carapace as wide as long, with prominent dorsal keel. *Perm.*, S.Am. (Brazil).—FIG. 161,1. **P. pachocoi*; 1a,b, dorsal views of carapace and abdomen, $\times 2$ (55).

SYNCARIDA

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[University of Florida]
[Chapter submitted February, 1964]

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INTRODUCTION

Syncarids possess a unique combination of characteristics that impart to them a decisive position in any phylogenetic discussion of the Eumalacostraca. This is not because they were ancestral to any other crustacean main groups, but rather because they are a relatively unmodified lineage

that differentiated early in the history of crustacean evolution.

The feature that most distinguishes the Syncarida is absence of a carapace. Some other Eumalacostraca (e.g., isopods, amphipods, cumaceans) have the carapace aborted or greatly reduced, but in these the absence or reduction can be proved to be secondary.

In the Syncarida no evidence indicates that a cephalothoracic shield ever was present.

Only a few syncarid species have survived to the present. The fossil record, however, indicates that they flourished during the late Paleozoic; indeed, representatives

of the Paleozoic fauna were discovered approximately 50 years before any extant species belonging to the assemblage was known. At first the fossils were interpreted as amphipods or isopods, but in 1885 PACKARD recognized their singularity and pro-

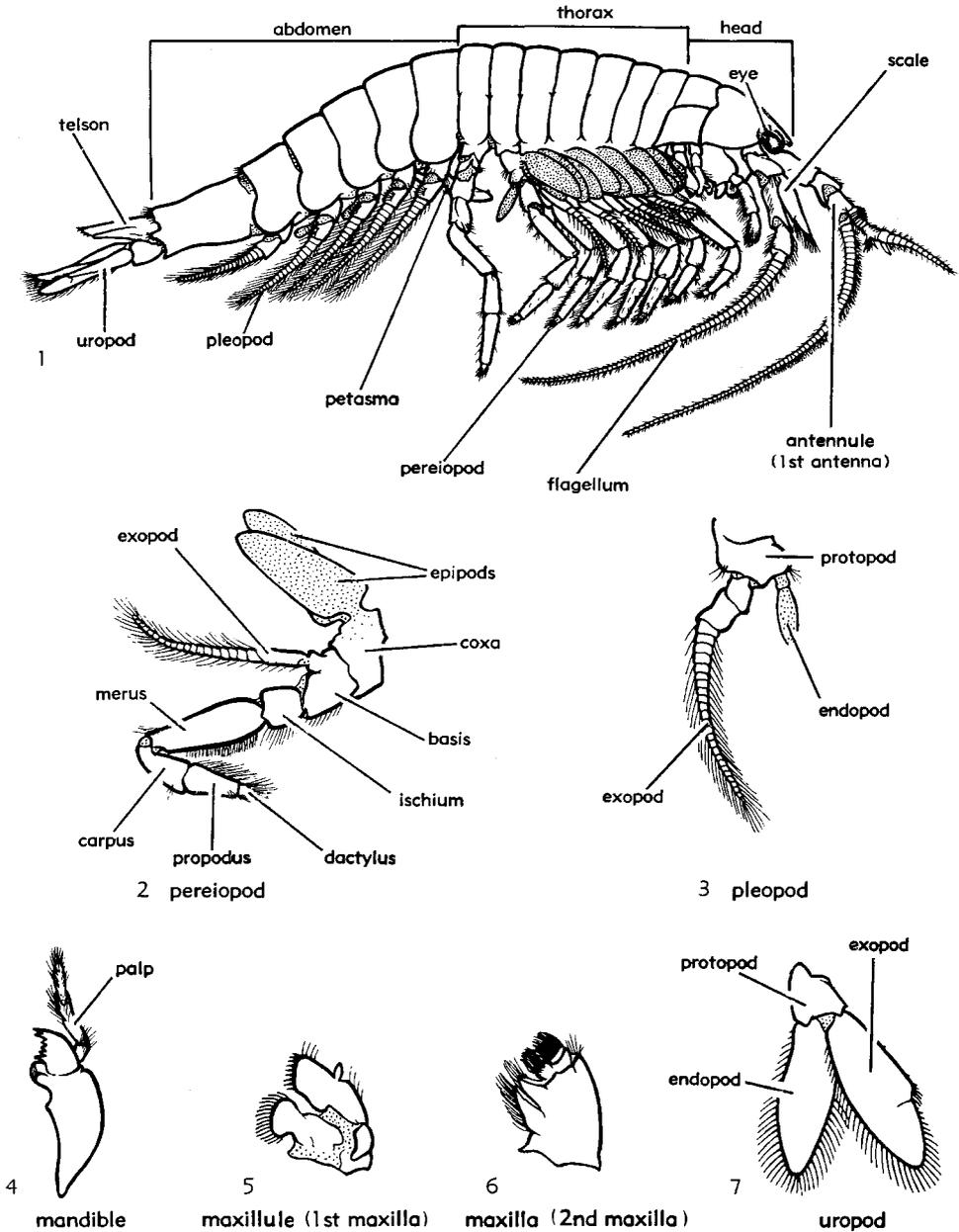


FIG. 162. Morphological features of syncarids illustrated by a generalized anaspidacean, *Anaspides tasmaniae* (THOMSON), Rec., Australia.—1. Lateral view of male, $\times 3$.—2. Second thoracic appendage, $\times 6$.—3. Second abdominal appendage, $\times 6$.—4. Mandible, $\times 10$.—5. Maxillule, $\times 10$.—6. Maxilla, $\times 10$.—7. Uropod, $\times 6$ (55).

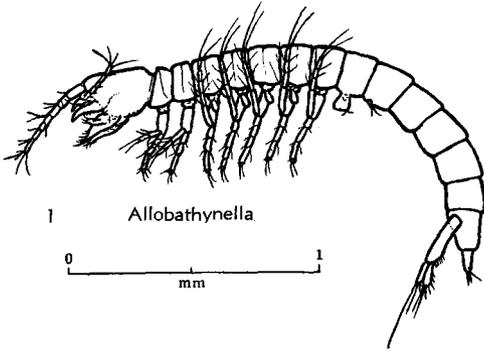


FIG. 163. Vestiges of furca in syncarids shown by bathynellacean *Allobathynella japonica* MORIMOTO & MIURA, male, Rec., Japan, $\times 32$ (290).

posed the name Syncarida for them. Subsequent discoveries of fossils and extant species have greatly enlarged our knowledge of these relics of the past. The taxon is now recognized as being distinct from the Peracarida and the Eucarida. It is best defined by three morphological features which individually are not definitive, but taken together provide a valid basis for systematic differentiation. These characteristics are biramous thoracopods, absence of a carapace, and absence of a marsupium on mature females.

MORPHOLOGY

The syncarid body is constructed upon the basic eumalacostracan plan (Fig. 162,1). Tagmosis of the 19 appendage-bearing somites is into (1) a **head**, bearing two pairs of antennae (**antennules**, **antennae**), a pair of **mandibles** and two pairs of **maxillae** (**maxillules**, **maxillae**), (2) a **thorax** composed of eight somites, each bearing a pair of **perciopods**, and (3) an **abdomen** composed of six somites, of which the first five bear **pleopods** and the last one a pair of **uropods**. The terminal body unit is a **telson**. The uropods and telson form a **caudal fan**. In the primitive extant Bathynellacea (Fig. 163) and in the recently discovered representative of a new family, the Stygocarididae (215) (Fig. 164), diminutive vestiges of **furca** are found. Cephalization has resulted in fusion of the first thoracic somite with the head in the Anaspidea,

whereas in the Bathynellacea the sixth abdominal somite is fused with the telson. All eight thoracic somites and six abdominal somites of the extinct Paleozoic order Palaeocaridacea (56) have retained their identity (Fig. 165).

No carapace or vestige of a carapace is found on any known syncarid, fossil or Recent. *Anthracocaris scotica* (PEACH) and *Acadiocaris novascotica* (COPELAND) (55) are peracarids with diminutive carapaces

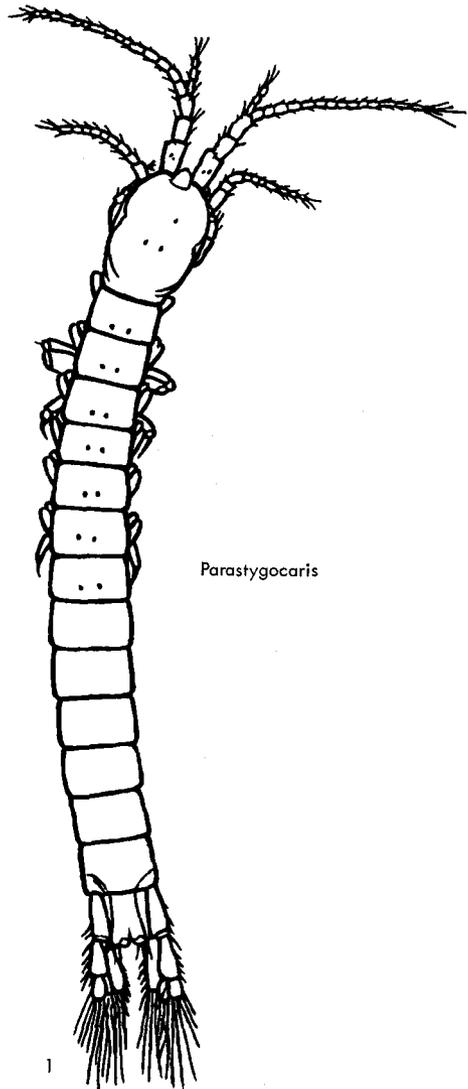


FIG. 164. Vestiges of furca in syncarids shown by stygocaridacean *Parastygocaris andina* NOODT, male, Rec., Argentina, $\times 60$ (215).

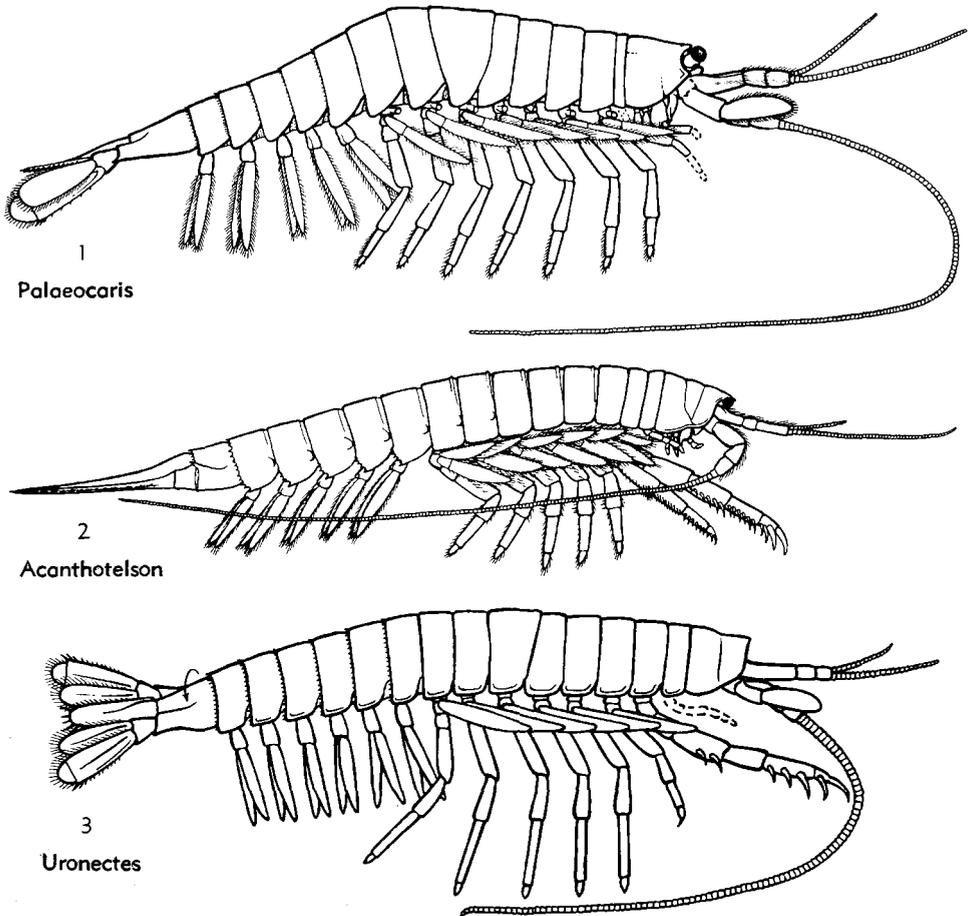


FIG. 165. Morphological features of syncarids shown by palaeocaridaceans (reconstr.).—1. *Palaeocaris typus* MEEK & WORTHEN, Penn., Ill., $\times 3$.—2. *Acanthotelson simpsoni* MEEK & WORTHEN, Penn., Ill., $\times 2$.—3. *Uronectes fimbriatus* (JORDAN), Perm., Ger., $\times 3$ (55).

occurring in Lower Carboniferous deposits of Scotland and Canada. Though both of these species were originally assigned to the syncarid *Palaeocaris*, their affinities are probably with the Tanaidacea or Spelaeogriffacea (55).

For purposes of homologous comparison between the different Eumalacostraca, the appendages of *Anaspides* (Rec., Tasmania) are most instructive (Fig. 162). The biramous thoracic legs are believed to have retained a primitive structure.

Each of the antennules consists of a **protopod** of three segments and two multiarticulate **flagella** (Fig. 162,1). Upon the proximal segment of this appendage is a slitlike

pore, which is the external opening of a **statocyst**.

The antennae have a two-segment **protopod**, a **bladelike exopod**, a **scaphocerite** (antennal scale), and two-segment **endopod**, and a **flagellum** (Fig. 162,1). In some of the benthonic Paleozoic species (e.g., *Acanthotelson simpsoni*) the caridoid eumalacostracan bladelike exopod has been lost (Fig. 166,1).

It is frequently stated that the retention of only two segments in protopods of the antennae is a feature distinctive of the Syncarida and the Eucarida, the latter having the **nephropore** of an antennal gland upon the proximal segment. For extant spe-

cies this observation is correct, but *Palaeocaris typus* (Penn., Ill.) probably had three distinct segments in protopods of its antennae (55, p. 244). It is definite that *Acanthotelson simpsoni* (Penn., Ill.) had a nephropore on the basal segment (55, p. 235) of its antennae (Fig. 166,1).

The body of the mandible of *Anaspides* is stout, with **gnathal lobe** differentiated into a thick **molar process** and distal toothed **incisor process** (Fig. 162,4). A three-seg-

ment **palp** arises on the outer surface of the body of the mandible. CALMAN (65, p. 148) and others have emphasized the absence of a lacinia mobilis on the mandibles of Syncarida. Bristles that may be homologous to this peracarid feature have been reported recently in species of *Parastygocaris* and *Stygocaris* (Rec., S.Am.) by NOODT (215, p. 571).

Both the maxillules and maxillae of *Anaspides* are small and highly specialized to

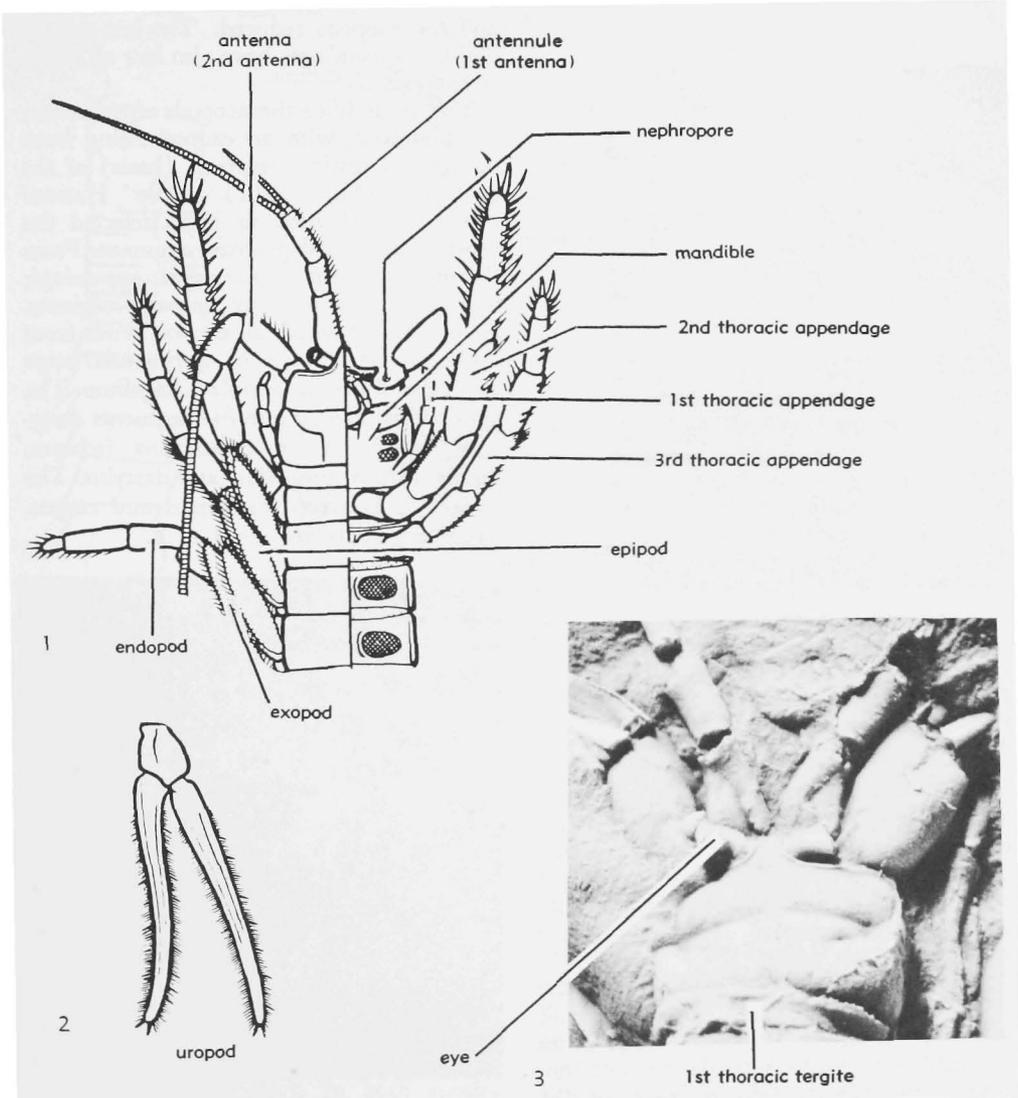


FIG. 166. Morphological features of syncarids shown by palaeocaridacean *Acanthotelson simpsoni* MEEK & WORTHEN, Penn., Ill.—1. Anterior portion of body, dorsal and ventral views, $\times 4$.—2. Uropod, dorsal view, $\times 4$.—3. Head and first thoracic tergite, dorsal view, $\times 8$ (Brooks, n).

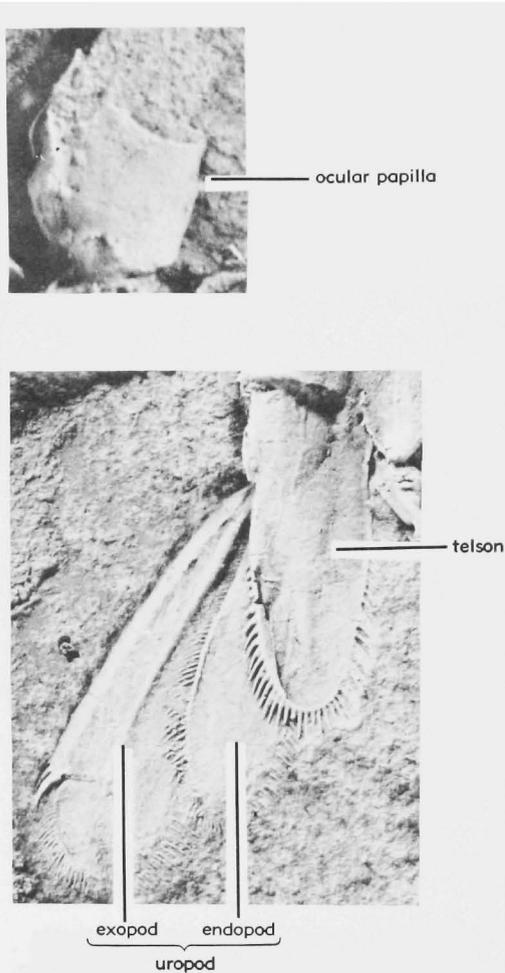


FIG. 167. Some morphological characteristics of *Palaeoecaris typus* MEEK & WORTHEN, Penn., Ill. (Brooks, n).—1. Peduncle of left eye with base of ocular papilla, $\times 14$.—2. Uropod (left) and telson, $\times 10$.

assist in food manipulation during mastication. They have little resemblance to legs. The maxillules have a small basal segment which gives rise to two plates that constitute the greater part of the appendage (Fig. 162,5).

A broad endite extends mesially. On the outer edge of the lateral plate is a small lobe that might represent the vestige of an endopod or exopod. A single segment constitutes the greater part of each of the maxillae (Fig. 162,6). The mesial margin bears two small setiferous endites, whereas

a movable bilobed structure with bristles is borne at its terminus.

The first pair of pereopods of *Anaspides* are modified as **maxillipeds**. Their **endopod** is adapted for grasping, but otherwise is unaltered from the plan of that of the succeeding pereopods. The **exopod** and **epipods** are reduced on the maxillipeds, but endites are present. The succeeding five pairs of appendages of *Anaspides* have retained their primitive structures, whereas the seventh pair have the epipods aborted and the exopods reduced. The last pair of thoracic appendages have also lost all traces of exopods.

The unmodified thoracopods of *Anaspides* are biramous, with an exopod rising from the second distinct segment (basis) of the protopod (Fig. 162,2). Only HANSEN (1925) has claimed to have detected the evasive theoretical precoxal segment. From the basal segment (coxa) of the appendage, two lobate, membranous epipods originate. As previously noted, an exopod arises from the basis; it consists of a proximal **stipe** and beyond this an annulate **flagellum**. The endopod is divided into five segments designated as in other crustaceans ischium, merus, carpus, propodus, and dactylus. The “knee” is between the merus and carpus. Three segments are distal to it.

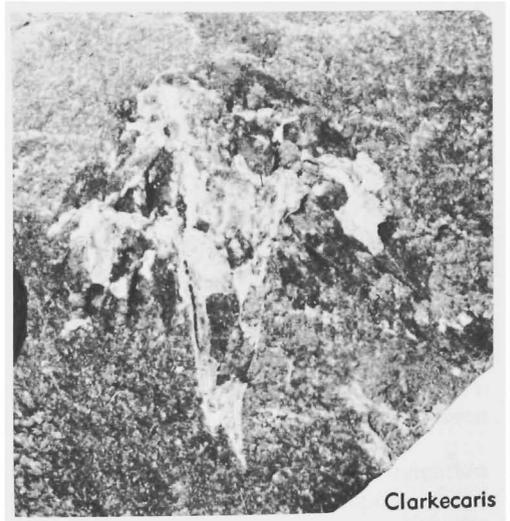


FIG. 168. Portion of caudal fan of *Clarkecaris brasiliensis* (CLARKE), Perm., Brazil, showing telson and right furcal lobe, $\times 6$ (Brooks, n).

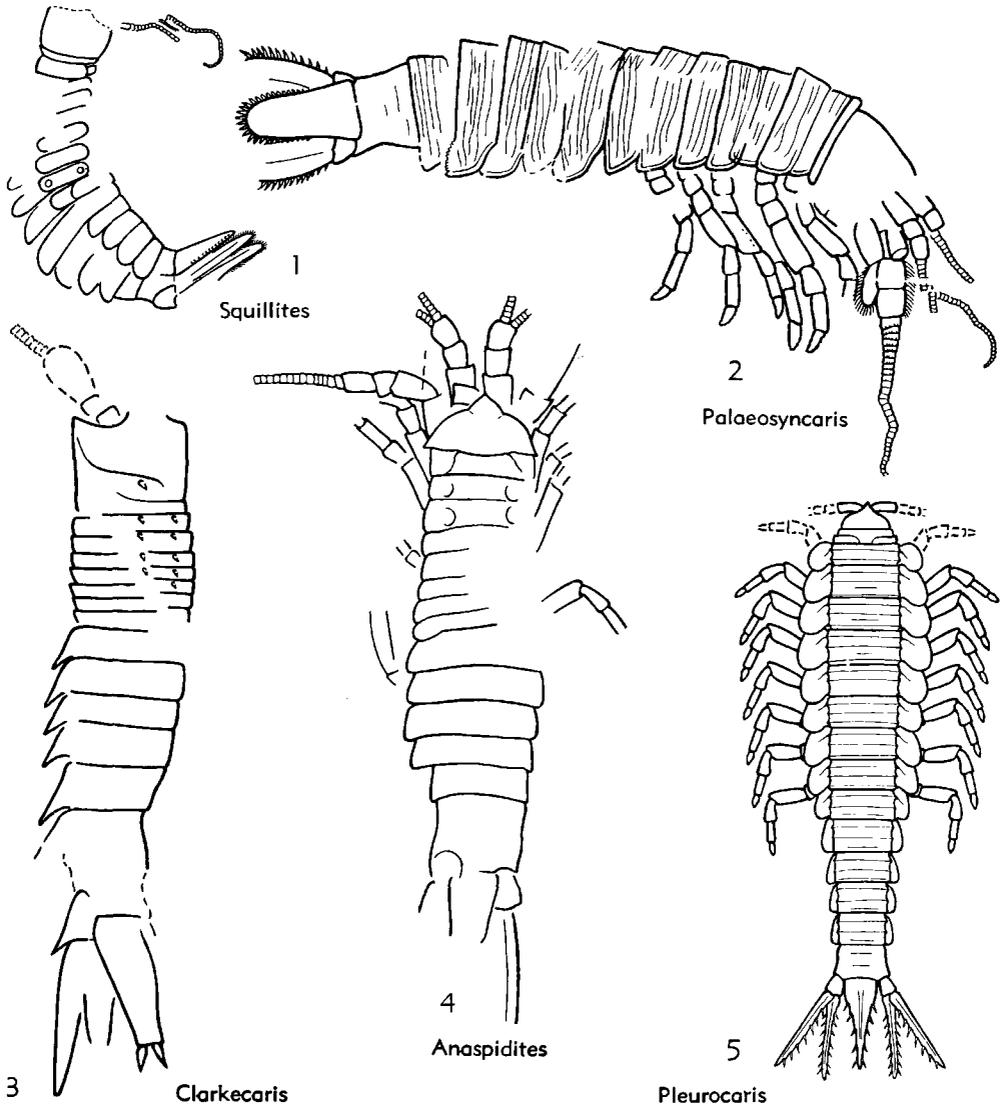


FIG. 169. Morphological features of fossil syncarids that are incompletely known (Brooks, n).—1. *Squillites spinosus* SCOTT, Miss., USA (Mont.), $\times 5$.—2. *Palaeosyncaris dakotensis* BROOKS, Miss., USA (N. Dak.), $\times 2$.—3. *Clarkecaris brasiliensis* (CLARKE), Perm., Brazil, $\times 3$.—4. *Anaspidites antiquus* (CHILTON), Trias., Australia, $\times 1.5$.—5. *Pleurocaris annulata* CALMAN, U. Carb., Eng., $\times 7$.

The pereiopods of Paleozoic syncarids have an identical structure (Fig. 165). In most species no maxillipeds are present, but *Acanthotelson stimpsoni* (Penn., Ill.) has massive grasping legs, as does *Uronectes fimbriatus* (Perm., Eu.). In both species they are the second pair of pereiopods.

Traces of the membranous epipods are rarely found on fossils, but remains of them

have been reported for *Palaeocaris typus* and *Acanthotelson stimpsoni* (55). Though the preservation of the fossils is not adequate for positive proof, it appears that the exopods were not flagellate in the Paleozoic fossils, but rather spatulate lobes somewhat resembling epipods (Fig. 166, I).

In the minute Recent Bathynellacea, adapted for living in interstitial spaces in

sand, the antennae and thoracic appendages are reduced and simplified (Fig. 163).

As to the pleopods and uropods of *Anaspides*, no morphological features of special importance call for notice. The pleopods of the first and second abdominal somites of males differ from those that follow and from female pleopods in that the endopods are produced as strong armlike gonapophyses—the petasma of stomatopods and eucarids—which projects forward between the last pair of thoracopods. The typical pleopod has a large basal segment (protopod), a much-reduced, soft lobate endopod, and an exopod consisting of two proximal segments followed by a long annulate, hairy flagellum (Fig. 162,3). In Recent syncarids adapted for living in interstitial spaces, the pleopods are reduced or aborted. Among Paleozoic fossils in which pleopods are known, the two rami are spatulate lobes of approximately equal size (Fig. 165).

The uropods are biramous on all known syncarids. Those of *Anaspides* (Fig. 162,1) and *Palaeocaris* (Fig. 167,2) are spatulate, but in many forms the rami are variously modified as styli (Fig. 166,2). A statocyst was reported by FRITSCH (97) in the basal segment of the uropod of *Uronectes fimbriatus*. Diligent restudy of the fossils has proved this observation to be in error.

The telson of *Anaspides* is a simple, spatulate terminal body unit with the anus situated on its ventral surface. In the Bathynellacea (Fig. 163) and Stygocaridacea (Fig. 164) are two small lobes representing rudiments of a furca. *Clarkecaris* (Perm., S.Am.), a primitive stygocarid, is the only Paleozoic fossil known to have preserved this fundamental crustacean structure (Fig. 168; 169,3).

The compound eyes of *Anaspides* are stalked, whereas those of *Koonunga* are sessile. The Bathynellacea are blind. All known fossil syncarids have stalked compound eyes (Fig. 166,3). A discovery of special interest on the peduncle of the eyes of *Palaeocaris typus* (55, p. 243) is an ocular papilla similar to that of the Mysidacea (Fig. 167,1).

For the most part, features of the internal morphology of the Syncarida are

primitive. Especially noteworthy is the so-called pars ampullaris on the entrance of the caeca into the pyloric chamber of the stomach, which is homologous to a similar structure in the Stomatopoda (275, p. 95). The stomach is small. A large number of liver caeca enter the stomach ventrally. Except for two small dorsal diverticula in the abdomen, the intestine is simple. In all Recent syncarids the excretory organs are maxillary nephridia, but in *Acanthotelson stimpsoni* nephropores are associated with the antennae (55, p. 235). Publications by SMITH (278) and SIEWING (273) give details of the internal morphology of the Recent Syncarida.

ONTOGENY

The eggs of Recent Syncarida are deposited, not carried by the mother. The nauplius and other ontogenetic stages are developed in the egg. No metamorphosis occurs, though the newly hatched animal is not completely developed; for example, in *Anaspides* the eyes are sessile and only two hepatic caeca are present (146). Whereas *Anaspides* is hatched with a full complement of body somites, *Bathynella* has only three abdominal somites (16).

ECOLOGY

It is customary to refer to the Syncarida as fresh-water Crustacea. Though all extant species, except *Thermobathynella amyxi* SIEWING, from brackish waters at the mouth of the Amazon, do live in fresh water, it is definite that many fossil syncarids were marine. In evaluating the paleontological environmental occurrence of animals with a chitinous exoskeleton, one must not neglect the fact that fossil arthropods without mineral-reinforced skeletons are practically unknown from marine deposits. This does not mean that highly diverse arthropods were lacking in seas of the past, but only that remains of those with chitinous exoskeletons were destroyed by normal biological and physicochemical vicissitudes during accumulation and diagenesis of the sediments.

It is believed that all Carboniferous syncarids were marine, but it is possible that some Permian species normally inhabited fresh water. *Clarkecaris brasiliicus* (Perm., S.Am.), from the Irati Shales, is from a marine lithotope (Fig. 168; 169,3). On the other hand, stratigraphic evidence and the associated fossils of *Anaspidites antiquus*, from the Triassic of Australia, suggest a fresh-water habitat (Fig. 169,4).

Paranaspides lacustris, a shrimplike syncarid, is nektonic, whereas *Anaspides tasmaniae* is benthonic. These relatively unspecialized Crustacea are from lakes and rivers of Tasmania. Species of *Koonunga* and *Micraspides* have been found in bottom detritus of lakes and pools in Australia and are intermediate between the true surface-dwellers mentioned above and highly specialized subterranean species. *Koonunga* has small sessile eyes and shuns strong light, whereas *Micraspides* lacks eyes. Species adapted for existence in interstitial spaces in sediment are geographically widespread, for North America and Australia are the only continents from which members of the Bathynellacea have not been reported. Fossil and extant members of the Stygocaridacea have been found only in South America.

Some syncarids are microphagous feeders. *Anaspides*, on the other hand, has maxillipeds adapted for grasping large detritus and prey. It has been observed to be carnivorous (213, p. 15). No question exists as to the predaceous habits of the extinct *Acanthotelson* and *Uronectes*, which possessed strong raptorial maxillipeds.

STRATIGRAPHIC OCCURRENCE

None of the Syncarida have carapaces strengthened by mineral matter. Chitinous exoskeletons rapidly decompose upon death of animals except when unusual physicochemical conditions exist to prevent destruction. Such fossils are found as compressions in black shales and in clay ironstone concretions from dark gray to black siltstone and shales. *Anaspidites antiquus* (Trias., Australia) is from a variegated gray to brick red, laminated lacustrine deposit (Fig. 169,4).

Though "*Palaeocaris*" has been reported from the Devonian of Belgium (VAN STRAELEN, 1943) and New York (WELLS, 1957), these fossils were misinterpreted (57). The original determinations were based on absence of a carapace in the fossils, but this is due to poor preservation. The oldest true syncarids are *Squillites spinosus* and *Palaeosyncaris dakotensis*, from the Heath Shale, of Late Mississippian age, in Montana and North Dakota (55) (Fig. 169,1,2). A large number of specimens are known from Carboniferous deposits in North America and Europe. Permian species are known from Europe and South America. The Paleozoic northern hemisphere species are all members of the order Palaeocaridacea, whereas *Clarkecaris*, from Brazil, is a primitive stygocaridacean. A single specimen of *Anaspidites antiquus* has been found in Triassic shales of Australia (Fig. 169,4). It is doubtful that *Triasocaris* (BILL, 1914), from the Triassic of France, has been interpreted correctly.

PHYLOGENY

Misinformation and insufficient knowledge of the morphology of fossil syncarids have resulted in many misconceptions of their phylogenetic relationships. Because of the erroneous interpretation of *Acanthotelson* by PACKARD (1886), many authors have postulated a relationship between the Syncarida and Isopoda (NICHOLLS, 1929; CALMAN, 1934; GLAESSNER, 1957). SIEWING (275, p. 95) has cited the presence of a seventh abdominal somite and the occurrence of statocysts in uropods of *Uronectes* (FRITSCH, 1901) as evidence for an affinity of syncarids with the Mysidacea, although it has been proved that FRITSCH was mistaken in reporting both of these morphological features (55, p. 239). In the light of present knowledge of Recent and extinct Crustacea, the Syncarida possess characteristics considered to be diagnostic of one or more of all other eumalacostracan taxa; thus they are of great phylogenetic interest.

The furca on the telson of Recent Bathynellacea and Stygocaridacea is a primitive crustacean feature that has been lost by most Eumalacostraca. Rudiments of a furca are present on some euphausiaceans and

in larval stages of the Eucarida. All known species of the extinct Eocarida have a furca or furcal lobes on the telson. None of the Paleozoic syncarids of the extinct order Palaeocaridacea are known to have had a furca. Restudy of the type specimens of *Clarkecaris brasiliensis*, a primitive stygocaridacean from South America, proves it to have had a furca (Fig. 168). These crustaceans, not the palaeocarids, must be closest to the ancestral syncarid stock.

The digestive tract, nervous system, reproductive system, and excretory system of Recent syncarids are those of a generalized eumalacostracan. This is true also for the stomatopods (275, p. 93), but the characteristics in each were inherited independently from the ancestral eumalacostracan stock.

Until nephropores were discovered in *Acanthotelson*, it was believed that all syncarids had maxillary glands. This, in addition to the presence of biramous pereopods and stalked or sessile compound eyes coupled with lack of a carapace and of an appendix interna on the pleopods of syncarids, has been construed as indicative of their affinities with Peracarida. Features that syncarids have in common with the Eucarida invalidate this interpretation. Female syncarids lack oostegites and the mature males have a petasma. These are characteristic of both the Stomatopoda and Eucarida. Characteristics that are distinctly eucarid in nature are presence of a statocyst in the basal antennal segments and presence of a seminal receptacle in females. The correlative morphological features mentioned above must be homeomorphic.

The evidence presented supports the conclusion that syncarid evolution has followed four distinct lines. These have led to differentiation of the groups now ranked as orders—Palaeocaridacea, Anaspidae, Bathynellacea, and Stygocaridacea. The archaic syncarid, which is unknown, must have had all thoracic and abdominal somites free, lacked a carapace, had biramous thoracic appendages, and possessed a furca on the telson.

The Palaeocaridacea are the oldest syncarid fossils yet discovered. Even so, they cannot be considered the ancestral stock of the Syncarida, as Noodt (1964) has pos-

tulated. Though highly specialized, the extant members of the orders Bathynellacea and Stygocaridacea have retained more fundamental primitive characteristics. These two orders must have been early derivatives of the original syncarids which thus far are unknown. The Stygocaridacea are restricted to the South American continent with the oldest known fossil, *Clarkecaris*, occurring in Permian strata. It is possible that the Anaspidae of Australia and Tasmania are their descendants.

The relationships of the Syncarida have been confused by the evolution of homeomorphic features. There is no proof of a relationship with any of the other Eumalacostraca other than through a common ancestor.

CLASSIFICATION

The Syncarida was originally defined by PACKARD (1885) as including only the Pennsylvanian fossil, *Acanthotelson simpsoni*, believed to be closely related to the Isopoda and Amphipoda. With the discovery of the Recent "Tasmanian mountain shrimp," *Anaspides tasmaniae* (THOMSON), CALMAN (1896) established the Syncarida as an order and extended it to include fossils such as *Palaeocaris*. Subsequently, several additional Recent genera have also been discovered. In his last published classification of these Crustacea, CALMAN (1909, p. 162) raised the Syncarida to division rank (i.e., superorder).

The attempts of CHAPPUIS (1915), COCKRELL (1916), SIEWING (1959), and VANDENBERGHE (1960) to establish a systematic classification of the Syncarida have failed because they were based upon erroneous interpretation of the Paleozoic fossils. BROOKS (55, 56) has restudied the fossils and proposed that three orders be recognized on the basis of fusion or lack of fusion of somites. One additional order (Stygocaridacea) subsequently has been defined by NOODT (1964, p. 96).

The Palaeocaridacea have all eight thoracic somites and six abdominal somites free. There is no furca. The known Anaspidae have the first thoracic somite fused with the head and in the Clarkecarididae and Stygocarididae the first thoracic somite is

fused with the head, but rudiments of a furca are present. The order Stygocaridacea, established for the extant forms (NOODT, 1964), should include also the extinct Clarkecarididae, which possess the same characteristics. The aberrant Bathynellacea all have a furca, and although their eight thoracic somites are free, the last abdominal somite is fused with the telson. Families are distinguished on the basis of their adaptive trends.

A tabulation of suprageneric divisions of the Syncarida showing their stratigraphic occurrence and numbers of contained genera is given on page R114.

SYSTEMATIC DESCRIPTIONS

Superorder SYNCARIDA

Packard, 1885

[*nom. transl.* CALMAN, 1904 (ex Syncarida PACKARD, 1885, *partim*)] [=Anomotraka VON GROBEN, 1910]

Carapace absent, pereopods biramous, with one or two epipods; seminal receptacle may be present but no oöstegites. *U.Miss.-Rec.*

Order PALAEOCARIDACEA

Brooks, 1962

[=Gampsonychidae SIEWING, 1959 (*pro* Gampsonychidae PACKARD, 1886, *partim*); Anaspidacea CALMAN, 1904 (*partim*); Simplicipoda FRITSCH, 1901 (*partim*)]

First thoracic somite not incorporated into cephalon; compound eyes stalked; caudal furca lacking. *U.Miss.-Perm.*

Family PALAEOCARIDIDAE

Meek & Worthen, 1865

[*non* Palaeocaridae SIEWING, 1959] [=Nectotelsonides BROCCHI, 1880; Eilecticidae VANDENBERGHE, 1960]

No thoracic endopods modified as raptorial appendages; rami of uropods lobate; telson spatulate. *U.Miss.-Perm.*

Palaeocaris MEEK & WORTHEN, 1865, p. 48 [**P. typus*; OD] [=Nectotelson BROCCHI, 1880; *Palaeoorchestia* ZITTEL, 1882; *Gasocaris* FRITSCH, 1901; *Praeanaspides* WOODWARD, 1908]. Thoracic and abdominal pleural lobes rounded anteriorly, posterior edge straight, without spines. *U.Carb. (Westphalian) - Perm.*, N. Am. (Ill.-N. Scotia)-Eu. (Eng.-Fr.-Belg.-Neth.).—FIG. 165,1; 170,1a. **P. typus*, Penn., Ill.; 165,1, $\times 3$; 170,1a, $\times 2$ (55).—FIG. 170,1b. *P. krejci* (FRITSCH), Perm., Eu.; $\times 4$ (Brooks, n).—FIG. 170,1c. *P. rochi* (BROCCHI), Perm., Eu.; $\times 4$ (Brooks, n).

Palaeosyncaris BROOKS, 1962, p. 250 [**P. dakotensis*; OD]. Thoracic and abdominal pleural lobes progressively larger, posterior margin at last thoracic and abdominal lobes rounded, spines on abdominal pleural lobes. *U.Miss.* or *L.Penn.*, N. Am. (N.Dak.).—FIG. 169,2; 170,2. **P. dakotensis*, 169,2; 170,2, both $\times 2$ (55).

Squillites SCOTT, 1938, p. 508 [**S. spinosus*; OD]. First thoracic tergite reduced; uropods with narrow spatulate rami; telson wedge-shaped. *U.Miss.*, N. Am. (Mont.).—FIG. 169,1; 170,3. **S. spinosus*; 169,1, $\times 5$; 170,3, $\times 6$ (55).

Family URONECTIDAE Cockerell, 1916

[=Gampsonychidae PACKARD, 1886]

Endopods of second thoracic appendages raptorial; rami of uropods and telson spatulate; antennae without scaphocerites. *L. Perm.*

Uronectes BRONN, 1850, p. 575 [**Gampsonyx fimbriatus* JORDAN, 1847; OD] [=Gampsonyx JORDAN, 1847 (obj.); *Carcinurus* BRONN, 1850; *Gampsonychus* BURMEISTER, 1855 (obj.)]. First thoracopods reduced; pleura truncate and posterior margin of abdominal tergites serrate. *L.Perm.*, Eu. (Saar B.).—FIG. 165,3; 173,1. **U. fimbriatus* (JORDAN); 165,3, $\times 3$; 173,1, $\times 4.5$ (Brooks, n).

Family ACANTHOTELSONIDAE

Meek & Worthen, 1865

[*non* COCKERELL, 1916]

Second and third pereopods raptorial; rami and uropods and telson styloid. *Penn.*

Acanthotelson MEEK & WORTHEN, 1865, p. 399 [**A. stimpsoni*; OD]. Thoracic pleura truncate, posterior margin of abdominal pleural lobes serrate; length of all abdominal somites approximately equal. *Penn.*, N. Am. (Ill.).—FIG. 165,2; 171,1. **A. stimpsoni*; 165,2, $\times 2$; 171,1, $\times 4.5$ (Brooks, 1962).

Family PLEUROCARIDIDAE

Chappuis, 1915

[*nom. correct* BROOKS, 1962 (ex Pleurocaridae CHAPPUIS, 1915)] [*non* Eilecticidae VANDENBERGHE, 1960]

No pereopods specialized for raptorial purposes; thoracic pleura large; rami of uropods and telson styloid. *Penn.*

Pleurocaris CALMAN, 1911, p. 156 [**P. annulatus*; OD]. Head small, 2 cephalic grooves not joining laterally; margins of uropod rami and telson spinose. *Penn.*, Eu. (Eng.-?Fr.).—FIG. 169,5; 172,1. **P. annulatus*, Eng.; 169,5, $\times 7$; 172,1, $\times 9$ (Brooks, n).

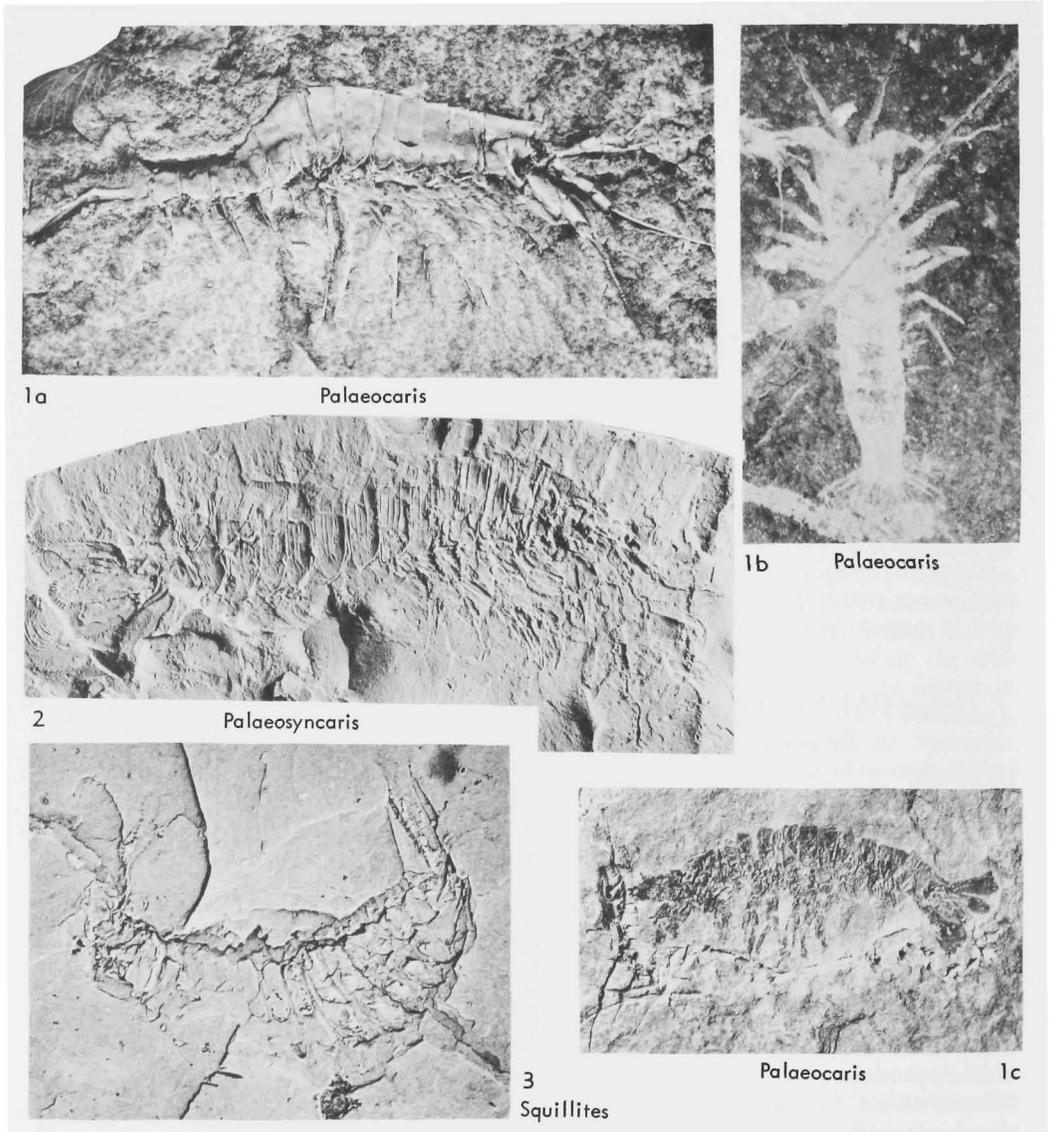


FIG. 170. Palaeocaridacea, Palaeocarididae (p. R355).

Order ANASPIDACEA Calman, 1904

[*nom. transl.* SIEWING, 1959]

First thoracic somite incorporated into cephalic tagma; seminal receptacle present. *Trias.-Rec.*

Family ANASPIDIDAE Thomson, 1894

Exopods on thoracic appendages 1 to 7;

endopods of pleopods reduced; with stalked compound eyes. *Trias.-Rec.*

Anaspides THOMSON, 1894, p. 285 [*Anaspis tasmaniae* THOMSON, 1892; OD]. Thoracic somites increasing only slightly in length posteriorly; antennal scales shorter than 1st 2 joints of endopod. *Rec.*, Tasmania. — FIG. 162, I. **A. tasmaniae* (THOMSON); ×3 (Brooks, n).

Paranaspides SMITH, 1908, p. 465 [*P. lacustris*; OD]. Thoracic somites increasing in length pos-

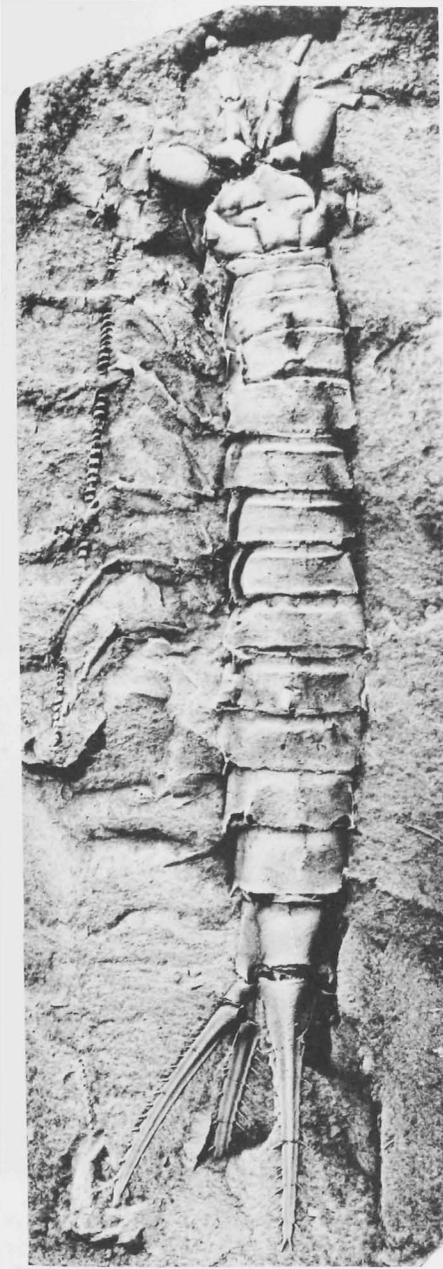
Anaspidites BROOKS, 1962, p. 234 [**Anaspides antiquus* CHILTON, 1929; OD]. Rostrum with broad base; thoracic somites reduced but position of origin of thoracic legs relatively widespread; scaphocerites with straight outer edge. *Trias.*, Australia.—FIG. 169,4; 174,1. **A. antiquus* (CHILTON); 169,4, $\times 1.5$; 174,1, $\times 2$ (Brooks, n).

Family KOONUNGIDAE Sayce, 1908

Eyes sessile, antennae lacking scaphocerites; last two pereopods uniramous, pleopods all uniramous except first two in males, which are copulatory organs. *Rec.*

Koonunga SAYCE, 1908, p. 353 [**K. cursor*; OD]. Eyes sessile. *Rec.*, Australia.

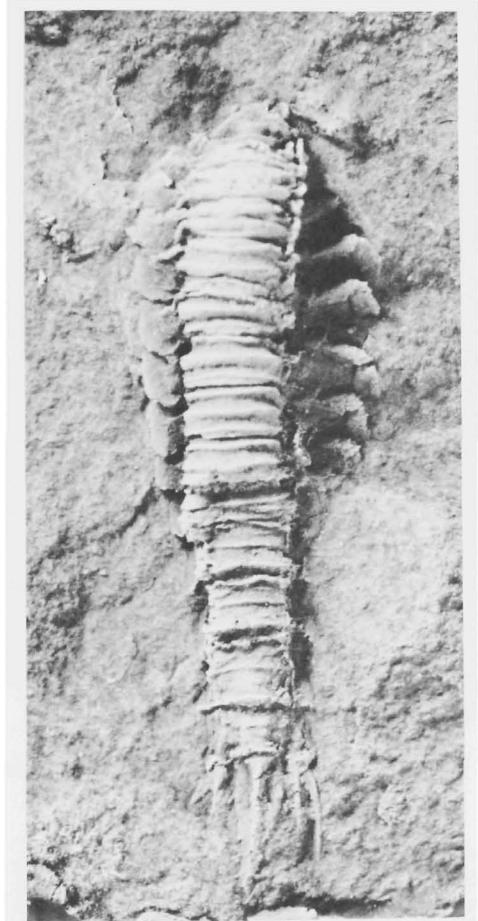
Micraspides NICHOLLS, 1931, p. 475 [**M. calmani*; OD]. Blind. *Rec.*, Tasmania.



1 Acanthotelson

FIG. 171. Palaeocaridacea, Acanthotelsonidae (p. R355).

teriorly and body flexed at 1st abdominal somite, which is largest; antennal scales longer than 1st 2 joints of endopod. *Rec.*, Tasmania.



1 Pleurocaris

FIG. 172. Palaeocaridacea, Pleurocarididae (p. R355)



FIG. 173. Palaeocaridacea, Uronectidae (p. R355).

Order BATHYNELLACEA Chappuis, 1915

[*nom. transl.* SIEWING, 1959]

Aberrant subterranean syncarids having last abdominal somite fused with telson; pleopods reduced or absent; furca present. *Rec.*

Family BATHYNELLIDAE Chappuis, 1915

Characters of order. *Rec.*

Bathynella VEJDovsky, 1882, p. 65 [**B. natans*; OD]. Pleopods 2-jointed, antennae with 5 or more joints; exopods present on pereopods 1 to 7. *Rec.*, Eu.-Japan.

Allobathynella MORIMOTO & MIURA, 1957, p. 145 [**A. japonica*; OD]. Pleopods single-jointed, rudi-

mentary. *Rec.*, Japan.—FIG. 163, I. **A. japonica*; $\times 32$ (290).

Brazilibathynella JAKOBI, 1961, p. 27 [**B. floriano-
polis* JAKOBI, 1958; OD]. Pleopods absent; 1st antennae with 6 joints; exopods of thoracopods with 2 joints. *Rec.*, S.Am. (Brazil).

Parabathynella CHAPPUIS, 1926, p. 7 [**P. stygia*; OD]. Pleopods entirely absent; antennae with 5 or fewer joints; exopods of pereopods 2 to 7, 2- or 3-jointed. *Rec.*, Eu.-Malay.Arch.-Japan-Madag.

Thermobathynella CAPART, 1951, p. 1 [**T. adami*; OD]. Pleopods entirely absent; antennae with 5 joints; exopods of pereopods 1 to 7 with only single joint. *Rec.*, Afr.-S.Am.

Order STYGOCARIDACEA Noodt, 1964

First thoracic somite fused with head; telson bearing furcal rudiment; petasma and antennal statocysts present. *Perm.-Rec.*

Family STYGOCARIDIDAE Noodt, 1962

[*nom. correct.* NOODT, 1964 (*pro* Stygocaridae Noodt, 1962)]

Specialized for living interstitially, eyes and pleopods aborted. First pereopods specialized as maxillipeds; antennae lacking exopod scaphocerites; rudiments of furca on telson. *Rec.*

Stygocaris NOODT, 1962, p. 577 [**S. gomezmillasi* NOODT, 1962; OD]. Exopods on pereopods aborted; segments of both antennules and antennae reduced in number. *Rec.*, S.Am. (Chile).

Parastygocaris NOODT, 1962, p. 576 [**P. andina* NOODT, 1962; OD]. Exopods on thoracic appendages 2 to 6; exopods of uropod divided into 2 segments. *Rec.*, S.Am. (Arg.).—FIG. 164, I. **P. andina*; $\times 50$ (215).

Family CLARKECARIDIDAE Brooks, 1962

Suture between head and first thoracic tergite vestigial; anterior sulcus on cephalon sigmoidal; abdominal pleura spinelike; furca present. *Perm.*

Clarkecaris MEZZALIRA, 1952, p. 47 [**Gampsonyx
brasiliicus* CLARKE, 1920; OD] [= *Gampsonyx*
CLARKE, 1920 (obj.)]. Thoracic somites shortened, paired dorsal spines on thoracic tergites. *Perm.*, S.Am. (Brazil).—FIG. 169, 3; 174, 2. **C. brasiliicus* (CLARKE), 169, 3, $\times 3$; 174, 2, $\times 6$ (Brooks, n).

Order and Family UNCERTAIN

Triasocaris BILL, 1914, p. 323 [**T. peachi*; OD] (*nom. dub.*). *Trias.*, Eu. (Fr.).

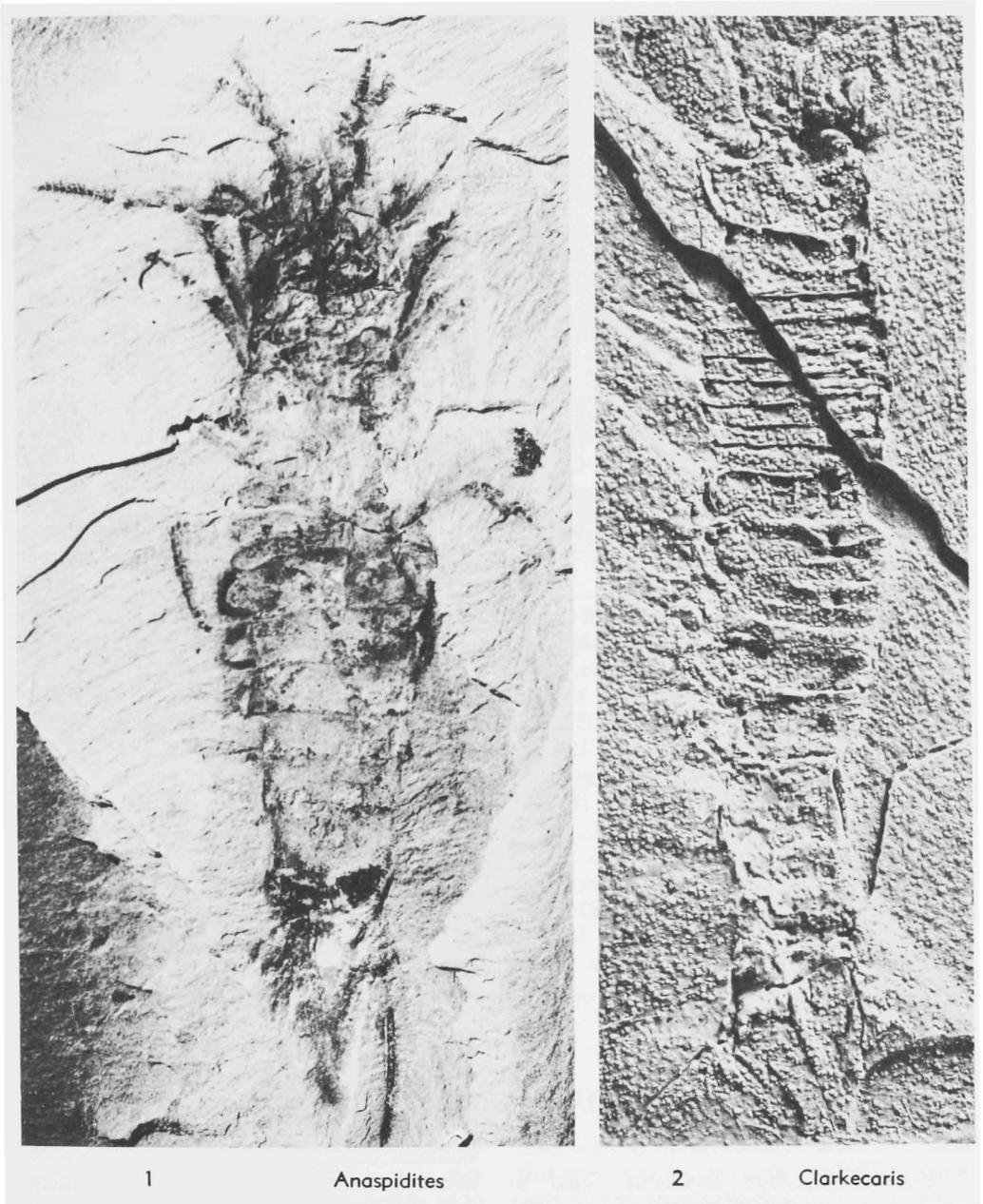


FIG. 174. Anaspidacea (Anaspididae) (1); Stygocaridacea (Clarkecarididae) (2) (p. R357-R358).

PERACARIDA

By ROBERT R. HESSLER

[Woods Hole Oceanographic Institution] [Acknowledgments are made to Dr. EDWARD L. BOUSFIELD, National Museum of Canada, and to Dr. ERIC L. MILLS, Queen's University, Ontario, Canada, for their advice on taxonomic placement of fossil amphipods. Appreciation also is expressed to Dr. ISABELLA GORDON, British Museum (Natural History), Lon-

don, and Dr. W. D. I. ROLFE, Hunterian Museum, University of Glasgow, for their criticism of the typescript. Work for the *Treatise* has been supported partly by the National Science Foundation under grants G-10744 and GB-563. This is contribution 1445 of the Woods Hole Oceanographic Institution.]

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Superorder PERACARIDA

Calman, 1904

First thoracomere invariably fused to cephalon; carapace fold (when present) never fused to all thoracomeres; protopod of antenna typically three-segmented; mandible with lacinia mobilis in all expect parasitic and other specialized forms (Fig. 175); first thoracopod modified as maxilliped; major flexure ("knee") of endopods of second to eighth thoracopods between merus and carpus; eggs and young nearly always carried in marsupium formed by medial lamellar outgrowths (oöstegites) of coxae of two

to seven pairs of thoracopods (Fig. 176); pleopods without appendix interna; young liberated from marsupium at late stage of development, not as nauplii. Hepatic caeca few and simple; heart usually elongate, extending through greater part of thorax or displaced into abdomen; spermatozoa usually threadlike. *Perm.-Rec.*

In both isopods and amphipods the coxae of the pereopods tend to be flattened and platelike, and may be quite large. These plates, called epimeres or coxal plates, are broadly joined to edges of the tergites and are the functional equivalent of pleura (lateral outfoldings of tergites), commonly fold-

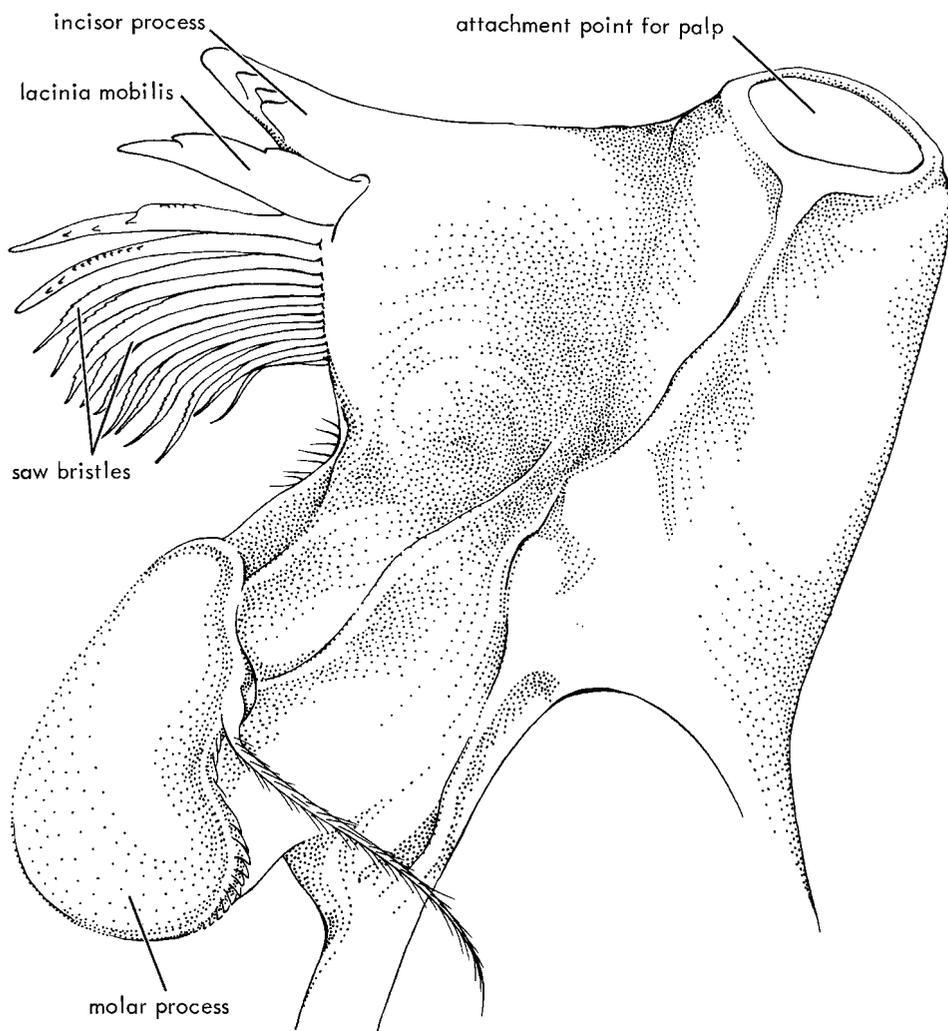


FIG. 175. Right mandible of the amphipod *Leptocheirus pinguis* (STIMPSON) (1853), dorsal view, showing the characteristic gnathic structures found in the Peracarida. The mandibular palp has been removed (Hessler, n).

ing down laterally over the basal portion of the rest of the limb (Fig. 176). The line of juncture of coxal plate and tergite may remain distinct, as in the Gammaridea or may be completely obscured through fusion, as in most Oniscoidea (GRÜNER, 1953). Epimeres are never developed on the pleon, where pleura of considerable size may occur instead.

Among many varied attempts at classifying the Malacostraca, only the few major systems having direct importance to the Peracarida are considered here.

LEACH (1815) divided the Malacostraca

into groups named Edriophthalma, having sessile eyes, and Podophthalma, with movable stalked eyes. Nearly coincident with this system is BURMEISTER'S (1834) division into Thoracostraca, having a carapace fold, and Arthrostraca, without one. Although most orders fall into either the edriophthalmid-arthrostracid or podophthalmid-thoracostracid assemblages, the living Tanaidacea, which possess a carapace and lack stalked eyes, and the equally equivocal Cumacea make such a bipartite division indefensible (1).

The Schizopoda of LATREILLE (1817), in-

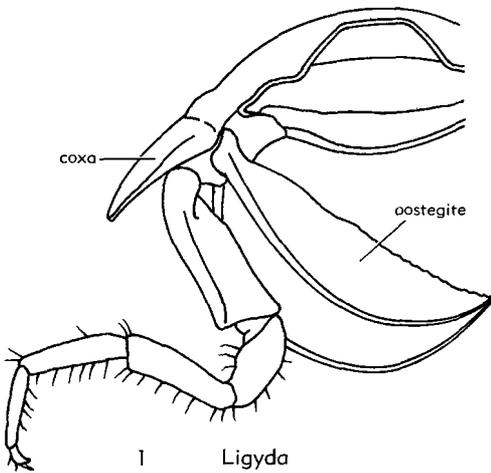


FIG. 176. Thoracic segment of *Ligyda exotica* ♀ showing one of oostegites which make up brood pouch, also illustrating how the coxa has become fused to the trunk, becoming modified as an epimeral plate, enlarged (379).

cluding the Mysidacea and Euphausiacea, is another taxonomic unit which existed for many years in good standing. BOAS (1883) pointed out the many differences between mysidaceans and euphausiids and discarded this grouping. HANSEN (1893) concurred with BOAS and united the mysidaceans with the cumaceans, tanaidaceans, isopods, and amphipods. CALMAN (1904) called this large group the Peracarida.

The Tanaidacea have had a very unsettled systematic position in the past. Early workers often included them with the amphipods, whereas G. O. SARS and other late 19th century taxonomists placed them in the isopods. CALMAN and HANSEN followed CLAUS (1888) in considering the Tanaidacea as an independent order.

The Peracarida, in addition to containing orders with highly unique morphologies, includes one group, the Mysidacea, which shares with a number of nonperacaridan orders a collection of important characters known as the caridoid facies (further noted in discussion of the mysidaceans). Unless one is willing to assume that the caridoid facies was acquired convergently, he is forced to conclude that mysidaceans are the most primitive living peracaridan group. Other primitive mysidacean features are the

presence of seven abdominal segments and a caudal furca in the embryo, large number of oostegites in lophogastrids, free telson, first maxillipeds not fused basally and not strongly differentiated from other thoracic limbs, and nature of the filter-feeding mechanism.

The Amphipoda and Isopoda, which comprise the heart of BURMEISTER'S Arthropoda, have been thought by many (e.g., REIBISCH, 1927) to be closely related, having in common sessile eyes and thoracic epimeres (see below), and lacking a carapace fold. However, CALMAN (65) and SIEWING (274) have considered these similarities to be superficial. Far more important differences in the excretory organs, respiratory and circulatory systems, modes of reproduction and development, structure of abdominal appendages, and morphology of the digestive tract indicate that these orders are the end products of two distinct lines of specialization which diverged from some mysidacean-like ancestor (Fig. 177).

The Cumacea and Tanaidacea are considered to represent intermediate grades of development in the evolution of the isopodan condition (274). Important facets of this evolution are the progressive reduction of the carapace fold, specialization of the first maxilliped (especially in relating cumaceans and tanaidaceans), and gradual loss of pereopodal exopods. SIEWING has mentioned changes in the structure of the digestive tract and shift in the respiratory organs, as well as similarity to the isopods

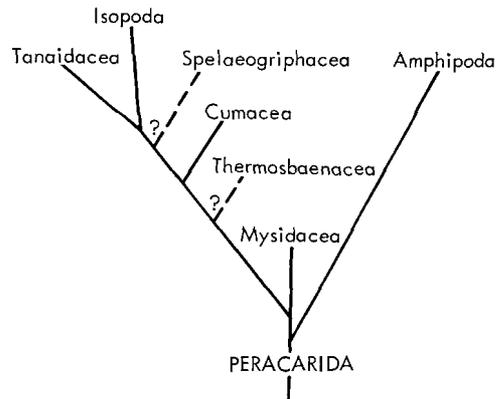


FIG. 177. Phylogeny of Recent Peracarida as interpreted by SIEWING (274) and modified by FRYER (101).

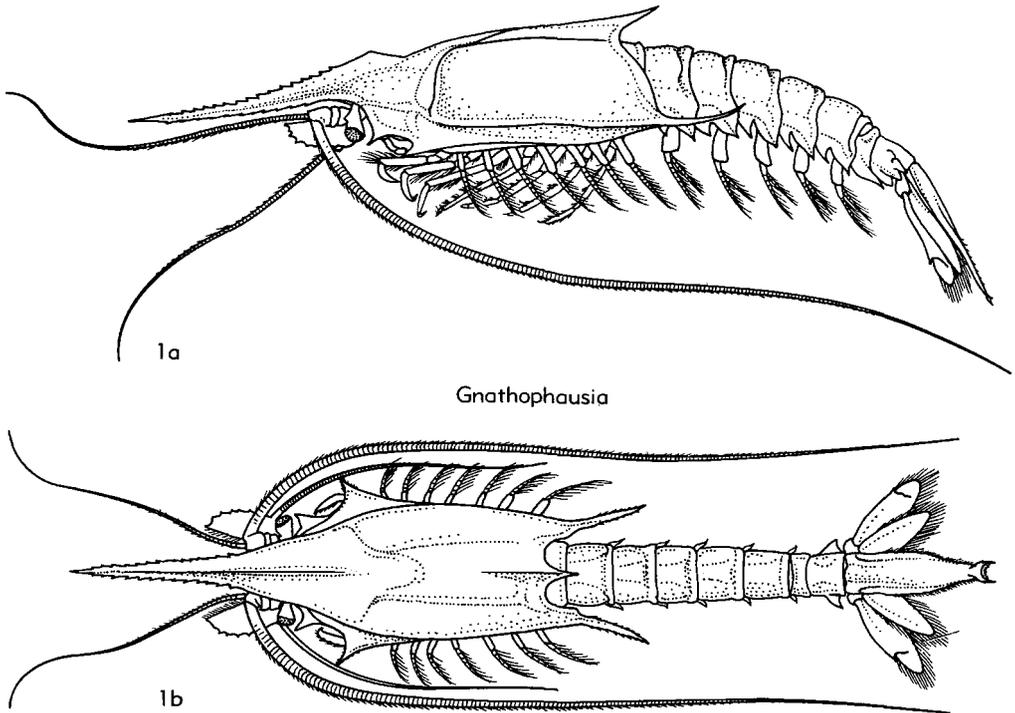


FIG. 178. Lophogastrida: *Gnathophausia calcarata* G. O. Sars; 1a,b, lateral and dorsal views, $\times 0.8$ (377c).

in such characters as distinguish the latter group from the amphipods.

The Spelaeogriffacea is clearly a primitive order, but its exact position within the Peracarida is uncertain.

A tabulation of suprageneric divisions of the Peracarida showing their stratigraphic occurrence and numbers of genera contained in each is given on page R114.

The Thermosbaenacea, included in the Peracarida in this volume, are probably the result of an early divergence in peracaridan evolution. SIEWING has considered the order to be a closely related but independent division.

Quite different from the above scheme, in which the Peracarida is construed to be a natural phyletic unit, is GLAESSNER'S (1957) suggestion that the Tanaidacea, Isopoda, and Amphipoda are related to the early Syncarida by way of the Acanthotelsonidae, and that the Mysidacea, Cumacea, Eucarida, and Hoplocarida are all derived from the Pygocephalomorpha. The Acanthotelsonidae and

Pygocephalomorpha then would be interpreted as derived from a common Paleozoic caridoid malacostracan. As such, the Peracarida would be a diphyletic group. TIEGS & MANTON (288), BIRSHTEYN (43), and SIEWING (275) do not agree to the syncarid origin of part of the Peracarida.

Order MYSIDACEA Boas, 1883

Exhibiting caridoid facies; carapace fold more or less enveloping thoracic region; eyes stalked, movable; antennule (first antenna) biramous; antenna (second antenna) with scalelike exopod; thoracopods bearing natatory exopods; abdomen large, elongate, ventrally flexed, terminating in tail fan formed by lamellar rami of uropods and telson; first one, two, three, or rarely four thoracomeres fused to cephalon; first one or two pairs of thoracopods modified as maxillipeds, in some forms lacking exopods, first with leaflike epipod; ramified gills at base of some or all thoracopods. Young

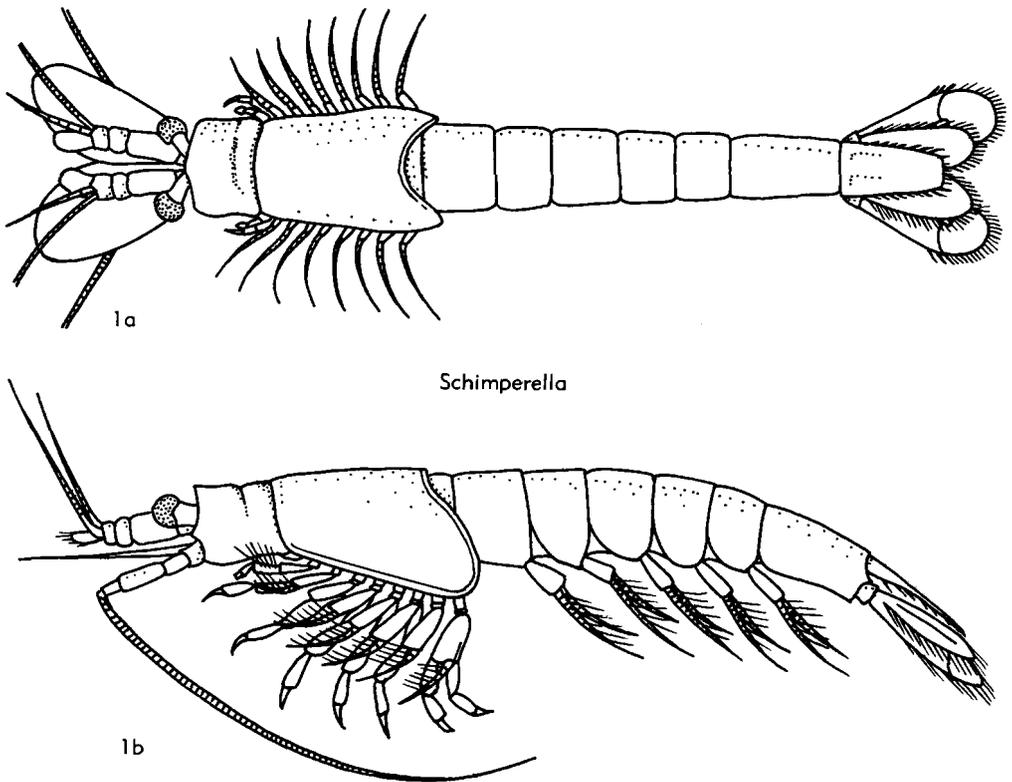


FIG. 179. Mysida: *Schimperella beneckeï* BILL; 1a,b, dorsal and lateral views, $\times 7$ (39).

leave marsupium with full complement of limbs. *Trias.-Rec.*

Among peracarids, the Mysidacea can be recognized at a glance because they possess the caridoid facies, but it is sometimes more difficult to distinguish members of this order from nonperacaridan forms (e.g., Euphausiacea, and lower Decapoda) which also exhibit the caridoid facies. This is particularly true of fossils in which diagnostic peracaridan traits usually are not preserved.

A number of Paleozoic genera have been included in the Mysidacea (299) in the past, some (e.g., *Pygocephalus*, *Tealliocaris*, *Crangopsis*) because of the presence of oöstegites. Brooks (55) has pointed out that all of these genera differ from any of the Recent eumalacostracan superorders in having an unsegmented sympod and caudal furca on which account he has included them in a new division named Eocarida.

Accepting this classification, at the present time no mysidaceans are known from the Paleozoic.

Of the two mysidacean suborders, the Lophogastrida are considered to be the more primitive in that all have seven pairs of oöstegites, well-developed unspecialized pleopods, and no uropodal statocysts. The Lophogastridae are especially primitive in that some show indications of a seventh abdominal segment (Fig. 178) and in having (*Gnathophausia*) a two-jointed maxillary palp, which is reflected into the branchial cavity.

Mysidaceans are found primarily in marine environments, but some species are markedly euryhaline, and a few live in fresh water. As a whole, the group is essentially pelagic, although commonly epibenthic. Species which exhibit vertical migration may be found on the bottom or even burrowed into it during the daytime.

Both carnivorous and detritus-feeding habits are characteristic. The detritus-feeders may filter fine particles from the water or pick up larger bits from the bottom.

The Mysidacea, including both suborders Lophogastrida and Mysida, are a very cosmopolitan assemblage.

Suborder LOPHOGASTRIDA
Boas, 1883

Ramified branchiae well developed on second to seventh thoracopods but rudimentary or absent on eighth; seven pairs of oöstegites; pleopods biramous, natatory, well developed in both sexes, may be slightly modified in males. No statocyst in endopod of uropods (Fig. 178). *Rec.*

Suborder MYSIDA Boas, 1883

Thoracopods lacking branchiae; usually two or three pairs of oöstegites present, rarely seven pairs; pleopods usually rudimentary in females, biramous and natatory in some males but more commonly with one or more pairs modified as accessory copulatory organs; uropodal endopod usually with statocyst. *Trias.-Rec.*

Family UNCERTAIN

Schimperella BILL, 1914, p. 310 [**S. beneckeï*; SD HESSLER, herein]. No obvious rostrum; carapace fold extended posteriorly to cover most of last pereionite, rounded posterolaterally, only moderately emarginate posteriorly; eyes well developed. Antennule with distal end of last peduncular segment modified in males; scaphocerites of antennae very large, broad; pereopods normal, more or less similar where known. Abdomen without evident pleura; telson elongate, truncate, entire; pleopods large, subequal, natatory, apparently unmodified. Uropodal rami broadly rounded posteriorly; exopod with transverse suture; no apparent statocyst. *Trias., Eu.*(Alsace).—FIG. 179, I. **S. beneckeï*; 1a, b, dorsal, lat. views (reconstr.), $\times 7$ (39).

[*Schimperella* is tentatively placed in the suborder Mysida on the basis of its general body form, especially that of the carapace, and the presence of an *appendix masculina* on the first antenna. The well-developed, unmodified pleopods and pereopods and the absence of a statocyst in the uropods suggest that this genus may be relatively primitive. It differs from some of the Lophogastridae in that no suture subdivides the last pleonite indicates fusion of the 6th and 7th abdominal somites.]

Francocaris BROILI, 1917, p. 429 [**F. grimmi*; OD]. Cephalon strongly produced anteriorly into long

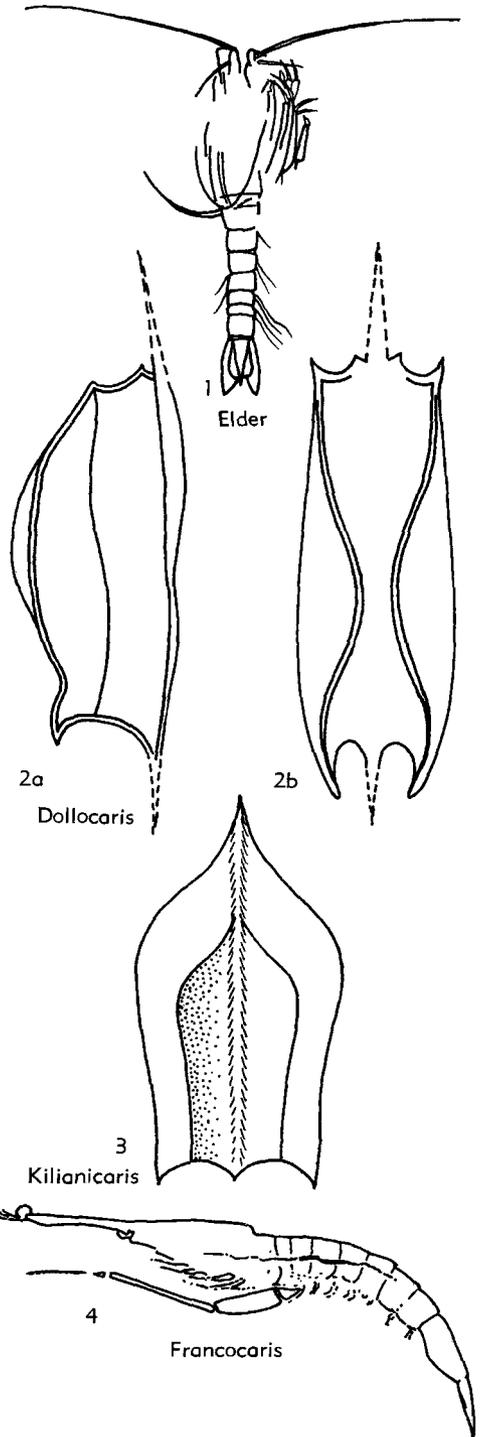


FIG. 180. Mysidacea, Family Uncertain (4), Suborder and Family Uncertain (1-3) (p. R365-R366).

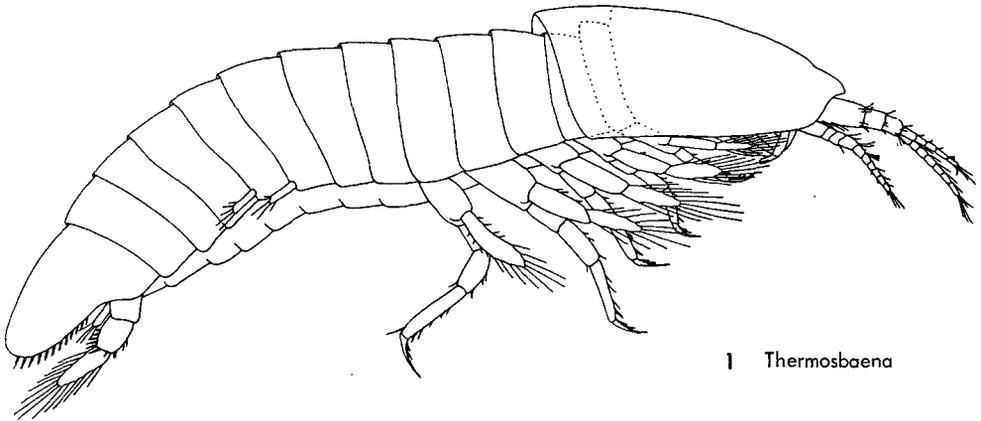


FIG. 181. *Thermosbaena mirabilis* MONOD, adult female, lateral view, $\times 30$ (347).

slender process with eyes at anterior end; carapace not strongly sclerotized; 8th thoracopods extremely long, with large basal segment. [BROILLI placed *Francocaris* among the Mysidacea because its carapace appears to be fused only to the anterior thoracic segments.] *U.Jur.*, Eu.(Ger.).—FIG. 180,4. **F. grimmi*; lat., $\times 1.4$ (346a).

Suborder and Family UNCERTAIN

Dollocaris VAN STRAELEN, 1923, p. 432 [**D. ingens*; OD]. Carapace with weak marginal furrow; dorso-medial carina running from posteromedial spine forward onto long rostrum; marked lateral carina halfway between dorsal mid-line and lateral edge, running length of carapace; posterolateral spines present. *U.Jur.*, Eu.(Fr.).—FIG. 180,2. **D. ingens*; 2a,b, carapace; lat., dorsal, $\times 0.6$ (383).

Elder MÜNSTER, 1839, p. 77 [**E. unguatus*; SD OPPEL, 1862] [=*Saga* MÜNSTER, 1839]. Cephalothorax of relatively delicate composition, rarely preserved in fossils where all other parts are in the proper relationship to each other; flagellum of antennae as long as body, much longer than those of antennules; pereopods with distinct distal claw. *U.Jur.*, Eu.(Ger.).—FIG. 180,1. **E. unguatus*; dorsal, $\times 0.8$ (369).

Kilianicaris VAN STRAELEN, 1923, p. 434 [**K. lerichei*; OD]. Carapace angular, subquadrate posteriorly, with strong dorso-medial and weak lateral carinae; rostrum broad; posteromedial and posterolateral spines weakly produced. *U.Jur.*, Eu.(Fr.).—FIG. 180,3. **K. lerichei*; carapace, lat., $\times 1.1$ (383).

[VAN STRAELEN (383) put *Dollocaris* and *Kilianicaris* in a new family, the Dollocaridae, which he placed near the Lophogastridae, but which differ in lack of a cervical furrow, in general form of the carapace, and in position of the carinae. *Dollocaris* and *Kilianicaris* are based on the carapace alone. Although in both this structure is much like that of *Gnathophausia*, not enough is known of these two fossil genera to demonstrate that they are definitely mysidaceans (287).]

Order THERMOSBAENACEA Monod, 1927

No oöstegites; instead eggs and embryos carried in dorsal brood pouch formed by shell fold. Maxilliped with two protopodal endites, most distal of which is very large, quadrate; epipod leaflike; slender exopod usually present in both sexes; slender endopod found in males of some species and female of one. Shell fold fused to first thoracomere, small, covering no more than next two somites. Eyes rudimentary or absent. Antennule biramous; antenna lacking exopod. Pereiopods with exopods. Pleopods on first two pleonites only. Uropod biramous, flattened. Young leave brood pouch before pereiopods 6 and 7 have developed. *Rec.*

STELLA (1953) and TARAMELLI (1954) placed the Thermosbaenacea between the Peracarida and Syncarida. SIEWING (272) noted the close relationship to the Peracarida, but concluded that the unique mode of brooding young and the different form of the maxilliped were of sufficient importance to warrant placing thermosbaenaceans in a separate, new division, the Pancarida. Subsequently, GORDON (1958), BARKER (14), and FRYER (101) have minimized the importance of these differences and have followed MONOD's original designation.

Thermosbaenaceans have been recorded from thermal springs, fresh and brackish subterranean lakes, and brackish coastal

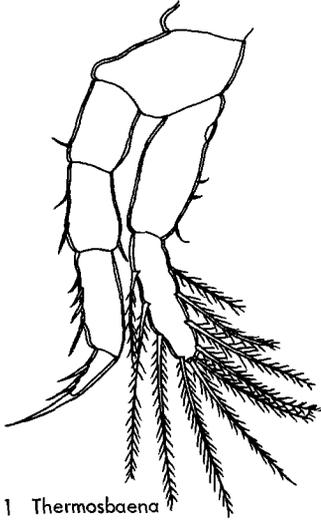
1 *Thermosbaena*

FIG. 182. Third pereopod of *Thermosbaena mirabilis* MONOD, $\times 90$ (206).

ground water. KARAMAN (163) and others consider the ancestors of this group to have been marine, thermosbaenaceans having invaded continental environments through the intermediate marine or brackish coastal ground water.

Family THERMOSBAENIDAE Monod, 1927

Characters of order. *Rec.*

Thermosbaena MONOD, 1924, p. 58 [**T. mirabilis*; OD]. Body short and stocky; pereopods absent from last 2 pereonites; endopod of uropod reduced; telson fused to pleonite 6. *Rec.*, N.Afr.—FIG. 181, 1; 182, 1. **T. mirabilis*, Tunisia; 181, 1, adult female, lat., $\times 30$ (347); 182, 1, 3rd pereopod, $\times 90$ (206).

Monodella RUFFO, 1949, p. 45 [**M. stygicola*; OD]. Body slender, elongate; pereopods on all pereonites; uropod with well-developed endopod; telson free. *Rec.*, USA (Tex.)-Italy-Yugosl.-Israel.—FIG. 183, 1. *M. halophila* KARAMAN, Yugosl.; maxilliped of male, $\times 90$ (163).

Order SPELAEOGRIPHACEA Gordon, 1957

Body elongate, subcylindrical; carapace short, fused dorsally to first thoracic somite, covering most of second to form lateral branchial cavities; trunk segments other

than first thoracomere free, including telson; pleon long; ocular lobe movable, but without visual elements. Antennules biramous; antennae with small exopodal scaphocerite and four-jointed peduncle; mandible with unjointed palp; maxilliped having large cup-like branchial epipod located in branchial chamber; thoracopods two to four with two-segmented natatory exopods, next three (in some forms four) pairs with unjointed branchial exopods; first four pleopods well developed, biramous, natatory, fifth pleopods vestigial; uropods biramous, flattened. *Rec.*

This order is known only from a cave at Table Mountain, South Africa, where its single known species was found in a freshwater pool. Because *Spelaeogriphus* possesses a lacinia mobilis and oostegites GORDON (121) included it in the Peracarida. Nevertheless, some of its features (e.g., large number of exopods, some respiratory) are reminiscent of the Syncarida. Although almost all characters of *Spelaeogriphus* are found in other peracaridan orders, in combination they are unique; the small carapace fold fused to a single thoracomere, the well-developed abdomen bearing large, natatory pleopods, and the movable ocular lobes are among the most important of these (Fig. 184). GORDON (1960) has placed *Spelae-*

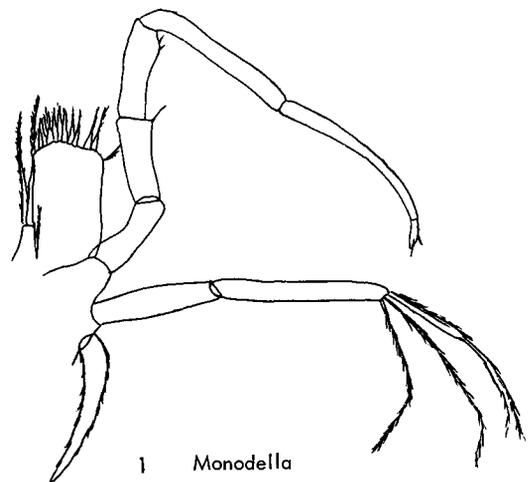
1 *Monodella*

FIG. 183. *Monodella halophila* KARAMAN, maxilliped of adult male, $\times 90$ (163).

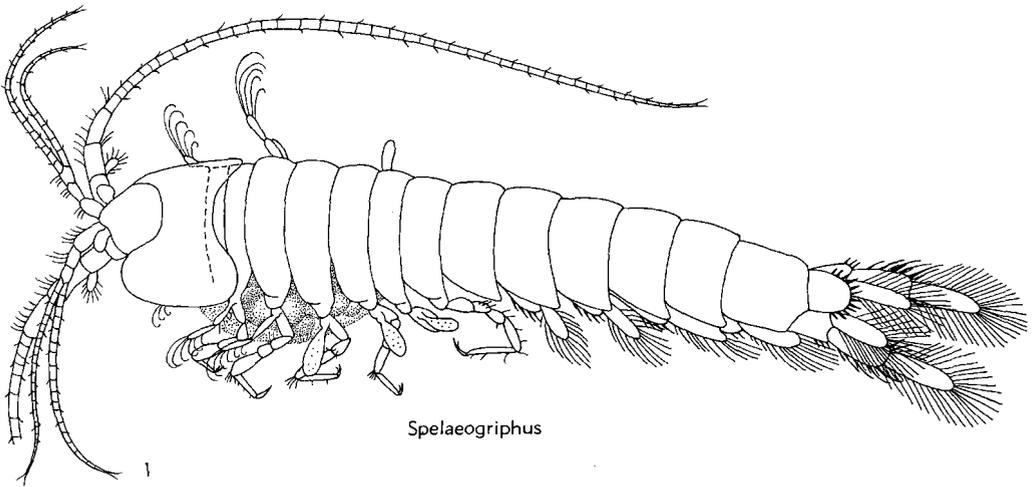


FIG. 184. *Spelaeogriphus lepidops* GORDON; dorsolateral view of adult female carrying eggs, $\times 7.5$ (358).

ogriphus closest to the Tanaidacea, mainly because of its small carapace, two-jointed antennal protopod, and the cuplike branchial epipod of the maxillipeds.

Order CUMACEA Kröyer, 1846

[=Symphoda STEBBING, 1900]

Carapace fold fused to at least three thoracomeres, in some to four, and very rarely to as many as six thoracomeres thus forming lateral branchial chambers which contain branchial epipodite of first maxilliped; anterolateral portions produced anteriorly, usually meeting in front of cephalon to form pseudorostrum. Eyes (when present) nearly always forming unpaired dorso-medial organ; antennules may be biramous; antennae lacking exopod; first three thoracopods modified as maxillipeds; natatory exopods may be present on thoracopods 3 to 7; pleon slender, long, usually defined distinctly from bulkier unit formed by cephalon and thorax; pleopods absent on female, present in varying numbers on male; uropods large, styliform; telson may or may not be fused to last pleomere. *U.Perm.-Rec.*

Cumaceans are easily recognized by the long, slim, subcylindrical pleon which is usually strongly differentiated from the broad, commonly inflated pereion and cephalon. The shape of the anterior end of the cephalon is also distinctive (Fig. 185). The

sessile eyes usually form an unpaired dorsal visual organ situated between the rostrum and pseudorostrum; this probably results from a dorsomedial migration of the originally lateral eyes in response to development of the pseudorostrum. Also contributing to the characteristic shape are the large, obvious uropods, each with its long, slender peduncle. Cumaceans are rarely more than 3.5 cm. long.

The inflated form of the carapace is mostly a result of the large, lateral branchial chambers. These serve respiration in being lined with a respiratory epithelium, and far more importantly, in housing a large branchial epipod of the maxillule. This epipod is subdivided into a complicated, posteriorly directed gill and an anteriorly directed exhalant siphon. The latter projects forward under the pseudorostral lobe and forms the siphonal apparatus, either in conjunction with this lobe or independently.

The Cumacea are dominantly marine, but some brackish and fresh-water forms exist. Although cumaceans, particularly reproductive males, can swim, they spend most of their time buried in the substrate. Many species are selective as to grain size of particles comprising this substratum. Cumaceans occur from intertidal to abyssal depths, and many species are quite eurybathic. For the most part, cumaceans are selective deposit-feeders.

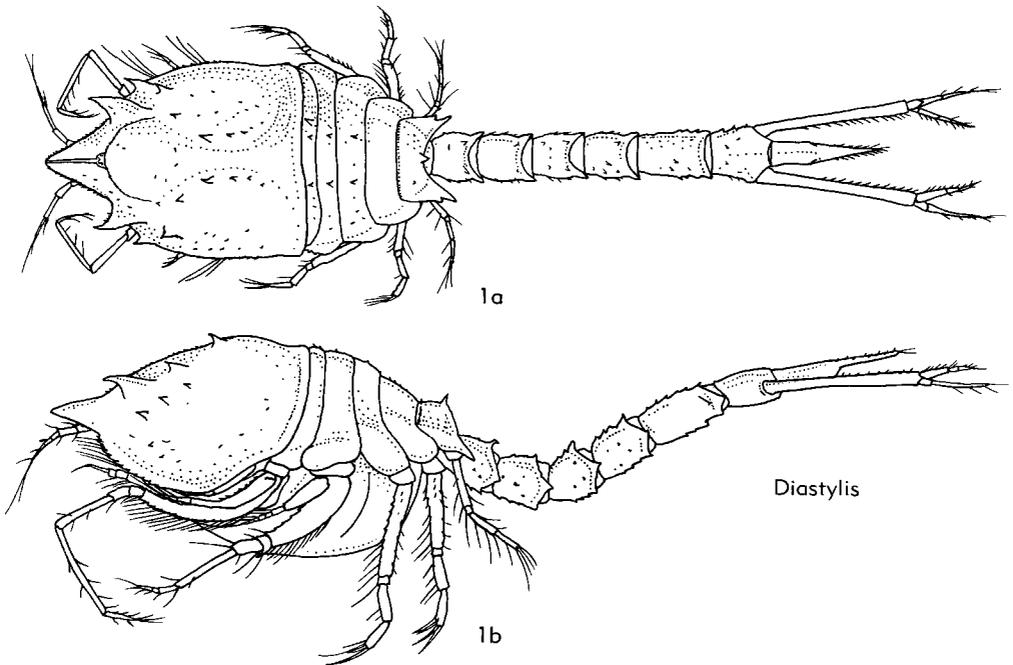


FIG. 185. *Diastylis cornuta* (BOECK, 1863), Rec.; 1a,b, adult female, dorsal, lateral views, $\times 7.5$ (377d).

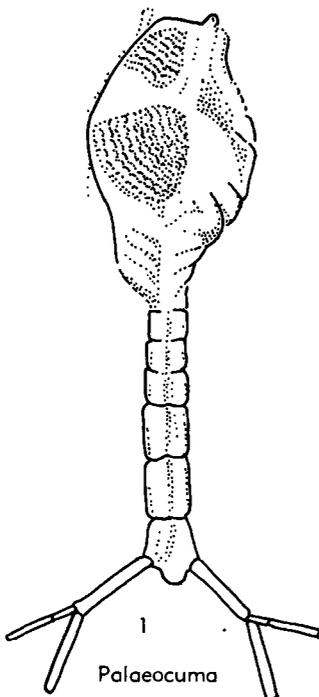


FIG. 186. Cumacea, Family Uncertain (p. R369).

ZIMMER (338) has divided the Cumacea into seven families, which, according to JONES (1960), contain 78 genera and about 645 species.

MALZAHN (personal communication; also see ROLFE, this volume, p. R313) has found cumacean remains in Upper Permian beds of Germany.

Family UNCERTAIN

Palaeocuma BACHMAYER, 1960, p. 422 [**P. hessi*; OD]. Telson small; cephalothorax egg-shaped, somewhat truncate anteriorly; pleonites 1 to 5 cylindrical, with strong dorsomedial keel; pleon only slightly longer than cephalothorax; exopod of uropods weaker, somewhat shorter than endopod. *M. Jur.*, Eu.(Fr.).—FIG. 186, 1. **P. hessi*; dorsal, $\times 2.5$ (9).

Order TANAIIDACEA Dana, 1853

[=Chelifera G. O. SARS, 1882; Anisopoda CLAUD, 1888]

Carapace fold short, covering first two thoracomeres to which it is fused dorsally, forming small lateral branchial cavities; body generally subcylindrical or tapering evenly posteriorly; pleon short; telson fused

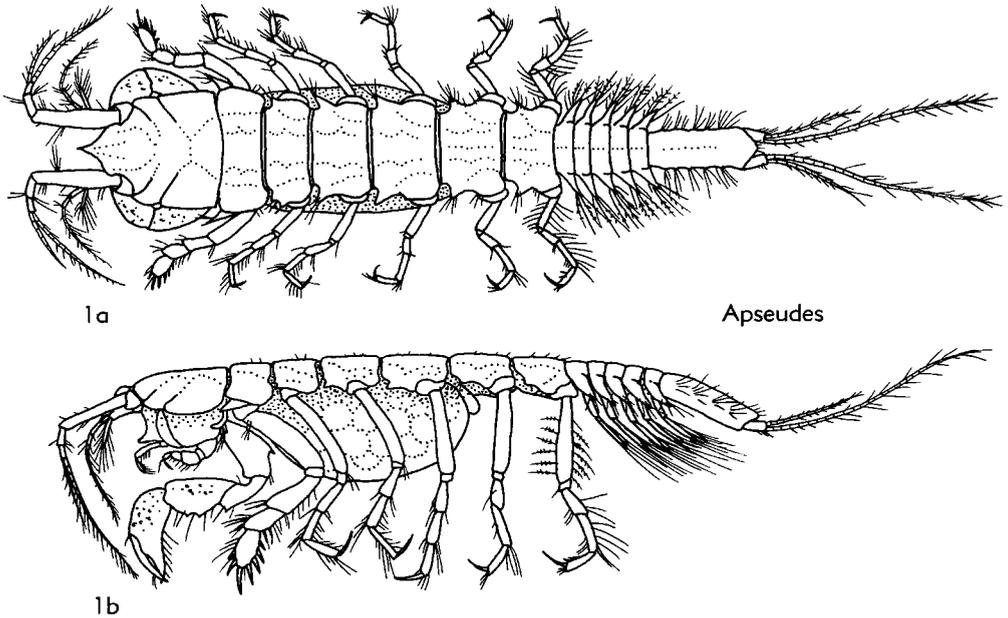


FIG. 187. Monokonophora: *Aapseudes spinosus* (M. Sars); 1a,b, dorsal and lateral views, $\times 10$ (261b).

to sixth pleonite; eyes (when present) set on short immovable lobes (except in *Ophthalmapseudes*). First thoracopods modified as maxillipeds having branchial epipodite; second thoracopods chelate, usually enlarged; vestigial exopods present in some forms on second and third thoracopods of adults; more posterior thoracopods with or without exopod in manca-stage larvae; pleopods usually present, biramous; uropods small, slender. *Perm.-Rec.*

The cylindrical or somewhat depressed body is generally slender and long. The pleon is commonly quite abbreviated, although its individual segments are almost never fused together. In the Monokonophora the body gradually narrows posteriorly, whereas in the Dikonophora it is common for body width hardly to vary. This body shape, in combination with the tagmosis and usually enlarged chelipeds, gives the tanaidaceans an appearance which is difficult to mistake. Tanaidaceans are small, rarely attaining a length of 2.5 cm.

In many differences between the two suborders, the Dikonophora consistently prove to be more degenerate than the Monokonophora.

Both antennules and antennae are biramous in the latter but uniramous in the former. In the Dikonophora a mandibular palp is lacking, the maxillules bear only a single endite and the maxillae are rudimentary. Indeed, in males of many Dikonophora most of the mouth parts are vestigial or absent. The monokonophoran maxillipeds bear a much larger, more complicated branchial epipodite. In the Dikonophora the coxae and even the bases of the maxillipeds tend to fuse. Small exopods may be present on some thoracopods of monokonophorans, but are always absent in the Dikonophora. The marsupium of the Tanaidae (Dikonophora) is formed by only a single pair of oöstegites. Finally, the uropodal rami tend to be shorter in the Dikonophora, and the exopod may even be absent. SIEWING (1954) has compared the internal anatomy of Aapseudidae (Monokonophora) and Paratanaidae (Dikonophora) and has found the latter to be reduced in a number of respects.

Tanaidaceans live almost exclusively in marine or brackish waters, from littoral to hadal depths (more than 6,000 m.). They are benthic organisms and burrow in mud,

crawl in rock crevasses, or live among plant or animal colonies. Some secrete a filamentous, feltlike mass in which they live; others build tubes. Walking is the predominant form of locomotion; a few also swim, but very poorly.

Both suborders of the Tanaidacea are very widespread, cosmopolitan crustacean groups.

Suborder MONOKONOPHORA

Lang, 1956

Antennules with two flagella; mandibles with palp; maxillules with two endites; marsupium formed by four pairs of oöstegites; males with one genital cone (Fig. 187). *Perm.-Rec.*

Family UNCERTAIN

Ophthalmapseudes GLAESSNER, in GLAESSNER & MALZAHN, 1962, p. 259 [*Decapoda cf. *Macrura rhenana* MALZAHN, 1957; OD]. General aspect of carapace and abdomen as in Apsseudidae (Fig. 187); eyes on elongate, apparently movable stalks. *U.Perm.-M.Jur.*, Eu.(Ger.).—FIG. 188, 1. **O. rhenanus* (MALZAHN); 1a, b, cephalic shield (reconstr.), lat., dorsal, showing eyestalks, $\times 30$ (186).

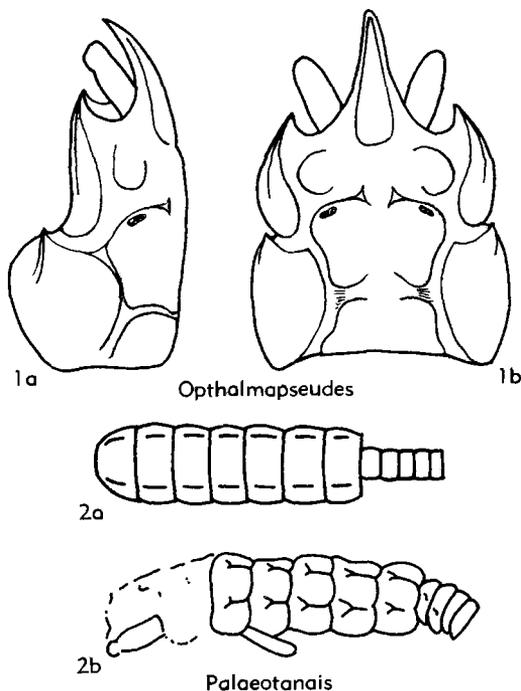


FIG. 188. Tanaidacea: Monokonophora, Family Uncertain (1); Suborder and Family Uncertain (2) (p. R371).

Suborder DIKONOPHORA Lang, 1956

Antennules with single flagellum; mandibles without palp; marsupium formed by one or four pairs of oöstegites; males with two genital cones (Fig. 189). *Rec.*

Suborder and Family UNCERTAIN

Palaeotanais REIFF, 1936, p. 86 [**P. quenstedti*; OD]. Pereonites well vaulted, each with pair of dorsolateral furrows; basis of third thoracopods long, broad; pleonites narrower, not vaulted, each pointed posterolaterally. *L.Jur.*, Eu.(Ger.).—FIG. 188, 2. **P. quenstedti*; holotype, 2a, dorsal, as figured by QUENSTEDT, $\times 5$ (374); 2b, same fossil, dorsal, refigured by REIFF, $\times 5$ (375).

[REIFF (375) has commented that the single known specimen is less complete than when QUENSTEDT (374) first figured it. The fossil originally consisted of seven large somites, of which the first was rounded off anteriorly, and four small posterior somites, the posterior end being missing. Assuming the first somite to be the cephalon, REIFF concluded that the fossil was most similar to tanaidaceans because of identical tagmosis, similar size and body form, and similar morphology of sole remnant limb fragment.]

Charassocarcinus (see p. R532 and p. R628).

Order ISOPODA Latreille, 1817

First thoracomere fused to cephalon, and rarely second as well; no distinct carapace fold; body most commonly somewhat depressed; pleon short, in many with segments fused; telson nearly always fused with last pleonite; eyes sessile, not stalked. Antennules usually uniramous; antennae nearly always lacking exopod; pereopods without exopods, coxae always short; first thoracopods modified as maxilliped with epipod (when present) not enclosed in branchial chamber; second thoracopods rarely also modified as mouth parts; pleopods biramous, specialized for respiration; heart located in pleon. [Young leave marsupium before appearance of last pair of thoracopods (manca stage).] *Trias.-Rec.*

Many different body shapes are found in this order. Most commonly isopods are somewhat depressed, as in the Oniscoidea (Fig. 202) or Flabellifera (Fig. 192). This

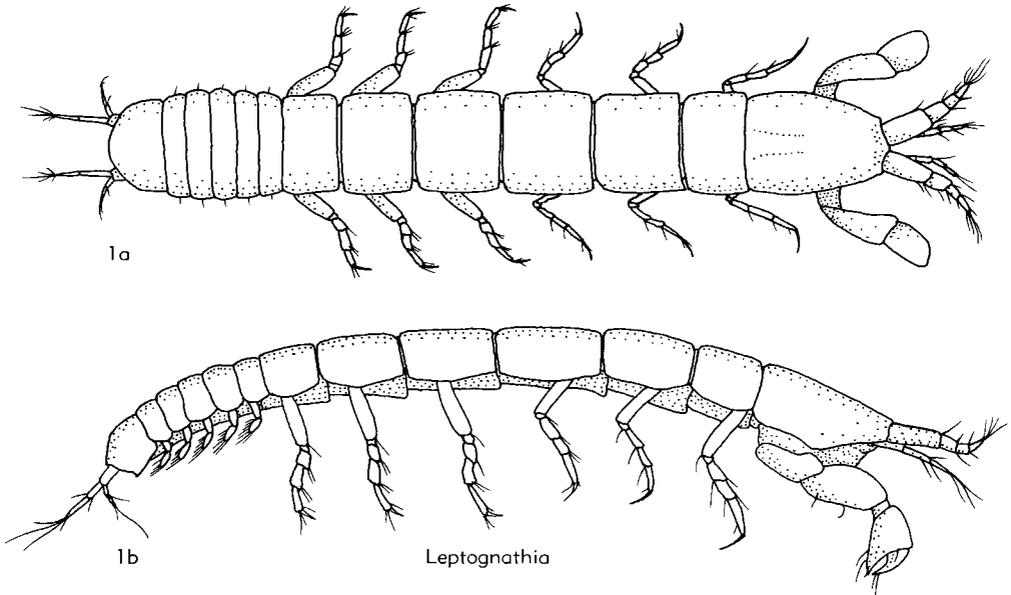


FIG. 189. Dikonophora: *Leptognathia longiremis* (LILLJEBORG); 1a, b, dorsal and lateral views, $\times 30$ (261b).

form is carried to the extreme in the Serolidae (Fig. 197). Some of the Phreatoicoidea (Fig. 203) exhibit the opposite pattern, appearing to be compressed laterally and are remarkably similar to the gammaridean amphipods. Many of the Asellota are cylindrical, as are the Anthuridea (Fig. 191) and Arcturidae (Valvifera). The latter two groups are, in addition, conspicuously elongate, this being achieved in the arcturids by lengthening of but a single segment.

As pointed out by ZIMMER (337), the name Isopoda is somewhat of a misnomer. Except in the Epicaridea, which are truly isopodous, pereopods one to three are directed anteriorly and pereopods five to seven point posteriorly, whereas the fourth pereopod commonly occupies an intermediate position. This is true even in the Oniscoidea, Limnoriidae (Flabellifera), and Gnathiidea, where the limbs are otherwise essentially alike.

More commonly the pereopods are specialized in blocks. A frequent pattern is one in which the posteriorly turned limbs are significantly longer than others and are "ambulatory" in form as in the Aegidae (Flabellifera). In many groups the first three pereopods are hooked or subchelate; the Anthuridea and many Idotheidae are

examples of this. In the Phreatoicoidea and many Asellota only the first pereopod is subchelate. The most extreme pereopodal specialization is seen in the Munnopsidae (Asellota). Here the first two pereopods are short and slender, the second two are thin and extremely elongate, while the last three are short paddles.

Because of the primarily respiratory function of all or part of a number of the pleopods, a variety of different adaptations serves to protect these delicate structures. For example, in many Cymothoidae the exopod of each pleopod protects the respiratory endopod. The first pleopods of some Anthuridea fold back over the rest. In female Paraselloidea (Asellota) the second pleopods form an unpaired operculum covering a ventral chamber in which the other pleopods lie. In the Valvifera the uropods are modified to form a pair of laterally hinged ventral plates which cover the ventral surface of the pleon. In addition to this respiratory or protective function, pleopods may also serve in locomotion or be modified for copulation.

The uropods may vary in form from valvelike opercula described above to relatively simple caudal processes, as found in the Asellota or Oniscoidea. A fanlike form,

such as that of the caridoid facies, appears in many Flabellifera and in the Gnathiidae.

The order Isopoda is the largest of the peracaridan orders. The majority of species are marine where they are found at all depths. Nevertheless they are well represented on land, primarily by the large suborder Oniscoidea. Members of the Asellota, Valvifera, Flabellifera, Anthuridea, and all of the Phreatoicoidea (except for a few terrestrial forms) may be found in fresh water and may even occur in interstitial and subterranean environments.

The feeding types found among the isopods are equally diverse. Most are detritus-feeders. Some are herbivorous, including wood-eaters, and yet others are carnivores, ranging in degree from predators to highly specialized parasites. Most of the nonparasitic isopods are primarily benthic.

Isopods are almost ubiquitous crustaceans, for each of the suborders can be classed as cosmopolitan, with qualification that living Phreatoicoidea now are known only from New Zealand, Australia, northern India, and South Africa.

Suborder GNATHIIDEA Leach, 1814

Second thoracomere fused to cephalon and its appendage modified to act as mouth part; eighth thoracomere and its appendage absent; as result, only five free thoracomeres and the same number of pereopods occur; peduncles of antennae consisting of four segments; pleonites not fused; uropods flattened, biramous, forming caudal fan in conjunction with pleotelson. Extraordinary sexual dimorphism and extensive metamorphosis; larvae parasitic and provided with suckorial mouth parts; those of adult male reduced to large, anteriorly protruding, pincer-like mandibles and modified maxillipeds, while in adult female only maxillipeds remain (Fig. 190). *Rec.*

Suborder ANTHURIDEA Leach, 1814

Body slender, elongate. Some forms with anterior pleonites fused but last somite never

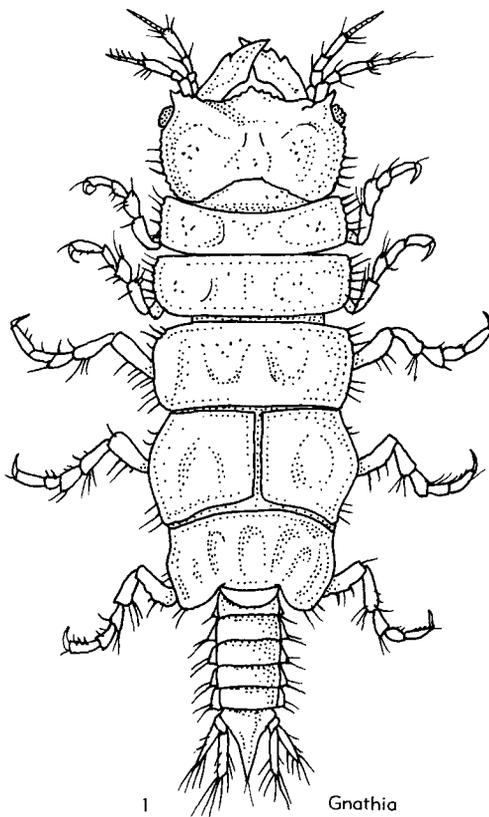


FIG. 190. Gnathiidea: *Gnathia elongata* (KRÖYER); ♂, dorsal view, $\times 18$ (261b).

fused to telson; peduncle of antenna with five segments; mouth parts suckorial in some forms; second, third, fourth thoracopods subchelate, second being enlarged; pleopods branchial, first long, somewhat opercular; uropods broad, flat, biramous, with exopod arching over telson (Fig. 191). *Rec.*

Suborder FLABELLIFERA G. O. Sars, 1882

Body more or less depressed; pleonites free or fused. Peduncle of antennae with five or six joints; mouth parts normal or suckorial; mandibles usually with reduced or modified molar process; coxae of pereopods developed as epimeres, in many forms partly or completely fused to thoracomeres;

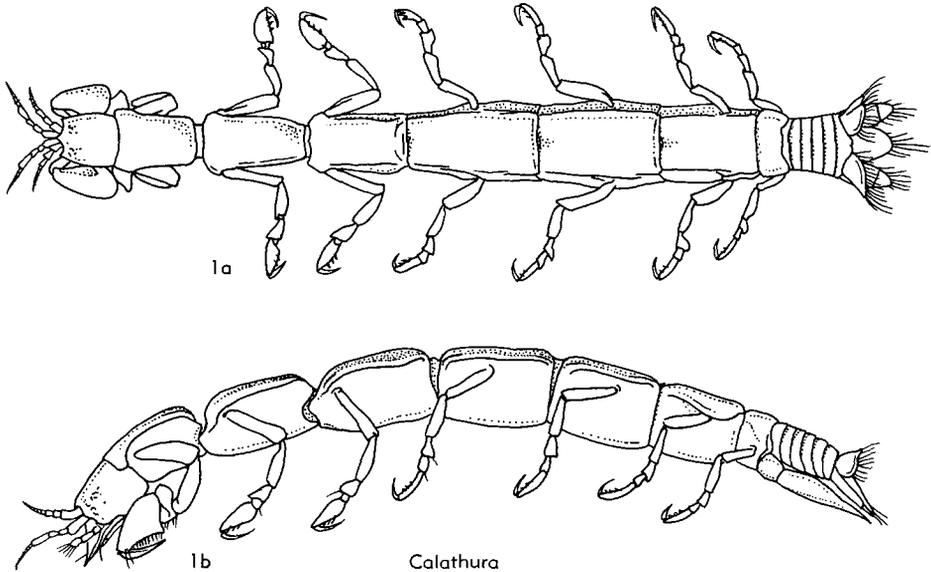


FIG. 191. Anthuridea: *Calathura norvegica* (G. O. Sars); 1a,b, dorsal and lateral views of female, $\times 9$ (261b).

uropods biramous, usually flattened and forming caudal fan in conjunction with pleotelson. *Trias.-Rec.*

Family CIROLANIDAE Hansen, 1890

Body ovoid; subsemicircular in cross section; labrum large; eyes usually small. Antennules and antennae unequal in length, with well-defined peduncles and flagella; mandibles with large lacinia mobilis; maxillipeds and both pairs of maxillae well developed, palp of former without hooks; well-developed epimeres defined on all pereonites except first; pereopods 1 to 3 prehensile, 4 to 7 ambulatory; all six pleonites distinct from each other, but last one fused to telson; biramous uropods lateral, forming caudal fan with flattened pleotelson. Free-living. ?*Mio., Rec.*

Bathynomus MILNE-EDWARDS, 1879, p. 21 [**B. giganteus*; OD]. Peduncle of antenna with 5 joints; rudimentary scaphocerite attached to distal end of peduncle of antennule; maxilliped with hooks on endite of basis; all 6 pleonites distinct; pleopods with accessory branchial rami on endopods. [IMAIZUMI (1953) has placed a fragmentary pleon from the Miocene of Japan in this genus and has claimed that specimens included in

Palaega WOODWARD (1870) more properly belong here.] ?*Mio., Rec.*, Carib.-Gulf Mex.-Indian O.-W. Pac.—FIG. 192, 1. **B. giganteus*; 1a,b, dorsal, lat., $\times 0.6$ (368).

Family SPHAEROMIDAE White, 1847

Body ovoid, well vaulted, capable of partial or complete enrollment. Antennules and antennae multiarticulate, clearly divided into peduncle and flagellum; mandibles with palp; epimeres firmly fixed to all pereonites, defined by furrow on all but first; pleon biarticulate, composed of large pleotelson and smaller anterior unit which is product of at least two fused pleonites; uropods lateral; endopod fused to protopod; exopod absent in some forms. *Trias.-Rec.*

The relationships between the modern genera of the Sphaeromidae are extremely subtle and difficult to interpret (142). This is in part a result of extensive sexual dimorphism. As usual in Recent groups, much of the systematics is based on structures seldom preserved in fossils. For all of these reasons the reference of fossil forms to Recent genera (e.g. *Sphaeroma*, *Cymodoce*) should be suspected and considered only tentative.

Group SPHAEROMIDAE
HEMIBRANCHIATAE Hansen, 1905

Body never strongly depressed; ability to enroll well developed; lateral margin of pereion not continuous. Proximal portion of antennae never protruding with free expansions in front of cephalon, fitted into oblique excavations. Pleopods 4 and 5

with thick fleshy endopods having deep transverse folds; exopods submembranous, rather pellucid, with two segments; neither ramus with plumose marginal setae; exopod of fifth pleopod with subapical squamiferous protuberance of lower surface very high; pleopod three with both rami having long closely set plumose setae, at least on distal

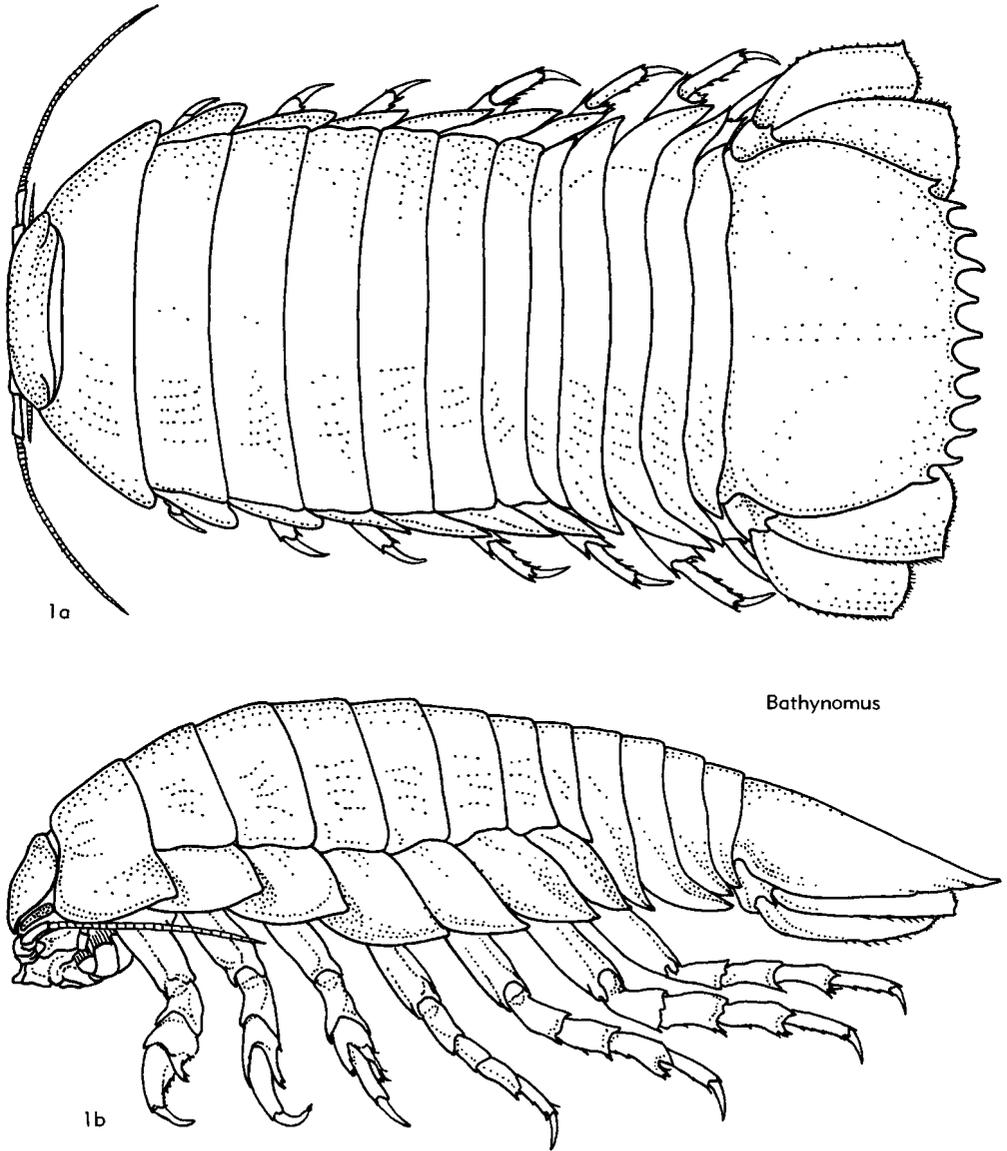


FIG. 192. Flabellifera, Cirolanidae: *Bathynomus giganteus* MILNE-EDWARDS; 1a,b, ♂ dorsal and lateral views, $\times 0.5$ (368).

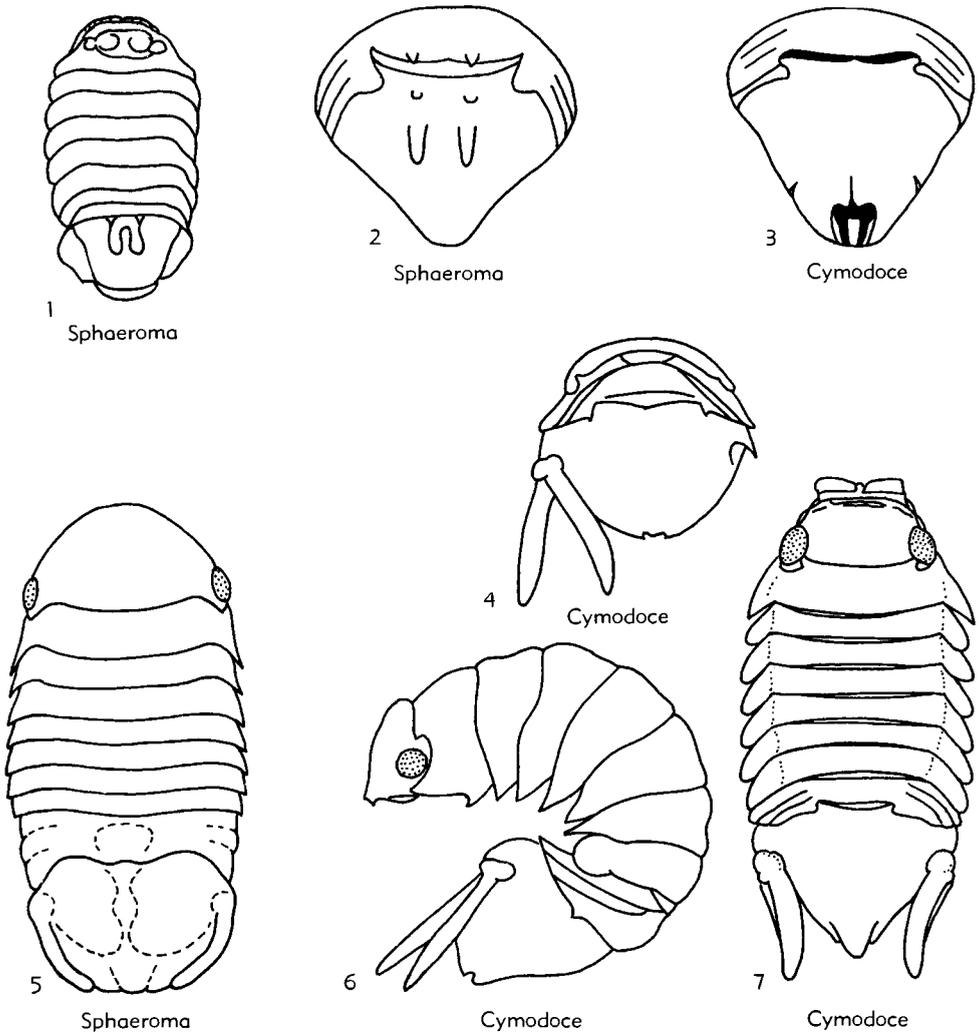


FIG. 193. Flabellifera, Sphaeromidae (p. R376-R377).

margin; pleopod one with rather broad endopod (scarcely ever 1.5 times longer than wide); uropods always with exopods, which may be exceedingly small. Brood develops in ventral pockets. ?*Mio.*, *Rec.*

Tribe CYMODOCINI Hansen, 1905

End of pleon in both sexes with notch which is semicircular in some forms but most commonly bilobed, being divided by mesial process, which rarely is large enough to overlap lateral teeth limiting notch, so that lateral teeth are visible only from side; mouth parts strongly metamorphosed in female; maxillipeds with long lobes on

joints 2 to 4 of palp; oostegites overlapping at mid-line; pleopod 3 with two-jointed exopod. ?*Mio.*, *Rec.*

Cymodoce LEACH, 1814, p. 433 [**C. truncata*; OD] [= *Cymodocea* LEACH, 1818; *Cymodice* LEACH, 1815]. Epistome without free process anteriorly; notch at posterior end of pleotelson at least with vestige of mesial lobe which generally is well developed, being commonly large or even very large; no medial process on anterior unit of pleon in male; rami of uropod generally well developed; exopod not able to fold under endopod. ?*Mio.*, *Rec.*, cosmop.—FIG. 193,4,6-7. *C.?* *exors* (VON EICHWALD), *Mio.*, Eu. (Rumania-S. USSR); 4, pleon, dorsal, $\times 3$ (4); 6, lat. (reconstr.), $\times 3.5$ (4); 7, dorsal (reconstr.), $\times 6$ (276).—FIG. 193,

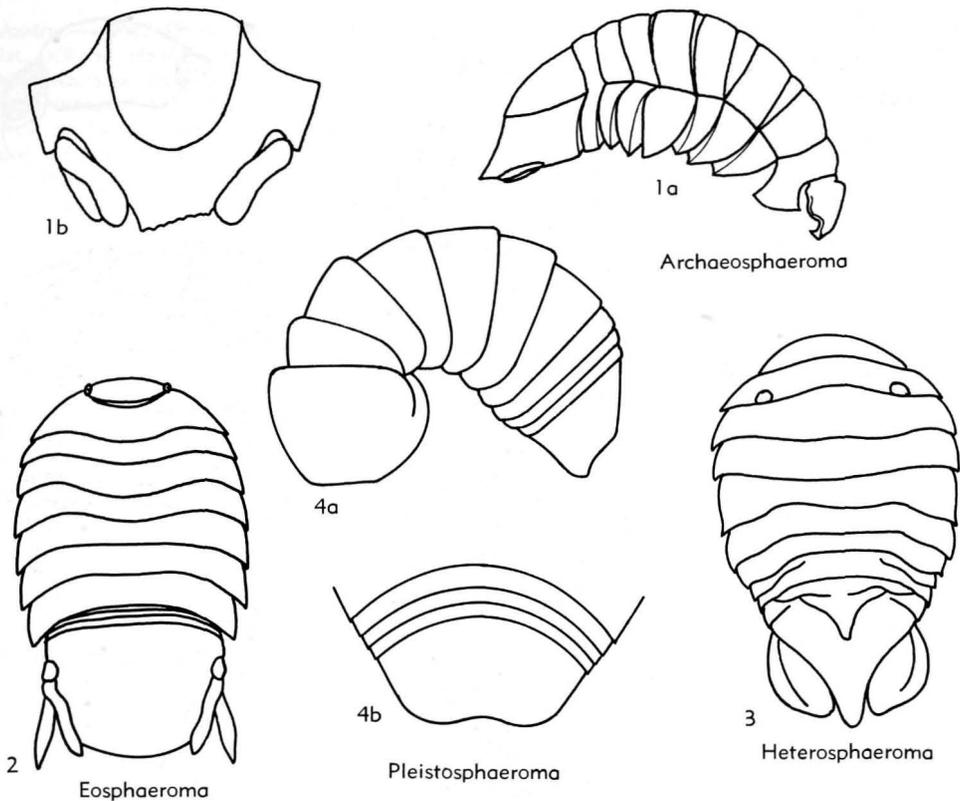


FIG. 194. Flabellifera, Sphaeromidae (p. R377-R378).

3. *C.?* *oroszyi* BACHMAYER, M.Mio., Aus., pleon, dorsal, $\times 6$ (341a).

Tribe SPHAEROMINI Hansen, 1905

End of pleon in female rounded or somewhat produced and more or less acute, without notch; in some forms end much produced, with pair of lateral notches, so that mesial part is shaped as process narrowed at base. Mouth parts similar in both sexes. ?*Mio.*, *Rec.*

Sphaeroma LATREILLE, 1804, p. 41 [**Cymothoa serrata* FABRICIUS, 1793; OD]. Body capable of complete enrollment. Mandible normal, incisor process not elongate, its end obtuse or with some small teeth; maxillipeds with low or rudimentary lobes on segments 2 to 4 of palp; 3 anterior pereopods with closely spaced, exceedingly long, stiff, plumose setae on outer margin of segments 3 and 4; oostegites overlapping at mid-line; pleon with side not expanded below lateral margin of pereion, tip rounded, not triangular or subacute; exopod of 3rd pleopod unjointed; uropodal rami subsimilar; exopod denticulate laterally, capable of fold-

ing under endopod, which is immovably fixed to side of pleotelson. ?*Mio.*, *Rec.*, cosmop.—FIG. 193,2. *S. weinfurteri* BACHMAYER, M.Mio., Ger.; pleon, dorsal, $\times 11$ (341).—FIG. 193,5. *S.?* *bachmayeri* TAUBER, M.Mio., Austria; dorsal, $\times 9$ (381).—FIG. 193,1. *S.?* *burkartii* BARCENA, Tert., Mex.; dorsal, $\times 4.5$ (342).

Group UNCERTAIN

Archaeosphaeroma NOVAK, 1872, p. 45 [**A. friči*; OD]. Body strongly vaulted, not capable of complete enrollment; epimeres transversely elongate, pointed, imbricating anteriorly and posteriorly from 5th pereionite; uropods with elongate, rounded, subequal rami much shorter than pleotelson, which tapers posteriorly and is strongly emarginated laterally to accommodate uropods. *Mio.*, Czech.—FIG. 194,1. **A. friči*; 1a, lat., $\times 4.5$; 1b, pleon, dorsal, $\times 6$ (370a).

Cyclosphaeroma WOODWARD, 1890, p. 530 [**C. trilobatum*; OD] [= *Palaeosphaeroma* REMES, 1903]. Body broad, strongly vaulted; cephalon also quite broad, but short, trilobate, only slightly surrounded by 1st pereionite; eyes large. Epimeres fused to pereionites, but still defined by

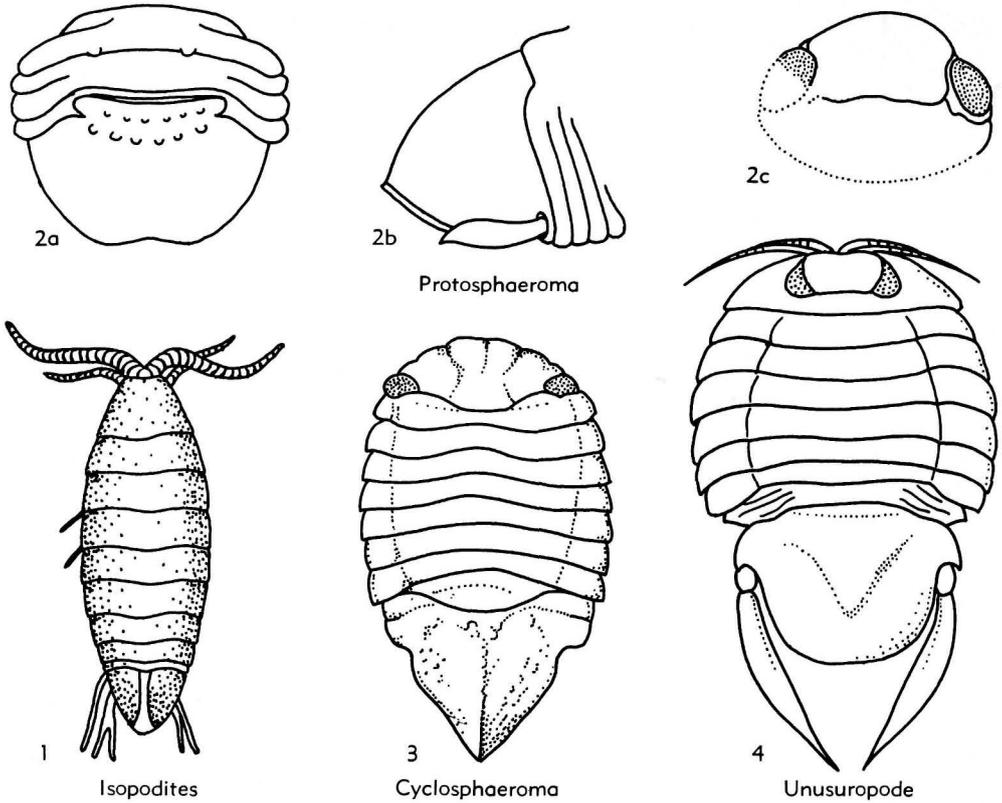


FIG. 195. Flabellifera, Sphaeromidae (p. R377-R379).

furrows except on 1st. Pleotelson triangular, pointed posteriorly, with lateral emargination for uropods; pleura of single fused pleonite defined by lateral furrows anteriorly; with strong medial ridge; pleura of anterior pleonal unit apparently obsolete, pleotelson and last pereonite coming together laterally. *Jur.*, Eng.-Czech.-Austria.—FIG. 195,3. **C. trilobatum*, Eng.; dorsal, $\times 1$ (386b).

Eosphaeroma WOODWARD, 1879, p. 346 [**E. fluviatile*; SD VAN STRAELEN, 1931] [= *Palaeoniscus* MILNE-EDWARDS, 1843]. Body broad, ovoid; cephalon small, much narrower than width of pereon, surrounded posterolaterally by 1st pereonite. Pleotelson subsemicircular, broadly rounded posteriorly; uropods biramous; rami subequal, sickle-shaped. *Oligo.*, Eng.-Fr.-Ger.—FIG. 194,2. *E. margarum* (DESMAREST), Fr.-Ger., dorsal, $\times 3.5$ (298).

Heterosphaeroma MUNIER-CHALMAS, 1872, p. 166 [**Sphaeroma priscum* MILNE-EDWARDS, 1868; OD]. Body broad; anterior pleonal unit with single pair of transverse lateral furrows; pleotelson subtriangular, strongly pointed posteriorly, with single pair of lateral furrows anteriorly; uropods apparently uniramous, broad, rounded posteriorly.

L.Eoc., Fr.—FIG. 194,3. **H. priscum* (MILNE-EDWARDS), dorsal, $\times 4$ (298).

[VAN STRAELEN (298) has misinterpreted the specimen at his disposal. His photograph (Fig. 9 of plate) shows clearly that what he called the fused 6th and 7th pereonites is actually the anterior unit of the pleon, and the part identified by him as cephalon is the 2nd pereonite; the specimen actually lacks a cephalon.]

Isopodites VON AMMON, 1882, p. 536 [**Sphaeroma triasina* PICARD, 1858; OD]. Body elongate, ovoid; cephalon relatively elongate, not surrounded posteriorly by pereonite 1; pleotelson subtriangular, with median carina; apparently no lateral emargination for uropods, which are biramous, scissors-like. *Trias.*, Ger.—FIG. 195,1. **I. triasinus* (PICARD), dorsal, $\times 4$ (373).

[VAN STRAELEN (298) has stated that this species is unrelated to the Sphaeromidae, being more like the Cymothoidae. However, the presence of only a single free pleonal unit anterior to the pleotelson is a strong argument for affinity to the Sphaeromidae.]

Pleistosphaeroma STROUHAL, 1954, p. 57 [**P. hundsheimensis*; OD]. Body strongly vaulted; 1st pereonite with posterolateral furrow which accommodates anterior edge of following pereonite during enrollment; epimeres completely fused to pereonites, rounded laterally; 3 free pleonal somites anterior to pleotelson, which is short, subtrapezoidal, and rounded posterolaterally. *Pleist.*,

Austria.—FIG. 194,4. **P. hundsheimensis*; 4a, lat., $\times 8$; 4b, pleon, dorsal, $\times 12$ (380).

Protosphaeroma BACHMAYER, 1949, p. 264 [**P. ernstbrunnense*; OD]. Body strongly vaulted; eyes well developed. Anterior pleonal unit with lateral furrows which demark fused segments that curve anteriorly at their lateral ends; pleotelson short, rounded posteriorly. *Jur.*, Czech.-Austria.—FIG. 195,2. **P. ernstbrunnense*, Austria; 2a,b, pleon, dorsal, lat., $\times 13$; 2c, cephalon, dorsal, $\times 10$ (7).

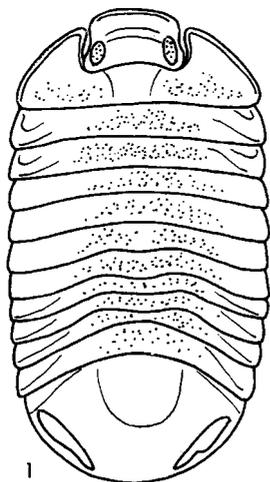
Unusuropode DUARTE & SANTOS, 1962, p. 58 [**U. castroi*; OD]. Cephalon small, set deeply back into pereionite 1; eyes large; epimeres defined on pereionites 2 to 7; anterior pleonal unit with 3 pairs of lateral sutures; pleotelson smoothly rounded posteriorly, entire, well vaulted, with strong anteromedial elevation; uropods apparently uniramous, very long, saber-like. *U.Cret.*, Brazil.—FIG. 195,4. **U. castroi*; dorsal, $\times 10$ (83).

Family ARCHAONISCIDAE Haack, 1918

Characters of type genus. *Jur.*

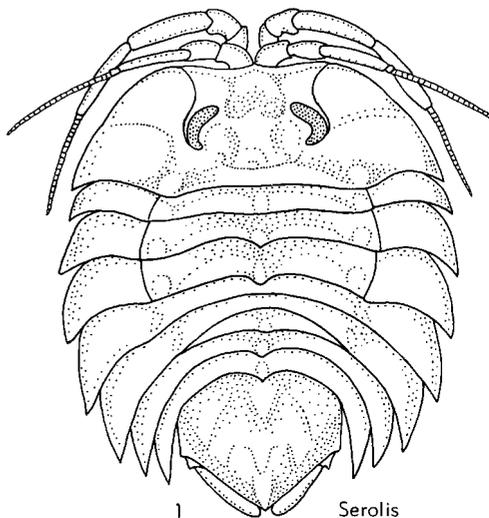
Archaeoniscus MILNE-EDWARDS, 1843, p. 328 [**A. brodiei*; OD]. Body broad, oval, only moderately vaulted; cephalon subquadrate, sunk deeply into 1st pereionite; eyes located dorsolaterally, of moderate size, prominent; 7 pereionites alike except for 1st; epimeres not defined; pleon as wide as pereion; 4 free pleonites subequal, essentially like pereionites; pleotelson large, subsemicircular. *Jur.*, Eng.-Ger.—FIG. 196,1. **A. brodiei*; dorsal, $\times 2.5$ (136).

[The broad, oval body, prominent eyes, absence of defined epimeres, and presence of only 4 free pleonites justifies placement of this monotypic genus in its own family.



1
Archaeoniscus

FIG. 196. Flabellifera, Archaeoniscidae (p. R379).



1 Serolis
FIG. 197. Flabellifera, Serolidae: *Serolis kempfi* SHEPPARD; ♂, dorsal view, $\times 3.4$ (378).

These are all features commonly occurring in the Oniscoidea, but as HAACK (136) has pointed out, the large pleotelson, well-developed antennules and form of antennae and uropods exclude *Archaeoniscus* from the latter suborder.]

Family SEROLIDAE Dana, 1852

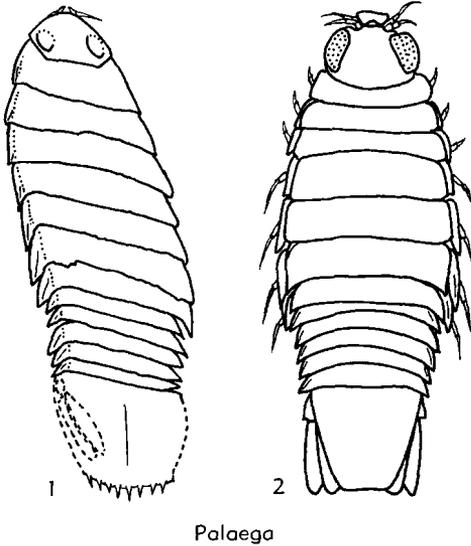
Body strongly flattened, broad; cephalon sunk deeply into first pereionite and fused to it posteriorly. Both antennules and antennae with well-defined peduncle and multiarticulate flagellum; mandible with palp; maxilliped with three-segmented palp; epimeres of pereionites extensive; tergum of last thoracomere usually absent; second pereiopod in both sexes, third pereiopod in male modified as prehensile organ; pleon composed of four units, three relatively subequal pleonites and one large pleotelson; first three pleopods natatory; fourth and fifth branchial, with outer pair of fourth forming operculum; uropod lateral, with free rami (Fig. 197). *Rec.*, S.Hemis.-N.Pac.-N.Atl.

Family UNCERTAIN

Anhelkocephalon BILL, 1914, p. 338 [**A. handlirschi*; OD]. Much like Serolidae, with number of pleonites reduced; terminal segment large, cephalon deeply embedded in 1st pereionite. *M. Trias.*, Fr.(Alsace).

[This monotypic genus is vaguely characterized and has not been figured. VAN STRAELEN (298) doubted that it should be put in the Serolidae.]

Cymatoga VON EICHWALD, 1863, p. 416 [**C. jazzy-*



Palaega

FIG. 198. Flabellifera, Family Uncertain (p. R380).

howii; OD]. Body very elongate (cephalon lacking); 7 pereonites and 6 free subequal pleonites; pleon narrower than pereon; telson large. *Cret.*, Eu.(USSR).

[This monotypic genus has not been figured. VON EICHWALD claimed that it belongs to the Cymothoidae, and therefore it may be assumed that its body is of the same general facies as seen in *Palaega*.]

Palaega WOODWARD, 1870, p. 496 [*emend.* HESSLER, herein] [**P. carteri*; OD] [= *Aegites* VON AMMON, 1882]. Body elongate, oval; eyes large (where known). Seven free pereonites (where known), not necessarily subequal; epimeres distinct on all but first; pereopods slender, ambulatory (where known); pleon not abruptly narrower than pereon, may taper posteriorly; five free pleonites subequal, with posteriorly pointed pleura; pleotelson large, commonly with median carina and rounded, posterior margin which may be denticulate; uropods biramous, lamellar. *Jur.-Plio.*, Eu.-N.Am.-Australia. —FIG. 198, 1. *P. scrobiculata* VON AMMON, U. Oligo., Austria; dorsal, $\times 0.5$ (340). —FIG. 198, 2. *P. kessleri* REIFF, L.Jur., Ger.; dorsal (reconstr.), $\times 2$ (375).

[Virtually all fossil flabelliferans having 7 free pereonites and 5 free pleonites have been included in *Palaega*. These fossils cover a range from Jurassic through Pliocene. Many of the species are based on the posterior half of the body, but in *P. kunthi* (VON AMMON) (1882), *P. scrobiculata* VON AMMON (1882), *P. maccoyi* CARTER (1899), *P. jurassica* STOLLEY (1910), *P. danica* VAN STRAELLEN (1928), *P. suevica* REIFF (1936), and *P. kessleri* REIFF (1936), the general form of the whole body is known. This body form, particularly that of pleon, is essentially the same in all and plays the major role in diagnosis of the genus. However, this very same body form is found in numerous families of modern flabelliferans (Cirolanidae, Exocorallanidae, Corallanidae, Aegidae, Cymothoidae) (251). These modern groups are discriminated mainly on the basis of appendages which are almost unknown in the fossils. Therefore, it is quite likely that *Palaega* is no more than a form genus. From the literature it appears that *Palaega*

can be divided into two groups on the basis of the cephalon. In one, characterized by *P. scrobiculata* (Fig. 198, 1), *P. kunthi*, *P. jurassica*, and *P. danica*, the cephalon is distinctly sunk back into the first pereonite. Its eyes are dorsally placed. In the other, composed of *P. maccoyi*, *P. suevica*, and *P. kessleri* (Fig. 198, 2), the cephalon is smoothly rounded and at the very most is only slightly engulfed by the 1st pereonite. Its eyes are anterolateral. In the 3 latter species the labrum protrudes strongly in front of the cephalon and where known is accompanied by a pair of scythelike mandibles. The palaegids which possess these protruding mouth parts are strongly reminiscent of the Urdidae, differing only in size of the eyes and number of pereonites. REIFF (375) has noted that the mandibles are formed as in the Exocorallanidae, but that the pleotelson differs. VAN STRAELLEN (1930) has reported a poorly preserved isopod from the Eocene of Jutland. This he placed in the vicinity of *Aega* LEACH (1815), on the basis of the pleotelson. Such an assignment makes the systematic position of this individual as vague as is that of *Palaega*.]

Suborder VALVIFERA G. O. Sars, 1882

Uropods modified to form laterally hinged opercula which fold over branchial pleopods like pair of swinging doors. Pleonites more or less fused; peduncle of antennae consisting of five segments; mouth parts normal but mandible usually without palp, and maxilliped commonly with reduced

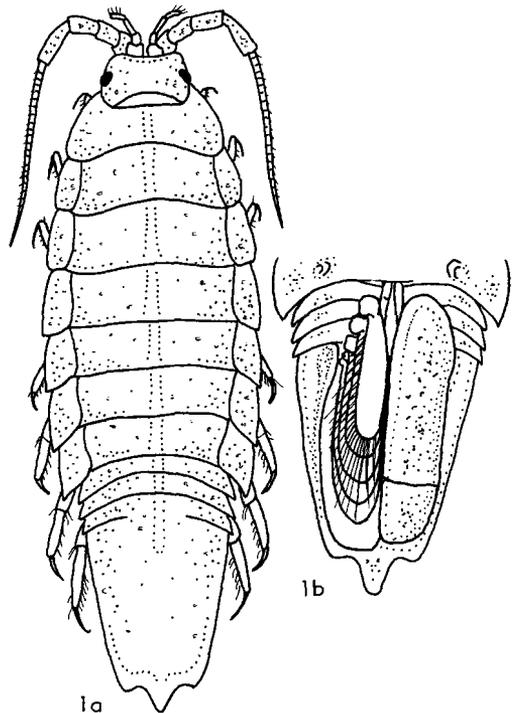


FIG. 199. Valvifera: *Idotea baltica* (PALLAS); 1a, ♂, dorsal view, $\times 1.6$; 1b, ventral surface of pleon, with uropod removed to show branchial pleopods in respiratory chamber, $\times 2$ (261b).

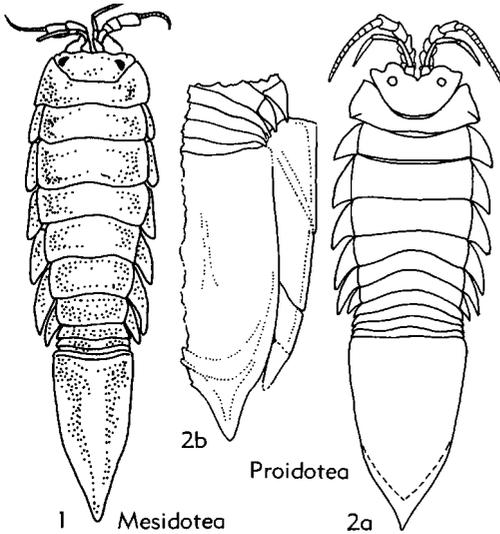


FIG. 200. Valvifera: Idotheidae (Mesidoteinae) (p. R381).

number of segments; coxae of pereopods usually developed as epimeres which are commonly fused to pereion. *Oligo.-Rec.*

Family IDOTEIDAE Leach, 1813

Body somewhat depressed. Pereionites subequal; epimeres distinct in some forms but fused to somites in others; some or all pleonites fused to form large pleotelson; antennule with uniaarticulate flagellum; antenna much longer than antennule, with multiarticulate flagellum; mandibular palp lacking; pereopods increasing in length posteriorly, first four subchelate on some forms, otherwise pereopods similar to each other (Fig. 199). *Oligo.-Rec.*

Subfamily MESIDOTEINAE Racovitza & Sevastos, 1910

[*nom. correct.* HESSLER, herein (*pro* subfamily Mesidoteini RACOVITZA & SEVASTOS, 1910)]

Anterolateral angles of cephalon produced into flattened lobes having submedial cleft; eyes dorsal. First pereionite strongly enveloping cephalon laterally; epimeres defined on all pereionites except first; pereopods distinctly dimorphic, first four subchelate, others ambulatory and longer; first three or four pleonites free; pleotelson more than 0.25 length of body; protopod of uropod at least

0.6 total length of limb, exopod present, rudimentary. *Oligo.-Rec.*

Mesidotea RICHARDSON, 1905, p. 347 [*?type sp.]. Flagellum of antennule with single segment, that of antenna multiarticulate; palp of maxilliped with five segments; pleonite four fused to pleotelson, but distinctly defined; protopod of uropod at least 0.8 total length of limb. *Pleist.-Rec.*, Holarctic-N. Atl.-NE. Pac.-Baltic-Caspian.—FIG. 200,1. *M. sabini* KRØYER, dorsal, $\times 0.7$ (359).

Proidotea RACOVITZA & SEVASTOS, 1910, p. 194 [**P. haugi*; OD]. Body elongate, tapering only slightly posteriorly; first four pleonites distinctly defined and probably free; protopod of uropod only 0.6 total length of limb. *L.Oligo.-M.Oligo.*, Romania-Pol.—FIG. 200,2. **P. haugi*; 2a, dorsal (reconstr.), $\times 2.25$; 2b, post. portion of body with uropod, dorsal, $\times 3$ (230).

Suborder ASELLOTA Latreille, 1803

Telson and last five (rarely four or six) pleonites fused into a single unit; anterior pleonites, when free, strongly reduced; one or two of more anterior pleopods forming posteriorly directed operculum over the other pleopods which are branchial in function. Various thoracomeres in some forms fused to each other or to pleotelson; peduncle of antenna consisting of six segments; mouth parts normal; coxae of pereopods small; uropods subterminal, styliform, commonly biramous (Fig. 201). *Rec.*

Suborder ONISCOIDEA Latreille, 1803

[*emend.* G. O. SARS, 1882]

Body more or less depressed; pleonites rarely fused. Antennules very small, never with more than three segments; peduncle of antennae with five segments; mouth parts normal, but mandible lacking palp and terminal portion of maxilliped reduced; coxae of pereopods expanded into epimeres which are usually not differentiated from tergites; uropods subterminal, styliform, generally biramous. Terrestrial, pleopods fitted for air-breathing. *Eoc.-Rec.*

Family TRICHONISCIDAE G. O. Sars, 1899

Cannot enroll. Cephalon without frontal line or occipital furrow; supra-antennary

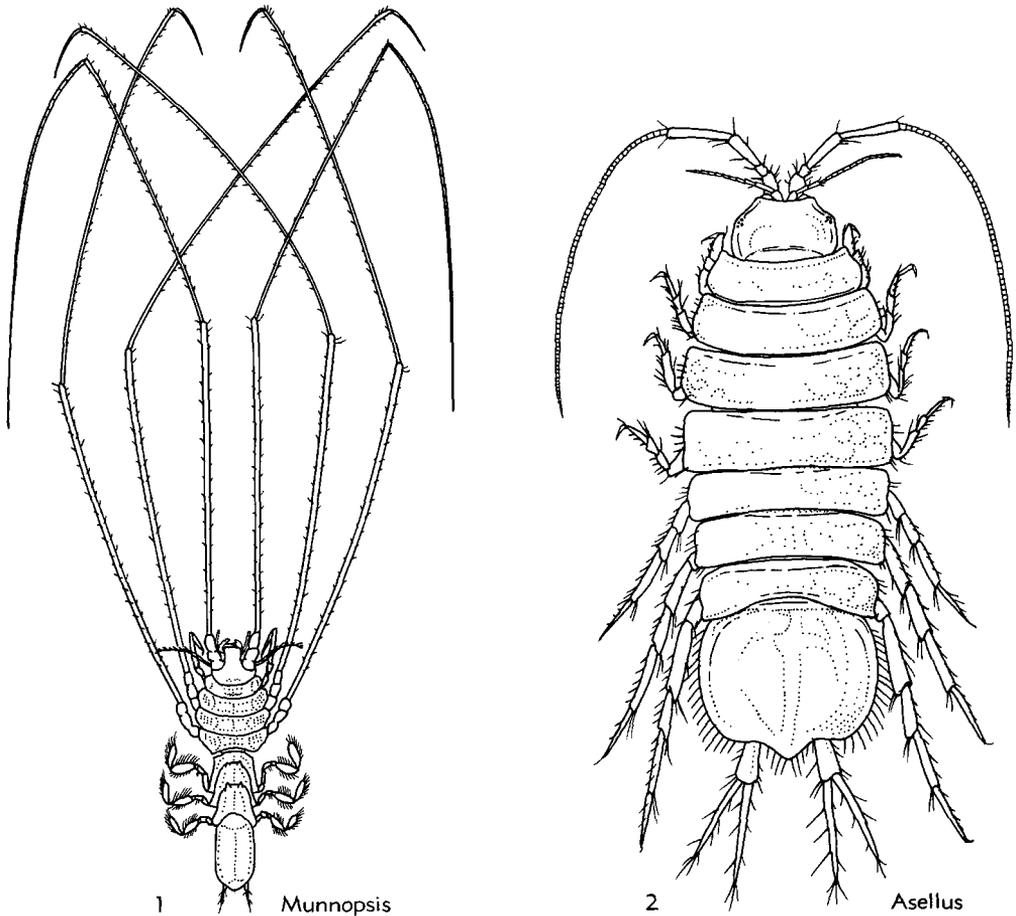


FIG. 201. Asellota: 1, *Munnopsis typica* M. Sars; ♂, dorsal view, $\times 2.7$ (261b); 2, *Asellus aquaticus* LINNÉ, ♀, dorsal view, $\times 8$ (261b).

line projecting broadly down between antennae nearly to clypeus, and also defining projecting antennary tubercles laterally; marginal line horizontal; clypeus flat, projecting strongly forward; mandible with well-developed molar process; genital apophysis unpaired, with single duct; no pseudo-trachea. *U.Eoc.-Rec.*

Subfamily TRICHONISCINAE Verhoeff, 1908

Body smooth or tuberculate, but lacking costae; pleura of pleonites short (transverse) so that pleon is abruptly narrower than pereion. *U.Eoc.-Rec.*

Trichoniscus BRANDT, 1833, p. 174 [**T. pusillus*; OD] [= *Spiloniscus* RACOVITZA, 1908]. Cuticle smooth or scaly, but not granular. Eyes triangular, with 3 ommatidia, rarely reduced. Flagellum of antennae with 3 or 4 poorly defined segments; left mandible with 2 penicilli, right with 1; pleopod 1 of male with triangular exopod lacking setae; endopod developed as 2-jointed paracopulatory organ; pleotelson with narrowly truncate tip. *U.Eoc.-Rec.*, Eu.-N.Afr.-N.Am.—FIG. 202, 3. **T. pusillus*; dorsal, $\times 11$ (261b).

Family ONISCIDAE Dana, 1852

[emend. VERHOEFF, 1918]

Cannot enroll (with rare exceptions). Eyes generally well developed; triturating

molar process of mandible replaced by brushlike setae; genital apophysis unpaired, with paired ducts and exit pores; pseudo-

trachea absent; uropod extending beyond posterior end of body; tip of pleotelson conically produced. *U.Eoc.-Rec.*

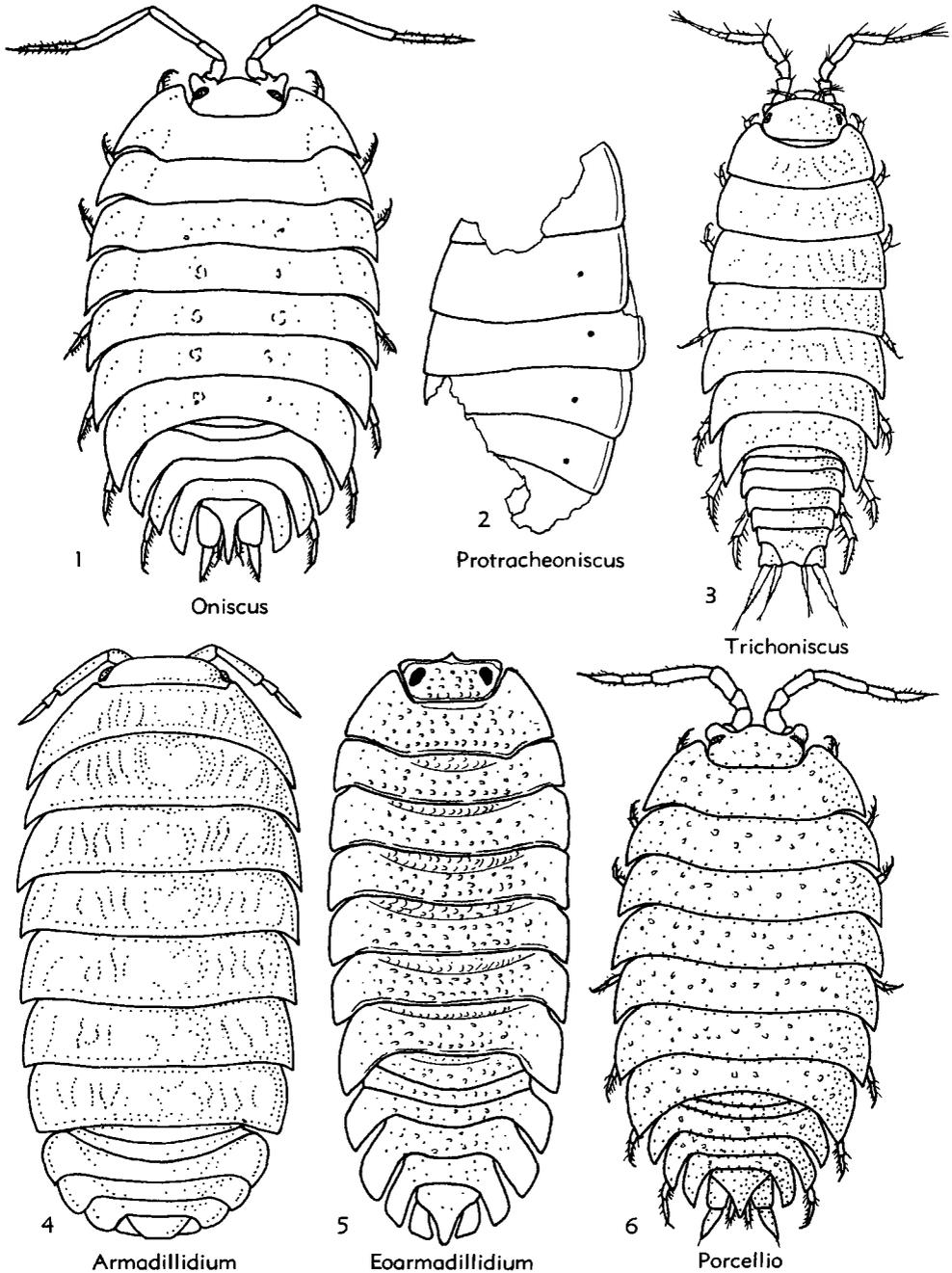


FIG. 202. Oniscoidea; Trichoniscidae (Trichoniscinae) (3); Oniscidae (Oniscinae) (1); Porcellionidae (2,6); Armadillidiidae (4-5) (p. R382-R384).

Subfamily ONISCINAE Vandel, 1952

Cephalon with strongly developed frontal line defining pair of lateral lobes and single median frontal lobe. Flagellum of antennae with three segments; glandular field on epimeres generally ovoid and reduced; pleura of pleonites large, causing outline of pleon to be continuous with that of pereion; genital apophysis simple. *U.Eoc.-Rec.*

Oniscus LINNÉ, 1758, p. 636 [**O. asellus*; SD DESMAREST, 1859]. Cephalon with indistinct supra-antennary line. Mandible with 3 to 5 penicilli; posterior margin of anterior pereionites strongly sinuous, forming acute posterolateral angles; epimeres large; articular process on pereionites 1-4; lateral edge of pleopodal exopods bearing well-differentiated respiratory region; pleotelson tapering to long narrow point. *U.Eoc.-Rec.*, Eu.—FIG. 202,1. **O. asellus*; dorsal, $\times 2.7$ (261b).

Family PORCELLIONIDAE
Verhoeff, 1918

Usually cannot enroll; where enrollment is possible, system is primitive. Flagellum of antennae with two or three segments; molar process of mandible reduced to brush-like setae; genital apophysis unpaired, with paired ducts and exit pores; pseudotrachea present; uropods extending beyond posterior end of body; tip of pleotelson conically produced. *U.Eoc.-Rec.*

Porcellio LATREILLE, 1804, p. 45 [**P. scaber*; SD ICZN Opinion 104, 1928]. Cuticular granulation distinct to absent. Cephalon without supra-antennary line; frontal line distinct, defining more or less developed median lobe and well-developed lateral lobes; eyes large; antennae long. Pleura of pleonites large, so that margin of pleon is continuous with that of pereion; pseudotrachea on exopods of pleopods 1 and 2 only; produced terminal portion of pleotelson usually distinctly defined from basal portion. *U.Eoc.-Rec.*, N.Am.-Central Am.-Eu.-N.Afr.-AsiaM.—FIG. 202,6. **P. scaber*; dorsal, $\times 3.3$ (261b).

Protracheoniscus VERHOEFF, 1917, p. 211 [**?type-sp.*]. Tergites smooth, not granulate. Cephalon without supra-antennary line; frontal line defining pair of small or medium-sized lateral lobes; median lobe not developed. Posterior margin of pereionites 1 and 2 rounded, not sinuous; all pleopodal exopods with weakly developed pseudotracheal system; exopod of pleopod 1 in male longer than wide. *?Pleist.-Rec.*, Asia-Japan-Philippines-Eu.—FIG. 202,2. *P. sp. cf. P. amoenus* KOCH, *Pleist.*, Austria; fragment of pereion, dorsal, $\times 7.5$ (380).

Family ARMADILLIDIIDAE Brandt,
1833

Median genital apophysis with paired ducts and exit pores; pseudotrachea in exopods of pleopods one and two only. Capable of complete enrollment and possessing many specializations related to this function; body very convex; cephalon enlarged transversely so that insertions of antennules and antennae widely separated; in enrollment two-jointed antennae rest against median scutellar lobe and in grooves formed by pair of lateral antennary lobes; primary marginal line almost completely obliterated in favor of secondary one; pleurepimeres fitted with specialized tongue-and-groove system; pleotelson broadly triangular or truncate; appendages generally short; uropodal exopod enlarged and flattened to fill gap between pleonite five and pleotelson. *Mio.-Rec.*

Armadillidium BRANDT, 1833, p. 184 [**Armadillo vulgare* LATREILLE, 1804; SD ICZN Opinion 104, 1928] [= *Uropodias* RICHARDSON, 1902; *Armadillo* CUVIER, 1792]. Cephalon with vertex separated from frontal region by parallel frontal and post-scutellar lines. Posterior edge of epimere of pereionite 1 rarely with horizontal cleft (schisma); uropodal endopod short, not extending beyond posterior border of telson. *Mio.-Rec.*, *Medit.-C.Eu.* —FIG. 202,4. **A. vulgare* (LATREILLE); dorsal, $\times 3.7$ (261b).

?Eoarmadillidium DOLLFUS, 1904, p. 146 [**E. granulatum*; OD]. Body moderately convex, slightly spread out laterally; cephalon with triangular median lobe. Pleotelson triangular; uropod with platelike exopod. *Pleist.*, Fr.—FIG. 202,5. **E. granulatum*; dorsal, $\times 5.4$ (354).

[This genus may not be a member of the Armadillidiidae in spite of its spatulate uropods. The flattened body and the form of the cephalon are more reminiscent of *Porcellio* than of *Armadillidium* (291).]

Suborder PHREATOICIDEA
Stebbing, 1893

Body more or less laterally flattened. Pleonal somites free, but telson fused to last somite; mouth parts normal; peduncle of antennae with five segments; second thoracopod subchelate; second to fifth thoracopods directed forward, sixth to eighth directed backward; coxae of thoracopods not expanded into epimeral plates; pleopods subequal, natatory as well as respiratory; uropod posterolateral, biramous, locomotory. *Perm.-Rec.*

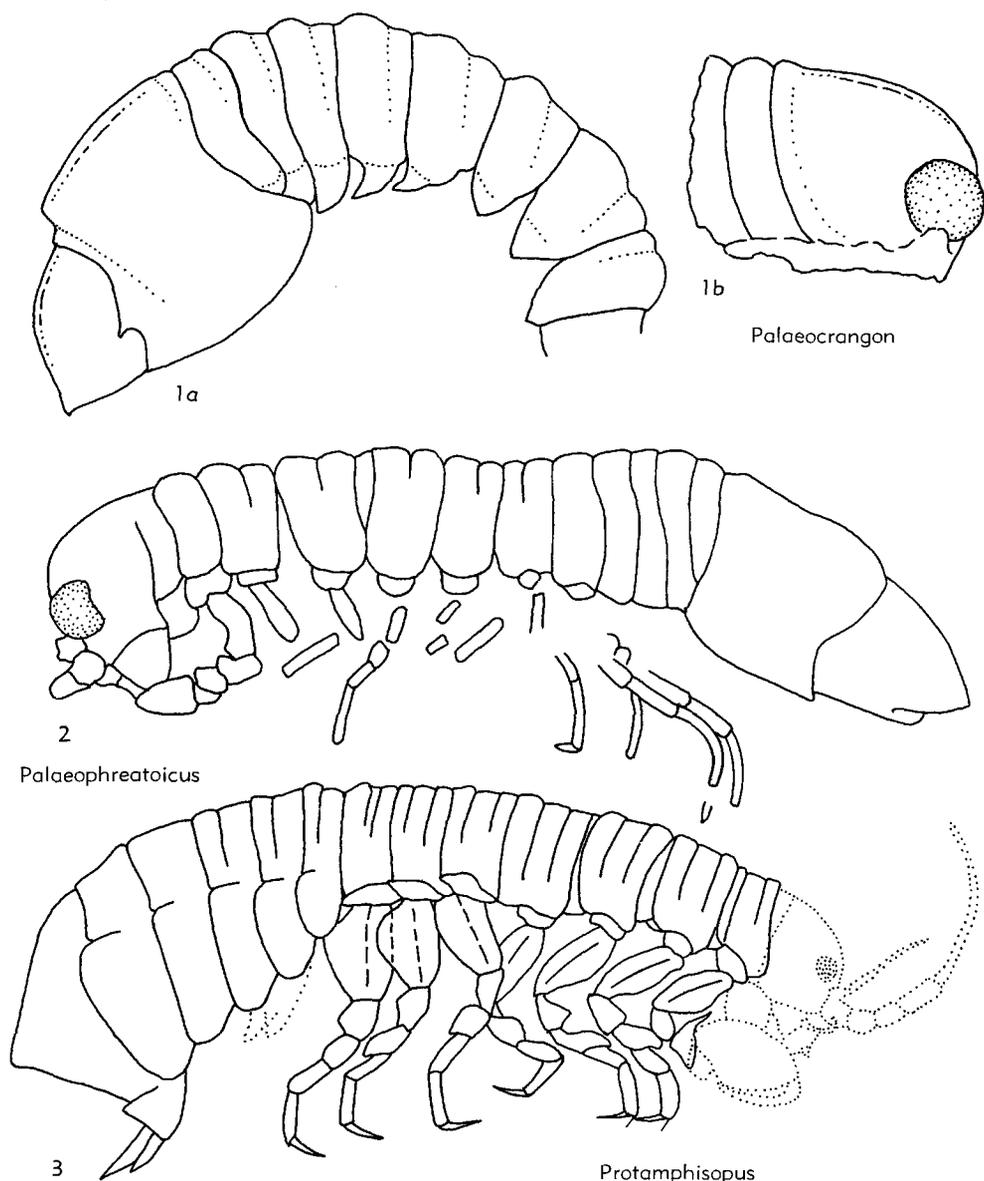
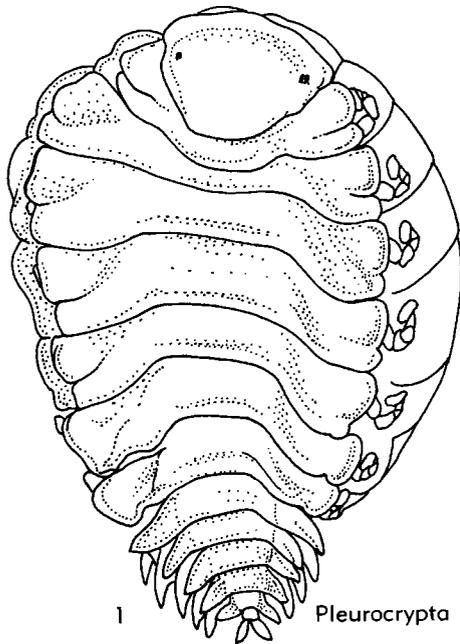


FIG. 203. Phreatoicida; Amphisopidae (3); Palaeophreatoicidae (1-2) (p. R385-R386).

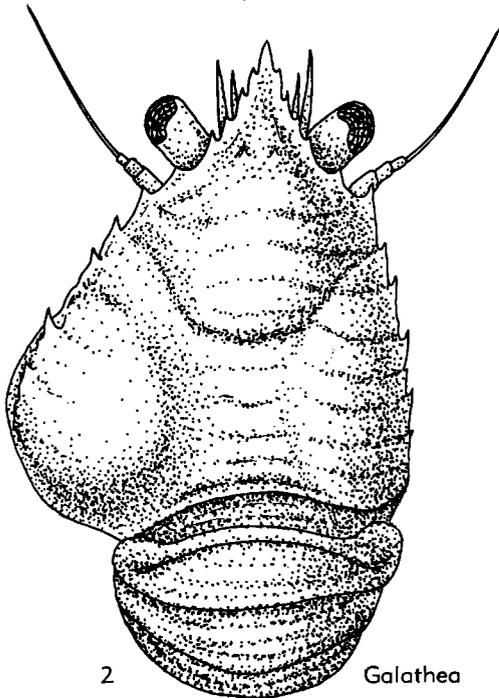
Family AMPHISOPIDAE Nicholls, 1943

Lacinia mobilis on both mandibles. Head relatively short; eyes (when present) prominent, many-faceted. Telson only slightly produced into terminal projection or not at all; coxae of pereopods generally fused with pleura; basis of more posterior pereopods usually well expanded. *Trias.-Rec.*

Protamphisopus NICHOLLS, 1943, p. 109 [*Phreatoicus wianamattensis* CHILTON, 1917; OD]. Pereionites deeper than long, some with marked transverse ridge; transition to pleon abrupt, pleonites being extremely deep; bases of at least last 5 pereopods well expanded; ischia relatively shorter than in Recent forms; merus produced strongly downward on 3rd and 4th pereopods; 3rd to 6th pereopods apparently subequal; uropod very short,



1 Pleurocrypta



2 Galathea

FIG. 204. Epicaridea: 1, *Pleurocrypta microbranchiata* G. O. Sars; ♀, dorsal view, $\times 12$ (261b); 2, dorsal view of decapod *Galathea intermedia* Lilljeborg showing left branchial cavity swollen to accommodate an individual of the epicaridean species *Pleurocrypta microbranchiata*, enlarged (261b).

with short peduncle expanded distally. *Trias.*, Australia.—FIG. 203,3. **P. wianamattensis* (CHILTON); lat. (reconstr.), $\times 2.4$ (211).

Family PALAEOPHREATOICIDAE Birshteyn, 1962

Head relatively long, with deep vertical cervical furrow; eyes very large, protruding anteriorly. First pereonite not expanded ventrolaterally; coxae of pereopods not fused to pleura; fifth pleonite extremely enlarged; pleotelson large, pointed, but telsonic projection not defined. *Perm.*

Palaeophreatoicus BIRSHTEYN, 1962, p. 66 [**P. sojanensis*; OD]. Body cylindrical; pleonites 1 to 4 shorter than pereonites, which bear transverse furrows. *U.Perm.*, Eu.(Ger.-USSR).—FIG. 203, 2. **P. sojanensis*, lat. (holotype), $\times 8$ (43).

Palaeocrangon VON SCHAUROTH, 1854, p. 560 [**Trilobites problematicus* VON SCHLOTHEIM, 1820; OD] [= *Prosoponiscus* KIRKBY, 1857 (non *Palaeocrangon* SALTER, 1861)]. Body laterally compressed, with mid-dorsal keel; pereonites and 1st 4 pleonites subequal in length; anterior pleonites with triangular pleurae. *Perm.*, Eu.(Eng.-Ger.).—FIG. 203,1. **P. problematicus* (SCHLOTHEIM); 1a, pleon and posterior portion of pereon (composite reconstr.), $\times 7.2$ (356); 1b, cephalon and 1st 2 pereonites, lat., $\times 6.4$ (362).

[The systematic position of this monotypic genus has been the subject of much disagreement. Indeed, it has been placed with the trilobites, decapods, amphipods, and isopods. Most recently GLAESSNER (1957) and BIRSHTEYN (43) have argued for phreatoicid affinities.]

Suborder EPICARIDEA Latreille, 1831

[= *Bopyroidea* RICHARDSON, 1904]

Ectoparasitic on other Crustacea (Copepoda, Ostracoda, Mysidacea, Euphausiacea, Isopoda, Amphipoda, parasitic Cirripedia, and Decapoda). Sexual dimorphism marked, female greatly modified, often asymmetrical and some lacking segmentation or appendages; male comparatively diminutive. Mouth parts suctorial and reduced or absent; thoracopods (when present) are prehensile; pleopods of adult all branchial. Development in form of regressive metamorphosis (Fig. 204). ?*U.Jur.*, *Rec.*

Adult female Epicaridea may be so specialized that in some groups they are no more than nearly formless sacs of eggs. Adult males and larvae of both sexes are more normal in form and are much like

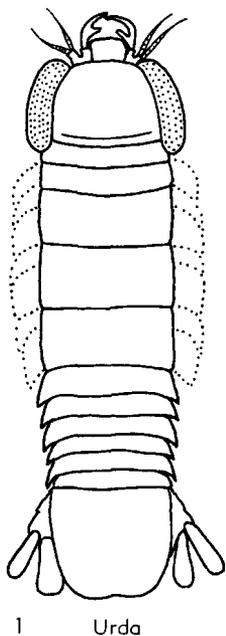


FIG. 205. Isopoda Suborder Uncertain; Urdidae (p. R387).

Flabellifera. Epicarideans exhibit a degree of host specificity. For instance, the Bopyridae are parasitic on Decapoda, and the various genera of Cryptoniscidae parasitize Ostracoda, Cirripedia, Mysidacea, Cumacea, Isopoda, or Amphipoda (337).

Where found in the branchial cavity of the host, the carapace of the latter may become asymmetrical distended to accommodate the parasite (Fig. 204,2). Such abnormally swollen carapaces have been found in a number of species of Decapoda from the Upper Jurassic and the Cretaceous of England, Germany, France, and Czechoslovakia. They are regarded as indicating the presence of epicarideans during these periods (6, 298, 314b).

Suborder UNCERTAIN

Family URDIDAE Kunth, 1870

[*nom. correct.* HESSLER, herein (*pro* Urdidae KUNTH, 1870)]

Characters of type genus. *Jur.-Cret.*

KUNTH (1870) placed this family between the Anceidae (=Gnathiidea) and Cymothoidea (Flabellifera). MONOD (205) denied

its affinity to the Gnathiidae, claiming that the missing pereionites of *Urda* are probably merely hidden from view. He included the Recent genus *Gnatholana* BARNARD (1920) in the Urdidae because it also possesses protruding mandibles and labrum, and he placed the family close to the cymothoids. MENZIES (1962) has considered the Gnathiidae to be derived from a cirolanid ancestor, with *Urda* being related to an intermediate form; *Gnatholana* was judged to be a relict that descended from this *Urda*-like ancestor.

Urda MÜNSTER, 1840, p. 21 [*emend.* HESSLER, herein] [**U. rostrata*; SD OPPEL, 1862] [= *Reckur* MÜNSTER, 1842]. Body elongate, with subparallel sides; cephalon large, not surrounded posteriorly by 1st pereionite; eyes lateral and very large, usually equal to the length of cephalon; labrum extending anterior to cephalon. Mandibles prominent, pincer-like, extending anteriorly beyond labrum; 6 pereionites; epimeres free; pleon slightly narrower than pereion, with 5 free, subequal pleonites and large, flat pleotelson; uropods biramous, lamellar. *Jur.-Cret.*, Eu. (Fr.-Ger.-Czech.).—FIG. 205,1. **U. rostrata*, dorsal, $\times 2.2$ (363).

[MÜNSTER (1840), KUNTH (1870), REMES (1912) and VAN STRALEN (298) claim that *Urda* has only 5 free pereionites. The first-mentioned three authors stated that the pleon has 6 free pleonites. STOLLEY (285) reported 6 pereionites and 5 free pleonites on *U. cretacea*, the last pereionite being smaller than the 5th and such that it might be confused as a pleonite in poorly preserved material.]

ISOPODA INCERTAE SEDIS

Two fossil isopod species, both from the Jurassic of Bavaria, which have never been figured and are too poorly described to be diagnosed are *Sphaeroma antiqua* DESMAREST (1822) and *Neosoma edwardsii* OPPEL (1865). The latter genus is monotypic.

Order AMPHIPODA Latreille, 1816

First and second thoracomeres in some fused to cephalon; no distinct carapace fold; eyes sessile, unstalked (except in Ingolfliidea). Antennules commonly biramous; antennae uniramous, with five-segmented peduncle. Thoracopods lacking exopods, some with branchiae; coxae short, but they may be expanded into plates which are more or less fused to body; first thoracopods modified as maxillipeds, next two commonly subchelate gnathopods; forms with pleon not reduced bearing pleopods with multiarticu-

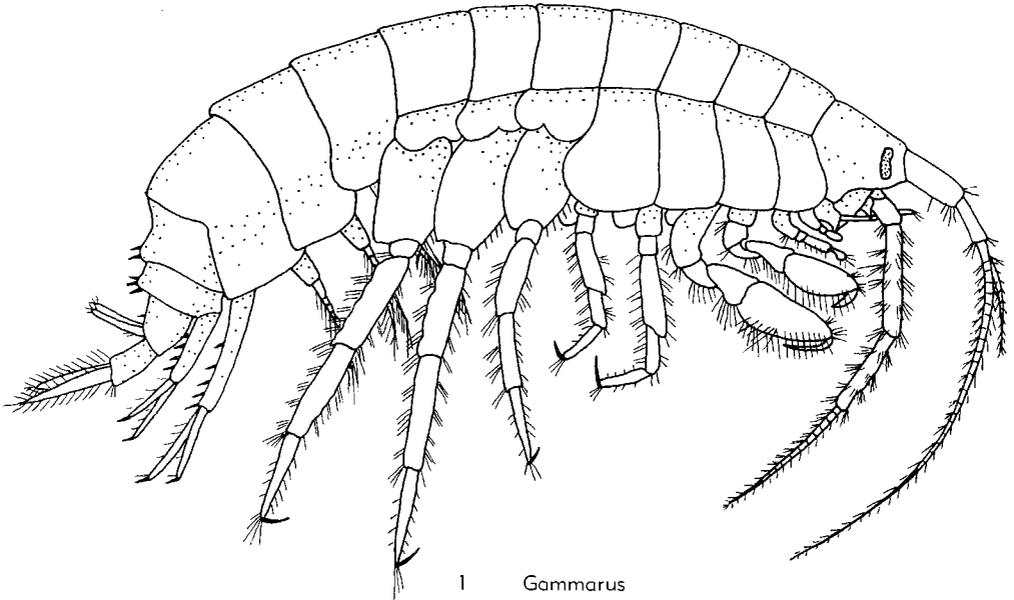


FIG. 206. Gammaridea, Gammaridae (p. R390).

late rami on first three somites and usually uropods with unsegmented rami on last three somites; telson usually not fused to last pleonite. Young leave marsupium with full number of appendages. *U.Eoc.-Rec.*

Amphipods are dominantly marine, occurring at all depths. Of the three major suborders, only the Gammaridea include freshwater and even terrestrial representatives. More than one-third of the known freshwater forms are found in Lake Baikal. Because of the long history and isolation of this lake, a small initial gammaridean stock located there is judged to have undergone extensive taxonomic differentiation, resulting in more than 290 species which live in Lake Baikal today (59).

The Hyperiidea are exclusively pelagic and commonly live a predaceous existence. Within the Caprelliidea, the Cyamidae live as ectoparasites on whales, whereas the Caprellidae are epifaunal, being found on seaweed, hydroids, and other living substrata. A few Gammaridea are truly pelagic; most are benthic, but possess the ability to swim. The majority of these benthic forms are detritus- or filter-feeders and may build a large variety of burrows or tubes in pursuit of these

ends. Gammarideans may also be epifaunal herbivores.

About 4,000 species of amphipods are known, and by far the greatest majority of these are gammarideans. This suborder is striking because, in relation to its large species composition and wide range of environments occupied, it displays a relatively small degree of morphological diversity. Thus, in the taxonomy of the Gammaridea minor structural differences play an important role, even at high taxonomic levels. This fact should be kept in mind when evaluating the placement of fossil forms in Recent genera.

Most amphipod groups are cosmopolitan in distribution but the Ingolfiellidea are as yet known only from Europe, North Atlantic, South America, Africa, and the South China Sea.

Suborder GAMMARIDEA Latreille, 1803

[=*Crevettina* CLAUS, 1880 (*pro Crevettines* MILNE-EDWARDS, 1830)]

First thoracomere only fused to cephalon; maxillipeds with palp; coxae of thoracopods two to eight usually giving rise to large

plates; body usually appearing to be laterally flattened; all pleonites well developed, free; three pairs of pleopods and three pairs of uropods well developed; eyes rarely very large. *U.Eoc.-Rec.*

Family GAMMARIDAE Leach, 1814

Body more or less slender; pleonites four to six usually well defined. Antennules and antennae generally rather slender, usually similar in both sexes; accessory flagellum of

antennule well developed in many forms but may be reduced or absent; mouth parts normal; labrum with distal border rounded, entire, or only slightly emarginate; labium with inner lobes well developed, poorly defined, or absent; mandibles with well-developed gnathic structures and three-segmented palp, second segment of palp almost never smaller than first; maxillules with both endites and palp well developed; gnathopods generally rather powerful, rarely less than subchelate; pereopods more or less slender,

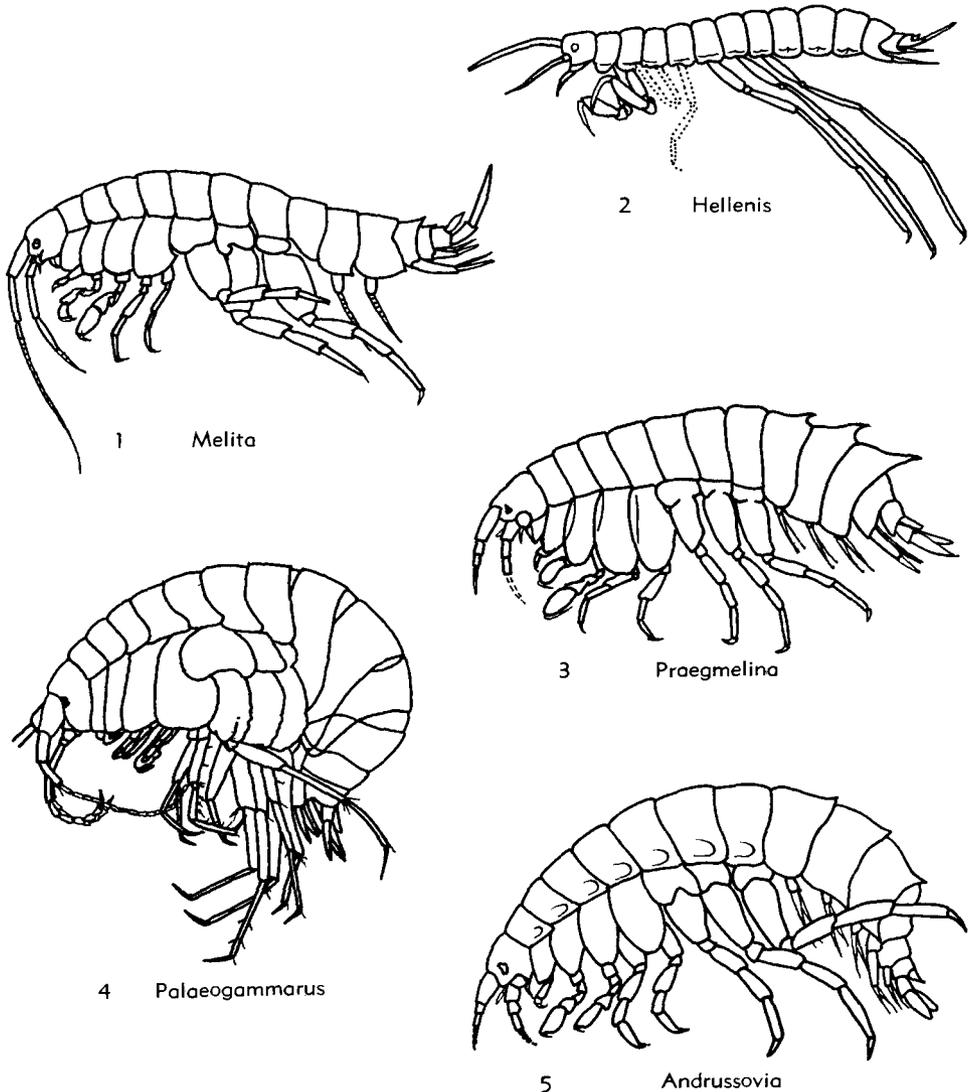


FIG. 207. Gammaridea, Gammaridae (p. R390).

few with basis little expanded in last three pereopods; pleopods only rarely uniramous; uropod 3 rarely losing one or both rami, which are often foliaceous, usually projecting beyond uropods 1 and 2; telson either entire, partially cleft, or cleft to base, in some forms sexually dimorphic. *U.Eoc.-Rec.*

Gammarus FABRICIUS, 1775, p. 418 [**Cancer pulex* LINNÉ, 1758; SD ICZN Opinion 104, 1928]. Cephalon without distinct rostrum; body lacking carinae, teeth, and tubercles; dorsal spicules in median and lateral groups on pleonites 4 to 6. Antennules usually longer than antennae but with shorter peduncle; accessory flagellum with 1 to 4 segments; basal endite of maxillules with continuous row of strong, plumose setae on inner margin; outer lobe with 10 or 11 serrate spines; tip of right palp with short thick spines, those of left palp being longer, thinner; coxal plates 1 to 4 usually deep, 4th with distinct lobe occupying distal portion of posterior border, gnathopods subchelate, 2nd usually larger than 1st, both stronger in male; 3rd uropods large, biramous; exopods with 2 segments, 2nd being short; telson deeply cleft. Branchiae simple. [Boreal-temperate-subtropical.] ?*U.Eoc.*, Rec.—FIG. 206,1. *G. locusta* (LINNÉ); lat., $\times 6$ (261a).

[None of the various reports compiled by VAN STRAELEN (299) and MAIKOVSKY (185) claiming the occurrence of *Gammarus* in the fossil record is convincing. Undoubtedly the fossils in question belong to the Gammaridea but need to be studied in far greater detail before trustworthy generic determinations can be made.]

Andrussovia DERJAVIN, 1927, p. 190 [**A. sokolovi*; SD BIRSHTEYN, 1960]. Rostrum small; 1st 3 pleonites and in one species posterior pereonites dorsally carinate; pleonites 2 and 3 with subquadrate posterolateral corners; antennules and antennae short, subequal, accessory flagellum apparently absent; gnathopods alike, subchelate; coxal plates 1 to 4 large, deep; basis of last 3 pereopods scarcely expanded; uropod 3 comparatively long, endopod well developed. *M.Mio.*, USSR (Caspian).—FIG. 207,5. **A. sokolovi*, lat., $\times 5.4$ (353).

Hellenis PETUNNIKOV, 1914, p. 153 [**H. saltatorius*; OD] [= *Prionchelius* PETUNNIKOV, 1914; *Tetrachelius* PETUNNIKOV, 1914]. B.dy slender; antennules and antennae short, antennules being longer; coxal plates 1 to 4 small, shallow; gnathopods subequal, large with proximal end of propodus slender; last 3 pereopods long, slender; uropod 2 short; uropod 3 much longer. *L.Mio.*, USSR (Caspian).—FIG. 207,2. **H. saltatorius*, lat., $\times 15$ (345).

Melita LEACH, 1814, p. 403 [**Cancer palmatus* MONTAGU, 1804; OD]. Cephalon not rostrate. Pereon smooth; pleon usually with one or more segments dorsally dentate and armed with bristles;

antennules longer, more slender than antennae, with accessory flagellum; mouth parts normal; several setae on basal endite of maxillules, 11 setae on more distal endite; 1st gnathopods small, subchelate, 2nd larger, in some species with left and right unequal in males, in some nearly chelate; 4th coxal plate largest, emarginate posteriorly; basis of last 3 pereopods well expanded, last 2 subequal, longer than others; 2nd uropod shortest; 3rd largest by far, with very large exopod and tiny endopod; telson small, deeply cleft. [МАЙКОВСКИЙ (185) has reported *M. palmata* from the Lower Oligocene of Alsace.] *L.Oligo.-Rec.*, cosmop.—FIG. 207,1. **M. palmata* (MONTAGU), *L.Oligo.*, Rec., lat., $\times 7$ (261a).

Palaeogammarus ZADDACH, 1864, p. 10 [**P. sambiensis*; OD]. Antennules longer than antennae, with thick 1st peduncular segment and accessory flagellum of 2 segments; coxal plates 1 to 4 very deep; gnathopods subequal, subchelate; propodus rounded; last pereopod shorter than preceding one; basis of last 3 pereopods expanded, oval; 4th and 5th pleonites with marginal denticles posteriorly; uropod 3 short, biramous; endopod reduced; telson deeply cleft. [According to BOUSFIELD (personal communication) this genus is much like *Crangonyx* BATE.] *U.Eoc. (Baltic amber)*.—FIG. 207,4. *P. balticus* LUCKS; lat., $\times 15$ (365).

Praegmelina DERJAVIN, 1927, p. 187 [**P. andrussovi*; SD BIRSHTEYN, 1960]. Cephalon without conspicuous rostrum; pereon with pair of low lateral ridges formed from single pair of prominences on each somite; 1st 3 pleonites dorsally carinate; 2nd and 3rd with acutely produced posterolateral corners; antennules and antennae short, subequal, accessory flagellum not obvious; mouth parts apparently normal; gnathopods subequal, subchelate, small; coxal plates large and deep; basis of last 3 pereopods not expanded; uropod 3 of moderate size with well-developed endopod. *M.Mio.*, USSR (Caspian).—FIG. 207,3. **P. andrussovi*, lat., $\times 2.5$ (353).

Suborder CAPRELLIDEA Leach, 1814

[= *Laemodipoda* LATREILLE, 1817]

First and second thoracomeres fused to cephalon; palp of maxilliped usually present; thoracopods four and five nearly always vestigial or absent; coxae of thoracopods small, commonly fused to body; pleon strongly reduced, with appendages vestigial or absent; body either slender and very elongate, or dorsoventrally flattened; eyes small. *Rec.*

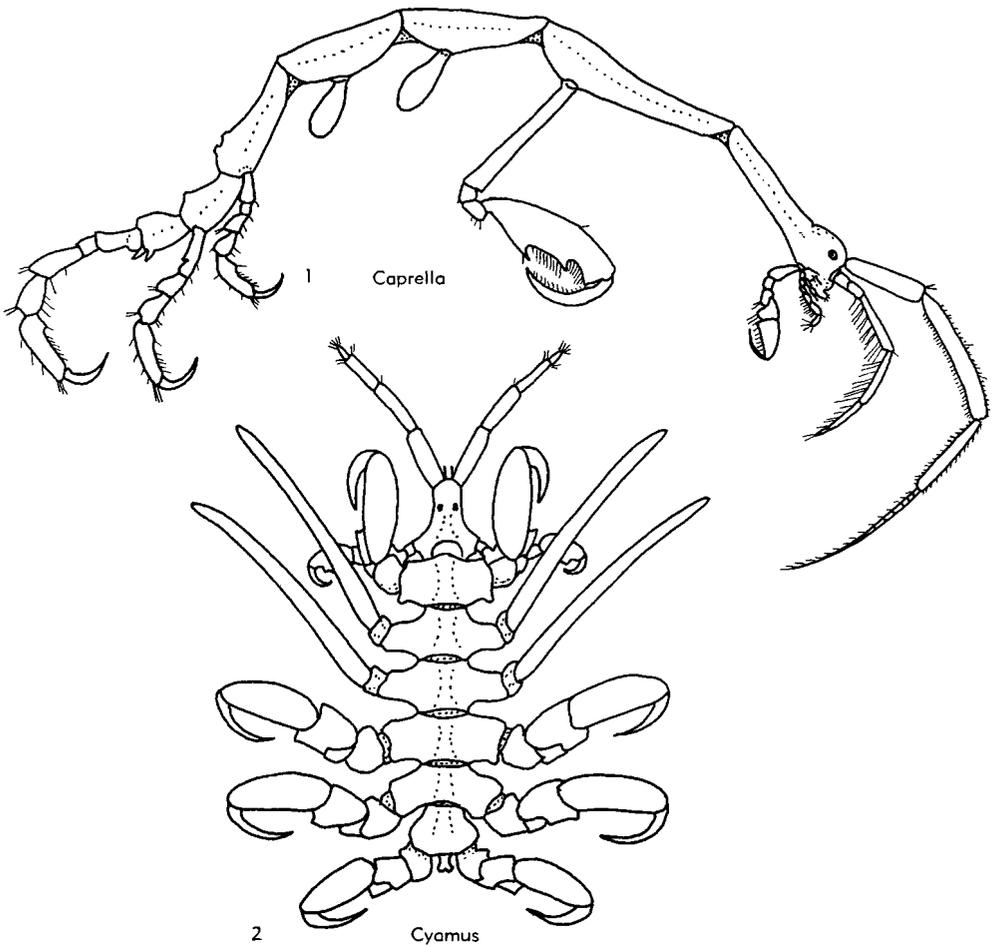


FIG. 208. Caprellidea: 1, *Caprella linearis* (LINNÉ) (Caprellidae); ♀, lat. view, $\times 5.2$ (261a); 2, *Cyamus boopis* LÜTKEN (Cyamidae); ♂, dorsal view, $\times 3$ (261a).

This suborder consists of two families, the Caprellidae DANA (1852), which are free-living forms (Fig. 208,1), and the Cyamidae WHITE (1847), which are ectoparasites on whales (Fig. 208,2).

Suborder HYPERIIDEA Latreille, 1831

First thoracomere fused to cephalon; maxilliped without palp; coxae of thoracopods two to eight small or fused to body; head usually enlarged, conspicuous; eyes generally very large, commonly covering

most of surface of head; pleon well developed; pleonites generally free with appendages well developed (Fig. 209). *Rec.*

Suborder INGOLFIELLIDEA Hansen, 1903

First thoracomere fused to cephalon; maxillipeds with palp; coxae of thoracopods two to eight small; body elongate; articulated eye lobes may occur, but without visual surfaces; pleon well developed; pleonites free; pleopods one to three and uropod three vestigial (Fig. 210). *Rec.*

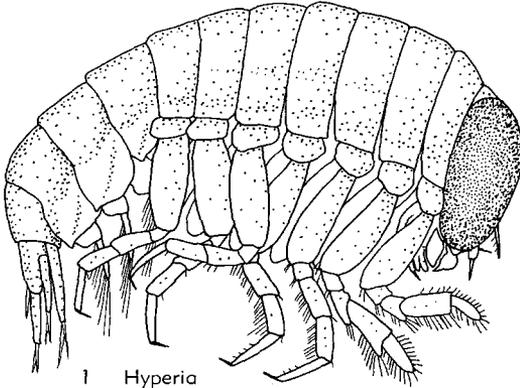


FIG. 209. Hyperiidea: *Hyperia medusarum* MÜLLER; ♀, lat. view, $\times 3.9$ (261a).

Suborder UNCERTAIN

Tracks or burrows supposed to have been made by amphipods have been reported from the Devonian (DAHMER, 1938), Triassic (RÜCKLIN, 1938), and Jurassic (PUTZER, 1938; WEISS, 1940) of Germany.

Order ANTHRACOCARIDACEA Brooks, 1962

Carapace short, covering only first two thoracomeres; sixth pleonite not fused to telson. *Miss.*

BROOKS (55), following CALMAN (1933), has placed this order tentatively in the Peracarida. The general form of its carapace and body suggests possible affinity with the Tanaidacea, Spelaeogriphacea, or Thermosbaenacea and indeed may prove eventually to belong to one of the extant orders.

Family ANTHRACOCARIDIDAE Brooks, 1962

Characters of order. *Miss.*

Anthracocaris CALMAN, 1933, p. 562 [**Palaeocaris scoticus* PEACH, 1882; OD]. Posterolateral expansions of cephalic shield defined by dorsolateral furrows, indicating probable branchial chambers; pleon not abbreviated, not clearly differentiated from pereion; telson large, styliform. *L. Carb., Scot.*—FIG. 211, 1. **A. scotica* (PEACH); dorsal, $\times 3$ (348b).

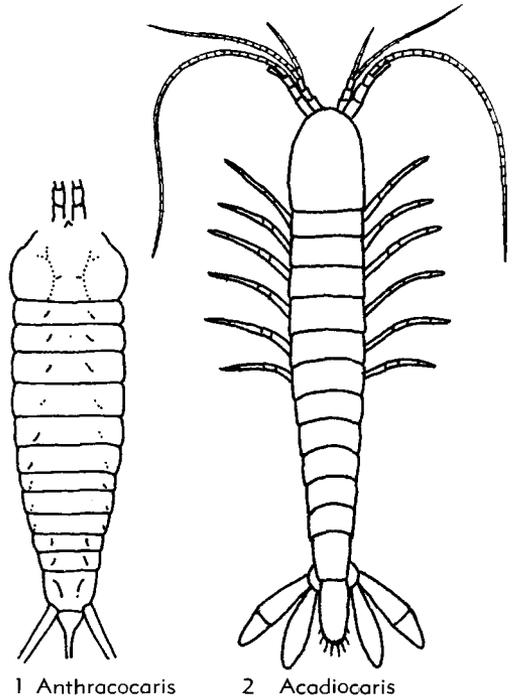


FIG. 211. Anthracocaridacea; Anthracocarididae (p. R392-R393).

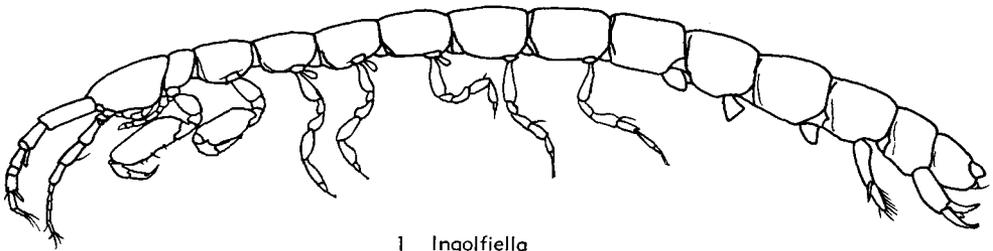


FIG. 210. Ingolfiellidea: *Ingolfiella abyss* HANSEN; lat. view, $\times 33$ (360).

Acadiocaris BROOKS, 1962, p. 273 [**Palaeocaris novascotica* COPELAND, 1957; OD]. Telson spatulate; uropods with narrow, lobate, leaflike rami. *M. Miss.*, Can.—FIG. 211,2. **A. novascotia* (COPELAND); dorsal (reconstr.), $\times 5$ (Hessler, n).

PERACARIDA INCERTAE SEDIS

A number of fossils from Europe and North America which have been referred to peracaridan orders either clearly do not belong to them or they are so fragmentary that the evidence for classifying them is insufficient (55, 299). Such fossils are: *Houghtonites* [*Mollisonia*] *gracilis* WALCOTT (1912) from the Cambrian; *Necro-*

gammarus salwayi WOODWARD (1871), from the Silurian; *Oxyuropoda ligioides* CARPENTER & SWAIN (1908), *Gitocrangon granulatus* RICHTER (1848), *Praearcturus gigas* WOODWARD (1871), and *Palaeoisopus problematicus* BROILI (1928) from the Devonian; *Camptophyllia eltringhami* GILL (1924), *Diplostylus dawsoni* SALTER (1863), and *Amphipeltis paradoxus* SALTER (1863) from the Carboniferous; *Diaphanosoma rare* BILL (1914) from the Triassic; *Mysis steinlai* GEINITZ (1843) from the Cretaceous; and *Opsipeton gracilis* HEER (1865) and *Norna lithophila* MÜNSTER (1840) from the Jurassic.

EUCARIDA

By R. C. MOORE

Superorder EUCARIDA Calman, 1904

Highly developed eumalacostracans having carapace fused dorsally with all thoracic somites, compound eyes located on movable stalks, adults without lacinia mobilis on mandibles, eggs usually attached to abdominal appendages, young typically developing with metamorphosis, free-swimming nauplius stage in primitive forms. *Permotrias-Rec.*

The Eucarida comprise the host of decapods—unnumbered kinds of shrimps, crayfishes, lobsters, and crabs—and the cos-

mopolitan oceanic nektonic crustaceans known as euphasiaceans, which are a very important food source for whales. Among decapods, the caridoid facies may be retained by adults, but the body shape and nature of appendages is greatly modified in crabs. The gills of decapods generally are developed in several series, all protected by the carapace. Three pairs of their thoracic limbs are specialized as maxillipeds. The young generally hatch at a postnauplius stage. In euphasiaceans the gills occur in a single exposed series and none of the pereopods are developed as maxillipeds. Instead, all may be specialized for filter-feeding.

EUPHAUSIACEA

By ROBERT R. HESSLER

[Woods Hole Oceanographic Institution]

ADULT MORPHOLOGY

All euphausiaceans conform to a narrowly circumscribed morphological pattern. The general body form is prawnlike (Fig. 212). The carapace, which is fused to all thoracic somites, is usually divided by a cervical furrow and terminates anteriorly in a short or moderately produced rostrum. Pleura, in contrast to those of the Decapoda, are weakly developed and do not enclose branchial chambers. They occur on all but the last of the abdominal somites.

The antennules consist of two flagella and a three-segmented peduncle. The antennae are composed of a two-segmented protopod, endopodal flagellum, and exopodal scaphocerite. The uniramous mandibles usually are provided with three-segmented palps. Their gnathal lobes lack saw bristles and lacinia mobilis. The three-segmented main body of the maxillules is produced medially into two endites and rather commonly bear a pseudoexopod laterally. The palp of maxillules is unjointed in all genera except *Bentheuphausia*, where it consists of two segments. The maxillae are composed of a three-segmented protopod,

with endites on the second and third segments, an exopod, and a palp. The palp is a single segment except in *Bentheuphausia* where it is three-segmented. Paragnaths are well developed.

All thoracic limbs are basically similar in structure (Fig. 213). Coxa and basis are distinct from each other and bear medial endites which are more strongly developed on the anterior thoracopods, but not to such a degree as to constitute gnathobases. Except where reduction has occurred, all limbs bear a leaflike, two-segmented exopod furnished with long, natatory setae. The five-segmented endopod is much larger and carries medially directed setae. Its knee occurs between the second and third segments. In all euphausiaceans except *Bentheuphausia* the eighth thoracopod is markedly reduced. The seventh thoracopod is also reduced in many members of the Euphausiidae.

Raptorial structures have been derived from the modification and elongation of the second thoracic endopod in *Thysanoessa* and *Nematoscelis*, the third thoracic endopod in *Nematobranchion* (Fig. 214) and

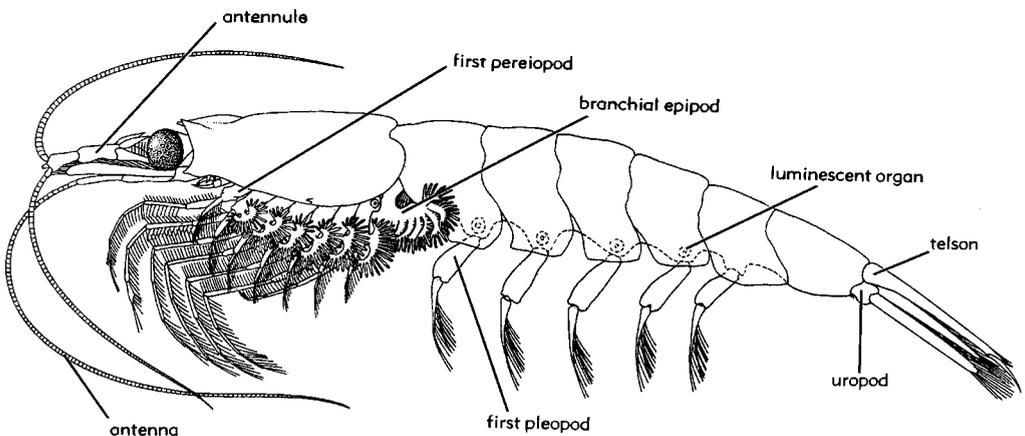


FIG. 212. Morphology of a typical euphausiid, *Meganycitiphanes norvegica* (M. Sars). Lateral view of adult, approx. $\times 7.8$ (361).

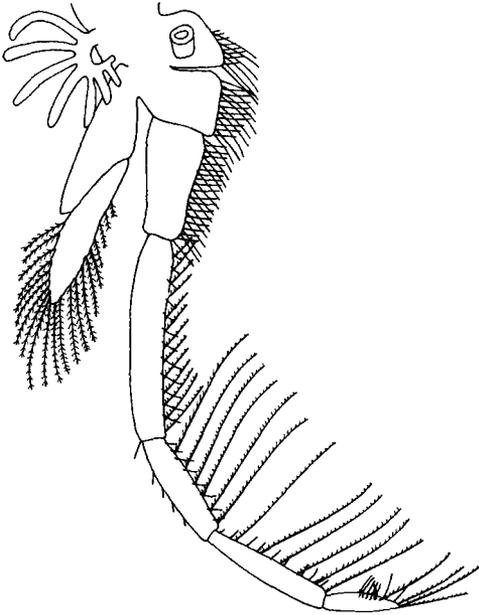


FIG. 213. Typical euphausiid second thoracopod, *Euphausia* sp. (=SARS' *E. pellucida*), $\times 25$ (377a).

Stylocheiron, and both the second and third endopods in *Tessarabrachion*.

In general, all thoracic limbs are provided with branchial epipods. The branchiae are simple on the first thoracopods, but become progressively larger and more complexly ramified posteriorly. On forms having raptorial limbs, branchiae may be absent anteriorly, but posteriorly, even when the rest of the limb is reduced or absent they remain well developed.

The pleopods consist of a two-segmented protopod and flat unjointed exopod and endopod, the latter provided with an appendix interna. In males of all genera except *Bentheuphausia* endopods of the first and second pairs of pleopods bear an additional medial lobe, the appendix masculina, which functions in copulation. The form of this structure may be quite complex, and it figures importantly in systematics of lower categories.

The uropods are composed of an unjointed protopod and two elongate, unjointed rami, except in *Bentheuphausia*, where the exopod is indistinctly two-segmented (Fig. 215).

Luminescent organs are found in all euphausiaceans except *Bentheuphausia*. They are located in stalks of the compound eyes, coxae of the second and seventh thoracopods, and sternites of the first four abdominal somites. In *Stylocheiron* many of these organs have disappeared.

The telson is provided with a pair of pointed, subapical spines (Fig. 215), which, although reminiscent of the caudal rami of the phyllocarids and many lower Crustacea, are actually enlarged marginal setae (Fig. 216).

The paired compound eyes are stalked and movable. In genera in which the second or third thoracic limb, or both of these limbs, has become modified into a raptorial structure, the visual surfaces of the compound eyes are divided into dorsoanterior and lateral portions (Fig. 214).

Euphausiaceans range in length from less than 7 mm. to almost 5 cm.

DEVELOPMENT

Euphausiacean development (Fig. 216) is divided into six smoothly intergrading stages designated as nauplius, metanauplius, calyptopis, furcilia, cyrtopia, and postlarval.

The oval, unsegmented body of the nauplius (Fig. 216,1) lacks compound eyes or mouth. Antennules, antennae, and mandibles are present, the latter two pairs being biramous and natatory.

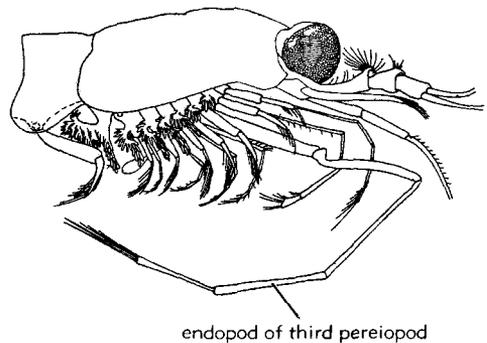


FIG. 214. *Nematobranchion boopis* (CALMAN); lateral view of anterior portion of adult, showing elongation of third pereiopod and subdivision of compound eye, approx. $\times 5.5$ (348a).

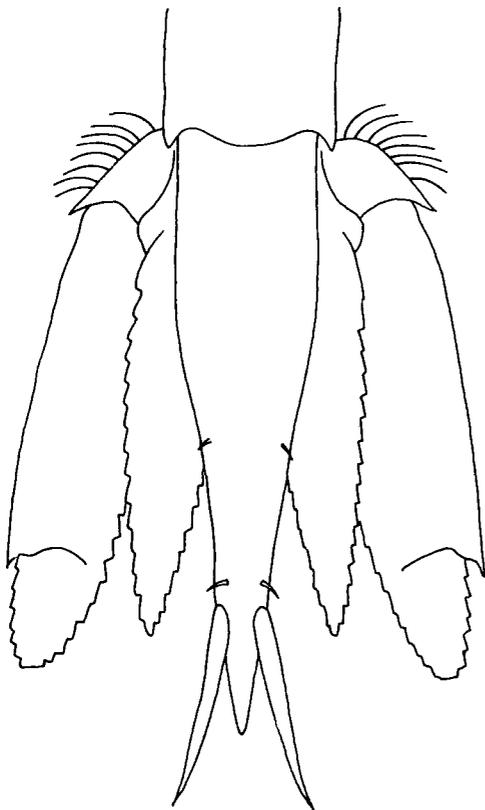


FIG. 215. *Bentheuphausia ambylops* (G. O. Sars), dorsal view of posterior end, showing uropods and telson (note paired subapical spines and compare with Fig. 216), $\times 25$ (377a).

In the metanauplius (Fig. 216,2) rudiments of the maxillules, maxillae, and first thoracopods appear, while the mandibular palp is lost.

The abdomen becomes distinct from the rest of the body in the calytopis stage (Fig. 216,3,4). Compound eyes develop, but they are immobile and covered by the newly developing carapace. The mandible, maxillules, maxillae, and first thoracopods develop further, and uropods appear.

In the furcilia stage (Fig. 216,5) the compound eyes become movable and project beyond the sides of the carapace, while the anterior thoracic limbs and the pleopods develop.

Up to this point the antennae have retained their naupliar form and natatory

function, but beginning with the cyrtopia stage they assume the basic adult morphology and no longer serve in locomotion. The posterior thoracic limbs develop.

In the postlarval stage further details of adult form are attained gradually.

MODE OF LIFE

Euphausiaceans invariably are members of the marine zooplankton, where they are second only to copepods in importance as part of the food chain. The vast majority of species are found in the open ocean, but some, particularly species of *Nyctiphanes*, *Meganyctiphanes*, and *Pseudeuphausia*, live in coastal waters. Most species occur at or near the ocean surface, and these usually exhibit diurnal migration. *Bentheuphausia*, on the other hand, is an abyssal form with vestigial eyes.

Temperature is probably the most important physical factor determining distribution. This being so, depth in the water column is as important as latitude as a distributional parameter (87).

Most euphausiaceans are filter-feeders, with detritus, algae, and copepods (? passively captured) making up the bulk of their stomach contents. Where copepods form a significant percent of the diet, such as that of *Meganyctiphanes*, active predation may occur (MACDONALD, 1927). Genera with raptorial limbs are considered to be more wholly predaceous, and with this is correlated specialized eyes and a modified or enlarged stomach (339). However, one representative of this group (*Thysanoessa raschi*) is known to feed on detritus, possibly using its elongate limbs to stir up mud.

FOSSIL RECORD

PEACH (226) has included the Carboniferous genera *Anthracophausia* and *Crangopsis* in the Euphausiacea. Most subsequent authors have not concurred, although ZIMMER & GRUNER (339) agree that *Anthracophausia* is a euphausiacean. Since PEACH clearly illustrated and described the eighth thoracic somite of *Anthracophausia* as being a complete, sclerotized ring, free from

the carapace, this genus cannot be a euphausiacean, although it may very well be related to a precursor of the order. An additional reason for the exclusion of these genera from the Euphausiacea is their possession of an unjointed sympod (55).

A tabulation of the suprageneric divisions of the Euphausiacea showing their stratigraphic occurrence and numbers of contained genera is given on page R114.

SYSTEMATIC DESCRIPTIONS

Order EUPHAUSIACEA Dana, 1852

Eucarida retaining primitive caridoid facies, no thoracopods modified as maxillipeds, all with branchial epipodites which are not covered by carapace; exopod present on thoracopods which are not reduced;

luminescent organs nearly always present. Young hatch as nauplii. *Rec.*

Family BENTHEUPHAUSIIDAE Colosi, 1917

Characters of type genus. *Rec.*

Bentheuphausia G. O. SARS, 1885, p. 108 [**Thysanopoda(?) ambylops* G. O. SARS, 1883; OD]. Eighth thoracopod reduced but with complete structure; endopods of maxillules 2-segmented, whereas those of maxillae are 3-segmented; 1st and 2nd pleopods not strongly modified for copulation; luminescent organs absent; eyes reduced. *Rec.*, cosmop.—FIG. 215. **B. ambylops* (G. O. SARS), cosmop.; telson and uropods, dorsal, $\times 25$ (377a).

Family EUPHAUSIIDAE Dana, 1850

[*nom. correct.* WILLEMES SUHM, 1875 (pro Euphausiidae DANA, 1850)]

Eighth and commonly seventh thoracopods reduced and simplified; endopods of

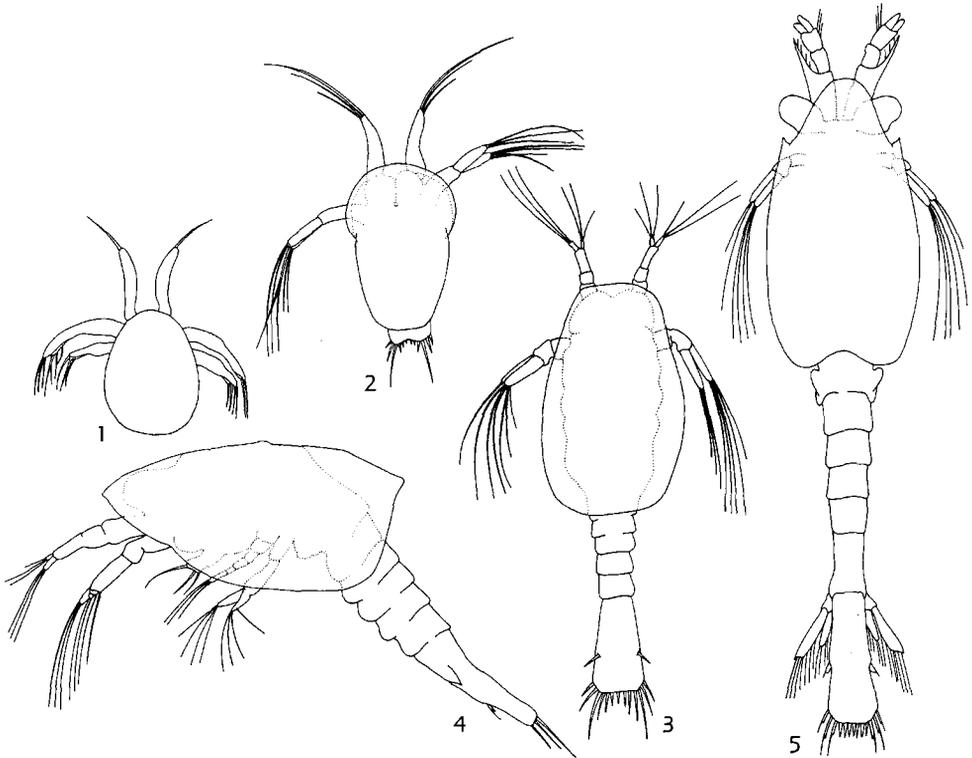


FIG. 216. Developmental stages of larval *Euphausia superba* DANA: 1, first nauplius, dors., $\times 25$; 2, metanauplius, dors., $\times 25$; 3, second calyptopis, dors., $\times 20$; 4, second calyptopis, lat., $\times 25$; 5, second furcilia, dors., $\times 35$ (97).

maxillules and maxillae unjointed; first and second pleopods of male strongly modified for copulation; luminescent organs present; eyes well developed. *Rec.*, cosmop.

Ten genera are recognized in this family, three representative ones being described and figured here.

Euphausia DANA, 1850, p. 130 [**E. superba*; SD HANSEN, 1905]. First 6 thoracopods approximately equal in length; eyes spherical; 7th and 8th thoracopods rudimentary in both sexes, forming small, unjointed, setose processes; antennular peduncle almost invariably alike in both sexes; first pleopods of male with setae on setiferous lobe of endopod. *Rec.*, cosmop. except high Arctic. —FIG. 213. *E. sp.* (= *E. pellucida* SARS, 1885; see HANSEN, 1905); 2nd thoracopod, $\times 25$ (377a).

—FIG. 216, 1-5. **E. superba* DANA, Antarctic; 1-5, developmental stages (97).

Meganyctiphanes HOLT & TATTERSALL, 1905, p. 103 [**Thysanopoda norvegica* M. SARS, 1857; OD]. Only 8th thoracopod rudimentary; 6th and 7th thoracopods with exopod in both sexes; both terminal and proximal processes of appendix masculina developed. *Rec.*, N.Atl., Medit. —FIG. 212. **M. norvegica* (M. SARS), N.Atl., Medit.; adult showing morphological features, lat., approx. $\times 5.5$ (361).

Nematobranchion CALMAN, 1905, p. 153 [**Nematodactylus boöpis* CALMAN, 1896; OD]. Third thoracopod elongate, 7th with 5 endopodal segments; full complement of luminescent organs; branchiae well developed. *Rec.*, trop.-temp. Atl.-Pac.-Ind.O. —FIG. 214. **N. boöpis* (CALMAN); anterior half of body, lat., approx. $\times 5.5$ (348a).

PART R

ARTHROPODA 4

By H. K. BROOKS, F. M. CARPENTER, M. F. GLAESSNER, GERHARD HAHN, R. R. HESSLER, R. L. HOFFMAN, L. B. HOLTHUIS, R. B. MANNING, S. M. MANTON, LAVON McCORMICK, R. C. MOORE, W. A. NEWMAN, A. R. PALMER, W. D. I. ROLFE, PAUL TASCH, †T. H. WITHERS, and V. A. ZULLO

VOLUME 2

DECAPODA

By M. F. GLAESSNER

[University of Adelaide, Australia] [The author wishes to acknowledge with gratitude the generous assistance with problems of nomenclature given by Dr. L. B. HOLTHUIS (Leiden), important information supplied by Professor L. VIA-BOADA (Barcelona), and the valuable help of Miss S. SUMMER (Adelaide) in compilation of data and preparation of the typescript.]

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INTRODUCTION

[By R. C. MOORE]

Decapods are highly organized malacostracan crustaceans having larger average size than other groups and containing the most gigantic representative of the whole superclass—the Japanese spider crab with “wing spread” of its extended limbs attaining nearly four meters. The carapace is fused to all thoracic segments, as in the subclass Eucarida generally. As the name Decapoda indicates, the order is distinguished by the presence of ten thoracic legs, which consist of the five pairs of limbs that follow the three pairs of maxillipeds (modified thoracic limbs) behind the mandibles, maxillules, and maxillae. A char-

acteristic feature of the decapods is the large exopod (scaphognathite) of the maxilla. Distinctive structures of the gills and other morphological attributes are described subsequently.

Exceptional variety of form which is found in the host of decapod crustaceans has inevitably led to numerous difficult problems in classification. These are reviewed in an appropriate chapter of the general discussion which precedes the systematic descriptions. Because reference is made in morphological descriptions to broad taxonomic assemblages (e.g., Natantia, Reptantia, Macrura) formerly adopted

for decapod groups but not recognized in *Treatise* classification, it is needful to explain the older names which are referred to but not now accepted. The Natantia (swimmers) essentially include the prawnlike or shrimplike forms belonging to the Penaeidea, Caridea, and some other decapod groups now distinguished. All natantian decapods are long-tailed forms and on this account they have been included in the Macrura (macrurous decapods or macrurans). The remaining Macrura are Reptantia (crawlers) including Astacidea (lobsters and crayfishes) and Palinura (containing spiny lobsters). The Macrura are distinguished by the development of their abdomen from the Anomura (containing

hermit crabs) and the Brachyura (short-tails). This group, which includes the host of true crabs, is recognized in *Treatise* classification. Except for historical reference, the formal names Natantia, Reptantia, and Macrura are not used in the *Treatise*.

Many fossil decapods are known, even though the remains of many are incomplete. Some species are represented by numerous beautifully preserved specimens, whereas many other species and even genera are known from unique specimens, which may be incomplete and poorly preserved. The known range of the Decapoda is from Permian to Recent. Some of the common species are useful index fossils.

MORPHOLOGY

GENERAL CHARACTERS OF SKELETON

The body of the decapod Crustacea, like that of all Eumalacostraca, consists basically of a **cephalothorax**, a segmented **abdomen**, and appendages attached to each of the body segments (**somites**) (Fig. 217). The individual somites in common practice are designated by Roman numerals (I-XIII) in sequence from front to rear.

The **carapace**, a backward extension of the head integument, takes the place of the terga of all thoracic segments, though exceptionally the last one or two may remain free. The lateral portions of the carapace overhang the sides of the thorax to form the **branchiostegite**, which encloses a **branchial chamber**. The anterior margin of the carapace may be medially produced to form a **rostrum** or a broadly truncated or downturned anterior area (**deflexed front**). This may connect medially with the antennal sternum (**epistome**), which may also come into contact anterolaterally with the carapace. The ventral integument of the posterior part of the head and of the thorax is formed by narrow or wide **sternites**, which may be fused to form a **sternal plate**. Attached to it are apodemes forming the endoskeleton. It consists of complex **endosternites** and the lateral **endopleurites**

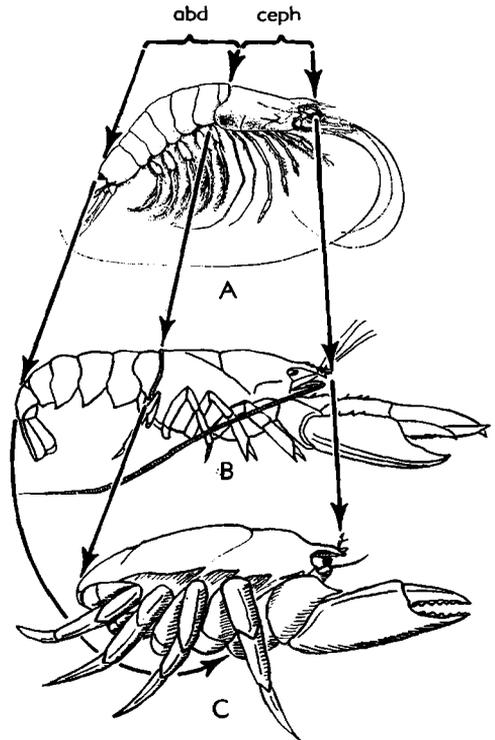


FIG. 217. Main divisions of the body in representative decapods (118).—A. *Penaeopsis*.—B. *Homarus*.—C. *Carcinus*. [EXPLANATION: *abd*, abdomen; *ceph*, cephalothorax (not to scale).]

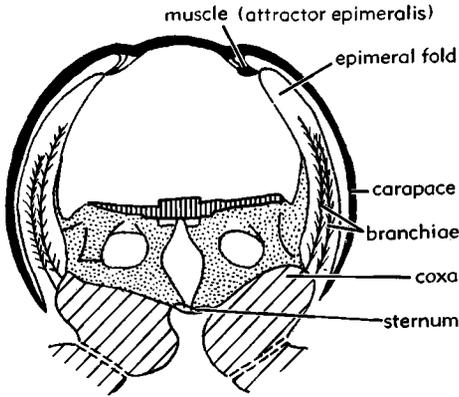


FIG. 218. Diagrammatic cross section of cephalothorax of reptantian decapod (118).

(epimera, BALSS) which connect through a steep fold (epimeral fold) with the margin of the branchiostegite, thus forming the walls and roof of the branchial chamber (Fig. 218). The posterior margin of the carapace overlaps the first somite of the abdomen and may be loosely hinged to it. Fusion of some of the six abdominal somites may occur.

CARAPACE

The carapace is the most significant part of any fossil decapod, though strongly calcified portions of appendages (e.g., chelae) are more commonly found. It deserves, therefore, more detailed study than it has received in the living Decapoda, where taxonomic characters and more significant functional differences may be observed in weakly calcified appendages and in other organs of the soft body (e.g., gills, which are not normally fossilized).

The carapace consists of an extension of the fused integument of the anterior (cephalic) part of the cephalothorax and reaches backward to the abdomen, overlapping the posterior thoracic somites which have lost their dorsal integument. It is not the product of simple fusion of the dorsal integument of all cephalic and thoracic somites. In macrurans it is basically a cylindrical tubular structure, but in many Brachyura and some Anomura it is modified to cover internal organs arranged in

more or less conical shape. In many it is shieldlike and may be weakened or variously reduced, particularly in the Paguroidea and in various burrowing Decapoda.

The carapace is marked by systems of grooves, elevated areas (regions), spines, keels, and other sculptures (Fig. 219). These were observed by early students of decapod Crustacea (DESMAREST, 1822; H. MILNE-EDWARDS, 1834), and since then with varying success many attempts have been made to establish homologies of elements of carapace sculpture and to use them in studies of phylogeny and classification. In recent years the value of such studies has been questioned with reference to extremes in closely related Brachyura (e.g., *Carpilius*, in which the carapace is almost perfectly smooth and *Zosimus*, in which the regions are extremely subdivided). The establishment of homologies in the carapace is difficult or impossible where it is weakly calcified, as in many natantian decapods. These difficulties, however, do not rule out the applicability of comparative studies on appropriate objects.

GROOVES

In Triassic and many Jurassic Decapoda the carapace shows clearly three transverse grooves, termed **cervical**, **postcervical**, and **branchiocardiac**. BOAS (1880) introduced a designation of carapace grooves by letters. A separate set of letters for natantians was later discarded in favor of that introduced for the reptantian forms, which, with modifications, is still widely used (Fig. 219). Though it is inconvenient in its employment of subscripts and lack of sequential order in morphological application of the letters, its continued use helps to keep earlier publications and illustrations readily intelligible and is preferable to introducing a new system. The letters correspond to descriptive names of carapace grooves as follows: *a*, branchiocardiac; *b*, antennar; *b*₁, hepatic; *c*, postcervical; *d*, gastroorbital (from junction of *e* and *e*₁ toward orbit); *e-e*₁, cervical; *i*, inferior.

GLAESSNER (118) and SECRETAN (267, 268) considered, simultaneously and independently, the three transverse grooves as remnants of somite boundaries (Fig. 219, 2,3). Earlier authors had recognized the

homology of $e-e_1$ with the cervical groove of other macrurans. SECRETAN interpreted the three transverse grooves as the somite boundaries II/III (=mandibular somite),

$III/IV+IV/V$ and V/VI (=1st maxilliped segment), with an inward displacement of somites IV and VII , which do not appear on the surface of the thorax. GLAESSNER

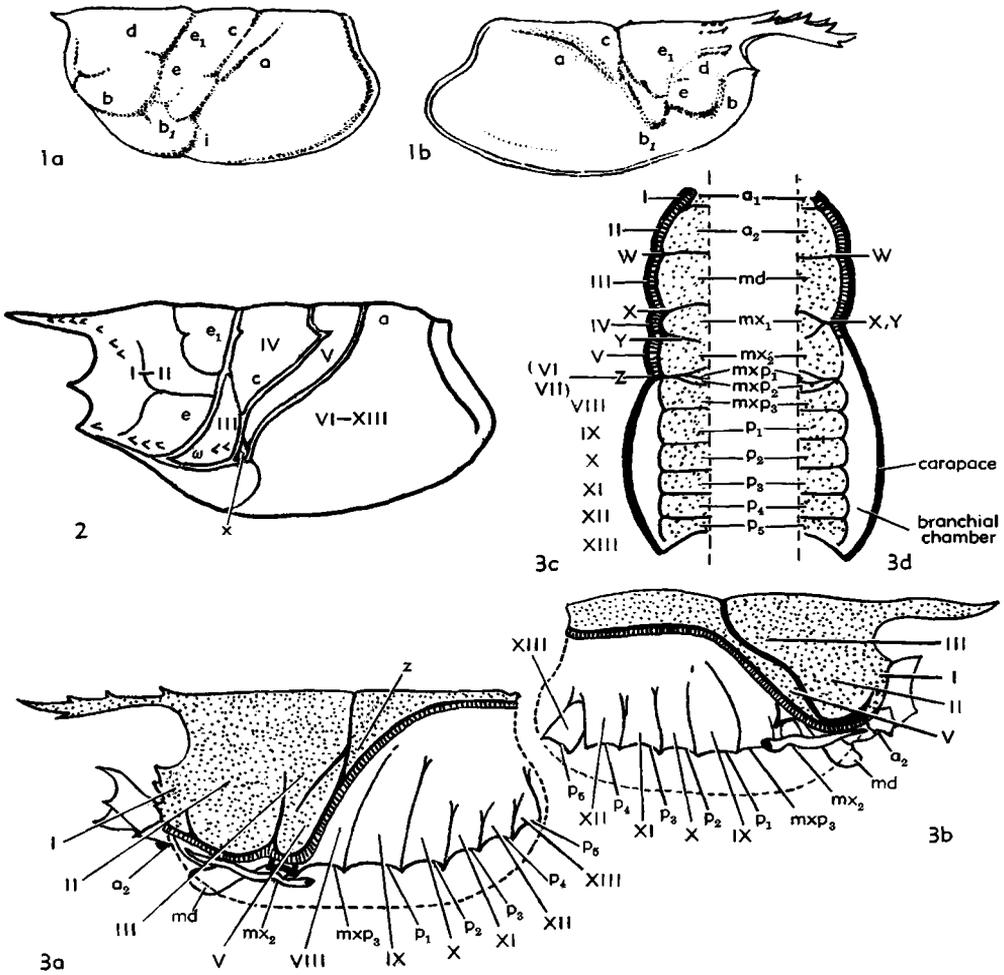


FIG. 219. Morphological features and relations of decapod carapace.

1. Carapace grooves in Nephropsidea according to BOAS & BOUVIER (51); 1a, *Klytia ventrosa* VON MEYER; 1b, *Nephrops norvegicus* (LINNÉ). [EXPLANATION: a, branchiocardiac; b, antennar; b_1 , hepatic; c, postcervical; d, gastroorbital; $e-e_1$, cervical; i, inferior.]

2. Triassic decapod carapace showing suggested correspondence of transverse grooves (double lines, lettered as in 1) with segmental boundaries (Glaessner, n). [EXPLANATION: ω , known position of mandibular external articulation; x, inferred position of attachment area of "adductor testis" muscle; somites numbered as in 3.]

3. Relation of carapace to cephalothoracic somites as interpreted by SECRETAN; 3a,b, lateral view of *Nephrops* and *Astacus* with branchiostegite removed (carapace stippled); 3c,d, diagrammatic horizontal sections of nephropsid (3c) and astacid (3d) (redrawn from Secretan, 268.) [EXPLANATION: carapace grooves—W, cervical; X-Y, postcervical; Z, branchiocardiac; somites—I, antennular (a_1); II, antennar (a_2); III, mandibular (md); IV, maxillular (mx_1); V, maxillar (mx_2); VI-VIII, maxillipedal (mxp_1 , mxp_2 , mxp_3); IX-XIII, pereopodal (p_1 - p_5); somites I and II not separately delineated in any decapod; branchiostegite covers thoracic somites VI-XIII.]

suggested that (in this numbering of somites, which is disputed) $e-e_1$ corresponds to III/III+III/IV, c to IV/V and a to V/VI, the tergal part of the mandibular somite being displaced downward rather than inward. The grooves are not boundaries of muscle attachments, nor do they serve for the attachment of membranes, but groove a corresponds to the boundary of the branchial chamber. The part of the carapace

posterolaterally from this groove is the branchiostegite. Groove i separates it in many Decapoda from the convex anterior portion of the branchial chamber, of which $b-b_1$ is the upper margin. This basic system of grooves is also recognizable in many Penaeidea (296). It is modified in many Caridea by the disappearance of c and in reptant decapods by the reduction of either c or e_1 , in which case the postcervical groove

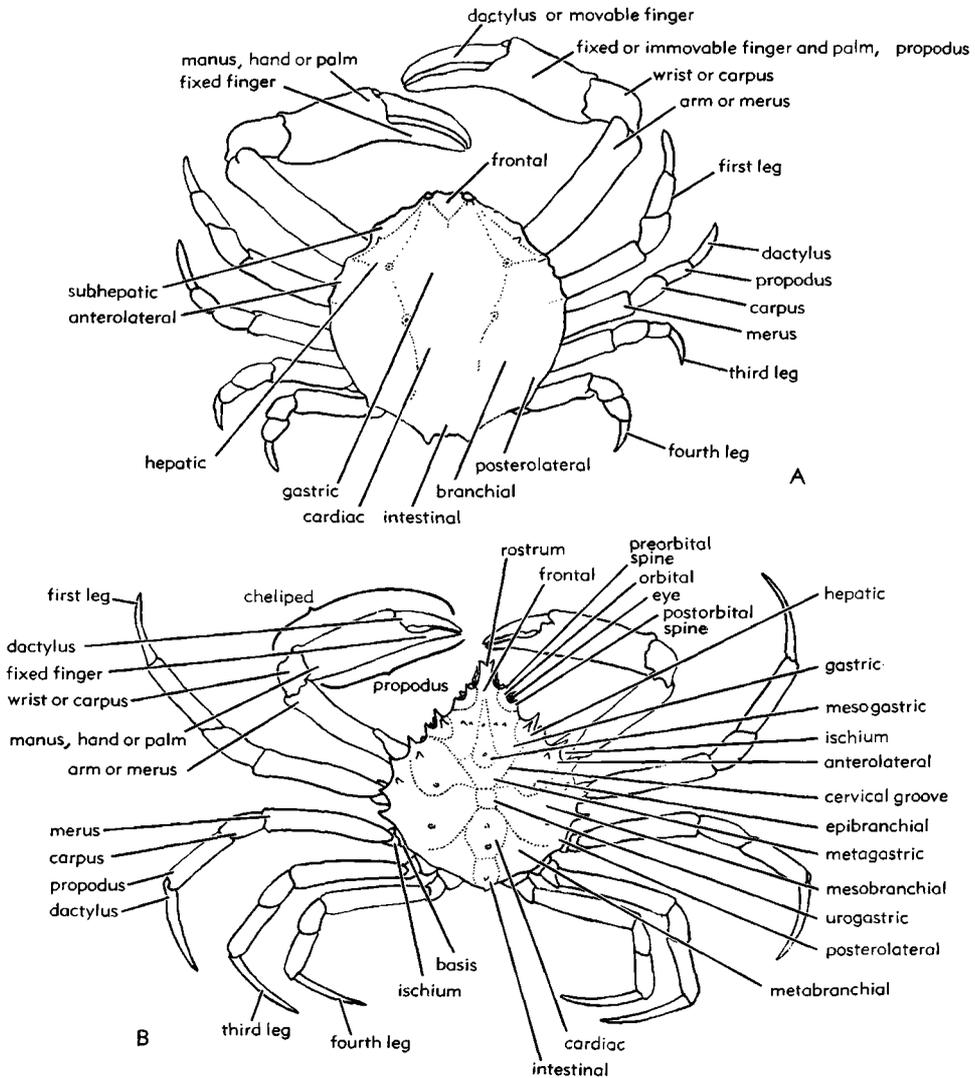


FIG. 220. Descriptive terminology of carapace regions and legs in crabs (redrawn from Rathbun, 234, 237, 243, 245).—A. Oxystomata (Leucosiidae).—B. Oxyrhyncha (Majidae).—C. Brachyrhyncha (Portunidae).—D. Brachyrhyncha (Grapsidae).

takes the place and appearance of the cervical groove in dorsal aspect—a fact misinterpreted by BOUVIER (51) and later by VAN STRAELEN but correctly noted by BOAS (44) and later by BOUVIER (52) and others. In the greatly modified carapace of the Brachyura, *a* and *e-e₁* are present in the Dromiacea, but groove *a* undergoes a progressive reduction in other crabs.

REGIONS

The terminology of the regions of the carapace, unlike that of the transverse grooves, is descriptive or topographic, without necessarily implying homology of the parts described or indicating the position of internal organs from which the names were taken. In the macrurans it is generally sufficient to distinguish anterior and

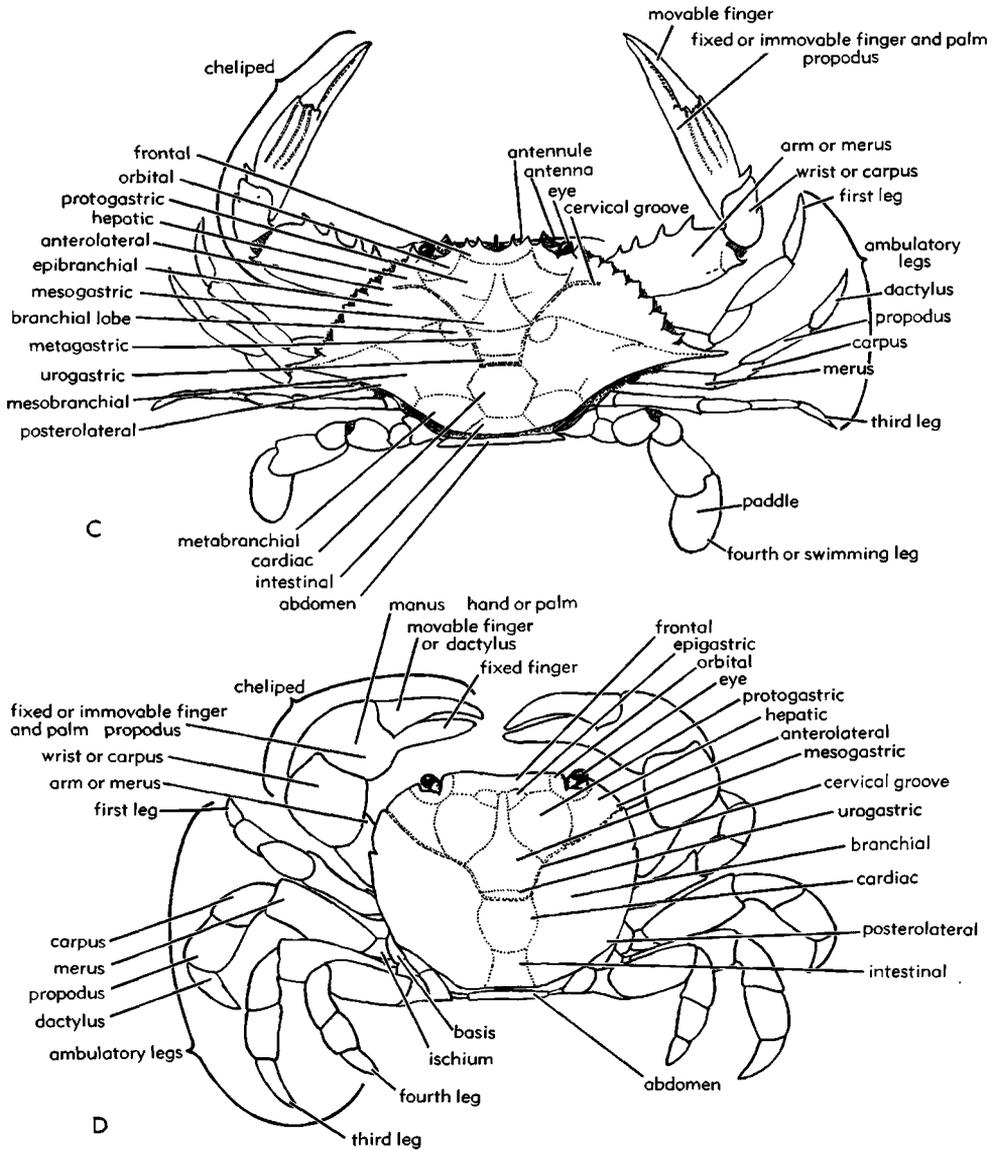


FIG. 220 (continued). See facing page.

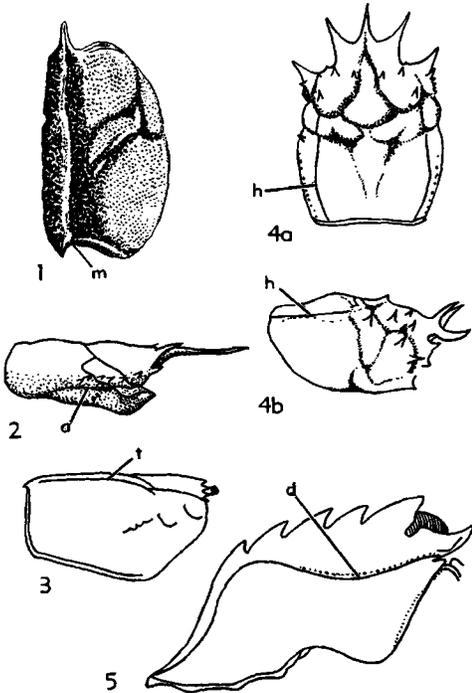


FIG. 221. Positions of lineae on decapod carapace.—1. *Klytia ventrosa* VON MEYER (*m*, median line).—2. *Munida bamfia* PENNANT (*a*, linea anomurica).—3. *Thalassinia anomala* (HERBST) (*t*, linea thalassinica).—4. *Paromola cuvieri* (Risso); 4*a*, *b*, dorsal and lateral views (*h*, linea homolica).—5. *Macropipus vernalis* (Risso) (*d*, linea dromica = pleural suture) (1, after Oppel, 219; 2-5, after Bouvier, 52).

posterior regions of the carapace, separated by the cervical groove, or in its absence by the postcervical groove, and in the posterior region the dorsal notum from the lateral branchiostegites. A median, usually pointed, anterior projection of the carapace is the rostrum. The posterior margin of the carapace may show a prominent rim delimited by a furrow (**marginal groove**). In many Brachyura the carapace is sculptured into a characteristic pattern of raised areas delimited by smooth grooves. Where these are more highly developed, in an anastomosing pattern, the regions are considered as divided into areoles, to which DANA applied index letters and numbers for descriptive reference. In most crabs a simpler descriptive terminology suffices (Fig. 220). Anteriorly to the cervical groove, the medial

gastric region is distinguished from the frontal region and the anterolaterally placed orbital and hepatic regions. A median triangular area is referred to as **mesogastric** and behind it is the **metagastric area**, bordered laterally by the **protogastric area** and (close to the tip of the mesogastric tongue) the **epigastric area**. Behind the cervical groove are, medially, the **urogastric, cardiac,** and **intestinal regions** and laterally the **branchial regions** divided into **epi-, meso-,** and **metabranial areas** situated between the anterolateral and posterior margins. Not all of these regions and areas (or subregions) are necessarily delimited. The position of the topographic regions is not fixed in relation to the branchiocardiac grooves. The grooves laterally delimiting the cardiac region and in many decapods also uro- and metagastric regions may be described as **lateral gastrocardiac**. An important evolutionary novelty in the carapace of some advanced macrurans and in many Brachyura is the acquisition of a **lateral margin**. The parts of the carapace placed ventrally from this margin are known, in accordance with the position of the corresponding dorsal regions, as **subbranchial, subhepatic,** and **suborbital**. These ventral regions commonly are delimited medially by a pleural suture (see below) from the **pterygostomial regions** on both sides of the buccal cavity.

A small, smooth protuberance on the carapace of many macrurans was observed by BOAS below the junction of grooves *e*, *b*, and *b*₁. He designated it as *ω*. It covers the external articulation of the mandible on its endosternum and is a valuable pointer to the homologies of carapace grooves.

LINEAE

In the living *Homarus* the mid-line of the carapace is weakly calcified and the carapace splits along this line in molting (Fig. 221). This is found also in fossil Astacidea. In the Thalassinioidea a longitudinal uncalcified line extends on each side from below the orbital notch on the anterior end to the posterior margin. It was named **linea thalassinica** by BOAS (44). A line in a similar position is found in a

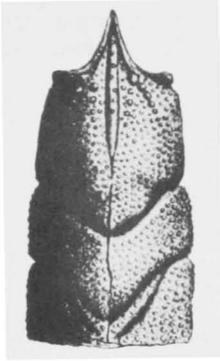


FIG. 222. Dorsal plate of *Klytia greppini* (OPPEL), M. Jur., Ger. (after Oppel, 219).

few living species of Penaeidae (*Parapenaeus*), Palaemonidae, and possibly Crangonidae. This is not, as BALSS surmised, a rudimentary boundary between notum and pleuron, as the lateral portions of the carapace are not homologous to pleura in the abdomen and in other arthropods.

The *linea thalassinica* may be comparable to the *linea anomurica* in Paguroidea, Galatheoidea (where it lies below the lateral margin), and Hippoidea; to the *linea homolica* in the Homolidae (above the lateral margin); and to the *linea dromica*, which is the name given in the Dromiidae to the **pleural suture**. This suture is found in all Brachyura. It opens and separates the pterygostomial regions from the rest of the carapace in molting. Possible homologies between these lines (which would exclude homologies between lateral margins) have been suggested by some and disputed by other authors. Some, if not all, lineae facilitate molting and are therefore comparable to facial sutures of trilobites, suggesting a reappearance of a latent character wherever calcification of the integument becomes strong enough to require it. It needs further investigation also in relation to the occurrence of transverse uncalcified sutures in Thalassinoidea and Paguroidea.

DORSAL PLATE

A spindle-shaped plate is intercalated in the median suture of the Erymidae, but not in other Astacidea (Fig. 222). VAN STRAELEN has noted a possible relation of this carapace element to the **dorsal organ** which

appears in Penaeidae, Sergestidae, and Caridea as a depression or projection in a similar position. It was considered by HANSEN as corresponding to the embryonic dorsal organ which may be concerned in the molting process.

RIDGES AND SPINES

In some natantian decapods the carapace bears strong longitudinal ridges. A median dorsal keel commonly continues backward from the rostrum. Lateral ridges are named after the adjoining regions of the carapace: gastroorbital or suborbital, antennal, hepatic, branchiocardiac. A sharp lateral margin develops in Eryonoidea, Scyllaridae, Anomura, and in most Brachyura. In the Leucosiidae a secondary anterolateral margin is situated below the pleural suture; the primary lateral margin is here named hepatic in its anterior part and branchial in its posterior part. The anterior margin in many forms is lobate, dentate, or spinose. Stridulating ridges are known on the anteroventral side but have not been described in fossils. The pterygostomial region may be modified by grooves facilitating the flow of water for respiration.

Spines on the anterior part of the carapace have an important function in protecting the eyes and antennules. They may occur on the upper and lower edges of the rostrum and in characteristic supraorbital, suborbital, and antennar positions. In the Brachyura, the first anterolateral spine or tooth is also extraorbital, and in Oxyrhyncha the development of supraorbital (supraocular) spines may be taxonomically important. Spines and tubercles on the dorsal surface of crabs vary greatly in position and are named after the regions. Transverse granulated ridges on the carapace of Portunidae are taxonomically important and are similarly named after the regions on which they occur. The carapace of Galatheididae shows such distinctive transverse ridging that even fragments can be correctly assigned to this family.

MUSCLE IMPRESSIONS AND APODEMAL PITS

Muscle attachment areas may be recognizable on the surface of the carapace as

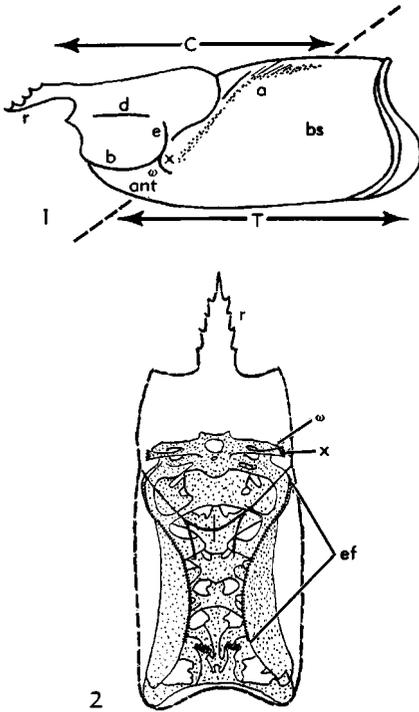


FIG. 223. Relations of carapace and internal skeleton in the lobster (*Homarus vulgaris*) (after Glaessner, 118).—1. Carapace, lateral view.—2. Diagrammatic dorsal view of internal skeleton (outline of carapace shown by broken lines). [EXPLANATION: C, cephalic portion; T, thoracic portion; ant, anterior chamber; bs, branchiostegite; ef, epimeral fold (dorsal edge, attractor epimeralis muscle attachment cross hatched); r, rostrum; other letters as in Fig. 219.]

reticulated or striated areas, but they are more pronounced on internal molds. They deserve more detailed comparative study than they have received in Recent or fossil Decapoda. The most important muscle insertion on the carapace is that of the **attractor epimeralis** muscle (tergoepimeral muscle) which follows the branchiocardiac groove, and leads to the top of the epimeral fold (Fig. 223). The transformation of the cylindrical cephalothorax of the macruran decapods to its conical shape in the brachyurans leads to the shifting forward of the posterior end of this muscle insertion, so that in the Dromiidae it is V-shaped on both sides of the cardiac region. After the loss of the branchiocardiac groove which it follows originally, only the inner arms

of the V remain, forming conspicuous **lateral gastrocardiac markings** (Fig. 224) in most Brachyura (2, 50).

Attachment areas of the stomach muscles are commonly conspicuous but less significant, as the muscles tend to divide into fiber bundles which can vary in position relative to the cervical groove and regions. A pair of these fiber bundles are attached to calcareous apodemes close to the midline of the carapace which are marked on the dorsal side by two small **posterior gastric pits** (Fig. 225).

Muscles moving the mandibles and maxillae are also attached to the inner dorsal and ventral surfaces of the carapace but are mostly not conspicuous. A muscle or tendon connecting the head apodeme with the dorsal side of the carapace (anterior to the large adductor mandibulae) was described in *Astacus* by SCHMIDT as *musculus dorsoventralis anterior* and is also known in natantian decapods. GROBBEN recognized it as the *tensor dorsoventralis maxillaris*. Of greater importance for homology problems is the muscle named *dorsoventralis posterior* by SCHMIDT in *Astacus*. It connects the head apodeme horizontally with the internal

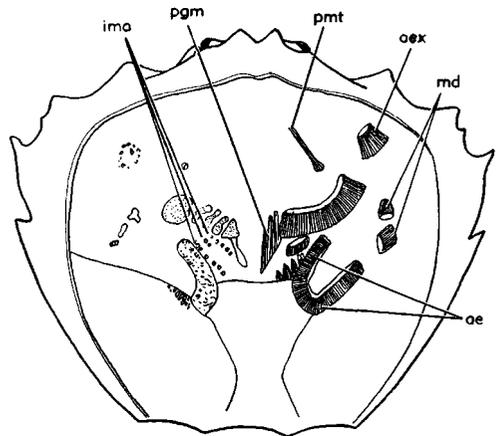


FIG. 224. Carapace of *Dromia personata* (LINNÉ) (middle part drawn as seen from inside, muscle attachments shown in left half, cut muscle in right half) (mod. after Abrahamczik-Scanzoni, 2). [EXPLANATION: ae, attractor epimeralis muscle; aex, antennar extensor muscle; ima, internal mandible adductor muscle; md, median dorsoventral muscle (attached to roof of branchial chamber); pgm, posterior gastric muscles (median part attached to apodeme); pmt, posterior mandible tendon.]

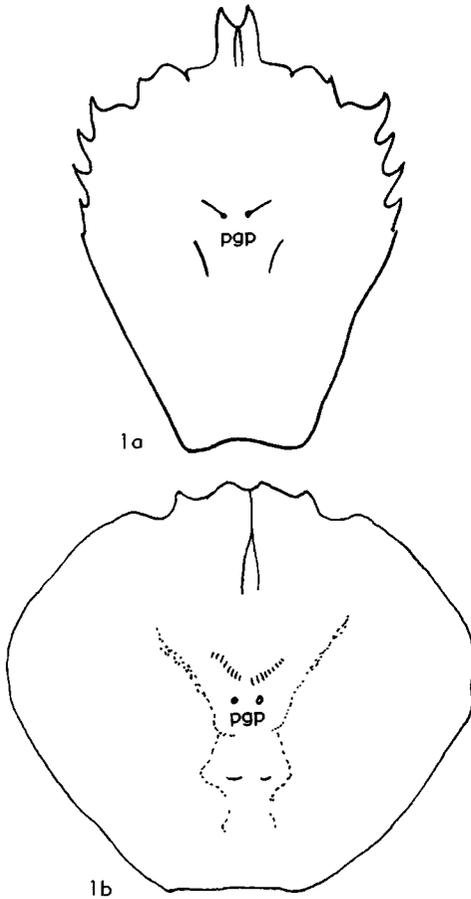


FIG. 225. Dorsal views of carapaces of (1a) *Noto-pocorystes (Cretacorantina) friischi* GLAESSNER and (1b) *Zanthopsis bittneri* LÖRENTHEY showing posterior gastric pits (*pgp*) (109, 184).

carapace surface (Fig. 226), where it is inserted just behind the cervical groove (but in *Astacus* groove *e* fuses with *c*). According to BALSS it is innervated from the maxillary ganglion. GROBBEN (127) recognized the homology of this muscle with the adductor testis in lower Malacostraca. It is also known in the Anomura and Brachyura, where (in *Eriphia*) ABRAHAMCZIK-SCANZONI (2) recognized it as the tensor of the roof of the branchial chamber occupying the same position when the head apodeme of *Astacus* is equated with the endopleurites of body segments 4 and 5 (maxillula and maxilla somites). Its attachment to the carapace lies in *Eriphia* in the ventral extension of

the cervical groove (Fig. 226). In *Homarus* and *Nephrops* it is attached behind the knob ω and thus lies anterior to groove *b*₁, the lateral end of the postcervical groove (Fig. 223). On this basis an attempt was made to establish the homology of this attachment area in relation to transverse carapace grooves in fossil reptantian decapods (118) (Fig. 227).

Some of the strong abductor and adductor muscles of the mandibles are attached to the carapace, the abductor minor and adductor lateralis laterally and the adductor posterior on the dorsal side, lateral from the stomach in Astacidea and on the meta-gastric region in Brachyura (Fig. 226). How large and conspicuous their impressions on the carapace are depends more on division of the muscles into bundles, which can be quite small, than on size of the entire muscle.

INTERNAL AND VENTRAL SKELETON

The internal (endophragmal) skeleton is very complex, but as it is only weakly calcified, it is rarely or poorly preserved and has not been studied in fossils. It serves

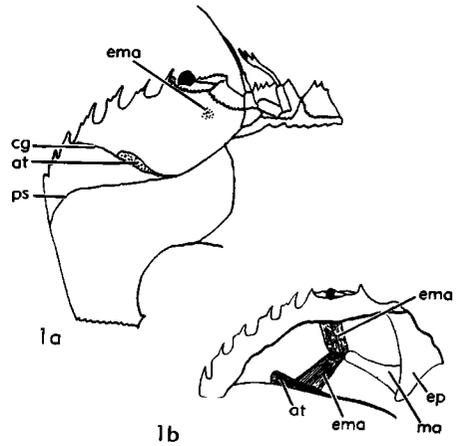
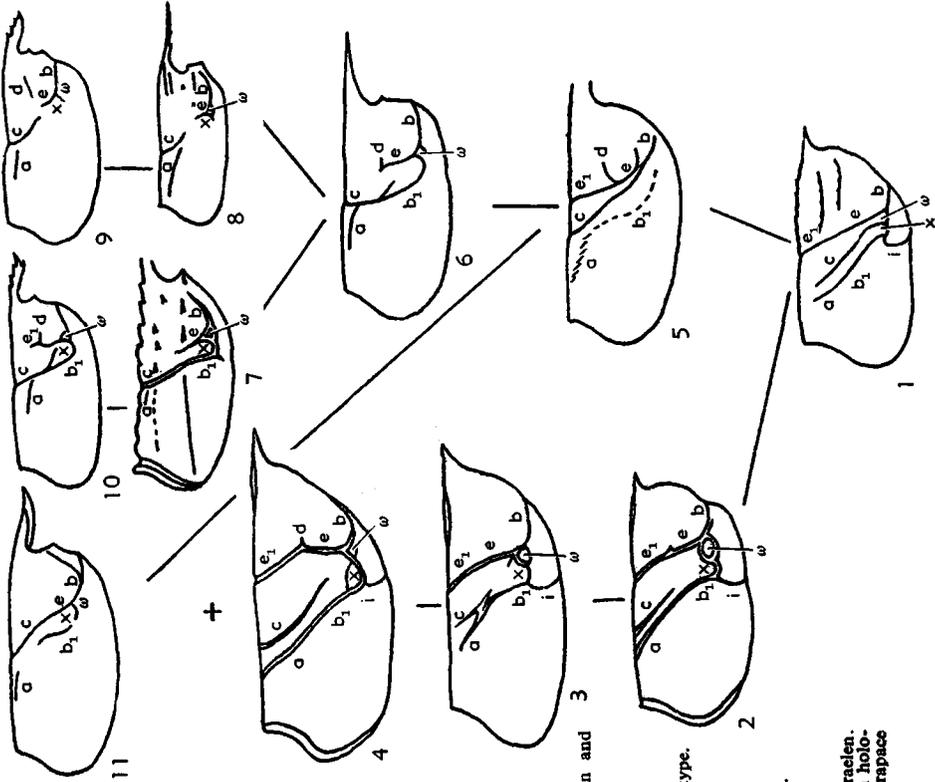


FIG. 226. Muscle insertions on anteroventral portion of carapace of *Eriphia spinifrons* HERBST; 1a, external ventral view; 1b, internal dorsal view with carapace opened (mod. from Abrahamczik-Scanzoni, 2). [EXPLANATION: *at*, adductor testis ("tensor of branchial chamber roof"); *cg*, cervical groove; *ema*, external mandible adductor (lateral); *ep*, epistome; *ma*, mandible apophysis; *ps*, pleural suture.]



A. Evolution of the carapace in Astacidea.

1. *Lissocardia silesiaca* H. v. Meyer. Triassic. After Assmann.
 2. *Eryma bedella* (Quenstedt). Jurassic. After Woods.
 3. *Klytia ventrosa* H. v. Meyer. Jurassic. Original drawing.
 4. *Enoploclytia leachi* (Mantell). Cretaceous. After Mertin.
 5. *Palaeophoberus suevicus* (Quenstedt). Jurassic. After Glaessner.
 6. *Hoplaria longimana* (Sowerby). Cretaceous. After Mertin.
 7. *Paraclytia boettcheri* Mertin. Cretaceous. After Mertin.
 8. *Palaeohomarus hemprichi* Mertin. Cretaceous. Original drawing.
 9. *Homarus vulgaris* H. Milne Edwards. Recent. Original drawing.
 10. *Nephrops norvegicus* L. Recent. Original drawing.
 11. *Astacus fluviatilis* Fabricius. Recent. Original drawing.
- Fam. Erymidae: 1-4. Fam. Nephropsidae: 5-10. Fam. Astacidae: 11.

B. Evolution of the carapace in other reptantian decapods.

1. *Pseudoglypheo spinosa* (Assmann). Triassic. After Assmann.
2. *Litogaster tiefenbachensis* Assmann. Triassic. After Assmann.
- 3a. *Pseudopemphix albertii* (H. v. Meyer). Triassic. After Assmann.
- 3b. *Pseudopemphix fritschii* Wüst. Triassic. After Scheffen.
- 4a. b. *Pemphix suwari* (H. v. Meyer). Triassic. After Glaessner.
5. *Mecochirus longimanatus* (Schlotheim). Jurassic. Modified after Beurlen and van Straelen.
6. *Meyeria ornata* (Phillips). Cretaceous. After Woods.
7. *Paraglypheo prestwichi* (Carter MS, Woods). Jurassic. After Woods.
8. *Glypheopsis cretacea* (McCoy). Cretaceous. After Woods.
9. *Megala latimana* Oppel. Jurassic. After Oppel.
10. *Schlaetaria tetracheles* Fritsch. Cretaceous. Reconstruction, from holotype.
11. *Gebicaria exigua* Alcock. Recent. After Alcock.
12. *Alpheus malleodigitatus* Bate. Recent. After Coulière.
13. *Coenobita peritata* H. Milne Edwards. Recent.
- 14a. b. *Eocarcinus praecursor* Withers. Jurassic. After Withers.
- 15a. b. *Proscopon mamillatum* H. Woodward. Jurassic. After Withers.
16. *Homolopsis edwardsi* Bell. Cretaceous. Reconstruction, from topotype.
17. *Dromiopsis rugosa* (Schlotheim). Danian. From topotype.
18. *Tetrachela railblana* Glaessner. Triassic. After Glaessner.
19. *Eryon* sp. Jurassic. After Woods.
20. *Polycheles andamanensis* Alcock. Recent. After de Man, from van Straelen type and paratype specimens.
21. *Palaeopallurus glaessneri* Bachmayer. Jurassic. Reconstruction, from holotype and paratype specimens. The unornamented areas believed to represent carapace furrows are marked by stippling.
- 22a. b. *Pallinurus vulgaris* Latreille. Recent. Original drawings.

FIG. 227. Evolution of carapace in Decapoda (Glaessner, 118). [Explanation as in Fig. 219.]

[For Erymidae, read Erymidae; for *Glypheopsis*, *Trachysoma*; for Nephropsidae, Nephropidae; for *Paraclytia*, *Paraclythia*; for *Paraglypheo*, *Glypheo*.]

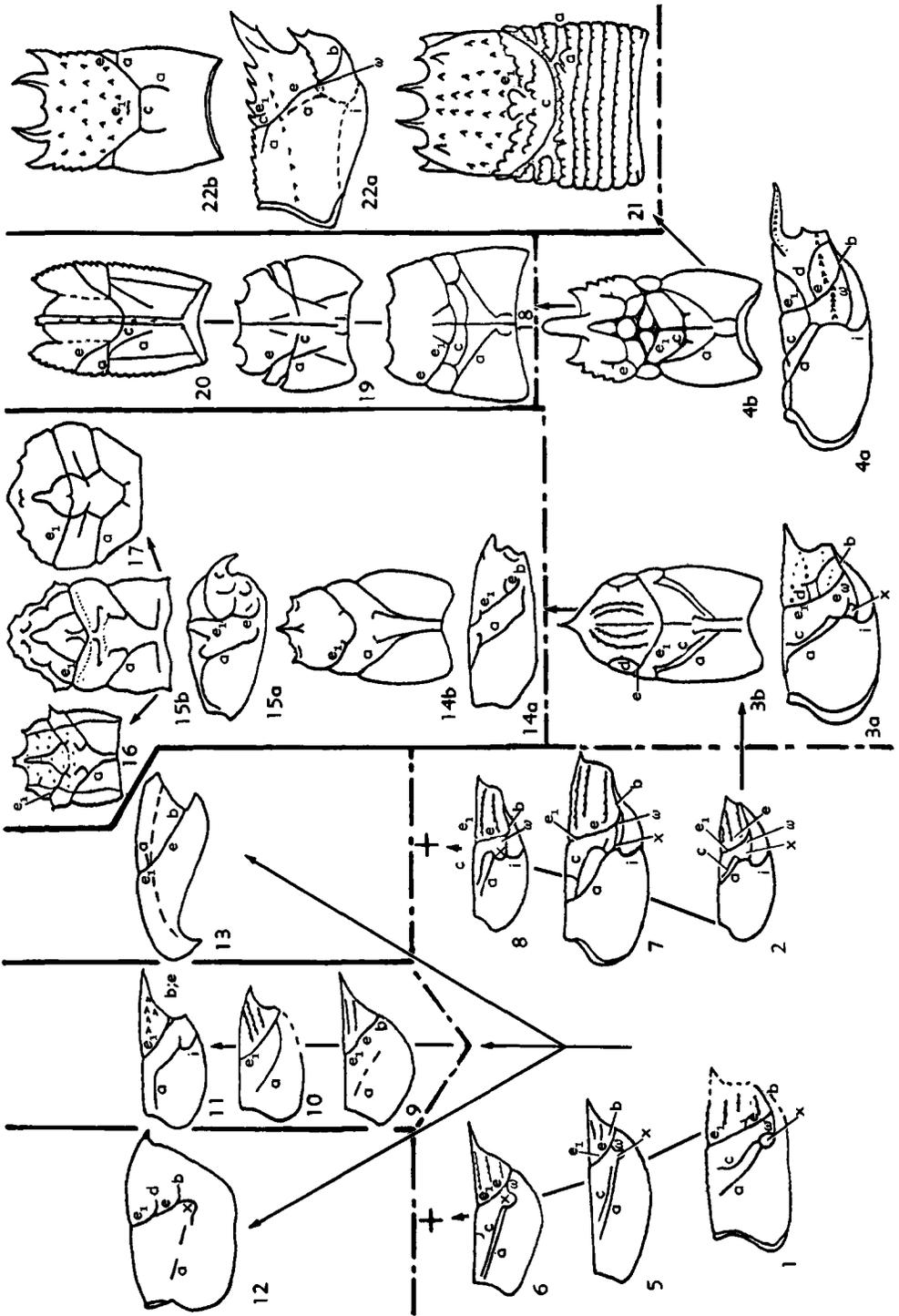


FIG. 227 (continued, see facing page).

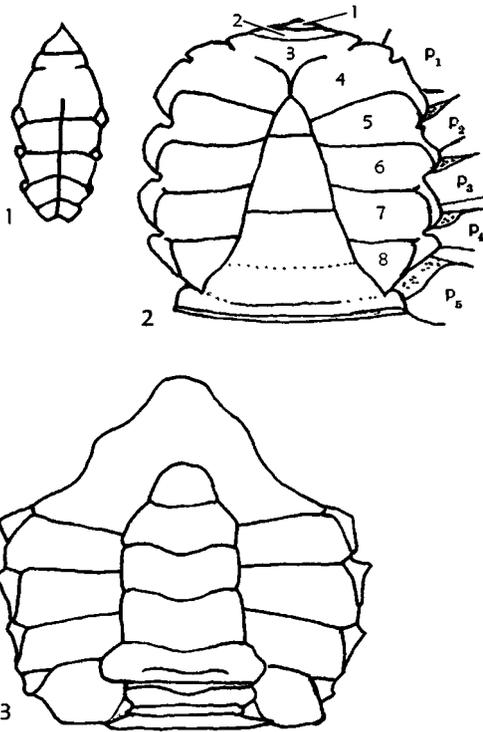


FIG. 228. Sternum and (in part) abdomen of some Recent male decapods.—1. *Corystes cassivelaunus* (PENNANT) (after Bals, 13).—2. *Portunus pelagicus* (LINNÉ) (Glaessner, n).—3. *Macrophthalmus latreillei* (DESMAREST) (after Reuss, 250). [EXPLANATION: 1-8, thoracic sternites; *pr-ps*, coxae of successive pereopods.]

as attachment for muscles and gills and as a protection for the nervous system and the intestines. The endophragmal skeleton consists of sternal (ventral) and endopleural or epimeral (lateral) elements of cuticular origin which are folded inward at the site of each somite to form muscle chambers and articulated frames for the coxae of the appendages, so that walls rise at each sternal somite boundary as intersomite apodemes (endosternites). The endopleurites arise from the epimeral walls (inner walls of the epimeral fold). Each of these apodemes divides into three branches (arthrodial branches externally). Considerable differences in the Brachyura are related to the conical shape of the internal skeleton. A median plate arising from the sternum is the mesosternum.

The endophragmal skeleton is simple in Penaeidae and also in Eryonidae, without interconnection of endosternites and endopleurites. It is more complex in Nephropidae and Thalassinidae, some more primitive Paguridae and Galatheidae, and the Homalodromiinae and Homolidae, with sutured connections. Finally, in Palinuridae, Lithodidae, advanced Galatheoidea, and Brachy-

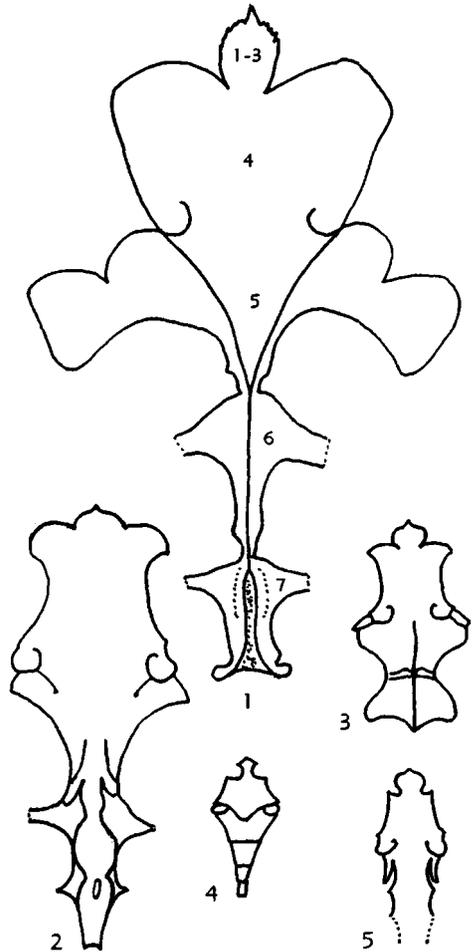


FIG. 229. Form of sternum in Raninidae.—1. *Ranina (Ranina) ranina* (LINNÉ) (after Gordon, 123).—2. *Lyreidus fossor* BENNETT (after Bennett, 20).—3. *Laeviranina ovalis* (RATHBUN) (after Rathbun, 244).—4. *Notopocorystes (Cretacorantina) schloenbachi* (SCHLÜTER) (after Martin, 193).—5. *N. (N.) stokesi* (MANTELL) (Glaessner, n). [EXPLANATION: 1-7, thoracic sternites.]

ura, it is completely fused. According to these stages of evolution, resorption preceding molting becomes localized at specific sites (82).

Fusion of endopleurites and endosternites at the anterior end in Astacidea forms the **head apodeme**, while fusion of the posterior thoracic endosternites in some Brachyura form the *sella turcica*.

The ventral skeleton of the cephalothorax consists of sterna (sternites) of the somites. Difficulties exist in the interpretation of anterior cephalic sterna. BALSS (13) has defined the **epistome** as the sternum of the antennal somite, suggesting the term **propistome** for the interantennular septum and the name **metopon** for the entire preoral area, including also parts of mandibular somite. In the Brachyura the epistome (or the entire metopon) is commonly well calcified and can be seen in fossils. Ventral cephalic skeletal elements have been described in very few fossil macrurans.

The eight thoracic sterna vary greatly in width and in degree of fusion. A median groove, which is conspicuous in crabs, has been interpreted as an indication of fusion of paired sclerites for each somite. In Penaeidea and most Caridea the sternites are narrow and separated from each other. In *Astacus* the last thoracic somite is free, others having a fused triangular sternal plate. A similar condition, but with considerable differences in details, is found in Palinuroidea, Galatheoidea, Paguroidea, and Brachyura. In the Dromiacea great variation in fusion of somites is found and grooves between them are extended anteriorly in connection with reproductive modifications (120). The width and shape of the sternum in higher Brachyura (Fig. 228) is taxonomically important, but comparative studies with the inclusion of fossils are lacking, except in Raninidae (295). In connection with the adaptation to burrowing in sand, the posterior sternites are narrowed progressively while the anterior portion of the plate between the first pereopods becomes shieldlike (Fig. 229). An anteromedian triangular projection of this shield, wrongly named episternum by VAN STRAELLEN, is interpreted as fused thoracic sterna 1 to 3 (corresponding to maxillipeds 1 to 3). The term **episternum** is applied to

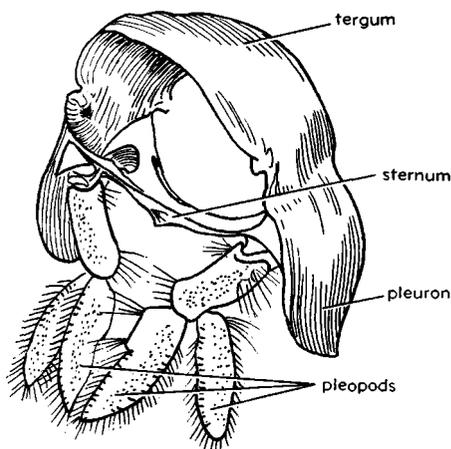


FIG. 230. Abdominal segment and attached appendages in Astacidea (from McGraw-Hill Encyclopedia of Science and Technology, p. 564, Crustacea section, by W. L. Schmidt, by permission of McGraw-Hill Book Company).

each of a series of posterolateral projections on all or some of the sterna 4 to 7 which may be separated from them by grooves (Fig. 228,2). They form the ventral supports for articulation of the pereopods (except the last pair). The median portion of the sternal plate is more or less depressed in the Brachyura, in which the abdomen is folded against the thorax.

ABDOMEN

The abdomen (or pleon) is simple in structure in the Decapoda. Its reduction in size or calcification and the concurrent changes in its function are the most important events in their evolution. The primitive, as well as various derived, conditions are observable in living Decapoda, which have been classified, accordingly, into macrurans, Anomura, and Brachyura. The morphology of the abdomen is best discussed under these headings.

In macruran decapods (Figs. 217, 230) the abdomen consists of six somites and a telson. In each somite, the convex tergum forms a strong dorsal covering, extending laterally into **pleura**. The ventral sternum is narrow and weakly calcified. In the Penaeidea the segments are of about equal

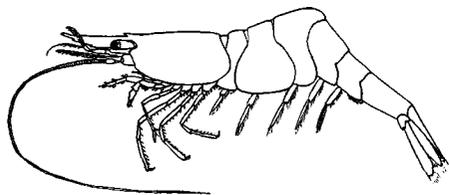


FIG. 231. Side view of caridean, *Hippolyte varians* LEACH, showing expanded second abdominal pleura (after Balss from Beurlen, 27).

length, except the sixth, which commonly is elongate. The posterior margin of each somite overlaps the anterior margin of the following one and they are movable in a vertical plane. The dorsal mid-line may bear a keel. The telson is narrowed posteriorly. In the Caridea (Fig. 231), the pleura of the second segment overlap those of the first and third, and the abdomen is strongly curved downward in normal position, commonly through curvature of the third segment. It is sculptured or spinose, particularly in living deep-water genera. The Stenopodidea resemble the Caridea in the curvature of segments 3 and 4 and the Penaeidea in the pleura 1 and 2.

In reptantian decapods the abdominal appendages do not function as locomotory organs, but a sudden ventral flexion of the abdomen effects a backward flight movement. This is assisted by the development of an anterior smooth portion of each tergum sliding under the posterior margin of the preceding somite and by the reduction of the first somite, which enables the abdomen to be moved more freely against the cephalothorax. The pleura of the second somite commonly are expanded. The terga and pleura are sculptured with ridges and tubercles in many and with spines in a few macruran reptantians. The telson is rectangular in the Astacidea, pointed in most Eryonoidea, and rectangular but only anteriorly calcified in the Palinuroidea.

A progressive reduction of the abdominal pleura is seen in the Thalassinioidea, in connection with their burrowing habit. In advanced Paguroidea the abdomen becomes adapted to concealment in gastropod shells by reduction of the calcified integument and by loss of symmetry and external segmentation. This asymmetry persists in free-

living Paguroidea, which assume a crab-like habit with inflexion of the reduced abdomen against the carapace.

In the Galatheoidea a reduction of the abdomen is achieved in a different manner, through curvature and infolding of the posterior extremity against the anterior somites. The telson is here subdivided by uncalcified sutures. In the crablike Porcellanidae, however, most of the abdomen comes to lie against the ventral side of the thorax. This is also found in the Hippoidea, where in some genera the pleura and the telson are extremely modified.

The higher Brachyura are characterized by the complete infolding of the abdomen against the thoracic sterna, but in Dromia-

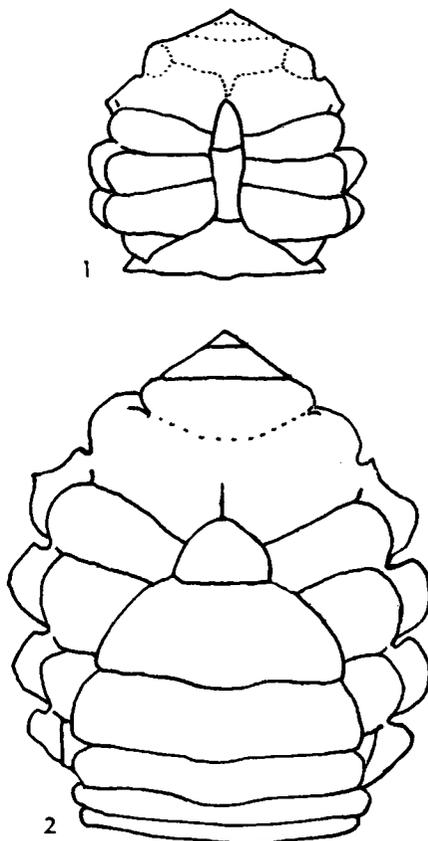


FIG. 232. Ventral views of crab abdomens.—1. *Callinectes sapidus* RATHBUN, male (mod. from Rathbun, 243).—2. *Scylla serrata* (FORSKÅL), female (mod. from A. Milne-Edwards, 198).

cea, Dorippidae, and Raninoidea, part of the abdomen remains visible from the dorsal side. Well-developed pleura are found only in the Homolodromiinae. In higher Brachyura, where some of the abdominal somites become fused, sutures between them may remain visible or disappear, and the shape of somites and degree of fusion may vary between the sexes and with growth. In many Brachyura the male abdomen is narrowly triangular and in some Portunidae (Fig. 232) it is T-shaped, whereas the female abdomen is generally broadly oval for protection of the eggs. It is commonly countersunk into a depression of the sternal plate.

APPENDAGES

The appendages of fossil Decapoda vary in their preservation, but even those most generally preserved have been neglected in paleontological studies, with exception of the strongly calcified claws of crabs and tail fans of macrurans. In Recent Decapoda the appendages are considered to be of great taxonomic importance. As in all Arthropoda, the appendages are divided into a series of articulating parts which in thoracic legs are collectively known as podomeres (coxa, basis, ischium, merus, carpus, propodus, dactylus), with epipods on the coxa and exopods on the basis (Fig. 233).

STALKED EYES

The eyes are best discussed separately from other appendages, as their stalks (**ocular peduncles**) are not considered homologous with arthropod limbs. The stalks consist typically of two articulating parts, the shorter proximal **basiophthalmite** and the longer **podophthalmite** which bears the **corneal surface**. In some forms the proximal part of the stalk may be elongated, or there may be three parts. The terminal segment may be thickened or provided with a projecting spine. The eyes are covered by the anterior margin of the carapace in *Alpheus* (Caridea); they are reduced in living deep-sea and burrowing Decapoda but fully developed in their free-living shallow-water ancestors (e.g.,

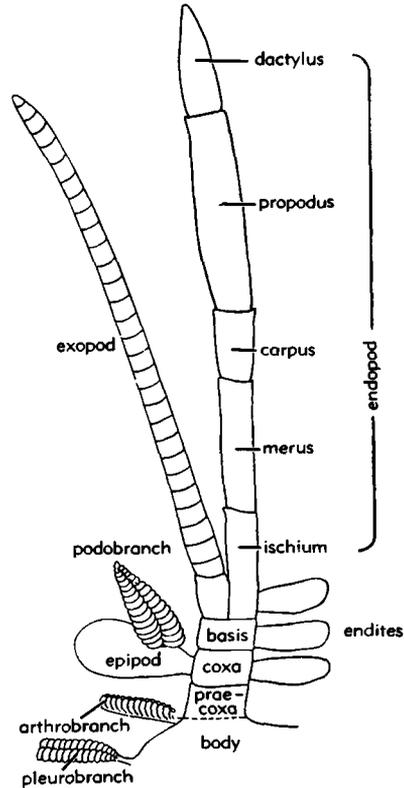


FIG. 233. Thoracopod podomeres in Decapoda, showing relations of exopod, endopod, endites, and gills (podobranch, arthrobranch, pleurobranch) (after Holthuis, 149).

Eryonoidea) and greatly lengthened in several not closely related crabs (e.g., *Podophthalmus*, *Ommatocarcinus*, *Macrophthalmus*). Eye stalks and corneal surfaces are commonly preserved in fossils, but they have not been studied in detail. Important modifications of the carapace arise in response to the need for protection for the eyes. Spines occur in Penaeoidea, Palinuroidea, and oxystomatous crabs; orbital emarginations are particularly noticeable in Eryonoidea and Scyllaridae, and elaborate orbits are found in Brachyura. Their construction involves not only the regularly fissured supra- and infraorbital margins of the carapace and a connecting **ocular bulla** on its inner surface, but also the basal segment of the antenna, which in advanced genera in various families is inserted be-

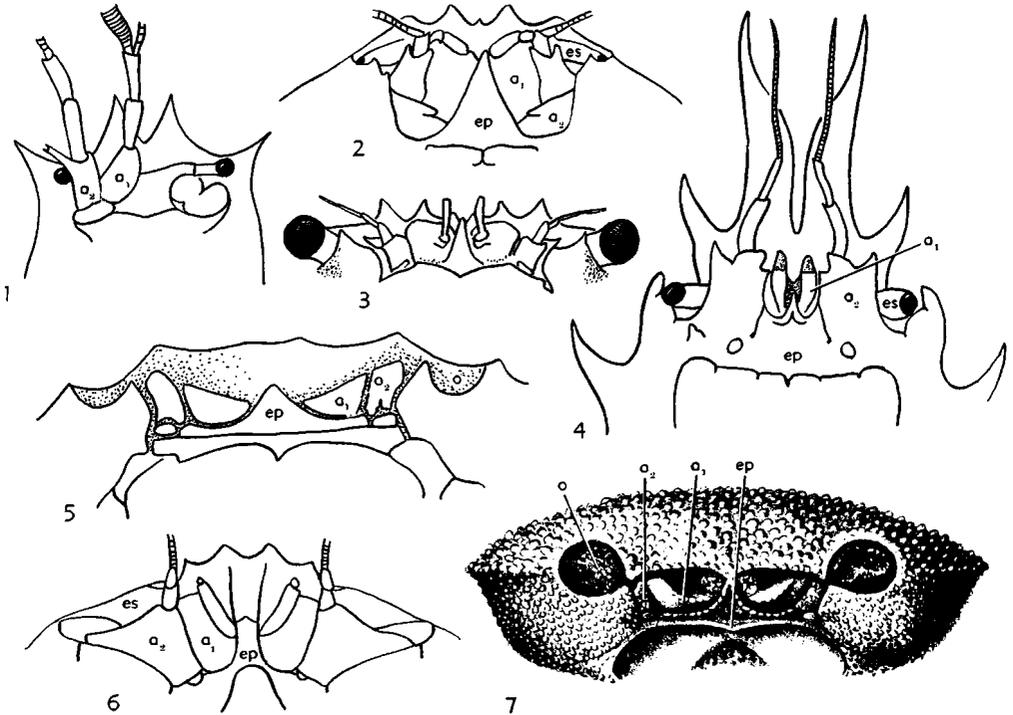


FIG. 234. Antennoorbital region in Brachyura shown in ventral (1-6) and frontal (7) views.—1. *Homolodromia paradoxa* A. MILNE-EDWARDS, with left a_1 and a_2 removed (52).—2. *Dromia* sp. (156).—3. *Portunus pelagicus* (LINNÉ) (15).—4. *Pisa tetraodon* (PENNANT) (52).—5. *Harpactocarcinus punctulatus* (DESMAREST), Eoc. (198).—6. *Calappa gallus* (HERBST) (301).—7. *Caloxanthus formosus* A. MILNE-EDWARDS, U.Cret. (198). [EXPLANATION: a_1 , antennula; a_2 , antenna (proximally fused with epistome in *Pisa*); ep, epistome; es, eye stalk; o, orbit.]

tween the infraorbital lobe and ventral projections of the front (Fig. 234).

ANTENNULES

The antennules (first antennae) are also considered as preoral appendages, not homologous with the biramous arthropod limb. They consist typically of a three-segmented stalk with two annulated flagella on the terminal segment. The basal segment of the stalk contains the **statocyst**, and in Penaeidea and Caridea it has also a pointed or rounded **stylocerite** (antennular scale) which protects the opening of the statocyst. One of the flagella may be divided into two (e.g., most Palaemonidae). In the higher Brachyura the antennules are placed in antennular grooves or cavities, separated by an interantennular septum under the front. They are folded longitudinally, ob-

liquely, or transversely in these grooves, with the short flagella projecting.

ANTENNAE

The antennae represent the structure of a biramous limb, with a five-segmented stalk consisting of a two-segmented proto-podite (coxa, basis) and a three-segmented endopodite (corresponding to **ischium, merus, carpus**), ending in an annulated **flagellum**. The first segment of the proto-podite contains ventrally the opening of the excretory antennal gland, commonly in a tubercle. The exopod joined to the second segment is the **scaphocerite** (antennal scale or squama). This becomes reduced in the course of evolution in the Decapoda but functions as a balancing organ in the natantian decapods. In reptantian decapods it is reduced in many to a spine or it is

absent (in the Palinuroidea). It is fixed in the Dromiacea and Raninidae and absent in other Brachyura. The stalk is also reduced by fusion of the coxa with the epistome and of the basis with the ischium in the Palinuroidea and in higher Brachyura, for which the term basis is commonly used instead of basiischium. This becomes incorporated in the orbit. The two remaining segments of the stalk and the flagella are commonly very small, but in burrowing crabs (e.g., Raninidae, *Corystes*) the antennae are modified to assist in directing the respiratory stream of water and their flagella may be long. In the Scyllaridae the flagellum is modified to a broad denticulate plate. The lateral expansion of the annulated flagella of *Cancrimos* is considered a step toward this modification.

MANDIBLES

The mandibles consist of a strongly calcified body and a palp with no more than three segments. The medial part of the body of the mandible may be divided into an anterior denticulate pars incisiva and a posterior pars molaris with a strongly developed crushing surface, but there is no lacinia mobilis in adult Decapoda. The mandible articulates primarily with its sternum, which commonly is fused with the epistome and secondarily, through a posterolateral extension, with a lateral projection of the head apodeme. This lies in many reptantians under a small convex circular field ω of the carapace below the junction of grooves, e , b , and b_1 .

MAXILLULES AND MAXILLAE

The appendages termed maxillules and maxillae (also known as first and second maxillae) are weakly calcified and have not been described in fossil Decapoda. They consist of several lobate segments carrying bristles which assist in food gathering. Another function is carried out by the exopod of the maxilla (scaphognathite) which is extended anteriorly and posteriorly and which pumps the respiratory stream of water out of the exhalant canal of the branchial cavity.

MAXILLIPEDS

The three pairs of maxillipeds in many decapods are transitional in form between maxillae and pereopods. Maxillipeds 1 and 2 are rarely preserved in fossils; maxillipeds 3 are mostly seen but rarely have been described in detail.

PEREIOPODS

The thoracopods 3 to 8 of the Decapoda are known as pereopods (p). They may be modified from the basic malacostracan limb by (1) loss of epipods and exopods, (2) fusion of segments, (3) annulation, (4) formation of subchelae and chelae, (5) flattening to paddle shape, and (6) reduction and loss of posterior limbs.

The epipod of the coxa is absent on pereopod 5 in all living forms. It is present on pereopod 4 of some natantians, Palinura, Astacidea, some Thalassinioidea, but absent in all other Anomura and Brachyura. The exopods are found in a rudimentary form in Penaeidea and better developed in some living families of the Caridea and in the Jurassic Udorellidae (13).

The basis and ischium are fused in all first pereopods and most others of reptantian decapods. The ischium and merus can also fuse.

Annulation is known in the carpus of the Cretaceous *Carpopenaeus*, the Jurassic *Blaculla*, and a number of living Caridea; also in other leg segments of Caridea and Stenopodidea and in the dactylus of a living penaeid and a hippid.

Subchelae (Fig. 235,1-3) are formed where a short outgrowth arises from the propodus, commonly at a right angle to its length; the generally long and projecting dactylus can be placed against it. In true chelae the tips of the outgrowth (fixed finger) and the dactylus (movable finger) meet or overlap slightly (Fig. 235,4-6). Chelae are absent in all Palinuridae, Scyllaridae, and Hippidae. Subchelae are found in Glypheoidea, Crangonidae, and Thalassinidae on pereopod 1, commonly on 2, and in other families on other pereopods. In the Penaeidea, Stenopodidea, and Astacidea the first three pereopods are chelate. The

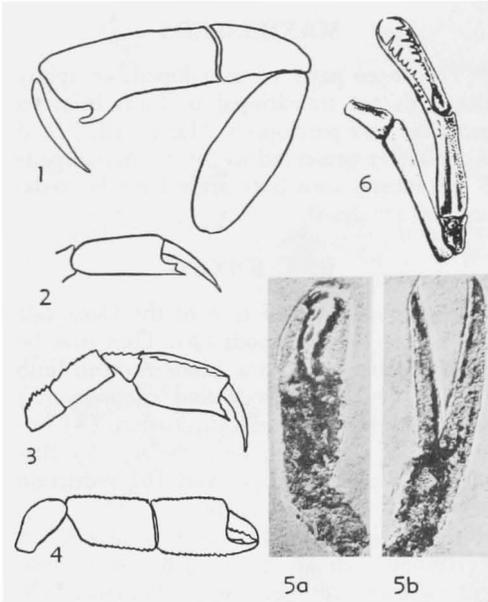


FIG. 235. Subchelae (1-3) and chelae (4-6) of first pereiopod in decapods.—1. *Glyphea udressieri* VON MEYER (34).—2. *Etallonia longimana* (MÜNSTER) (34).—3. *Thalassinia anomala* (HERBST) (34).—4. *Axius* sp. (34).—5. *Homarus hakelensis* (FRAAS); 5a,b, right and left chelae (115, 219).—6. *Palaeopentacheles roetenbacheri* (MÜNSTER), right chela (219).

Eryonoidea can have chelae on all five pereiopods. Other Decapoda have them only on pereiopods 1 (chelipeds) or 1 and 2. The chelae, or at least their fingers, are very strongly calcified. They can grow to enormous size, reaching a maximum in the crabs *Pseudocarcinus* and *Macrocheira* and showing not only taxonomic differences in shape and sculpture but also age and sex differences. Right and left chelae are commonly different in size and shape (**heterochelous**). *Homarus* illustrates the functional difference between a stout crusher claw and a slender finely denticulate nipper claw (Fig. 235,5). This is common in Brachyura. In many Xanthidae and in some other crabs the finger tips of the claws are spoon-shaped. A distinctive elongate prism shape develops in advanced Portunidae. It is correlated with transversely elongate body shape and with fast-swimming and predatory habits.

The last pair or pairs of pereiopods are also commonly differentiated. The fifth

pereiopods are well developed and flattened to form swimming paddles in most Portunoidea.

A reduction of fifth pereiopods is seen in Thalassinioidea and Galattheoidea, where they function as cleaning organs, in Dromiidae, where they are shifted to a dorsal position to hold protective sponges or other camouflage over the carapace, and in Homolidae, Palicidae, and Retroplumidae. In the Hexapodiinae pereiopods 5 are absent and in Dromiidae pereiopods 4 can be reduced. It appears that the reduction of the posterior pereiopods is related to early stages in the reduction of the abdomen and that their change of function from locomotion to cleaning and so forth is secondary.

Insufficient information is available on the articulation of pereiopods. In dorsal view the movable finger of pereiopod 1 is on the inner side of the fixed finger in the Astacidea, whereas in the Eryonoidea it is on the outer side. This is the result of different orientation of the various axes of the joints in the limb rather than a difference in the position of the fingers.

PLEOPODS

Pleopods are biramous appendages of the abdominal segments with a short coxa and longer basis. They are originally swimming organs, but the anterior pleopods may be modified for reproductive functions. An appendix interna (44) or stylamblys (18) is developed on the median side of the endopod, mostly in pleopods 2 to 5, in the Caridea, Palinuroidea, and Axiidae among decapods, as in many other Malacostraca. It connects by means of hooks with the appendix interna of the opposite side, thus facilitating synchronous swimming movements.

In all Decapoda, with exception of the Penaeidea, the eggs are attached to pleopods of the females. The pleopods 1 and 2 of the males are modified as gonopods, except in the Stenopodidea, Palinuroidea, and Hippoidea. In the Brachyura (except Dromiacea) pleopods 3 to 5 of the males and 1 of the females are absent. The second pleopods of male Caridea and Axiidae carry an appendix masculina, which commonly is similar to the appendix interna

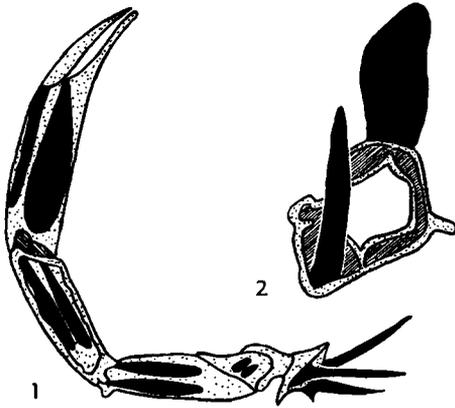


FIG. 236. Cheliped tendons in crab, *Maja verucosa* H. MILNE-EDWARDS; 1, entire cheliped; 2, proximal view of coxa showing flexor (above), extensor (below), articulations appearing as right and left projections, and articulations of basiischium appearing as upper and lower projections of internal outline (after Abrahamczik-Scanzoni, 2).

but without hooks. Where the first pleopods of males are developed as copulatory organs, their form, which is more or less tubular, is important in classification. In Penaeidea their endopods form the *petasma*, a leaf-shaped or tubular structure which is known in some fossils. Its function is transfer of spermatophores to the *thelycum*, a thoracic sternal pocket developed in females. In the Brachyura, modified first and second pleopods introduce the spermatophores into the internal seminal receptacle (*receptaculum seminis*).

UROPODS

The pleopods of the sixth abdominal somite form a tail fan, together with the telson. Coxa and basis are fused. Endo- and exopod are leaf-shaped. In hermit crabs (Paguroidea) the tail fan loses its swimming function and is used for attachment in the protective gastropod shell. In secondarily free-living Paguroidea and in Brachyura it is absent, except for two small rudiments of the coxa of the uropods in Dromiidae. Where the exopod is well developed, it is commonly divided by a transverse suture (*diaeresis*). In Palinuridae and Scyllaridae the distal parts of the telson and uropods are not calcified.

INTERNAL ANATOMY

MUSCLES

In the macrurous Decapoda the trunk muscles are located mainly in the abdomen, where they effect its sudden flexion in backward flight movements. The thorax, being inflexible, contains mainly thoracoabdominal muscles, in addition to those connecting the internal with the external skeleton. The ventral abdominal muscles, which are flexors, exceed the dorsal extensors in strength. They consist of complex longitudinal, transverse, and oblique (intersegmental) systems (13) which are bilaterally symmetrical (except in Paguroidea). The sixth abdominal somite contains the complex muscles of the tail fan. In the Brachyura, flexor and extensor muscles connect the proximal abdominal somites mainly with the internal skeleton and the muscles within the abdominal somites are reduced in number and strength.

The muscles of the decapod appendages are complex (2, 13). Those of the coxa and basis are located in chambers formed by the internal skeleton. The other podomeres have two tendons attached to the proximal margin, corresponding to extensor and flexor muscles which are attached to the inner wall of the preceding podomere (Fig. 236). Muscles attached to the carapace have been mentioned in the description of its morphology (p. R408).

NERVOUS SYSTEM

The nervous system comprises the supraesophageal ganglion (*syncerebrum*), the

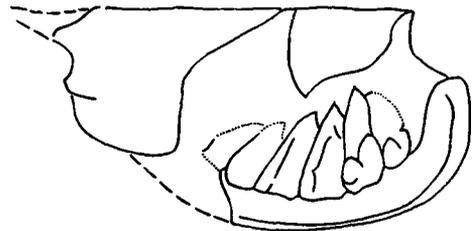


FIG. 237. Broken cephalothorax of *Oncopareia muncki* (PELSENEER) with partly preserved branchiae (podobranchs) in exposed branchial chamber, U.Cret., Belg. (mod. from Pelseeneer, 227).

subesophageal ganglion, and the ventral nerve chain. In most Brachyura (with exception of the Raninidae) the ventral ganglia are fused in a rounded mass from which the nerves radiate outward.

ALIMENTARY SYSTEM

The alimentary system consists of the stomodeum, mesenteron, and proctodeum. The stomodeum forms the complex stomach. The triturating gastric mill contains calcified ossicles and has a complicated system of muscles some of which are inserted in the exoskeleton. The gastroliths (p. R432) are located in the anterior part of the stomach. Attached to the mesenteron are caeca and the digestive gland (hepatopancreas), consisting of a large mass of ramified tubules spread through the cephalothorax. In the Paguroidea it extends into the abdomen. The proctodeum has strong longitudinal internal ridges.

HEART

The heart is located under the posterior part of the carapace ("cardiac region"), above the gut. It is polygonal, surrounded by a pericardial sinus, and has generally three pairs of ostia and seven arteries.

BRANCHIAE

Branchial morphology and pattern (i.e., numbers of differently placed gills present on the thoracic segments and limbs, commonly expressed in branchial formulae) provide important evidence for relationships among Recent Decapoda. Further evidence is obtained from the ontogeny of these patterns (i.e., branchial formulae of larval stages). The branchiae are only exceptionally and never completely preserved in fossils (Fig. 237).

According to their position, a distinction is made between (1) **podobranchs**, arising from the coxal epipods or the coxae, (2)

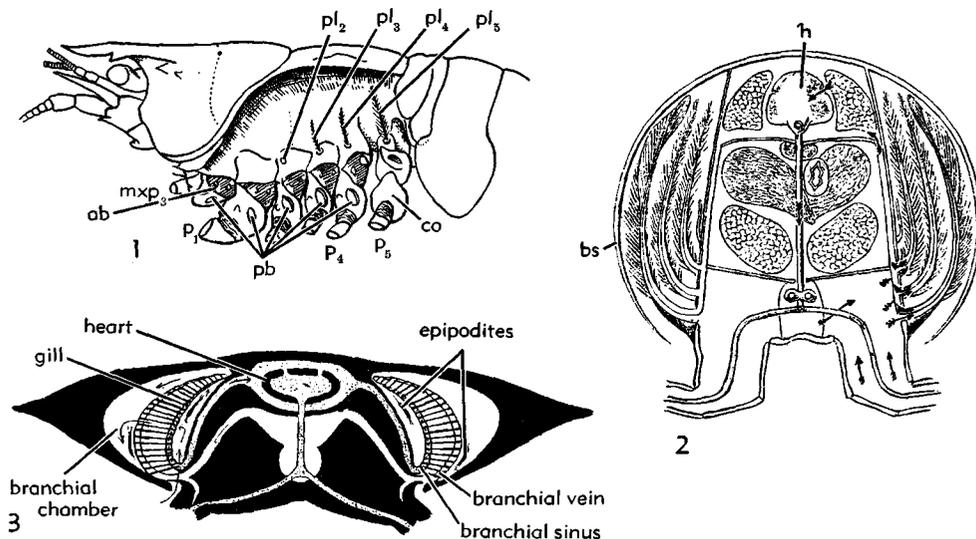


FIG. 238. Gill positions in decapods.—1. *Astacus pallipes* LEREBOULLET, showing left side of cephalothorax (branchiostegite removed) and anterior abdominal somites (mod. from Bouvier, 52).—2. *A. astacus* LINNÉ, diagrammatic cross section, arrows indicating direction of blood flow (mod. from Huxley, 155).—3. *Cancer pagurus* LINNÉ, diagrammatic cross section showing branchial chambers and blood supply of gills, directions of blood flow and water currents indicated by arrows (mod. from Wolvekamp & Waterman, 316). [EXPLANATION: *ab*, arthrobranch insertions, two in each arthrodistal membrane of 3rd maxilliped (mxp_3) and 1st to 4th pereiopods (p_1 to p_4); *bs*, branchiostegite; *co*, coxae; *h*, heart; *mxp*, maxilliped; *p*, pereiopod; *pb*, podobranch insertions, on coxae of 3rd maxilliped and 1st to 4th pereiopods; pl_2 to pl_5 , pleurobranch insertions corresponding to 2nd to 5th pereiopods, rudimentary on 2nd pereiopod.]

arthrobranchs, arising from the articular membranes between coxae and body wall, and (3) **pleurobranchs**, arising from the epimeral wall dorsal of the articular membranes (Fig. 238). The coxal epipods (**mastigobranchs** in some maxillipeds, **laminae** in some pereiopods) can have respiratory functions. The maximum number found on each side (not counting epipods) is one podobranch, two arthrobranchs, and one pleurobranch, which would give a maximum number of 32 for the eight thoracic somites. This does not occur, as there are no podo- or pleurobranchs on any first maxilliped and no podo- or arthrobranchs on any fifth pereiopod. The maximum number is found in the primitive penaeid genus *Benthescymus* (24) and reduction is observed in more advanced Decapoda, with nine in most Brachyura and a minimum number (three) in the crab *Pinnotheres*. The branchial formulae of the larvae are no more complete than those of the adults, so that there is no recapitulation of phylogeny in this respect.

According to their structure, a distinction is made between **trichobranchs**, long thin tubes attached in rows to a shaft, **dendrobranchs**, which have the tube divided into arborescent bundles, and **phyllobranchs**, in which the tubes are expanded into numerous flat leaves (Fig. 239). The trichobranchs appear to be morphologically most primitive. They occur in Stenopodidae, Astacidea, Palinura, Thalassinoidea, primitive Paguroidea, Galattheoidea, and Homolodromiinae. Dendrobranchs characterize the Penaeidea exclusively. Phyllobranchs are found in Caridea, most Paguroidea and Galattheoidea, all Hippoidea, and most Brachyura (13).

EXCRETORY SYSTEM

The main excretory organ is the **green gland** (antennal gland). Its duct opens to the surface in an elevated **nephropore** on the coxa of the antenna. The Brachyura have a voluminous bladder; in the Paguroidea it is displaced in the abdomen.

REPRODUCTIVE SYSTEM

The reproductive organs are generally placed in the thorax, between intestine and

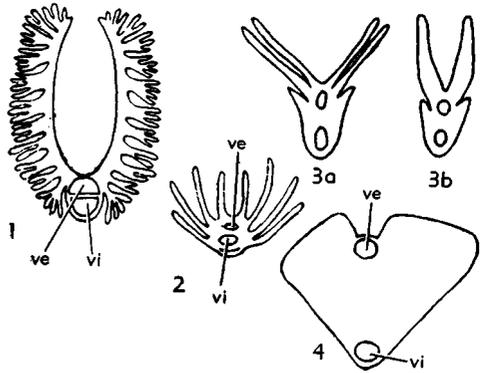


FIG. 239. Types of decapod branchial structures illustrated by cross sections (after Bouvier, 52).—1. *Penaeus*, dendrobranch.—2, 3a, b. *Astacus*, *Dicranodromia*, trichobranch.—4. *Carcinus*, phyllobranch. [EXPLANATION: *ve*, *vi*, blood vessels.]

heart; they may extend into the abdomen. The male genital openings (**gonopores**) usually are located in the coxae of the fifth pereiopods, but in some crabs (e.g., Goneplacidae, Ocypodidae, and others) they are sternal. The oviducts usually end in gonopores on the coxae of the third pereiopods. In the Brachyura this **podotreme** position is maintained in the Dromiacea, Dorippidae (subfamily Tymolinae only), and Raninidae. In all other crabs the female gonopores are located in the sternum of the third pereiopods (sixth thoracic sternum); in the Palicidae they are found in the sternum of the second pereiopods. The **sternotreme** position is related to the widening of the sternum in the Brachyura, in which the male abdomen remains narrow. The male first pleopods (and mostly second also), modified to **gonopods** for transmittal of spermatophores to the females, are closer to the median line than the female coxae of the third pereiopods. The spermatophores may be affixed on the ventral surface of the body of the females or placed in a depression of the thoracic sternum (**spermatheca**, **thelycum** in Penaeidea), which may be connected with the gonopore by sternal furrows on or near the boundary of the seventh and eighth thoracic sterna. In the Raninidae the spermathecal opening is a deep median pit in the seventh thoracic sternum (120). The evolutionary morphology of these structures remains to be studied in fossils.

ONTOGENY AND GROWTH

LARVAL AND POSTLARVAL STAGES

The ontogeny of the Decapoda comprises the embryonic, larval, postlarval, and adult periods. In the Penaeidea the eggs are laid in the water and hatch soon at the **nauplius** stage. The nauplius larva is unsegmented, with an externally unsegmented oval body, a median eye, simple antennules, antennae, and mandibles adapted for swimming. In the following **metanauplius** stage, four additional pairs of appendages and the masticatory part of the mandible are developed. In the **protozoa** stage the larva has a carapace, stalked eyes, and an abdomen with forked telson. At the **zoea** stage, the eye stalks become movable, a rostrum develops, and all thoracic appendages and rudimentary abdominal appendages appear. In the **mysis** stage, biramous thoracopods are developed, the rostrum is long, and antennules and antennae approach their adult form. At the **postlarval** stage, the exopods are reduced and the pleopods function in locomotion. GURNEY (133), who has described numerous larvae, has criticized these traditional distinctions and recognized only nauplius, protozoa, and zoea-mysis as "really distinct phases," dividing them further into numbered stages.

Numerous cenogenetic adaptations and evolutionary acceleration and retardation in morphogeny make phylogenetic and taxonomic conclusions from ontogeny in Decapoda extremely difficult and controversial, though by no means irrelevant.

In most Decapoda the nauplius and similar early stages are completed in the eggs, which are carried under the abdomen of the females, and the young animals hatch at the zoea stage. In the Palinuroidea the first postembryonic larva is a disc-shaped, long-legged **phyllosoma**, while the postlarval forms are benthonic and more adult-like. In the living Eryonoidea the early larvae are bathypelagic, with a spiny, globular carapace (e.g., *Eryoneicus*). In pagurids, the postzoea larva is the **glaucothoe**, which

is entirely or almost symmetrical. In the Brachyura the last zoea, which is generally armed with long dorsal spines, metamorphoses into a **megalopa** with ambulatory pereopods and extended abdomen bearing functional pleopods (but weak muscles), and an elongate carapace which may be prosopon-like.

No decapod larvae have been found as fossils. *Phalangites priscus* MÜNSTER, 1836, from the Upper Jurassic of Solnhofen, Germany, long considered as a phyllosoma larva of a palinurid, has also been assigned to the Pantopoda (?Nymphonidae). A report (254, 255) of "*Eryoneicus*" from the Upper Cretaceous (Senonian) of Lebanon is considered to be erroneous.

The larval stages are further reduced in fresh-water Decapoda. Terrestrial decapods lay their eggs in the sea, where the usual larval stages develop. Embryonic development occupies seven or eight months in *Astacus*, about a year in *Homarus*, but only one to four months in Brachyura. The postembryonic development occupies weeks to months.

MOLTING

Growth in Decapoda involves periodic molting. This term is being used (PASSANO in WATERMAN, 316) to include the physiological "processes of preparation for withdrawal from the old integument, ecdysis and postecdysis increase in linear size, as well as subsequent tissue growth." The shedding of the old integument (**ecdysis**, **exuviation**) and its paleontological effects are discussed later (p. R431). "There is scarcely a time when all aspects of the crustacean's life processes (feeding, behavior, sensory capabilities, reproductive activity, etc.) are not dominated by its saltatory growth pattern, its recurrent renewal of skeleton, and its material storage metabolism."

Molting is controlled by the molting gland or Y-organ (which in crabs lies at the anterior end of the branchial chamber above the branchiostegite and below the insertion of the external adductor muscle of

the mandible), and inhibited by the neurosecretory activity of the X-organ, situated in the eye stalk. It is also affected by external conditions. It may continue periodically throughout the life of the animal,

occur with decreasing frequency in adults (as in *Homarus*), or cease after a terminal molt. It consists in the withdrawal not only from the old exoskeleton of the carapace and abdomen but also from that of the ap-

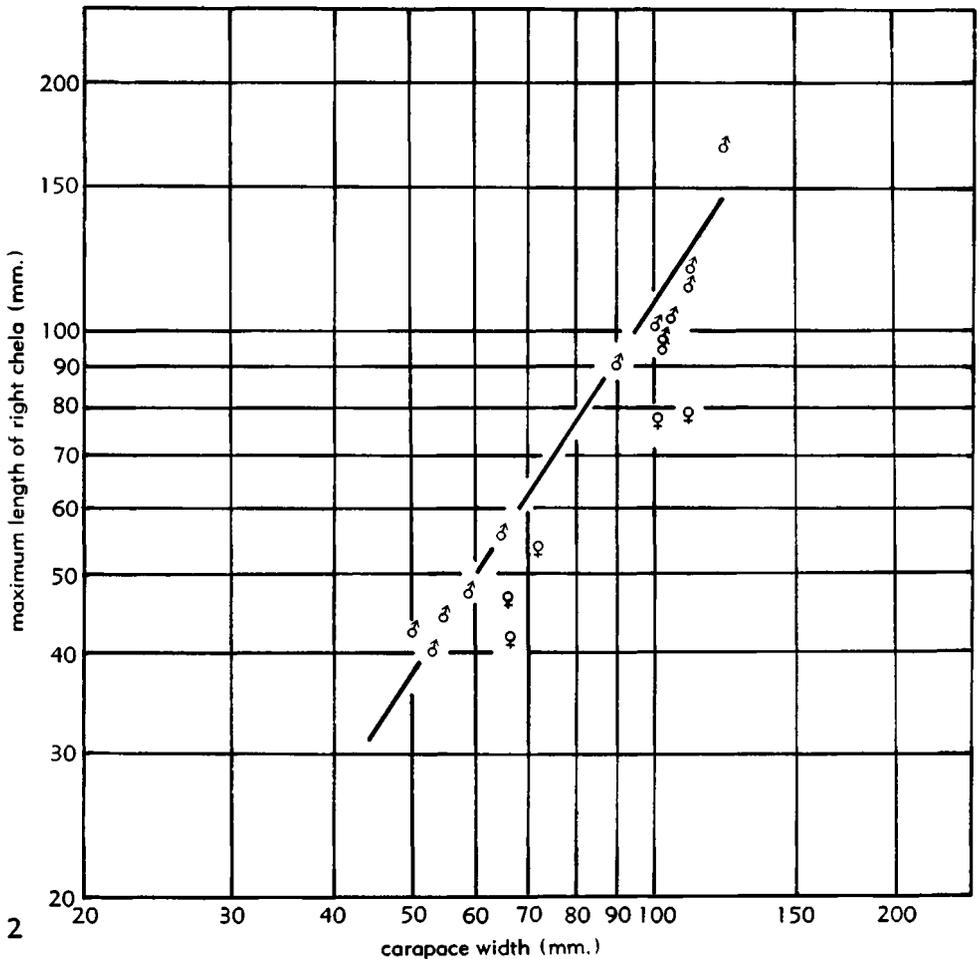
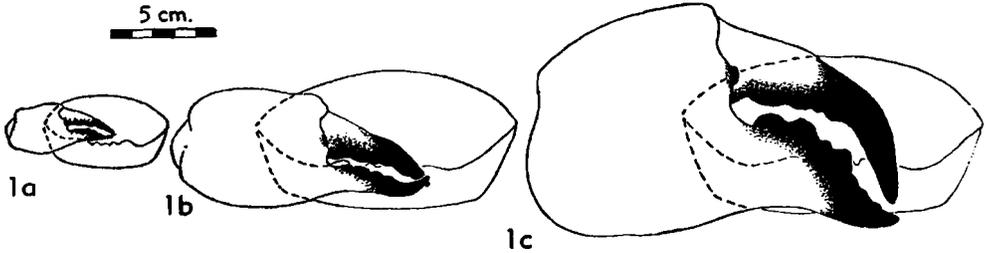


FIG. 240. Allometric growth of right chela of the crab *Tumidocarcinus giganteus* GLAESSNER, Mio., N.Z. (after Fleming, 93).—1a-c. Outlines of carapace and right chela of males.—2. Graph showing positive allometric growth of chela in males (each symbol representing one measured individual).

pendages, including antennae, eye stalks, mouth parts, legs, branchiae, and the lining of the digestive tract. Mineral storage in gastroliths of fresh-water crayfish and remineralization of tissues have been described in detail by TRAVIS (289).

GROWTH RATES

The different growth rates of various parts of the decapod skeleton have been illustrated by means of deformation of

cartesian coordinates (D'ARCY THOMPSON) and later investigated by biometric studies of allometric growth (references given by TEISSIER in WATERMAN, 316). The relative increase in carapace width in portunid crabs, in width of the female abdomen during growth to maturity, or the size increase of the major claw in heterochelous male crabs are allometric. The last of these examples has also been demonstrated on fossil material (Fig. 240).

PALEOECOLOGY

HABITATS

Most Decapoda are marine, some are found in brackish water, few live in fresh water, and only some Paguroidea and Brachyura are adapted to life on land. The ecology of living Decapoda was extensively reviewed by BALS (13). Only points of special paleontological significance will be mentioned here.

MARINE

The littoral zone is today conspicuously rich in crabs. They are common in Tertiary and Upper Cretaceous shallow-water deposits, but their usually fragmental remains rarely attract attention. In the Lower Cretaceous they occur less commonly, in the Upper Jurassic they are confined to calcareous rocks, and in the Lower Jurassic only one crab, with distinctly ancestral characters, is known. Crabs living on rocky shores have little chance of preservation. Grapsidae, which are common today, are rare fossils probably for this reason. Crabs living on soft sand and clay and others adapted to coral reefs are more common, while burrowers in shifting sands of the tidal zone are rare or entirely unknown as fossils (e.g., Hippoidea). Other burrowers are distinctly favored in preservation, with the result that the picture of fossil littoral and sublittoral communities is biased. A distinctive fauna lives today in the phytal, in algal and other marine plant growths. The Caridea are too weakly calcified to be preserved, but some fossil Oxyrhyncha may indicate this envi-

ronment. Others live on muddy ground below wave base. A distinctive decapod fauna occurs in dark bituminous shales of Oligocene age in the Carpathians and the Caucasus. It consists of small portunids, *Planes*, *Inachinae*, and a *Palaemon*-like caridean shrimp. It resembles the fauna of the Sargasso Sea and lived probably in floating vegetation rather than on the bottom, which was poisoned by H₂S (euxinic conditions). The fauna of the mangrove swamps is not definitely recognizable as a fossil assemblage, but the common subfossil occurrences along the coasts of southeastern Asia and northern Australia of *Macrophthalmus*, *Scylla serrata*, and other crabs, together with *Thalassinia anomala*, originated probably as concretions in mangrove mud. They are washed out by currents and found on beaches and in estuaries.

Chelae assigned to *Callianassa* and its Mesozoic predecessors *Protocallianassa* and *Protaxius* are among the most common fossil Decapoda because of their burrowing habit in areas of sedimentation, and strong calcification of the claws and fingers which are used in burrowing.

Paguroidea, which also have strongly calcified claws, are fairly common in shallow-water sediments from Jurassic to Recent. They are known not only as skeletal remains (chelae and fingers) but also from their effect on molluscan shells.

Decapoda are found in reef limestones from Jurassic to Tertiary age. The Jurassic reefs of central Europe contain an amazing variety of crabs which all belong to the

Dromiacea. Parallels in carapace shape and sculpture with later Oxystomata, Oxyrhyncha, and Brachyrhyncha can be seen, but complete descriptions of these forms are not yet available. Many Galatheoidea, a few Palinuroidea, and a number of Paguroidea occur with these crabs. During the Cretaceous the coral-reef Decapoda changed only slowly, and in the Danian reefs of Faxø (Denmark) the dynomenid genus *Dromiopsis* dominates. In the Eocene the fauna of similar habitats is more modern, and in the Miocene (of the Vienna Basin) it is close to the present Indopacific fauna, with *Daira* and other xanthoids dominant, associated with *Calappa*, etc. As can be expected, the thin-shelled Trapeziidae, Caridea, and Stenopodidea, which are common among coral reefs today, are not preserved in this environment.

An entirely different association is found in calcareous shales and thin-bedded limestones which are known from the Late Triassic to the Tertiary. Most of them are rich in fish remains. These shales contain benthonic macrurans with flat (depressiform) bodies and short legs, associated with nectonic macrurans, most of which have long legs. Crablike forms join this association only in the Cretaceous. The benthonic forms include some Glyphoidea and Palinuroidea in the Jurassic, and Astacidea. These are very rare in the Lower Jurassic and more common in the Upper Jurassic and in the Cretaceous. The assemblages, though mostly thanatocoenoses, demonstrate "relay evolution," as certain adaptive types are represented by successions of more advanced taxonomic groups. This is illustrated by the following Table 1.

The present bathyal decapod fauna comprises, among others, many Penaeidae, Caridea, all living Eryonoidea, some Nephropidae, Lithodidae, Galatheidae, and crabs belonging to the Homolodromiinae (all), Dorippidae, Majidae, Geryonidae, and Retroplumidae. Many of these taxa have fossil representatives in assemblages which indicate shallow-water conditions, particularly Penaeidae, Eryonoidea, *Palaeophoberus* and *Oncopareia* (related to the bathyal *Neophoberus* and *Thaumastocheles*), Galathei-

TABLE 1. *Assemblages of Decapod Crustacea from Calcareous Shales and Thin-bedded Limestones*

Age	Depressiform benthonic reptantians	Penaeidea	Natantians Caridea
Early Tertiary	<i>Ibacus</i> <i>Palinurus</i> (?)		<i>Palaemon</i>
Late Cretaceous	<i>Eurycarpus</i> <i>Ibacus</i>	<i>Penaeus</i> <i>Benthescymus</i> <i>Acanthochirana</i> <i>Carpopenaeus</i>	" <i>Palaemon</i> " <i>Oplophorus</i>
Middle and Late Jurassic	<i>Eryon</i> <i>Cycleryon</i> <i>Coleia</i> etc.	<i>Antrimpos</i> <i>Aeger</i> <i>Acanthochirana</i> <i>Bombur</i> etc.	<i>Udora</i> <i>Udorella</i> <i>Hefriga</i> <i>Blaculla</i>
Early Jurassic	<i>Coleia</i> <i>Proeryon</i>	<i>Antrimpos</i> <i>Aeger</i>	<i>Uncina</i> (?) Caridea indet.(?)
Late Triassic	<i>Tetrachela</i>	<i>Antrimpos</i> <i>Aeger</i> <i>Bombur</i>	

dae, Prosopidae, Geryonidae, Retroplumidae. BEURLEN (28) has shown convincingly that the Eryonoidea and Prosopidae retreated to deep water at the end of the Jurassic; many Nephropidae followed at the end of the Cretaceous, and Geryonidae in the Tertiary. Later work has added some Nephropidae to the first group, Penaeidae, *Oncopareia*, and Galatheidae to the second, and Retroplumidae to the third. BEURLEN has suggested that the cause of these changes of habitat is extensive regressions at critical times, reducing the extent of the shelf seas in which these decapods had flourished. The regression of the Nephropidae, which are abundant Jurassic and Cretaceous fossils and reduced in numbers during the Tertiary, coincides with the increase of Brachyura in the littoral habitat and was probably the result of competition.

BRACKISH-WATER

It is known (13) that at present some marine and some fresh-water Decapoda can tolerate brackish water, but Stenopodidea, Palinura, Galatheoidea, Hippoidea, Dromi-

acea, and Oxyrhyncha are exclusively marine. One of the oldest known decapod faunas, from the upper part of the Lower Triassic of Alsace, comes from a brackish or lagoonal facies. It comprises Penaeidea and primitive Astacidea. No Jurassic brackish-water decapods are known but in the Upper Cretaceous of northern Germany, MERTIN (192) collected *Linuparus*, *Palaeohomarus*, *Protocallianassa*, and *Necrocarcinus* from a bed in a brackish-water facies of Early Senonian age. In the Tertiary, the brackish-water Sarmatian (Upper Miocene) of Austria contains only the crab *Mioplax*, in contrast to the rich decapod fauna of the preceding fully marine stage.

FRESH-WATER

According to BALSS (13), the only Decapoda living in fresh water are Atyidae and Palaemonidae (Caridea), the genus *Aegla* (Galatheidae), Astacidae, Parastacidae, and Potamidae. The oldest of these are the Astacidae, which date back to the Late Jurassic or Early Cretaceous of Eurasia and the early Eocene of North America. Both families of fresh-water Caridea are known from the Tertiary. *Potamon* appears first in the Late Tertiary of Europe and India. *Aegla* is not known as a fossil.

TERRESTRIAL

Some tropical marine Decapoda have become adapted to life on land, particularly Paguroidea (Coenobitidae) and crabs (Gecarcinidae). They have developed lungs but lay their eggs in the sea. Both are questionably reported from the Late Tertiary.

ADAPTATIONS

Decapoda develop extreme adaptations to specialized functions and habitats which are often cited as examples of extreme diversification and specialization on various taxonomic levels. Only selected examples of adaptations for locomotion, respiration, reproduction, and protection (defense and concealment) will be given, particularly from fossil material. Recent reviews by LOCHHEAD of locomotion and by SCHÖNE of

complex behavior in living Crustacea, mainly Decapoda (in WATERMAN, 316) will assist in the functional interpretation of structures in fossil Decapoda.

LOCOMOTION

Adaptations are developed in adult Decapoda for swimming, walking, and climbing. Most decapod larvae show adaptations for planktonic life.

In macrurous natantian forms the long pleopods are well-developed swimming paddles. In the Brachyura, a flattening and expansion of pereopods, particularly dactyli of the fifth pereopods, produce paddles for propulsion, but it should be noted that similar shapes develop as adaptations for burrowing. Streamlining of the body in connection with fast movement occurs only in macrurous natantian decapods and to some extent in portunid crabs which swim sideways.

Walking legs differ greatly in shape according to the nature of the ground (mud, sand, dry beach, or dry land), still or current-swept water, speed of movement, and whether the body is carried close to or high above the ground. Climbing can be effected either by very long or by very short legs.

SCHÄFER (264) has studied the functions of the chelae in Brachyura in detail. Their shapes are closely related to (1) different modes of locomotion and feeding, and (2) different shapes of the cephalothorax and its anterior margin. This relation is particularly striking in the rapidly swimming Portunidae (e.g., *Portunus pelagicus*), where a greater width of the carapace is related to the great length and reach of the cheliped; the chela is here lightly built but strengthened by longitudinal ridges. This contrasts with the massive chelae in *Dromia* which are used in walking.

RESPIRATION

Apart from the few terrestrial Decapoda with lungs (respiratory surfaces inside the carapace), respiration requires a stream of water which is moved by the scaphognathites of the maxillae. The water is drawn in from openings between the carapace

margin and the bases of the legs and expelled near the bases of the antennae, but the current direction is reversible, so that all water in the branchial chamber can be kept fresh and clean. This is particularly important in crabs which burrow in sand. Here the reversed stream can continue for long periods. Inhalant respiratory tubes are formed by modified opposed antennules in a penaeid and in Hippoidea, by the antennae of the crab *Corystes*, and between the claws and the pterygostome of *Calappa*. The Oxystomata, which live mostly buried in sand with only the fronto-orbital region projecting, have elaborate pterygostomial grooves for the inhalant respiratory current. They deserve more detailed study in fossils. The branchiae vary greatly in number and position and are important in the taxonomy of living Decapoda. They can be seen occasionally in fossils but are never well preserved.

REPRODUCTION

The only characters related to reproduction which are observable in fossils are the position of the genital openings (gonopores), and only very rarely other primary sexual characters such as the petasma in male Penaeidea or the copulatory appendages of male Brachyura (appendages of the coxae of the fifth pereopods and first pleopods).

Secondary sexual characters are found more frequently. Differences in the shape of the abdomen were tentatively described in *Hoploparia stokesi* (WELLER) by BALL (10). They are obvious in the Brachyura, where the abdomen is triangular in males and broadly rounded in adult females (Fig. 232). There are also sexual differences in the fusion of abdominal segments. Others occur in the development of the chelae, usually larger in males.

PROTECTION

The most striking adaptations observable in fossils are related to defense and concealment. The strong calcification of the integument of slow-moving reptantian Decapoda (Palinuroidea, *Pemphix*, many Brachyura) and the weak calcification of swim-

ming forms (natantian Decapoda, most Portunidea) are such adaptations. The characteristic backward flight movement effected by sudden flexure of the abdomen in Caridea and macrurous reptantians is a defense mechanism which leads to further elaborate adaptations in the articulations between abdominal segments, the shortening of the first segment, which increases the mobility of the abdomen against the cephalothorax, the lengthening of the sixth somite, which contains the muscles operating the tail fan, the permanent curvature of the third somite in many Caridea, and a characteristic sculpture which is directed forward on most of the body but backward on the posterior abdominal somites, so as not to impede the backward movement. Distinctive spines and ridges protect the eyes, not only in macrurous forms (283) but also in some Brachyura (*Oxyrhyncha*). Many crabs have frontal, anterolateral, and lateral and a few also posterior protective spines. Many Decapoda defend themselves with their chelae, but they are not primarily defensive adaptations.

Concealment is achieved in various ways, particularly in Brachyura, where it has influenced the shape of the carapace and chelipeds. It is effected by covering the carapace with a sponge or shell (e.g., *Dromia*) or with plant debris fastened to hooked setae (e.g., Majidae), or in the development of mimetic shapes of the body which resemble corals (e.g., *Daira*, *Actaea*), stones, or irregular plant or animal growth (e.g., Parthenopidae, Majidae). Only this type of concealment adaptation can be established in fossils.

It should be understood clearly that burrowing for concealment in Decapoda is often strictly temporary. In these instances no burrow is formed, though lamination of the sediment is disturbed. SCHÄFER (264) has described the process of digging in for many Brachyura and macrurous decapods and the disturbance resulting from this action in *Corystes* and *Carcinus*. In other Decapoda (e.g., Astacidae, Thalassinidea, Grapsidae, *Scylla*, etc.) the burrows are more lasting tunnels of varying shape. Digging of these tunnels is done either with the aid of the chelae of the first and second

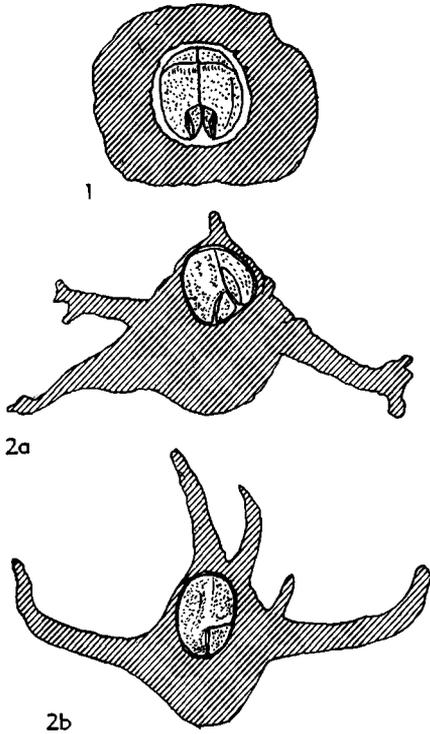


FIG. 241. Adaptation of chelipeds in Paguroidea (various sources).—1. *Pylocheles agassizi* A. MILNE-EDWARDS with 2 symmetrical chelae closing hole in rock.—2. *Pagurus* with chelae closing hole in shell overgrown by bryozoans; 2a, *P. alcocki* (BALSS) with 2 heterochelous chelae; 2b, *P. varians* (BENEDICT), with right chela only. [EXPLANATION: Substance surrounding crab-occupied hole indicated by oblique-ruled pattern.]

pereiopods or with posterior pereiopods. Many of these have sharpened and flattened dactyli, while the chelae may be square and sharp-edged (trowel-shaped).

Outstanding examples of adaptation for concealment are found in the Paguroidea (13, p. 1385-94). The primitive Pylochelidae have elongate symmetrical bodies and live in scaphopod shells or bamboo tubes. The advanced forms live in coiled gastropod shells which are mostly dextrally coiled. The abdomen is uncalcified, the right third to fifth pleopods are lost, the animal attaches itself to the shell by the tail fan and fourth and fifth pereiopods, which also clean the gills. The second and third pereiopods are walking legs. Chelipeds of the first pereiopods

can be used to close the shell in the manner of an operculum and can be accordingly modified in shape (Fig. 241).

MULTIPLE FUNCTIONS

The fact that single organs in Decapoda may be adapted to multiple functions is particularly important in the functional interpretation of the morphology of extinct forms. Carapace sculpture may be simultaneously a mechanical strengthening and a means of concealment on an irregular background. Spines may be a protection from predators as well as an aid to balancing in locomotion. Chelae may be organs of attack as well as defense, warning, or recognition; they may be used in locomotion, feeding, and burrowing, and also be so shaped as to direct the respiratory stream of water when at rest (263). Locomotive organs may be alternatively used also for cleaning or protection, and the abdomen and its appendages, while still functioning in locomotion, may carry the eggs in fertile females.

Various filtering mechanisms in feeding and respiration depend largely on setae on mouth parts or on the carapace, which are rarely preserved in fossils. Other setae may significantly alter the shape of the surfaces to which they are attached, particularly the limbs of Natantia or the bodies of crabs.

The similarity of the mechanics of digging in soft sand and swimming may lead to alternative uses of flattened dactyli in portunid crabs for both purposes. The agility necessary for climbing, which is a slow process, is also used for active protective masking of the body by many Oxyrhyncha.

COMMENSALISM, SYMBIOSIS, AND PARASITISM

Observations which could be interpreted according to one or other of these concepts will be discussed under this heading, without reference to the problem of distinctions between these ecological relationships.

The commensalism of Decapoda with sponges, coelenterates, mollusks, echinoderms, and ascidians, common in living forms, has not been observed in fossils.

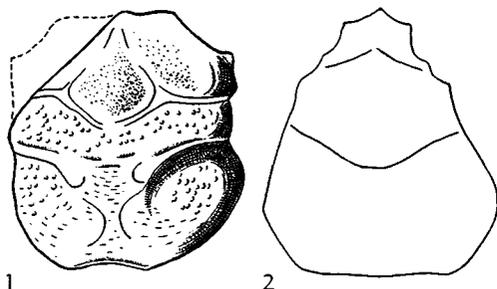


FIG. 242. Distortion of branchial chamber of Jurassic decapods owing to growth of parasites (after Houša, 1953).—1. *Pithonoton marginatum* VON MEYER.—2. *Mesogalthea striata* (REMÉŠ).

Common commensal natantians are Palaeomonidae and other Caridea, Stenopodidae, some Porcellanidae and Thalassinidae, and, among the crabs, some Parthenopidae (Eumedoninae) and Pinnoteridae (13). Specialized living crabs of uncertain systematic position (Hapalocarcinidae) cause growth deformation on hermatypic corals which are potential fossils.

The well-known symbiosis of pagurids and Actinaria cannot be recognized in fossils, as fossil Actinaria are unknown. A distinctive smoothly worn area on the last whorl of suitably shaped gastropod shells inhabited by hermit crabs and overgrown elsewhere by *Hydractinia* has been reported (84) in living and Miocene material. The epizoon growth can consist also of bryozoans and may extend beyond the apertural margin of the gastropod shell. Peculiar outgrowths can extend horizontally and vertically (in the position in which the shell is carried), producing the *Kerunia*-symbiosis (1), originally described as a genus of cephalopods from the upper Eocene of Egypt by MAYER-EYMAR but soon correctly explained by DOUVILLÉ. Not all associations of gastropods and bryozoan epifauna with tubular openings are necessarily to be interpreted as inhabited by pagurids. Tubes with constantly small diameter could have contained sipunculid worms, similar to *Aspidosiphon*, which inhabits solitary corals growing on small gastropods (Miocene to Recent).

Obvious evidence of parasitism is found frequently in Jurassic Decapoda (Galathei-

dae, Dromiacea) (Fig. 242) in which one side of the carapace is strongly inflated in the branchial region (6, 153, 247). This was also observed in Lower Cretaceous *Palaeastacus* ("*Phlyctisoma*") and *Notopocorystes*. Identical effects are produced in living Caridea, Galatheoidea, Paguroidea, and other Decapoda by Bopyridae (Isopoda), which are exclusively parasitic on Decapoda.

Balanid barnacles have been observed on several carapaces of *Leptomithrax atavus* from the Miocene of New Zealand. Other associations of cirripeds with decapods are common in the living fauna, particularly occurrences of the parasitic Rhizocephala, but they have not been found in fossils.

INDIRECT FOSSIL EVIDENCE OF LIFE ACTIVITIES

BURROWS

Infilled burrows of decapod Crustacea are fairly common objects. They can be definitely identified when they contain remains of burrowing Decapoda (e.g., *Protocallianassa*, *Callianassa*). Such finds (Fig. 243) have

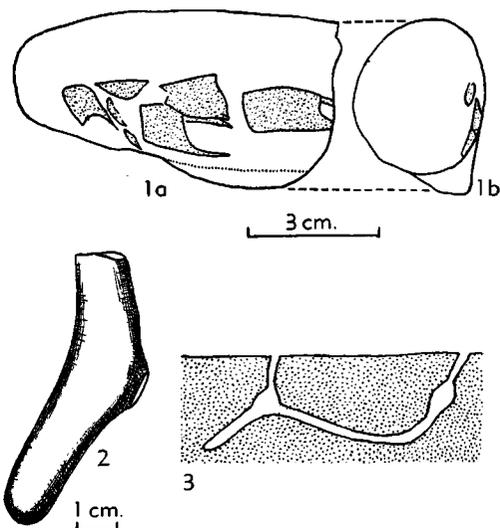


FIG. 243. Burrows of Callianassidae.—1. Burrow cast containing remains of *Protocallianassa* sp., U.Cret., Ger.; 1a,b, side and end views (after Mertin, 193).—2. Burrow cast of *Callianassa* sp., Paleoc., Australia (after Glaessner, 116).—3. Burrow of *C. californiensis* (after MacGinitie from Mertin, 193).

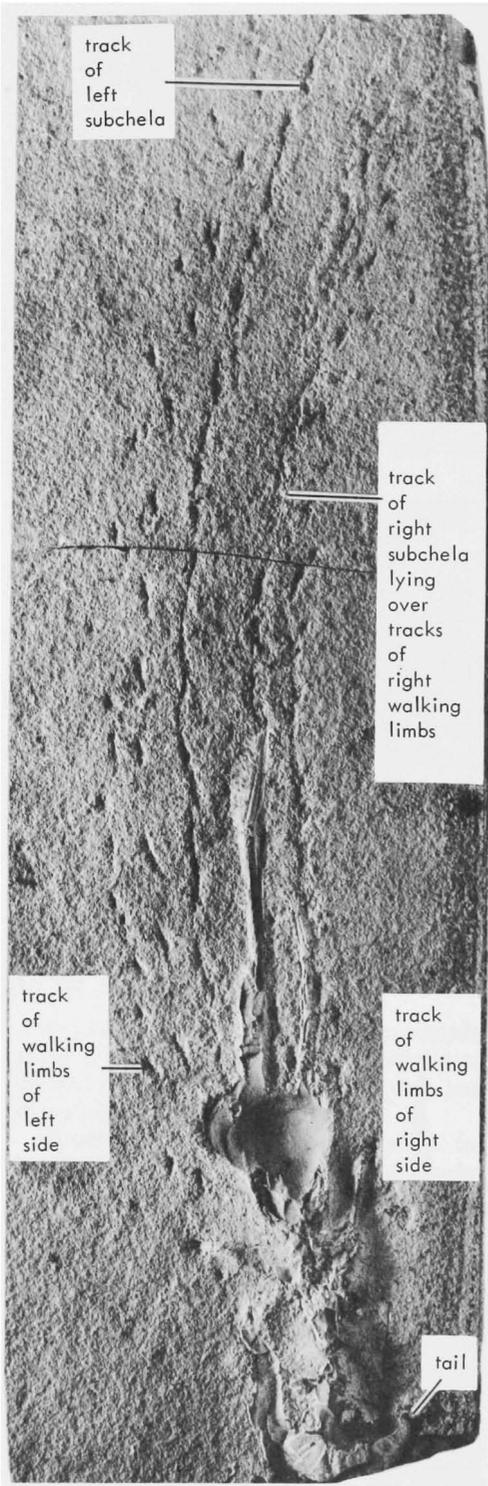


FIG. 243A. *Mecochirus longimanatus* (SCHLOT-HEIM), with walking track, U.Jur., Ger. (343a).

been reported from the Upper Cretaceous of Germany and the Miocene of western and central Europe. Similar infillings with the distinctive features of *Callianassa* burrows (Y-shaped branching, combination of vertical and horizontal or inclined tubes, local widening where the animal can reverse its direction of movement), occurring together with *Callianassa* chelae in the sediments, are also known from the Paleocene of southeastern Australia, the Lower Tertiary of Central Asia, and the Miocene of Japan. The burrows from the Miocene of the Vienna Basin were named *Thalassinoides callianassae* EHRENBERG, 1944. Similar burrows from the Upper Cretaceous had been known as *Spongites saxonicus* GEINITZ, while others, possibly made by Glypheoidea, occur in the Middle Triassic of northwest Germany (e.g., *T. visurgiae* FIEGE, 1944). Another type of burrow from these Triassic sediments is subcylindrical, horizontal, with two terminal vertical tubes. It resembles the burrows of *Cambarus*, was named *Pholeus abomasoformis* FIEGE, 1944, and could have been made by other macrurous reptantians. It must be remembered that similar burrows indicate possibly similar body shape and behavior, not systematic identity of the burrower. The comparison of the flat-lying U-shaped *Rhizocorallium* with crab burrows cannot be generally conclusive, since this type of burrow is well known from Cambrian to Triassic sediments which antedate the first appearance of crabs, as well as from younger Mesozoic rocks. This comparison was based mainly on the imprints of scratches on walls similar to those made by crab dactyli (but probably made by worm bristles or limbs of other arthropods). No definite fossil crab burrows are known. Most burrowing crabs do not make lasting burrows like those of the Thalassinioidea or Astacidae but dig in for concealment or temporary feeding, often in ephemeral beach deposits, and remain more mobile.

The distinctive cylindrical trace fossil *Ophiomorpha* LUNDGREN, 1891, with a diameter of 15 to 25 mm. and a nodular wall, known from Upper Cretaceous through Tertiary deposits of North America, Europe, and Japan, was considered by HÄNTZSCHEL (138) to be a decapod burrow lined with mud pellets.

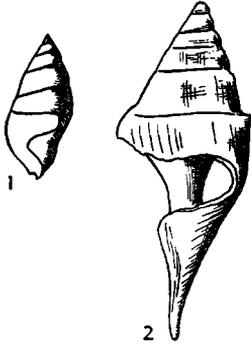


FIG. 244. Fossil gastropod shells damaged by pagurids (after Zapfe in Papp *et al.*, 224).—1. *Euthria intermedia* (regenerated), Mio., Austria. —2. *Clavilites parisiensis*, Eoc., Fr.

TRAILS

Walking trails of fossil Decapoda have been observed rarely and are identifiable only if the animal is preserved at the end of its trail (Fig. 243A). SCHÄFER (264) has stated that shallow-water crabs make deep stabs in the sediment with their dactyli, which are provided with chemoreceptors indicating buried food.

FEEDING

Observations on the feeding of Paguridae explain characteristic fractures of the apertural margin of Tertiary gastropods (Fig. 244). If the attack by the pagurid was interrupted, the gastropod could regenerate the fractured shell. Similar damage on the proximal margins of the scaphopod *Dentalium* could have been caused by pagurids or crabs (224).

Coprolites, or fecal pellets, with distinctive straight or transversely curved internal structures have been described from Jurassic to Tertiary shallow-water marine limestones from Europe, Africa, the Middle East, and America (e.g., *Favreina* BRÖNNIMANN, 1955; *Palaxius* BRÖNNIMANN & NORTON, 1960) and are said to be closely comparable with those of living Thalassinoidea (e.g., *Upogebia*, *Axius*).

MOLTING

Fossil Decapoda are frequently found in molting position (107, 193). Articulated

skeletons of macrurous decapods occur mainly in deposits formed under quiet conditions in which the relative positions of parts of a molted skeleton also remain undisturbed (e.g., Mesozoic bedded aphanitic limestones, Eocene London Clay). In *Homarus* the molting animal rests on its side, the integument opens between the carapace and the first abdominal somite, the carapace splits dorsally along the median line and the molted animal emerges, leaving the carapace displaced from the abdomen, with their axes forming almost a right angle. This occurs also in fresh-water crayfishes (Fig. 245,1). The same displacement and the splitting of the carapace are seen in *Hoploparia* (Fig. 245,2) from the Eocene and Cretaceous, in *Palaeohomarus* and *Oncopareia* from the Upper Cretaceous, and in the Jurassic *Glyphea* and *Protaxius*. Not all molts of *Oncopareia* are found lying on their sides; dorsoventrally compressed forms displace their carapaces in a horizontal plane (e.g., *Pemphix*, Triassic).

The molting proceeds differently in Brachyura, which remain standing with their sternal side downward. Here also the first opening occurs between carapace and abdomen, but the abdomen is freed first. The carapace is lifted upward and forward, remaining in hingelike contact with the anterior portion of the ventral skeleton but separating along the pleural suture. This separation is complete in Brachyrhyncha, but in *Maja* (Oxyrhyncha) the lower part of the carapace only moves outward along the pleural suture without separation. It is not known how the decalcified lineae in Homolidae function during molting, but the frequently occurring median parts of homolid carapaces may be molts. Fossil *Ranina*, *Notopocorystes*, *Coeloma*, *Potamon quenstedti* ZITTEL, and subfossil *Macrophthalmus latreillei* DESMAREST (Fig. 245,3) have been found in molting position, the carapace forming approximately a right angle with the sternum and abdomen and with the pleural suture opened. This is clear evidence that the abandoned molted skeleton was held in position in the soft mud during fossilization (SCHÄFER, 1951). Not all molts are recognizable as such; some disintegrate but in others the carapace falls back into normal position. Decalcifica-

tion of the exoskeleton (apart from lineae) is not noticeable, compared with effects of fossilization. The endoskeleton is corroded to facilitate molting, but it is only rarely and incompletely fossilized.

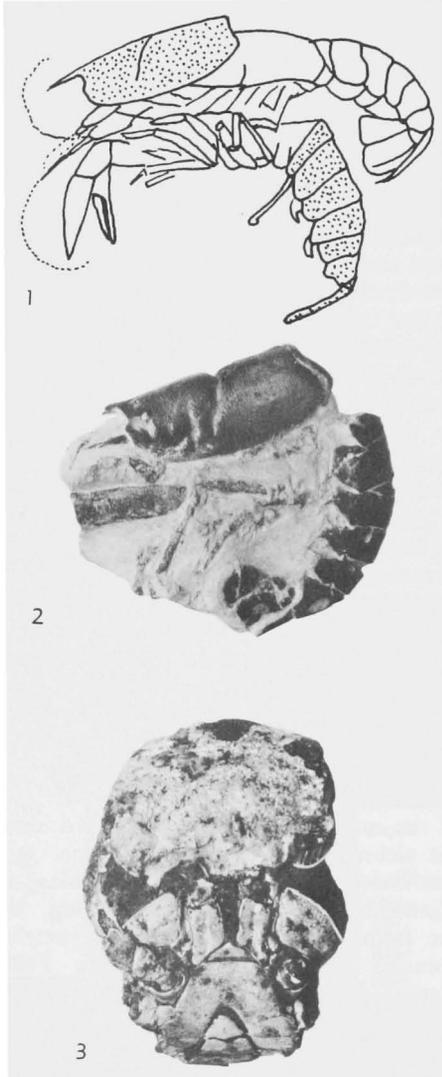


FIG. 245. Molting in decapods.—1. Fresh-water crayfish, *Parachaeraps* (Parastacidae), in process of molting (carapace and abdomen of shed exoskeleton, stippled) (redrawn from Hale, 139).—2. Molting position of *Hoploparia gammaroides* M'COY, L.Eoc., Eng. (after Glaessner, 107).—3. Molting position of *Potamon quenstedtii* (ZITTEL), enclosed in fresh-water limestone, U.Mio., Ger.; frontal view showing opening of pleural suture (from Glaessner, 107).

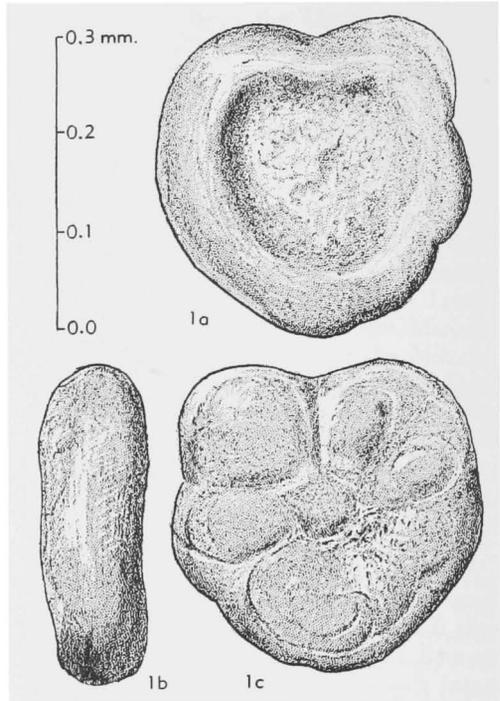


FIG. 246. Presumed gastrolith of larval nephropsidean, *Wechesia pontis* FRIZZELL & EXLINE, M.Eoc., USA (Tex.); 1a-c, int., lat., ext. views (from Frizzell & Exline, 99).

GASTROLITHS

Calcium carbonate resorbed prior to molting is deposited in the gastroliths of fresh-water Astacidea, but it is uncertain whether they have any significance for the calcification of the new skeleton in adult marine Decapoda, since Ca is abundantly available from sea water (see also PASSANO in WATERMAN, 316, and TRAVIS, 289). Small fossils from the marine middle and upper Eocene sediments of Texas and Louisiana have been described as gastroliths of larval Astacidea (*Wechesia pontis* FRIZZELL & EXLINE, 1958; *W. louisianae* FRIZZELL & HORTON, 1961) (Fig. 246).

AUTOTOMY AND REGENERATION

Specific instances of these processes have not been recorded in fossils, but it is very likely that they occur and will be observed.

Some Decapoda have the ability to drop an appendage at a preformed breaking

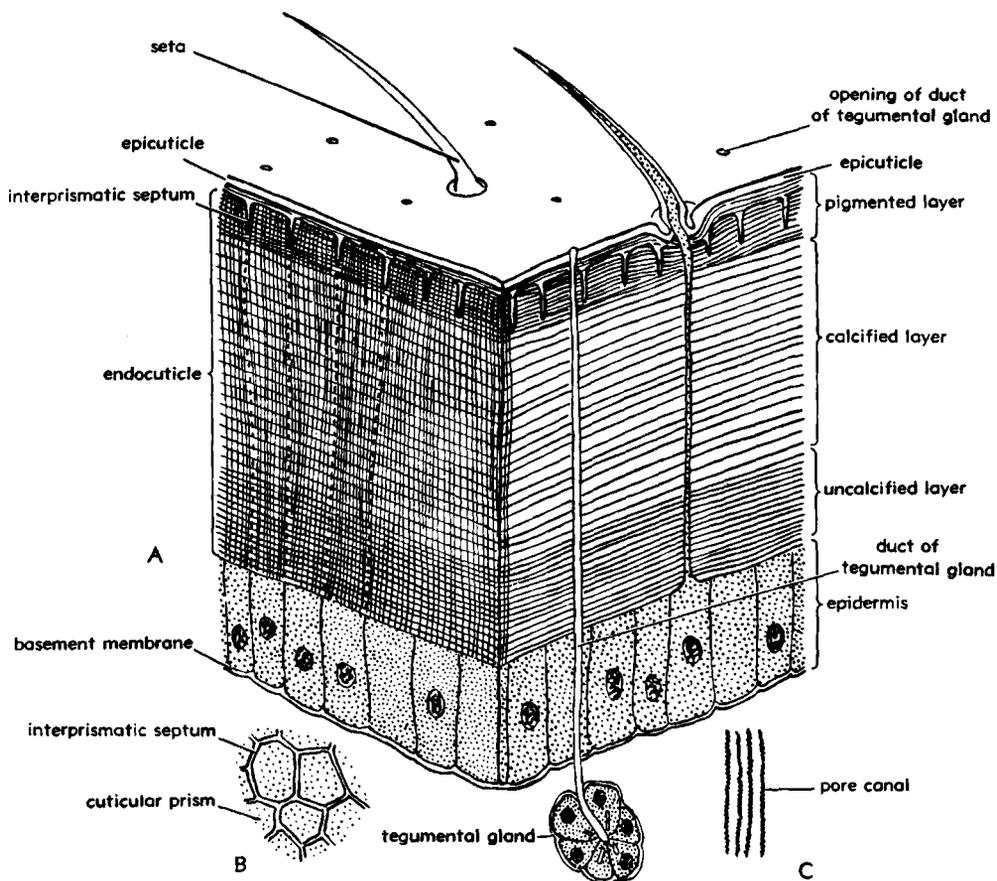


FIG. 247. Structure of decapod cuticle (from Dennell in Waterman, "The Physiology of the Crustacea," 316, by permission of Academic Press, Inc.). *A*. Diagram illustrating structure seen in vertical sections. —*B*. Pigmented layer of endocuticle in horizontal section. —*C*. Pore canals in vertical section of epicuticle seen at magnification higher than those of *A* and *B*.

plane by means of a reflex muscle action. This plane lies in the proximal part of the basiischium. An isolated fossil decapod limb ending proximally with a partial basiischium may have been shed by autotomy. Decapoda regenerate limbs or parts of limbs most readily at or near the preformed breaking plane (BLISS in WATERMAN, 316). The regenerate may differ from the original limb, and extreme instances such as replacement of an eye by an antenna have been described as heteromorphoses. Reversal of regenerated left and right chelae can occur in heterochelous forms. When two injured surfaces occur at the end of a limb, triple dactyls are regenerated (BUDENBROCK in BALSS, 1954, 13).

FOSSILIZATION

Conditions and effects of fossilization in decapod Crustacea vary greatly and affect morphological interpretations considerably. Few detailed studies have been carried out. Preservation varies from almost complete fossilization of external and internal skeleton, setae, branchiae, and even muscles, to fragmentation, and from almost unchanged composition of the integument to complete decalcification. Formation of concretions around decapod remains occurs frequently. The lamination of the pigmented and calcified layers of the decapod cuticle (Fig. 247) leads to varying degrees of decortication which may produce spurious surface

sculptures. This effect remains often unrecognized in descriptions and can lead to serious taxonomic errors. MERTIN (193) has found that chelae and abdominal terga of *Enoploclytia leachi* are coarsely pitted on their external and internal surfaces, with strong asymmetry of the external pits which have partly raised margins. The internal molds thus appear coarsely granulated. The thick integument of the carapace of this species shows reversal of sculpture compared with the internal mold.

Chitin is subject to slow bacterial decomposition. It may be preserved under conditions of rapid burial, particularly in bituminous sediments rich in organic matter. The completeness of decapod remains in Triassic, Liassic, and Oligocene black shales is due to the absence of scavengers and to anaerobic conditions of sedimentation. The most perfect preservation occurs in the lithographic limestones of the Upper Jurassic of Solnhofen (Bavaria), where even the setae fringing the appendages are preserved.

The preservation of branchiae of a macruran (Fig. 237) in phosphatic chalk was described by PELSENER, and phosphatized bundles of muscles are preserved in macrurans from the Senonian chalk of Lebanon but have not been described.

The frequent occurrence of Decapoda in spheroidal and ellipsoidal concretions in shales and sandstones is probably the result of decomposition of bodies rapidly buried in

sediment. It is not confined to Brachyura and Anomura actively burrowing in sediment and killed *in situ* by rapid sedimentation. The thalassinid remains preserved in infillings of their burrows must be dead bodies rather than molts, since molting does not take place in the burrow (264).

Fossilization is selective in various ways, distorting the record of fossil biocoenoses; (1) weakly calcified forms are at a disadvantage, except when buried in a reducing (and acid) environment; thus natantian forms will be less frequently represented in the fossil record; (2) since the most strongly calcified parts of skeletons will be preserved preferentially, claws and spines are most commonly found; most thalassinids and all pagurids are known from claws only, as their bodies are soft; (3) Decapoda living in areas of quiet sedimentation are favored, occurring commonly in well-bedded aphanitic limestones; (4) Decapoda living in areas of rapid sedimentation are favored; they occur in reef limestones and in bedded sands, silts and shales; (5) Anomura and Brachyura living in the intertidal zone where the sediment is frequently reworked are discriminated against and some (Hippoidea) are missing from the record; (6) decapod skeletons disintegrate rapidly in the water and in transport; only the resistant claws can be transported; (7) decapods are eaten by other decapods, cephalopods, and fishes; shell breccias consisting of decapod remains originating in this way are known but are rare.

STRATIGRAPHIC DISTRIBUTION

The earliest occurrences of Decapoda are not well documented stratigraphically. One species, *Antrimpos madagascariensis* VAN STRAELEN, 1933 (301), was found in the "Permotriassic" of northern Madagascar "without any possibility of determining its age precisely." Another, *Protoclytiopsis antiqwa* BIRSHTEYN, 1958 (42), comes from a core from a bore in the north of western Siberia from delta deposits containing Lower Triassic or Upper Permian Conchostraca, plant remains of Permian appearance, Low-

er Triassic insects, and unidentified *Posidonia*-like mollusks. It should be noted that among the Malacostraca found by MALZAHN in the Zechstein limestone (lower Upper Permian) of northwestern Germany, Isopoda, Tanaidacea, and probably Cumacea and Mysidacea were recognized, but no Decapoda.

The Penaeidae and Erymidae are definitely represented in the Lower Triassic, and Glypheidae of that age have been found recently. Middle and Upper Triassic Deca-

poda are more varied. They include *Pemphix sueuri*, the first common fossil representative of this order, but it is geographically restricted to the German Muschelkalk. The first Eryonoidea appear in the Alpine Upper Triassic.

The first great systematic and geographic expansion occurred in the Early Jurassic, but only a few unidentified specimens of Caridea have been found. The Astacidea are represented only by Erymidae; there are a few Palinuroidea, Thalassinoidea, and Paguroidea, and there is only one very primitive brachyuran species. The Lower Jurassic decapod fauna thus consists mainly of Penaeoidea, Erymidae, Glypheoidea, and Eryonoidea.

A further expansion in the Middle and Late Jurassic is at least partly due to adaptation of Decapoda to the reef environment in which primitive but very varied crabs (mainly Prosopidae) flourished. They are known only from Europe but could also be expected elsewhere. Another specially important addition to the Upper Jurassic Decapoda is the result of extremely favorable conditions for preservation in the lithographic limestones of Solnhofen in southern Germany.

The oldest fresh-water crayfishes have been found in Late Jurassic or Early Cretaceous sediments of Mongolia and China. In the Cretaceous the more advanced Nephropsidae began to replace the Erymidae. Similarly, the advanced Palinura (Palinuridae) gradually outnumbered the primitive Glypheoidea. Thalassinoidea resembling *Callianassa* were well established by mid-Cretaceous time. Their claws and the re-

mains of some reptant macrurans (e.g., *Hoploparia*, *Linuparus*) are locally fairly common Late Cretaceous fossils, but they lack general stratigraphic importance. Crabs were still rare in the Early Cretaceous, but they increased in numbers and geographic range at the top of the Lower Cretaceous (Albian) and in the Upper Cretaceous.

The rich crab fauna of the reef facies in the type Danian of Denmark is transitional in composition between the Upper Cretaceous and the Lower Tertiary (*Plagiophthalmus*, *Homolopsis*, *Dromiopsis*, *Necrocarcinus*, *Raninella*, *Caloxanthus*, "Panopeus," *Xantholithes*).

In the Tertiary a gradual approach to the modern fauna is found, with a rapid advance in numbers and diversification of crabs corresponding to a reduction in reptant macrurans. Recent Indopacific genera and families are widespread in mid-Tertiary sediments, because of the warmer climate of this period. The primitive Dromiacea and Raninidae, however, showed a remarkable reduction during this period, while the Oxyrhyncha appeared for the first time and flourished. The Xanthidae became widespread and varied but their Early Tertiary genera differed significantly from the Late Tertiary representatives, and many Late Tertiary crabs have survived to the present. *Callianassa* chelae are almost ubiquitous in Tertiary sediments. "Crab-beds" filled with carapaces of *Xanthopsis* or *Harpactocarcinus* and other similar genera are widespread in Lower Tertiary warm-water deposits, but the stratigraphic value of fossil decapods in the Tertiary is still very limited. Fresh-water prawns appeared in mid-Tertiary and fresh-water crabs in Late Tertiary time.

EVOLUTION

ORIGIN OF DECAPODA

The Decapoda are closely related to the Euphausiacea. These, although in many characters more primitive and presumably at least as ancient as the Decapoda, are unknown as fossils, presumably because of their weak integument. This creates a

major problem in tracing the history of the Decapoda to their origin.

The earliest known Decapoda are rare Permian Triassic Penaeoidea (Natantia) and Astacidea (Reptantia). A genus *Palaeopemphix* GEMMELLARO, 1890, has been described from the mid-Permian Sosio Limestone of Sicily, but its carapace furrows are

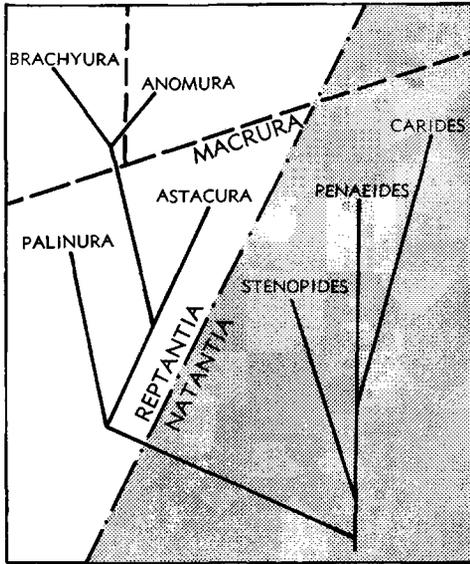


FIG. 248. Phylogeny of Decapoda inferred by BORRADAILE and BOUVIER (after Borradaile, 48, Bouvier, 1917).

unlike those of any known decapod and it requires re-examination before being accepted as an early representative of this order. The rich and well-preserved crustacean fauna of the Zechstein limestone (lower Upper Permian) of northwestern Germany has not so far yielded any eucarid Malacostraca. In a re-examination of Paleozoic Eumalacostraca, BROOKS (226) has suggested that among the pre-decapod Eumalacostraca, the benthonic, superficially eryonid-like, Pennsylvanian *Anthracaris* (order Pygocephalomorpha, which BEURLEN, 1930, had earlier placed in ancestral relationship to Decapoda), or the superficially penaeid-like *Anthracophausia*, now placed in the order Eocaridacea, or both, may be close to decapod ancestors. BURKENROAD (62) has given reasons why these fossils are unlikely to indicate the ancestry of the Decapoda or their polyphyletic origin, expecting that a Carboniferous eucarid will be found which may link the decapods with the Devonian-Lower Mississippian *Palaeopalaemon* (Eocaridacea). There is no evidence on the relations between Dendrobranchiata (Penaeidea) and other Decapoda (Pleocyemata), to indicate which suborder was older or

whether they evolved from a common decapod ancestor belonging to neither of these suborders. BURKENROAD described the hypothetical "stem-decapod" as "probably achelate, petasma-lacking, appendix-internabearing." It is also to be considered as trichobranchiate.

PHYLOGENY OF RECENT DECAPODA

Until recently, zoologists have been inclined to consider the Penaeidea as the ancestral Decapoda and to assume that early in their history the Stenopodidea and Caridea evolved from them, forming the suborder named Natantia. According to this view, the Palinura and Astacidea branched off later, giving rise to the remaining members of the so-called suborder Reptantia. They were the Anomura and the Brachyura. The main difficulties inherent in this hypothesis are the combination of primitive with advanced characters in the Penaeidea, the numerous ambiguities in the position of the Stenopodidea which have characters in common not only with Penaeidea but also with Caridea, Astacidea, and Thalassinoida, the profound and unbridged differences between Penaeidea and Caridea, and the lack of evidence for a derivation of Palinura and Astacidea from Penaeidea. In contrast, there was little doubt about the phyletic unity of the Reptantia (i.e., the necessity to postulate a common ancestor for Palinura and Astacidea), the derivation of the Anomura from Astacidea with the Thalassinoida nearest to the origin of this branch (48), and the "origine homarienne des crabes" which had been proposed in a brilliant discussion of then-existing knowledge of fossils and comparative anatomy by BOUVIER (51). This simple scheme (Fig. 248) was widely accepted. Suggestions for modifications resulted from work on larval stages, mainly by GURNEY, and on the morphology of Raninidae ("Tribe" Gymnopleura, BOURNE, 1922). This work suggested a separate polyphyletic origin of different brachyuran crabs (Dromiacea, Gymnopleura, Oxystomata, Brachyrhyncha) from Astacidea. The only fossil Decapoda consistently taken into

consideration at that stage of evolutionary study were Jurassic Eryonidae and Mesozoic Erymidae and Prosopidae. All authors noted the controversial character of their phylogenetic hypotheses.

EVALUATION OF PALEONTOLOGICAL DATA

The work of VAN STRAELEN, WITHERS, BEURLEN, and GLAESSNER during the period from about 1922 to 1932 provided new paleontological data which could be evaluated from the viewpoints of evolution and classification. BEURLEN and GLAESSNER rejected a number of assumptions of the zoological phylogeny and replaced them by the following conclusions, which seemed to be in better agreement with paleontological evidence: (1) Penaeidea, Stenopodidea, and Astacidea, the only Decapoda with three pairs of chelae, have a common origin, probably in a penaeid-like but trichobranchiate form. (2) The origin of all other Decapoda is seen in a glypheid-like benthonic form; this presumably achelate form was considered by BEURLEN as more primitive than the trichelate branch. (3) The fossil Glypheididea and *Pemphix* indicate very clearly the origin of the Thalassinoidea (and Paguroidea), Eryonoidea, and Brachyura through known transitional forms, while the origin of the Palinuroidea and of the remaining Anomura (Galatheoidea, Hippoidea) from different members of the same ancestral complex was inferred. (4) BEURLEN argued strongly in favor of deriving the Caridea from ancestral Thalassinoidea in Jurassic time, since they were absent from Triassic faunas containing natantians and subordinate to and less differentiated than the Penaeidea in the Jurassic; forms with exopodites are to be considered paedomorphic. The presence of phyllobranchiae and the variability of chelae with exclusion of the trichelate condition, as well as the main articulation between merus and carpus in pereiopods and presence of a stylamblys on pleopods, seem to be in agree-

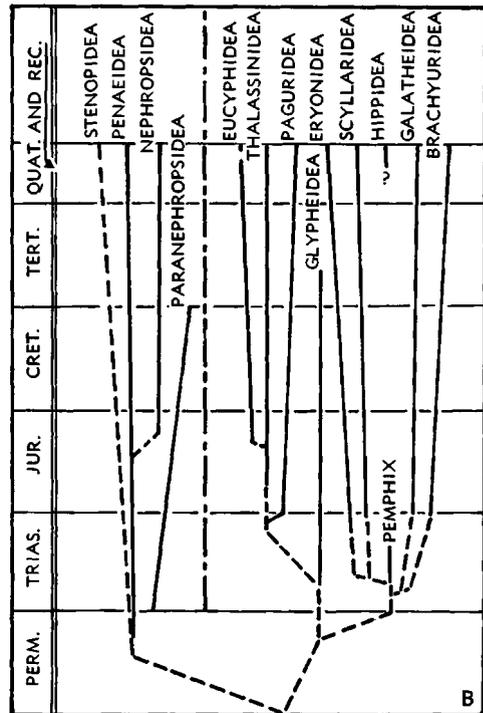
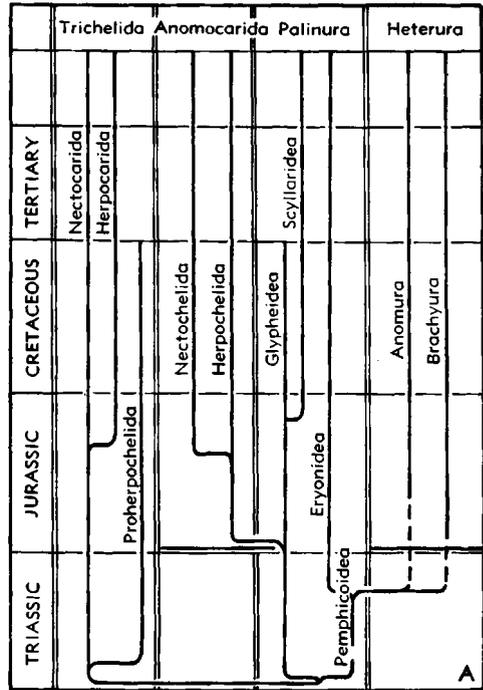


FIG. 249. Phylogeny of Decapoda (A) inferred by BEURLEN (1930) (27) and (B) inferred by BEURLEN & GLAESSNER (1930) (34).

ment with this phylogenetic hypothesis. The carapace furrows, where developed in Caridea, similarly suggest a glypheid-thalassinid rather than a penaeid origin of the Caridea (Fig. 249).

REVISIONS OF DECAPOD PHYLOGENY

MAJOR PROBLEMS

The revised phylogeny and the resulting reclassification of the Decapoda have been accepted in most textbooks and handbooks on invertebrate paleontology published after 1930. They were not generally accepted by zoologists and were criticized promptly by GROBBEN and later in detail by BALSS. After a revised summary had been published by GLAESSNER (118) (see Fig. 227, p. R410), a critical survey of the evolution of the eucaurids in relation to the fossil record was undertaken by BURKENROAD (62). A detailed discussion of the contentious questions of decapod phylogeny would be out of place here, but the main points of agreement and disagreement need to be summarized as a basis for discussion of the development of classification.

(1) The close relationship of the Penaeidea (and Stenopodidea) with the Astacidea was not accepted by BURKENROAD, who considered all other Decapoda as derived from Penaeidea in Permian time.

(2) This concept is contrary to the acceptance of the Natantia (Penaeidea, Caridea) as a natural grouping. None of the zoologists, however, has accepted BEURLEN's view that the Caridea originated from Thalassinoidea, entirely independently from the evolutionary line of the Penaeidea. The strictly paleontological evidence, based on rare fossils with thin integument, cannot be considered decisive, and only further investigations and discussion will clarify the important question of the origin of the Caridea.

(3) It is considered that derivation of the Eryonoidea and Palinuroidea from Glypheoidea (including *Pemphix*) rests on clear and at present undisputed evidence.

(4) There is also good evidence for the

derivation of Thalassinoidea from Glypheoidea (though BURKENROAD was inclined to regard the ancestor as thalassinid-like and the Glypheoidea as an offshoot.

(5) The question whether all or any of the Paguroidea, Galattheoidea, and Hippoidea are descendants of the Thalassinoidea, as BALSS believed, is debatable. At present zoological arguments carry more weight than the meager paleontological data.

(6) The origin of the Astacidea is not as problematic as their place in the classification. At first appearance of the Decapoda, the early Astacidea seem to be morphologically equally close to Penaeidea, with which they share three pairs of chelae ("Trichelida") and Glypheoidea which are achelate but benthonic ("Reptantia"). As the ancestral decapods are not known, it is impossible to evaluate fully the phyletic relations of the three different early branches of the order (Penaeidea, Astacidea, Glypheoidea). The last-named, being extinct, are not known in sufficient detail to be compared with the two groups with living representatives as to structure of branchiae and internal organs.

(7) The paleontologists' answer to the question of origin of the Brachyura from the group of *Pemphix* and *Pseudopemphix* among the Glypheoidea is well supported by abundant Jurassic material, including one transitional form (*Eocarcinus*). Zoologists still adhere to BOUVIER's view that the Brachyura originated from Astacidea (BALSS) or Thalassinoidea (GURNEY, BURKENROAD), but this is not supported by paleontological data. This controversy has little, if any, effect on classification.

A tentative phylogenetic scheme representing the views here expressed and conforming with the classification here adopted is shown in Fig. 250.

Serological data have been applied to the study of relationships among Decapoda (180). These data confirm in general current concepts of decapod evolution but occasionally reveal anomalies, some of which are explicable on the basis of paleontological observations similarly at variance with traditional zoological classification. An example is the closer link between *Dromia* and Palinura which was observed as early as 1930

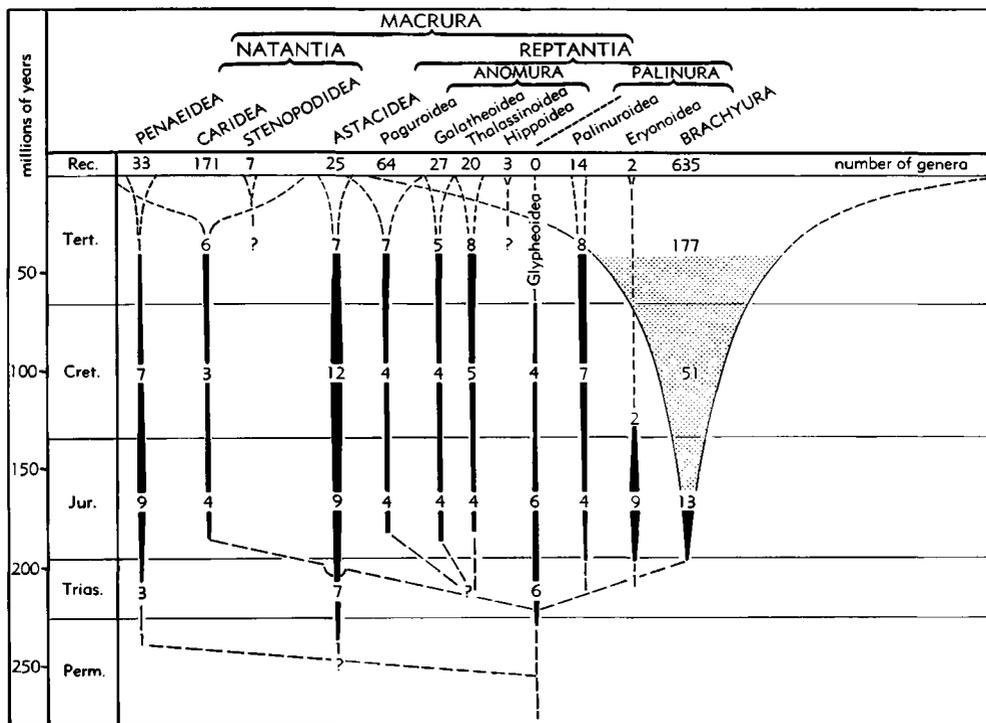


FIG. 250. Phylogeny and stratigraphic distribution of Decapoda. The numbers of pre-Quaternary genera are indicated approximately for each period. Numbers of Recent genera after CHACE (1951) (Glaessner, n).

and again more recently. This conflicts with the traditional views on astacidean ancestry of crabs but agrees with the paleontological data.

EVOLUTION OF BRACHYURA

The relatively greater abundance of fossil crabs permits more detailed phylogenetic studies compared with those based on fossil macrurous decapods. More precise descriptions of the fossils are required before evolutionary trends and genetic relationships can be reliably established. Present views on the phylogeny of the Brachyura are generally considered tentative.

A polyphyletic origin of the Brachyura which had been proposed by students of larval development in Dromiacea (GURNEY, LEBOUR) was found unacceptable by BALSS and others who upheld the view that the Dromiacea are primitive Brachyura. BEUR-

LEN (30) turned away from his earlier monophyletic constructions and considered the Dromiacea, Xanthimorpha, and "Oxymorpha" (Cancridea, Oxyrhyncha, Oxystomata, "Gymnopleura") as three parallel and independent phyletic groups. The paleontological basis of his argument is, however, faulty, as the Liassic age of the supposed xanthimorph ancestor "gen. nov. (cf. *Goniodromites*) *liassicus*" BEURLEN is unconfirmed and unlikely. *Oxythyreus* is an aberrant dynomenid resembling Oxystomata only in carapace outline.

BOURNE (50) considered the Raninoidea ("Gymnopleura") not as Oxystomata but as a group derived independently from Astacidea. They retain a number of primitive characters and have an elongate and posterolaterally incomplete carapace, not because of origination directly from macrurous forms but because of early adaptation to burrowing. The Brachyura are derived

monophyletically from extinct *Pseudopemphix*-like Glypheoidea in early Jurassic time. The Recent *Homolodromia* still resembles the earliest crabs. During Jurassic time the Brachyura did not rise above the organizational level of the Dromiacea. The Oxystomata appear in the Lower Cretaceous, but the details of the origination of Dorippoidea and Calappoidea are still obscure. The Raninoidea appear first in the Albian. Except for the elongation of the cephalothorax, the earliest Raninoidea do not differ substantially from contemporaneous Calappoidea.

The relative abundance and diversity of fossil Raninoidea compared with their Recent representatives shows that this group is now in a stage of decline. The family Leucosiidae is known only from the Cenozoic and appears to be derived from Calappidae. It is most strongly diversified in Recent faunas. The Dorippidae were also considered as derived from Calappidae (26), but they may be older; Cretaceous representatives have lately been recognized. An early Cretaceous diversification and later decline of the Oxystomata (except the more recent and more specialized Leucosiidae) is clearly demonstrated. Their ancestors have to be sought among the Dromiacea, but the mouth parts of Late Jurassic and Early Cretaceous crabs are not sufficiently well known to establish the origin of the main character of the Oxystomata.

GORDON (123) has pointed out that whereas most female decapods have genital openings in coxal position, the Brachyura, with exception of the Dromiacea, Raninidae, and Tymolinae, have sternal female gonopores. Therefore, she has suggested the separation of these exceptional groups from the sternitreme true Brachyura. Separation of a group on the basis of an obviously primitive character is an extreme application of "horizontal classification" which is not acceptable, particularly as the steps in the evolution from the primitive peditreme to the advanced sternitreme conditions have not yet been studied on fossil material.

The origin of the Oxyrhyncha is obscure. They appear first in the Eocene, with the families Majidae and Parthenopidae well

differentiated. Oxystomata and Homoloidea (*Latreillia*) have been suggested as ancestors, mainly because of similarities in form and sculpture of the carapace.

The Cancridae, Atelecyclidae, and Corystidae were separated from the Brachyrhyncha because of their rounded carapace bearing characteristic sculpture. These closely related families are not known in deposits older than Eocene, in which primitive Atelecyclidae (*Montezumella*) and also very advanced Cancridae (*Lobocarcinus*) occur. The Corystidae, which combine primitive characters with advanced adaptations for burrowing, are unknown as fossils. A derivation of the Cancridae from a form like the Upper Cretaceous *Avitelmessus* (Dakotiancridae, originally placed in Atelecyclidae) seems possible.

The origin of the highly diversified Brachyrhyncha remains problematical, mainly because of gaps in our knowledge of Cretaceous crabs, not only in general but also in details of the morphology of forms which have been described only superficially.

The origin of the Portunoidea, when considered on the basis of living forms, was sought near the Cancridae because of their resemblance with the Carcininae. These were thought to be primitive compared with the advanced Portuninae and the aberrant Podophthalminae. The available fossils show that the history of crabs adapted for active swimming is more complicated, and they could even be polyphyletic. There are early Tertiary xanthid-like forms (*Portunites*), but also highly specialized genera (*Enoplonorus*). The Cretaceous Carcineretidae are unlike typical xanthids. They have a number of advanced portunoid characters, such as adaptation of the fifth pereopod (where known) for swimming, transverse ridges on the carapace, keeled chelae, and long *Podophthalmus*-like eye stalks. There are also resemblances with the aberrant Palicidae and, according to BEURLEN, with *Necrocarcinus* (Calappidae).

The Xanthoidea are definitely represented in the Upper Cretaceous, the earliest undoubted genus of the Xanthidae being rather featureless *Caloxanthus*, from the Cenomanian. The representation of the

superfamily in the Lower Cretaceous is probable but at present obscure. *Etyus*, which because of its triangular front and small eyes has been placed in the Dynomenidae, conforms closely with *Xanthosia*, which also resembles Xanthidae. The origin of this family cannot be clearly demonstrated without further studies of *Xanthosia*. Another Lower Cretaceous genus, *Actaeopsis*, which was thought to have xanthid relationships, is even less well known. The problem was further confused in the literature by erroneous references to various Tertiary and later specimens as Cretaceous ("*Podopilumnus*," = *Galene*, *Glyphothyreus*). The Xanthidae were well established as a highly differentiated family at the beginning of the Tertiary, together with the related Geryonidae, Goneplacidae, and Pinnotheridae, but the fresh-water Potamidae appear only in the Upper Tertiary. The Grapsidae are generally rare in the Tertiary, possibly because of their littoral habitat. Only one record of Late Tertiary Gecarcinidae is found. The fossil material throws little light on the intricate problems of the relationships between these families. The Geryonidae, which are now insignificant, comprise important extinct Tertiary genera.

BEURLEN (26) established the superfamily Ocyropodoidea, which appears to have developed independently of the other Brachyrhyncha. It is known only from the Cenozoic, where the occurrence of the aberrant *Retropluma* is of particular interest. It resembles in some respects the Eocene *Retrocypoda*, here tentatively and questionably placed in the Palicidae, together with *Actaeopsis* and *Archaeopus*. The relationships of the living Palicidae have been interpreted in widely different ways; they have been placed with the Dorippidae by some authors and with the "Catometopa" (Brachyrhyncha with a square cephalothorax) by others.

BALSS has also drawn attention to characters of the Dromiacea in this enigmatic family. It is possible that the difficulty in placing it in the system results from the status of living Palicidae as relict forms of a group of genera which was more widespread in the Cretaceous and early Tertiary and which linked the early Dorippidae with Portunidae and with Ocyropodoidea. This hypothesis will have to be explored further when some tentatively placed and other as yet undescribed genera are studied in detail.

The evolution of the Brachyura is a striking example of an adaptive radiation of which the starting point is reasonably well established phylogenetically, morphologically, and in geologic time, and which is still going on. The first bursts of morphological differentiation occurred in Late Jurassic time within the limits of the Dromiacea grade of organization and mainly within the diversified family Prosopidae. This grade of organization survived to the present, partly in deep-water habitats, and partly through special adaptations for concealment (*Dromia*). In the Lower Cretaceous, the Oxystomata developed a special trend in the disposition of the mouth parts. The likely recognition of some fossil genera of uncertain relationships as ancestors of Dorippidae and Palicidae is expected to clarify the transition from Dromiacea to Oxystomata and also to Brachyrhyncha, which appear to have branched off in different directions about the same time. Abundant fossil material is available for the study of the evolution of the Raninoidea within the Oxystomata, which is characterized by retention of primitive together with development of adaptively specialized characters. The Oxyrhyncha, Cancridea, Portunoidea, Xanthoidea, and Ocyropodoidea became highly divergent in adaptation and diversified in early Tertiary time and continue to flourish.

CLASSIFICATION

EARLY CLASSIFICATIONS

The long history of decapod classification has been reviewed in detail by BALSS (1940, 1957). For the purpose of introducing the

systematic treatment adopted for the *Treatise*, it will suffice to begin with the major classification used in the reports of the Challenger Expedition. BATE (1888) used the following divisions:

Classification of Bate (1888)

Suborder MACRURA

Division Trichobranchiata

Group Aberrantia (Galatheidae, Pylochelidae, Thalassinidae, Callianassidae, Axiidae, Thaumastocheilidae)

Group Normalia (tribe Synaxidea—Scyllaridae, Palinuridae; tribe Astacidea—Eryonidae, Homaridae, Astacidae; tribe Stenopidea—Stenopidae [Stenopodidae])

Division Dendrobranchiata (Penaeidea)

Division Phyllobranchiata [including Caridea]

HENDERSON (1888) included in the Anomura the present Dromioidea, Raninoidea, Hippoidea, Paguroidea, and Galatheoidea. MIERS (1886) described some of the crabs, grouped according to H. MILNE-EDWARDS as Oxyrhyncha, Cyclometopa (Cancriidea), Catometopa (Ocyopodoidea), Oxystomata (Leucosiidae).

BOAS (1880), in the first fundamental study on phylogenetic relations of the Decapoda on the basis of their comparative morphology, divided them into the Natantia (comprising the Penaeides, including *Stenopus*, and the Eukyphotes, a new name replacing the older name Carides), and the Reptantia, comprising Nephropidae, Loricata (Palinuridae and Scyllaridae), Eryonidae, Thalassinidae, Anomala (Paguridae, Galatheidae, Hippidae), and Brachyura (Brachyura genuina and Dromiacea). ORTMANN, BOUVIER, and ALCOCK subsequently elaborated and improved this classification in detailed studies on various groups. BOUVIER tried to reconcile H. MILNE-EDWARDS' earlier and BOAS' later major subdivisions, giving them finally (1940) the following form.

Classification of Bouvier (1940)

Suborder MACRURA NATANTIA

Suborder REPTANTIA

Section Macrura reptantia (comprising "tribes"

Homaridea, Palinura—including Eryonidea—and Thalassinidea)

Section Anomura

Section Brachyura

This classification found little favor, partly because of the awkwardness involved in the use of the first three names on the list.

In the meantime, BORRADAILE (1907) had published a complete formal classification,

together with hypothetical phylogenetic schemes, which was widely accepted. The following major taxa were used:

Classification of Borradaile (1907)

Suborder NATANTIA

Tribe Penaeides

Tribe Carides

Tribe Stenopides

Suborder REPTANTIA

Tribe Palinura (incl. superfamilies Eryonidea, Scyllaridea)

Tribe Astacura

Tribe Anomura (incl. superfamilies Galatheidea, Thalassinidea, Paguridea, Hippidea)

Tribe Brachyura

Subtribe Dromiacea (incl. superfamilies Dromiidea, Homolidea)

Subtribe Brachygnatha (incl. superfamilies Brachyrhyncha, Oxyrhyncha)

Subtribe Oxystomata

The term tribe which plays an important part in this and subsequent classifications is defined in the *International Code of Zoological Nomenclature* (1961) as subordinate to subfamily. The terms infraorder and section are available to replace terms between the rank of suborder and superfamily.

CLASSIFICATIONS BY BEURLEN AND GLAESSNER

In 1928, BEURLEN criticized the traditional classifications. On the hypothesis that the Decapoda could be divided into two conservative phyletic lines, one nektonic and the other benthonic, with "iterative" sidelines repeatedly and independently evolving similar characters, he divided the order into two groups named Rostralia and Arostralia. This phylogeny and the resulting grouping were soon discarded and the names were not used.

BEURLEN & GLAESSNER (34) and BEURLEN (26) revised current classification so as to express new conclusions and hypotheses on phylogeny based on much more information on fossil Decapoda than had been available to previous systematists. This led to a radical alteration of the traditional system, eliminating the taxa Macrura, Natantia, Reptantia and introducing many new terms. Critical reviews of this classification make

it possible to eliminate now some of these terms which expressed hypothetical phylogenetic concepts without underlying morphological realities. The BEURLEN & GLAESSNER (1930) classification included the following units (newly introduced names are here followed by "B. & G.").

Classification of Beurlen & Glaessner (1930)

- Suborder TRICHELIDA B. & G.
 - Division Nectochelida B. & G.
 - Tribe Penaeidea
 - Tribe Stenopidea [Stenopodidea]
 - Division Proherpochelida B. & G.
 - Tribe Paranephropsidea (Erymidae [Erymidae], Stenochiridae)
 - Division Herpochelida B. & G.
 - Tribe Nephropsidea (Nephropsidae, Potamobidae, Parastacidae)
- Suborder HETEROCHELIDA B. & G.
 - Division Anomocarida B. & G.
 - Tribe Thalassinidea
 - Subtribe Axioida B. & G. (Axiidae)
 - Subtribe Thalassinoida B. & G.
 - Tribe Paguridea
 - Tribe Eucyphidea (eight subtribes)
 - Division Glypheocarida B. & G.
 - Tribe Glypheidea (Glypheidae, Mecochiridae)
 - Division Gastralida B. & G.
 - Subdivision Palinura
 - Tribe Pemphicidea B. & G.
 - Tribe Eryonidea
 - Tribe Scyllaridea
 - Subdivision Heterura B. & G.
 - Tribe Galatheidea
 - Tribe Hippidea
 - Tribe Brachyuridea (divided into six "Superfamilies or Subtribes")

At about the same time BEURLEN (27) published another classification which expresses similar views on phylogenetic relationships but gives different taxonomic importance to some of the major taxa.

Classification of Beurlen (1930)

- Suborder TRICHELIDA
 - Division Nectochelida
 - Tribe Penaeidea
 - Tribe Stenopidea
 - Tribe Uncinoidea
 - Division Proherpochelida
 - Tribe Paranephropsidea
 - Division Herpochelida
 - Tribe Nephropsidea
- Suborder ANOMOCARIDA
 - Division Nectocarida
 - Tribe Eucyphidea

- Division Herpocarida
 - Tribe Thalassinidea (not divided into subtribes)
 - Tribe Paguridea
- Suborder PALINURA
 - Division Glypheidea
 - Tribe Pemphicoida
 - Tribe Glypheoida
 - Division Eryonidea
 - Division Scyllaridea
- Suborder HETERURA
 - Division Anomura
 - Tribe Galatheidea
 - Tribe Hippidea
 - Division Brachyura
 - Tribe Dromiomorpha (including subtribes Dromiacea, Oxyrhyncha, Ocypodoida, Cancriformia)
 - Tribe Xanthimorpha (including subtribes Portunoida, Xanthoidea)
 - Tribe Oxystomata (including subtribes Gymnopleura, Calappoida)

The main differences between BEURLEN'S system and that published earlier by BEURLEN & GLAESSNER are (1) elevation of divisions of the Heterochelida to the rank of suborders, (2) corresponding elevation of the Eucyphidea [=Caridea] and the Thalassinidea+Paguridea to the rank of divisions under new names, (3) transfer of the Pemphicidea to the Glypheidea and elevation of Eryonidea and Scyllaridea to divisions (all constituting the Palinura *sensu lato*), and (4) placement of the residual Anomura *sensu stricto* (Galatheidea+Hippidea) as a division with the same rank as Brachyura. The brachyuran tribes were reconstituted by the inclusion of several subtribes of Brachyrhyncha in the Dromiomorpha.

REVISIONS SUBSEQUENT TO 1930

An early correction of the 1930 classifications eliminated the Proherpochelida and Paranephropsidea, as the Erymidae were found (112) to be directly related to early Nephropsidea. The lines of evolution are divergent rather than "iterative," as BEURLEN (25) had claimed. This eliminated, in turn, need for the terms Herpochelida and Nectochelida.

The Pemphicidea were subordinated to the infraorder Glypheocarida, and the Bra-

chyura were restored to the same rank, which was also given to Anomocarida, Palinura, and Anomura (*sensu stricto*), while the "Division Gastralida" was eliminated in a revised synopsis (118) which otherwise followed BEURLEN & GLAESSNER (34).

This left three major contentious innovations of decapod classification: (1) the suborder Trichelida, (2) the infraorder Anomocarida, and (3) the infraorder Anomura (*sensu stricto*). The question whether the Glypheidea should be subordinated to the Palinura or coordinated with them as Glypheocarida is a comparatively minor problem of vertical versus horizontal classification.

The concept of a taxon Natantia is no longer acceptable because of evidence for early separation of the Penaeidea and Caridea and lack of evidence for linkage of these groups. The origin of the Caridea from early Thalassinioidea, on which the taxon Anomocarida was based, cannot be well documented by fossils, because of the weak calcification of the integument of swimming and burrowing forms. BEURLEN's morphological arguments and supporting negative paleontological evidence, which seemed convincing to GLAESSNER, have been rejected by zoologists. The wide divergence of adaptations makes a satisfactory diagnosis of the Anomocarida impossible. Hence, it is a hypothetical phylogenetic rather than a practical taxonomic concept, which will not be included in the *Treatise* classification. Similarly, the separation of the Galatheidea+Hippidea from the Thalassinidea+Paguridea is a phylogenetic hypothesis rather than a convenient taxonomic division and has been rejected by zoologists. BALSS (1954) accepted BORRADAILE's Anomura (*sensu lato*) with all four subdivisions, while BURKENROAD (1963) separated the Thalassinidea from the Anomala, following BOAS. Admittedly, there is no convincing paleontological evidence on these relationships, as fossil Paguroidea are only known from chelae and fossil Hippoidea are unknown. BALSS & GRUNER (13) have given morphological evidence for close relationships between Anomura (*sensu lato*), and this category is here retained. These authors had included the Glypheidea in the

Anomura, but this is an inconvenient application of vertical classification. The Glypheoidea are probable ancestors of the Anomura, and of other phyletic lines as well, so that they are not now included in the Anomura.

The suborder Trichelida was defined (26) as follows: Macrura with well-developed abdomen. Carapace laterally compressed or cylindrical, with well-developed rostrum. Either all pereopods or pereopods 2 to 5 with seven segments; pereopods 1 to 3 chelate, with the dactylus placed medially. Pleopods well developed, without stylamblys. Antennal stalk always with scaphocerite. Mandible undivided. First maxilliped without caridean expansion ("Eucyphidenanhang"); maxilliped 3 mostly seven-jointed, resembling pereopod. Pleura of second abdominal segment not markedly enlarged. Gills consisting of trichobranchiae of dendrobranchiae.

This diagnosis excludes the Caridea and all non-nephropsid Reptantia. It reflects the view of a derivation of Nephropsidea from Penaeidea or of their common origin. [The question of the place of the Stenopodidea will not be discussed here, because of the lack of fossil evidence.] This is generally accepted. The recognition of the suborder Trichelida implies, however, that the Caridea had a different origin. In BEURLEN's view this was within the Glypheidea, which were the ultimate and remote ancestors of the Trichelida (Fig. 249, A). This view is hypothetical and unacceptable to zoologists. As their arguments against relationships being closer among Trichelida than between them and others (e.g., Glypheoidea, Caridea) cannot readily be refuted, it is best to hold the taxon Trichelida in abeyance for the present. This has the practical advantage that the sequence of major taxa in the *Treatise* classification can be kept close to that used in zoological classifications. The content of the taxa Macrura, Natantia, and Reptantia can thus be indicated readily in terms of classification used in a general descriptive sense without giving them formal recognition, which is unwarranted, since they refer to units with common adaptations and habit, rather than origin.

BURKENROAD (62) separated the Penaeidea from all other Decapoda as a suborder Dendrobranchiata. The others are placed in a new suborder Pleocyemata. It is noted that BURKENROAD retained a "supersection Natantia" (Stenopodida+Eukeyphida) and a "supersection Reptantia" with the diagnosis "loss of all pleurobranchs anterior to the 5th thoracic somite, specializations for benthonic life." His revision of the Recent Eucarida has not yet been published.

TREATISE CLASSIFICATION

The classification adopted for the *Treatise* takes the following form (to the level of superfamilies):

Classification Adopted in Treatise

Order DECAPODA

Suborder DENDROBRANCHIATA (1)

Infraorder Penaeidea (2)

Superfamily Penaeoidea (3)

Superfamily Sergestoidea (4)

Suborder PLEOCYEMATA (5)

Infraorder Stenopodidea (6)

Infraorder Uncinidea (7)

Infraorder Caridea (8)

Infraorder Astacidea (9)

Infraorder Palinura (10)

Superfamily Glypheoidea (11)

Superfamily Eryonoidea (12)

Superfamily Palinuroidea (13)

Infraorder Anomura (14)

Superfamily Thalassinoidea (15)

Superfamily Paguroidea (16)

Superfamily Galatheoidea (17)

Superfamily Hippoidea (18)

[Macrura include nos. 1-10; Natantia (*sensu lato*) nos. 1-8, Natantia (*sensu stricto*) nos. 6-8; Reptantia (*sensu lato*) nos. 9-18, Reptantia (*sensu stricto*) nos. 9-13.]

Infraorder Brachyura

Section Dromioidea

Superfamily Dromioidea

Superfamily Homoloidea

Superfamily Dakoticancroidea

Section Oxystomata

Superfamily Dorippoidea

Superfamily Calappoidea

Superfamily Raninoidea

Section Oxyrhyncha

Section Cancridea

Section Brachyrhyncha

Superfamily Portunoidea

Superfamily Xanthoidea

Superfamily Ocypodoidea

The purpose of this *Treatise* is best served by a cautious approach to taxonomy. A systematic review is its main objective and should be meaningful to both zoologists and paleontologists. It should include only such higher taxonomic categories as are necessary for a coherent presentation of our present knowledge of relationships and omit those which were introduced to present particular and subsequently disputed hypotheses of decapod phylogeny. As phylogeny cannot be perfectly represented by any sequential arrangement of taxa, and as such an arrangement is the main part of this *Treatise*, it is not considered desirable that disputed hypotheses which would substantially affect the traditional sequence should dominate it, to the exclusion of more generally acceptable and less hypothetical views. Hence, without prejudice to further discussion and development of phylogenetic views based mainly on paleontological data, these views and their taxonomic expression are partly held in abeyance until they can be more fully discussed. The critical points raised by the zoologists are therefore given full weight as far as they support traditional as against (for zoologists) unfamiliar groupings and sequential order of Decapoda.

A tabulation of suprageneric divisions of the Decapoda showing their stratigraphic occurrence and numbers of contained genera is given on pages R114-116. Stratigraphic and geographic distribution of major taxonomic divisions is shown in Figure 251.

SYSTEMATIC DESCRIPTIONS

Order DECAPODA Latreille, 1803

Eucarid malacostracans in which the first three pairs of thoracopods are modified as maxillipeds, so that no more than five

pairs are locomotory pereiopods; one or more pairs of pereiopods end in chelae, those of first pair commonly very strong; exopods of pereiopods mostly lost in adults but may be present in larvae. Abdomen is

either fully developed, with locomotory pleopods, or reduced in various ways, finally being incurved under thorax so as to protect gonopods in males and eggs in females. *Permotrias*.-Rec.

Suborder DENDROBRANCHIATA Bate, 1888

Natantian decapods with dendrobranchiate gills; first three pereopods chelate; eggs not carried by females, hatched as nauplius. *Permotrias*.-Rec.

Infraorder PENAEOIDEA de Haan, 1849

Carapace laterally compressed, thin-walled; rostrum strong; first thoracic somite not shortened, not overlapped by pleura of second somite; abdomen long; antennular stalk long; scaphocerite large, oval; chelae of first three pereopods similar in shape. Males with petasma on first pleopods, females with spermatheca (thelycum) on last thoracic sternum. [Includes at least 30 Recent genera containing more than 300 species. Rare as fossils.] *Permotrias*.-Rec.

Superfamily PENAEOIDEA Rafinesque, 1815

[*nom. transl. et correct.* GLAESSNER, herein (*ex* family *Pencidia* RAFINESQUE, 1815, =*Penaeidae* RAFINESQUE, 1815, ICZN)]

Third pereopods not stronger than first two pairs, maxillipeds with seven segments; antennules with stylocerite; branchiae numerous, dendrobranchiate; eggs not carried on pleopods. *Permotrias*.-Rec.

Family PENAEIDAE Rafinesque, 1815

[*nom. correct.* WHITE, 1847 (*pro* family *Pencidia* RAFINESQUE, 1815) (*Penaeidae* on official list, ICZN)] [=*Pencidea* DANA, 1852]

Rostrum laterally compressed and well developed so that it overlaps ocular segment, pereopods four and five not reduced. [This family was divided by BALSS into subfamilies named *Penaeinae*, *Aristaeinae*, and *Sicyoninae*. These are considered families of the superfamily *Penaeoidea* by HOLTTHUIS, who divides the *Penaeidae* into *Penaeinae* and *Haliporinae*, the *Aristaeidae*

into *Aristaeinae* and *Benthescyminae*, the *Sicyonidae* being undivided. The distinguishing characters are only rarely and very incompletely preserved in fossils.] *Permotrias*.-Rec.

Penaeus FABRICIUS, 1798 [on official list, ICZN] [**P. monodon*; SD LATREILLE, 1810] [=*Pseudocrangon* SCHLÜTER, 1862 (type, *Palaemon tenuicauda* VON DER MARCK, 1858); *Machaerophorus* VON DER MARCK, 1863 (type, *M. spectabilis*)]. Rostrum with teeth dorsally and ventrally; antennular flagella short. *U.Cret.*(*Senon.*), Ger.; *L. Tert.*, India; *Rec.*, cosmop.—FIG. 252.4. *P. latesulcatus* (KISHINOUE), *Rec.*; $\times 0.5$ (139).

Acanthochirana STRAND, 1928 [*nom. subst. pro Acanthochirus* OPPEL, 1862 (*non* PETERS, 1861)] [**Udora cordata* MÜNSTER, 1839; SD GLAESSNER, 1929]. Carapace smooth, rostrum with spines; antennules short; antennae twice length of body; 1st pereopod shorter than others, with spinose merus and carpus, 3rd pereopod longest; 3rd maxilliped as in *Aeger*, spinose. *U.Jur.*, Ger.; *U.Cret.*(*Cenoman.*), Lebanon.—FIG. 253.1. **A. cordata* (MÜNSTER), *U.Jur.*, S.Ger.; $\times 0.7$ (219).

Aeger MÜNSTER, 1839 [**Macrowrites tipularius* VON SCHLOTHEIM, 1822; SD WOODS, 1925]. Rostrum long, sides granulate; 3rd maxilliped with thin long multiple spines; pereopods 1 to 3 spinose, increasing in length, 3rd one with long chelae; surface of carapace finely granulate; uropods with diaeresis. [A monotypic family (*Aegeridae* BURKENROAD, 1963) has been proposed, but re-examination of other fossil *Penaeoidea* is required before it can be defined adequately.] *U.Trias*.-*U.Jur.*, Eu.—FIG. 252.3. **A. tipularius* (SCHLOTHEIM), *U.Jur.*, Ger.; reconstr., $\times 0.5$ (11).

Antrimpos MÜNSTER, 1839 [**A. speciosus*; SD WOODS, 1925] [=*Kölga* MÜNSTER, 1839 (no type)]. Antennules very short, antennae twice length of body; rostrum dentate, carapace smooth, thin; length of pereopods increasing from 1 to 3; 6th abdominal somite longest. [According to BALSS (1922, p. 130) a synonym of *Penaeus* FABRICIUS. This is a "collective" genus in which many fossil species not showing diagnostic characters of Recent *Penaeidae* have been placed.] *Permotrias*.-*Cret.*, Eu.-Madagascar.—FIG. 253.6. **A. speciosus* (MÜNSTER), *U.Jur.*, Ger.; $\times 0.7$ (219).—FIG. 252.1. *A. kiliani* (VAN STRAELEN), *U.Jur.*, Fr.; reconstr., $\times 1$ (296).

Benthescymus BATE, 1881 [**B. crenatus*; SD BATE, 1888]. Rostrum short, compressed, forming crest; cervical groove strongly marked; carapace with lateral longitudinal ridges; abdomen compressed; antennular stalk excavated to accommodate eye; pereopods slender, pleopods long. [Deep-water benthos of warm seas.] *U.Cret.*(*Senon.*), Lebanon; *Rec.*—FIG. 253.2. *B. libanensis* (BROCCHI), *U. Cret.*(*Senon.*), Lebanon; reconstr., $\times 0.5$ (115).

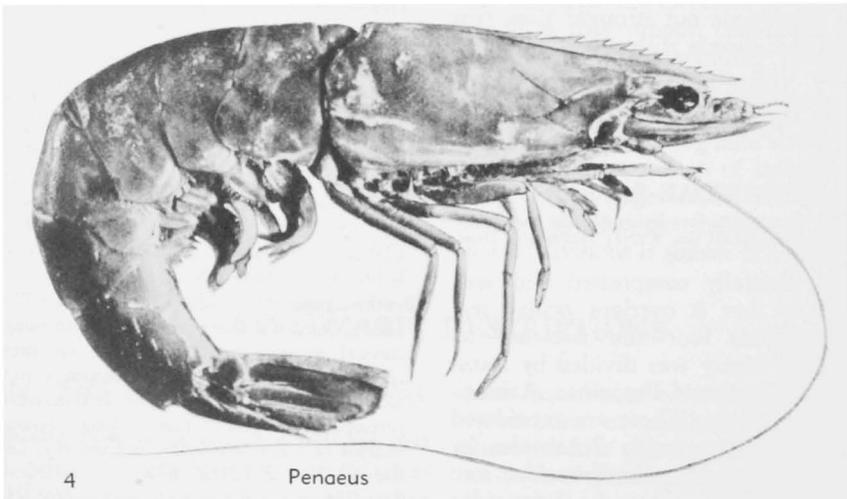
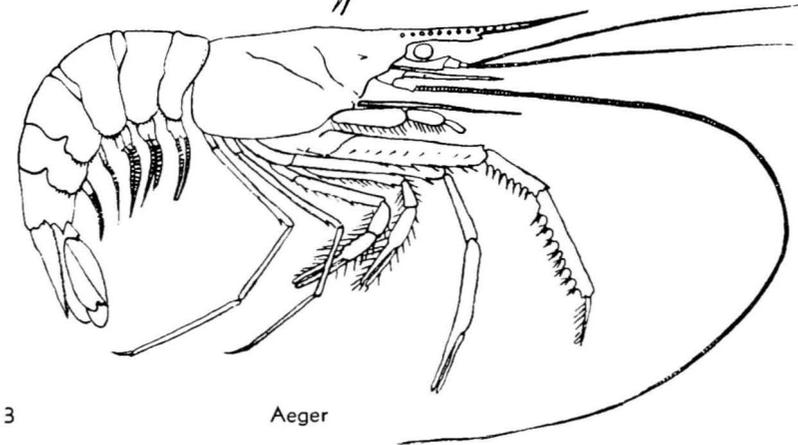
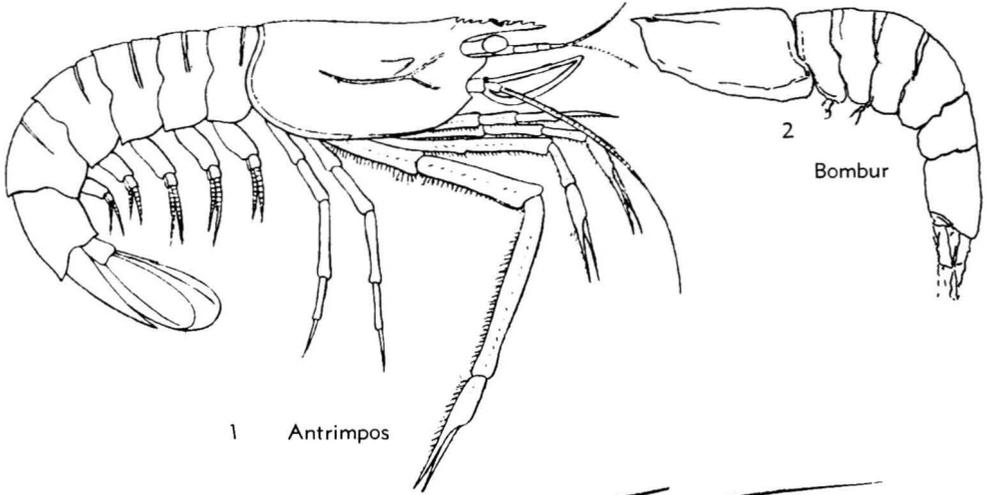


FIG. 252. Penaeidae (p. R447).

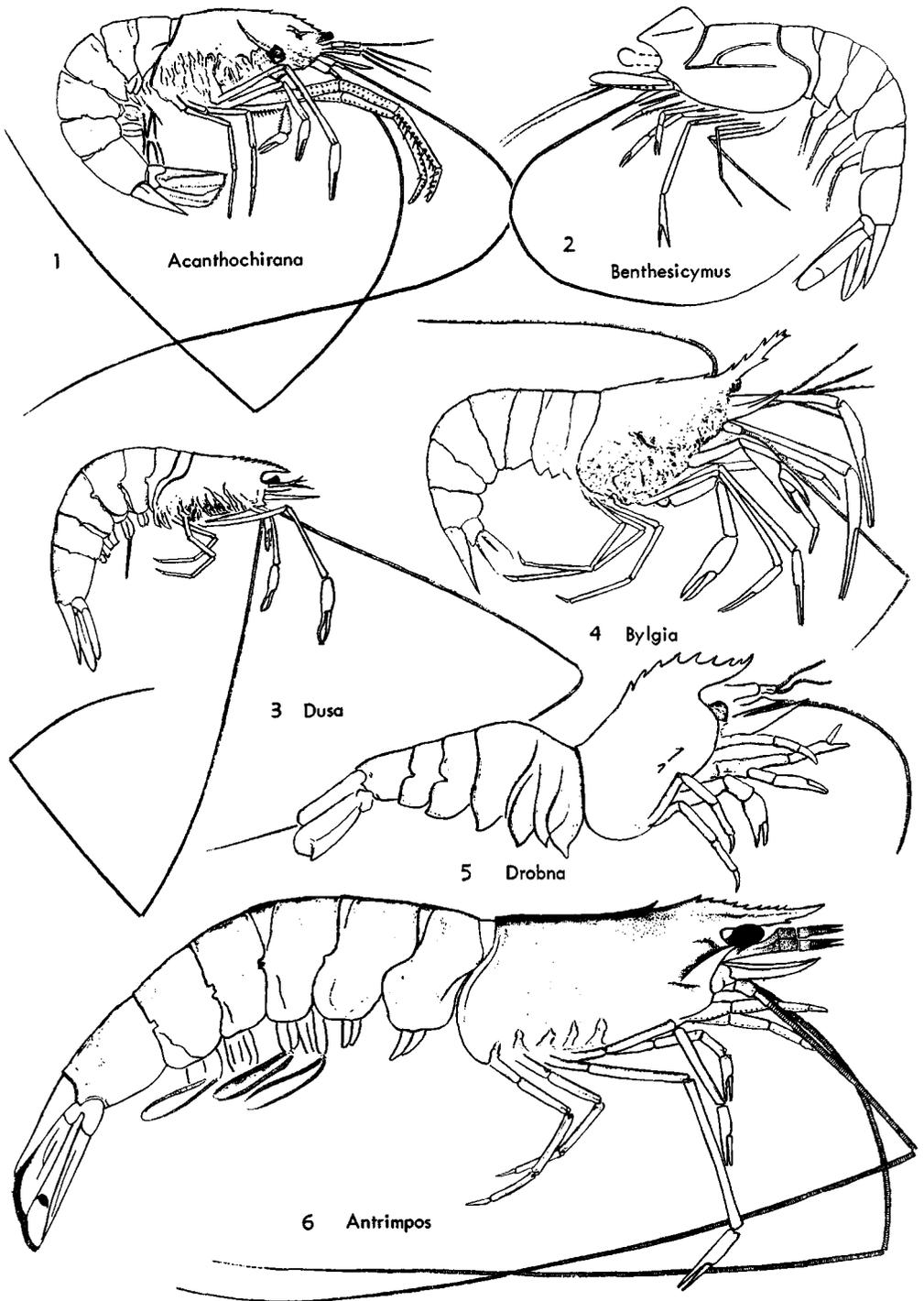


FIG. 253. Penaeidae (p. R447, R450).

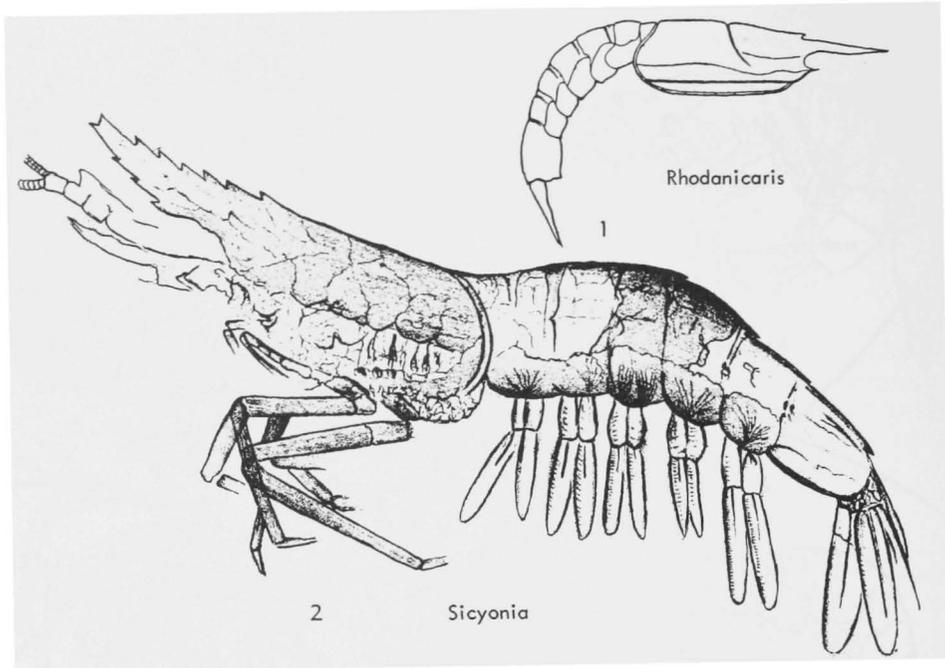


FIG. 254. Penaeidae (p. R450).

Bombur MÜNSTER, 1839 [**B. complicatus*; SD GLAESSNER, 1929]. Small forms with small rostrum, short cephalothorax, bent abdomen and long 6th somite. *U.Trias.-U.Jur.*, Eu.—FIG. 252,2.

**B. complicatus*, U.Jur., Ger.; $\times 0.5$ (Glaessner, n).

Bylgia MÜNSTER, 1839 [**B. spinosa*; SD GLAESSNER, 1929]. Differs from *Penaeus* and *Antrimpos* in shorter cephalothorax, upturned rostrum and more strongly developed pereopods. *U.Jur.*, S. Ger.—FIG. 253,4. **B. spinosa*; $\times 0.7$ (219).

Drobna MÜNSTER, 1839 [**D. deformis*; SD GLAESSNER, 1929]. Antennae long; rostral keel strongly curved and dentate, 3rd maxilliped thick, 1st pereopod short and thick, abdomen curved, 3rd somite large. *U.Jur.*, S.Ger.—FIG. 253,5. **D. deformis*; $\times 0.7$ (219).

Dusa MÜNSTER, 1839 [**D. monocera*; OD, M]. Antennae twice length of body, rostrum denticulate, carapace and abdomen finely granulate; chelae of 1st 3 pereopods with wide propodus and curved fingers; abdomen as in *Penaeus* and *Antrimpos*. *U.Jur.*, S.Ger.—FIG. 253,3. **D. monocera*; $\times 0.7$ (219).

Rauna MÜNSTER, 1839 [**R. angusta*; OD, M]. Small; carapace smooth, pleopods long. [Poorly preserved.] *U.Jur.*, S.Ger.

Rhodanicaris VAN STRAELEN, 1925 [**R. depereti*; OD]. Carapace with deep cervical groove and laterally 2 ridges and groove; rostrum long. *M. Jur.*, Fr.—FIG. 254,1. **R. depereti*; carapace and abdomen (reconstr.), $\times 1.3$ (296).

Sicyonia H. MILNE-EDWARDS, 1830 [*nom. conserv.*, ICZN, Op. 382] [**S. sculpta*; SD DEMAREST, 1858]. Integument hard, carapace compressed laterally, rostrum short, denticulate dorsally, 1st 3 pereopods short, pleopods very short. [Littoral, warm seas.] *U.Cret.*, Ger.; *Rec.*—FIG. 254,2. *S.?* *roemeri* (VON DER MARCK), Senon., N.Ger.; $\times 0.7$ (191).

Family UNCERTAIN

Tiche VON DER MARCK, 1863 [**T. astaciformis*; OD]. [Based on single incompletely known specimen.] *U.Cret.(Senon.)*, N.Ger.—FIG. 255,1. **T. astaciformis*; $\times 1$ (191).

Carpopenaeus GLAESSNER, 1945 [**C. callirostris*; OD]. Carapace short, with longitudinal fissure; rostrum with 1 ventral and 7 or 8 dorsal teeth; carpus of pereopods 2 and 3 multiarticulate as in some Caridea; telson lanceolate. *U.Cret.(Cenoman.)*, Lebanon.—FIG. 255,2. **C. callirostris*; reconstr., $\times 1$ (115).

Superfamily SERGESTOIDEA Dana, 1852

[*nom. transl.* HOLTHUIS, herein (ex Sergestidae DANA, 1852)]

Carapace moderately compressed, rostrum shorter than eye stalks, small, lower flagellum of antennule modified; antennal flagellum with bend; chelae on first three

pereiopods, pereiopods 4 and 5 and branchiae all reduced. *Rec.*

Family SERGESTIDAE Dana, 1852

Characters of superfamily. [Two subfamilies and seven genera are currently recognized.] *Rec.*

Sergestes H. MILNE-EDWARDS, 1830 [*S. atlanticus*; OD]. Carapace thin, 1st 3 pereiopods elongate, slender, 1st without proper chela. [Pelagic, mainly tropical.] *Rec.*

Suborder PLEOCYEMATA Burkenroad, 1963

Decapoda without secondary rami of branchiae; eggs carried by females on pleopods, hatching at zoea stage. *Permotrias-Rec.*

Infraorder STENOPODIDEA Huxley, 1879

[*nom. correct.* HOLTHUIS, 1946 (*pro* Stenopidea BATE, 1888)]

Carapace cylindrical, with cervical and branchiocardiac grooves; pleura of second abdominal somite not overlapping first, pereiopods 1 to 3 chelate, one or both third pereiopods considerably longer than first two; no exopodites on pereiopods; females without spermatheca; branchiae numerous, trichobranchiate; first pleopods reduced, others long, carrying eggs in females. *Rec.*

Family STENOPODIDAE Huxley, 1879

[*nom. correct.* SMITH & WELDON, 1909 (*pro* Stenopidae HUXLEY, 1879)]

Characters of infraorder. *Rec.*

Stenopus LATREILLE, 1819 [**Palaemon hispidus* OLIVIER, 1811; OD]. Rostrum long; carapace and abdomen spinose, scaphocerite long and flat; 4th and 5th pereiopods with carpus and propodus multiarticulate. *Rec.*, *Medit.-W.Indies-IndoPac.*

Infraorder UNCINIDEA Beurlen, 1930

[*nom. correct.* GLAESSNER, herein (*pro* tribe Uncinoidea BEURLEN, 1930)]

Carapace incompletely preserved; abdomen with small first and large second somite with pleura expanded anteriorly and posteriorly; ?first pereiopod very long,

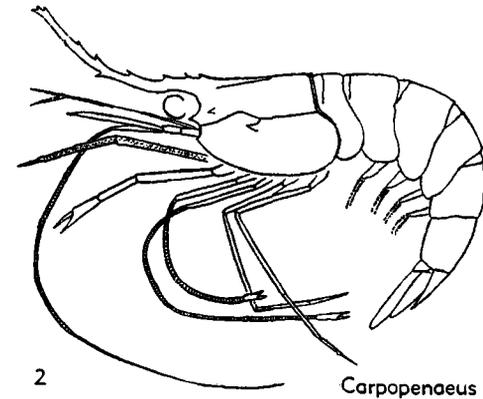
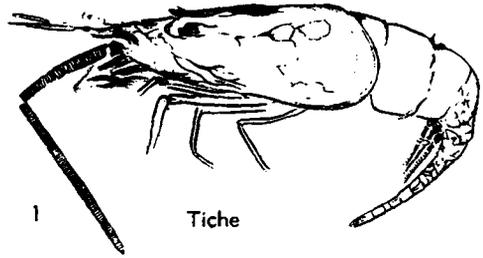


FIG. 255. Family Uncertain (p. R450).

strong and spinose, with elongate carpus and propodus and strong curved fingers; pereiopods 2 and 3 with small chelae; uropods without diaeresis. *L.Jur.*

Family UNCINIDAE Beurlen, 1928

Characters of infraorder. *L.Jur.*

Uncina QUENSTEDT, 1850 [**U. posidoniae*; OD] [= *Leptochirus* KRAUSE, 1891 (no species named)]. Characters of infraorder. *L.Jur.*, *Ger.*—FIG. 255A, 1. **U. posidoniae*, *Lias.*, *S.Ger.*; $\times 0.3$ (360a).

Infraorder CARIDEA Dana, 1852

[= *Eukyphotes* BOAS, 1880; *Eucyphidea* ORTMANN, 1890; *Carides* BORRADAILE, 1907]

Carapace cylindrical, laterally or (slightly) dorsoventrally compressed, mostly with well-developed rostrum; third maxilliped with four or five segments, first two pereiopods chelate or subchelate, pereiopod 3 chelate; abdomen well developed, second segment with rounded pleura overlapping those of both adjoining segments, third segment commonly with longitudinal

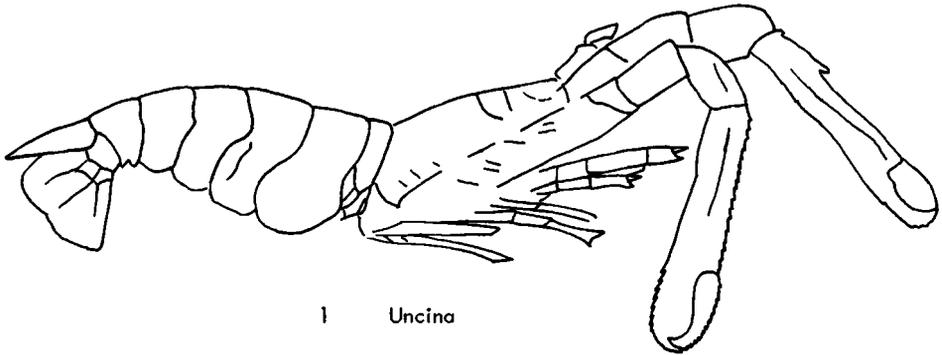


FIG. 255A. Uncinidae (p. R451).

downward bend. [The Recent Caridea were classified in nine superfamilies by HOLTHUIS (1955) and in seven superfamilies by BORRADAILE (1907) and BALSS (1957, with a doubtful additional new superfamily). BALSS considered the subdivision as not altogether satisfactory because of uncertain limits. There are 22 living families with more than 170 genera. In the few known fossils only very few distinctive characters of the living taxa are recognizable and their listing in a work on paleontology would serve no useful purpose.] *M.Jur.-Rec.*

Family ATYIDAE de Haan, 1849

[*nom. correct.* DANA, 1852 (*pro* family Atyidea DE HAAN, 1849)]

Rostrum compressed; first two pereopods subequal, chelate, all pereopods may bear exopods. [Fresh-water.] *Tert.-Rec.*

Atya LEACH, 1816 [**Atya scaber* LEACH, 1815; OD] [= *Atyoida* RANDALL, 1839 (type, *A. bisulcata*)]. Rostrum not compressed; carpus of 2nd pereopod very short, anteriorly deeply excavated, chelae divided to base; 3rd pereopod large and long. [Two new species of Tertiary prawns from Brazil were placed in *Atyoida* by BEURLEN (1950), considered close to *A. potimirim* MÜLLER, 1881 (= *Caridina mexicana* DE SAUSSURE, 1857), the type-species of *Potimirim* HOLTHUIS, 1954.] *Rec.*, C.Am.-W.Indies-W.Afr.-IndoPac.-S.Australia. — FIG. 256,5. *A. crassa* (SMITH), *Rec.*; $\times 0.7$ (149, from Bouvier).

Caridina H. MILNE-EDWARDS, 1837 [**C. typus*; OD]. Rostrum generally compressed, smooth or serrate; carpus of 2nd pereopod hardly excavated anteriorly; no exopods on pereopods. *Oligo.*, Fr.; *Rec.*, Afr.-SE.Asia-Pac.Is.

Family OPLOPHORIDAE Dana, 1852

[*nom. transl.* RATHBUN, 1902 (*ex* Oplophorinae DANA, 1852)]

Rostrum compressed, dentate, antennal scale long, third maxilliped long, pediform, first two pereopods chelate. [Marine.] ?*U. Jur.*, ?*U. Cret.*, *Rec.*

Oplophorus H. MILNE-EDWARDS, 1837 [**O. typus*; OD] [= *Hoplophorus* AGASSIZ, 1846 (*nom. van.*)]. Abdominal somites 2 to 4 or 3 to 5 with long mediodorsal teeth; telson acutely triangular. ?*U. Jur.*, C.Afr.; ?*U. Cret.* (*Senon.*), Ger.-Lebanon; *Rec.*, cosmop. — FIG. 256,1. *O. marcki* SCHLÜTER, *Senon.*, Ger.; $\times 0.7$ (191).

Notostomus A. MILNE-EDWARDS, 1881 [**N. gibbosus*; OD]. Carapace with oblique hepatic and horizontal lateral keel, last 4 abdominal somites keeled; telson truncate. ?*U. Cret.* (*Cenoman.-Senon.*), Lebanon; *Rec.*, bathypelagic. — FIG. 257,1. *N.?* *cretaceus* ROGER, *Cenoman.*, Lebanon; $\times 2$ (255).

Family PALAEMONIDAE Rafinesque, 1815

Antennules mostly three-flagellate, chelae of second pereopod stronger than those of first, all pereopods lacking exopods. [Marine and fresh water.] *Tert.-Rec.*

Palaemon WEBER, 1795 [**P. adpersus* RATHKE, 1837; SD ICZN (Opinion 564)]. Carapace with antennal and branchiostegal spines; no hepatic spine; antennules 3-flagellate, telson with 4 apical spines. [Mostly marine.] ?*Oligo.*, Eu.; *Rec.* cosmop. — FIG. 256,2. *P. longirostris* H. MILNE-EDWARDS, *Rec.*; $\times 0.7$ (149).

Bechleja HOUŠA, 1956 [**B. inopinata*; OD]. Rostrum dentate, pereopod 1 with small chela, pereopod 2 with large chela, pereopods 3 to 5 equal in length; telson little shorter than uropods; an-

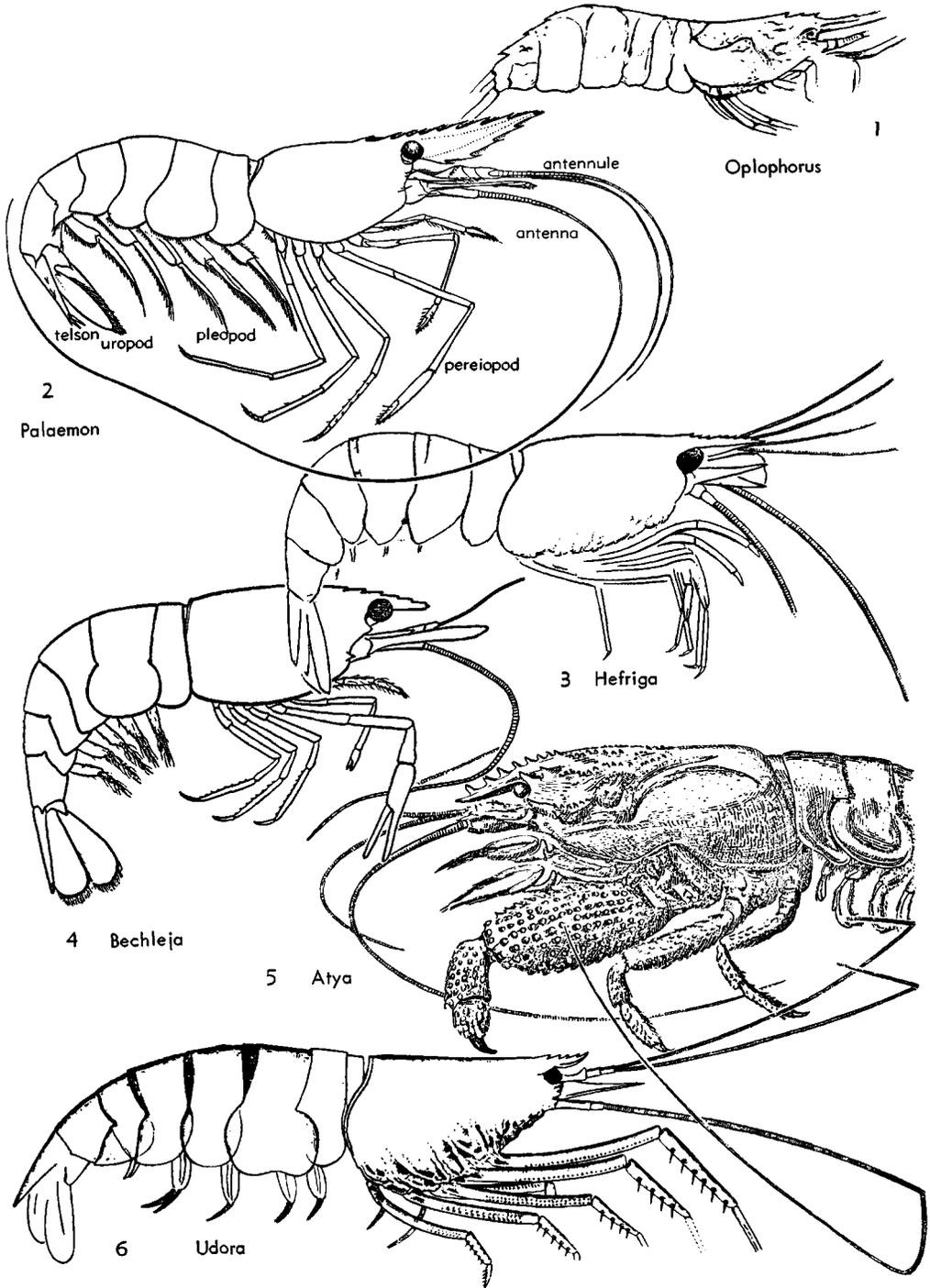


FIG. 256. Atyidae (5); Oplophoridae (1); Palaemonidae (2, 4); Family Uncertain (3, 6) (p. R452, R454-R455).

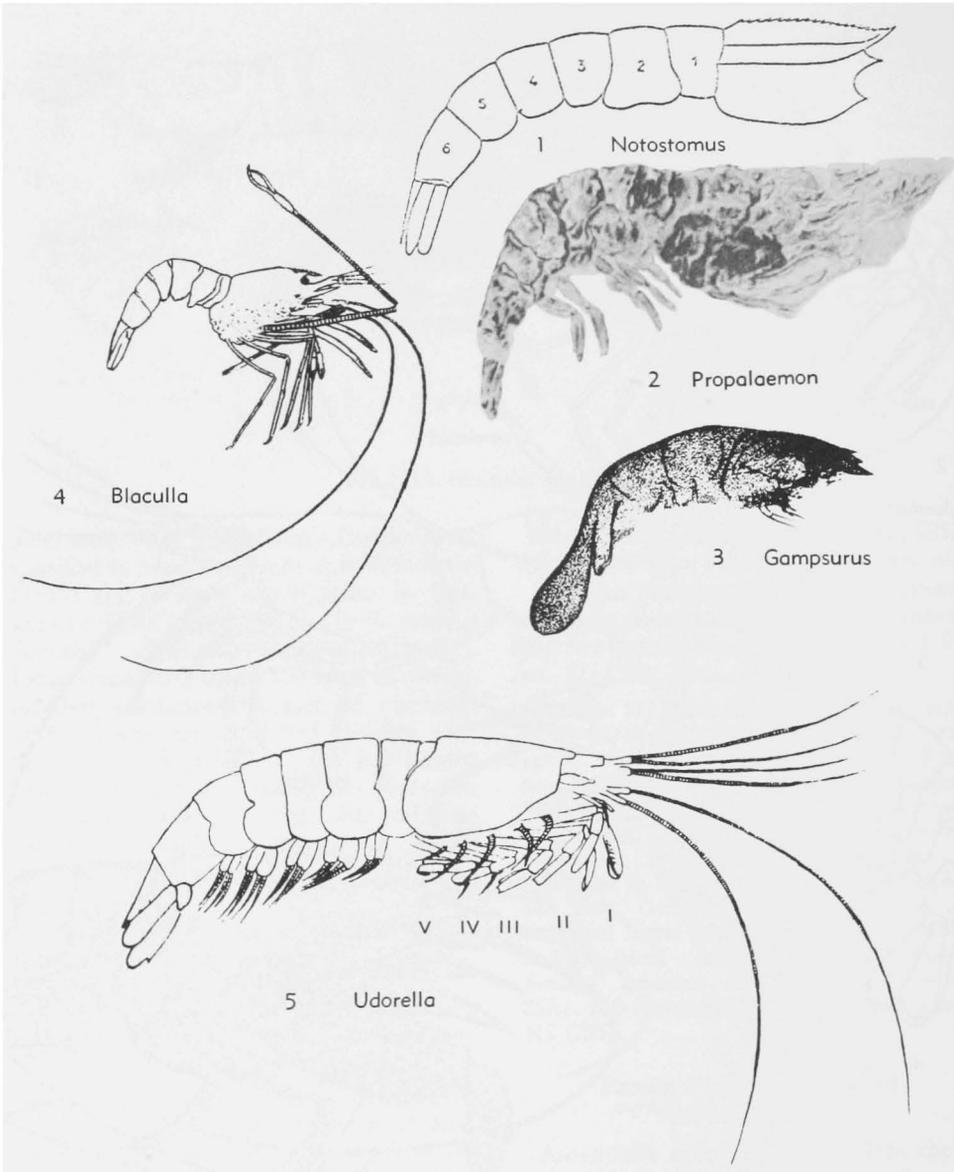


FIG. 257. Oplophoridae (1); Palaemonidae (2); Udorellidae (5); Family Uncertain (3,4) (p. R455).

tennae 1.5 times length of cephalothorax. *U. Oligo.* or *L.Mio.*, Czech.—FIG. 256,4. **B. inopinata*, reconstr.; $\times 3$ (152).

?*Homelys* VON MEYER, 1862 [**H. minor*; OD]. *U.Mio.*, Eu.

?*Micropsalis* VON MEYER, 1859 [**M. papyracea*; OD]. Rostrum smooth, 1st pereopod with long chelae, antennae 3 times length of cephalothorax. *Oligo.*, Eu.

Propalaemon WOODWARD, 1903 [**P. osborniensis*; SD WOODS, 1925]. Rostrum serrate; pereopods

long and slender, pleopods long. *L.Oligo.*, Eng.—FIG. 257,2. **P. osborniensis*; $\times 1$ (326).

Family UDORELLIDAE Van Straelen, 1924

Third maxilliped ending in long thin terminal segment and finely spinose; pereopods spinose, subchelate, decreasing in length from first to fifth, with annulated

exopods. [This was made a "subtribe" *Udorellida* BEURLEN & GLAESSNER (1931) =superfamily Udorelloidea, *nom. transl.* BIRSHTEYN (1960).] *U.Jur.*

Udorella OPPEL, 1862 [**U. agassizi*; OD]. Characters of family. *U.Jur.*, S.Ger.—FIG. 257,5. **U. agassizi*; (I-V, pereopods 1 to 5), $\times 1$ (11).

Family UNCERTAIN

Blaculla MÜNSTER, 1839 [**B. nicoides*; OD, M]. Rostrum denticulate, 1st pereopod chelate, 2nd annulate, ending in small chela, left much shorter than right, pereopods 3 to 5 without chelae; telson pointed, uropods with diaeresis. *U.Jur.*, S.Ger.—FIG. 257,4. *B. sieboldi* OPPEL, $\times 1$ (219).

Hefriga MÜNSTER, 1839 [**H. serrata*; OD, M]. Rostrum denticulate, 1st 2 pereopods with chelae, 3rd pereopod longest. *U.Jur.*, S.Ger.—FIG. 256, 3. **H. serrata*; $\times 2$ (219).

Gampsurus VON DER MARCK, 1865 [**Euryurus dubius* VON DER MARCK, 1863; OD]. Carapace short, with short triangular rostrum and 2 or 3 spines near orbit; abdomen with pleura of 2nd somite expanded. [Some confusion exists as to the name of this incompletely known genus. VON DER MARCK stated that he introduced *Gampsurus* to replace his earlier proposed name *Euryurus*, because of prior use of the latter name by KOCH (1864). However, *Euryurus* VON DER MARCK appears to have been published in 1863.] *U.Cret.* (*Senon.*), Ger.—FIG. 257,3. **G. dubius*; $\times 1$ (191).

Udora MÜNSTER, 1839 [**U. brevispina*; OD, M]. Antennae long, rostrum denticulate, 2nd abdominal somite largest; 1st pereopod chelate, all pereopods spinose. *M.Jur.-U.Jur.*, Eu.—FIG. 256,6. **U. brevispina*, *U.Jur.*, Ger.; $\times 1.3$ (219).

Infraorder ASTACIDEA

Latreille, 1803

[=ASTACURA BORRAIDAILE, 1907]

Cephalothorax subcylindrical, rostrum and abdomen well developed; frontal portion of carapace not fused with epistome; antennae with five-segmented stalk and scale; third maxilliped pediform; first three pereopods chelate, chelae of third pereopods largest; abdominal pleura well developed; uropods with diaeresis; genital openings coxal. *Permotrias.-Rec.*

Family ERYMIDAE Van Straelen, 1924

[*nom. correct.* GLAESSNER, 1929 (*pro* Erymidae VAN STRAELEN, 1924)] [=Paranephropsidae BEURLEN, 1927]

Carapace with well-developed cervical, postcervical and branchiocardiac grooves,

mostly with median suture and small fusiform intercalated plate. *Permotrias.-U.Cret.*, ?*Paleoc.*

[A revision of the Erymidae and related forms by Dr. R. FÖRSTER (Munich) is in the press in "Palaeontographica" (pers. comm., Oct., 1965). His taxonomic conclusions differ from the following treatment of the genera concerned in important points: *Klytia* is placed in the synonymy of *Eryma*. *Palaeastacus* and *Phlyctisoma* are considered valid genera of the Eryminae. Only *Clytiopsis* and doubtfully *Paraclytiopsis* are included in the Clytiopsinae. *Lissocardia* is seen as "intermediate between Erymidae, Glypheidae and Pemphicidae." *Protoclytiopsis* and *Clytiella* are placed in the Eryminae.] (See Addendum to Decapoda, p. R626.)

Subfamily ERYMINAE Van Straelen, 1924

[*nom. transl. et correct.* BEURLEN, 1927 (*ex* Erymidae VAN STRAELEN, 1924)]

Carapace with median suture and intercalated plate; chelae of first pereopods large. *Jur.-U.Cret.*, ?*Paleoc.*

Eryma VON MEYER, 1840 [**Macrourites modestiformis* VON SCHLOTHEIM, 1822; OD] [?= *Aura* MÜNSTER, 1839 (*nom. neg.*)]. Carapace granulate or punctate; cervical groove deep and moderately inclined, not strongly sinuous; postcervical and branchiocardiac grooves nearly parallel, joined near their lower ends; tubercle *w* usually distinct, rostrum short; 1st chelae stout, fingers not much longer than palm; surface of shell granulate to punctate. *L.Jur.-L.Cret.*, Eu.-E.Afr.-Indonesia; *U.Cret.*, N.Am.—FIG. 258,4. **E. modestiformis* (SCHLOTHEIM), *U.Jur.*, Ger.; $\times 2$ (219).—FIG. 259,3. *E. bedelta* (QUENSTEDT), *M.Jur.*, Eng.; $\times 0.7$ (326).

Enoploclytia M'COY, 1849 [**Astacus leachi* MANTELL, 1822; OD]. Carapace and 1st pereopods more coarsely ornamented than in *Eryma*; rostrum strongly dentate. [The distinction of some Jurassic species from *Eryma* is uncertain.] ?*M.Jur.*, Eu.; *U.Jur.-U.Cret.*, Eu.-N.Am.; ?*Paleoc.*, N.Am.(Ala.); *L.Cret.* (*Apt.-Alb.*), E.Australia.

E. (*Enoploclytia*). Chelae long and slender, fingers long, without spines. *L.Cret.* (*U.Alb.*)-*U.Cret.*, ?*Paleoc.*, Eu.-W.Afr.-N.Am.; *L.Cret.* (*Apt.-Alb.*), E.Australia.—FIG. 259,1. **E.* (*E.*) *leachi* (MANTELL), *U.Cret.*, Eng.; chela, $\times 0.7$ (326).—FIG. 258,2. *E.* (*E.*) *leachi granulicauda* (SCHLÜTER), *U.Cret.*, Ger.; carapace, $\times 0.7$ (193).

E. (*Palaeastacus*) BELL, 1850 [**P. dixonii* BELL, 1850 (= *Astacus sussexiensis* MANTELL, 1833); OD] [= *Phlyctisoma* BELL, 1862]. Chelae stout, spinose; fingers equal in length to palm. ?*U.Jur.*, *U.Cret.* (*Cenoman.*), Eu., *L.Cret.* (*Alb.*)-*U.Cret.*, N.Am.—FIG. 259,2. **E.* (*P.*) *sussexiensis* (MANTELL), *U.Cret.*, Eng.; 2a, dorsal view; 2b, cheliped; $\times 0.5$ (326).

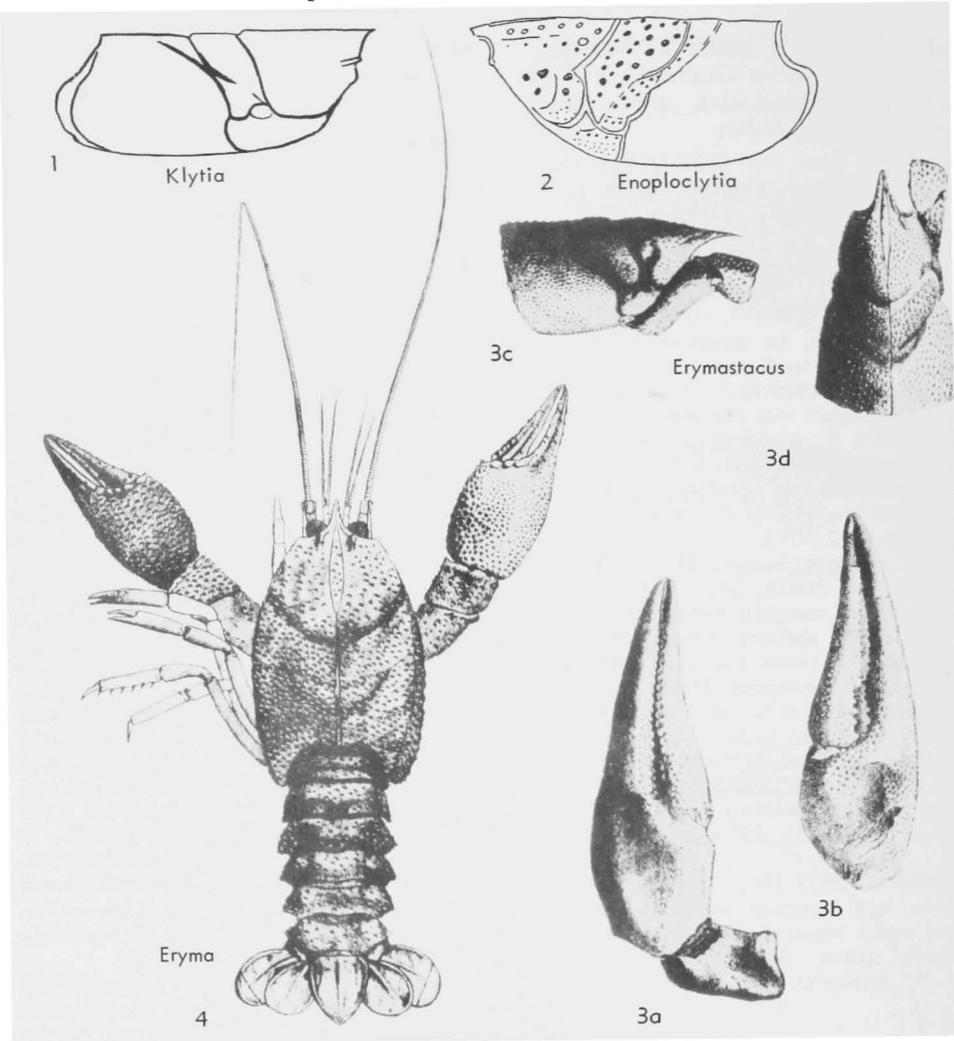


FIG. 258. Erymidae (Eryminae) (p. R455-R456).

Erymastacus BEURLEN, 1928 [**Glyphea ornati* QUENSTEDT, 1857; SD GLAESSNER, 1929]. Anterior portion of carapace narrow; cervical groove deep, all 3 transverse grooves straight; 1st chelae with short square palm and long denticulate fingers; dactylus thin, with slight upward curvature. *L.Jur.*, Can.; *L.Jur.-U.Jur.*, Eu.; *M.Jur.-U.Jur.*, E. Afr.—FIG. 258,3. **E. ornati* (QUENSTEDT), *U. Jur.*, Ger.; 3a,b, chelae, 3c, carapace, side view, 3d, carapace, dorsal view, $\times 0.7$ (219).

Klytia VON MEYER, 1840 [**Glyphea ventrosa* VON MEYER, 1835]. Carapace with cervical groove deep, sinuous, inclined, but less sloping than post-cervical and branchiocardiac grooves, which are fused near middle of flank; 1st chelae long, fingers longer than palm. *Jur.*, Eu.—FIG. 258,1. **K. ventrosa* (VON MEYER); carapace, lat. view, $\times 0.7$ (Glaessner, n).

Stenodactylina BEURLEN, 1928 [**S. liasina*; OD]. Chela with stout, spinose, short palm and very long thin finger. *L.Jur.*, S.Ger.

Subfamily CLYTIOPSINAE Beurlen, 1927

Carapace without median intercalated plate; first chelipeds not significantly different from second and third pairs. *?Permotrias.*, *L.Trias.-U.Trias.*

Clytiopsis BILL, 1914 [**C. argentoratensis*; SD GLAESSNER, 1929]. Carapace thin, with short triangular rostrum and 3 parallel transverse grooves; lateral keels continuing on carapace; chelae weak. *L.Trias.*, Eu.—FIG. 260,1. **C. argentoratensis*, Alsace; 1a, dorsal, 1b, lateral, $\times 2$ (39).

Clytiella GLAESSNER, 1931 [**C. spinifera*; OD]. Carapace with closely granulate surface and with

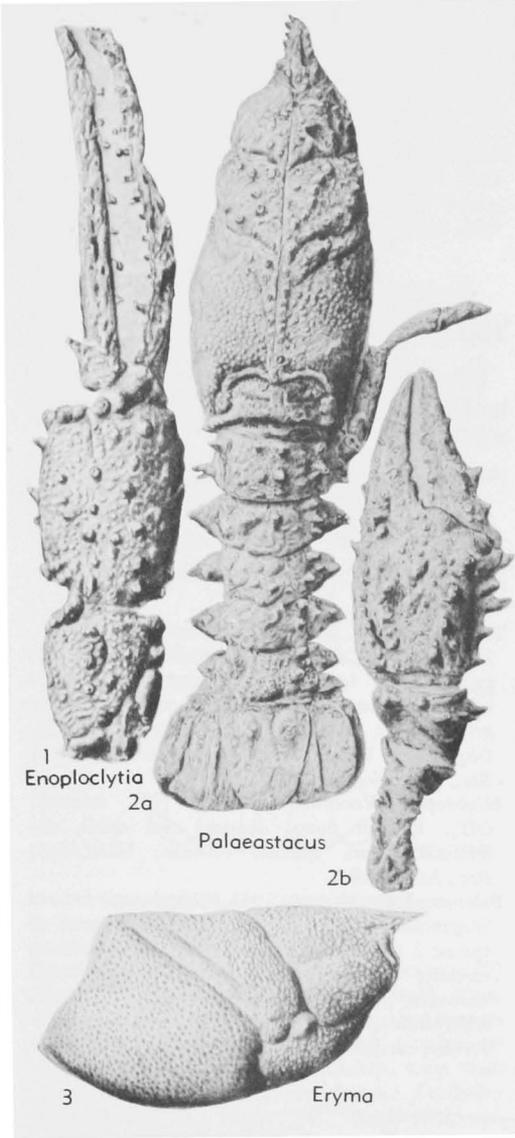


FIG. 259. Erymidae (Eryminae) (p. R455).

median keel bearing row of curved sharp spines; 1st pereopods with massive chelae, fingers short. *U.Trias.*, Aus.—FIG. 261,1. **C. spinifera*; holotype, $\times 1$ (111).

?*Piratella* ASSMANN, 1927 [**P. badensis*; OD]. Carapace thin, median keel with spines as in *Clytiella*, but chelae long and slender; fingers long, with teeth. *M.Trias.*, Ger.—FIG. 261,2. **P. badensis*; 2a, carapace, 2b, chelae, $\times 1$ (5).

Lissocardia VON MEYER, 1851 [**L. silesiaca*; SM ASSMANN, 1927]. Carapace thin, with weak

granulated median keel, rostrum short, gastral region with longitudinal ridges, cervical and post-cervical grooves parallel; branchiocardiac groove weak, sigmoidal; chelae long, with long denticulate fingers. *M.Trias.*, Eu.—FIG. 261,3. **L. silesiaca*; carapace and chela, $\times 1$ (5).

Paraclytiopsis ORAVEC, 1962 [**P. hungaricus*; OD]. Resembling *Clytiopsis* but cervical groove deep; postcervical groove very weak and close to branchiocardiac; groove *i* near vertical; appendages unknown. *U.Trias.*, Hung.—FIG. 262,1. **P. hungaricus*; 1a,b, carapace, side, dorsal, $\times 1.5$ (221).

?*Protoclytiopsis* BIRSHTEYN, 1958 [**P. antiqua*; OD]. Possibly synonym of *Lissocardia* from which it differs only in apparent absence of anterolateral

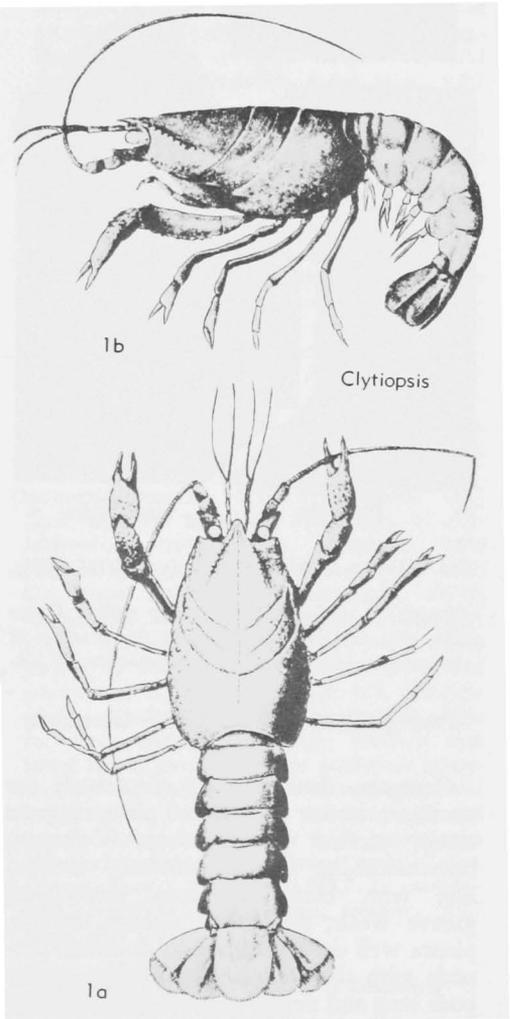


FIG. 260. Erymidae (Clytiopsinae) (p. R456).

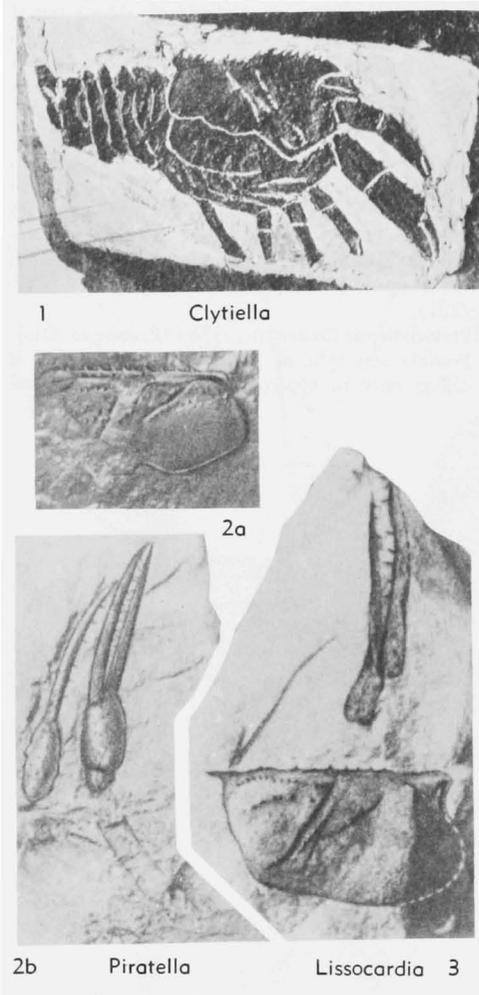


FIG. 261. Erymidae (Clytiopsinae) (p. R456-R458).

(“gastral”) ridges. [The name is spelled *Protoclytiopsis*, obviously by error, in the heading of the generic description only.] *Permotrias.*, W.Sib.

Family PLATYCHELIDAE Glaessner, n. fam.

Carapace dorsoventrally depressed; no median suture or intercalated plate; rostrum small; cervical groove deep, V-shaped; branchiocardiac groove crossing median line with backward loop; postcervical groove weak; abdominal somites smooth, pleura well developed, telson rounded, uropods with diaeresis; chelae of first pereopods long and slender, second chelae smaller

by about one-half, third chelae very small. *U.Trias.*

Platychele GLAESSNER, 1931 [**P. trauthi*; OD]. Characters of family. *U.Trias.*, Aus.—FIG. 263, 1. **P. trauthi*; reconstr., $\times 0.7$ (111).

?**Platypleon** VAN STRAELEN, 1936 [**P. nevadense*; OD]. Fragmentary abdomen resembling *Platychele*; 5th and 6th abdominal somites smooth, with large triangular pleura. *U.Trias.*, Nev.

Family NEPHROPIDAE Dana, 1852

[*nom. correct.* GLAESSNER, herein (*pro* Nephropsidae DANA, 1852)] [=Homaridae HUXLEY, 1879; Herpochelida BEURELEN, 1930]

Carapace with mainly postcervical and branchiocardiac grooves; fifth thoracic somite fused. *M.Jur.-Rec.*

Subfamily NEPHROPINAE Dana, 1852

[*nom. transl.* MERTIN, 1941 (*ex* Nephropsidae DANA, 1852)]

Carapace with longitudinal keels or rows of spines; abdomen with median keel. *U. Cret.-Rec.*

Nephrops LEACH, 1814 [**Cancer norvegicus* LINNÉ, 1758; OD]. Carapace with distinct postcervical groove, with long spinose rostrum and longitudinal spinose keels; abdomen with transverse grooves, 1st chelipeds long, slender, keeled. *Oligo.-Mio.*, W.Ind.; *Plio.*, Eng.; *Pleist.*, Panama; *Rec.*, Atl.-IndoPac.

Nephropsis WOOD-MASON, 1872 [**N. stewarti*; OD]. Rostrum long, dentate, eyes small, abdominal pleura spinose. ?*Paleoc.*, USA (Ala.), *Rec.*, Atl.-IndoPac.

Palaonephrops MERTIN, 1941 [**Hoploparia browni* WHITFIELD, 1907; OD]. Carapace with rows of spines; 2 transverse grooves, cervical groove almost reaching median line; abdominal somites with transverse grooves and median keel. *U.Cret.*, N. Am.(Mont.).—FIG. 264, 2. **P. browni* (WHITFIELD); carapace, $\times 1$ (193).

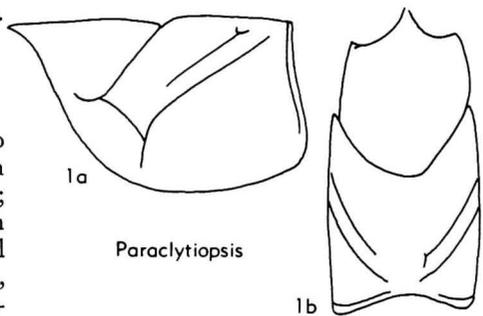


FIG. 262. Erymidae (Clytiopsinae) (p. R457).

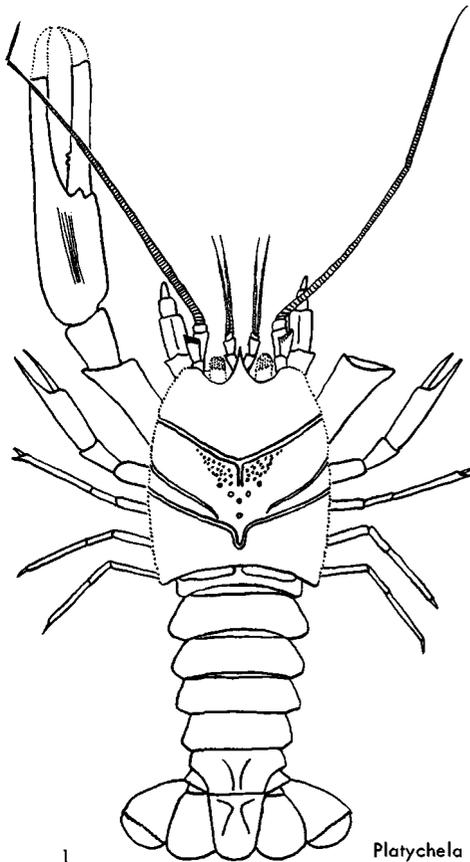


FIG. 263. Platychelidae (p. R458).

Paraclythia FRITSCH, 1877 [**P. nephropica*; OD] [= *Paraclythia* ZITTEL, 1885 (*nom. van.*)]. Carapace with 4 longitudinal ridges; abdominal somites with deep transverse grooves and longitudinal ridges or bosses; chelae heterochelous, long, with rows of spines. *U.Cret. (Turon.-Senon.)*, Eu. (Boh.-N.Ger.).—FIG. 264, 1. **P. nephropica*; reconstr., $\times 0.7$ (98).

Subfamily HOMARINAE Huxley, 1879

[*nom. transl.* MERTIN, 1941 (*ex* Homaridae HUXLEY, 1879)]

Carapace and abdomen mostly without coarse spines or carinae and only lightly granulated; chelae usually without carinae, heterochelous. *Cret.-Rec.*

Homarus WEBER, 1795 [**Cancer gammarus* LINNÉ, 1758 (= *H. vulgaris* H. MILNE-EDWARDS, 1837); SD RATHBUN, 1904]. Rostrum rather short and spiny, carapace without ridges or spines behind suborbital spine, cervical groove clearly developed

only below gastro-orbital groove, postcervical groove long and smoothly curved, connecting lowest part of cervical with posterior part of branchiocardiac groove; chelae stout, heterochelous. *Cret.-Rec.*, N.Am.-Eu.

H. (Homarus). Abdomen smooth, palm of 1st chela without median ridge. *Cret.-Rec.*, N.Am.-Eu.-S.Afr.—FIG. 265, 1a. **H. gammarus* (LINNÉ), Rec.; $\times 0.2$ (341a).—FIG. 265, 1b. *H. americanus* H. MILNE-EDWARDS, Rec.; carapace (r , rostrum; 1-3, rostral spines; a , supra-orbital spine; β , suborbital spine; γ , antennal spine; $c-e$, postcervical groove; a , branchiocardiac groove), $\times 0.4$ (283).

H. (Palaeohomarus) MERTIN, 1941 [**H. (P.) hemprichi*; OD]. Differs from *H. (Homarus)* in its longer rostrum, longer postcervical and branchiocardiac grooves, weak lateral ridges on abdomen, median ridge or spines on manus of 1st chela. *L.Cret. (Alb.)-U.Cret. (Senon.)*, Madag.-Eu.-N. Am. (Tex.).—FIG. 265, 3. **H. (P.) hemprichi*; 3a, lateral, 3b, dorsal view, $\times 0.7$ (193).

Hoploparia M'COY, 1849 [**Astacus longimanus* SOWERBY, 1826; SD RATHBUN, 1926] [= *Palaeno* ROBINEAU-DESVOIDY, 1849 (type, *P. roemeri*)]. Rostrum thin, long, smooth or denticulate, cervical groove clearly developed above and below gastro-orbital groove, postcervical groove distinct, connecting with cervical groove through semicircular arc; chelae strong, long, heterochelous. [The distinction between some species of *Hoploparia* and *Homarus* is difficult and disputed.] *L.Cret.-L.Tert.*, cosmop.—FIG. 265, 4a. **H. longimana* (SOWERBY), *U.Cret. (Cenoman.)*, Eng.; $\times 0.7$ (326).—FIG. 265, 4b, c. *H. stokesi* (WELLER), *U.Cret. (Campan.)*, Antarctic; reconstr., 4b, female, 4c, abdominal somites 2-5 of ?male, $\times 0.7$ (10).

Oncopareia BOSQUET, 1854 [**O. bredai*; OD] [= *Nymphaeops* SCHLÜTER, 1862 (type, *N. coesfeldiensis*); ?*Ischnodactylus* PELSENEER, 1886 (type, *Hoploparia macrodactyla* SCHLÜTER, 1862; SD) (*non Ischnodactylus* CHEVROLAT, 1877); ?*Sienocheles* FRITSCH, 1887 (type, *S. esocinus*; SD)]. Rostrum strongly spinose; only ventral portion of cervical groove present; postcervical groove distinct, extensively fused with branchiocardiac groove; several weak longitudinal ridges on anterior portion of carapace; abdomen with lateral ridges, pleura short; 1st pereopods heterochelous, one chela with short stout palm and long, narrow fingers with acicular teeth and strongly curved points; other with longer palm and thicker fingers with shorter teeth. *U.Cret. (Turon.-Senon.)*, Eu.—FIG. 265, 2. *O. coesfeldiensis* (SCHLÜTER), Senon., Ger.; reconstr., $\times 0.7$ (orig., after 193).

Subfamily NEOPHOBERINAE Glaessner, n. subfam.

[= *Phoberinae* MERTIN, 1941]

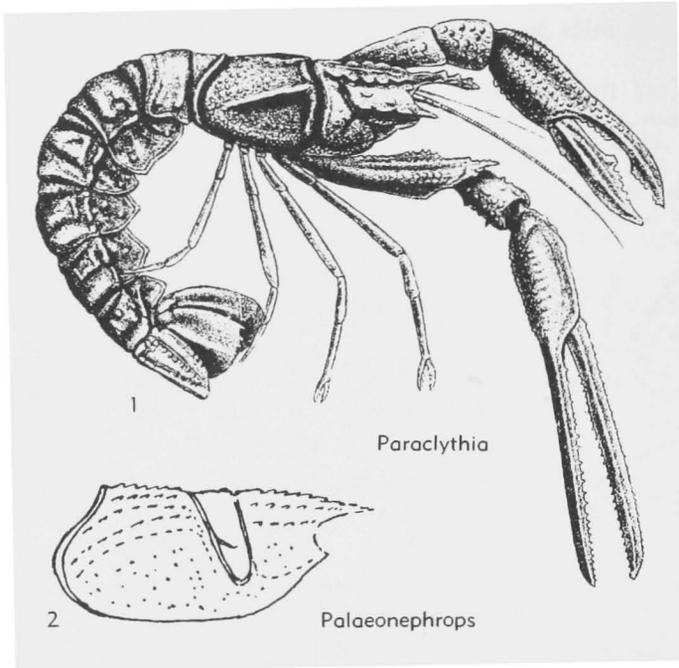


FIG. 264. Nephropidae (Nephropinae) (p. R458-R459).

Carapace spinose, with rows of spines on anterior part. *M.Jur.-Rec.*

Neophoberus *nom. subst.* [*pro Phoberus* A. MILNE-EDWARDS, 1881 (*non* MACLEAY, 1819, *nec* KIRSCH, 1873)] [**P. caecus*; OD]. Carapace strongly spinose, with long curved denticulate rostrum; postcervical groove joining short lateral portion of cervical groove with semicircular loop; chelae very long and slender, spinose; abdominal pleura pointed. *Rec.*, W.Indies-IndoPac.—FIG. 266,1. **P. caecus tenuimanus* BATE, *Rec.*; $\times 0.2$ (112).

Palaeophoberus GLAESSNER, 1932 [**Stenochirus suevicus* QUENSTEDT, 1867; OD]. Carapace spinose, with distinct cervical and postcervical grooves, joining laterally with acute angle; abdominal pleura truncate, chelae very long and strong. *M.Jur.*, Eu.—FIG. 266,2. **P. suevicus* (QUENSTEDT), S.Ger.; reconstr., $\times 0.2$ (112).

?**Tillocheles** WOODS, 1957 [**T. shannonae*; OD]. Rostrum spinose, anterior region of carapace longitudinally carinate, antennal furrow semicircular, cervical groove short, postcervical groove distinct, branchiocardiac groove diverging from it posteriorly high on carapace; branchial region finely spinose; abdomen with median keel; 1st chelipeds heterochelous, palms tuberculate, dactylus keeled. *L.Cret.(Alb.)*, Australia.—FIG. 266,3. **T. shannonae*; left side of carapace, $\times 0.7$ (328).

Subfamily UNCERTAIN

Cardirhynchus SCHLÜTER, 1862 [**C. spinosus*;

OD]. Insufficiently known. *U.Cret.(Senon.)*, N. Ger.

Pseudastacus OPPEL, 1861 [**Bolina pustulosa* MÜNSTER, 1839; OD] [= *Alvis* MÜNSTER, 1840 (type, *A. octopus*); *Bolina* MÜNSTER, 1839 (type, *B. pustulosa*) (*non* RAFINESQUE, 1815; *nec* MERTENS, 1833)]. Carapace granulate, with deep transverse groove, weak branchiocardiac groove branching off on middle of flank, rostrum triangular, with 3 lateral teeth, antennal stalks long, with pointed scale; 1st chelae long, slender, with straight fingers. ?*M.Jur.*, *U.Jur.*, Eu.—FIG. 267,1. **P. pustulosus* (MÜNSTER), *U.Jur.*, S.Ger.; $\times 1$ (219).

?**Stenochirus** OPPEL, 1861 [**S. meyeri* OPPEL, 1862; SD GLAESSNER, 1929]. Small; antennal flagella long, 1st pereopods with long, slender chelae, propodus rectangular, fingers with acicular teeth. [A new subfamily Stenochirinae was proposed by BEURLEN (1928) and later given family rank (BEURLEN, 1930). The type-species of *Stenochirus* is imperfectly preserved; according to BEURLEN nothing is recognizable of the carapace. His definition of the family was largely based on "*S.*" *suevicus* QUENSTEDT, which is the type of *Palaeophoberus* GLAESSNER.] *U.Jur.*, S.Ger.—FIG. 267,2. **S. meyeri*; $\times 1$ (219).

Family ASTACIDAE Latreille, 1802

[*nom. correct.* SAMUELLE, 1819 (*pro* Astacini LATREILLE, 1802)] [= Potamobiidae HUXLEY, 1878]

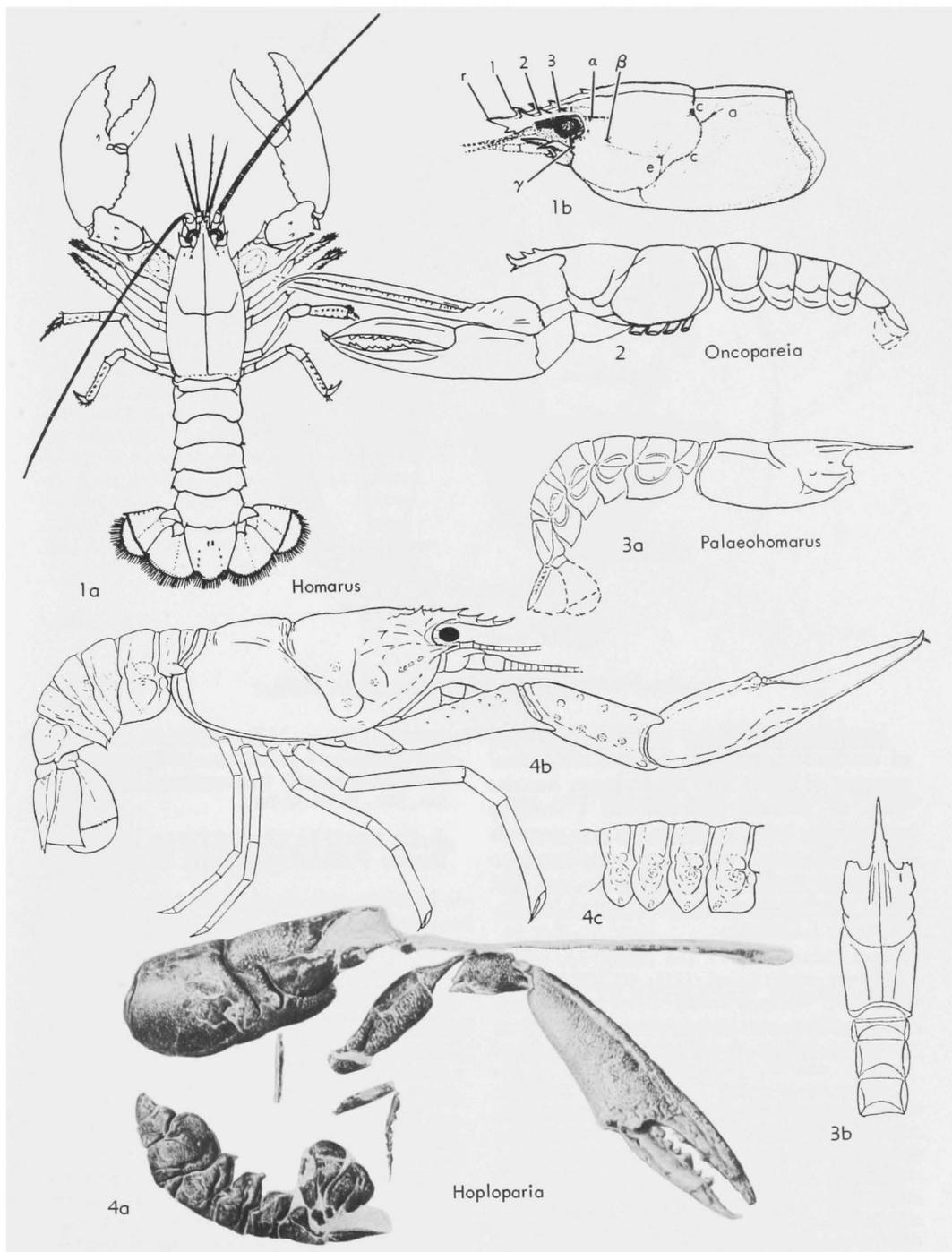


FIG. 265. Nephropidae (Homarinae) (p. R459).

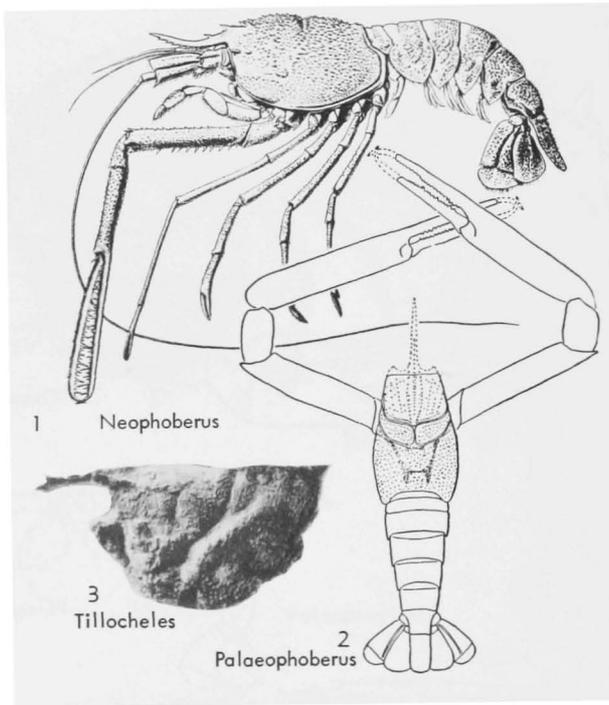


FIG. 266. Nephropidae (Neophoberinae) (p. R460).

Last thoracic segment movable; first rami of antennules subequal in size; abdominal segment of males with appendages; females with or without spermatheca ("annulus ventralis"); telson and exopod of uropods divided by transverse suture; podobranchiae of second and third maxillipeds and first three pereopods with broad plaited lamina. *U. Jur.* or *L. Cret.-Rec.*

Astacus FABRICIUS, 1775 [on official list, ICZN] [**Cancer astacus* LINNÉ, 1758; SD ICZN (Direction 12)]. Carapace usually with 2 pairs of post-orbital ridges, one behind other; males without hooks on ischium of pereopods, females without annulus ventralis. [The generic position of Recent species is mainly determined on characters of first pleopods in males which are unknown in fossils; the generic assignment of some fossils currently placed in this genus requires revision.] *U. Jur.* or *L. Cret.*, E. Mongolia-China (Jehol); *L. Cret.*, Ger.; *Paleoc.*, Fr.; *Plio.*, N. Am.-USSR; *Pleist.*, Eu.; *Rec.*, Eu.-W. Asia-N. Am.—FIG. 268, 1. **A. astacus* (LINNÉ), *Rec.*; $\times 0.5$ (49).

Cambarus ERICHSON, 1846 [**Astacus bartonii* FABRICIUS, 1798; SD FAXON, 1898]. Carapace ovate, generally depressed, never with 2 pairs of postorbital ridges, males without hooks on ischium of pereopods 3 or 3-4, females with annulus

ventralis. [HOBBS, 1942, established a subfamily Cambarinae, and LAGUARDA (1961) recognized Cambaroidinae and Cambarellinae.] *L. Eoc.*, N. Am., *Rec.*, N. Am.-C. Am.

Family PARASTACIDAE Huxley, 1878

Last thoracic somite movable, rami of antennules subequal in size, first abdominal somite of males without appendages; females without annulus ventralis; telson usually without transverse suture; exopod of uropods with transverse suture, podobranchiae with rudimentary laminae. [In addition to the genera here listed, one occurs in Madagascar, eight in Australia and one in New Zealand.] *Pleist.-Rec.*

Parastacus HUXLEY, 1879 [**Astacus pilimanus* VON MARTENS, 1869; SD FAXON, 1898]. Carapace and abdomen comparatively smooth, without prominent spines or tubercles; rostrum never with more than terminal spine and pair of lateral spines or tubercles; telson partially membranous and without transverse suture. *Rec.*, S. Am.

Astacopsis HUXLEY, 1879 [**Astacus franklinii* GRAY, 1845; OD]. Carapace with numerous small tubercles and punctures; rostrum always with

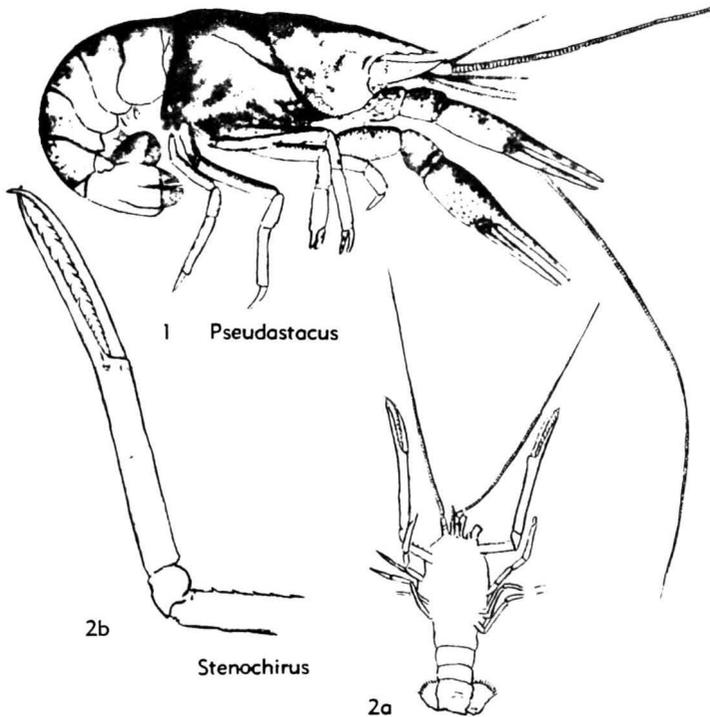


FIG. 267. Nephropidae (Subfamily Uncertain), (p. R460).

more than terminal and 1 pair of lateral spines or tubercles; telson without transverse suture. *Pleist.*, SE.Australia, *Rec.*, Tasmania.

Family AUSTRIOASTACIDAE Clark, 1936

Carapace strongly vaulted posteriorly; abdomen small; first somite without lateral lobes; telson and uropods not divided by transverse sutures; antennules with second flagellum small or absent. *Rec.*

Austroastacus CLARK, 1936 [**Engaeus hemicirratulus* SMITH & SCHUSTER, 1913; OD]. Characters of family. *Rec.*, Australia.

Infraorder PALINURA Latreille, 1803

Carapace cylindrical or dorsoventrally compressed, without prominent rostrum (except in *Pemphix*) but commonly spinose, fused laterally with epistome; antennal stalk with five segments; maxilliped pediform; abdomen well developed. ?*L.Trias.*, *M.Trias.-Rec.*

Superfamily GLYPHEOIDEA Winckler, 1883

[*nom. transl.* GLAESSNER, herein (ex Glypheidae WINCKLER, 1883)]

Carapace subcylindrical and slightly compressed laterally, with longitudinal ridges on anterior part; rostrum small, triangular; first pereiopods without chelae. ?*L.Trias.*, *M.Trias.-L.Tert.*

Family GLYPHEIDAE Winckler, 1883

Cephalothorax and abdomen strongly calcified, first pereiopod strong, flattened. ?*L.Trias.*, *M.Trias.-L.Tert.*

Glyphea VON MEYER, 1835 [**Palinurus regleyanus* DESMAREST, 1822; OD] [= *Orphnea* MÜNSTER, 1839 (type, *Macrowrites pseudoscyllarus* VON SCHLOTHEIM, 1820); *Brisa* MÜNSTER, 1839 (type, *B. lucida*); ?*Selenisca* VON MEYER, 1847 (type, *S. gratiosa*); *Paraglyphea* BEURLIN, 1928 (type, *G. ambigua* FRITSCH, 1870)]. Carapace with short pointed rostrum; tuberculate longitudinal carinae on anterior part; cervical groove deep and steeply inclined in side view, postcervical and branchio-cardiac grooves very oblique, joined medially and laterally and in some species at additional points;

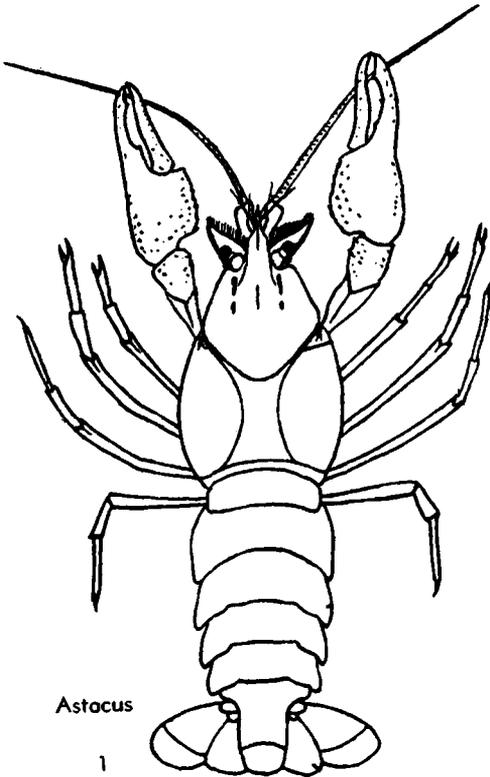


FIG. 268. Astacidae (p. R462).

anterior portion of carapace rectangular in outline in dorsal and lateral views, branchiostegite with long narrow anterior extension; abdominal terga smooth, telson rounded, exopods of uropods with diaeresis; antennal scale pointed; 1st pereopods subchelate. ?*U.Trias.*, *Jur.-Cret.*, *Eu.-Greenl.-E.Afr.-Australia-N.Am.*

G. (*Glyphea*). Carapace granulose or with granules and pits. ?*U.Trias.*, *Jur.-Cret.*, *Eu.-Greenl.-N.Am.-E.Afr.-Australia*.—FIG. 269,3a. **G. (G.) regleyana* (DESMAREST), *U.Jur.*, *Fr.*; $\times 1$ (219).—FIG. 269,3b. *G. (G.) prestwichi* WOODS, *L. Jur.*, *Eng.*; $\times 1$ (326).

G. (*Squamosoglyphea*) BEURLEN, 1930 [**G. adressieri* VON MEYER, 1840; OD]. Carapace with scalelike sculpture. *U.Jur.*, *Eu.*—FIG. 269,4. **G. (S.) adressieri* (VON MEYER), *Fr.*; $\times 1$ (219).

Litogaster VON MEYER, 1847 [*nom. subst. pro Litogaster* VON MEYER, 1844 (*non* PERTY, 1830)] [**L. obtusa*; OD] [= *Aphthartus* VON MEYER, 1847 (type, *A. ornatus*); *Myrtonius* VON MEYER, 1851, *nom. subst. pro Brachygaster* VON MEYER, 1847 (*non* LEACH, 1817) (type, *M. serratus*); ?*Aspidogaster* ASSMANN, 1927 (*non* BAER, 1826) (type, *Litogaster limicola* KÖNIG, 1920) (doubtfully dis-

tinguishable from *Litogaster*]. Differs from *Glyphea* in thin-shelled carapace, spatulate rostrum, parallel postcervical and branchiocardiac grooves. ?*L.Trias.*, *M.Trias.*, *Ger.*—FIG. 269,1. *L. ornata* (VON MEYER), *M.Trias.*, *Ger.*; carapace in side view and 2nd pereopod, $\times 2$ (5).

Trachysoma BELL, 1858 [**T. scabrum*; OD] [= *Glypheopsis* BEURLEN, 1928 (type, *Orphnea ornata* QUENSTEDT, 1858)]. Carapace long, low and narrow, with deep, straight cervical groove, postcervical and branchiocardiac grooves straight. *Jur.-Cret.*, *Eu.*; *U.Jur.*, *N.Z.*; *L.Cret.*, *Australia*; *L.Eoc.*, *Eng.*; ?*M.Eoc.*, *USSR.*—FIG. 269,2. *T. ornatum* (QUENSTEDT), *U.Jur.*, *Ger.*; 2a, dorsal view of carapace, 2b, lat. view, $\times 1$ (219, from Quenstedt).

Triasiglyphea VAN STRAELEN, 1936 [**T. mulleri*; OD]. Based on fragment of carapace which resembles *Litogaster*. *U.Trias.*, *N.Am.(Nev.)*. [A "genus *Glypheinarum*" BEURLEN, 1928, does not exist. References to it in the literature are based on a misunderstanding of the author's intentions who gave an indication in Latin (*gen. plur.* of "Glypheinae") that the Triassic *G. tantalus* WÖHRMANN (abdomen and pereopods only) may require a new name.]

Family MECOCHIRIDAE Van Straelen, 1925

Carapace thin, with short anterior portion, cervical groove distinct, straight, other transverse grooves weak, first pereopods strongly elongate. *M.Trias.-U.Cret.*

Mecochirus GERMAR, 1827 [**M. locusta* (= *Macrourites longimanatus* VON SCHLOTHEIM, 1820; SD WOODS, 1927)] [= *Megachirus* BRONN, 1837 (type, *M. locusta* GERMAR, 1827 = *M. longimanatus*); *Pterochirus* MÜNSTER, 1839 (type, *P. elongatus*, = *M. longimanatus*); *Norna* MÜNSTER, 1840 (type, *N. lithophila*); *Carcinium* VON MEYER, 1841 (type, *C. sociale*) (*non* *Carcinium* BANKS & SOLANDER, 1773; *nec* MEYEN, 1834); *Ammonicolax* PEARCE, 1842 (type, *Mecochirus pearcei* M'COY, 1849); *Eumorphia* VON MEYER, 1847 (type, *Carcinium sociale* VON MEYER, 1841)]. Carapace very thin, anterior portion carinate, cervical groove very oblique, postcervical and branchiocardiac grooves straight and shallow, joining cervical groove through semicircular arc; 1st pereopods very long, slender, subchelate, 2nd pereopods subchelate. *L.Jur.-U.Jur.*, *Eu.-N.Z.*—FIG. 270,1. **M. longimanatus* (SCHLOTHEIM), *U. Jur.*, *Ger.*; $\times 0.7$ (219).

Meyeria M'COY, 1849 [**Astacus ornatus* PHILLIPS, 1829; OD]. Differs from *Mecochirus* in granulate or spiny sculpture on carapace and abdomen, length of 1st pereopods not exceeding body length, 1st abdominal somites reduced. *L.Cret.-*

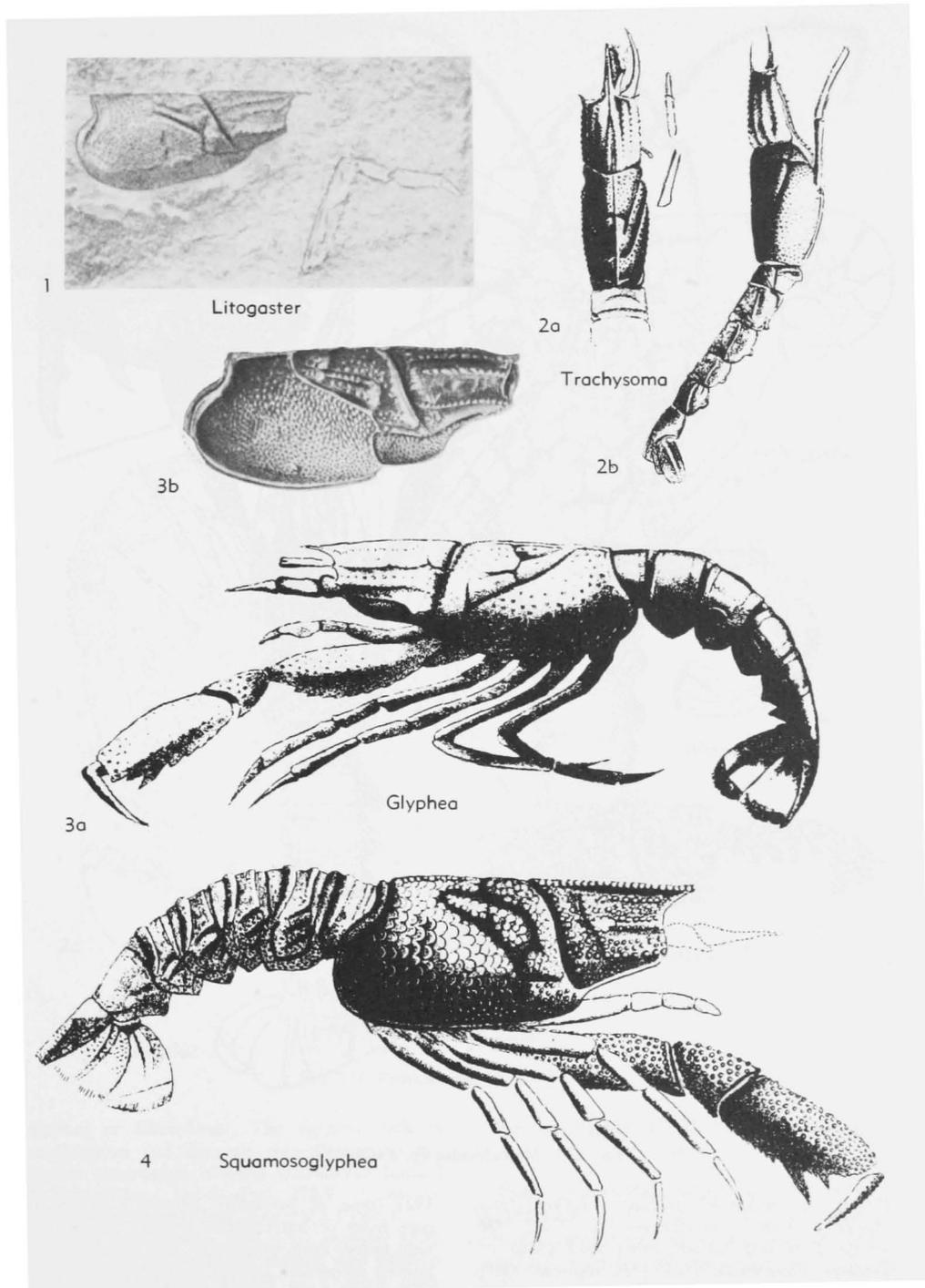


FIG. 269. Glypheidae (p. R463-R464).

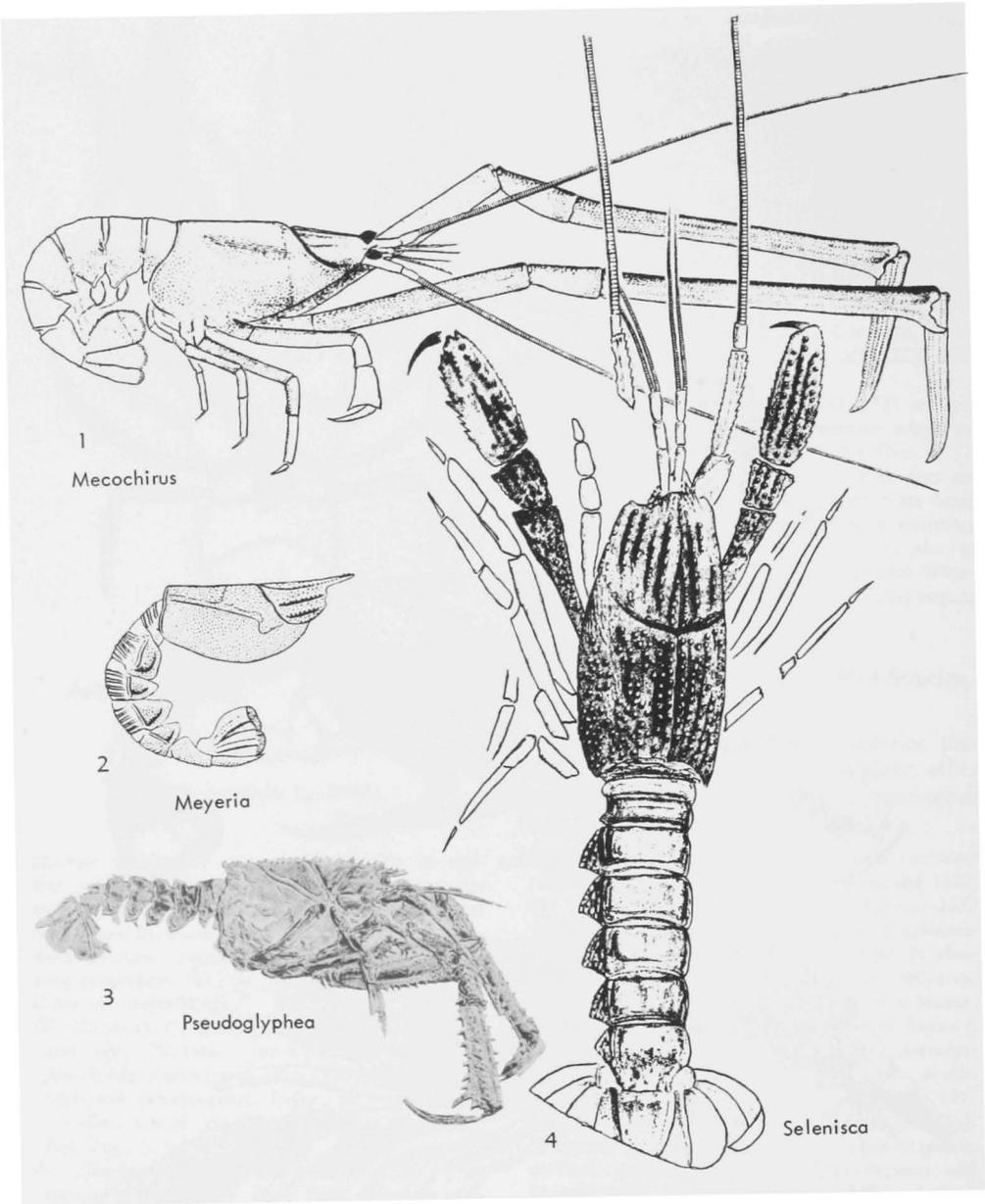


FIG. 270. Mecochiridae (p. R464-R466).

U.Cret., Eu.-N.Am.-W.Afr.-S.Afr.; *L.Cret.*(*Apt.*), Mexico; *U.Cret.*, Antarctic.—FIG. 270,2. **M. ornata* (PHILLIPS), *L.Cret.*, Eng.; $\times 0.7$ (326).

?*Pracatya* WOODWARD, 1868 [**P. scabrosa*; OD]. Carapace with short rostrum, 1st 2 pereopods not chelate. [Incompletely known.] *L.Jur.*, Eng.

Pseudoglypheia OPPEL, 1861 [**Glypheia grandis* VON MEYER, 1837; OD] [= *Scapheus* WOODWARD, 1863 (type, *S. ancylochelis*); *Heteroglypheia* COLOST,

1921 (type, *H. paronai*)]. Anterior part of carapace more or less carinate, rostrum spinose, cervical groove deep, postcervical and branchiocardiac grooves subparallel, sinuous, joining cervical groove with semicircular connection; inferior groove weak or absent; 1st pereopods long, uropods with diaeresis. [BEURLIN (1930) reinstated *Eumorphia* VON MEYER, 1847 (type, *E. socialis*) for several species which other authors include in *Pseudo-*

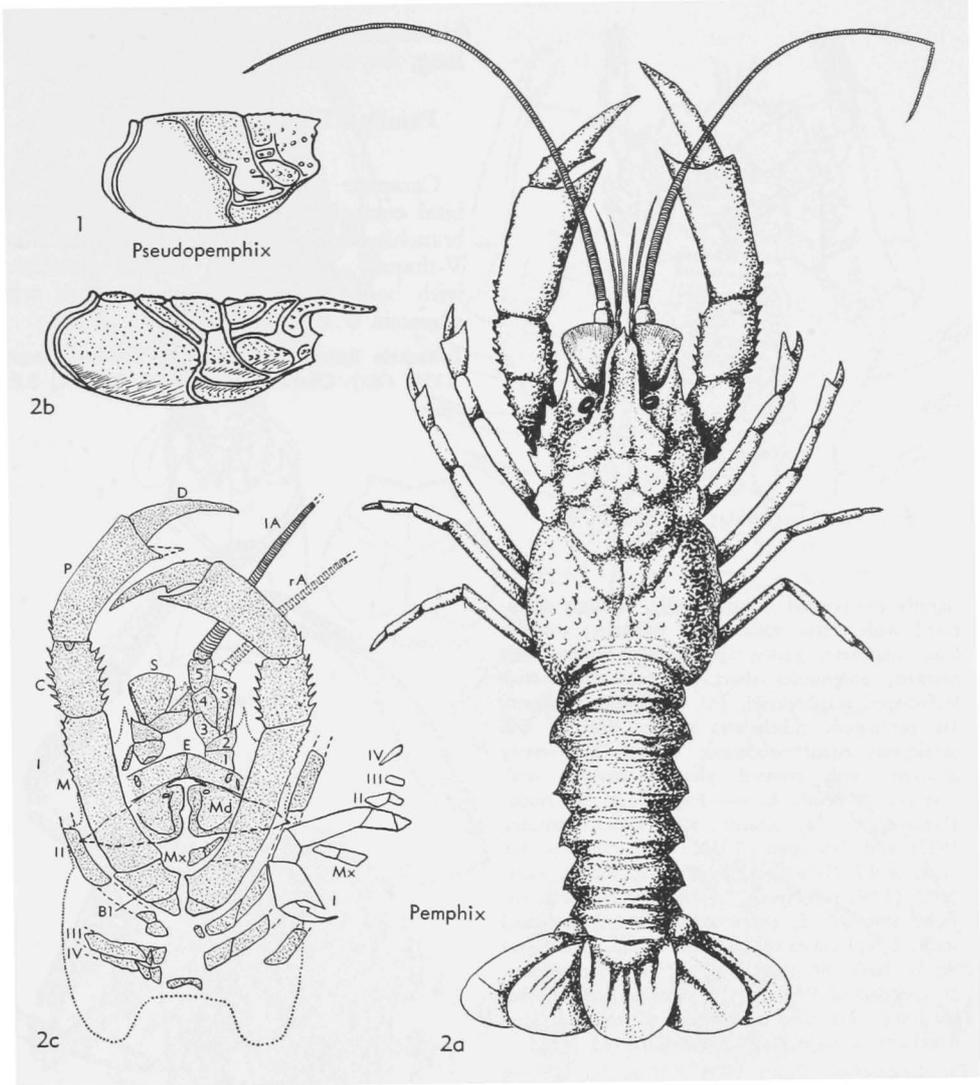


FIG. 271. Pempficidae (p. R467-R468).

glyphea or *Mecochirus*. The apparent lack of scaphocerites and diaeresis may be due to imperfect preservation of these thin-shelled forms.] *M.Trias.-M.Jur.*, Eu.—FIG. 270,3. *P. ancylolichelis* (WOODWARD), Lias., Eng.; $\times 0.3$ (326).

?*Selenisca* VON MEYER, 1847 [**S. gratiosa*; OD]. Carapace and 1st pereopods covered with tubercles in longitudinal rows. [Based on a single specimen which OPPEL and VAN STRAELEN placed in *Glyphea*, whereas BEURLIN included it in the *Mecochiridae*.] *U.Jur.*, Ger.—FIG. 270,4. **S. gratiosa*; $\times 2$ (219).

Family PEMPHICIDAE Van Straelen, 1928

Body cylindrical, carapace with cervical, postcervical and branchiocardiac grooves equally developed, latter joining on flank; anterior portion of carapace with longitudinal ridges; first three pereopods subchelate; telson rounded. *M.Trias.*

Pemphix VON MEYER, 1840 [**Palinurus suevii* DESMAREST, 1822; OD]. Carapace cylindrical,

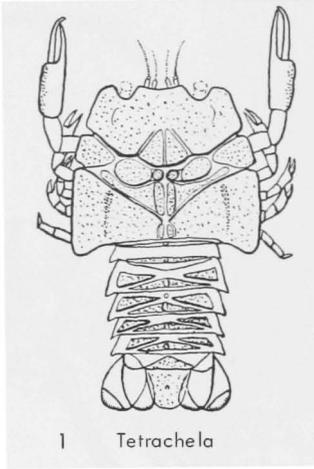


FIG. 272. Tetrachelidae (p. R468-R470).

slightly compressed dorsoventrally, strongly sculptured with crests, spines, and tubercles; rostrum long, spatulate; gastric and hepatic regions well marked; antennules short, antennae long with leaf-shaped scaphocerite; 3rd maxilliped pediform, 1st pereopods subchelate, strong, 2nd to 5th pereopods equal; abdomen strong, transversely grooved, with pointed pleura; uropods with diaeresis. *M.Trias.*, Eu.—FIG. 271,2. **P. sueuri* (DESMAREST); 2a, reconstr., $\times 0.7$ (after Assmann, 1927, and Glaessner, 1932); 2b, carapace, lat. view, $\times 0.7$ (Glaessner, 1932); 2c, ventral view, $\times 0.5$ [I-IV, pereopods 1-4; LA, left antenna; RA, right antenna; S, antennal scale; 1-5, antennal stalk; E, epistome; Md, mandible; Mx, maxilliped 3; BI, basis; M, merus; C, carpus; P, propodus; D, dactylus of P1]. First 4 pereopods of another specimen also shown; outline of carapace and flagellum of right antenna reconstructed (112).

Pseudopemphix WÜST, 1903 [**Pemphix albertii* VON MEYER, 1840; OD] [= *Seebachia* WÜST, 1903 (non NEUMAYR, 1882) (type, *Pemphix meyeri* ALBERTI, 1864)]. Differs from *Pemphix* in shorter carapace and rostrum, weaker sculpture, 1st pereopods almost chelate. *M.Trias.*, Eu.—FIG. 271,1. **P. albertii* (VON MEYER); carapace, lat. view, $\times 0.7$ (112).

Superfamily ERYONOIDEA de Haan, 1841

[*nom. transl. et correct.* GLAESSNER, herein (ex family Eryonidae DE HAAN, 1841)]

Carapace dorsoventrally compressed, with sharp lateral margins, front truncated; first to fourth or fifth pereopods chelate, dacty-

lus normally in lateral position; abdomen long, flat, medially keeled. *U.Trias.-Rec.*

Family TETRACHELIDAE Beurlen, 1930

Carapace almost quadrangular, with orbital emarginations, granulate, cervical and branchiocardiac grooves strongly marked, V-shaped, postcervical groove connected with both; telson rounded, uropods with diaeresis. *U.Trias.*

Tetrachela REUSS, 1858 [**Bolina raiblana* BRONN, 1858; OD]. Characters of family. *U.Trias.*, S.Eu.

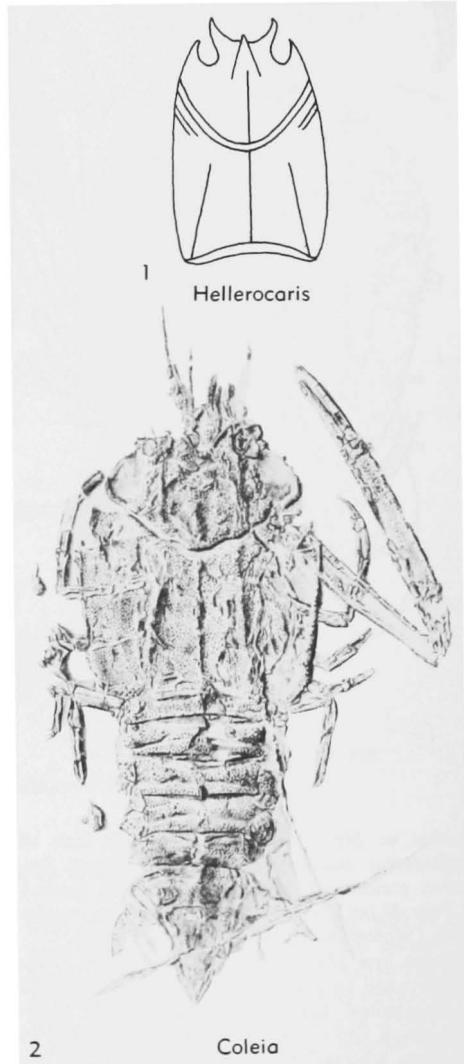


FIG. 273. Coleiidae (p. R470).

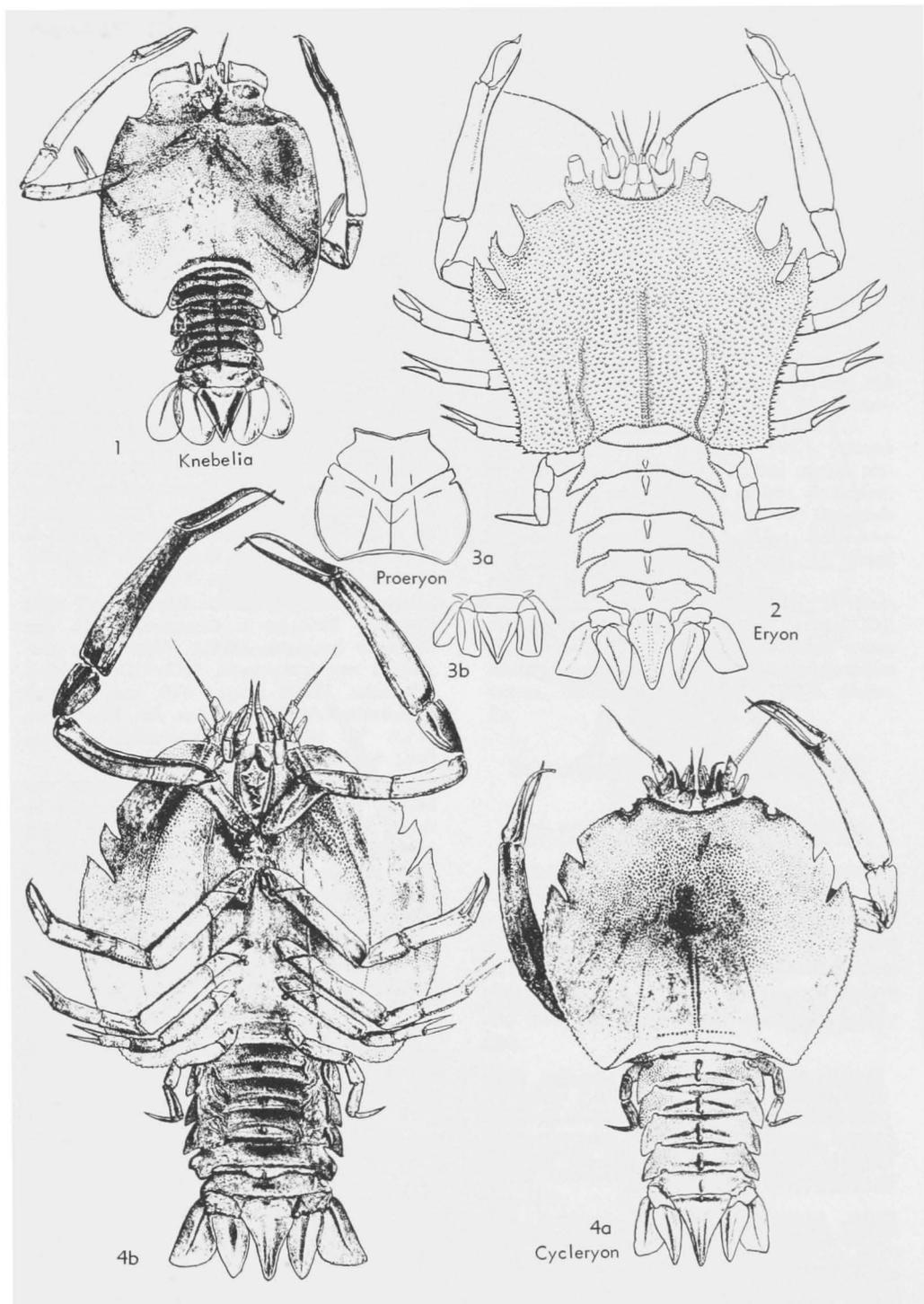


FIG. 274. Eryonidae (p. R470).

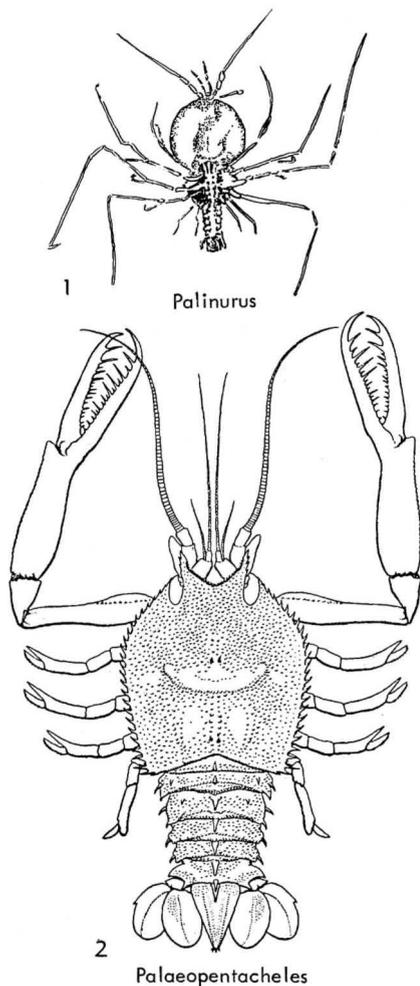


FIG. 275. Polychelidae (2); Palinuridae (1)
(p. R471, R473).

—FIG. 272,1. **T. raiblana* (BRONN); reconstr.,
×1.3 (109).

Family COLEIIDAE Van Straelen, 1924

Carapace longer than wide, with indented frontal margin and orbital emarginations, dorsally three longitudinal keels; uropods with diaeresis. *L.Jur.-L.Cret.*

Coleia BRODERIP, 1835 [**C. antiqua*; OD] [= *Archaeoastacus* BATE, 1884 (type, *A. willemoesi*)]. Carapace with distinct cervical and branchiocardiac grooves forming lateral indentations; 1st 4 pereiopods chelate. *Jur.*, Eu.-W.Sib.; *L.Cret.*, India.—FIG. 273,2. **C. antiqua*, L.Lias., Eng.; ×1 (326).

Hellerocaris VAN STRAELEN, 1925 [**Palaeopolycheles falloti* VAN STRAELEN, 1923; OD]. Carapace narrow, with weak rostral spine and deep orbital indentations and supraorbital spines; without lateral indentations, cervical groove distinct. *M.Jur.*, Fr.—FIG. 273,1. **H. falloti* (VAN STRAELEN); carapace, ×0.7 (296).

Family ERYONIDAE de Haan, 1841

[*nom. correct.* DANA, 1852 (pro Eryonidea de HAAN)]

Carapace outline rectangular to subcircular, cervical groove and longitudinal keels short or absent, eyes well developed; first four pereiopods chelate, uropods without diaeresis. *L.Jur.-L.Cret.*

Eryon DESMAREST, 1822 [**E. cuvieri* (= *Macrourites arctiformis* VON SCHLOTHEIM, 1820); OD]. Carapace angular, with cervical and branchiocardiac grooves indistinct or absent; scaphocerite elongated; uropods pointed. ["*Eryon*" *yehoachi* REMY & AVNIMELECH, 1956, (U.Cret., Israel) is based on a *Squilla*-like stomatopod telson.] *M.Jur.-L.Cret.*, Eu.—FIG. 274,2. *E. arctiformis* (SCHLOTHEIM), U.Jur., Ger.; reconstr., ×0.7 (11).

Cycleryon [*nom. subst.* GLAESSNER, 1965 (pro *Cyclocaris* BEURLEN & GLAESSNER, 1930, non *Cyclocaris* STEBBING, 1888)] [**Macrourites propinquus* VON SCHLOTHEIM, 1822; OD]. Carapace subcircular, frontal margin wide, eyes in small semicircular orbital indentations. *Jur.*, Eu.—FIG. 274,4. **C. propinquus* (SCHLOTHEIM), U.Jur., Ger.; 4a, dorsal, 4b, ventral, ×0.7 (219).

Proeryon BEURLEN, 1928 [**Eryon hartmanni* VON MEYER, 1835; OD]. Carapace with broadly V-shaped frontal margin and lateral shallow orbital indentations; lateral margins convex, widest behind middle; V-shaped parallel cervical and branchiocardiac grooves; endopodite of uropods truncated. *L.Jur.*, Eu.-W.Sib.—FIG. 274,3. *P. macrophthalmus* (KRAUSE), Ger.; 3a, carapace, 3b, tail fan, ×0.5 (25).

Knebelia VAN STRAELEN, 1922 [**Eryon bilobatus* MÜNSTER, 1839; OD, M] [= *Muensteria* KNEBEL, 1907 (non STERNBERG, 1838)]. Carapace with oval outline, without marginal indentations; telson large, uropods rounded. *U.Jur.*, S.Ger.—FIG. 274,1. **K. bilobata* (MÜNSTER); ×0.7 (219).

Family POLYCHELIDAE Wood-Mason, 1874

Carapace longer than wide, orbital indentations deep, lateral margins denticulate or spinose, median keel strong, cervical groove well marked, not strongly curved, eyes reduced in Recent forms, first four or five pereiopods chelate; telson narrow, uropods without diaeresis. *M.Jur.-Rec.*

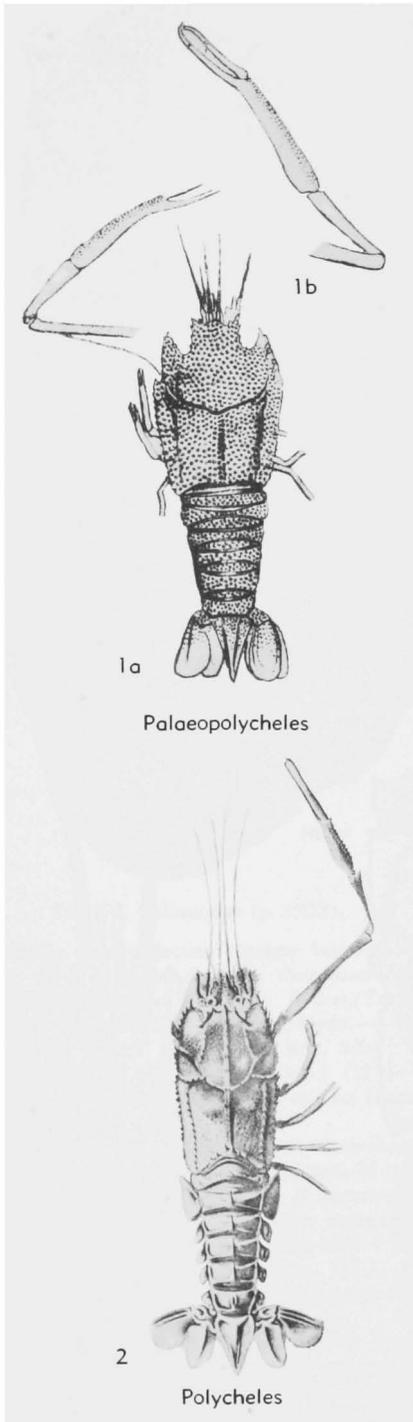


FIG. 276. Polychelidae (p. R471).

Polycheles HELLER, 1862 [**P. typhlops*; OD] [= *Pentacheles* BATE, 1878 (type, *P. euthrix*; SD FAXON, 1895); *Stereomastis* BATE, 1888 (type, *Pentacheles suhmi* BATE, 1878); SD HOLTHUIS, 1962); *Eryoneicus* BATE, 1882 (post-larval stage) (type, *E. coecus*; OD)]. Anterior margin of carapace with 3 frontal spines and deep oblique orbital indentations; lateral margins almost straight; 1st pereopods slender; uropods rounded; postlarval stage with ovoid inflated carapace. [Abyssal and subabyssal.] *Rec.*, cosmop.—FIG. 276,2. **P. typhlops*, *Rec.*; $\times 0.7$ (52).

Palaeopentacheles VON KNEBEL, 1907 [**Eryon röttenbacheri* MÜNSTER, 1839; OD]. Carapace with projecting front and oval orbital indentations, lateral margins convex, denticulate, cervical groove and median ridge weak, 1st pereopods long and robust. *U.Jur.*, S.Ger.—FIG. 275,2. **P. roettenbacheri* (MÜNSTER); reconstr., $\times 0.7$ (11).

Palaeopolycheles VON KNEBEL, 1907 [**Eryon longipes* FRAAS, 1855; OD]. Frontal margin projecting, lateral margins almost straight, denticulate, cervical groove distinct, curved, 1st pereopods with long merus and carpus. *U.Jur.*, S.Ger.—FIG. 276,1. **P. longipes* (FRAAS); 1a, dorsal view, 1b, cheliped, $\times 1$ (219).

Willemoesiocaris VAN STRAELEN, 1925 [**Palaeopentacheles ovalis* VAN STRAELEN, 1923; OD]. Frontal margin with rostrum and lateral spines, orbital emarginations rounded, lateral margins convex, denticulate, no median ridge. *M.Jur.*, Fr.

Superfamily PALINUROIDEA Latreille, 1803

[*nom. transl.* DE HAAN, 1849 (ex *Palinurini* LATREILLE, 1802)] [= *Loricata* BOAS, 1880; *Synaxidea* BATE, 1888]

Carapace cylindrical or dorsoventrally compressed, mostly without projecting rostrum. Base of antenna fused with epistome and lateral carapace margin, no scaphocerite; first four pereopods without chelae; abdominal pleura well developed; telson and uropods only partly calcified. *L.Jur.-Rec.*

Family PALINURIDAE Latreille, 1802

[*nom. correct.* GRAY, 1847 (pro *Palinurini* LATREILLE, 1802)]

Carapace subcylindrical, without lateral keels; antennal flagella long and strong. *L.Jur.-Rec.*

Palinurus WEBER, 1795 [**Astacus elephas* FABRICIUS, 1787 (= *Palinurus vulgaris* LATREILLE, 1804; OD)]. Rostrum very short, supraorbital spines large and obliquely flattened; median portion of

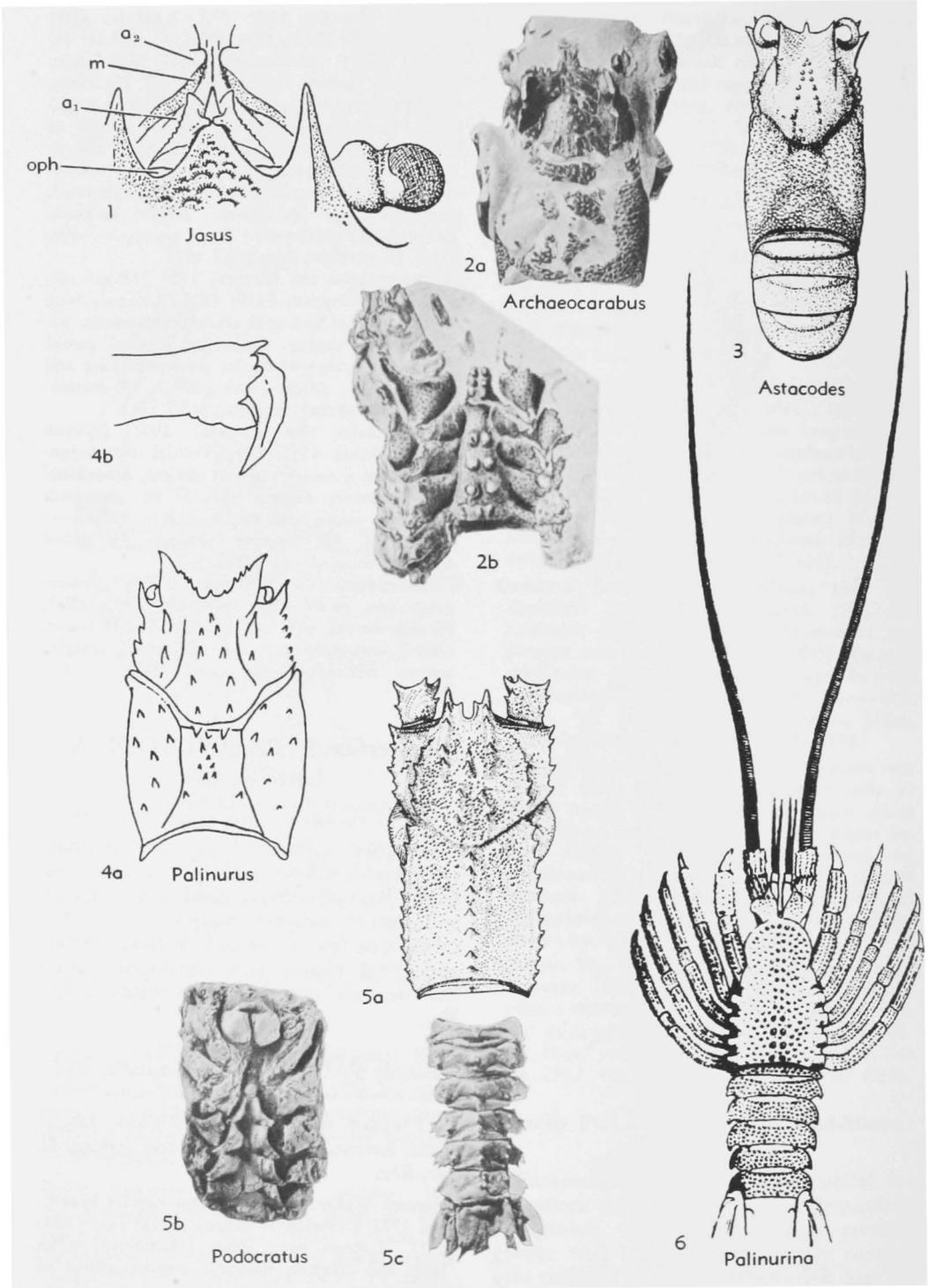


FIG. 277. Palinuridae (p. R471, R473-R474).



FIG. 278. Palinuridae (p. R473).

antennular base projecting strongly between segments 2+3 of antennal stalks; their bases fused medially in front of epistome. *U.Cret.*(*Turon.-Senon.*), ?*L.Tert.*, Eu.; *Rec.*, Atl.-Medit.—FIG. 277,4. **P. elephas* (FABRICIUS), *Rec.*, S.Eu.; 4a, carapace, 4b, end of pereopod 1, $\times 0.1$ (52).—FIG. 275,1. *Phyllosoma* larva of *P. elephas* (FABRICIUS), *Rec.*; $\times 0.7$ (52).

Archaeocarabus M'COY, 1849 [**A. bowerbanki*; OD]. Differs from *Palinurus* in rostrum of moderate size which is clasped by 2 processes of ophthalmic somite as in *Jasus*, but supraorbital spines widely separated; sternal plate with 4 pairs of tubercles. *L.Eoc.*, Eng.—FIG. 277,2. **A. bowerbanki*; 2a, dorsal view, $\times 1$, 2b, ventral view, $\times 1$ (326).

Astacodes BELL, 1863 [**A. falcifer*; OD]. Resembling *Palinurus* but rostrum and supraorbital spines of similar length, abdominal terga without transverse grooves. *U.Jur.*, Czech., *L.Cret.* (*Hauteriv.*), Eng.; *U.Cret.*(*Turon.-Santon.*), Tex.—FIG. 277,3. *A. maxwelli* STENZEL, *U.Cret.*, Tex.; reconstr., $\times 0.5$ (283).

Eurycarpus SCHLÜTER, 1868 [**E. nanodactylus*; OD]. Antennular stalks long, antennal stalks strong and spiny, pereopods long and slender, carapace unknown. *U.Cret.*(*Senon.*), Eu.

Jasus PARKER, 1883 [**Palinurus lalandii* H. MILNE-EDWARDS, 1837; SD HOLTHUIS, 1960] [= *Palinostus* BATE, 1888]. Rostrum clasped by 2 processes of ophthalmic somite and projecting almost as far as supraorbital spines; antennular bases not projecting strongly, close-set medially. *Oligo.*, N.Z.; *Rec.*, S.Oceans.—FIG. 277,1. **J. lalandii* (MILNE-EDWARDS), *Rec.*, S.Afr.; frontal area (a₂, base of antenna; m, articulating membrane; a₁, antennular base; oph, eye stalk), $\times 1$ (15).—FIG. 278, 1. *J. flemingi* GLAESSNER, *Oligo.*, N.Z.; $\times 0.4$ (118).

Linuparus WHITE, 1847 [**Palinurus trigonus* VON SIEBOLD, 1824; OD]. Carapace with 3 longitudinal keels; no rostrum; supraorbital spines close to median line, fused to form plate or separated by indentation. *L.Cret.-Rec.*

L. (Linuparus). Supraorbital spines dorsoventrally flattened, medially joined; posterolateral ridges on carapace smooth; abdominal pleura with 3 marginal spines. *Rec.*, E.Afr.-E.Asia-Australia.

L. (Podocratus) GEINITZ, 1849 [**P. duelmense*; OD] [= *Thenops* BELL, 1858 (type, *T. scyllariformis*); *Podocrates* SCHLÜTER, 1862 (obj.); *Eolinuparus* MERTIN, 1941 (type, *Linuparus*

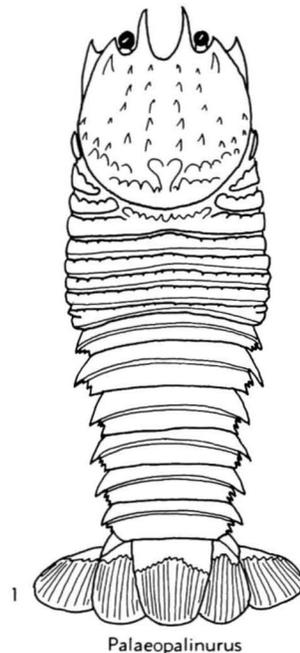


FIG. 279. Palinuridae (p. R474).

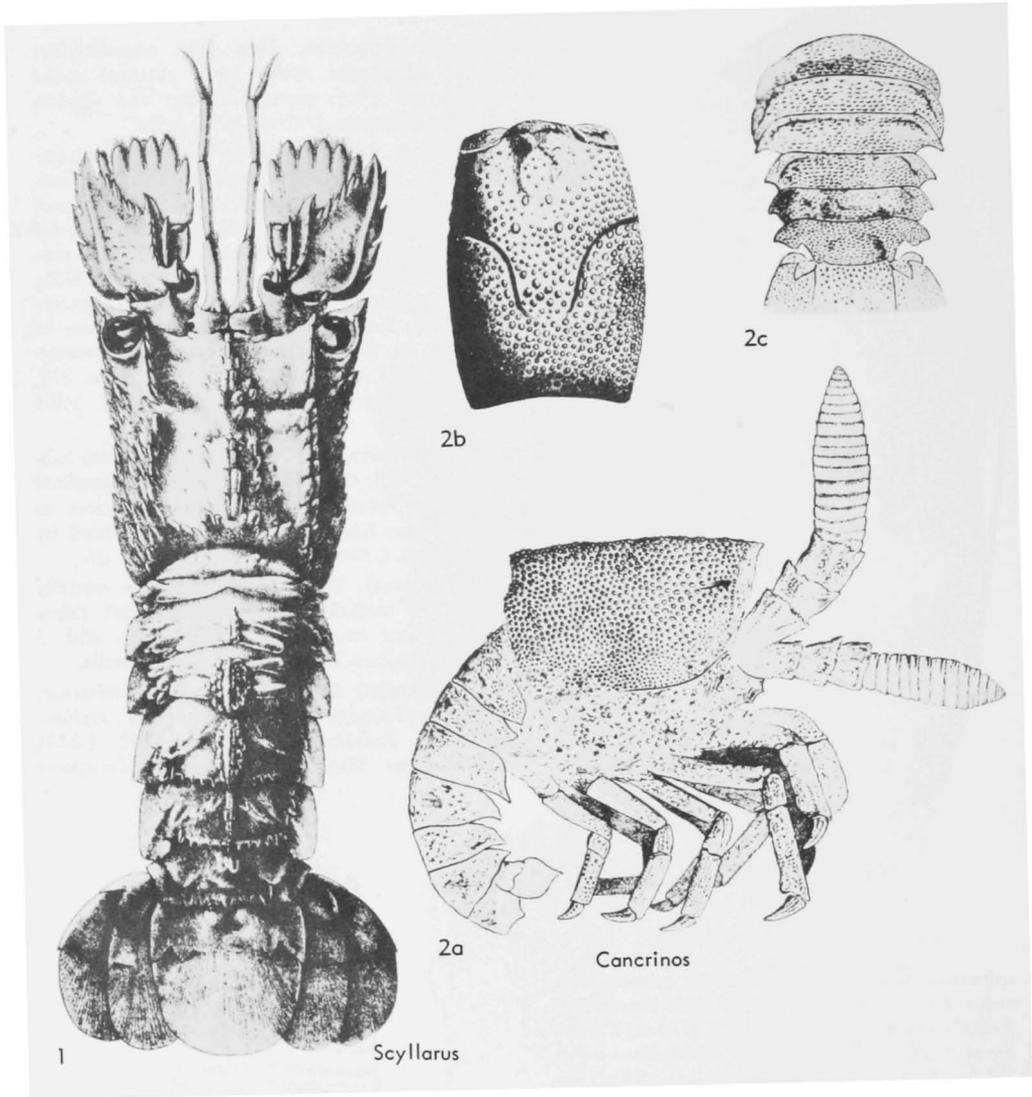


FIG. 280. Cancrinidae (2); Scyllaridae (1) (p. R475).

carteri REED, 1911)]. Supraorbital spines separate, carapace with granulate or spinose longitudinal ridges. *L.Cret.-U.Cret.*, N.Am.-Eu.; *U.Cret.*, W.Afr.-Japan-Kamchatka; *L.Tert.(Paleoc.)*, USA (Tex.-Ala.); *L.Tert.*, Eu. [Attempts to subdivide the fossil forms have been made by MERTIN and BIRSHTEYN, but diagnoses do not agree with descriptions of species referred to the subgenera *Podocrates*, *Thenops*, and *Eolinuparus*, which therefore cannot be satisfactorily distinguished.] —FIG. 277,5. *L. (Podocratus) watkinsi* STENZEL, *U.Cret.*, Tex.; 5a, reconstr. of carapace with part of antennae, 5b, sternum, mandibles and

parts of pereopods 1-5, 5c, abdomen, $\times 1$ (283). **Palaeopalinurus** BACHMAYER, 1954 [**P. glaessneri*; OD]. Carapace cylindrical, with distinct post-cervical groove, anterior portion with large supra-orbital and other spines, posterior part transversely grooved and ridged. *U.Jur.*, Eu.—FIG. 279,1. **P. glaessneri*; reconstr., $\times 0.5$ (Glaessner, n). **Palinurina** MÜNSTER, 1839 [**P. longipes*; SD Woods, 1926]. Antennae thick and long, with setae, on strong short stalks; 1st pereopods shorter than others; carapace and abdomen incompletely known. *L.Jur.*, Eng.; *U.Jur.*, Ger.—FIG. 277,6. **P. longipes*, *U.Jur.*, S.Ger.; reconstr., $\times 1$ [accord-

ing to OPPEL, "outlines of the body are too definite") (219).

?*Phalangites* MÜNSTER, 1839 [**P. priscus*] [= *Palpipes* ROTH, 1851 (obj.); *Palaeonymphon* LÉON, 1933 (no species named)]. Considered either as a larva, probably of *Palinurina*, or as belonging to the Pantopoda. *U.Jur.*, Ger.

Family CANCRINIDAE Beurlen, 1930

Antennae thick, with short stalks and 13 to 19 rings, widest in middle part, with long setae on inner edge; carapace coarsely, abdomen finely granulate; telson wide; dactyli thick and wide. *U.Jur.*

Cancrinus MÜNSTER, 1839 [**C. claviger*; OD]. Characters of family. *U.Jur.*, S.Ger.—FIG. 280, 2. **C. claviger*; 2a, lateral view, 2b, dorsal view of carapace; 2c, dorsal view of abdomen, $\times 0.7$ (219).

Family SCYLLARIDAE Latreille, 1825

[*nom. correct.* WHITE, 1847 (*pro* *Scyllarides* LATREILLE, 1825)]

Carapace dorsoventrally more or less flattened, with sharp lateral margins, orbits in anterior margin, no supra-orbital spines; antennae short, flagella replaced by plates with dentate or lobulate margins. *L.Cret.-Rec.*

Scyllarus FABRICIUS, 1775 [**Cancer arctus* LINNÉ, 1758; OD]. Carapace convex, not broader than long, rostrum short, exopod of 3rd maxilliped without flagellum, terminal plate of antenna with distinct teeth. *L.Mio.*, Java; *Rec.*, littoral, cosmop.—FIG. 280, 1. *S. rugosus* H. MILNE-EDWARDS, *Rec.*; $\times 2$ (18).

Ibacus LEACH, 1815 [**I. peronii*; OD]. Carapace much wider than long, dentate lateral margins converging posteriorly, with deep emargination; orbits nearer to median line than to anterolateral angles. ?*U.Cret.*, Lebanon; ?*Oligo.*, Eu.; *Rec.*, IndoPac.-W.Pac.-Cape Verde Is.—FIG. 281, 1. **I. peronii*, *Rec.*; cephalothorax and antennae, $\times 0.4$ (15).

Parribacus DANA, 1852 [**Scyllarus antarcticus* LUND, 1793; SD HOLTHUIS, 1956]. Differs from *Ibacus* in orbits being midway between median line and anterolateral angles. ?*U.Cret.* (*Cenoman.*), Lebanon; *Rec.*, IndoPac.-W.Ind.

Scyllarella RATHBUN, 1935 [**S. gibbera*; OD]. Carapace broader than long, with sloping sides and very prominent cardiac region; cervical and branchiocardiac grooves deep, lateral margin carinate and dentate. *Paleoc.*, USA (Ala.).—FIG. 281, 2. **S. gibbera*; 2a-c, dorsal, ventral, post. views of incomplete carapace, $\times 1.5$ (244).

Scyllarides GILL, 1898 [**Scyllarus aequinoctialis* LUND, 1793; OD] [= *Scyllaridia* BELL, 1858

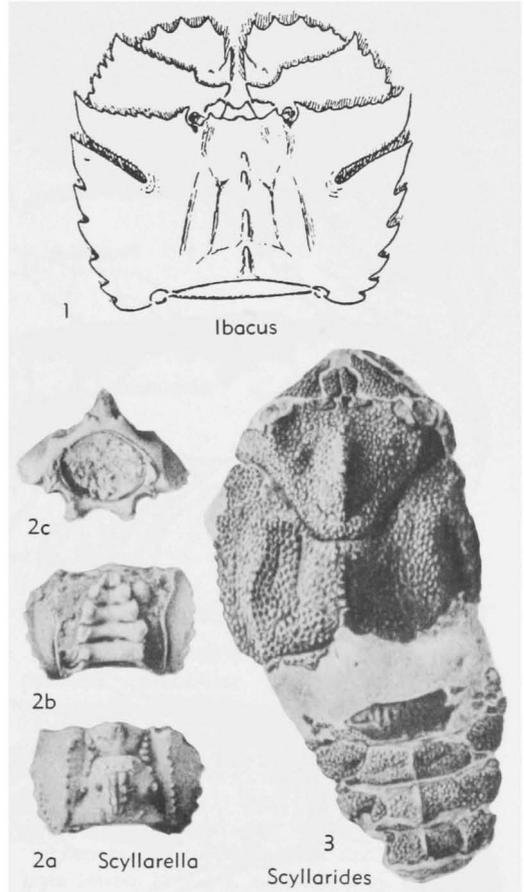


FIG. 281. Scyllaridae (p. R475).

(type, *S. koenigi*; OD)]. This name was suppressed by ICZN (Op. 293). If the fossil is not congeneric with the Recent genus as claimed by Woods (1926), it must therefore be given a new name.] Eyes near anterolateral angles; lateral margins of carapace without deep fissures, rostrum salient. ?*L.Cret.* (*Alb.*), ?*L.Eoc.*, Eng.; *Rec.*, Medit.-E.Atl.—FIG. 281, 3. *S. ?koenigi* (BELL), *L.Eoc.*, Eng.; $\times 1$ (326).

Infraorder ANOMURA H. Milne-Edwards, 1832

[*nom. transl.* BORRADAILE, 1907]

Carapace not fused with epistome; last thoracic sternite free; third maxilliped narrow, third pereiopods lacking chelae, fifth modified in shape and position; abdomen not strongly calcified, mostly reduced in length. *L.Jur.-Rec.*

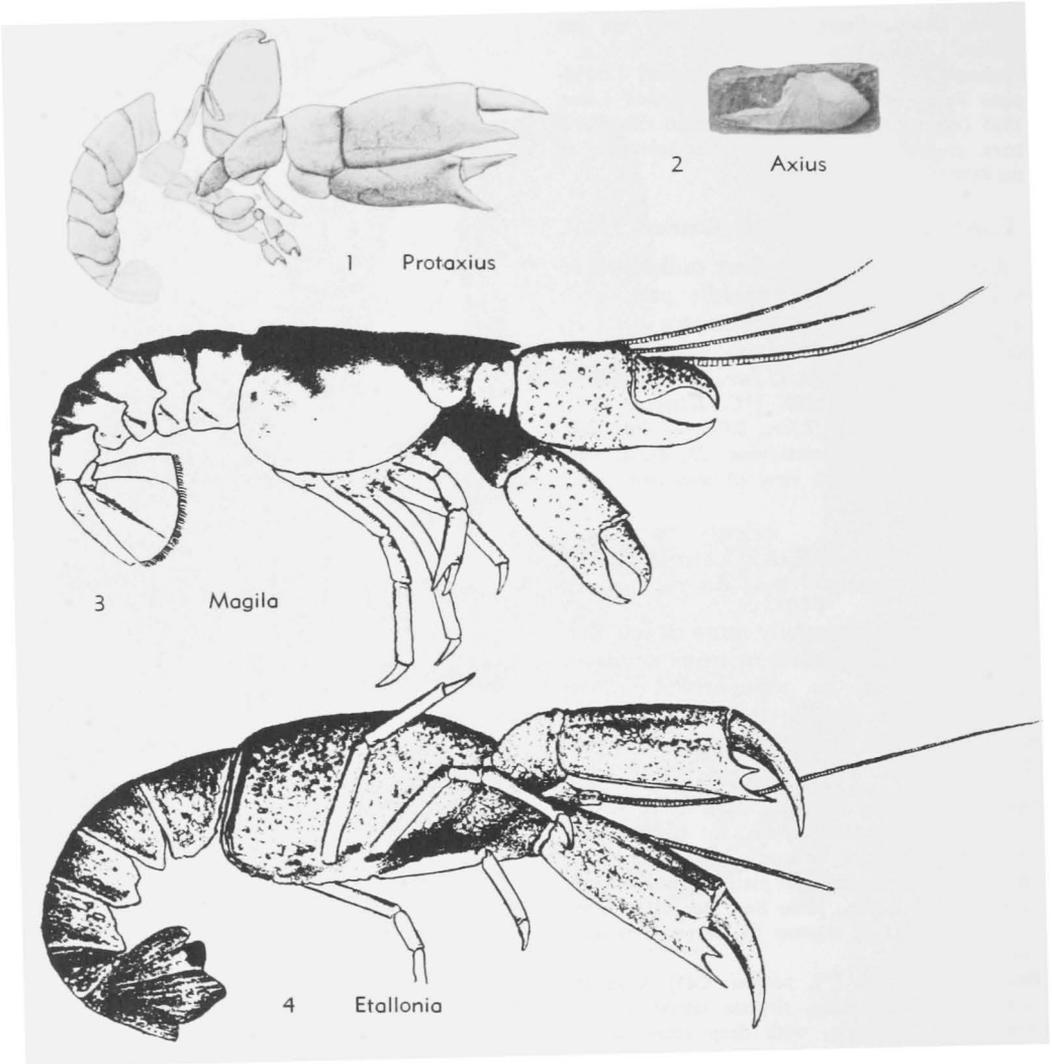


FIG. 282. Axiidae (p. R477).

Superfamily THALASSINOIDEA Latreille, 1831

[*nom. transl.* DANA, 1852 (*ex* family Thalassinides LATREILLE, 1831)]

Abdomen well developed but pleura more or less reduced; first pereopods mostly chelate. *L.Jur.-Rec.*

Family THALASSINIDAE Latreille, 1831

[*nom. correct.* WHITE, 1847 (*pro* family Thalassinides LATREILLE, 1831)]

Large, rostrum moderately developed, linea thalassinica present, first and second

pereopods subchelate, pleura reduced, uropods without diaeresis, lanceolate. [Monotypic, with probably only one species.] *?Pleist., Rec.*

Thalassina LATREILLE, 1806 [**T. scorpionides* LATREILLE, 1806 (= **Cancer (Astacus) anomalus* HERBST, 1804); OD]. Characters of family. *?Pleist., Rec.*, IndoPac. [Common in concretions in mangrove mud of undetermined (but probably Holocene) age.]

Family AXIIDAE Huxley, 1879

Carapace with rostrum and cervical groove, without linea thalassinica; antennu-

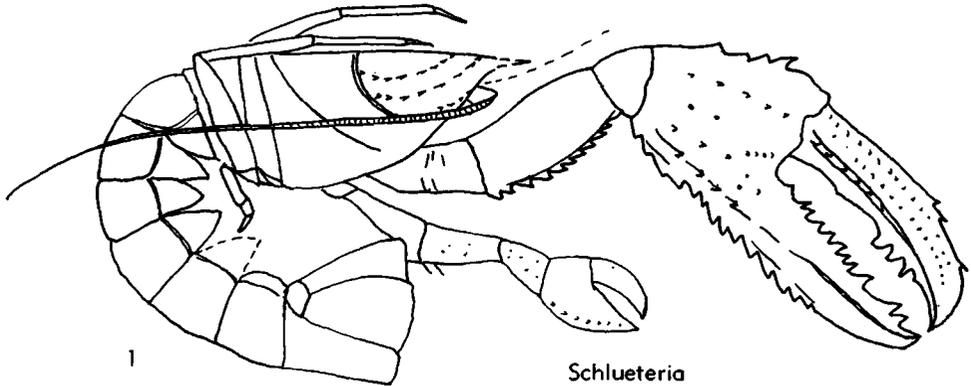


FIG. 283. Axiidae (p. R477).

lar flagella well developed; first pereopods with large chelae, second pereopods with small chelae. *L.Jur.-Rec.*

Axius LEACH, 1815 [**A. stirhynchus*; OD]. Rostrum dentate, carapace without median keel. *Oligo.*, Panama; *Plio.*, Fr.; *Rec.*, cosmop.—FIG. 282,2. *A. reticulatus* RATHBUN; *Oligo.*, Panama; propodus of left 1st pereopod, $\times 1.5$ (234).

Etallonia OPPEL, 1861 [**Magila longimana* MÜNSTER, 1839; OD] 1st pereopods subchelate, with long rectangular manus and curved dactylus; abdominal pleura pointed. *U.Jur.*, S.Ger.—FIG. 282,4. **E. longimana* (MÜNSTER); $\times 3$ (219).

Magila MÜNSTER, 1839 [**M. latimana*; SD GLAESSNER, 1929]. Carapace not strongly calcified, straight keels on short anterior portion; first chelipeds with square manus about equal in length to fingers, abdominal pleura well developed. *L.Jur.-U.Jur.*, Eu.—FIG. 282,3. **M. latimana*; *U.Jur.*, S.Ger.; reconstr., $\times 3$ (219).

Protaxius BEURLEN, 1930 [**Callianassa isochela* WOODWARD, 1876; OD]. First pereopods with large chelae differing slightly in size only, with long manus and short dactylus; 2nd pereopods with small symmetrical chelae; first abdominal somite not much reduced, abdominal pleura 2 to 5 well developed. *U.Jur.*, Eu.—FIG. 282,1. **P. isochelus*, *U.Jur.*, Eng.; $\times 1.5$ (331).

Schlueteria FRITSCH, 1887 [**S. tetracheles*; OD]. Carapace with curved longitudinal keels on anterior portion, with cervical and branchiocardiac grooves; abdomen large; 1st pereopods long, with very large spiny chelae; 2nd pereopods flattened, chelate; 3rd and 4th pereopods slender; 5th pereopod reduced. *U.Cret.(Turon.-L.Senon.)*, Eu.—FIG. 283,1. **S. tetracheles*, Czech.; reconstr., $\times 0.8$ (Glaessner, n. mod. from 98).

Family LAOMEDIIDAE Borradaile, 1903

Rostrum well developed, linea thalassinica present, antennular flagella short; first pereopods large, chelate or subchelate, isochelous; abdominal pleura well developed. *Mio.-Rec.*

Laomedia DE HAAN, 1841 [**L. astacina*; OD].

First pereopods with stout chelae, subequal; 2nd pereopods with simple dactylus. *Rec.*, Japan.

Jaxea NARDO, 1847 [**J. nocturna*; OD]. Chelae of 1st pereopods slender, elongate, with long fingers; 2nd pereopods subchelate. *Mio.*, Aus.; *Rec.*, Medit.-North Sea.—FIG. 284,4. *J. kuemeli* BACHMAYER, *Mio.*, Aus.; 4a, carapace and 3 abdominal somites (compressed); 4b, left chela, $\times 3$ (8).

Family CALLIANASSIDAE Dana, 1852

Carapace weakly calcified, mostly with linea thalassinica, with cervical groove; antennular flagella short to medium in length; first pereopods chelate or subchelate, heterochelous; abdominal pleura reduced or absent. *U.Jur.-Rec.*

Subfamily CALLIANASSINAE Dana, 1852

Rostrum small or absent, linea thalassinica present; third maxillipeds with exopodite; first pereopods chelate, heterochelous; second pereopods isochelous. *U.Cret.-Rec.*

Callianassa LEACH, 1814 [**Cancer (Astacus) subterraneus* MONTAGU, 1808; OD]. Carapace with cervical groove extended far back medially; 1st

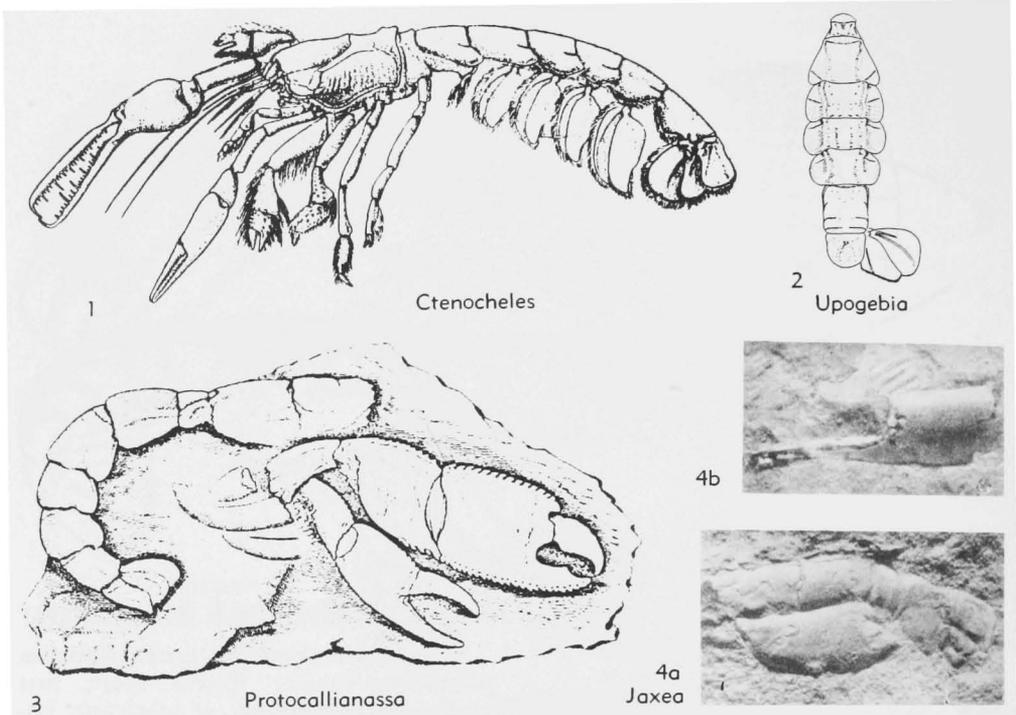


FIG. 284. Laomedidae (4); Callianassidae (Callianassinae) (1), (Protocallianassinae) (3), Upogebinae (2) (p. R477-R479).

peraeopods strongly heterochelous, carpus very narrow proximally, widened abruptly to equal propodus, which is rectangular; fingers short, curved; abdominal pleura rudimentary. [*Callianassa*-like chelae are very common fossil decapod Crustacea, because of strong calcification and because the burrowing habits of these organisms favor fossilization. It is not known how many species based on chelae actually represent the genus *Callianassa* or even the subfamily or family to which it belongs.] *U.Cret.-Rec.*, cosmop.—FIG. 285, 1. *C. sp.*, Rec., Papua; diagrammatic (LT, linea thalassinica), $\times 0.7$ (Glaessner, n).

Ctenocheles KISHINOUE, 1926 [**C. balssi*; OD]. Differs from *Callianassa* in larger chela of 1st peraeopods with inflated palm and very long and slender fingers, with comblike teeth, resembling *Oncopareia*. [It is possible that a chela from the Upper Cretaceous of Holland described by PELSENNEER as *Ischnodactylus* (see p. R459) *inaequidens* belongs to *Ctenocheles*, rather than to *Oncopareia*.] *Paleoc.*, S.Australia-N.Am.(Ala.); *Eoc.*, N.Am.(Miss.)-Japan; *M.Oligo.*, Hung.; *Pleist.*, N.Z.; *Rec.*, Pac.—FIG. 284, 1. **C. balssi*, Rec.; $\times 0.7$ (362a).

Subfamily PROTOCOLLIANASSINAE Beurlen, 1930

Carapace with linea thalassinica; first peraeopods with well-developed chelae, heterochelous; abdomen with pleura developed on second to sixth somites; uropods without diaeresis. ?*L.Cret.*, *U.Cret.-Paleoc.*

Protocallianassa BEURLEN, 1930 [**C. archiaci* A. MILNE-EDWARDS, 1860; OD]. Characters of subfamily. [Single chelae are hardly distinguishable from those of *Protaxius* or *Callianassa*.] ?*L.Cret.*, *U.Cret.*, Eu.-N.Am.; *Paleoc.*, W.Australia.—FIG. 284, 3. **P. archiaci* (A. MILNE-EDWARDS), *U. Senon.*, Neth.; $\times 1$ (197).

Subfamily UPOGEBIINAE Borradaile, 1903

Carapace with well-developed rostrum, cervical and branchiocardiac grooves, and linea thalassinica; first peraeopods chelate or subchelate, subequal. *U.Jur.-Rec.*

Upogebia LEACH, 1814 [**Cancer (Astacus) stellatus* MONTAGU, 1808; OD]. Rostrum triangular, with marginal ridges extended back on carapace; 1st peraeopods with strong propodus and short fixed finger, dactylus strong, gently curved; telson square, uropods without diaeresis. *U.Jur.*, *U.Cret.*, *U.Tert.*, Eu.; *U.Cret.-L.Tert.*, N.Am.; *Rec.* cosmop.—FIG. 286, 1. *U. littoralis* RISSO, Rec.; 1a, b, dorsal and lateral views of carapace; 1c, claw,

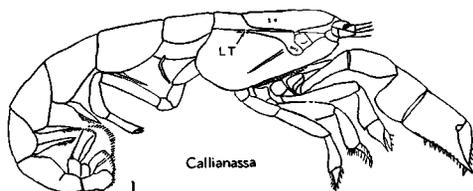


FIG. 285. Callianassidae (Callianassinae)
(p. R477-R478).

×0.7 (52).—FIG. 284,2. *U. rhacheochir* STENZEL, U.Cret., USA(Tex.); abdomen, ×1 (283).

Superfamily PAGUROIDEA Latreille, 1803

[*nom. transl.* BORRADAILE, 1907 (*ex* Pagurii LATREILLE, 1802)]

Carapace ovate, with more or less well-defined regions, tending to be weakly calcified behind "cervical groove"; first pereopods chelate, second and third or second to fourth well developed, fifth reduced; abdomen mostly asymmetrical, soft, or folded under cephalothorax; uropods (where present) adapted for attachment to interior of empty mollusk shells or tubes. *L.Jur.-Rec.*

Family PYLOCHELIDAE Bate, 1888

Body straight and symmetrical; rostrum absent; third maxillipeds approximated basally, first pereopods similar and strong; abdominal terga articulating. *Rec.*

Pylocheles A. MILNE-EDWARDS, 1880 [**P. agassizi*; OD]. Characters of family. *Rec.*, W.Indies-Ind.O.

Family PAGURIDAE Latreille, 1802

[*nom. correct.* SAMOUELLE, 1819 (*pro* family Pagurii LATREILLE, 1802)]

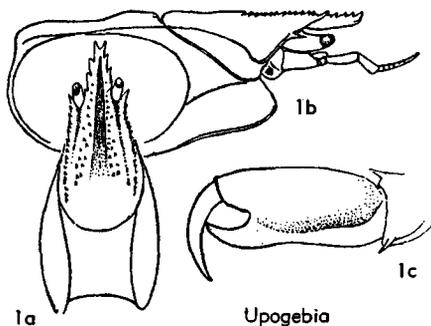


FIG. 286. Callianassidae (Upogebiinae)
(p. R478-R479).

Carapace elongate, widened and weakly calcified posteriorly, rostrum very short, abdomen uncalcified and coiled or secondarily symmetrical externally; first pereopods with chelae which are more or less heterochelous; second and third pereopods elongate and ambulatory, fourth and fifth pereopods reduced, commonly subchelate; abdominal appendages in many forms on left side only. *Jur.-Rec.*

Subfamily PAGURINAE Latreille, 1802

[*nom. transl.* ORTMANN, 1892 (*ex* Paguridae LATREILLE, 1802)] [=Eupagurinae ORTMANN, 1892]

Third maxillipeds distant at base, right chela commonly much larger than left, rarely chelae almost equal. *L.Cret.-Rec.*

Pagurus FABRICIUS, 1775 [**Cancer bernhardus* LINNÉ, 1758 (on official list, ICZN); SD LATREILLE, 1810 [=Eupagurus BRANDT, 1851 (type, *Cancer bernhardus* LINNÉ, 1758; SD STIMPSON, 1858) (obj.)]. Chelipeds usually dissimilar and unequal, right being much larger than left, very rarely subequal; 4th pereopods subchelate. *L.Cret. (Alb.)*, USA(Tex.); *Paleoc.*, USA(Ala.); *Plio.*, Eng.; *Pleist.*, USA(Calif.)-Eu.; *Rec.*, cosmop.—FIG. 287,1. *P. longicarpus* SAY, *Rec.*; ant. part, ×4 (229).

Anapagurus HENDERSON, 1886 [**Pagurus laevis* BELL, 1845; SD HOLTHUIS, 1962]. Chelipeds unequal, right larger than left, finger tips calcareous; ambulatory legs long and slender. ?*Plio.*, *Pleist.*, Neth.; *Rec.*, Atl.-Medit.-IndoPac.

Subfamily DIOGENINAE Ortmann, 1892

[=Dardaninae SCHMIDT, 1926; Paguristinae MAKAROV, 1938]

Third maxillipeds approximated basally, chelipeds equal or subequal, or left much larger than right, abdominal tergites not divided into two paired pieces, first somite not fused with last thoracic sternites. *U. Cret.-Rec.*

Diogenes DANA, 1851 [**Pagurus miles* FABRICIUS, 1787; OD (on official list, ICZN)]. Chelipeds with elongate carpus, manus with fixed finger slightly deflected downward; 2nd and 3rd pereopods laterally compressed. *Rec.*, E.Hemis.(littoral).

Eocalcinus VIA, 1959 [**E. eocenicus*; OD]. Left chela robust, plano-convex, with semicircular or circular profile; carpo-propodial articulation markedly oblique. *Eoc.*, Spain.—FIG. 288,2. **E. eocenicus*; left chela, ×0.5 (314).

Clibanarius DANA, 1852 [**Cancer clibanarius* HERBST, 1791; OD]. Chelipeds equal or subequal, tips of fingers corneous and spooned. ?*U.Eoc.*, Egypt; *Rec.*, warm seas (littoral).

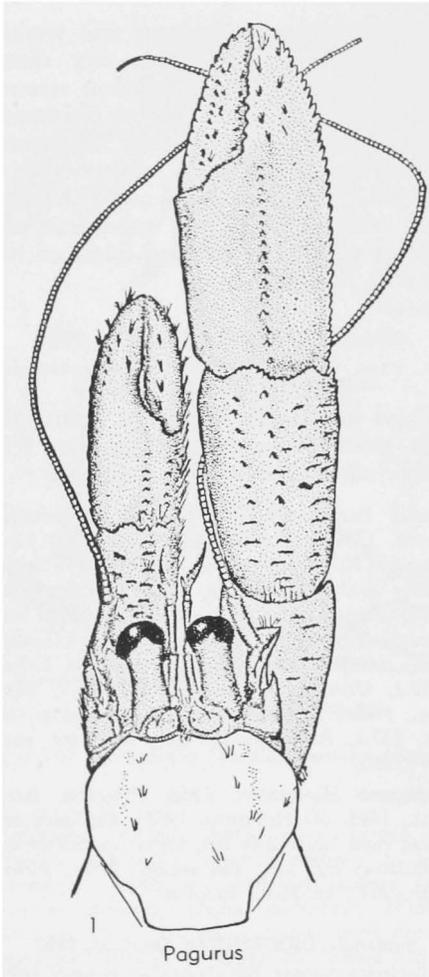


FIG. 287. Paguridae (Pagurinae) (p. R479).

Dardanus PAULSON, 1875 [**D. hellerii*; OD (on official list, ICZN)] [= *Pagurites* (*Propagurites*) BEURLIN, 1929 (type, *P. hungaricus* LÖRENTHEY, 1929)]. Chelipeds (with few exceptions) dissimilar and unequal, left being much larger than right; finger tips corneous, blackened and somewhat spooned, especially those of smaller chela. *Eoc.*, USA (Calif.)-Egypt; *L.Oligo.*, C.Asia; *Mio.*, Eu.; *Plio.*, Ital.-Fiji; *Pleist.*, USA (Calif.); *Rec.*, littoral in all warm seas.—FIG. 288,6. **D. subaequalis* RATHBUN, *Eoc.*, USA (Calif.); left chela, $\times 1.5$ (238).

Paguristes DANA, 1851 [**P. hirtus*; SD STIMPSON, 1858] [= *Pagurites* LÖRENTHEY, 1929, erroneous spelling]. Chelipeds similar, equal, subequal, or one (usually left) larger. *U.Cret.* (*U.Senon.*)-*Paleoc.*, USA (Ala.); *Mio.*, USA (Calif.); *Rec.*, warm seas.—FIG. 288,1. *P. johnsoni* RATHBUN;

Paleoc., Ala.; 1a,b, outer views of left and right chelae, $\times 1.5$ (244).

Petrochirus STIMPSON, 1859 [**Pagurus granulatus* OLIVIER, 1811 (= **Cancer bahamensis* HERBST, 1791); OD]. Chelae large, heterochelous, fingers with calcareous tips, surfaces of chelae covered with clustered granules. *U.Cret.*, USA (Tex.); *Oligo.*, W.Ind.; *Mio.*, Panama-N.Am.-N.Afr.; *Plio.*, N.Am.; *Rec.*, E.Atl.-W.Atl. coasts.—FIG. 288,7.

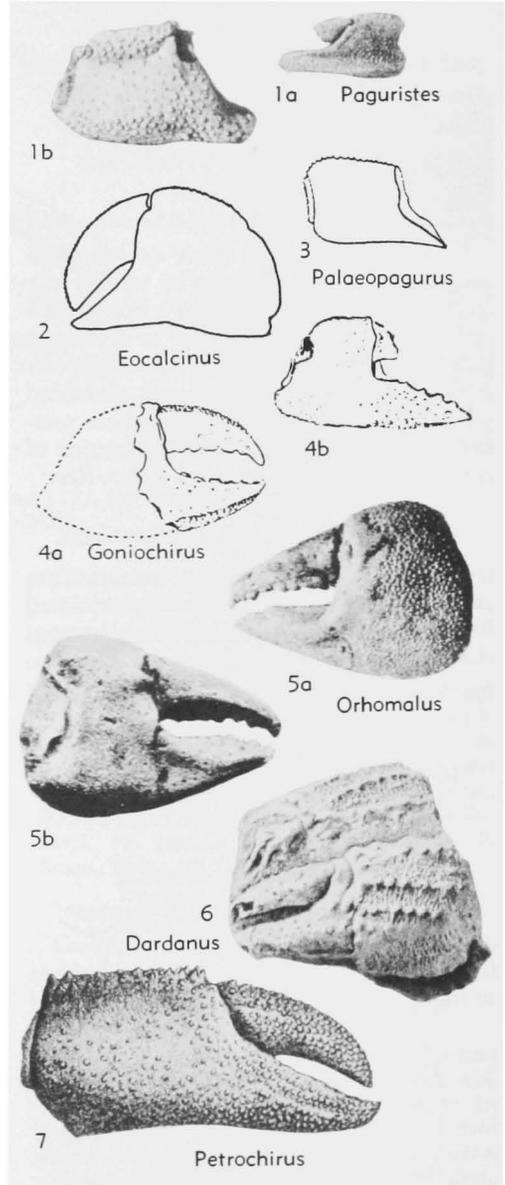


FIG. 288. Paguridae (Diogeninae) (1-2,6,7), (Subfamily Uncertain) (3-5) (p. R479-R481).

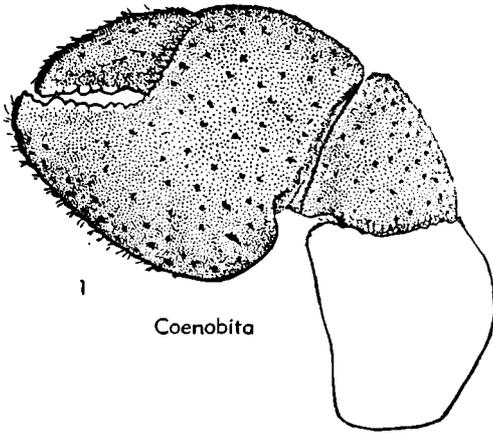


FIG. 289. Coenobitidae (p. R481).

P. priscus (BROCCHI), *Mio.*, Hung.; right chela, $\times 1$ (184).

Subfamily UNCERTAIN

Goniochirus ÉTALLON, 1861 [**G. babeau*; OD]. Chela inflated externally, flat internally, fixed finger short, proximal articulation of propodus strongly oblique. *Jur.*, Eu.—FIG. 288,4. *G. cristatus*, U.Jur., Eng.; 4a, right chela, outline restored, 4b, left chela, $\times 1$ (349a).

Orhomalus ÉTALLON, 1861 [**O. virgulinus*; SD GLAESSNER, 1929]. Chela wider than long, with convex outer surface, fixed finger short and thick, proximal articulation of propodus straight and placed on inner side; fingers with rounded teeth. *M.Jur.-U.Jur.*, ?*L.Cret.*, Eu.—FIG. 288,5. *O. deslongchamps* HÉE, U.Jur., Fr.; 5a,b, outer and inner sides of left chela, $\times 1$ (296).

Palaeopagurus VAN STRAELLEN, 1925 [**P. deslongchamps*; SD GLAESSNER, 1929]. Chela elongate, with rectangular propodus, convex external and flat internal surface, carpo-propodial articulations slightly oblique, dactylus articulation oblique. *L.Jur.*, ?*U.Cret.*, Eu.—FIG. 288,3. **P. deslongchamps*, Lias., Fr.; right chela, $\times 1$ (296).

Pustulina QUENSTEDT, 1858 [**P. suevica*]. Single small granulous chela. *U.Jur.*, Ger.

Family COENOBITIDAE Dana, 1851

Carapace well calcified; third maxillipeds basally approximated, left cheliped larger than right; second and third pereopods long, fourth and fifth shorter, fourth chelate or subchelate, fifth chelate. [Terrestrial.] ?*L.Mio.*, *Rec.*

Coenobita LATREILLE, 1829 [**Cancer clypeatus* HERBST, 1791; OD]. Left cheliped much shorter

than right, all segments short, broad; legs stout. ?*L.Mio.*, Java; *Rec.*, tropical.—FIG. 289,1. **C. clypeatus* (HERBST), *Rec.*; $\times 1.5$ (229).

Family LITHODIDAE Samouelle, 1819

Carapace well calcified, crablike, with projecting rostrum and with lateral edge, linea anomurica, and well-marked regions; last thoracic and first abdominal sternum fused; chela of right first pereopod larger than left, fifth pereopods reduced, in branchial chamber; female abdomen asymmetrical. *Rec.*

Lithodes LATREILLE, 1806 [**Cancer maja* LINNÉ, 1758; OD]. Rostrum long, spinose; abdomen with paired calcified plates. *Rec.*, N.Pac.-N.Atl.-E.Atl.-S.Ind.O.

Family LOMIDAE Bouvier, 1895

[*nom. correct.* GLAESSNER, herein (pro Lomisidae BOUVIER, 1895)]

Carapace flat, resembling Porcellanidae, well calcified; abdomen wide, turned under cephalothorax; first pereopods with flat chelae, second to fourth ambulatory, fifth reduced, in branchial chamber. *Rec.*

Lomis H. MILNE-EDWARDS, 1837 [**Porcellana hirta* LAMARCK, 1818; OD]. Characters of family. *Rec.*, S.Australia-Tasmania.

Superfamily GALATHEOIDEA

Samouelle, 1819

[*nom. transl.* HENDERSON, 1888 (ex Galatheadae SAMOUELLE, 1819)]

Carapace with well-developed rostrum and lateral margin, not fused with epistome. Eye stalks short; antennal stalks with four or five segments; third maxillipeds pediform or slightly flattened; pereopods with six segments, first pereopods with well-developed chelae, fifth pereopods reduced, with small chelae. Abdomen more or less reduced, with well-developed pleura. Telson subdivided by sutures. *M.Jur.-Rec.*

Family GALATHEIDAE Samouelle, 1819

[*nom. correct.* WHITE, 1847 (pro Galatheadae SAMOUELLE, 1819)]

Carapace longer than wide, rostrum triangular or styliform, last thoracic sternum free, abdomen curved ventrally under cephalothorax; antennal stalks four-segmented. *M.Jur.-Rec.*

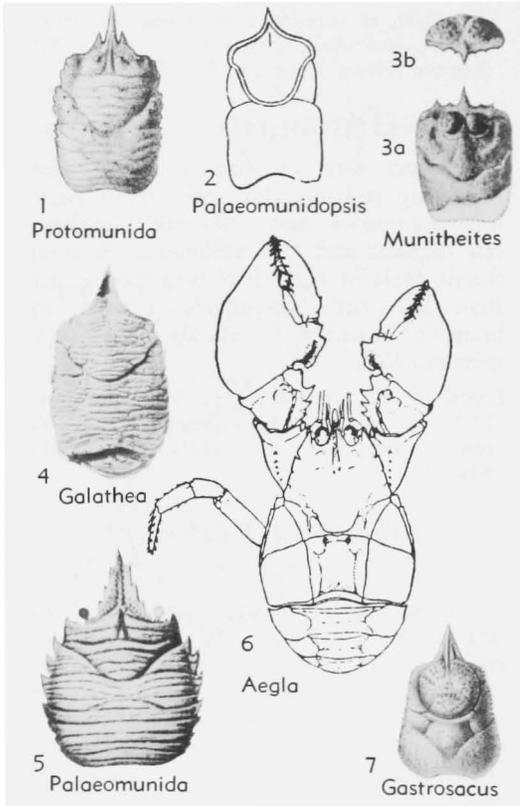


FIG. 290. Galatheidae (Galatheinae) (1,4-5), (Subfamily Uncertain) (2-3,7); Aegliidae (6) (p. R482-R483).

Subfamily GALATHEINAE Samouelle, 1819

[*nom. transl.* ORTMANN, 1898 (*ex Galatheidae SAMOUELLE*, 1819)]

Carapace with transverse sculpture, eyes well developed. *L.Cret.-Rec.*

Galathea FABRICIUS, 1793 [**Cancer strigosus* LINNÉ, 1761; SD LATREILLE, 1810]. Carapace with denticulate curved lateral margins; rostrum triangular, with denticulate sides and without median ridge. *L.Cret.(U.Alb.)*, USA(Tex.); *U. Cret.-Tert.*, Eu.; *Rec.*, cosmop.—FIG. 290,4. *G. cretacea* STENZEL, U.Alb., USA(Tex.); carapace and first somite of turned-down abdomen, $\times 3$ (283).

Munida LEACH, 1820 [**Pagurus rugosus* FABRICIUS, 1775; OD]. Lateral carapace margins dentate, surface transversely ridged; rostrum developed as a long spine with a pair of lateral spines. *Paleoc.(Dan.)*, N.Eu.; *Rec.*, cosmop. (warm and temperate seas).—FIG. 291,1. *M. bamfia tenuimana* SARS, *Rec.*; $\times 0.7$ (52).

Palaeomunida LÖRENTHEY, 1902 [**P. defecta*; OD]. Like *Galathea*, but rostrum spiniform, with 2 or

3 pairs of lateral teeth, with median ridge. *M. Eoc.-U.Eoc.*, Hung.-Sicily.—FIG. 290,5. **P. defecta*, Hung.; $\times 1$ (184).

Protomunida BEURLIN, 1930 [**Galathea munidoides* SEGERBERG, 1900; OD]. Rostrum smooth, triangular, with short basal spines. Carapace as in *Galathea*. *Paleoc.(Dan.)-Paleoc.*, Denm.-Sweden-Spitz.—FIG. 290,1. **P. munidoides* (SEGERBERG), Dan., Denm.; $\times 3$ (333).

Subfamily MUNDOPSINAE Ortman, 1898

Carapace well calcified, with rectangular outline, mostly without transverse sculpture, rostrum triangular, narrow or wide. Eyes reduced in living forms. [The fossil genus *Gastrosacus* (= *Galatheites*) is close to *Munidopsis*, in which most or all living genera formerly placed in this family are now included. BEURLIN (1930) has conditionally proposed a "subfam. Galatheitinae," as the eyes in the fossil forms were probably not reduced, but information is insufficient to distinguish them definitely as a subfamily. They also resemble the Recent Chirostylidae ORTMANN, 1892.] *Rec.*

Munidopsis WHITEAVES, 1874 [**M. curvirostra*; OD]. Carapace rugose or spinose, rostrum triangular. *Rec.*, cosmop.

Subfamily UNCERTAIN

Gastrosacus VON MEYER, 1851 [**G. wetzleri* VON MEYER, 1854; OD] [= *Galatheites* BALSS, 1913 (type, *Galathea zitteli* MOERICKE, 1889)]. Carapace elongate, surface with transverse grooves and ridges or lines of granulations, rostrum broadly triangular, with smooth sides, with or without median keel. [The genus was placed in synonymy with *Galathea* by MOERICKE (1889) but re-established under a new name by BALSS. It is not possible, on present evidence, to distinguish *Galatheites* from *Gastrosacus*.] *U.Jur.-L.Cret.*, Eu.—FIG. 290,7. **G. wetzleri*, U.Jur., S.Ger.; $\times 1.5$ (367).

Mesogalathea HOUŠA, 1963 [**Galathea striata* REMEŠ, 1895]. Lateral margins of carapace without teeth; rostrum broadly triangular, slightly deflexed, without lateral teeth but with lateral angular projections; surface transversely striated; gastric region not delimited. *U.Jur.*, Czech.; *U. Cret.*, Spain.

Munitheites LÖRENTHEY, 1929 [**M. palfyi*; OD]. Carapace with small, narrowly triangular rostrum and 2 pairs of supraorbital spines. Epigastric regions well marked. *U.Jur.(Tithon.)*, Hung.—FIG. 290,3. **M. palfyi*; 3a,b, dorsal and frontal views, $\times 1$ (184).

Palaeomunidopsis VAN STRAELEN, 1925 [**Gastrosacus moutieri* VAN STRAELEN, 1923; OD]. Cara-



FIG. 291. Galatheidae (Galatheinae) (p. R482).

pace flat, sides parallel, rostrum narrowly triangular, gastric region raised. *M.Jur.*, Fr.—FIG. 290,2. *P. moutieri* (VAN STRAELEN); $\times 2$ (296).

Family AEGLIDAE Dana, 1852

Carapace widened posteriorly, divided by longitudinal and transverse sutures and cervical groove; last thoracic sternum present, telson divided longitudinally, chelae stout, legs short. *Rec.*

Aegla LEACH, 1820 [**Galathea laevis* LATREILLE, 1818; OD]. Characters of family. [Fresh-water.] *Rec.*, S.Am.—FIG. 290,6. **A. laevis* (LATREILLE); $\times 1$ (266).

Family PORCELLANIDAE Haworth, 1825

Carapace crablike, with oval outline, flat, smooth; front wide, short, triangular; antennal stalks with four segments; third maxillipeds with flattened ischium and merus; first pereopods with flattened chelae. Abdomen thin, turned under cephalothorax. *U.Cret.-Rec.*

Porcellana LAMARCK, 1801 [**Cancer platycheles* PENNANT, 1777; OD]. Frontal margin prominent, dentate; chelipeds moderately flattened, hetero-

chelous in males. *U.Cret.*(*Cenoman.*), Fr.; *Rec.*, cosmop.

Petrolisthes STIMPSON, 1858 [**Porcellana violacea* GUÉRIN, 1829; OD]. Front triangular, depressed, undulate but not dentate; first segment of antennal stalk short, cheliped broad and flat. ?*Plio.*, Fiji; *Rec.*, tropical and temperate seas except Medit.

Superfamily HIPPOIDEA Latreille, 1825

[*nom. transl.* DANA, 1852 (*ex Hippidae* LATREILLE, 1825)]

Cephalothorax subcylindrical, abdomen loosely turned under it, with pleura and uropods; carapace not fused with epistome; first pereopods with or without chelae, fifth pereopods reduced. *Tert.-Rec.*

Family ALBUNEIDAE Stimpson, 1858

[*nom. correct.* ORTMANN, 1896 (*pro Albuniidae* STIMPSON, 1858)]

Carapace subquadrangular, without posterolateral extensions; first pereopods subchelate, second to fourth with last segment curved and flattened; telson oval. *Tert.-Rec.*

Albunea WEBER, 1795 [**Cancer symmysta* LINNÉ, 1758; SD HOLTHUIS, 1956]. Carapace with serrated fronto-orbital border and median notch; antennular and antennal stalks long. *Rec.*, warm seas.

Blepharipoda RANDALL, 1840 [**B. occidentalis*; OD]. Eye stalks very slender, elongated; 3rd maxillipeds with merus and carpus similar, narrow. *Oligo.*, N.Am.; *Rec.*, S.Am. [The fossil record of this genus, and hence of the family and superfamily, rests only on 2 small fragments of a merus and propodus of a cheliped.]

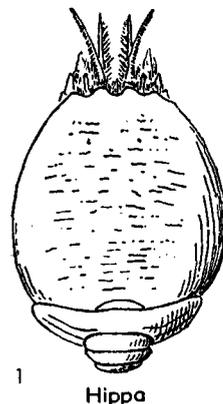


FIG. 292. Hippidae (p. R484).

Family HIPPIDAE Latreille, 1825

[*nom. correct.* BORRADAILE, 1907 (*pro* Hippides LATREILLE, 1825)]

Carapace ovoid, with posterolateral extensions covering posterior pereopods, first ones without chelae; telson lanceolate. *Rec.*

Hippa FABRICIUS, 1787 [**H. adactyla*; SD RATHBUN, 1900] [= *Remipes* LATREILLE, 1804]. Carapace broadly ovoid, with sinuous frontal border. Eye stalks slender and short; 3rd maxillipeds with merus dilated; last thoracic somite free. *Rec.*, cosmop.—FIG. 292,1. **H. adactyla*; $\times 1$ (15).

Infraorder BRACHYURA Latreille, 1803

[= Brachyuridea GLAESSNER, 1929]

Carapace progressively shortened and widened, developing lateral margin; fused with epistome; last thoracic sternite fused with anterior sternites; first pereopods invariably chelate, third ones never chelate. Abdomen short, flattened, symmetrical, without complete uropods, turned under sternum, commonly with some somites fused. *L.Jur.-Rec.*

Section DROMIACEA de Haan, 1833

Carapace elongate to subcircular, front narrow, triangular, either without orbits and antennular grooves or with orbito-antennular grooves; antennal stalk with four movable segments; buccal frame quadrangular, commonly widened anteriorly; first pereopods chelate, fifth ones in dorsal position and tending to be reduced, fourth and fifth pereopods commonly similar. Abdomen wide in both sexes, commonly with seven somites. Seminal ducts perforate coxa of fifth pereopods, oviducts open in coxa of third pereopods. *L.Jur.-Rec.*

Superfamily DROMIOIDEA de Haan, 1833

[*nom. transl.* GLAESSNER, herein (*pro* Dromiidea, *nom. transl.* ALCOCK, 1899, *ex* Dromiidae DE HAAN, 1883)]

Carapace with elongate or rounded outline, without dorsal lineae, without or with orbits; fourth and fifth pereopods or only fifth ones dorsal. *L.Jur.-Rec.*

Family EOCARCINIDAE Withers, 1932

Characters of type-genus. *L.Jur.*

Eocarcinus WITHERS, 1932 [**E. praecursor*; OD]. Carapace elongate, no orbits, no lateral margin, cervical and branchiocardiac furrows well developed, latter extending to posterior margin; abdomen 0.7 length of carapace, not folded under sternum, with pleura and small 7th somite; 1st pereopods with long chelae, 4th and 5th pereopods probably elevated on back. *L.Lias.*, Eng.—FIG. 293,7. **E. praecursor*; 7a,b, dorsal and side views of carapace (reconstr.), $\times 1$ (321).

Family PROSOPIDAE von Meyer, 1860

[*nom. correct.* GLAESSNER, herein (*pro* Prosoponidae VON MEYER, 1860)]

Carapace mostly cylindrical, elongate, without or with incompletable lateral margin; without orbits but commonly with elongate orbital grooves; strong cervical and branchiocardiac grooves. *M.Jur.-Cret.*, *Rec.*

Subfamily PROSOPINAE von Meyer, 1860

[*nom. correct.* GLAESSNER, herein (*pro* Prosoponinae, *nom. transl.* GLAESSNER, 1933, *ex* Prosoponidae VON MEYER, 1860)]

Carapace with strong surface sculpture, without sharp lateral margin, rostrum projecting. *M.Jur.-L.Cret.*

Prosopon VON MEYER, 1835 [**P. tuberosum* VON MEYER, 1840; SD BEURLEN, 1928] [= *Protocarcinus* WOODWARD, 1865 (type, *P. longipes* = *Homolus auduini* EUDES-DESLONGCHAMPS, 1835); *Palaeinachus* WOODWARD, 1866 (obj. syn. of *Protocarcinus*); *Avihomola* VAN STRAELEN, 1925 (obj. syn. of *Protocarcinus*)]. Carapace strongly convex, front sloping, no orbital grooves, posterior margin wide, branchiocardiac groove strong. *M. Jur.-L.Cret.*, Eu.—FIG. 294,1. **P. tuberosum* VON MEYER, Neocom., Fr.; $\times 1.3$ (367).—FIG. 293,1. *P. mamillatum* H. WOODWARD; 1a, female abdomen, $\times 0.5$; 1b-d, dorsal, lat., and frontal views of carapace (reconstr.), $\times 1$ (324).

Laeviprosopon GLAESSNER, 1933 [**Prosopon laeve* VON MEYER, 1860; OD]. Carapace outline rectangular, front bilobed, regions smoothly convex; orbital grooves shallow, semicircular. *U.Jur.*, Eu.—FIG. 294,2. *L. laeve punctatum* (VON MEYER), Ger.; $\times 2$ (367).

Lecythocaris VON MEYER, 1860 [**Prosopon paradoxum* VON MEYER, 1860; OD]. Carapace small, hexagonal, wider than long, greatest width across branchial regions; front large, bilobed. *U.Jur.*, Eu.—FIG. 294,4. **L. paradoxa* (VON MEYER), Ger.; $\times 3$ (367).

Nodoprosopon BEURLEN, 1928 [**Prosopon ornatum* VON MEYER, 1860; OD]. Carapace elongate, rostrum bilobed, branchial regions inflated, posterior

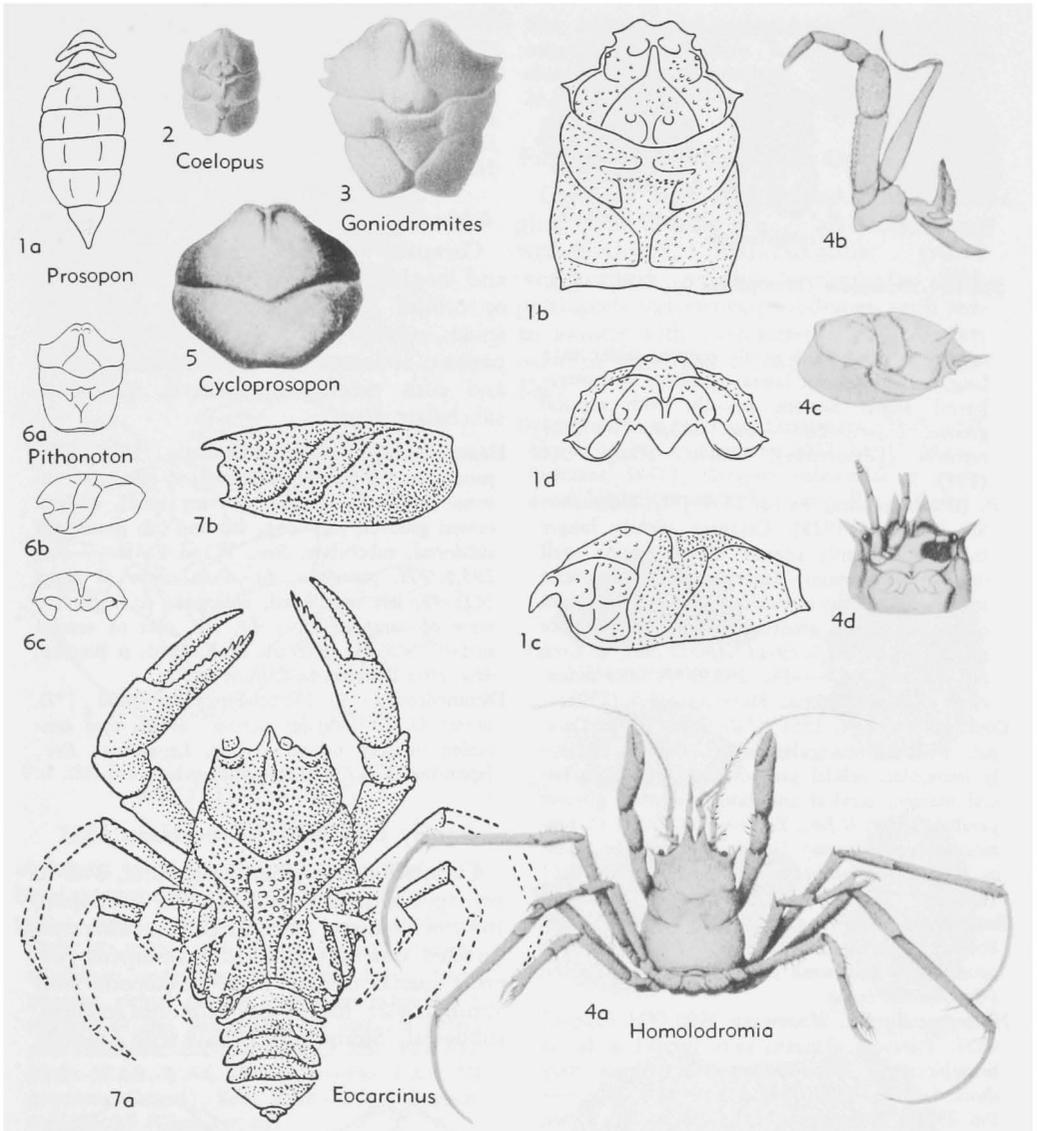


FIG. 293. Eocarcinidae (7); Prosopidae (Prosopinae) (1), (Pithonotinae) (2-3,5-6), (Homolodromiinae) (4) p. R484-R486.

margin narrow. *U.Jur.*, Eu.—FIG. 294,3. **N. ornatum* (VON MEYER), Ger.; $\times 2$ (367).

Subfamily PITHONOTINAE Glaessner, 1933

Carapace smooth, in some forms with partial lateral margin, fronto-orbital margin wide. *M.Jur.-U.Cret.* [See Addendum, p. R627.]

Pithonoton VON MEYER, 1842 [**P. marginatum*; SD BEURLEN, 1928]. Carapace convex transversely and longitudinally; cervical and branchio-cardiac grooves equally strong; front wide, orbital

grooves well developed. [*Ogydromites* A. MILNE-EDWARDS, 1865 (type, *O. nitidus* A. MILNE-EDWARDS, 1865) was considered by GLAESSNER (1929) to be a synonym of *Pithonoton* but as a different genus by VAN STRAELEN (1936). *Ogydromites* has not been clearly diagnosed.] *M.Jur.-U.Cret.*, Eu.

P. (Pithonoton). Carapace longer than wide, convex, lateral margins weak; cervical and branchio-cardiac furrows equally strong. *M.Jur.-U.Jur.*, Eu.—FIG. 293,6. **P. (P.) marginatum*, Tithon., Moravia; 6a-c, dorsal, lat., and frontal views, $\times 1$ (324).

P. (Cycloprosopon) LÖRENTHEY, 1928 [**C. typi-*

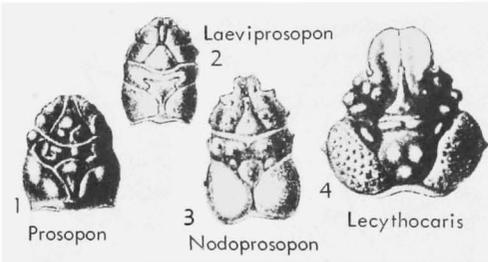


FIG. 294. Prosopidae (Prosopinae) (p. R484-R485).

cum; OD]. Carapace gently convex, wider than long, well-developed lateral margins, no antero-lateral angle. Surface smooth, with cervical groove. *U. Jur.*, Eu.—FIG. 293,5. **P. (C.) typicum* (LÖRENTHEY), Tithon., Hung.; $\times 1$ (184).

P. (Goniodromites) REUSS, 1859 [**G. bidentatus*; SD BEURLEN, 1928]. Carapace slightly longer than wide, gently convex, lateral margin well developed, commonly denticulate; cervical groove stronger than branchiocardiac; front wide, straight or bilobed, orbital grooves long and deep; surface granulate. *U. Jur.-L. Cret. (?Apt.-L. Alb.)-U. Cret. (Cenoman.)*, Eu.—FIG. 293,3. **P. (G.) bidentatus* (REUSS), Tithon., Moravia; $\times 1.5$ (250).

Coelopus ÉTALLON, 1861 [**C. jolyi*; OD]. Carapace with subrectangular outline, rostrum narrowly triangular, orbital grooves deep, no sharp lateral margin, cervical and branchiocardiac grooves parallel. *M. Jur.-U. Jur.*, Eu.—FIG. 293,2. *C. pustulosus* (VON MEYER) [incorrectly cited by REUSS as *Pithonoton rostratum*], Tithon., Moravia; $\times 1$ (250).

Iberihomola VAN STRAELLEN, 1940 [**I. laevis*; OD]. Possibly differing from *Plagiophthalmus* in less ovoid shape and weak transverse sutures. *U. Cret. (Cenoman.)*, Spain.

?**Mesodromilites** H. WOODWARD, 1900 [**M. birleyae*; OD]. Carapace elongate, sides parallel as far as branchiocardiac groove, branchial region very short. *L. Cret. (Alb.)-U. Cret. (Cenoman.)*, Eng.—FIG. 297,1. **M. birleyae*; 1a,b, dorsal and lat. views, $\times 1.5$ (332).

Microcrystes FRITSCH, 1893 [**M. parvulus*; OD]. Carapace small, with parallel sides, large orbits, raised mesogastric and cardiac bosses. *U. Cret. (Coniac.)*, Boh.—FIG. 296,2. **M. parvulus*; $\times 3$ (96).

Plagiophthalmus BELL, 1863 [**P. oviformis*; OD]. Carapace elongate, strongly convex transversely and longitudinally; lateral margins complete and distinct, rostrum bilobed, orbital grooves deep, cervical and branchiocardiac grooves equal. *Cret. (L. Alb.-Cenoman.-Dan.)*, Eu.—FIG. 295,1. **P. oviformis*, Cenoman., Eng.; 1a-c, dorsal, frontal and lat. views of internal mold, $\times 1.5$ (335).

?**Vectis** WITHERS, 1945 [**V. wrighti*; OD]. Carapace ovoid, widening posteriorly, lateral margin marked by tubercles, orbits deep. [This genus was placed by its author in the Prosoponidae (Prosopidae) but transferred by BALS to the Dromiidae.] *L. Cret. (L. Apt.)*, Eng.—FIG. 296,1. **V. wrighti*; 1a-c, dorsal, frontal, and lat. views, $\times 6$ (323).

Subfamily HOMOLODROMIINAE Alcock, 1899

Carapace elongate, convex transversely and longitudinally, without lateral margins or orbital grooves, front with two long spines, cervical and branchiocardiac grooves present; abdomen with weak pleura; fourth and fifth pereopods reduced, subdorsal, subchelate. *Rec.*

Homolodromia A. MILNE-EDWARDS, 1880 [**H. paradoxa*; OD]. Carapace narrow, antennae inserted below eye stalk, eyes very small, without orbital grooves; legs long, 4th and 5th pereopods subdorsal, subchelate. *Rec.*, W. Ind.-E. Afr.—FIG. 293,4. **H. paradoxa*; 4a, dorsal view of male, $\times 1$; 4b, left maxilliped, enlarged; 4c, right lat. view of carapace, $\times 1$; 4d, ant. part of ventral surface, $\times 3$ (4a, after A. M. Edwards & Bouvier, 4b,c, after Bouvier, 4a-d, from 245).

Dicranodromia A. MILNE-EDWARDS, 1880 [**D. ovata*; OD]. Carapace narrow, ovoid, eyes concealed in deep orbital cavities. Legs short. *Rec.*, Japan-Ind. O.-E. Atl.-W. Indies-deep seas.

Family DROMIIDAE de Haan, 1833

Carapace convex, outline circular, oval to pentagonal, lateral margins well developed; front with three teeth, median weaker and directed downward; third maxillipeds covering buccal cavity. First pereopods with strong chelae, fourth and fifth ones reduced, subdorsal. Sternum of female with grooves;

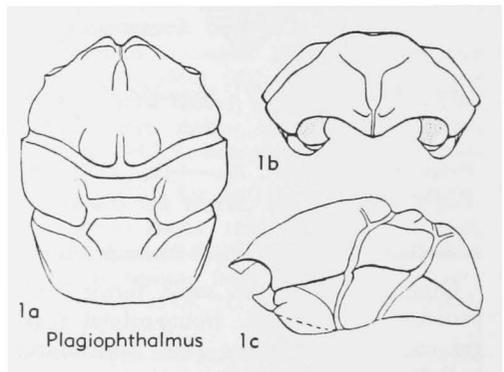


FIG. 295. Prosopidae (Pithonotinae) (p. R486).

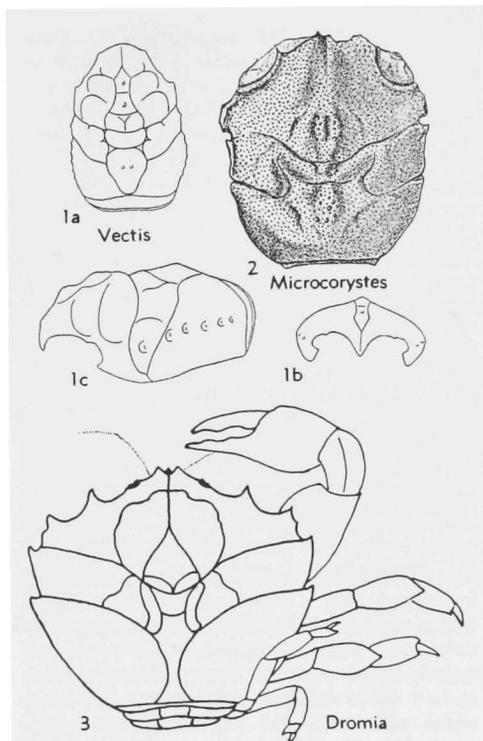


FIG. 296. Prosopidae (Pithonotinae) (1,2); Dromiidae (3) (p. R486-R487).

abdomen with seven somites, mostly with basal remnants of uropods. *Paleoc.-Rec.*

Dromia WEBER, 1795 [*Cancer personatus* LINNÉ, 1758; SD ICZN, 1964 (Opinion 688)]. Carapace subglobose, wider than long, with dentate lateral margins, sternal grooves in females extending to segment of 2nd pereopods, 4th and 5th pereopods subchelate. *Eoc., Pleist., Eu.; Plio., Fiji; Rec., Medit.-W.Afr.-W.Atl.-IndoPac.*—FIG. 296,3. **D. personata* (LINNÉ), *Rec., E.Atl.-Medit.*; diagrammatic, $\times 0.5$ (Glaessner, n).

Dromilites H. MILNE-EDWARDS, 1837 [*Dromia bucklandi*; OD] [= *Pseudodromilites* BEURLÉN, 1928 (*Pseudodromilitis*, error) (type, *Dromia hilarionis* BITTNER, 1883); *Basinotopus* M'COY, 1849 (type, *Inachus lamarckii* DESMAREST, 1822)]. Carapace with dentate or spiny margins, regions distinct, branchial regions larger than in *Dromia*, branchiocardiac and cervical grooves well marked. *Paleoc., N.Am.(Gulf Coast); L.Eoc.-M.Eoc., Eu.; Mio., Aus.*—FIG. 297,3. **D. bucklandi*, *L.Eoc., Eng.*; 3a,b, dorsal and frontal views, $\times 1$ (19).

Noetlingia BEURLÉN, 1928 [*Dromia claudiopolitana* BITTNER, 1893; OD]. Carapace ovoid, strongly inflated, median rostral spine more prominent

than lateral, lateral margin rounded, marked by tubercles. *U.Eoc.-L.Oligo., Eu.*—FIG. 297,2. **N. claudiopolitana* (BITTNER), *U.Eoc., Rumania*; 2a,b, dorsal, lat., $\times 1$ (184, after Bittner, 1893).

Family DYNOMENIDAE Ortmann, 1892

Carapace with well-defined lateral margins, front broadly triangular, short; orbits well-developed, branchiocardiac groove weak; third maxillipeds opercular, fifth pereopods rudimentary; abdomen with seven somites with intercalated lateral platelets between sixth and seventh somites. *U.Jur.-Rec.*

Dynomene LATREILLE in DESMAREST, 1825 [**D. hispida* H. MILNE-EDWARDS, 1837; SD H. MILNE-EDWARDS, 1837]. Carapace subcircular to pentagonal, slightly broader than long. *Rec., Atl.-Indo-*

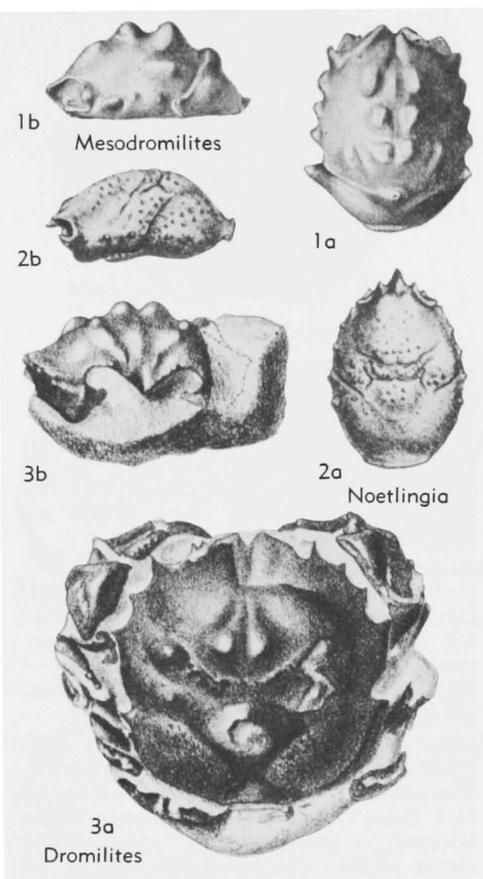


FIG. 297. Prosopidae (Pithonotinae) (1); Dromiidae (2, 3) (p. R486-R487).

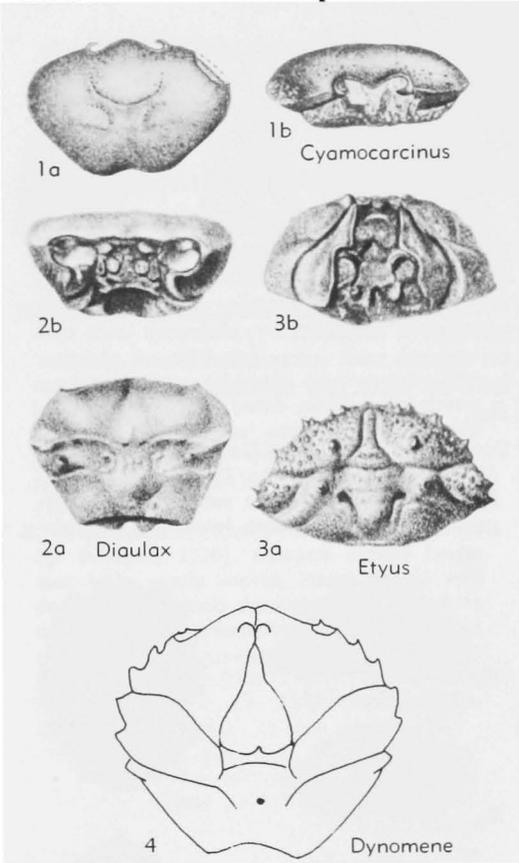


FIG. 298. Dynomenidae (p. R487-R488).

Pac.-N.Am.(W.coast).—FIG. 298,4. *D. filholi* BOUVIER, Pac. (tropic); carapace, $\times 2$ (345a).

Cyamocarcinus BITTNER, 1883 [**C. angustifrons*; OD]. Carapace wider than long; lateral margins smooth, outline rounded. *U.Eoc.*, Eu.—FIG. 298, 1. **C. angustifrons*; 1a,b, dorsal, frontal, $\times 1$ (183).

Cylothyreus REMEŠ, 1895 [**C. strambergensis* (= **Prosopon reussi* GEMMELLARO, 1870); OD]. Carapace outline subcircular, rostrum steeply sloping, lateral margin sharp to posterior margin, mesogastric region not delimited. *U.Jur.*, Eu.—FIG. 299,2. **C. reussi* (GEMMELLARO), Tithon., Moravia; carapace, $\times 1$ (375a).

Cyphonotus BELL, 1863 [**C. incertus*; OD] [= *Distefania* CHECCHIA-RISPOLI, 1917 (type, *D. himeraensis*); *Palaeodromites* A. MILNE-EDWARDS, 1865 (type, *P. octodentatus*)]. Carapace outline subcircular to pentagonal, front truncated, lateral margin lobulate, mesogastric region distinct. *U. Jur.-Cret.(Cenoman.)*, Eu.—FIG. 299,1. **C. incertus*, Cenoman., Eng.; 1a,b, dorsal, frontal, $\times 1.5$ (335).

Diaulax BELL, 1863 [**D. carteriana*; OD]. Carapace wider than long, greatest width in front of cervical groove, branchiocardiac groove transverse, weak, orbits large. *U.Jur.-Cret.(Alb.-Cenoman.)*, Eu.—FIG. 298,2. **D. carteriana*, Cenoman., Eng.; 2a,b, dorsal, frontal, $\times 1$ (344).

Dromiopsis REUSS, 1859 [**Brachyurites rugosus* VON SCHLOTHEIM, 1820; SD BEURLEN, 1928]. Carapace pentagonal, convex, front forming large triangular lobe, lateral margins tuberculate, transverse grooves strong. *U.Cret.(Cenoman.)*, Eu.; *Paleoc.(Dan.)*, Eu.-N.Am.(N.J.).—FIG. 300,1. **D. rugosa* (SCHLOTHEIM), Dan., Denm.; 1a,b, dorsal, frontal, $\times 1.3$ (Glaessner, n).

Etyus MANTELL, 1822 [**E. martini* MANTELL, 1844; SM MANTELL, 1844] [= *Reussia* M'COY, 1854 (type, *R. granosa*)]. Carapace about twice as wide as long, margins and surface tuberculate, cervical groove transverse, branchiocardiac groove curving back posterolaterally. *L.Cret.(Alb.)*, Eng.-Fr.—FIG. 298,3. **E. martini*; 3a,b, dorsal, ventral, $\times 1.3$ (Glaessner, n).

Gemmellarcarcinus CHECCHIA-RISPOLI, 1905 [**G. loerentheyi*; OD]. Differs from *Cyamocarcinus* in well-marked gastric regions and transverse grooves on carapace. *M.Eoc.*, Sicily.

Glyptodynomene VAN STRAELEN, 1944 [**G. alsasuensis*; OD]. Carapace small, wider than long, widest across branchial regions, strongly sculptured, with anterolateral and posterolateral spines. *U.Cret.(Cenoman.)*, Spain.—FIG. 301,6. **G. alsasuensis*; dorsal, $\times 2$ (311).

Graptocarcinus ROEMER, 1887 [**G. texanus*; OD]. Carapace transversely oval in outline, with narrow posterior margins and raised lateral margin; surface granulate, with posterior mesogastric and lateral cardiac grooves only. *L.Cret.(Alb.)*, Mexico; *Cret.(Alb.-Cenoman.)*, USA (Tex.); *U. Cret.(Cenoman.)*, Eng.—FIG. 301,4. **G. texanus*, Cenoman., Tex.; carapace, dorsal view, $\times 3$ (282).

Family UNCERTAIN

Mithracites GOULD, 1859 [**M. vectensis*; OD]. Carapace elongate, lateral margins distinct, diverg-

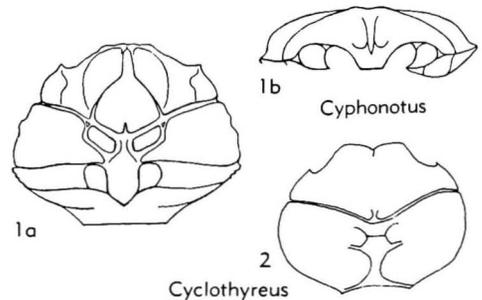


FIG. 299. Dynomenidae (p. R488).

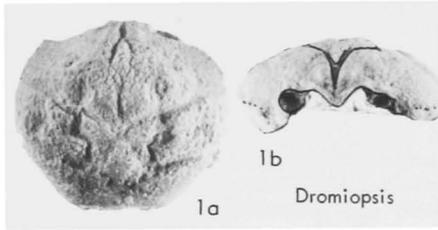


FIG. 300. Dromiopsis (p. R488).

ing, posterior margin wide, orbits large; 5th pereopods reduced, dorsal. *L.Cret.(Apt.)*, Eng.—FIG. 301,7. **M. vectensis*; carapace (reconstr.), $\times 1$ (324).

Oxythreus REUSS, 1858 [**O. gibbus*; OD]. Carapace ovoid, strongly convex longitudinally, widest in posterior third, front turned downward, grooved medially, posterior margin narrowly semicircular, lateral margin lobate, cervical groove more distinct than branchiocardiac groove. *U.Jur.*, Eu.—FIG. 301,2. **O. gibbus*, Tithon., Moravia; dorsal, $\times 2$ (250).

Rathbunopon STENZEL, 1945 [**R. polyakron*; OD]. Carapace ovoid, slightly longer than wide, orbits distinct, lateral margin indistinct, posterior margin long, cervical and branchiocardiac grooves deep. *U.Cret.(Cenoman.)*, USA(Tex.); *Cret.(Alb.-Cenoman.)*, Eng.—FIG. 301,5. **R. polyakron*, Cenoman., Tex.; $\times 2$ (283).

Stephanometopon BOSQUET, 1854 [**S. granulatam*; OD]. Anteromedian portion of carapace resembling *Cyphonotus*, chela short, stout. [Incompletely known.] *U.Cret.(U.Senon.)*, Neth.

Trachynotus BELL, 1863 [**T. sulcatus*; OD]. Carapace ovoid, differing from *Cyphonotus* in rounded outline and transversely ridged branchial regions. *U.Cret.(Cenoman.)*, Eng.—FIG. 301,3. **T. sulcatus*; $\times 1$ (344).

Xanthosia BELL, 1863 [**X. gibbosa*; SD GLAESSNER, 1929]. Carapace wider than long, wide fronto-orbital and denticulate anterolateral margins; orbits large, otherwise close to *Etyus*. *Cret.(Alb.-Cenoman.)*, Eu.; *L.Cret.(Alb.)*, USA(Tex.); *U.Cret.(Campan.)*, USA(N.J.-Del.); ?*Paleoc.*, W. Afr.—FIG. 301,1a,b. **X. gibbosa*, Cenoman., Eng.; 1a,b, dorsal, frontal, $\times 1$ (344).—FIG. 301,1c. *X. wintoni* RATHBUN, Alb., Tex.; ant. view showing antennular bases, $\times 2$ (244).

Superfamily HOMOLOIDEA

White, 1847

[*nom. correct.* GLAESSNER, herein (*pro Homolidea* ALCOCK, 1899, *nom. transl. ex Homolidae* WHITE, 1847)] [= *Thelxiopeidea* RATHBUN, 1937]

Carapace longer than broad, with longitudinal lineae, without orbits, eye stalks

jointed, fifth pereopods dorsal, reduced. *U.Jur.-Rec.*

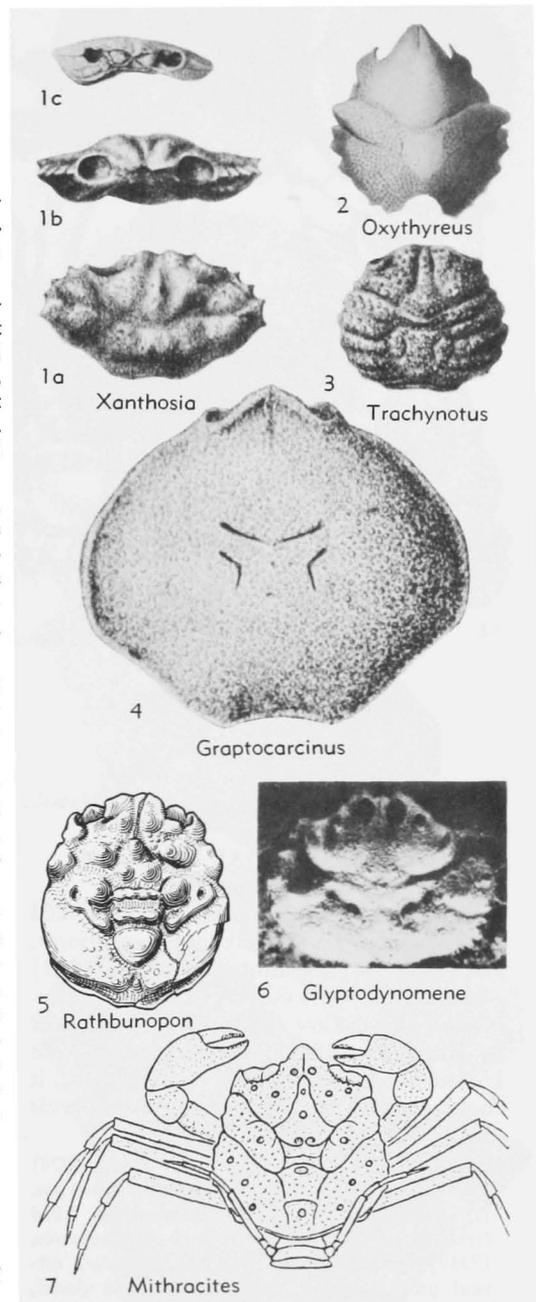


FIG. 301. Dromiopsis (4,6); Family Uncertain (1-3,5,7) (p. R488-R489).

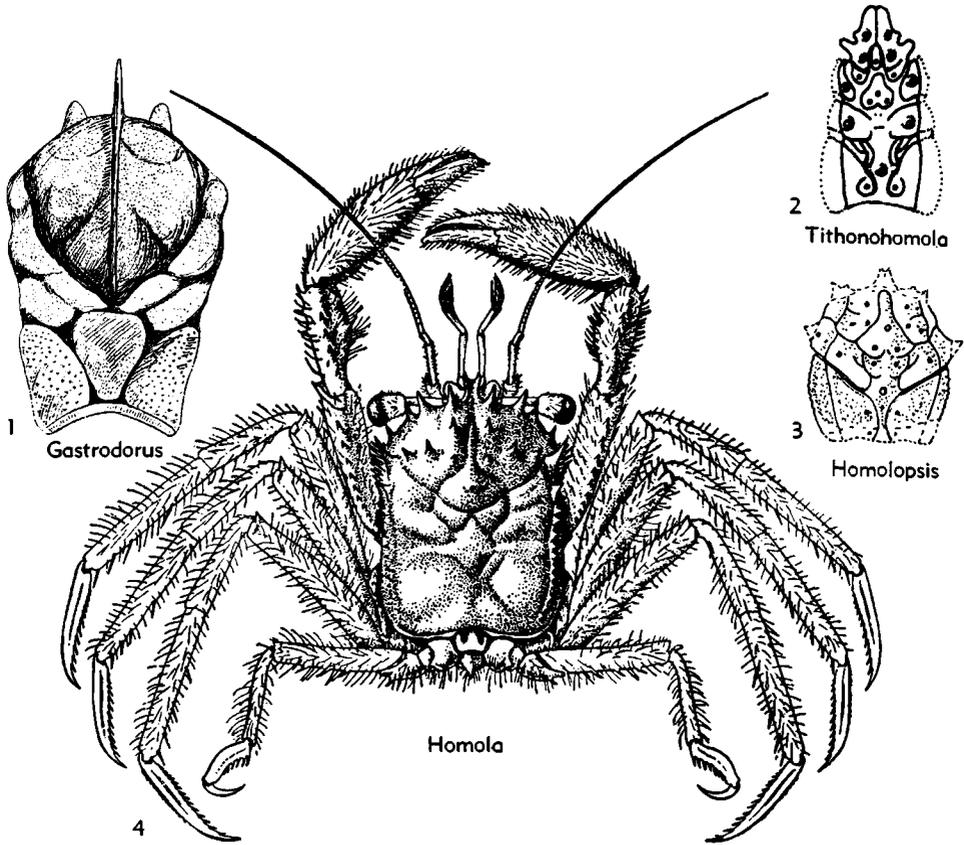


FIG. 302. Homolidae (p. R490-R491).

Family HOMOLIDAE White, 1847

[=Thelxiopidae RATHBUN, 1937]

Carapace elongate or ovoid, antennal flagella long. Third maxillipeds pediform. [The family Latreilliidae ALCOCK (1899) including *Latreillia* ROUX (1830) and *Latreillopsis* HENDERSON (1888) was recognized by RATHBUN (1937) but included in the Homolidae by BALSS (1957). If accepted, it could include the fossil forms *Palehomola* and *Tithonohomola*.] *U. Jur.-Rec.*

Homola LEACH, 1815 [nom. conserv., ICZN] [**H. spinifrons* (= **Cancer barbatus* FABRICIUS, 1793); OD] [= *Thelxiop* RAFINESQUE, 1814 (type, *T. palpigera*, = *Cancer barbatus* FABRICIUS, 1793)]. Carapace elongate, subrectangular, cervical groove distinct, lineae distinct and dorsal, 5th pereopods subchelate. *Rec.*, IndoPac.-Medit.-W.Afr.-N.Am. (E. coast-W. coast).—FIG. 302,4. **H. barbata* (FABRICIUS); dorsal view of male, $\times 1$ (245, after Smith).

Gastrodorus VON MEYER, 1864 [**Prosopon* (*Gastrodorus*) *neuhausense*; OD] [= *Eopagurus* BEURLEN, 1925 (obj.)]. Carapace small, elongate; rostrum with median spine continued as ridge, lateral parts outside lineae unknown, posterior margin rounded, gastric region inflated. *U. Jur.*, Ger.—FIG. 302,1. **G. neuhausensis* (VON MEYER); median part of carapace, dorsal view, $\times 7.5$ (24).

Homolopsis BELL, 1863 [**H. edwardsi*; OD] [= *Hoplitocarcinus* BEURLEN, 1928 (type, *H. joh-boehmi*)]. Carapace longer than wide, anterior regions spinose, strongly subdivided branchial regions well delimited by branchiocardiac groove, granulate; lineae distinct. *Cret. (Alb.-Senon.-Dan.)*, Eu.; *U. Cret.*, W. Can.-USA (S. Dak.-N. J.); *Cret. (Alb.-Cenoman.)*, Australia.—FIG. 302,3. **H. edwardsi*, Alb., Eng.; carapace (reconstr.), $\times 1$ (Glaessner, n).

?**Palehomola** RATHBUN, 1926 [**P. gorrelli*; OD]. Carapace broadly ovate, narrowing anteriorly, with 2-horned rostrum. Chelipeds very long and strong. *Oligo.*, N. Am.

?*Tithonohomola* GLAESSNER, 1933 [**Oxythyreus armatus* BLASCHKE, 1911; OD]. Carapace elongate, lateral parts outside lineae unknown, rostrum flattened, triangular, with supraorbital projections; anterior regions strongly inflated and tuberculate; cervical and branchiocardiac grooves distinct. *U.Jur.*, Moravia.—FIG. 302,2. *T. longa* (MOERICKE); carapace (reconstr.), $\times 2$ (Glaessner, n).

Superfamily DAKOTICAN-CROIDEA Rathbun, 1917

[*nom. correct.* GLAESSNER, herein (*pro* Dakoticancroideae RATHBUN, 1917)]

Carapace rectangular to transversely ovoid, front narrow; orbits well developed, median part of cardiac groove weak, branchiocardiac groove strong, no lineae; third maxillipeds elongate; sternum of female without longitudinal grooves, fifth pereopods subdorsal, small. *U.Cret.*

Family DAKOTICANCRIDAE Rathbun, 1917

Characters of superfamily. *U.Cret.*

Dakoticancer RATHBUN, 1917 [**D. overanus*; OD]. Carapace wider than long, strongly grooved, eyes small, gastric regions hardly separated from cardiac. *U.Cret.*, N.Am.—FIG. 303,2a. **D. overanus*, USA (S.Dak.); ventral side, $\times 1.5$ (Rathbun, 1917).—FIG. 303,2b. *D. overanus australis* RATHBUN, SENON., USA (Miss.); dorsal side, $\times 1.5$ (244).

Avitelmessus RATHBUN, 1923 [**A. grapsoides*; OD]. Carapace with rounded outline, not strongly grooved, orbits wide, second to fourth pereopods flattened. *U.Cret.* (Senon.), N.Am. (N.Car.-Tenn.-Ala.-Miss.).—FIG. 303,3. **A. grapsoides*, U.Senon., Tenn.; 3a,b, dorsal and ventral surface of male; 3c, left chela, 3d, female abdomen; all $\times 0.7$ (239).

Tetracarcinus WELLER, 1905 [**T. subquadratus*; OD]. Carapace small, subquadrate, grooves well marked, weak transverse groove separating gastric and cardiac regions; eyes small. *U.Cret.* (Senon.), N.Am. (N.J.-Wyo.).—FIG. 303,1. **T. subquadratus*, USA (N.J.); $\times 2$ (244).

Section OXYSTOMATA H. Milne-Edwards, 1834

Buccal cavity elongate, subtriangular, antennules folded mostly longitudinally or obliquely; gonoducts coxal or sternal, fourth pereopods normal or subdorsal. *L.Cret.* (*Alb.*)-*Rec.*

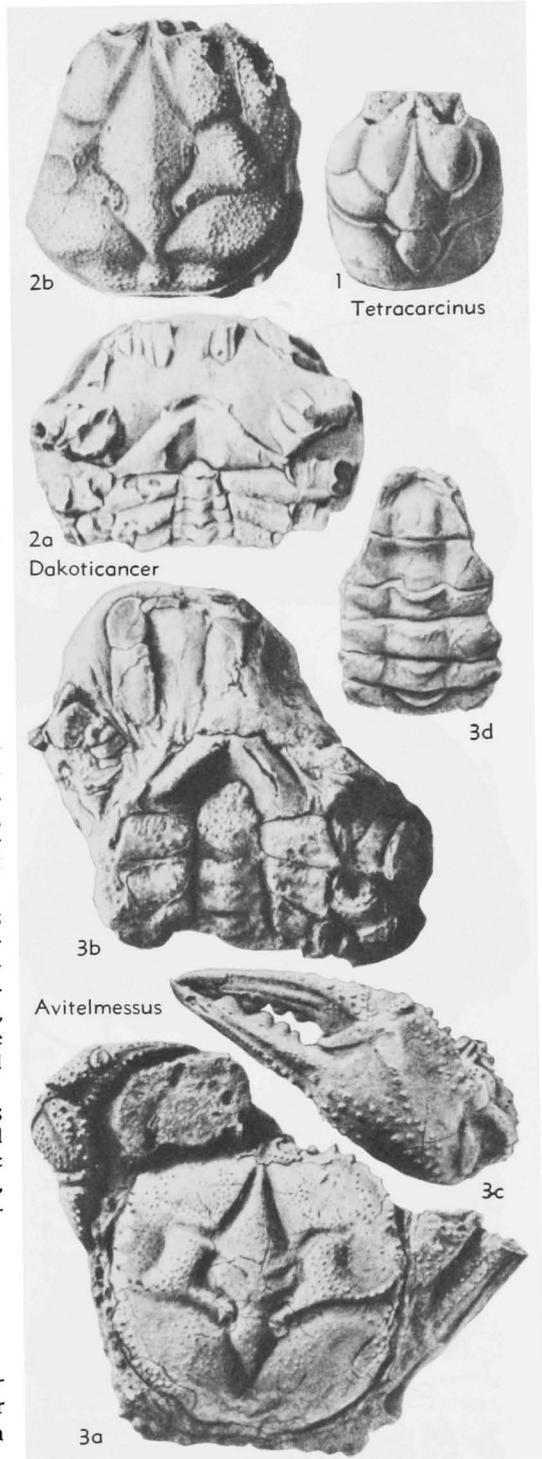


FIG. 303. Dakoticancridae (p. R491).

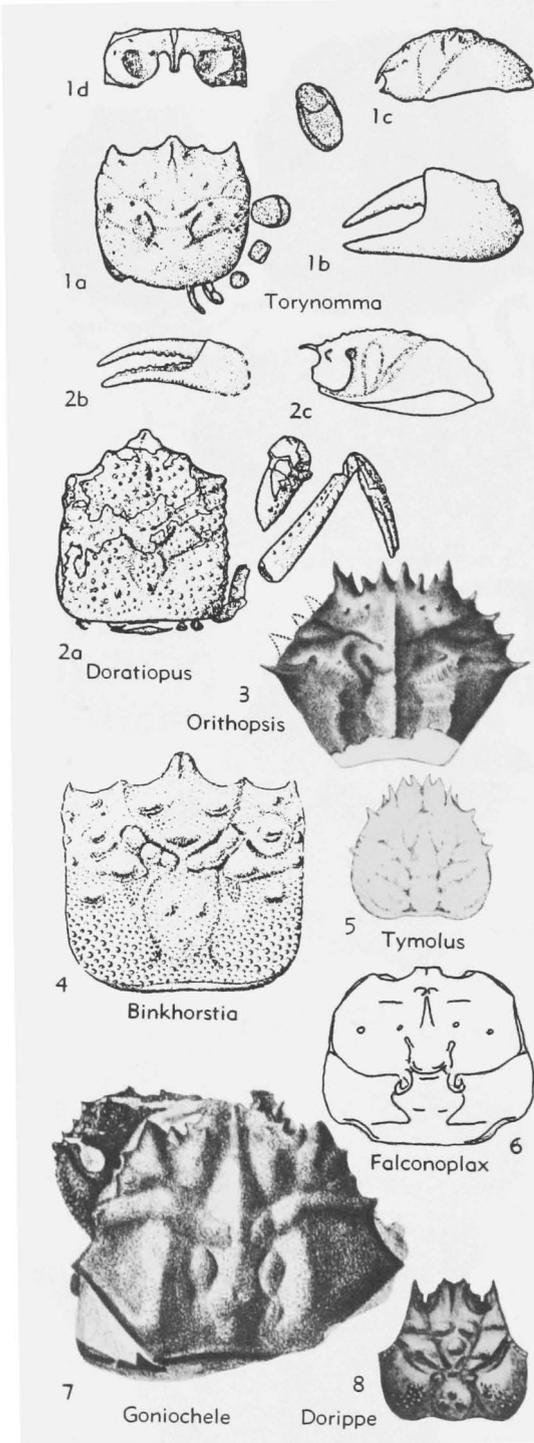


FIG. 304. Dorippidae (Dorippinae) (3,7-8), (Tymolinae) (1-2,4-6) (p. R492-R493).

Superfamily DORIPPOIDEA de Haan, 1841

[*nom. transl.* GLAESSNER, herein (ex Dorippidae DE HAAN, 1841)]

Carapace short, not covering the first two or three abdominal somites; fourth and fifth pereopods reduced, dorsal. *L.Cret. (Alb.)-Rec.*

Family DORIPPIDAE de Haan, 1841

Characters of superfamily. *L.Cret. (Alb.)-Rec.*

Subfamily DORIPPINAE de Haan, 1841

[*nom. transl.* ALCOCK, 1896 (ex Dorippidae DE HAAN, 1841)]

Carapace with lateral margins converging anteriorly; third maxillipeds not covering entire buccal area; oviducts opening on sternum. *L.Cret. (Alb.)-Rec.*

Dorippe WEBER, 1795 [**Cancer quadridens* FABRICIUS, 1793 (= **C. frasco* HERBST, 1785); SD LATREILLE, 1810]. Carapace flat, with anterolateral spines, widest in posterior 3rd, regions well marked, chelae small, 2nd and 3rd pereopods large, 4th and 5th ones small, subchelate. *Mio.-Pleist.*, Eu.; ?*Pleist.*, IndoPac.; *Rec.*, Medit.-W.Afr.-IndoPac.—FIG. 304,8. *D. margaretha* (LÖRENTHEY), *Mio.*, Hung.; dorsal, $\times 1$ (184).

Goniochele BELL, 1858 [**G. angulata*; OD]. Carapace hexagonal, wider than long, anterior margin spinose, chelae large, compressed. *L.Eoc.*, Eu.; *Oligo.*, Panama.—FIG. 304,7. **G. angulata*, L. Eoc., Eng.; $\times 1$ (19).

Orithopsis CARTER, 1872 [**O. bonneyi*]. Carapace wider than long, outline hexagonal, surface flattened, granulated, with transverse grooves and metabranchial longitudinal ridges, rostrum bifid, orbits with 2 supraorbital lobes, anterolateral border spinose. *Cret. (Alb.-Cenoman.)*, Eng.—FIG. 304,3. **O. bonneyi*, Cenoman., Eng.; dorsal view of carapace, $\times 0.7$ (69).

Subfamily TYMOLINAE Alcock, 1896

Third maxillipeds covering buccal area completely. Oviducts opening in coxa of third pereopods. Sixth and seventh abdominal somites fused. *L.Cret. (Alb.)-Rec.*

Tymolus STIMPSON, 1858 [**T. japonicus*; OD]. Carapace inflated, front with 4 teeth, supraorbital margin deeply notched. ?*Mio.*, *Rec.*, Japan.—FIG. 304,5. **T. japonicus*, *Rec.*; dorsal view of carapace, $\times 1$ (157, after Sakai).

Binkhorstia NOETLING, 1881 [**Dromilites ubaghsi* BINKHORST, 1857; OD]. Carapace outline square, orbital margins long, transverse. *U.Cret. (U.Senon.)*,

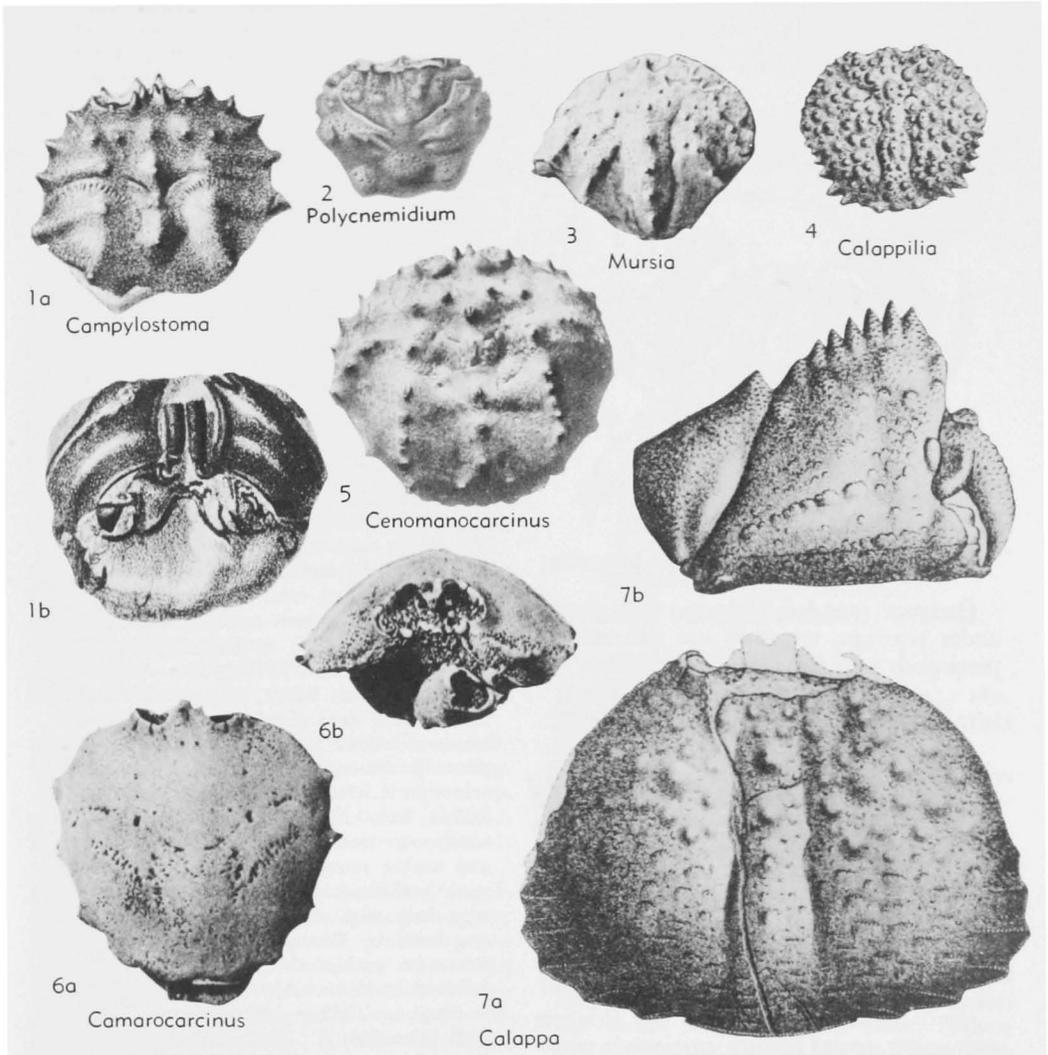


FIG. 305. Calappidae (Calappinae) (p. R494-R495).

Eu.—FIG. 304,4. **B. ubaghsi* (BINKHORST), Neth.; dorsal view of carapace, $\times 2$ (214).

Doratiopus WOODS, 1953 [**D. salebrosus*; OD]. Carapace pentagonal, orbital margins long, diverging backward. *Cret.(Alb.-Cenoman.)*, Australia.—FIG. 304,2. **D. salebrosus*, Alb.; 2a, dorsal view of holotype, 2b, right chela, 2c, left side of carapace, $\times 1$ (327).

Falconoplax VAN STRAELEN, 1933 [**F. kugleri*; OD]. Carapace transversely oval, convex longitudinally, front narrow, deflected, orbits small, fronto-orbital margin less than 0.5 width of carapace, anterolateral angles rounded, lateral margins diverging posteriorly, lateral gastrocardiac

grooves deep, with faint groove and ridge extending across branchial regions; sternal plate wide, with deep sternal grooves leading medially from 5th pereopod coxae of females, abdominal depression deep. *U.Eoc.*, Venez.—FIG. 304,6. **F. kugleri*; carapace drawn from int. mold, $\times 1$ (Glaessner, n).

Torynomma WOODS, 1953 [**T. quadrata*; OD]. Carapace subquadrate, widest anteriorly, orbital grooves large, rostrum narrow, oviduct opening on coxa of 3rd pereopods. *Cret.(Alb.-L.Turon.)*, Australia.—FIG. 304,1. **T. quadrata*, Alb.; 1a, dorsal view of holotype, 1b, left chela, 1c,d, left and ant. sides of carapace, $\times 1$ (327).

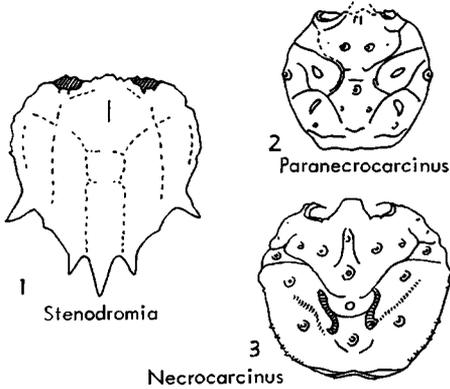


FIG. 306. Calappidae (Calappinae) (p. R495).

Superfamily CALAPPOIDEA de Haan, 1833

[*nom. transl.* BEURLEN, 1930 (*ex* Calappidea DE HAAN, 1833)]
[="subtribe" Calappoida BEURLEN, 1930]

Carapace rounded, abdomen fully turned under sternum, which is not reduced; all pereiopods well developed. *L.Cret.-Rec.*

Family CALAPPIDAE de Haan, 1833

[*nom. correct.* DANA, 1852 (*ex* Calappidea DE HAAN, 1833)]

Carapace with rounded outline and spinose or lobate margin; front and orbits of equal width; chelae large; male third to fifth abdominal somites fused; oviducts opening on sternum. *L.Cret.-Rec.*

Subfamily CALAPPINAE de Haan, 1833

[*nom. transl.* ALCOCK, 1896 (*ex* Calappidae DE HAAN, 1833)]

Merus of third maxillipeds not elongate and acute, second to fifth pereiopods walking legs. *L.Cret.-Rec.*

Calappa WEBER, 1795 [**Cancer granulatus* LINNÉ, 1758; SD LATREILLE, 1810]. Carapace strongly convex, expanded to maximum width posterolaterally, front and orbits small, chelipeds very large, fitting front of carapace, dactylus of one hand with strong curved basal tooth. ?*M.Eoc.*, *Oligo.* - *Pleist.*, Eu.-N. Am.-C. Am.-Egypt-Burma-E. Indies; *Rec.*, W. Eu.-Atl.-Pac.-Ind. O.—FIG. 305,7. *C. heberti* (BROCCHI), Mio., Hung.; 7a, carapace; 7b, right chela, $\times 1$ (184). [= *Aparnondylus* ROSS, LEWIS, & SCOLARO, 1964 (type, *A. ocalanus*)]

Acanthocarpus STIMPSON, 1871 [**A. alexandri*; OD]. Carapace ovate, convex, as broad as long,

with posterolateral spines. Chelipeds with long spine on merus, pointing outward. *Oligo.*, Panama; *U.Oligo.* or *L.Mio.*, Brazil; *Rec.*, N.Am.(W.coast). *Calappella* RATHBUN, 1919 [**C. quadrispina*; OD]. Resembling *Calappa* but with long spines on anterior and posterior ends of posterolateral borders. *Oligo.*, C.Am.-W.Indies.

Calappilia A. MILNE-EDWARDS, 1873 [**C. verrucosa*; SD GLAESSNER, 1929] [= *Paracyclois* MIERS, 1886 (type, *P. milne-edwardsi*)]. Greatest width of carapace in anterior or middle portion, rostrum narrow, surface tuberculated, sternum longer than wide. *M.Eoc.-U.Oligo.*, Eu.-N.Am.(Tex.)-Mex.-E. Indies; *Rec.*, Australia-Pac.-W.Indies.—FIG. 305,4. *C. dacica* (BITTNER), U.Eoc., Rumania; dorsal view of carapace, $\times 0.7$ (184).

Camarocarcinus HOLLAND & CVANCARA, 1958 [**C. arnesoni*; OD]. Differs from *Campylostoma* in absence of dorsal tubercles and in having greatest width of carapace between anterolateral margins. *Paleoc.*, N.Am.(N.Dak.)—FIG. 305,6. **C. arnesoni*; 6a,b, dorsal and ant. views of carapace, $\times 1$ (148).

Campylostoma BELL, 1858 [**C. matutiforme*; OD]. Carapace rounded, with very strong lateral and several weaker antero- and posterolateral spines; surface with tubercles on longitudinal and transverse ridges. *L.Eoc.*, ?*U.Eoc.*, Eu.—FIG. 305,1. **C. matutiforme*, L.Eoc., Eng.; 1a,b, dorsal and anteroventral views of carapace, $\times 1$ (19).

Cenomanocarcinus VAN STRAELEN, 1936 [**C. inflatus* (= *Neocarcinus inflatus* A. MILNE-EDWARDS in A. GUILLIER, 1886, *nom. nud.*); OD]. Differs from *Neocarcinus* in having strong continuous median and branchial longitudinal and weaker anterior, median and posterior transverse granulated ridges on the carapace. [The type designation and validity of the genus were questioned by STENZEL (1945). However, VAN STRAELEN established the genus as monotypic, followed by the remark that it is fitting to refer to this genus another species.] *Cret.(Alb.-Turon.)*, USA (Tex.-Okla.); *U. Cret.(Cenoman.-Turon.)*, Fr.; *U. Cret.(Cenoman.)*, Palest.—FIG. 305,5. **C. inflatus* (VAN STRAELEN), Cenoman., Fr.; dorsal view of carapace, $\times 0.5$ (306).

Cycloes DE HAAN, 1837 [**C. granulosa*; OD] [= *Cryptosoma* BRULLE in H. MILNE-EDWARDS, 1837 (*non* BERTHOLD, 1827)]. Carapace elongate to subcircular, orbits as in *Mursia*, chelipeds as in *Calappa* or *Mursia*, legs shorter than chelipeds. *Mio.*, Fiji; *Rec.*, At.-IndoPac.-E.Pac.

Mursia DESMAREST, 1823 [**M. cristata* H. MILNE-EDWARDS, 1837; SD H. MILNE-EDWARDS, 1837]. Carapace transversely oval, rounded anteriorly, contracted posteriorly, with long lateral spines; orbits rather large; chelipeds similar to those of *Calappa* but chelae more elongate, legs large. *Oligo.*, N.Am.-Panama; *Mio.*, Japan; *Rec.*, Pac.

—FIG. 305,3. *M. marcusana* (RATHBUN), Oligo., USA (Wash.); dorsal view of carapace, $\times 1.3$ (238).

Mursilia RATHBUN, 1919 [**M. ecristata*; OD]. Based on manus of cheliped which resembles that of *Mursia* but lacks ridge on inferior margin. Mio., Panama.

Mursiopsis RISTORI, 1889 [**M. pustulosus*; OD]. *U.Oligo.*, N.Italy.

Necrocarcinus BELL, 1863 [**Orithya labeschei* DESLONGCHAMPS, 1835; SD GLAESSNER, 1929] [= *Neocarcinus* STOLICZKA, 1873 (erroneous spelling)]. Carapace convex dorsally with subcircular to polygonal outline, wider than long, with weak transverse grooves; regions marked by strong tubercles arranged medially, and also along curved longitudinal lines on branchial region and transverse lines on gastric and hepatic regions. Orbits turned obliquely upward, with 2 supraorbital fissures. Lateral margins granulate to denticulate. *Cret.(Alb.-Senon.)-Eoc.*, Eu.-N.Am.-W.Afr.-India.

—FIG. 306,3. **N. labeschei* (DESLONGCHAMPS), Alb., Eng.; carapace, $\times 1$ (Glaessner, n).

Paranecrocarcinus VAN STRAELEN, 1936 [**P. hexagonalis*; OD]. Differs from typical *Necrocarcinus* in hexagonal outline of carapace and reduced ornamentation. *L.Cret.*, Fr.; *U.Cret.(Campan.)*, USA (N.J.). —FIG. 306,2. **P. hexagonalis*, *L.Cret.(Neocom.)*, Fr.; dorsal view of carapace, $\times 2$ (after 306).

Polyncemidium REUSS, 1859 [**Dromilites pustulosus* REUSS, 1845; OD]. Carapace wider than long, orbits large, front grooved, lateral margin sharp, surface pustulose and granulated. *U.Cret.(Coniac.)*, Boh. —FIG. 305,2. **P. pustulosum* (REUSS); 305,2, dorsal view, $\times 1.5$.

Stenodromia A. MILNE-EDWARDS, 1873 [**S. gibbosa*; OD]. Carapace pyriform, long, narrow, very convex, with or without weak posterior gastric grooves; front short and narrow; orbits large, surface smooth, with medial and branchial longitudinal tuberculated ridges. *M.Eoc.*, Spain; *M.Oligo.*, Fr. —FIG. 306,1. *S. calasanctii* (VIA), Eoc., Spain; dorsal view of carapace, $\times 2$ (314).

Subfamily MATUTINAE McLeay, 1838

Merus of third maxillipeds elongate and acute, covering palp. Pereiopods are swimming legs. ?*L.Cret.*, *M.Tert.-Rec.*

Matuta FABRICIUS, 1798 [**Cancer victor* FABRICIUS, 1786 (= *Cancer lunaris* FORSKÅL, 1775); SD LATREILLE, 1810]. Carapace depressed, slightly wider than long, anterolateral margin with spines, last spine slightly or considerably larger than others. Posterolateral margins strongly convergent. Chelae strongly ridged and tuberculate. *Mio.*, Eu.; *Rec.*, IndoPac.-W.Afr. —FIG. 307,2. *M. brocchii* [nom. nov. GLAESSNER, herein, pro *M. inermis*

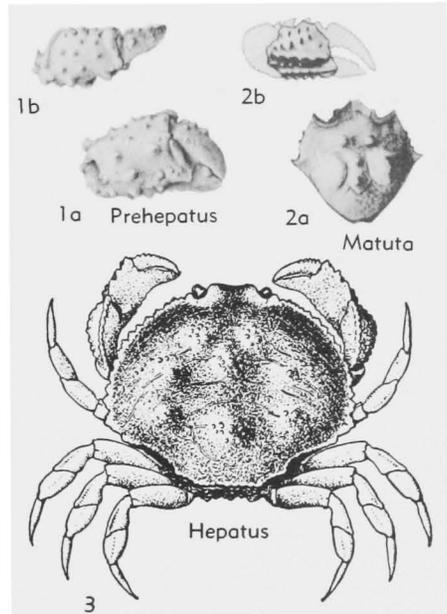


FIG. 307. Calappidae (Matutinae) (p. R495).

(BROCCI), 1883 (*non* MIERS, 1882)], Mio., Hung.; 2a, dorsal view of carapace; 2b, right chela, $\times 0.7$ (184).

Hepatella SMITH, 1869 [**H. amica*; OD]. Differs from *Hepatus* in subrectangular carapace, prominent fronto-orbital border, lateral regions concave above. *U.Oligo.* or *L.Mio.*, Brazil; *Rec.*, W. coast of Mexico to Peru.

Hepatus LATREILLE, 1802 [**Calappa angustata* FABRICIUS, 1798; OD] [= *Hepatoides* BALSS, 1957 (obj.)]. Carapace broad, convex, outline arcuate in front, strongly narrowed behind; fronto-orbital margin narrow, elevated; chelipeds strong, keeled; legs smooth. ?*Oligo.*, Panama; *Pleist.*, Panama-USA (Calif.); *Rec.*, N.Am. (E.coast-W.coast). —FIG. 307,3. *H. lineatus* (RATHBUN), *Rec.*; dorsal view, $\times 1$ (245).

?**Prehepatus** RATHBUN, 1935 [**P. cretaceus*; OD]. Chelae only, which differ from those of other Calappidae in being flattened above to form horizontal face instead of crest. *Cret.(Alb.-Campan.)*, USA (Tex.-N.J.). —FIG. 307,1. **P. cretaceus*, Alb., Tex.; 1a,b, ext. and aboral views, $\times 2$ (244).

Family LEUCOSIIDAE Samouelle, 1819

[nom. correct. MIERS, 1886 (pro Leucosidae SAMOUELLE, 1819)]

Carapace round, oval or polygonal. Eyes and orbits very small, front narrow but

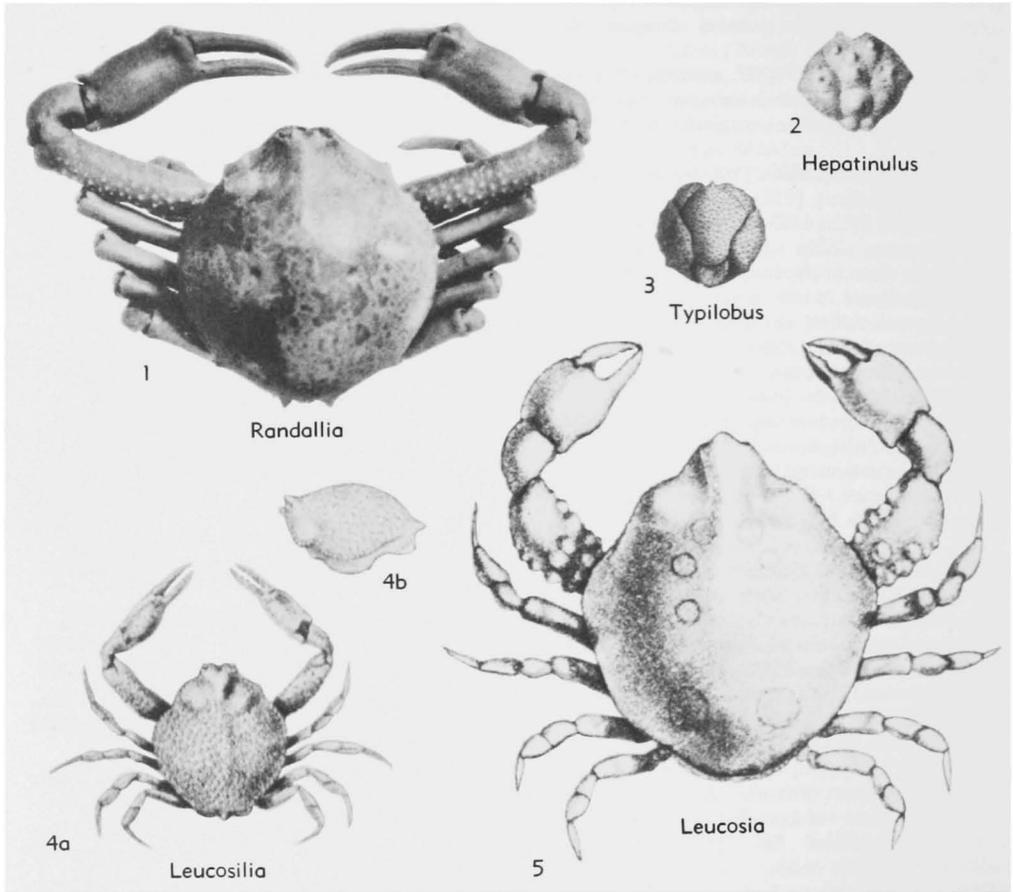


FIG. 308. Leucosiidae (p. R496-R498).

wider than orbits, antennules infolded obliquely, antennae small, third maxillipeds covering buccal area, inhalant canals covered by their wide exopods; abdominal terga 3 to 5 or 6 commonly fused; chelipeds symmetrical. [This family is commonly divided into subfamilies which are constituted and defined differently by different authors (MIERS, ALCOCK, IHLE, RATHBUN, BALSS) and are not considered helpful to paleontologists at the present stage of our knowledge of the family.] ?*L.Eoc.*, *M. Eoc.-Rec.*

Leucosia WEBER, 1795 [**Cancer craniolaris* LINNÉ, 1758; SD HOLTHUIS, 1959] [= *Leucosides* RATHBUN, 1897 (obj.)]. Carapace porcelaneous, convex, smooth, narrow frontal region projecting (snoutlike), "thoracic sinus" in side walls under epibranchial angles; chelipeds massive. *Mio.-Rec.*,

IndoPac.—FIG. 308,5. *L. australiensis* (MIERS), *Rec.*; $\times 2.25$ (139, after Miers).

Ebalia LEACH, 1817 [**Cancer tuberosus* PENNANT, 1777; SD RATHBUN, 1922]. Carapace convex, rhomboidal to hexagonal, with tumid regions, nodose, granulate, front narrow, truncate, chelipeds moderately developed. *Mio.-Pleist.*, Eu-Burma; *Rec.*, IndoPac.-Atl.-Medit.-W.N.Am.—FIG. 309,2. *E. tuberculosa* (H. MILNE-EDWARDS), *Rec.*; $\times 2$ (139).

Hepatinulus RISTORI, 1886 [**H. seguenzai*; OD]. Carapace finely granulated, convex, rhomboidal, length equal to width, regions marked by tubercles and faint grooves; 2 rounded posterior lobes. *Mio.-Plio.*, Italy.—FIG. 308,2. **H. seguenzai*, *Plio.*; $\times 3$ (253).

Ilia LEACH, 1817 [**Cancer nucleus* LINNÉ, 1758; OD]. Carapace globular, 4 spines on posterior and posterolateral margins, front narrow with median indentation; chelipeds long, with long, thin fingers, 2nd to 5th pereopods much shorter

and decreasing in length. ?*Eoc.*, *Plio.*, Italy; *Rec.*, *Medit.-W.Afr.*—FIG. 310.2. **I. nucleus* (LINNÉ), *Rec.*, *Medit.*; $\times 0.7$ (redrawn from 13, after 259).

Ixa LEACH, 1815 [**Cancer cylindrus* FABRICIUS, 1777; OD]. Sides of carapace produced transversely into 2 large cylindrical processes; median regions separated from lateral by broad channels. *Pleist.-Rec.*, IndoPac.

Ixoides M'GILCHRIST, 1905 [**I. cornutus*; OD]. Cephalothorax subglobular, with pair of large conical lateral spines. *Plio.-Rec.*, IndoPac.

Leucosilia BELL, 1855 [**Guaia (Ilia) jurinei* DE SAUSSURE, 1853; OD]. Carapace orbicular, granu-

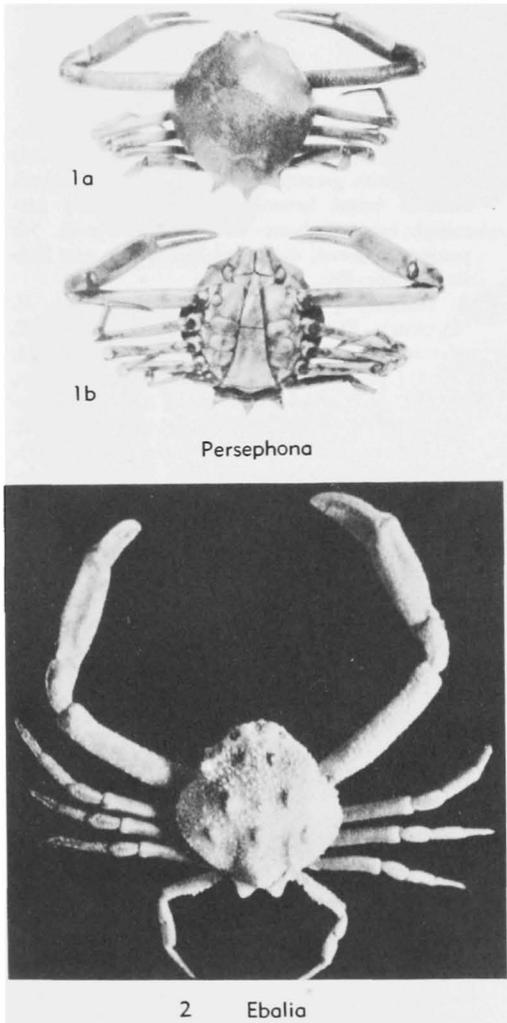


FIG. 309. Leucosiidae (p. R496, R498).

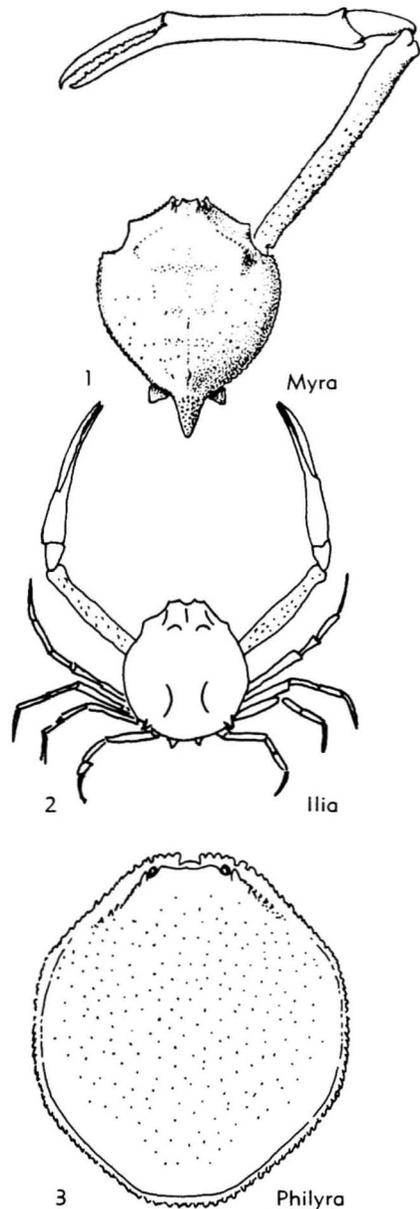


FIG. 310. Leucosiidae (p. R496-R498).

late, front narrow with median indentation, single posterior spine. *Mio.-Pleist.*, Panama; *Rec.*, Panama-Peru.—FIG. 308.4. **L. jurinei* (SAUSSURE), *Rec.*; 4*a,b*, dorsal and lat. views of carapace, $\times 1$ (245).

Myra LEACH, 1817 [**Leucosia fugax* FABRICIUS, 1798; OD]. Carapace ovoid, front narrow with

- median indentation, 3 spines on posterior margin, surface smooth and granulate, regions scarcely marked, chelipeds elongate, slender. *Mio.*, Eu.-India-Fiji; *Mio.-Plio.*, Java; *Pleist.*, Celebes; *Rec.*, IndoPac.-Hawaii-Gulf Calif.-Panama.—FIG. 310, 1. **M. fugax* (FABRICIUS), *Rec.*; $\times 1$ (15).
- Nucia DANA, 1852 [**N. speciosa*; OD]. Carapace convex, broader than long, lateral margins spinose, chelipeds short, legs stout. *L.Mio.*, Java; *Rec.*, IndoPac.
- Palaeomyra A. MILNE-EDWARDS, 1861 [**P. bispinosa*; OD]. *M.Mio.*, N.Italy.
- Pariphiculus ALCOCK, 1896 [**Randallia coronata* ALCOCK & ANDERSON, 1894; SD RATHBUN, 1922]. Carapace subglobular, margins spinose, surface vesiculose; intestinal region distinctly isolated; front narrow, orbits obliquely elongate. Chelipeds about 1.5 times length of carapace, fingers long. *L.Mio.*, E.Indies; *Rec.*, IndoPac.
- Persephona LEACH, 1817 [**P. latreillii* (= **Cancer punctatus* LINNÉ, 1758); SD RATHBUN, 1922]. Close to *Myra*, distinguished by bidentate, not tridentate, anterior margin of pterygostomal groove (BARNARD, 1950). *Plio.-Pleist.*, N.Am.; *Rec.*, Am.(E.coast-W.coast).—FIG. 309, 1. **P. punctata punctata* (LINNÉ), *Rec.*; 7a,b, dorsal and ventral views, $\times 0.7$ (245).
- Philyra LEACH, 1817 [**Cancer globus* FABRICIUS, 1775; SD H. MILNE-EDWARDS, 1837]. Carapace circular, smooth to finely granulate, surrounded by beaded margin, edges of pterygostome extending beyond front, regions scarcely defined, chelipeds elongate and slender. *Plio.-Rec.*, IndoPac.; *Rec.*, W.Afr.—FIG. 310, 3. *P. punctata* BELL, *Rec.*; $\times 1$ (15).
- Randallia STIMPSON, 1857 [**Ilia ornata* RANDALL, 1840; OD]. Carapace almost globular, granulate, front narrow, with front edge of buccal cavity projecting beyond it; regions usually marked by grooves, chelipeds stout. *Mio.*, Aus.-?Brazil; *Pleist.*, N.Am.; *Rec.*, Indo Pac.-N. Am.(E. coast-W. coast).—FIG. 308, 1. **R. ornata* (RANDALL), *Rec.*; $\times 0.7$ (245).
- Typilobus STOLICZKA, 1871 [**T. granulosus*; OD]. Carapace small, ovoid, rostrum pointed, gastric, cardiac, hepatic and branchial regions well marked by grooves; female abdomen not greatly expanded. *M.Eoc.-L.Oligo.*, *L.Mio.-M.Mio.*, Eu.-Egypt-India.—FIG. 308, 3. *T. semseyanus* LÖRENTHEY, U. Eoc., Hung.; $\times 1$ (184).
- posteriorly, chelae flat, with fixed finger more or less deflected; oviducts opening in coxae of third pereopods, fifth ones subdorsal. *L.Cret.(Alb.)-Rec.*
- BOURNE (1922) distinguished the Raninidae as a "subtribe Gymnopleura" of the "tribe" Brachyura. BALSS (1957) retained them in the "tribe" Oxystomata as a family. BEURLEN (1930) separated a family Raninellidae but based this distinction only on the degree of reduction of the posterior sternites.

Family RANINIDAE de Haan, 1841

[*nom. correct.* ALCOCK, 1896 (pro Raninoidea DE HAAN, 1841)]

Characters of superfamily. *L.Cret.(Alb.)-Rec.*

Ranina LAMARCK, 1801 [**R. serrata* (= **Cancer raninus* LINNÉ, 1758; OD)]. Carapace evenly convex, with granulated surface, rostrum pointed, sternum broad between chelipeds, rapidly narrowed between bases of 2nd pereopods, 5th pereopods dorsal, dactyli of 2nd to 5th ones leaf-shaped. *Eoc.-Rec.*, IndoPac.

R. (Ranina) [= *Hela* MÜNSTER, 1840 (type, *H. speciosa*); *Eteroranina* FABIANI, 1910 (type, *R. dentata* LATREILLE = **Cancer raninus* LINNÉ, 1758)]. Carapace with granulated surface. *Eoc.*, N.Am.-?Eu.; *Oligo.*, Eu.-N.Am.; *Mio.-Plio.*, Alg.-Malta-Italy-Fiji; *Rec.*, IndoPac.—FIG. 311, 8. **R. (R.) ranina* (LINNÉ); adult male, $\times 0.3$ (137).

R. (Lophoranina) FABIANI, 1910 [**Ranina marestiana* KÖNIG, 1825; OD] [= *Palaeonotopus* BROCCHI, 1877 (type, *Ranina barroisi*; name, based on incomplete, wrongly described specimen, has not been used and therefore should be set aside by ICZN)]. Carapace with parallel transverse granulated ridges. *M.Eoc.-U.Eoc.*, Eu.-Egypt-Iran-India-W. Pac.-W. Indies, *Oligo.*, USA (Ala.)-Borneo-W.Indies.—FIG. 311, 6. **R. (L.) marestiana* (KÖNIG), ?N.Italy; fragmentary carapace (holotype) showing sculpture, $\times 1$ (322).

Eumorphocorystes BINKHORST, 1857 [**E. sculptus*; OD]. Carapace with strong anteriorly directed anterolateral spines. Surface covered with longitudinal and oblique granulated ridges. *U.Cret.(U. Senon.)*, Neth. [Also recorded, probably wrongly, from *Oligo.*, USA(Ore.)].—FIG. 311, 2. **E. sculptus*; dorsal view, $\times 1$ (41). [According to PELSENER, 1886, the drawing is incorrect in that it should show a ridged rostrum 4 mm. long.]

Hemioon BELL, 1863 [**H. cunningtoni*; OD]. Carapace ovoid, strongly convex transversely, rostrum small, orbits sloping; surface smooth, sternites of 1st and 2nd pereopods equally wide. *U.Cret.(Cenoman.)*, Eng.—FIG. 311, 4. **H. cunningtoni*; frontal view, $\times 1$ (344).

Superfamily RANINOIDEA de Haan, 1841

[*nom. trans.* DANA, 1852 (ex Raninoidea DE HAAN, 1841)]
[=Gymnopleura BOURNE, 1922]

Carapace elongate, not covering proximal abdominal terga or posterior thoracal epimera; sternum broad anteriorly, narrow

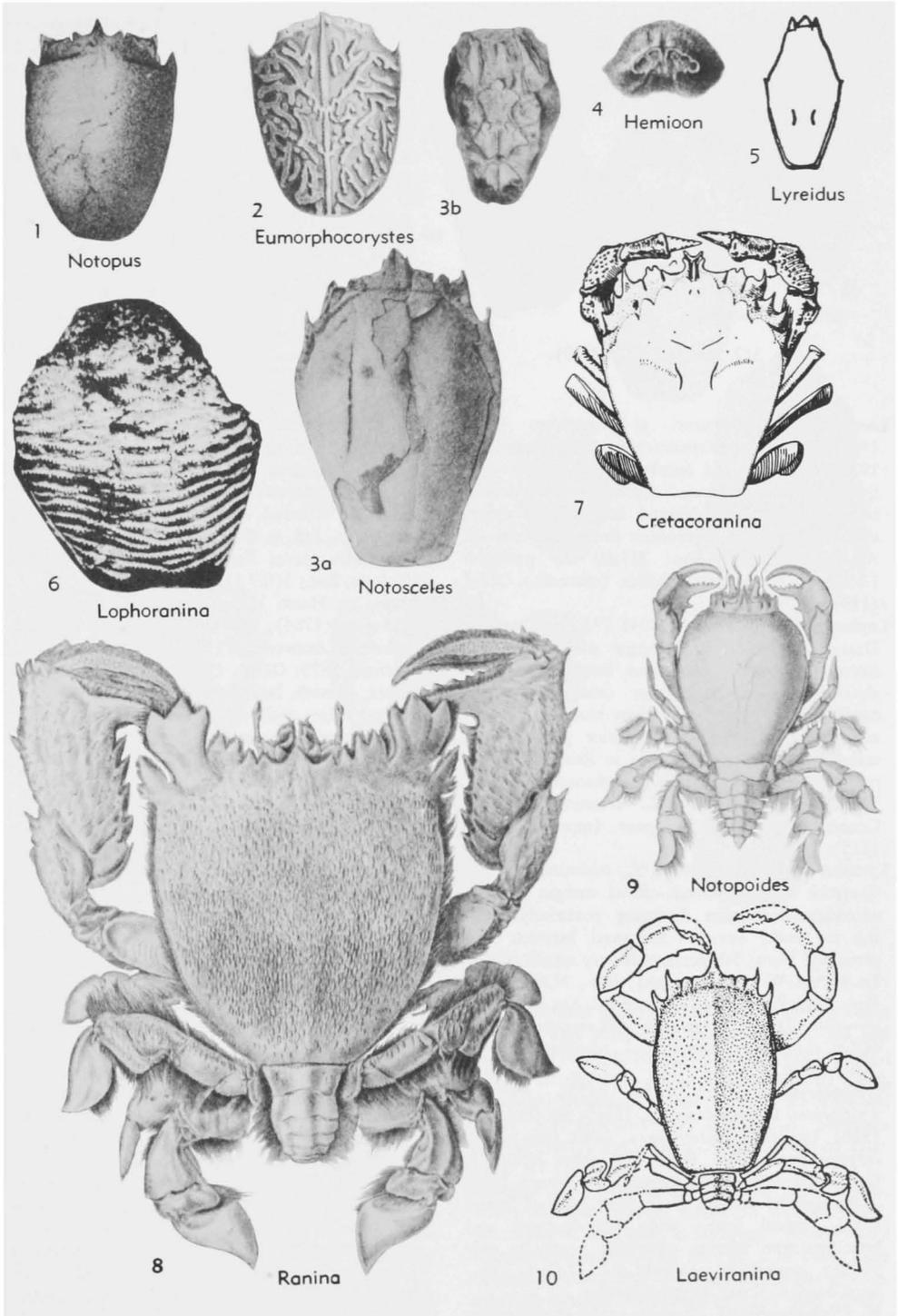


FIG. 311. Raninidae (p. R498, R500).

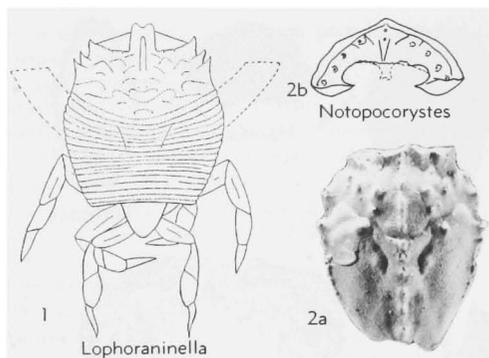


FIG. 312. Raninidae (p. R500).

Laeviranina LÖRENTHEY & BEURLEN, 1929 [**Ranina* (L.) *budapestinensis*; SD GLAESSNER, 1929]. Differs from *Raninoides* in greater relative width of carapace, narrower fronto-orbital border, and more advanced anterolateral spine; sternal plate as in *Raninoides*. *Eoc.*, Eu.-N.Am.-S. Am.-W.Afr.-N.Z.—FIG. 311,10. *L. gottschei* (BÖHM), *L.Eoc.*, Eu.; carapace (reconstr.), $\times 1.7$ (119).

Lophoraninella GLAESSNER, 1945 [**Ranina cretacea* DAMES, 1886; OD]. Carapace ovoid; rostrum, extraorbital, anterolateral and lateral teeth well developed; anterior portion ornamented with curved, short, granulated ridges marking regions, or uniformly granulated, posterior portion with transverse granulated ridges as in *Ranina* (*Lophoranina*). *U.Cret.*(*Cenoman.*), Lebanon; ?*Paleoc.*, W.Afr.—FIG. 312,1. **L. cretacea* (DAMES), *Cenoman.*, Lebanon; carapace (reconstr.), $\times 1$ (115).

Lyreidus DE HAAN, 1841 [**L. tridentatus*; OD]. Carapace elongate, fronto-orbital margin narrow, anterolateral margins diverging posteriorly, ending in tooth; sternum narrowed between 2nd pereopod bases; 5th pereopods very small. *Oligo.*, Eu.-N.Am.-W.Indies-Australia; *Mio.*, N.Italy-N.Z.; *Rec.*, IndoPac.-N. Am.(E. coast)-C. Am.(E. coast).—FIG. 311,5. *L. elegans* (GLAESSNER), *Mio.*, N.Z.; carapace, fronto-orbital margin restored, $\times 0.7$ (118).

Notopocorystes M'COY, 1849 [**N. mantelli* (= *Corystes stokesi* MANTELL, 1844); SD WITHERS, 1928] [= *Palaeocorystes* BELL, 1863 (obj.); *Eucorystes* BELL, 1863 (type, *N. carteri* M'COY)]. Carapace ovoid to shield-shaped; front narrow, bifid, 2 supraorbital fissures, 2 or more pairs of lateral spines; buccal frame wide, pterygostome and branchiostegite narrow. Sternites gradually narrowing posteriorly. *L.Cret.*(*Alb.*)-*U.Cret.*, Eu.-Syria-Madag.-N.Am.-Japan-Australia.

N. (Notopocorystes). Carapace ovoid, with median

ridge, regions at least partly marked by grooves and tubercles or ridges, posterolateral margins straight; 5th pereopods dorsal, with short, broad and flat segments and leaf-shaped dactylus. *Cret.* (*Alb.-Cenoman.*), Eu.-Syria-N.Am.-Japan-Australia.—FIG. 312,2. **N. (N.) stokesi* (MANTELL), *Alb.*, Eng.; 2a,b, carapace, dorsal and frontal, $\times 1$ (Glaessner, n).

N. (Cretacorantina) MERTIN, 1941 [**Raninella? schloenbachi* SCHLÜTER, 1879; OD]. Carapace finely granulate or smooth, shield-shaped, posterior part narrowed, with concave posterolateral margins; fronto-orbital and anterolateral margins dentate, only median parts of cervical and branchiocardiac grooves marked. *U.Cret.*, Eu.-N. Am.-W.Indies.—FIG. 311,7. *N. (C.) dichrous* STENZEL, Turon., USA(Tex.); carapace (reconstr.), $\times 1$ (283).

Notopoides HENDERSON, 1888 [**N. latus*; OD]. Carapace ovate, convex; fronto-orbital border 0.5 width of carapace, which widens abruptly behind it; sternum narrowed between bases of 2nd pereopods and widened again towards bases of 3rd pereopods, 3rd to 5th ones similar in size and shape. *Mio.*, Java; *Rec.*, E.Indies.—FIG. 311,9. **N. latus*, *Rec.*; $\times 0.7$ (145).

Notopus DE HAAN, 1841 [**Cancer dorsipes* LINNÉ, 1758 (*non* 1764); SD (ICZN pend.)] [= *Notoporanina* LÖRENTHEY, 1929 (type, *N. beyrichi* BITTNER, 1875; OD)]. Carapace oval, transversely convex, smooth, but with lateral spines joined by serrated ridge; wide straight fronto-orbital margin with narrowly triangular, prominent rostrum and supraorbital spines and fissures; sternum narrowed behind chelipeds; not strongly reduced. *M.Eoc.-U. Eoc.*, Eu.; *Rec.*, IndoPac.—FIG. 311,1. *N. beyrichi* BITTNER, *Eoc.*, Hung.; $\times 1$ (184).

Notosceles BOURNE, 1922 [**N. chimmonis*; SD RATHBUN, 1928]. Carapace ovate, smooth, with postfrontal ridge, fronto-orbital border about 0.5 width of carapace, rostrum pointed, with 2 basal lateral teeth; 1 pair of curved lateral spines; abdomen wide, 5th pereopods raised. *U.Cret.*, USA (Tex.); *Paleoc.*, USA (Tex.-Ark.-Ala.); *Rec.*, IndoPac.—FIG. 311,3. *N. bournei* (RATHBUN), *Paleoc.*, Tex.; 3a, carapace, $\times 2$; 3b, ventral view, $\times 1$ (240).

Pseudoraninella BEURLEN, 1929 [**Notopocorystes muelleri* BINKHORST, 1857; SD GLAESSNER, herein]. Carapace small, ovoid, with spinose rostrum, 2 pairs of supraorbital, 1 pair each of extra-orbital and lateral teeth; anterior part of carapace granulated, otherwise smooth, buccal frame narrow. [Other species formerly placed in *Raninella* and included by BEURLEN in his new genus are now separated as *Notopocorystes* (*Cretacorantina*).] *U.Cret.*(*Senon.*), Eu.; ?*Eoc.*, Borneo.—FIG. 313, 4. **P. muelleri* (BINKHORST), *U.Senon.*, Neth.; 4a, carapace, dorsal view, $\times 1$ [according to PEL-

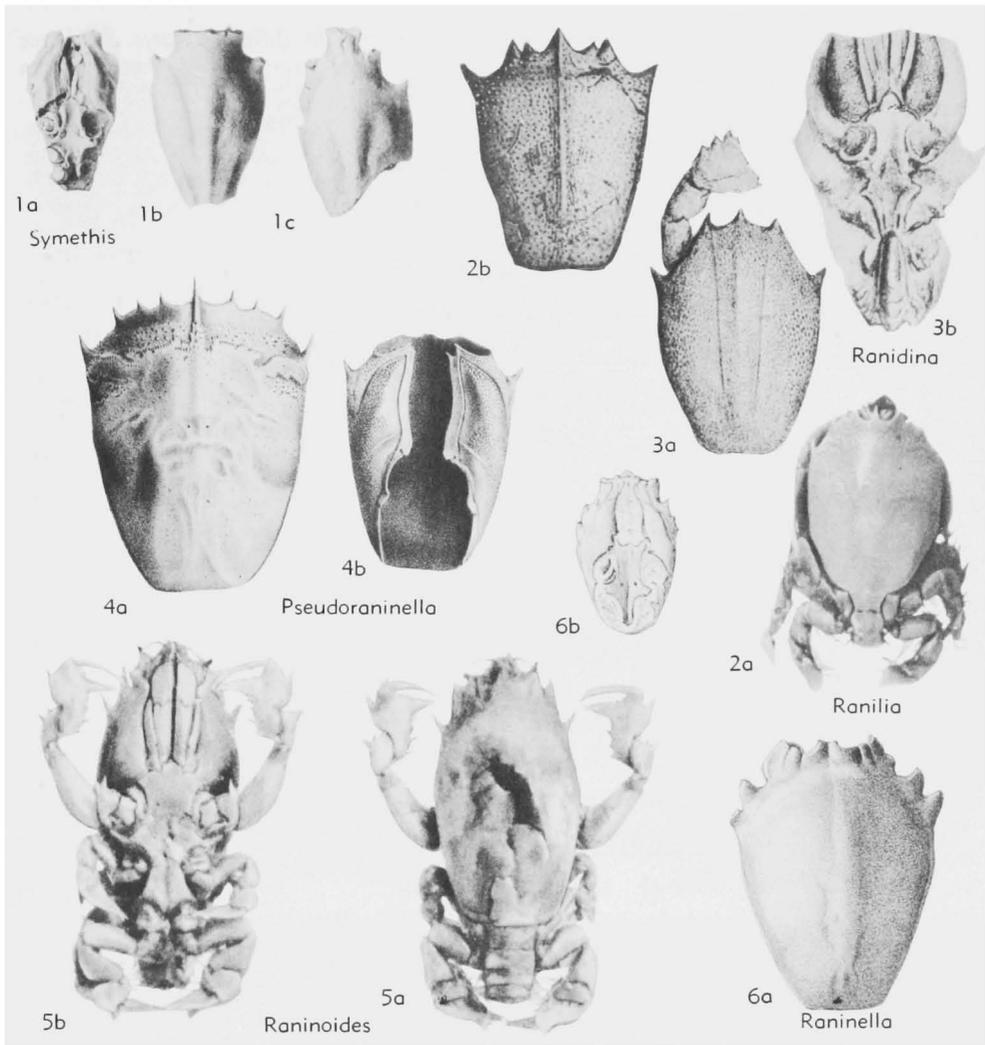


FIG. 313. Raninidae (p. R501).

SENEER (1886) the drawing is incorrect since the spines are flattened teeth, those nearest the rostrum being longer than outer ones], 4b, ventral view, $\times 1.5$ (41).

Ranidina BITTNER, 1893 [**R. rosaliae*; OD]. Like *Ranilia*, fronto-orbital margin narrow, one pair of extraorbital spines between rostrum and lateral spines; sternum not very narrow between 2nd pereopods. *Oligo.*, N.Am.; *Mio.*, Aus.-Hung.—FIG. 313,3. **R. rosaliae*, *Mio.*, Aus.; 3a,b, dorsal, ventral, $\times 1$ (184, after Bittner).

Ranilia H. MILNE-EDWARDS, 1837 [**R. muricata*; OD] [= *Notopella* LÖRENTHEY, 1929 (type, *N. vareolata*)]. Carapace ovoid, strongly granulated anteriorly, rostrum triangular; 2 or 3 pairs of spines between rostrum and strong lateral spines;

orbits inclined downward-outward; sternum linear between 2nd pereopods, wider between 3rd and 4th ones, 5th not strongly reduced. *Eoc.*, Hung.; *Tert.*, Eu.-N.Am.; *Rec.*, W.Atl.(tropical)-E.Pac. (tropical)-IndoPac.—FIG. 313,2a. **R. muricata*, *Rec.*; $\times 1$ (245).—FIG. 313,2b. *R. vareolata* (LÖRENTHEY), *Eoc.*, Hung.; dorsal view of carapace, $\times 1$ (184).

Raninella A. MILNE-EDWARDS, 1862 [**R. trigeri*; OD]. Carapace ovoid, widest in anterior third, posterolateral margins converging, fronto-orbital margin with supraorbital fissures, 1 or more pairs of anterolateral spines. Only lateral cardiac grooves marked; sternum narrowed between 2nd pereopods; buccal frame long and narrow. *U.Cret.*, Eu.; *?Paleoc.*, USA (Ala.).—FIG. 313,6. **R. trigeri*,

Cenoman., Fr.; 6a, dorsal, $\times 0.7$ (53); 6b, ventral view of smaller specimen (described as *R. elongata*), $\times 1$ (53).

Raninoides H. MILNE-EDWARDS, 1837 [**Ranina laevis* LATREILLE, 1825; OD] [= *Symnista* PHILIPPI, 1887 (non RAFINESQUE, 1815) (type, *S. araucana*); *Raninellopsis* BÖHM, 1922 (type, *R. javana*)]. Carapace elongate, greatest width behind middle part, transversely convex, surface smooth, fronto-orbital border less than greatest width of carapace, sternum broad between chelipeds and between bases of 2nd pereopods, narrow between bases of 3rd pereopods, 5th ones short and slender. *Oligo-Mio.*, NW.N.Am.-Chile-E.Indies; *Rec.*, Indo-Pac.-W.Afr.-C.Am.—FIG. 313,5. **R. laevis* (LATREILLE); *Rec.*, Colombia; 5a,b, dorsal and ventral views, $\times 1$ (after 245).

Symethis WEBER, 1795 [**Hippra variolosa* FABRICIUS, 1793; OD] [= *Zanclifera* HENDERSON, 1888 (type, *Eryon caribensis* DE FREMINVILLE, 1832)]. Fronto-orbital margin very narrow, front trilobate, produced; sternum linear between 2nd pereopods, chelae long, inflated. *Paleoc.*, USA(Ala.); *Rec.*, C.Am.—FIG. 313,1. *S. johnsoni* (RATHBUN), *Paleoc.*, USA(Ala.); 1a,b, ventral and dorsal views of carapace (holotype); 1c, dorsal view of carapace with rostrum, $\times 1$ (244).

Tribolocephalus RISTORI, 1886 [**T. laevis*; OD]. Differs from *Lyreidus* in greater length of fronto-orbital spines and absence of lateral teeth. *Plio.*, Italy.

Section OXYRHYNCHA

Latreille, 1803

Carapace narrowed anteriorly, with rostrum; branchial regions well developed, inflated; epistome wide, buccal frame square; antennules infolded longitudinally, second segment of antennae mostly completely fused with epistome. ?*U.Cret.*, *Eoc.-Rec.*

Family MAJIDAE Samouelle, 1819

[*nom. correct.* ALCOCK, 1895 (pro *Majidae* SAMOUELLE, 1819)]

Chelipeds not much longer than second and third pereopods; second segment of antenna well developed. Orbits more or less incomplete. ?*U.Cret.*, *Eoc.-Rec.*

Subfamily MAJINAE Samouelle, 1819

[*nom. transl.* ALCOCK, 1895 (ex *Majidae* SAMOUELLE, 1819)]

Basal segment of antenna very wide, orbits developed sufficiently to cover long eye stalks and eyes, with orbital spine. [ALCOCK (1895) and BALSS (1929) divided

this subfamily in different ways. Evidence is lacking for grouping of fossil genera below subfamily level.] ?*U.Cret.*, *Eoc.-Rec.*

Maja LAMARCK, 1801 [**Cancer squinado* HERBST, 1788 (on official list, ICZN)] [= *Mamaja* STEBBING, 1904]. Carapace pear-shaped, granular or spinose, with spinose lateral margins, rostrum with 2 straight, divergent horns; interantennular and intermediate spines present; chelipeds slender, fingers straight. *Mio.-Pleist.*, Eu.-N.Afr.; *Mio.*, Fiji; *Rec.*, IndoPac.-E.Atl.-Medit.—FIG. 314,9. *M. arambourgi* VAN STRAELEN, *Plio.*, Alg.; $\times 1$ (303).

Leptomithrax MIERS, 1876 [**Paramithrax* (*Leptomithrax*) *longimanus* MIERS, 1876; SD MIERS, 1879]. Postorbital spine excavated, close to intercalary supraorbital spine; carpus of cheliped without ridges, commonly granular. *U.Mio.-L.Plio.*, N.Z.; *Rec.*, W.Pac.—FIG. 314,7. *L. uruti* GLAESSNER, *U.Mio.*, N.Z.; $\times 1$ (118).

Micromithrax NOETTLING, 1881 [**M. holsaticus*; OD]. Differs from *Maja* in frontal horns not diverging, extraorbital spines small, few anterolateral spines. *Mio.*, N.Ger.—FIG. 315,1. **M. holsaticus*; $\times 0.7$ (214).

Periicanthus BITTNER, 1875 [**P. horridus*; OD]. Carapace triangular, with long spines on lateral and posterior margins, orbital roof an obliquely projecting convex plate. [BEURLEN (1929) proposed a monotypic family Periicanthidae, but withdrew it later (1930). BALSS (1957) placed the genus in the Majinae or (“possibly”) Acanthonychinae.] *M.Eoc.*, Italy-Spain; *U.Eoc.*, Hung.—FIG. 314,8. **P. horridus*, *U.Eoc.*, Hung.; $\times 1$ (184).

Stenocionops DESMAREST, 1823 [**Maja taurus* LAMARCK, 1818 (= **Cancer furcatus* OLIVIER, 1791); SD RATHBUN, 1925]. Orbits tubular, not strongly projecting, postorbital spine of moderate size, triangular; chelipeds well developed in adult males, chelae elongate. [Only fragmentary claws have been reported as fossil representatives of this genus. The otherwise unrecognized occurrence of Majidae in the Cretaceous cannot be deduced from such material.] ?*U.Cret.*, USA(Ark.); *U.Eoc.*, USA(Fla.); *Rec.*, N.Am.(coasts).

Thoe BELL, 1836 [**T. erosa*; OD]. Carapace moderately wide, lobulate; rostrum small; no pre-orbital spine; chelipeds long; fingers spoon-shaped, gaping in adult. ?*Plio.*, Fiji; *Rec.*, USA(Fla.)-Mexico-Panama.

Subfamily MICROMAJINAE Beurlen, 1930

[*nom. correct.* GLAESSNER, herein (pro *Micromajinae* BEURLEN, 1930)]

Second segment of antennae free; carapace as in Majinae, orbits as in Inachinae. [Considered by BEURLEN (1930) as provisional.] *Eoc.-Oligo.*

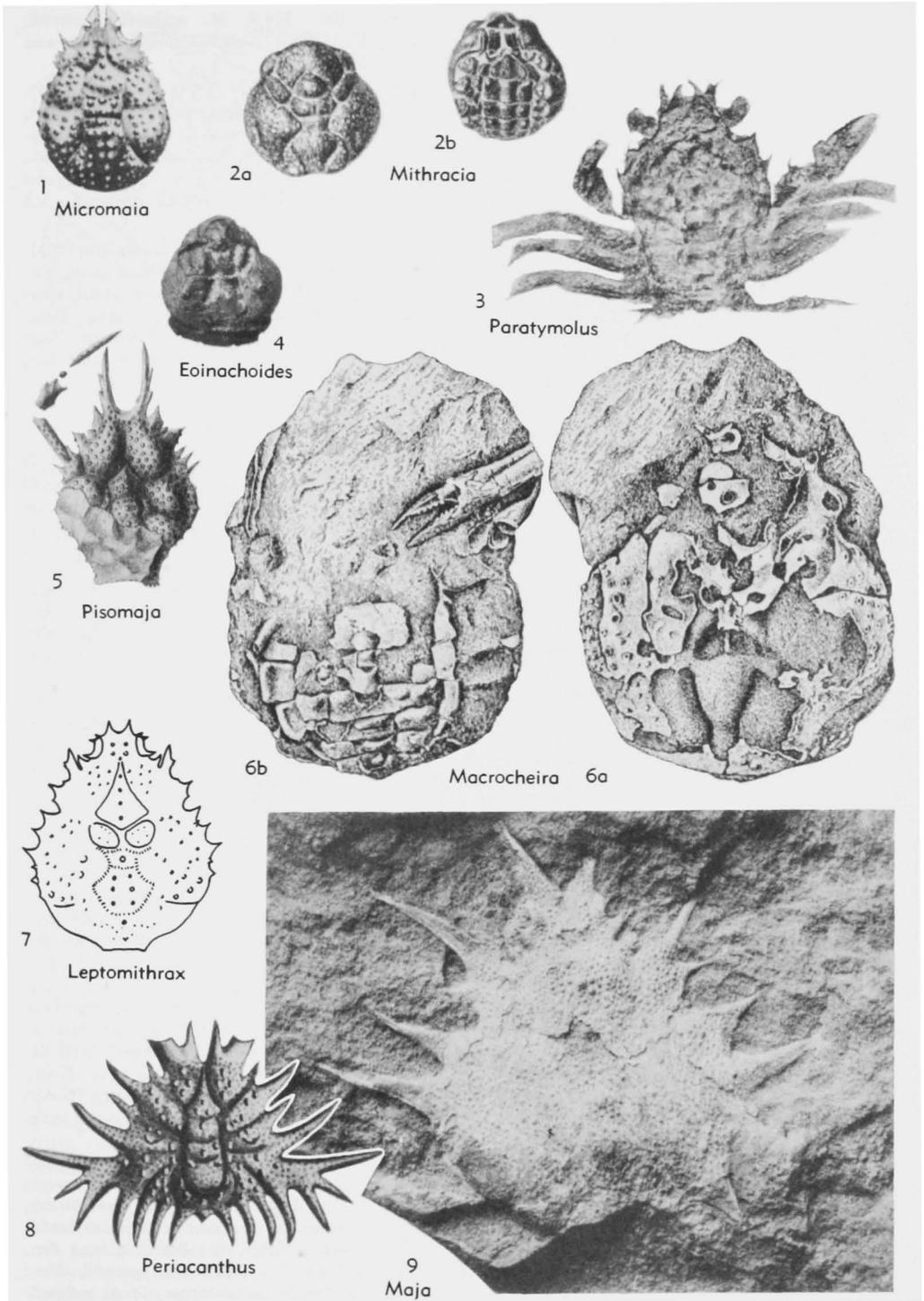


FIG. 314. Majidae (Majinae) (7-9), (Micromaiinae) (1-2, 5), (Inachinae) (3-4, 6) (p. R502-R504).

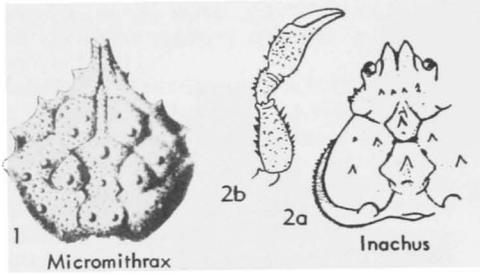


FIG. 315. Majidae (Majinae) (1), (Inachinae) (2) (p. R502, R504).

Micromaia BITTNER, 1875 [**M. tuberculata*; OD] [= *Micromaja* BITTNER, 1883]. Carapace ovoid, rostrum bilobed, orbits incomplete, postorbital spine separated. *M.Eoc.-L.Oligo.*, Eu.-Egypt; *M.Eoc.*, W.Afr.—FIG. 314,1. **M. tuberculata*, *U.Eoc.*, Hung.; $\times 1$ (184).

Mithracia BELL, 1858 [**M. libinoides*; OD]. Carapace subglobular, with grooved rostrum and clearly defined regions. *L.Eoc.*, Eng.—FIG. 314,2. **M. libinoides*; 2a,b, dorsal, ventral, $\times 1$ (19).

Pisomaja LÖRENTHEY, 1929 [**P. tuberculata*; OD]. Carapace broadest across middle, with long rostral spines and spinous margins, posterolateral margins concave. *U.Eoc.*, Hung.—FIG. 314,5. **P. tuberculata*; $\times 1$ (184).

Subfamily INACHINAE McLeay, 1838

Basal segment of antenna long and slender, no orbits, pointed postorbital spine. *U.Eoc.-Rec.*

Inachus WEBER, 1795 [**Cancer scorpio* FABRICIUS, 1779 (= **Cancer dorsettensis* PENNANT, 1777); SD H. MILNE-EDWARDS, 1837]. Carapace widened posteriorly, rostrum short, 4 main tubercles on gastric, cardiac and branchial regions; chelipeds much stronger in males, 2nd pereopods long. *Oligo.*, Eu.(USSR); *Plio.*, Eng.; *Rec.*, E.Atl.-Medit.—FIG. 315,2. **I. dorsettensis* (PENNANT), *Rec.*; 2a, left part of carapace, $\times 1$, 2b, male right cheliped, $\times 1$ (52).

Eoinachoides VAN STRAELEN, 1933 [**E. senni*; OD]. Carapace with branchial, cardiac and gastric regions inflated; cardiac region with 2 tubercles. *U.Eoc.*, Venezuela.—FIG. 314,4. **E. senni*; $\times 1.5$ (300).

Euprogna STIMPSON, 1871 [**E. rastellifera*; OD]. Carapace pyriform, rostrum short, with 2 small teeth; chelipeds with palms dilated, 2nd pereopods longest. *U.Mio.*, USA(Fla.); *Rec.*, N. Am.(E. coast-W. coast).

Macrocheira DE HAAN, 1839 [**Maja kaempferi* TEMMINCK, 1836; OD]. Carapace subtriangular, rostrum long, with 2 divergent spines, inner orbital spine small, legs very long. *Oligo.*, N.Am.; *Rec.*,

Japan.—FIG. 314,6. *M. teglandi* RATHBUN, *Oligo.*, USA(Wash.); 6a,b, female, dorsal and ventral, $\times 1$ (238).

Paratymolus MIERS, 1879 [**P. pubescens*; OD]. Carapace elongate-subpentagonal, rostrum short, no orbits or pre- or postocular spines, basal segment of antenna short, legs not elongate. *Mio.*, Japan; *Rec.*, IndoPac.—FIG. 314,3. *P. yabei* IMAIZUMI, *Mio.*, Japan; crushed specimen, $\times 3$ (158).

Pyromaia STIMPSON, 1871 [**P. cuspidata*; OD]. Carapace pyriform, with tubercles and spines, rostrum simple, well developed, supraorbital spine usually present, postorbital spine large, basal article of antenna long, chelipeds moderately long; 2nd to 5th pereopods long. *Pleist.*, N.Am.; *Rec.*, N.Am.(E. coast-W. coast).

Subfamily PISINAE Dana, 1852

Eyes with commencing orbits, with large, cupped, postocular process into which eyes can be partly retracted; basal segment of antenna broad; rostrum with two spines or teeth, legs usually very long. *Mio.-Rec.*

Pisa LEACH, 1814 [**Cancer biaculeatus* MONTAGU, 1813 (= **Maja armata* LATREILLE, 1802); OD]. Carapace with raised sculpture, preocular spine long, basal segment of antenna uniformly wide. *Pleist.*, Italy; *Rec.*, E.Atl.-Medit.

Chorilia DANA, 1851 [**C. longipes*; OD]. Carapace subpyriform, convex, spinous or tuberculate, rostral spines long, divergent, basal segment of antenna long and narrow; chelipeds large, manus compressed. *Pleist.*, N.Am.; *Rec.*, N.Pac.

Hyas LEACH, 1814 [**Cancer araneus* LINNÉ, 1758; OD]. Carapace broad, shield-shaped, tuberculate, rostrum triangular, bifid, incomplete orbits with fissures above and below, chelipeds stout, chelae compressed, pereopods subcylindrical. *Mio.*, Eu.-Japan; *Plio.*, N.Afr.; *Pleist.*, Eu.; *Rec.*, N.Pac.-N.Atl.—FIG. 316,1. **H. araneus* (LINNÉ), *Rec.*; male, dorsal view, $\times 0.7$ (237).

Libinia LEACH, 1815 [**L. emarginata*; OD]. Carapace convex, tuberculate or spinous, triangular with rounded posterior margin, rostrum bifid at apex, incomplete orbits small, chelipeds well developed, with elongate palms. ?*Plio.*, Fiji; *Pleist.*, N.Am.; *Rec.*, N.Am.(E. coast-W. coast)-?W.Afr.—FIG. 316,2. **L. emarginata*, *Rec.*; young male, $\times 0.7$ (237).

Loxorhynchus STIMPSON, 1857 [**L. grandis*; SD MIERS, 1879]. Carapace large, pyriform, rough, rostrum bifid, deflexed, preorbital tooth strong, postorbital acute; basal segment of antenna broad; chelipeds of male large. *Plio.-Pleist.*, N.Am.; *Rec.*, USA(Calif.).—FIG. 316,3. **L. grandis*, *Plio.*, Calif.; 3a,b, female cephalothorax, dorsal and ventral, $\times 0.5$ (238).

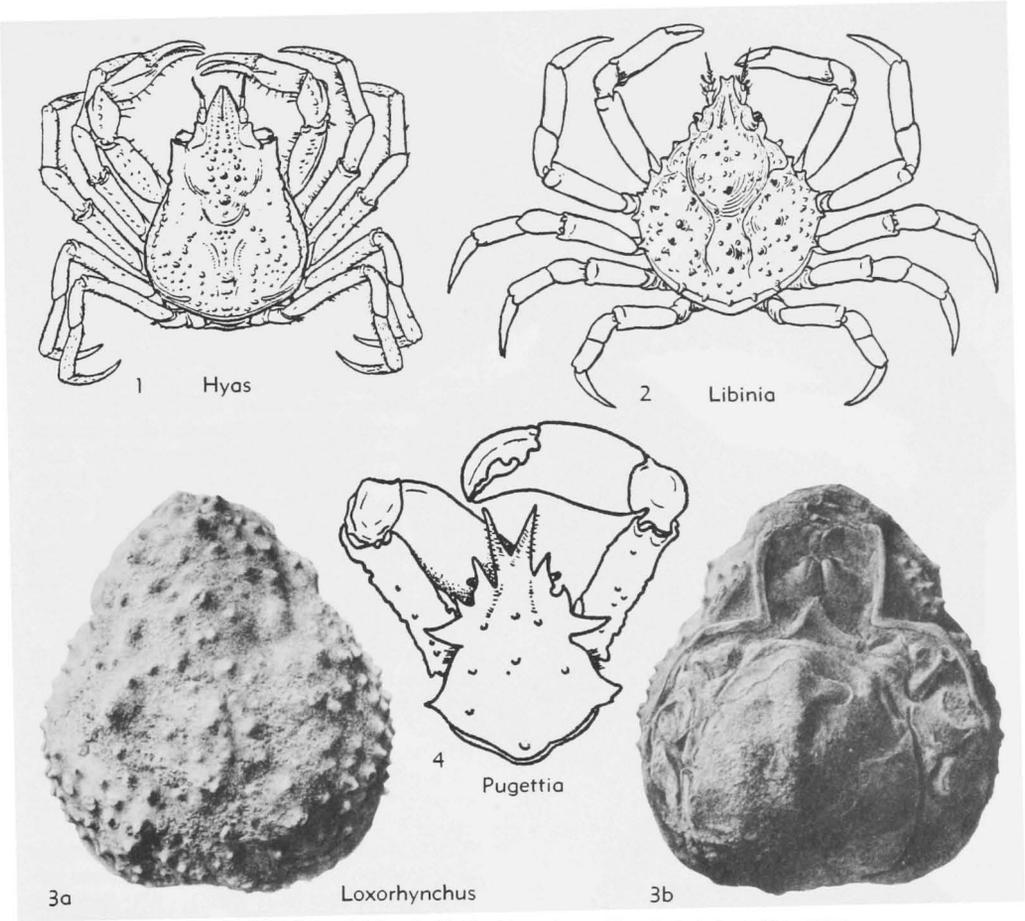


FIG. 316. Majidae (Pisinae) (1-3), (Acanthonychinae) (4) (p. R504-R505).

Scyra DANA, 1851 [**S. acutifrons*; OD]. Carapace subpyriform, with few or no spines; rostral horns flattened, sharp-pointed; orbits small, manus compressed, carinate above. *Pleist.*, N.Am.; *Rec.*, N. Pac.

Subfamily ACANTHONYCHINAE Stimpson, 1870

[*nom. transl.* ALCOCK, 1895 (ex Acanthonychidae STIMPSON, 1870)]

Carapace mostly with parallel lateral margins, without orbits, eye stalks short, rostrum simple or bifid, basal segment of antenna triangular. *Plio.-Rec.*

Acanthonyx LATREILLE, 1827 [**Maia lunulata* RISSO, 1816; OD]. Anterolateral angles prominent; all pereiopods short and strong. *Rec.*, N.Am.(E. coast-W. coast).-IndoPac.-E.Atl.-Medit.

Epialtus H. MILNE-EDWARDS, 1834 [**E. bituberculatus*; SD]. Carapace broad, oblong, smooth, with

2 lateral laminate projections on each side; rostrum broadly triangular or oblong; male chelipeds strong. *Plio.*, Fiji; *Rec.*, S.Calif. to Chile-Fla.-Brazil.

Pugettia DANA, 1851 [**P. gracilis* DANA, 1852; SD MIERS, 1879]. Carapace oblong, with 2 prominent lateral extensions, supraorbital cave forming preocular tooth; palm dilated and compressed. *Pleist.*, N.Am.; *Rec.*, N.Pac.-Ind.O.-Australia.—FIG. 316,4. *P. richii* DANA, *Rec.*; carapace and chelipeds, $\times 0.6$ (237).

Family PARTHENOPIDAE Macleay, 1838

[*nom. correct.* MIERS, 1879 (pro Parthenopina MACLEAY, 1838)] [=Lambridae ALCOCK, 1895]

Chelipeds longer and stronger than second to fifth pereiopods, with fingers short, fixed finger inflexed, dactylus curved; antennal segment short, not fused with epi-

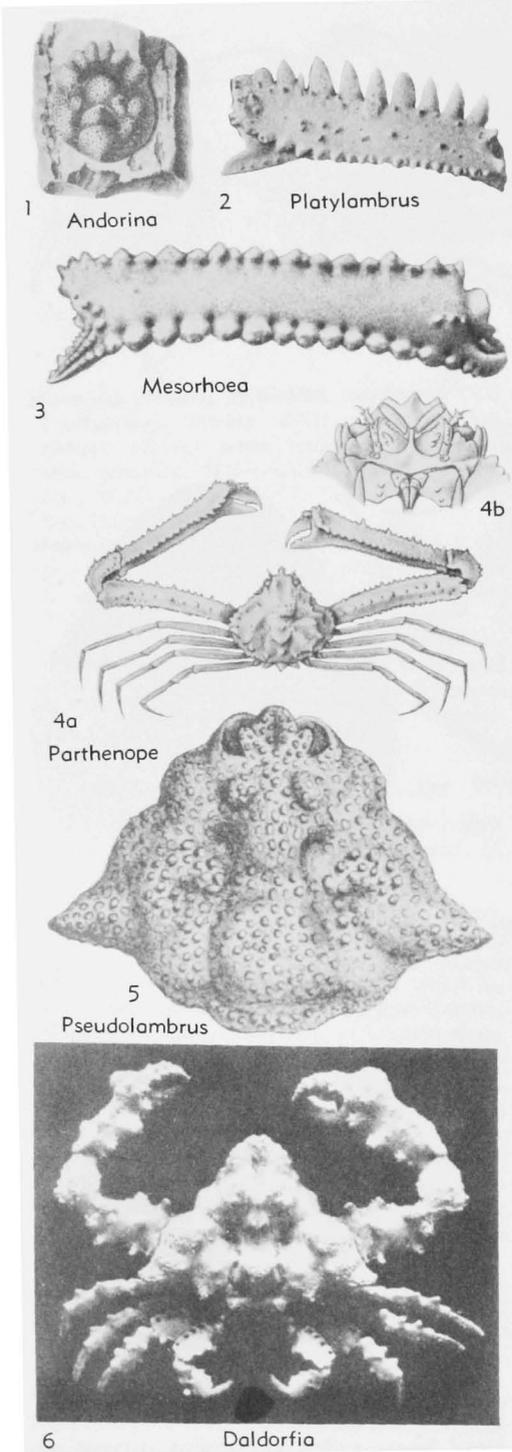


FIG. 317. Parthenopidae (Parthenopinae) (2-6); Family Uncertain (1) (p. R506, R508).

stome or front, orbits well developed. Male genital openings coxal. *Eoc.-Rec.*

Subfamily PARTHENOPINAE Macleay, 1838

[*nom. transl.* MIERS, 1879 (ex Parthenopidae MACLEAY, 1838)]

Carapace mostly triangular to pentagonal in outline, gastro-cardiac regions clearly delimited laterally, rostrum simple or obscurely trilobed, first pereiopods very long and strong. *M.Eoc.-Rec.*

Parthenope WEBER, 1795 [**Cancer longimanus* LINNÉ, 1758; SD RATHBUN, 1904] [= *Lambrus* LEACH, 1815 (obj.)]. Carapace granular, tubercular, or spiny, front short, infraorbital gap filled by 2nd segment of antennal stalk; short antennal basal segment wedged between antennular fossa and infraorbital lobe; chelipeds very long, 2nd to 5th pereiopods very short and slender. [The assignment of some fossil species to this genus and its subgenera is doubtful because of long-standing confusion between *Parthenope* and *Daldorfia* and insufficient data.] *M.Eoc.-Pleist.*, Eu.-Venezuela-Panama-W.Indies; *Rec.*, Atl.-Pac.-Medit.

P. (Parthenope). Carapace ovate-pentagonal or subcircular, surface granular or pustulate, without strong carinae, rostrum very short. *U.Eoc.-Pleist.*, Eu.-Venezuela-Panama-W.Indies; *Rec.*, Atl.-Pac.-Medit.—FIG. 317,4. *P. (P.) agonus* (STIMPSON), *Rec.*; 4a, dorsal view, $\times 1$; 4b, ventral view of anterior part, $\times 3$ (237, after A. Milne-Edwards).

P. (Platylambrus) STIMPSON, 1870 [**Lambrus crenulatus* DE SAUSSURE, 1858 (= **Lambrus serratus* MILNE-EDWARDS, 1834); SD RATHBUN, 1924]. Carapace carinate or tuberculate, broadly triangular, rostrum broad, acute, projecting; chelipeds with strongly serrate edges. ?*Mio.*, Brazil-Venezuela; *Plio.*, USA (Fla.); *Rec.*, warm seas.—FIG. 317,2. *P. (P.) charlottensis* RATHBUN, *Plio.*, Fla.; propodus of left cheliped, $\times 1$ (244).

P. (Pseudolambrus) PAULSON, 1875 [**Lambrus calappoides* ADAMS & WHITE, 1848; OD] [= *Parthenolambrus* A. MILNE-EDWARDS, 1878 (type, *Lambrus tarpeius* ADAMS & WHITE, 1850); = *Phrynotlambrus* BITTNER, 1893 (type, *P. corallinus*)]. Carapace with nearly straight posterior margin, posterolateral angles strongly produced; rostrum medially grooved, deflexed, orbits deep; chelipeds not very long, not sharply serrate, contorted. *U.Eoc.*, ?*Mio.*, Eu.; *Rec.*, IndoPac.-Australia-Atl.-C.Am.-Medit.—FIG. 317,5. **P. (P.) corallinus* (BITTNER), *U.Eoc.*, Rumania; $\times 1$ (184, after Bittner).

Daldorfia RATHBUN, 1904 [**Cancer horridus* LINNÉ, 1758; OD]. Carapace with rough surface, but not deeply grooved; basal segment of antenna strongly developed, separating base of antennula from infraorbital gap; rostrum very short, turned down-

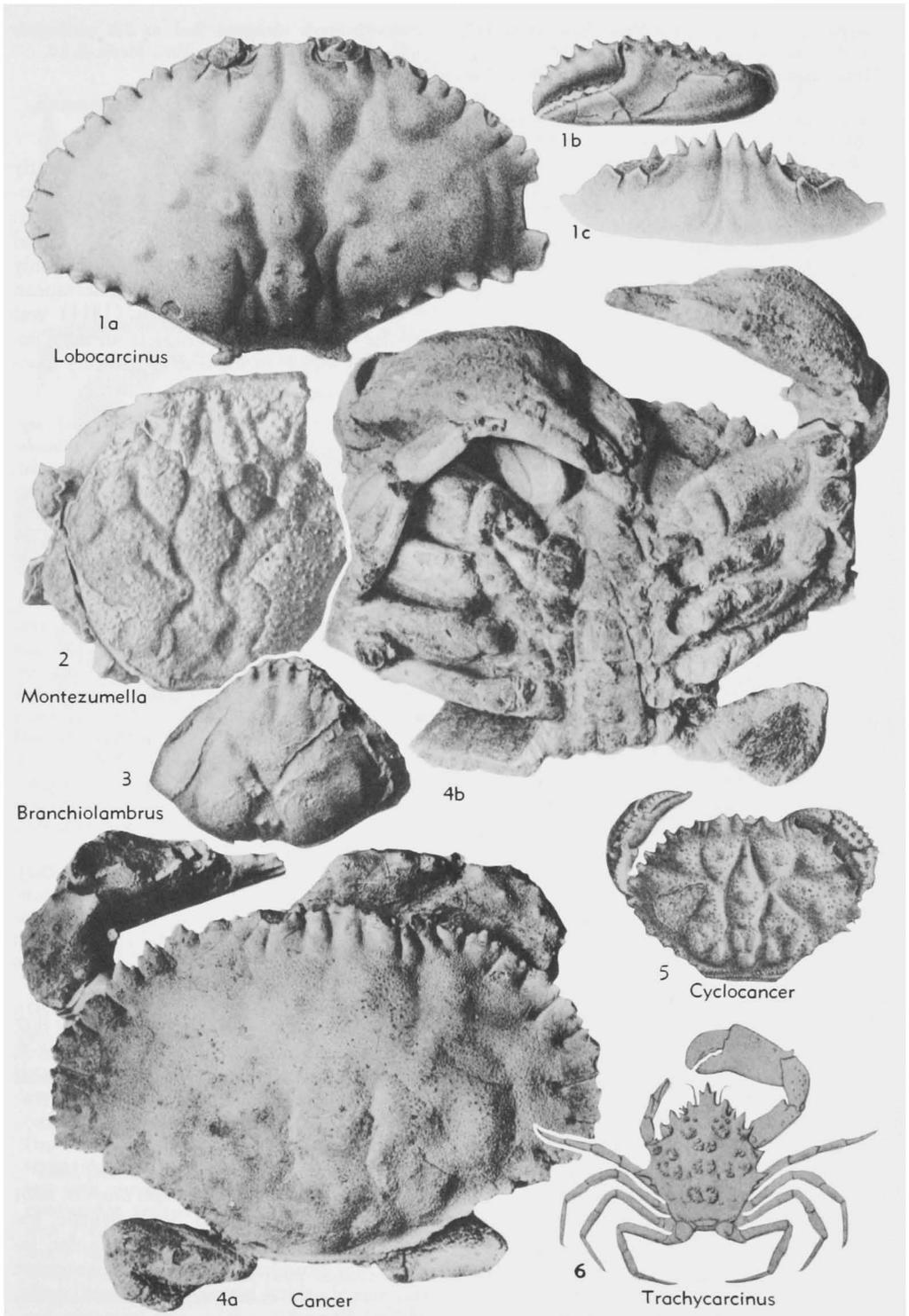


FIG. 318. Atelecyclidae (2,5-6); Cancridae (Cancrinae) (3-4), (Lobocarcininae) (1) (p. R508-R510).

ward. *Rec.*, IndoPac.-Cape Verde Is.—FIG. 317, 6. **D. horrida* (LINNÉ), male, $\times 1$ (232).

Heterocrypta STIMPSON, 1871 [**Cryptopodia granulata* GIBBES, 1850; OD]. Carapace broadly triangular but not covering legs, with posteriorly divergent dorsal and ventral granular ridges. *Pleist.*, N.Am.; *Rec.*, Atl.-Medit.-IndoPac.-N.Am. (E. coast-W. coast).

Mesorhoca STIMPSON, 1871 [**M. sexspinosa*; OD]. Carapace pentagonal, broader than long, posterior margin short, eyes very small, cheliped with very short fingers. *Oligo.*, W.Indies; *Pleist.*, N.Am., *Rec.*, N. Am. (E. coast-W. coast).—FIG. 317,3. *M. idae* RATHBUN, *Pleist.*, USA (Calif.); propodus of left cheliped, $\times 1$ (238).

Subfamily EUMEDONINAE Miers, 1879

Carapace pentagonal or rhomboidal, front two- or four-lobed, first pereopods moderately long, branchial and cardiac regions not sharply separated. *Rec.*

Eumedonus H. MILNE-EDWARDS, 1834 [**E. niger*; OD]. Carapace pentagonal, rostrum large, projecting, bifid, antennules folded obliquely, basal segment of antennal stalk partly filling infra-orbital hiatus. *Rec.*, IndoPac.

Family UNCERTAIN

Andorina LÖRENTHEY, 1901 [**A. elegans*; OD]. Carapace oval, granulate, frontal margin lobate, hepatic regions projecting, lateral and posterior margins convex. *Mio.*, Hung.—FIG. 317,1. **A. elegans*; $\times 2$ (184).

Section CANCRIDEA Latreille, 1803

[*nom. transl.* DANA, 1852 (*ex* Cancridae LATREILLE, 1802) [=Cancriformia GLAESSNER, 1929]

Carapace elongate to transversely oval, front narrow, mostly with median and lateral teeth, orbits with two supraorbital fissures; lateral margins dentate; gastric and cardiac regions not clearly separated; antennules infolded longitudinally or obliquely; male gonoducts opening on coxae. *Eoc.-Rec.*

Family CORYSTIDAE Samouelle, 1819

Carapace elongate, suboval, convex, without sharp lateral margin, front with two or three teeth, antennulae infolded longitudinally, antennae long. *Rec.*

Corystes LATREILLE, 1802 [**Hippa dentata* FABRICIUS, 1793 (= **Cancer cassivelaunus* PENNANT, 1777); OD]. Carapace convex, with convex, dentate, lateral margin, gastrocardiac regions marked,

male chelipeds elongate; 2nd to 5th pereopods with pointed short dactyls. *Rec.*, Medit.-E.Atl.

Family ATELECYCLIDAE Ortman, 1893

Carapace suboval to pentagonal, slightly elongate, front dentate, buccal frame elongate; antennulae infolded longitudinally. [Subfamilies Thiinae ALCOCK (1899) and Acanthocyclusinae ALCOCK (1899) are only Recent. The Atlantic and Mediterranean monotypic genus *Thia* LEACH (1814) was reported by RATHBUN (1945) from the Pliocene of Fiji, on insufficient evidence.] *Eoc.-Rec.*

Atelecyclus LEACH, 1814 [**Cancer (Hippa) septemdentatus* MONTAGU, 1813 (= **Cancer rotundatus* OLIVI, 1792); OD]. Carapace subcircular, lateral margins dentate, front with 3 teeth, gastrocardiac regions well marked, chelipeds strong, with longitudinal granulations externally on manus. ?*M. Eoc.*, W.Afr.; *Mio.-Pleist.*, Eu.; *Rec.*, Medit.-E. Atl.

?**Cyclocancer** BEURLEN, 1958 [**C. tuberculatus*]. Carapace transversely oval, width moderate, front and orbits small, anterolateral and anterior part of posterolateral margins lobulate; concave posterolateral and straight posterior margins with granulate ridges; regions well marked, inflated, granulate. [Transitional between *Atelecyclus* and *Cancer*, therefore the position of *Cyclocancer* in the Atelecyclidae, assigned by BEURLEN, is questionable.] *U.Oligo.* or *L.Mio.*, Brazil; *Mio.*, Eu.—FIG. 318,5. *C. szontaghi* (LÖRENTHEY), *Mio.*, Hung.; $\times 0.7$ (184).

Montezumella RATHBUN, 1930 [**M. tubulata*; OD]. Carapace elongate to subcircular, anterolateral margins dentate, front with 2 or 4 teeth, orbit tubular. *Eoc.*, Mex.-USA (Calif.)-W.Indies-Egypt-Spain; *M.Tert.*, Panama.—FIG. 318,2. **M. tubulata*, U.Eoc., USA-Mex.; $\times 1$ (242).

Trachycarcinus FAXON, 1893 [**T. corallinus*; OD]. Carapace pentagonal, convex, anterolateral margins long, dentate, front projecting, with 3 teeth, orbits large. *Mio.*, Japan; *Plio.*, Fiji; *Rec.*, Gulf Mexico-Panama-IndoPac.—FIG. 318,6. **T. corallinus*, *Rec.*; $\times 0.7$ (243, after Faxon).

Family CANCRIDAE Latreille, 1803

[*nom. correct.* DANA, 1852 (*pro* Cancrines LATREILLE, 1803)]

Carapace broadly oval, front dentate, anterolateral margins dentate, antennulae infolded longitudinally or obliquely, antennae in internal orbital hiatus, with short flagella. *M.Eoc.-Rec.*

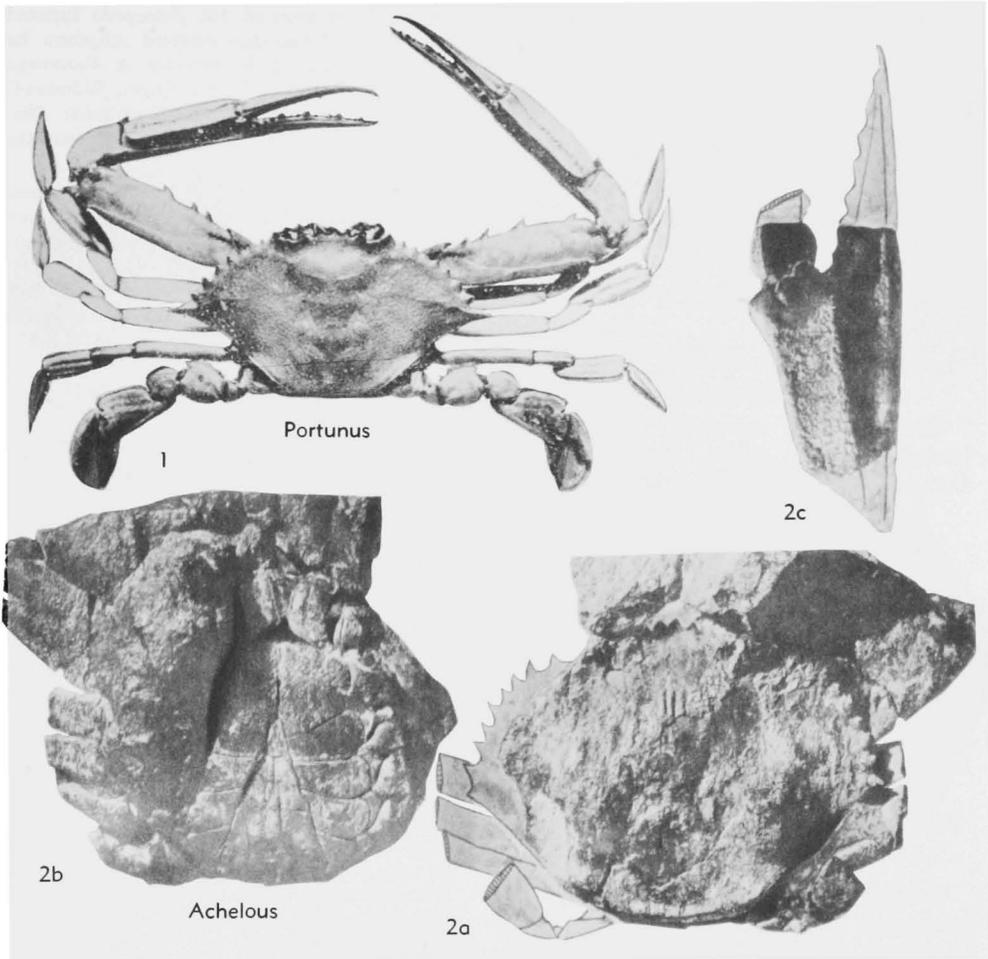


FIG. 319. Portunidae (Portuninae) (p. R510).

Subfamily CANCRINAE Latreille, 1803[*nom. transl.* ALCOCK, 1899 (*ex* Cancridae LATREILLE, 1803)]

Front with median and lateral teeth, lateral angles of carapace distinct, chelae stout. *Mio.-Rec.*

Cancer LINNÉ, 1758 [**C. pagurus*; SD LATREILLE, 1810] [= *Platycarcinus* H. MILNE-EDWARDS, 1834 (*obj.*); *Metacarcinus* A. MILNE-EDWARDS, 1862 (*type*, *Cancer magister* DANA, 1852)]. Carapace very wide, finely granulate, anterolateral margins very long, curved, with about 10 denticulate lobes; gastroducardic regions marked; orbits small, deep, with 2 fissures; front narrow, with 3 teeth, epistome narrow, chelae subequal, with 5 longitudinal blunt ridges on their outer surfaces. *Mio.-Pleist.*, Eu.-N.Afr.-Burma-Japan-N.Am.; *Rec.*, cold and temperate seas.—FIG. 318,4. *C. deshayesi*

A. MILNE-EDWARDS, *Mio.*, Spain; 4*a,b*, dorsal, ventral, $\times 0.7$ (297).

Branchiolambrus RATHBUN, 1909 [**B. altus*; OD]. Carapace rhomboidal, with widely divergent, straight, dentate anterolateral margins; posterolateral margins sinuous; branchial regions nearly touching medially. *Mio.*, USA (Calif.).—FIG. 318,3. **B. altus*; dorsal view of carapace, $\times 1.5$ (238).

Parapirimela VAN STRAELEN, 1937 [**P. angolensis*; OD]. Carapace wider than long, front with median and 2 lateral teeth, orbits large and deep, anterolateral margin with 4 teeth, regions well marked, chelae stout. *Mio.*, W.Afr.

Subfamily LOBOCARCININAE Beurlen, 1930[*nom. transl.* GLAESSNER, *herein* (*ex* Lobocarcinidae BEURLEN, 1930)]

Front with four to six teeth, carapace very wide, with lobulate and dentate anterolateral and dentate posterolateral margins, with oblique posterolateral projections, chelae elongate. *M.Eoc.-U.Eoc.*

Lobocarcinus REUSS, 1857 [**Cancer paulinowurtembergensis* VON MEYER, 1847; OD]. Characters of subfamily. *M.Eoc.-U.Eoc.*, Egypt-Eu.-India.—FIG. 318, 1. **L. paulinowurtembergensis* (VON MEYER), Egypt; 1a, dorsal view, $\times 0.7$; 1b, chela, $\times 0.7$; 1c, fronto-orbital margin, $\times 1$ (198).

Section BRACHYRHYNCHA Borradaile, 1907

Carapace wide anteriorly, without projecting rostrum; orbits mostly complete. *Cret.-Rec.*

Superfamily PORTUNOIDEA Rafinesque, 1815

[*nom. transl.* GLAESSNER, herein (ex Portunidae RAFINESQUE, 1815)] [=subtribe Portunoidea BEURLÉN, 1930]

Carapace flat, square or oval, with front narrow or wide, dentate or lobed; surface mostly with transverse ridges; chelae ridged; fifth pereopods flattened, commonly with oval dactylus. *U.Cret.-Rec.*

Family PORTUNIDAE Rafinesque, 1815

[*nom. correct.* DANA, 1852 (pro family Portunidia RAFINESQUE, 1815)]

Carapace broad and flat, greatest width commonly marked by lateral spine; front dentate or lobate, orbits and eye stalks moderately large or elongate, anterolateral margin dentate; antennules infolded obliquely or transversely, fifth pereopods mostly flattened, with leaf-shaped dactylus. *Eoc.-Rec.*

Subfamily PORTUNINAE Rafinesque, 1815

[*nom. transl.* ALCOCK, 1899 (ex Portunidae RAFINESQUE, 1815)]

Carapace broad, anterolateral margin with up to nine teeth, chelipeds very long, fifth pereopods flattened, paddle-shaped. *Eoc.-Rec.*

Portunus WEBER, 1795 [**Cancer pelagicus* LINNÉ, 1758; SD RATHBUN, 1926 (ICZN Opinion 394, v. 12, no. 17, p. 315-316, 1956)] [= *Lupa* LEACH, 1814 (obj.); *Neptunus* DE HAAN, 1833 (obj.)]. Carapace usually very broad, front with 3 to 6 teeth, anterolateral margin mostly with 9 teeth, basal antennal segment very short, chelipeds with dentate merus, carpus and propodus and costate

palms; all segments of 5th pereopods flattened. [The value of currently accepted subgenera has been questioned by STEPHENSON & CAMPBELL, 1959.] *Eoc.-Mio.*, Eu.-Egypt; *Oligo.*, W.Indies-C. Am.; *Mio.*, ?Brazil-E.Afr.-Java-India; *Plio.-Pleist.*, IndoPac.; *Rec.*, all warm and temperate seas.

P. (Portunus). Carapace wide, anterolateral margin approximating arc of circle with center near posterior margin; lateral spine long, produced laterally. *Eoc.-Mio.*, Eu.-Egypt-W.Afr.; *Oligo.*, W.Indies-C.Am.; *L.Mio.*, ?Brazil-E.Afr.-Java; *Pleist.*, IndoPac.; *Rec.*, all warm and temperate seas.—FIG. 319, 1. **P. (P.) pelagicus* (LINNÉ), *Rec.*, S.Australia, $\times 0.25$ (139).

P. (Achelus) DE HAAN, 1833 [**Portunus spinimanus* LATREILLE, 1819; OD]. Carapace relatively narrow, anterolateral margins approaching arc of circle with center near center of cardiac region; lateral tooth not much larger than others. [This subgenus is based on a Recent American species. Indo-Pacific species are distinguished by the antero-external angle of the merus of 3rd maxillipeds being strongly produced laterally and are now mostly placed in *Cycloachelous* WARD (1942). Fossil species from *Oligo-Mio.* of Eu.-Iran require re-examination; others belong to *Scylla*.] *Oligo.*, W.Indies; *Pleist.*, N.Am.; *Rec.*, N. Am. coasts-Galapagos-?IndoPac.—FIG. 319, 2. *P. (Achelus) withersi* GLAESSNER, *Mio.*, Iran; 2a, b, dorsal, ventral, $\times 0.7$; 2c, right chela, $\times 0.7$ (113).

P. (Lupocycloporus) ALCOCK, 1899; **P. (Monomia)** GISTEL, 1848 (= *Amphitrite* DE HAAN, 1833, non A. MUELLER, 1771); **P. (Xiphonectes)** A. MILNE-EDWARDS, 1873 (= *Hellenus* A. MILNE-EDWARDS, 1879), are all *Rec.* subgenera not known as fossils.

Callinectes STIMPSON, 1860 [**C. sapidus* RATHBUN, 1896; SD RATHBUN, 1896]. Differs from *Portunus* in T-shaped male abdomen; front with 2 or 4 teeth; manus of cheliped with 5 external costae and no more than 2 spines. *Eoc.-Mio.*, Brazil-C. Am.-W.Indies; *Pleist.*, N.Am.; *Rec.*, C.Am.-W. Afr.-IndoPac.

Charybdis DE HAAN, 1833 [**Cancer feriatus* LINNÉ, 1758 (= *C. sexdentatus* HERBST, 1783); SD GLAESSNER, 1929] [= *Goniosoma* A. MILNE-EDWARDS, 1860 (obj.)]. Carapace hexagonal, with transverse granular ridges, front with about 6 lobes or teeth, anterolateral margins with 5 to 7 teeth, usually 6; chelipeds long and massive, spinose, propodus costate. *Oligo.*, Eu.; *Mio.*, Arabia; *Plio.-Rec.*, IndoPac.

Colneptunus LÖRENTHEY, 1929 [**Neptunus hungaricus* LÖRENTHEY, 1898; SD GLAESSNER, herein] [= *Allogoneplax* VAN STRAELEN, 1930 (*nom. nud.*), 1934 (type, *A. dallonii*); *Gonioneptunites* VIA, 1959 (obj.)]. Carapace subhexagonal, wider

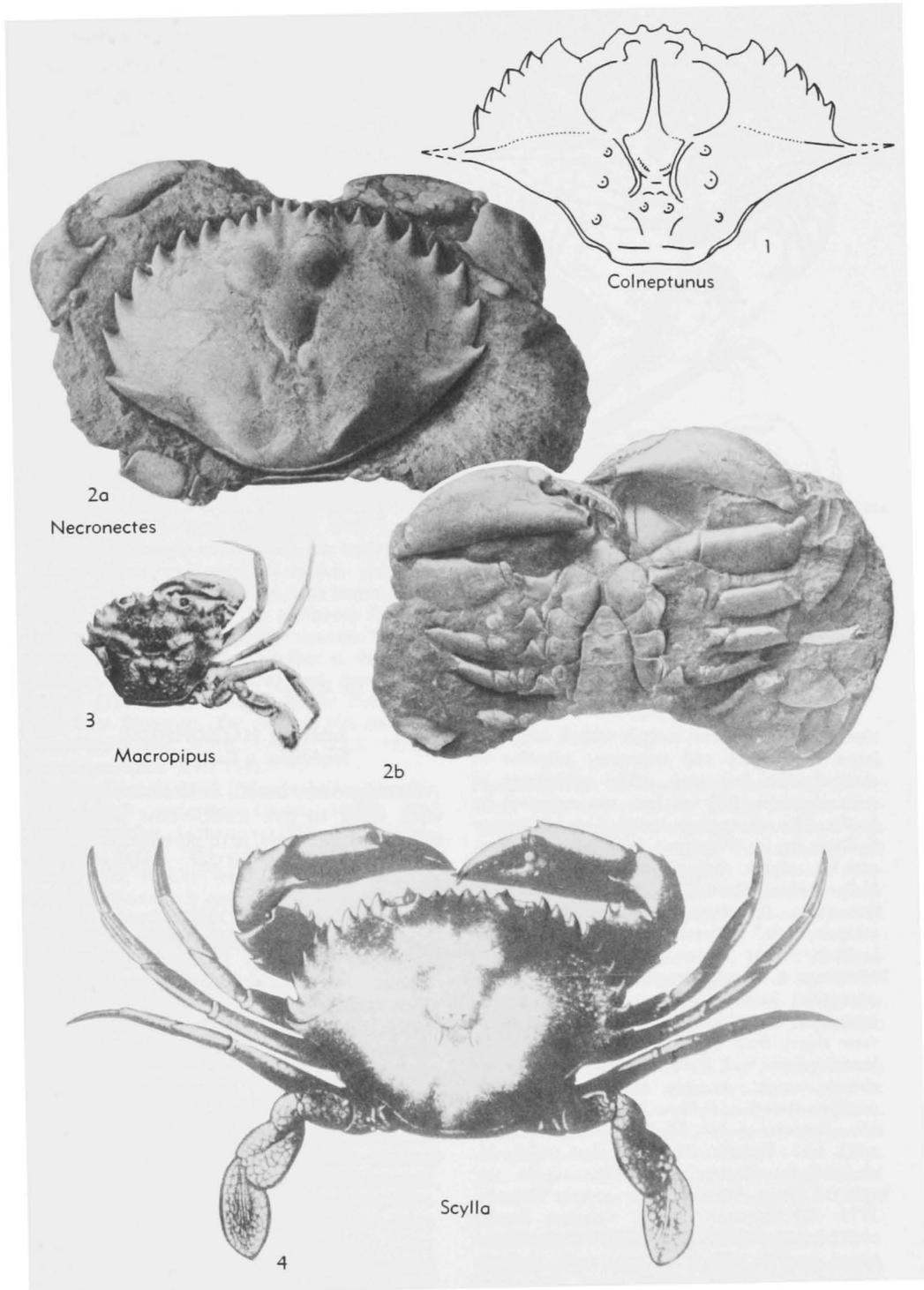


FIG. 320. Portunidae (Portuninae) (1-2,4), (Macropipinae) (3) (p. R510, R512).

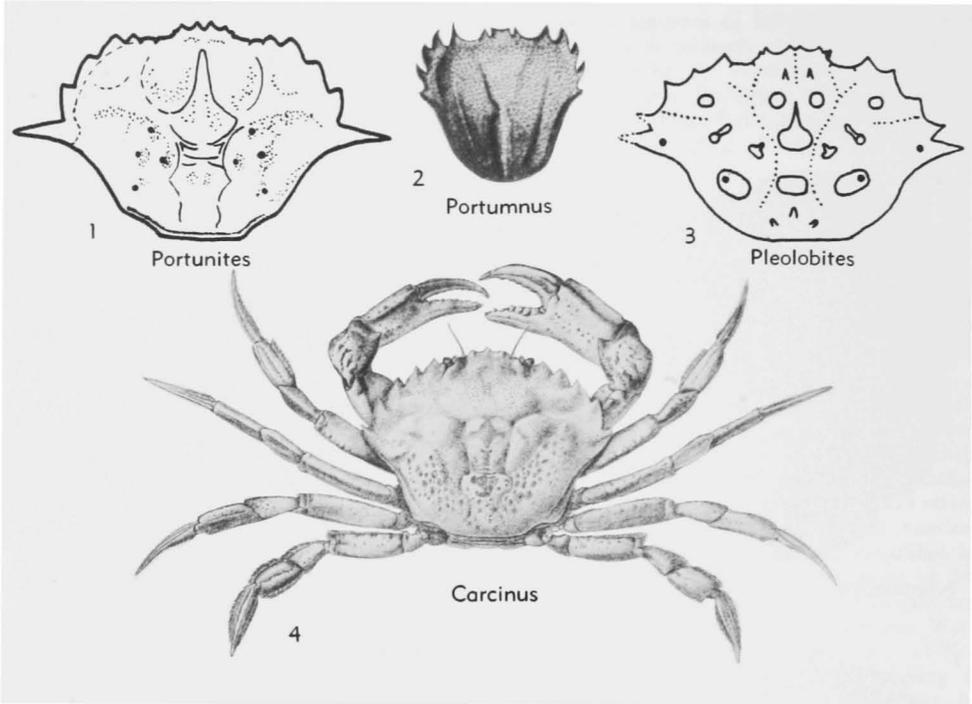


FIG. 321. Portunidae (Carcininae) (p. R513).

than long, anterolateral margin with 6 teeth, last larger than others and transverse; propodus of cheliped with few keels. [The adjustment of nomenclature carried out here was suggested by L. VIA. The other species included by LÖRENTHEY & BEURLEN in "*Neptunus (Colneptunus)*" cannot be reliably distinguished from *Portunus*.] *M.Eoc.*, Hung.-Spain-W.Afr.—FIG. 320,1. **C. hungaricus* (LÖRENTHEY), Spain; diagram of carapace, $\times 0.7$ (Glaessner, n, from photos by L. VIA).

Necronectes A. MILNE-EDWARDS, 1881 [**N. vidalianus*; OD] [= *Gatunia* RATHBUN, 1919 (type, *G. proavita*)]. Carapace broadly oval, without transverse ridges, front dentate, orbits narrow, anterolateral margins with 8 teeth, posterolateral margins almost straight, strongly convergent; chelipeds massive, smooth. ?*U.Eoc.*, *M.Oligo.*, *Mio.*, Eu.; *Mio.*, Panama.—FIG. 320,2. *N. proavitus* (RATHBUN), *Mio.*, Panama; 2a, dorsal view, $\times 0.5$; 2b, chelipeds, frontal view, $\times 0.5$ (235).

Scylla DE HAAN, 1833 [**Cancer serratus* FORSKÅL, 1775; SD RATHBUN, 1922]. Carapace broadly oval, almost smooth. Front with 4 teeth, anterolateral margins with 9 subequal teeth, chelipeds massive, with spines, without costae. *Eoc.*, Java-Eu.; *Oligo.*, Eu.-?W.Indies; *Mio.*, Eu.-Madag.-India; *Pleist.*, *Rec.*, IndoPac.—FIG. 320,4. **S. serrata* (FORSKÅL), *Rec.*; $\times 0.5$ (198).

Subfamily MACROPIPINAE Stephenson & Campbell, 1960

Carapace not broad, anterolateral margin with three to five teeth, some pereiopods as long as chelipeds, fifth pereiopods paddle-shaped. *Oligo.-Rec.* [See Addendum, p. R627.]

Macropipus PRESTANDREA, 1833 [**Portunus macropipus* PRESTANDREA, 1833; OD] [= *Portunus* FABRICIUS, 1798 (non WEBER, 1795)] [ICZN Opinion 394]; *Liocarcinus* STIMPSON & POURTALÉS, 1870 (type, *Portunus holsatus* FABRICIUS, 1798; OD)]. Carapace with transverse striations, front simple or 3-lobed, anterolateral margin with 5 teeth, chelae with 5 longitudinal costae on external surface of propodus. *Oligo.-Pleist.*, Eu.; *Mio.*, Celebes; *Rec.*, E.Atl.-Medit.-IndoPac.—FIG. 320,3. *M. depurator* (LINNÉ), *Rec.*; $\times 0.5$ (52).

Ovalipes RATHBUN, 1898 [**Cancer ocellatus* HERBST, 1799; OD] [= *Platyonichus* LATREILLE, 1825 (non LATREILLE, 1818); *Anisopus* DE HAAN, 1833 (non MEIGEN, 1803); *Aenaeacancer* WARD, 1933 (type, *A. molleri*; OD)]. Carapace little broader than long, front with 3 or 4 teeth, anterolateral margins with 5 subequal teeth, chelipeds keeled, granulated and spinose, dactylus of 5th pereiopods oval. *Plio.-Pleist.*, N.Z.; *Rec.*, N.Am. (E. coast)-IndoPac.-N.Z.-Australia.

Subfamily CARCININAE Macleay, 1838

Carapace not very broad, with four or five anterolateral teeth; basal segment of antenna fixed, elongate, in longitudinal position; chelae not much elongated; second to fifth pereopods similar, rather stout, fifth pereopods with lanceolate dactylus. *L. Eoc.-Rec.*

Carcinus LEACH, 1814 [**Cancer maenas* LINNÉ, 1758; OD] [= *Carcinides* RATHBUN, 1897 (type, *C. maenas*) (non *Carcinus* LATREILLE, 1796) (on official list, ICZN)]. Carapace hexagonal, broader than long, regions well defined, no transverse ridges; front 3-lobed; 1 supraorbital notch, 5 anterolateral teeth; chelipeds massive, slightly heterochelous; abdominal terga 3 to 5 fused. *Eoc.*, USA (Wash.); *Mio.-Plio.*, Eu.; *Rec.*, N.Am.(coasts)-S. Am.(coasts)-Eu.-S. Afr.-E. Asia-Australia-N. Z. —FIG. 321,4. **C. maenas* (LINNÉ), *Rec.*; $\times 0.5$ (243).

?**Pleolobites** REMY, 1960 [**P. erinaceus*; OD]. Carapace broader than long, front with 4 teeth, anterolateral margin with 5 teeth, last most prominent; regions well marked, surface granulate; chelipeds slightly heterochelous, with longitudinally keeled propodus; 2nd to 5th pereopods flattened, said to be without "palette nataoire." [This monotypic genus is said to be close to the Recent *Bathynectes* STIMPSON (1871) and *Parathranites* MIERS (1886), but it seems hardly distinguishable from *Portunites*. The carapace also resembles *Xanthilites*.] *Eoc.*, W.Afr. —FIG. 321,3. **P. erinaceus*; carapace, $\times 0.7$ (48).

Portumnus LEACH, 1814 [**Cancer latipes* PENNANT, 1777 (= *P. variegatus* LEACH, 1815); OD] [= *Platyonichus* LATREILLE, 1818 (obj.); *Platyonychus* VOIGT, 1836 (*nom. van.*)]. Carapace elongate or slightly wider than long, front 3-lobed, projecting, 5 anterolateral teeth, male abdomen narrow. *Mio.*, Hung.; *Rec.*, Eu.-Azores. —FIG. 321,2. *P. tricarinatus* LÖRENTHEY, *Mio.*, Hung.; carapace with incompletely preserved rostrum, $\times 1$ (184).

Portunites BELL, 1858 [**P. incertus*; OD] [= *Leiochilus* REUSS, 1859 (type, *L. morrissi*)]. Carapace hexagonal, not much broader than long, front with 4 teeth, anterolateral margin with 4 or 5 teeth, last one longest, posterolateral margin straight or slightly concave; gastroducardiac regions well marked; arcuate ridge extending from lateral teeth to their sides; 5th pereopods not flattened. *Eoc.*, Eu.-N.Am.-N.Z.; *Oligo.*, N.Am.; *Mio.*, Japan-Chile. —FIG. 321,1. *P. grimaldifer* GLAESSNER, *Eoc.*, N.Z.; carapace (reconstr.), $\times 0.7$ (118).

Subfamily PSAMMOCARCININAE Beurlen, 1930

Carapace subhexagonal, with anterolateral teeth, last being greatly elongated and modified. *L.Eoc.-L.Oligo.*

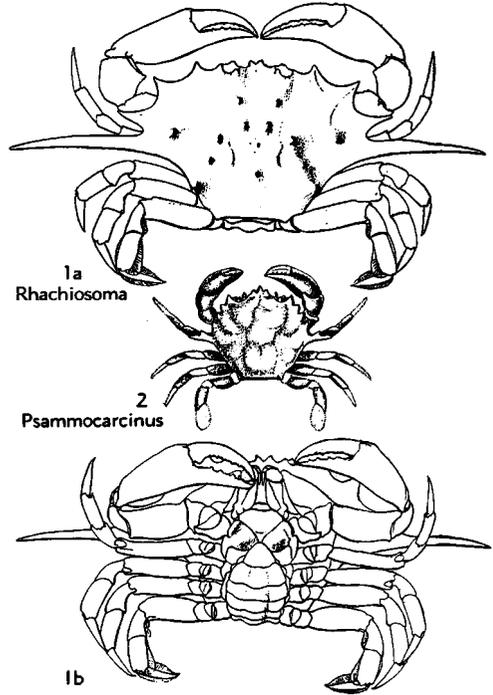


FIG. 322. Portunidae (Psammocarcininae) (p. R513).

Psammocarcinus A. MILNE-EDWARDS, 1860 [**Portunus hericarti* DESMAREST, 1822]. Carapace hexagonal, length equal to width, 5 anterolateral teeth including large lateral spine with accessory anterior denticle; 5th pereopods compressed. *Eoc.-L.Oligo.*, Eu. —FIG. 322,2. **P. hericarti* (DESMAREST), *Eoc.*, Fr.; carapace (reconstr.), $\times 1$ (196).

Enoplnotus A. MILNE-EDWARDS, 1860 [**E. armatus*; OD]. Carapace with greatly elongated lateral spines bearing sawlike denticles on anterior edge. *M.Eoc.*, N.Italy. —FIG. 323,2. **E. armatus*; dorsal, $\times 1$ (196).

Rhachiosoma WOODWARD, 1871 [**R. bispinosum*; SD]. Carapace much wider than long, with 2 or 3 anterolateral and long, pointed, lateral spines, with or without accessory denticles; surface of carapace tuberculate. *L.Eoc.*, Eng. —FIG. 322,1. **R. bispinosum*, S.Eng.; 1a,b, dorsal and ventral views of carapace (\varnothing) (reconstr.), $\times 0.5$ (330).

Subfamily PODOPHTHALMINAE Miers, 1886

Front very narrow, T-shaped, orbits very long, occupying entire anterior border of carapace. Chelipeds elongate. *Oligo.-Rec.*

Podophthalmus LAMARCK, 1801 [**P. spinosus*

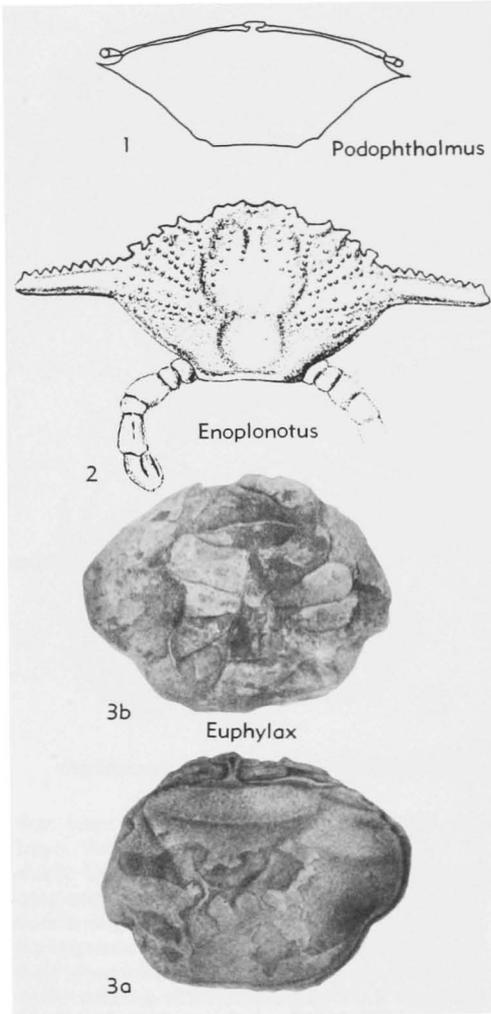


FIG 323. Portunidae (Psammocarininae) (2), (Podophthalminae) (1-3) (p. R513-R514).

(=*Portunus vigil* FABRICIUS, 1798; OD)]. Length of carapace less than 0.5 of width, with strong extraorbital spine directed outward and followed by smaller tooth on strongly converging lateral margins. *Pleist.-Rec.*, IndoPac.—FIG. 323, 1. **P. vigil* (FABRICIUS), *Rec.*, Australia; outline of carapace and eyestalks, $\times 0.5$ (after 379a).

Euphyllax STIMPSON, 1860 [*E. dovii*; OD]. Carapace transversely oval, with short, dentate, anterolateral margins and longer, straight, posterolateral margins. *Oligo.*, W.Indies; *U.Oligo.-L.Mio.*, Brazil-Panama; *Rec.*, C.Am.—FIG. 323, 3. *E. callinectias* RATHBUN, *Mio.*, Panama; 3a,b, dorsal, ventral, $\times 0.7$ (235).

Family CARCINERETIDAE Beurlen, 1930

Carapace square or transversely extended, flat to convex longitudinally, with straight lateral margins converging posteriorly, supraorbital margin long, ending in forward pointing spines; regions well marked by grooves and transverse ridges. *U.Cret.*

Carcineretes WITHERS, 1922 [*C. woolacotti*; OD]. Supraorbital margins with 2 fissures, front deflected, protogastric lobes with transverse ridge; sternal plate narrow. Chelipeds massive, heterochelous, with keels on upper and lower edges of propodus; 5th pereopods with flattened propodus and oval dactylus. *U.Cret.*, Jamaica.—FIG. 324, 3. **C. woolacotti*; dorsal, $\times 1.6$ (319).

Cancrixantho VAN STRAELEN, 1934 [*C. pyrenaiacus*; OD] [= *Cancrixantho* VAN STRAELEN, 1930 (*nom. nud.*)]. Carapace rectangular, wider than long; front very narrow, spiniform; orbits and eye stalks very long; supraorbital margin divided into 3 lobes; proto- and mesogastric regions large, clearly marked; transverse ridges on both and also on epi-, meso-, and metabranchial regions, former 2 ridges directed posterolaterally on either side; differing from *Carcineretes* in narrow front and distinct mesogastric region, from *Lithophylax* in supraorbital lobes and smoother anterolateral carapace surface. *U.Cret.(Campan.)*, Spain.—FIG. 325, 1. **C. pyrenaiacus*; carapace and eye stalks, $\times 2.5$ (Via in 17).

?**Lithophylax** A. MILNE-EDWARDS & BROCCHI, 1879 [*L. trigeri*; OD] [= *Petrocarcinus* GUILLIER, 1886 (*obj.*)]. Carapace subhexagonal, width almost twice length, with transverse ridges on protogastric, cardiac and mesobranchial regions; front very narrow, orbits very long, sternal plate subcircular, chelae long and keeled; pereopods long and strong. [VAN STRAELEN (1936) proposed a monotypic family Lithophylacidae but on present evidence the only distinctive character of *Lithophylax* are its wide carapace and narrow front, comparable with the distinction of Podophthalminae among Portunidae.] *U.Cret.(Cenoman.)*, Fr.

Ophthalmoplax RATHBUN, 1935 [*O. stephensoni*; OD]. Carapace square, front about 0.25 of anterior margin, with median fissure, orbits long, with supraorbital fissure and prominent extraorbital spine; few lateral spines; dorsal surface with transverse ridges and tubercles; chelipeds with spinous keels; 5th pereopods with flat and wide propodus and dactylus (portunoid). *U.Cret.(Maastricht.)*, USA(Gulf Coast)-Brazil.—FIG. 324, 1. **O. stephensoni*, USA(Tex.); carapace, $\times 0.4$ (284).

Woodbinax STENZEL, 1953 [*W. texanus*; OD]. Front with 4 teeth, equal in width to orbits;

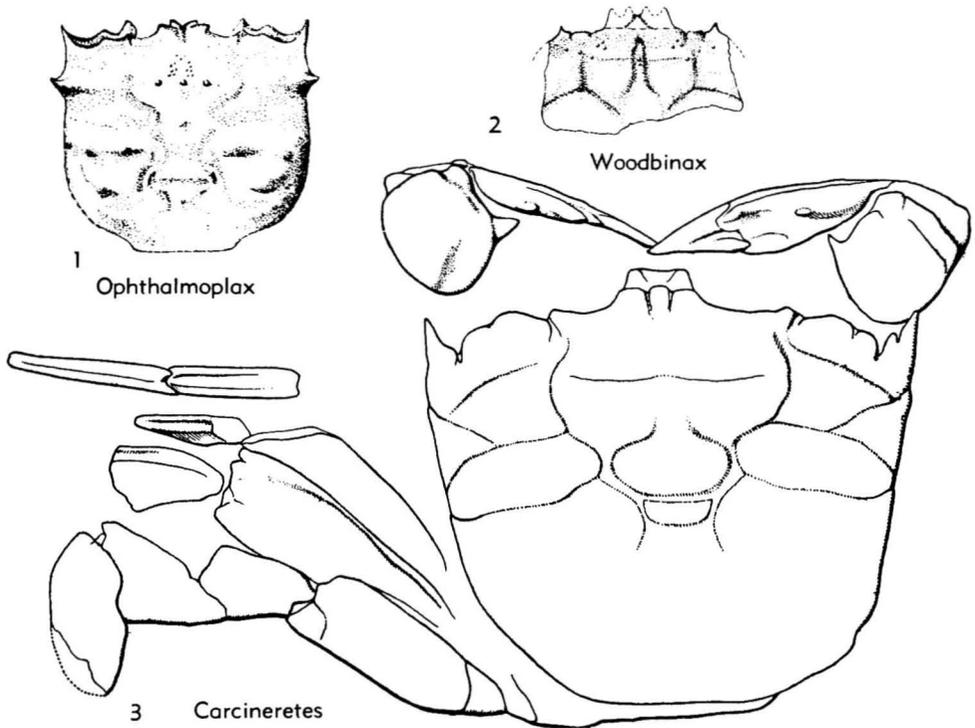


FIG. 324. Carcineretidae (p. R514-R515).

regions well marked, protogastric region with transverse ridge. *U.Cret.(Cenoman.)*, USA(Tex.). —FIG. 324,2. **W. texanus*; anteromedian part of carapace, $\times 1.2$ (284).

recently BALSS (1957), who also placed in them some fossil genera, following BEURLEN (1930). It is generally recognized that definitions of these subfamilies are not satisfactory, particularly for the placing of extinct genera on which further studies are required.] *U.Cret.-Rec.*

Superfamily XANTHOIDEA
Dana, 1851

[*nom. transl.* BEURLEN, 1930 (*ex* Xanthidae DANA, 1851)]

Carapace transversely oval or square; front wide, notched; orbits well developed, margin commonly dentate; antennules infolded obliquely or transversely; antennal flagella short; second to fifth pereiopods ambulatory, male gonoducts opening on coxae or sternum. *U.Cret.-Rec.*

Family XANTHIDAE Dana, 1851

Carapace almost invariably broader than long, transversely oval, hexagonal, subrectangular, rarely subcircular, anterior margin of buccal frame not covered by third maxillipeds; male genital openings coxal. [Many authors have attempted to divide this large family into subfamilies, most

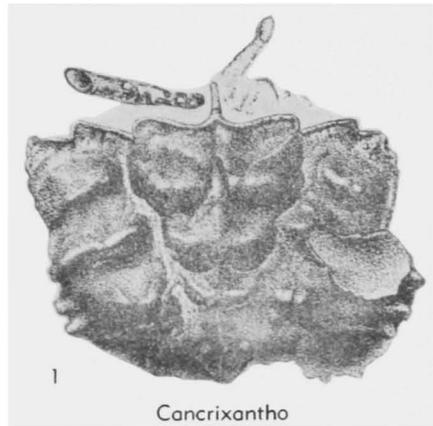


FIG. 325. Carcineretidae (p. R514).

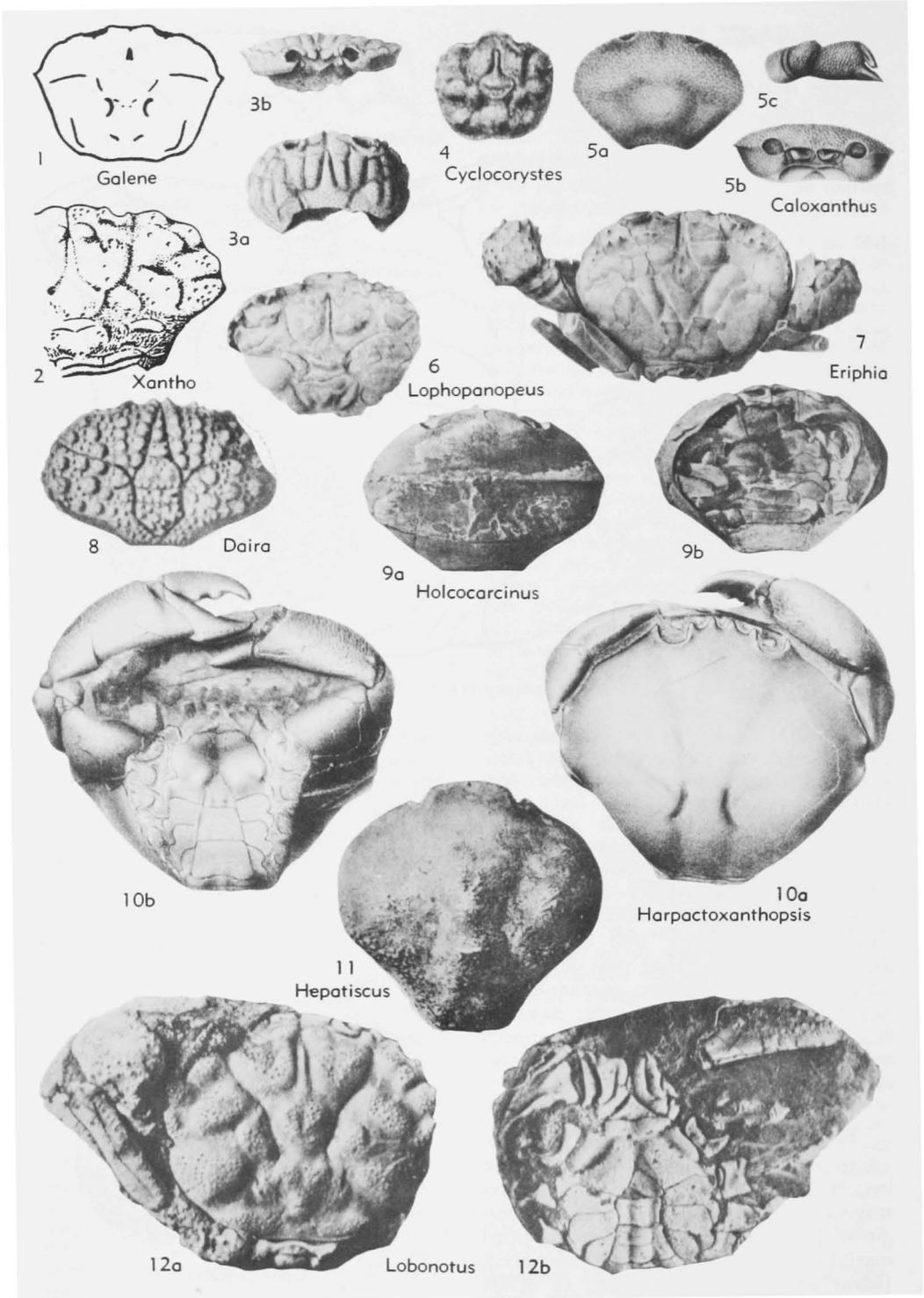


FIG. 326. Xanthidae (p. R517-R518, R520).

- Xantho** LEACH, 1804 [**Cancer incisus* (= *C. floridus* MONTAGU, 1808); OD]. Carapace broad, moderately convex anteriorly, flat posteriorly, regions well defined, anterolateral margin lobed or dentate, posterolateral margin not strongly concave, fronto-orbital width not more than 0.5 of carapace width; male abdomen with 2nd to 5th somites fused. *Mio.-Pleist.*, Eu.-Fiji; *Rec.*, IndoPac.-Medit.-E.Atl.—FIG. 326,2. *X. impressus* (LAMARCK), *Rec.*; right half of carapace, $\times 0.7$ (15).
- Actaea** DE HAAN, 1833 [**Cancer (Actaea) granulatus* (non *C. granulatus* LINNÉ, 1758) (= **C. savignyi* H. MILNE-EDWARDS, 1834); SD RATHBUN, 1922]. Carapace convex, transversely oval, regions well marked, granulate, anterolateral margin usually shallowly 4-lobed, posterolateral margin usually concave, chelipeds isochelous. ?*Pleist.*, Iran; *Rec.*, cosmop. in warm seas.—FIG. 326,3. *A. persica* A. MILNE-EDWARDS, ?*Pleist.*, Iran; *3a,b*, dorsal, frontal, $\times 0.7$ (198).
- Atergatis** DE HAAN, 1833 [**Cancer integerrimus* LAMARCK, 1818]. Carapace wider than long, smooth, with smooth marginal ridge; orbits small, front wide. *Oligo.*, Fr.; *Plio.-Rec.*, IndoPac.
- Caloxanthus** A. MILNE-EDWARDS, 1864 [**C. formosus* A. MILNE-EDWARDS, 1863; OD] [= *Carpiliopsis* FISCHER-BENZON, 1866 (type, *C. ornata*); *Creticarcinus* WITHERS, 1928 (type, *C. purleyensis*)]. Carapace wide, convex, anterior margin entire, smoothly convex; front wide, steeply sloping, straight; orbits rounded, without supra-orbital fissures, lateral angles rounded, entire surface of carapace and chelipeds granulated. *U.Cret.* (*Cenoman.-Santon.*), Fr.-Eng.; *Paleoc.* (*Dan.*), Denm.—FIG. 326,5. **C. formosus* A. MILNE-EDWARDS, *Cenoman.*, Fr.; *5a,b*, dorsal, frontal, $\times 2$; *5c*, cheliped, $\times 2$ (198).
- Carpilius** DESMAREST, 1823 [**Cancer maculatus* LINNÉ, 1758; OD]. Carapace broadly oval, convex, smooth, anterolateral margin entire, ending in lateral blunt tooth; front 4-lobed, chelipeds massive, heterochelous, with large blunt tooth on fixed finger of larger chela. *Mio.*, Eu.; *Rec.*, IndoPac.
- Carpilodes** DANA, 1851 [**C. tristis* DANA, 1852; SD]. Carapace very broad, convex, regions well marked; anterolateral margins with 4 rounded lobes; front deflexed, slightly notched medially; orbits small; posterior margin narrow; chelipeds equal or subequal; male abdominal somites 3 to 5 fused. *Plio.*, Fiji; *Rec.*, IndoPac.-C.Am. (E. coast-W. coast).
- Chlinocephalus** RISTORI, 1886 [**C. demissifrons*; OD]. Carapace slightly wider than long, front wide, projecting, orbits large, placed at anterolateral angles, main regions delimited by shallow grooves; with 2 parallel transverse ridges, one across middle and other across cardiac region; male abdomen with 7 somites. *Plio.*, Italy.
- Chlorodiella** RATHBUN, 1897 [*nom. subst. pro Chlorodius* H. MILNE-EDWARDS, 1834 (*nom. van.*) (non *Clorodius* LEACH in DESMAREST, 1823)] (non *Chlorodius* RUEFFEL, 1830; nec AGASSIZ, 1846) [**Cancer niger* FORSKÅL, 1775; OD]. Carapace depressed, hexagonal, regions faintly or not demarcated; front broad, anterolateral margin 4-lobed; chelae heterochelous, finger tips spooned. *Mio.*, Java-Fiji; *Rec.*, IndoPac.-W.Indies.
- Cyclocorystes** BELL, 1858 [**C. pulchellus*] [= *Necrozius* A. MILNE-EDWARDS, 1863 (type, *N. bow-erbankii*)]. Carapace small, subcircular, front projecting, horizontal, wide, wavy; orbits round, without fissures; anterolateral margin with few small teeth; regions well marked, granulate. *L. Eoc.*, Eng.—FIG. 326,4. **C. pulchellus*; carapace, $\times 1$ (19).
- Cycloxanthops** RATHBUN, 1897 [*nom. subst. pro Cycloxanthus* A. MILNE-EDWARDS, 1863 (non H. MILNE-EDWARDS, 1850)] [**Xantho sexdecim-dentatus* A. MILNE-EDWARDS & LUCAS, 1844; OD]. Carapace ovoid, front horizontal, prominent, medially notched; orbits small; anterolateral borders long, curved, with denticulation extending far backward; chelipeds moderately heterochelous, fingers pointed. *Plio.*, Fiji; *Pleist.*, N.Am.; *Rec.*, IndoPac.-N.Am. (W. coast).
- Daira** DE HAAN, 1833 [**Cancer perlatus* HERBST, 1790; OD] [= *Phymatocarcinus* REUSS, 1871 (type, *P. speciosus*)]. Carapace broad, convex, regions well delimited and subdivided; anterolateral margins strongly arched, crenulated; posterolateral margins concave, short; front deflexed, 2-lobed; orbital margin thickened, chelae heterochelous, finger tips blunt, hollowed. *U.Eoc.-Mio.*, Eu., *Plio.*, Fiji; *Rec.*, IndoPac.-C.Am. (W. coast).—FIG. 326,8. *D. speciosa* (REUSS), *Mio.*, Hung.; $\times 1$ (184).
- Eriphia** LATREILLE, 1817 [**Cancer spinifrons* HERBST, 1785 (= **Cancer verrucosus* FORSKÅL, 1775); SD H. MILNE-EDWARDS, 1837]. Carapace subquadrilateral, not highly convex, only gastric region well defined; lateral margins convex, fronto-orbital margin wide, front deflexed, in contact with infraorbital lobe, closing orbit; chelipeds massive, heterochelous. Male abdomen with 7 somites. *Oligo.-Pleist.*, Eu.; *Rec.*, IndoPac.-Medit.-Atl.-C. Am. (W. coast)-S. Am. (W. coast).—FIG. 326,7. *E. cocchii* RISTORI, *Plio.*, Italy; $\times 0.3$ (283).
- Etisus** H. MILNE-EDWARDS, 1834 [**Cancer dentatus* HERBST, 1785; SD GLAESSNER, 1929] [= *Etisus* LEACH in DESMAREST, 1825 (*nom. nud.*); *Etisodes* DANA, 1852 (type, *E. frontalis*)]. Carapace broad, regions moderately well marked, anterolateral margins with 4 to 8 lobes or spines, antennules folded obliquely, antennal base fused with front, orbit closed, chelae heterochelous with spoon-shaped ends of fingers; male abdominal somites 3 to 5 fused. ?*U.Eoc.*, Fr.; *Plio.-Rec.*, IndoPac.
- Eumorphactaea** BITTNER, 1875 [**E. scissifrons*; OD]. Carapace rounded, slightly wider than

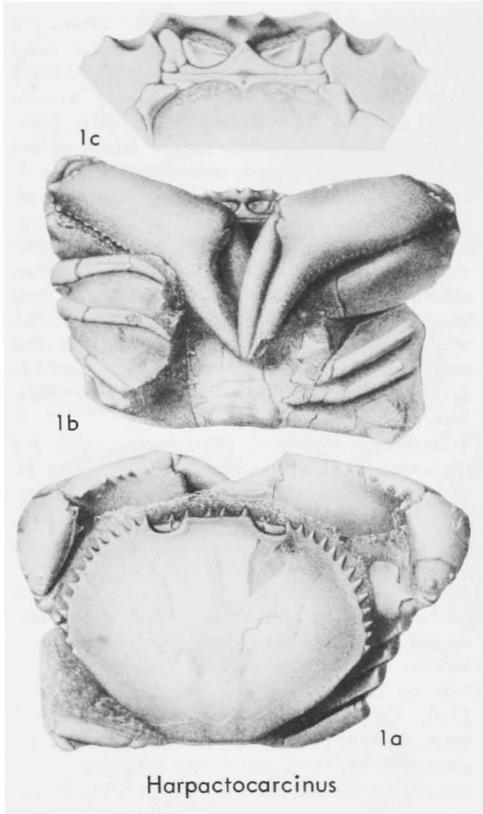


FIG. 327. Xanthidae (p. R518).

long, convex, front deflected, wide, deeply incised medially, granulated; orbits 0.5 width of front; anterolateral margin with 4 blunt lobes; mesogastric lobe strong. *L.Tert.*, S.Eu.(Italy-Fr.).

Eurytium STIMPSON, 1859 [**Cancer limosa* SAY, 1818; OD]. Carapace very broad, convex, regions slightly marked; anterolateral margins with 5 short teeth, 1st and 2nd fused; front deflexed, almost 0.3 width of carapace; chelipeds massive. *Pleist.*, Panama; *Rec.*, N.Am.(E.coast-W.coast).

Galene DE HAAN, 1833 [**Cancer bispinosus* HERBST, 1783; OD] [= *Podopilumnus* M'COY, 1849 (type, *P. fitonii*, = *Gecarcinus trispinosus* DESMAREST, 1822)]. Carapace subquadrate, wider than long, smooth, with branchiocardiac grooves; front sloping, medially grooved, with 4 lobes, anterolateral margins with 2 lobes or teeth, branchial regions posteriorly inflated and ridged longitudinally; chela robust. *Mio.*, Formosa-N.Z.; *Plio.*, E.Indies; *Pleist.-Rec.*, IndoPac.—FIG. 326, 1. *G. proavita* GLAESSNER, *Mio.*, N.Z.; carapace (with damaged front), $\times 0.7$ (118).

Harpactocarcinus A. MILNE-EDWARDS, 1862 [**Cancer punctulatus* DESMAREST, 1822; SD RATHBUN,

1928]. Carapace wider than long, with rounded outline, flatly convex dorsally, punctate; front and anterolateral margins denticulate; regions not marked, chelae heterochelous, propodus cylindrical, dorsal margin denticulate. *L.Eoc.-U.Eoc.*, Eu.-N. Am.(Tex.)-E.Afr.—FIG. 327, 1. **H. punctulatus* (DESMAREST), *Eoc.*, Italy; 1a,b, dorsal and ventral views of adult male, $\times 0.5$; 1c, fronto-orbital region, ventral view, $\times 0.8$ (198).

Harpactoxanthopsis VIA, 1959 [**Cancer quadrilobatus* DESMAREST, 1822; OD]. Carapace convex, front with 4 teeth, anterolateral margins with about 5 blunt teeth, surface with regions more or less faint, branchiocardiac grooves deep; chelae heterochelous, massive. *M.Eoc.-U.Eoc.*, ?*M.Oligo.*, Eu.—FIG. 326, 10. **H. quadrilobatus* (DESMAREST), *Eoc.*, Fr.; 10a,b, dorsal and ventral views of male, $\times 0.5$ (198).

Hepaticus BITTNER, 1875 [**H. neumayri*; SD GLAESSNER, 1929]. Carapace with wide, slightly bilobed front, lateral margins convex to level of cardiac region, then concave to straight, narrow, posterior margin; main regions separated by shallow grooves, convex or tuberculate; chelipeds short, stout, granulate. *M.Eoc.-U.Eoc.*, Eu.-Egypt-Java.—FIG. 326, 11. **H. neumayri*, *M.Eoc.*, Italy; $\times 2$ (355).

Heteractaea LOCKINGTON, 1877 [**H. pilosa* (= *Pilumnus lunatus* H. MILNE-EDWARDS & LUCAS, 1843); OD]. Carapace as in *Xantho*, fronto-orbital borders thick; carpus of 2nd to 5th pereopods with raised crests and spines. *Plio.*, Panama; *Rec.*, C.Am.(coasts).

Heteropanope STIMPSON, 1858 [**H. glabra*; SD BALSS, 1933]. Carapace moderately broad, flattish, regions hardly marked; anterolateral margins short, with 4 lobes or teeth, posterior margin rather long; front bilobed; chelae heterochelous, with short, pointed fingers. ?*Mio.*, Iran; *Rec.*, IndoPac.

Holcocarcinus WITHERS, 1924 [**H. sulcatus*; OD]. Carapace transversely oval, smooth but with 2 prominent subparallel transverse ridges across middle; front notched medially; posterior margin short, straight. *U.Eoc.*, W.Afr.—FIG. 326, 9. **H. sulcatus*, Nigeria; 9a,b, dorsal, ventral, $\times 2$ (320).

Lipasthesius RATHBUN, 1898 [**L. leeanus*; OD]. Anterior portion of carapace very broad, posterior fourth very narrow; anterolateral margin arcuate, front deflexed, medially grooved; orbits small, sub-circular; chelipeds concave on inner side; surface granulate. ?*Plio.*, Fiji; *Rec.*, W.Pac.

Lobonotus A. MILNE-EDWARDS, 1864 [**L. sculptus*; OD] [= *Archaeopilumnus* RATHBUN, 1919 (type, *A. caelatus*)]. Carapace flat, as wide as long, regions well marked, anterolateral margins short, denticulate, orbits large, with 2 supra-orbital fissures, antennal base joined to front, antennular fossa transversely elongate. ?*Eoc.*,

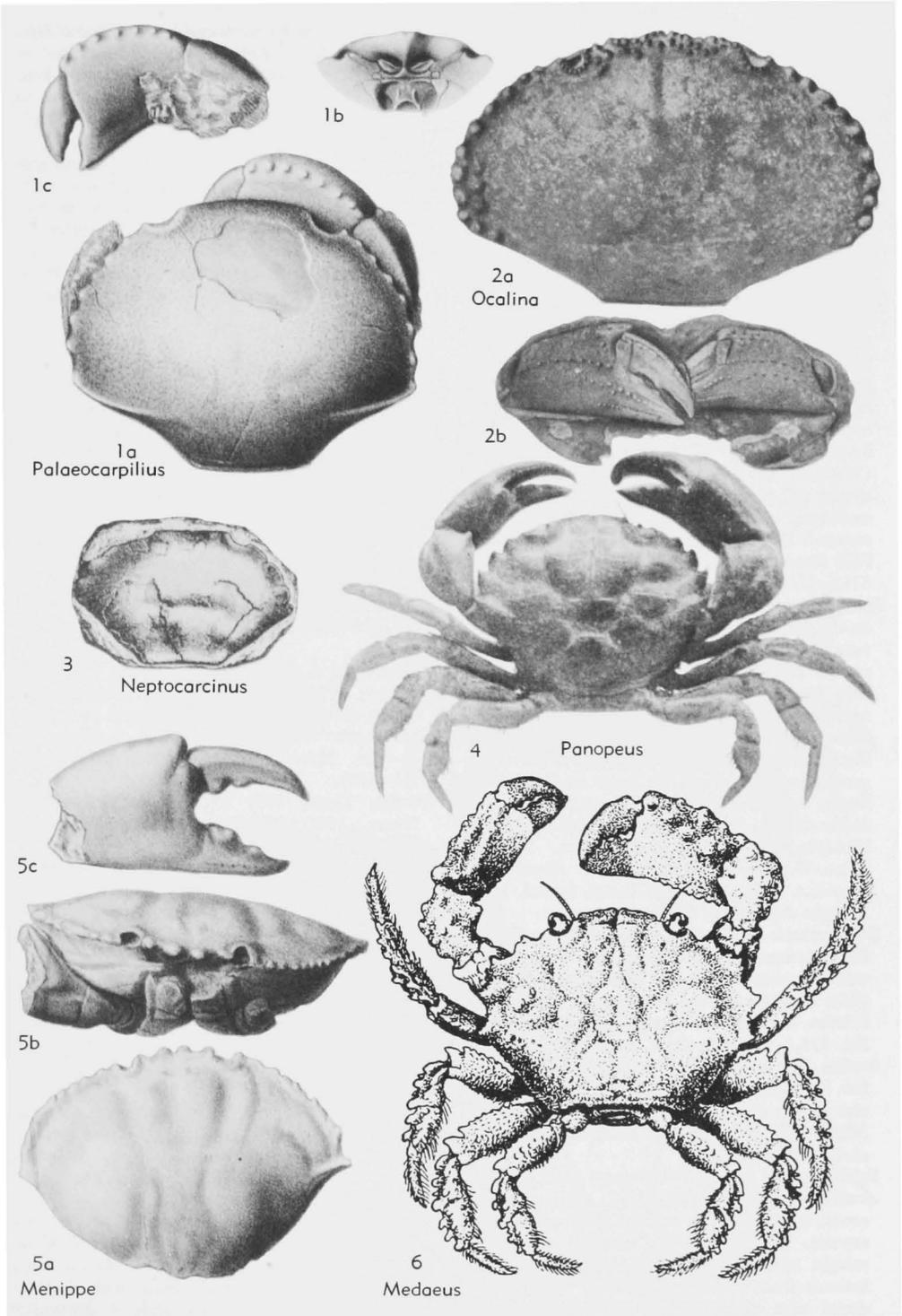


FIG. 328. Xanthidae (p. R520).

- Borneo; *M.Eoc.*, USA (Tex.); *U.Eoc.*, Mex.; *Oligo.*, W. Indies.—FIG. 326, 12. *L. mexicanus* RATHBUN, *U.Eoc.*, Mex.; 12*a, b*, dorsal, ventral, $\times 1$ (242).
- Lophopanopeus** RATHBUN, 1898 [**Xantho bella* STIMPSON, 1860; OD]. Carapace hexagonal, front short, divided into 2 sinuous lobes, postorbital tooth small, followed by 3 prominent teeth; chelae short. *Oligo.*, Alaska; *Pleist.*, USA (Calif.), *Rec.*, N. Am. (W. coast)—W. Indies—W. Afr.—FIG. 326, 6. *L. olearis* RATHBUN, *Oligo.*, Alaska; $\times 1$ (238).
- Medaeus** DANA, 1851 [**M. ornatus* DANA, 1852; SM DANA, 1852]. Carapace not very broad, hexagonal, regions well defined and areolated; anterolateral border with 4 thick tuberculiform teeth; front prominent, notched, chelae covered with nodules; fingers pointed. [A specimen from the upper Pliocene of Java was assigned by VAN STRAELEN (1938) to "*Lophoxanthus scaberrimus* (WALKER, 1887)," following ALCOCK, 1896, a species not now placed in this American Recent monotypic genus but in the synonymy of *M. reynaudi* H. MILNE-EDWARDS.] *Mio.*, Java; *Plio.*, Fiji; *Rec.*, IndoPac.—Medit.—W. Afr.—W. Pac.—FIG. 328, 6. *M. lobipes* RATHBUN, *Rec.*; $\times 1.5$ (243).
- Menippe** DE HAAN, 1833 [**Cancer rumphii* FABRICIUS, 1798; SD GLAESSNER, 1929]. Carapace transversely oval, moderately convex longitudinally; regions little defined; anterolateral margins long, with broad teeth; posterior margin short; front narrow, bilobed; orbits small; antennules infolded transversely; antennal base not reaching front, flagellum in orbital hiatus; chelipeds massive, fingers stout, with large flat basal tooth on fixed finger, male abdomen broad, segments not fused. *M.Eoc.-U.Eoc.*, Eu.—W. Afr.; *Oligo.*, N.Z.; *U.Mio.*, USA (Fla.)—Fiji; *Pleist.*, N. Am.; *Rec.*, IndoPac.—C. Am.—W. Afr.—FIG. 328, 5. *M. chauvini* DE BERVILLE, *M.Eoc.*, Fr.; 5*a, b*, dorsal, frontal, $\times 0.5$; 5*c*, right chela, $\times 0.5$ (198).
- Neptocarcinus** LÖRENTHEY, 1898 [**N. millenaris*; OD]. Carapace small, broader than long, smooth, with gastrocardiac region faintly marked; front wide, medially sulcate; anterolateral margin with 4 lobes, last most prominent. *U.Eoc.*, Hung.—FIG. 328, 3. **N. millenaris*; $\times 0.7$ (184).
- Ocalina** RATHBUN, 1929 [**O. floridana*; OD]. Differs from *Phlyctenodes* in lobate front and irregular surface tubercles. *U.Eoc.*, USA (Fla.).—FIG. 328, 2. **O. floridana*; 2*a*, carapace, $\times 0.5$; 2*b*, chelae, $\times 0.3$ (241).
- Palaeocarpilius** A. MILNE-EDWARDS, 1862 [**Cancer macrochelus* DESMAREST, 1822; SD]. Carapace ovoid, smooth, highly convex, front wide, subtriangular, deflected, orbits narrow, anterolateral margin tuberculate, antennal base long, inserted between front and suborbital lobe, chelae plump, dorsal edge tuberculate. *M.Eoc.-U.Eoc.-Oligo.-?L. Mio.*, Eu.; *M.Eoc.*, Somaliland—India; *U.Eoc.*, Egypt; *L.Mio.*, Zanzibar—India—Java—Saipan.—FIG. 328, 1. **P. macrochelus* (DESMAREST), *Eoc.*, Italy; 1*a*, dorsal view, $\times 0.7$; 1*b*, ventral view of frontal region, $\times 0.7$; 1*c*, internal view of right cheliped, $\times 0.7$ (198).
- Palaeoxanthopsis** BEURLEN, 1958 [**Xanthopsis cretacea* RATHBUN, 1902; OD]. Carapace wider than long; anterolateral margin arcuate, dentate, ending in long spines directed obliquely backward; front notched, supraorbital margins with 2 fissures; surface with rounded and granulated bosses on major regions; chelae carinate and spinose. *U.Cret. (Maastricht.)*, Brazil.—FIG. 329, 5. **P. cretacea*; dorsal view of carapace, $\times 1$ (32).
- Panopeus** H. MILNE-EDWARDS, 1834 [**P. herbstii*; SD FOWLER, 1912]. Carapace moderately wide, moderately convex, regions distinct, marked by raised transverse lines on anterior half; anterolateral margins with 5 teeth, shorter than posterolateral; front 0.2 to 0.3 width of carapace, laminar, notched medially; orbital margin with 2 fissures; chelipeds heterochelous, fingers pointed, dactylus of larger chela with large basal tooth; male abdomen 5-segmented. *Paleoc. (Dan.)-Eoc.*, Eu.—USA (N.J.); *?Plio.*, Fiji; *Oligo.*, *Pleist.*, W. Indies—Panama; *Rec.*, N. Am. (E. coast—W. coast)—W. Afr.—Pac.—FIG. 328, 4. **P. herbstii*, *Rec.*; $\times 1$ (243).
- Phlyctenodes** A. MILNE-EDWARDS, 1862 [**P. tuberculatus*; SD GLAESSNER, 1929]. Carapace with convex surface with tubercles arranged in more or less regular rows. *M.Eoc.-U.Eoc.*, *L.Oligo.*, Eu.—FIG. 329, 4. **P. tuberculatus*; L. Tert., Fr.; $\times 1$ (198).
- Pilodius** DANA, 1852 [**Chlorodius pilumnoides* WHITE, 1847; SD FOREST & GUINOT, 1961]. [= *Chlorodopsis* A. MILNE-EDWARDS, 1873 (type, *C. melanochirus*)]. Differs from *Chlorodiella* in its well-defined regions and areoles and granulation of carapace; basal joint of antennae extending between front and suborbital tooth, its outer angle projecting into orbit. *?Mio.*, Eu.; *Rec.*, IndoPac.
- Pilumnus** LEACH, 1815 [**Cancer hirtellus* LINNÉ, 1761; OD]. Carapace transversely oval, not much broader than long, anterolateral border with spini-form teeth; front 1.3 or more of width of carapace, bilobed; orbital borders with notches; antennules folded transversely; chelipeds and legs stout, chelae tuberculate, fingers short and pointed; male abdomen 7-segmented. *Oligo.*, W. Indies; *Mio.*, *Pleist.*, Eu.; *Rec.*, cosmop.—FIG. 329, 3. *P. sayi* RATHBUN, *Rec.*; $\times 1$ (243).
- Pseudocarcinus** H. MILNE-EDWARDS, 1834 [**Cancer gigas* LAMARCK, 1818; SD MIERS, 1886]. Carapace up to 50 cm. wide and nearly 30 cm. long, transversely oval, inflated, front with 4 short teeth, anterolateral margins with 4 denticulate

lobes, chelipeds massive, strongly heterochelous in males, with long, curved strongly dentate fingers. *Mio.-Plio.*, Australia-N.Z.; *Rec.*, S.Australia. *Simonella* VINASSA DE REGNY, 1897 [**S. quiri-*

censis; OD]. Carapace oval, slightly wider than long, flat and smooth; front short, wide; antero-lateral margins with single tooth; lateral margins convex, posterior margin wide; sternal plate wide;

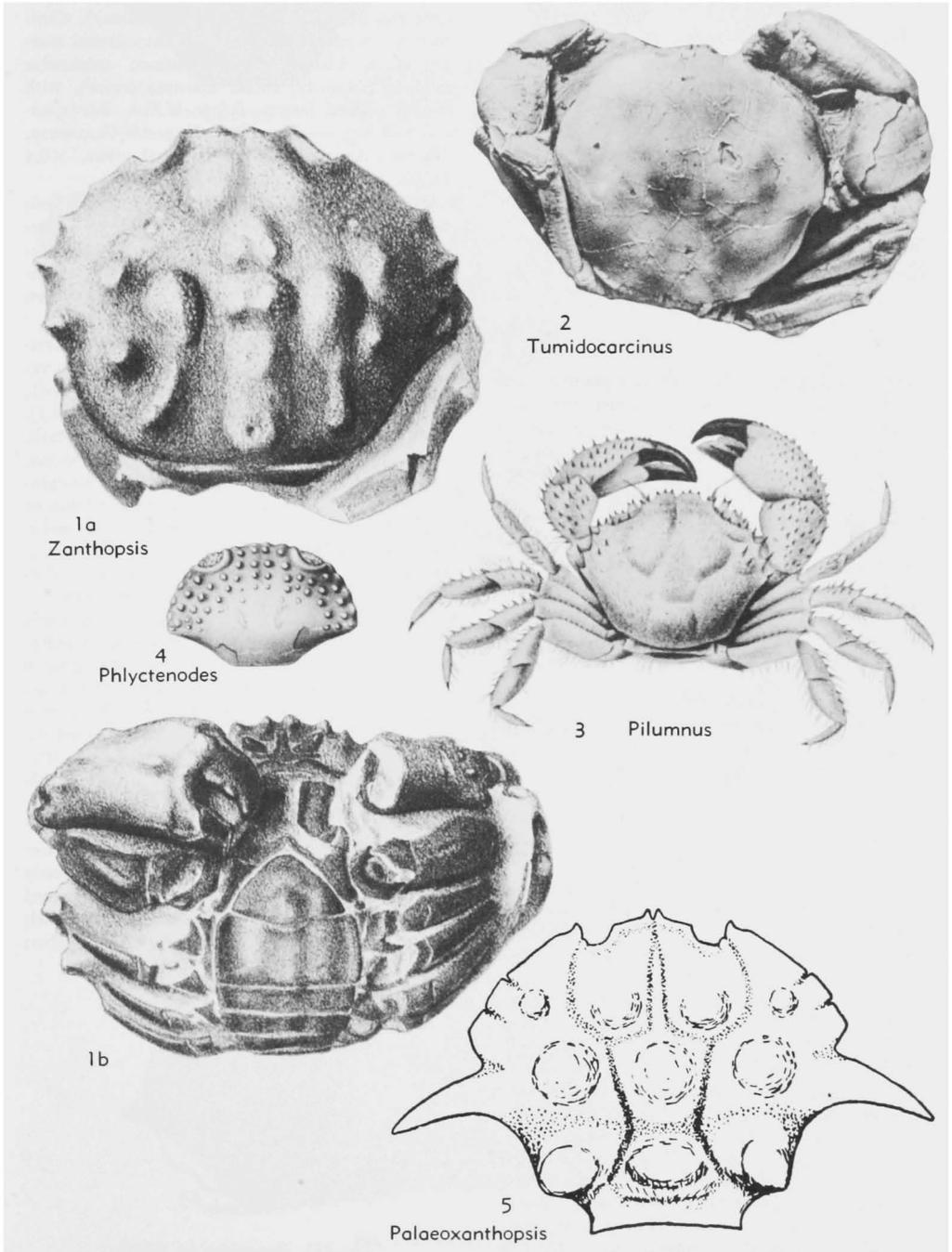


FIG. 329. Xanthidae (p. R520-R522).

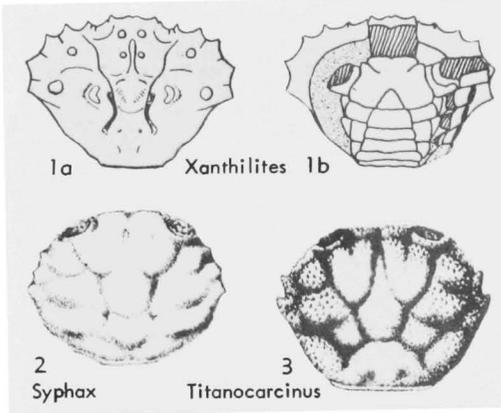


FIG. 330. Xanthidae (p. R522).

male abdomen triangular, narrowly pointed; right cheliped large, with long dactylus; pereopods long, compressed. Differs from *Chlinocephalus* in flat smooth carapace, shape of sternum, and abdomen, from Recent *Quadrella* in shorter anterolateral margins and front. *Plio.*, Italy.

Syphax A. MILNE-EDWARDS, 1863 [**S. crassus* A. MILNE-EDWARDS, 1864; OD]. Carapace ovoid, front wide, orbits small, anterolateral margins with 4 blunt teeth, regions distinct, surface smooth. *L.Tert.*, S.Fr.—FIG. 330,2. **S. crassus* (MILNE-EDWARDS); carapace, $\times 1.3$ (198).

Thelecarcinus BÖHM, 1891 [**T. gümbeli*; OD]. *U. Cret. (Senon.)*, S.Ger.

Titanocarcinus A. MILNE-EDWARDS, 1863 [**T. serratifrons*; SD]. Carapace hexagonal, slightly wider than long, flattened, front straight, medially notched, orbital margins with 2 fissures, anterolateral margins dentate or denticulate, posterior margin about equal in length to posterolateral margin; regions well marked, surface granulate. *U.Cret. (U.Senon.)-Eoc.*, *Mio.*, Eu.—FIG. 330,3. **T. serratifrons*, *U.Cret.*, Belg.; $\times 2$ (198).

Tumidocarcinus GLAESSNER, 1960 [**Harpactocarcinus tumidus* WOODWARD, 1876; OD]. Differing from *Harpactocarcinus* in inflated carapace, weak or absent anterolateral spines, smooth dorsal edge of chela; carapace finely granulated and pitted, cardiac and branchial regions faintly marked. *?M.Eoc.-U.Eoc.*, *L.Oligo.*, *M.Mio.-U.Mio.*, N.Z.; *L.Mio.*, Australia.—FIG. 329,2 **T. tumidus* (WOODWARD), *U.Eoc.-L.Oligo.*, N.Z.; $\times 0.5$ (118).

Xanthias RATHBUN, 1897 [**Xanthodes granosomanus* DANA, 1852 (= *Xantho lamarchii* H. MILNE-EDWARDS, 1834); OD] [= *Xanthodes* DANA, May, 1852 (non GUÉNÉE, Jan., 1852)]. Carapace transversely oval, front wide, bilobed, anterolateral margins with 4 lobes or teeth, chelae isochelous, propodus tuberculate. *?U. Cret.*

(*Campan.*), USA(N.J.); *Rec.*, IndoPac.-W.Indies-Brazil.

Xanthilites BELL, 1858 [**X. bowerbanki*; OD] [= *Pseuderiphia* REUSS, 1859 (type, *P. maccoyi*, = *Xanthilites bowerbanki* BELL, 1858); *Colpocaris* VON MEYER, 1862 (type, *C. bullata*)]. Carapace not much wider than long, anterolateral margin short, 4-lobed; regions distinct; antennulae infolded obliquely; chelae massive, smooth, with strong, pointed fingers. *Paleoc.-M.Eoc.*, Eu.-Japan-C.Am.-S.Am.—FIG. 330,1. *X. gerthi* GLAESSNER, *?Paleoc.*, Arg.; *1a,b*, dorsal, ventral views, $\times 0.4$ (110).

Xanthodius STIMPSON, 1859 [**X. sternbergii*; OD]. Carapace broadly oval; anterolateral margin lobate or dentate, with rim continuing behind widest part of carapace; orbits small, subcircular; regions well marked; chelae heterochelous. *Mio.*, Fiji; *Rec.*, N.Am. (E.coast-W.coast)-Pac.

Zanthopsis M'COY, 1849 [**Cancer leachi* DESMAREST, 1822; OD] [= *Cycloxanthus* H. MILNE-EDWARDS in D'ARCHIAC, 1850 (type, *C. dufourii*); *Xanthopsis* BELL, 1858 (obj.) (*nom. van.*)]. Carapace oval, convex, front 4-lobed, orbits small, with prominent extra- and infraorbital spines, anterolateral margin without fissures; margins arcuate, with few more or less indistinct lobes or teeth; posterior margin short; surface with nodular bosses; antennulae infolded obliquely; chelae massive, heterochelous, propodus tuberculate dorsally and exteriorly; male abdominal somites 3 to 5 fused. [VIA (1959) proposed a subfamily Xanthopsinae for this genus together with *Harpactocarcinus* and *Harpactoxanthopsis*. Recognition of subfamilies of the Xanthidae seems premature, but if accepted, this subfamily must be named Zanthopsinae and should also include *Tumidocarcinus*.] *Paleoc.-Oligo.*, Eu.-W. Afr.-N. Am.-Panama-W. Indies. — FIG. 329,1. **Z. leachi* (DESMAREST), *L.Eoc.*, Eng.; *1a,b*, dorsal view δ and ventral view η , $\times 1$ (19).

Zosimus LEACH in DESMAREST, 1823 [**Cancer aeneus* LINNÉ, 1758; OD]. Carapace moderately broad, moderately convex, regions well delimited and areolated, front sloping, medially grooved; orbits large, anterolateral margin with 4 lobes;

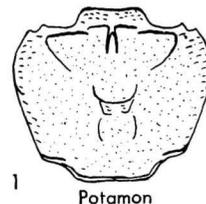


FIG. 331. Potamidae (p. R524).

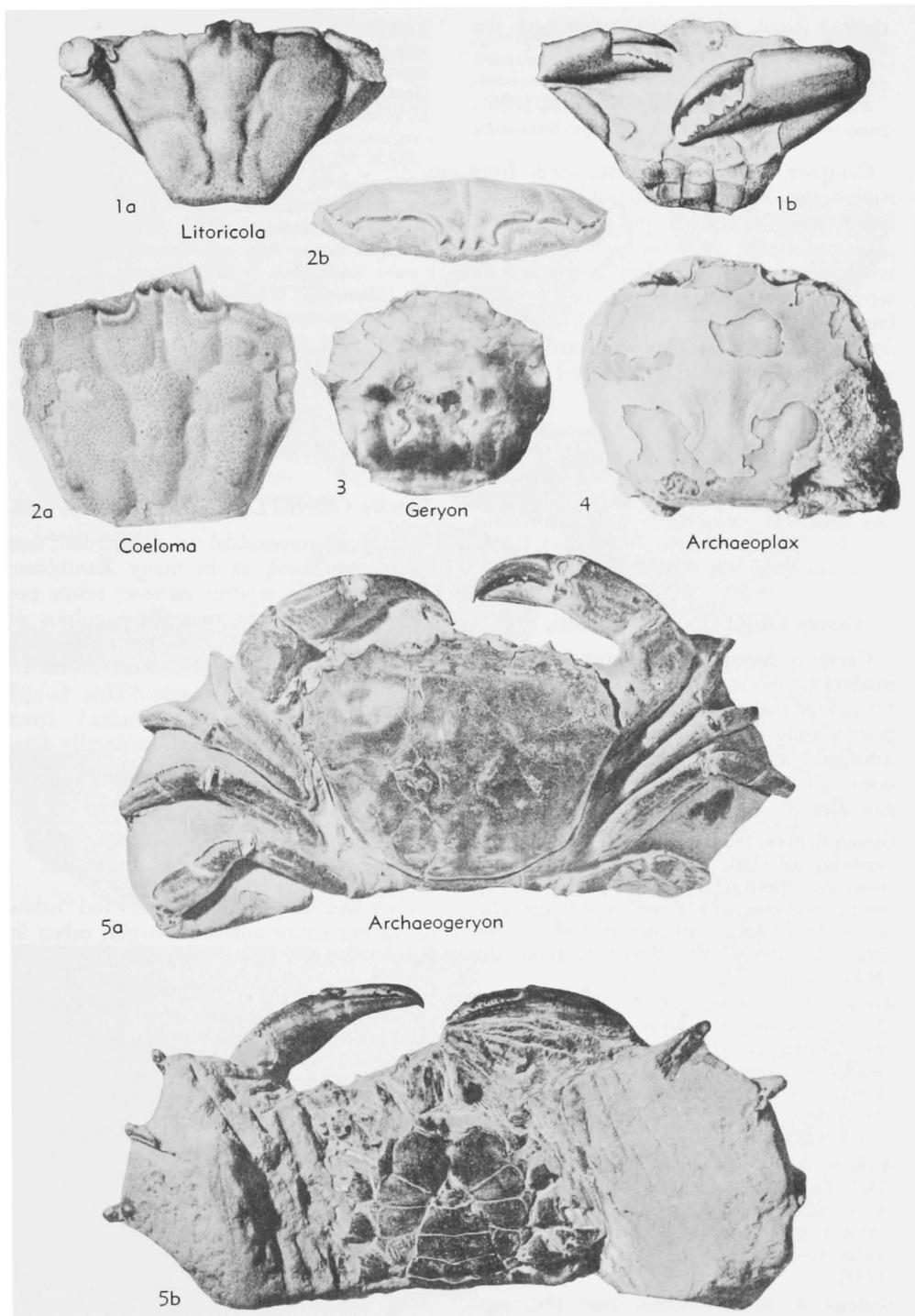


FIG. 332. Geryonidae (p. R524).

chelipeds equal, fingers with hollowed-out tips. ?*Mio.*, Hung., *Rec.*, IndoPac.

Family POTAMIDAE Ortmann, 1896

[*nom. correct.* ICZN, 1964, Op. 712, p. 342 (*pro* Potamonidae ORTMANN, 1896)]

Carapace rectangular to rounded, front straight or bilobed, mostly wide; anterolateral margins convex, posterolateral margins converging posteriorly; sternal plate wide; chelae more or less heterochelous; second to fifth pereopods ambulatory. [This family of freshwater crabs is divided into four subfamilies but known fossils represent only the nominate subfamily.] *U.Tert.-Rec.*

Potamon SAVIGNY, 1816 [**P. fluviatilis*; OD] [= *Telphusa* LATREILLE, 1819 (obj.)]. Front large, carapace with epigastric and proto gastric lobes ending anteriorly in ridges. *U.Mio.-Plio.*, Eu.-India; *Rec.*, S.Eu.-Afr.-S.Asia-E.Asia-E.Indies. —FIG. 331,1. *P. speciosus* (VON MEYER), *U.Mio.*, S.Ger.; carapace, $\times 0.7$ (241).

Family GERYONIDAE Colosi, 1924

Carapace hexagonal to trapezoidal, front moderately wide, dentate, orbits large, anterolateral margin with three to five teeth, posterolateral margins straight; antennulae infolded obliquely, antennae well developed; male abdomen broadly triangular. *Eoc.-Rec.*

Geryon KRÖYER, 1837 [**G. tridens*; OD]. Carapace subhexagonal, little broader than long, regions obscurely defined; chelipeds subequal, strong; legs strong; abdomen with 7 somites. *U.Oligo.-Plio.*, Eu.-N. Afr.; *Rec.*, Atl.-IndoPac.-Medit. —FIG. 332,3. *G. latifrons* VAN STRAELEN, *Plio.*, Alg.; $\times 0.7$ (303).

Archaeogeryon COLOSI, 1924 [**A. juegianus*; OD]. Differs from *Geryon* in flattened carpus, propodus, and dactylus of 5th pereopods and in greater width of carapace and orbital margins. *Mio.*, S.Am. —FIG. 332,5. *A. peruvianus* (D'ORBIGNY), Arg.; *5a,b*, dorsal and ventral views of male, $\times 0.5$ (113).

Archaeoplax STIMPSON, 1863 [**A. signifera*; OD]. Differs from *Geryon* in subquadrilateral carapace, wide orbits, short anterolateral margin, strongly marked branchiocardiac grooves. *U.Mio.*, USA (Mass.). —FIG. 332,4. *A. signifera*; $\times 0.7$ (244).

Coeloma A. MILNE-EDWARDS, 1865 [**C. vigil*; OD]. Carapace flat, trapezoidal, with projecting

4-toothed front, supraorbital margin with 2 fissures; anterolateral margin short, with 4 teeth; regions well marked, surface granulate. *L.Eoc.*, Greenl.-USA (Calif.)-Eng.; *M.Eoc.-L.Mio.*, Eu.

C. (Coeloma). Supraorbital margin long; branchial regions subdivided. *U.Eoc.-M.Oligo.*, Eu. —FIG. 332,2. **C. vigil*; *Oligo.*, Italy; *2a,b*, dorsal and frontal views, $\times 0.7$ (198).

C. (Paracoeloma) BEURLIN, 1929 [**Coeloma rupeliense* STAINIER, 1886; OD]. Supraorbital margin shorter than anterolateral, branchial regions subdivided. ?*L.Eoc.*, Greenl.; *Oligo.*, Eu.

C. (Litoricola) WOODWARD, 1873 [**L. dentata*; SD GLAESSNER, 1929]. Supraorbital margin shorter than anterolateral, sinuous; carapace nearly smooth, branchial regions not subdivided. *L.Eoc.*, Eng.-USA (Calif.); *M.Eoc.*, S.Ger. —FIG. 332,1. **C. (L.) dentata*, *L.Eoc.*, S.Eng.; *1a*, dorsal and ant. view of front, *1b*, ventral view, $\times 1$ (330).

Family GONEPLACIDAE Macleay, 1838

Carapace trapezoidal to rectangular, not transversely oval, as in many Xanthidae; interantennular septum narrow; orbits not clearly divided into two parts; palpus of maxillipeds inserted on antero-internal angle of merus; male gonoducts sternal or coxal with sternal grooves. [This family cannot be sharply distinguished from Xanthidae, particularly the subfamily Carcinoplacinae, which is transitional.] ?*U. Cret.*, *Paleoc.-Rec.*

Subfamily GONEPLACINAE Macleay, 1838

[*nom. transl.* MIERS, 1886 (*ex* Goneplacidae MACLEAY, 1938)]

Carapace trapezoidal; front and orbits occupying entire anterior margin; orbits in form of long narrow grooves. *Eoc.-Rec.*

Goneplax LEACH, 1814 [**Ocypoda bispinosa* LAMARCK, 1801 (= *Cancer rhomboides* LINNÉ, 1758); OD] [= *Gonoplax* LEACH, 1816 (obj.)]. Carapace with extraorbital teeth at points of greatest width; lateral margins straight, converging; front deflected, truncate, about 0.25 of anterior margin in width. Chelipeds very long. *M.Mio.-Plio.*, Eu.; *Rec.*, Medit.-Atl.-IndoPac. —FIG. 333,5. *G. formosa* RISTORI, *Plio.*, Italy; *5a*, dorsal view, *5b*, right chela, $\times 1$ (253).

Mioplax BITTNER, 1883 [**M. socialis*; OD]. Carapace flat, square, only cardiac region marked; front wide, straight, anterolateral teeth directed forward; chelae with deflected fingers; legs long. *Mio.*, Yugosl.-Aus. —FIG. 333,1. **M. socialis*; $\times 1$ (184).

Ommatocarcinus WHITE, 1852 [*O. macgillivrayi*; OD]. Differing from *Goneplax* in narrow front, very long anterior margin, strong, laterally directed extraorbital spines; posterolateral margins

converging. *Eoc.*, Spain; *Oligo.-Mio.*, N.Z.; *M.Mio.*, Australia; *Rec.*, IndoPac.-N.Z.—FIG. 334, 1. *O. corioensis* WHITE, *M.Mio.*, Australia; carapace, $\times 0.7$ (118).

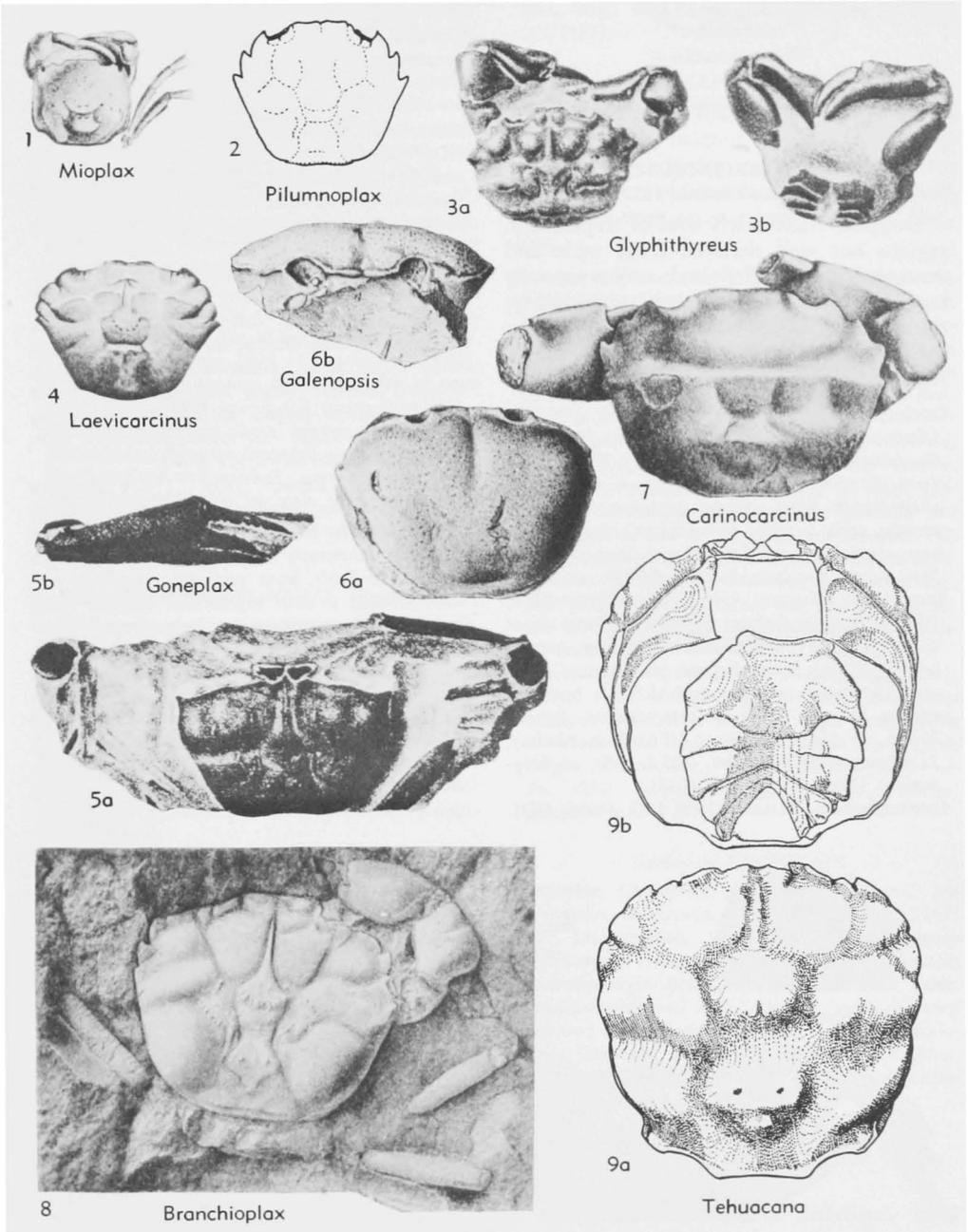


FIG. 333. Goneplacidae (Goneplacinae) (1-5), (Carcinoplacinae) (2-4,6-9) (p. R524, R526-R527).

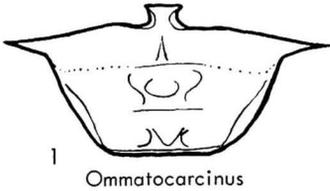


FIG. 334. Goneplacidae (Goneplacinae) (p. R525).

Subfamily CARCINOPLACINAE
H. Milne-Edwards, 1852

Carapace transversely oval to trapezoidal, regions not well defined; front wide and truncated, slightly deflected; orbits not very long; antennulae infolded transversely; third male abdominal segment covering entire space between pereopods. *Paleoc.-Rec.*

Carcinoplax H. MILNE-EDWARDS, 1852 [**Cancer (Curtonotus) longimanus* DE HAAN, 1833; SD GLAESSNER, 1929] [= *Curtonotus* DE HAAN, 1833 (non STEPHENS, 1828)]. Carapace transversely oval, convex, front straight, anterolateral margins arcuate, with 3 teeth, posterolateral margins convex; chelipeds heterochelous, very long in males. *Mio.*, Japan; *Rec.*, trop. IndoPac.-W.Afr.

Branchioplax RATHBUN, 1916 [**B. washingtoniana*; OD]. Carapace slightly wider than long; front straight, orbital margins moderately long; anterolateral margins short, dentate; posterolateral margins convergent; regions well defined, branchial regions inflated; chelipeds heterochelous. *Paleoc.*, *M.Eoc.*, W.Afr.; *Eoc.-Oligo.*, USA (Wash.-Alaska), ?*L.Oligo.*, C.Asia.—FIG. 333,8. **B. washingtoniana*, *Oligo.*, Alaska; $\times 1$ (238).

Carcinoplaoides KESLING, 1958 [**C. flottei*; OD].

Carapace transversely oval, convex, smooth, differing from *Carcinoplax* in absence of anterolateral teeth. ?*Pleist.*, Guam.

Carinocarcinus LÖRENTHEY, 1898 [**C. zitteli*; OD]. Carapace transversely oval, convex longitudinally, front wide, orbits rather small, anterolateral margin with 4 teeth; straight transverse smooth ridge connecting lateral teeth across middle of carapace; chelae massive, heterochelous. *M.Eoc.*, S.Ger.—FIG. 333,7. **C. zitteli*; $\times 1$ (182).

Eucrate DE HAAN, 1835 [**Cancer (E.) crenatus*; OD]. Carapace subquadrilateral, convex; front straight, fronto-orbital margin nearly as wide as carapace; anterolateral borders dentate, slightly arched; chelipeds massive. ?*Oligo.*, USA (Ore.); *Rec.*, IndoPac.

Galenopsis A. MILNE-EDWARDS, 1865 [**G. typica*; SD]. Carapace transversely oval, smooth, moderately convex, front deflexed, medially sulcate, orbits small; anterolateral margins curved, short, with weak teeth; posterolateral margin long, straight, posterior margin long; branchial regions inflated. *M.Eoc.-Oligo.*, Eu.-E.Afr.-India; *Plio.*, Fiji.—FIG. 333,6. **G. typica*, *Eoc.*, Fr.; 6a,b, dorsal and frontal views, $\times 1$ (198).

Glyphithyreus REUSS, 1859 [**G. formosus* (= **Plagiolophus wetherelli* BELL, 1858); OD] [= *Plagiolophus* BELL, 1858 (non POMEL, 1847)]. Carapace transversely oval, wider than long, longitudinally convex; front projecting, medially sulcate, as wide as each supraorbital margin, which has 2 fissures; anterolateral margins short, tuberculate; regions well marked by wide, smooth grooves, strongly elevated and granulate; base of antennae closing orbital gap; chelae massive, propodus with external blunt ridge; male abdominal somites 3 to 5 fused. *L.Eoc.-M.Eoc.*, Eu.; *M.Eoc.*, USA (Calif.); *U.Eoc.*, Egypt.—FIG. 333,3. **G. wetherelli* (BELL), *L.Eoc.*, Eng.; 3a,b, dorsal, ventral, $\times 1$ (19).

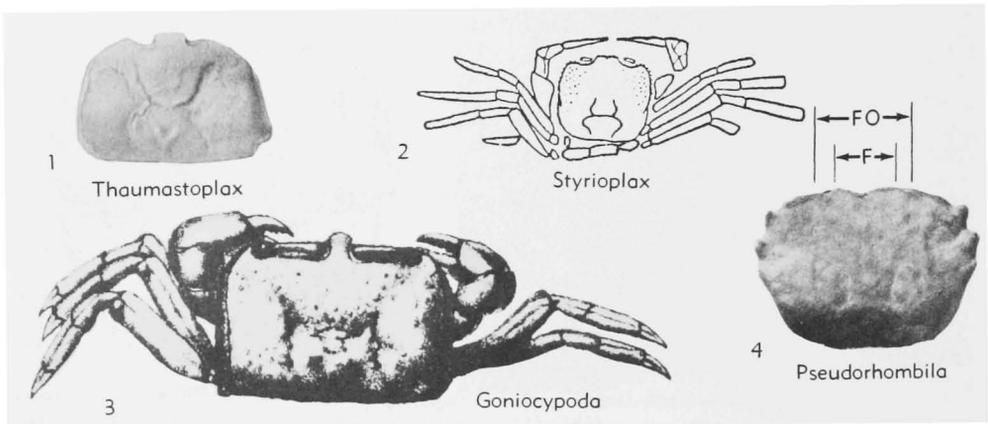


FIG. 335. Goneplacidae (Prionoplacinae) (4), (Hexapodinae) (1,3), (Subfamily Uncertain) (2) (p. R527).

Laevicarcinus LÖRENTHEY & BEURLEN, 1929 [**L. egerensis*; SD GLAESSNER, 1929]. Carapace wider than long, flat; front medially notched, antero-lateral margin arcuate, 4-lobed, shorter than posterolateral, posterior margin long; anterior regions well marked; surface of carapace and legs smooth. *M.Eoc.-U.Eoc., Mio.-Plio., Eu.*—FIG. 333,4. **L. egerensis*, U.Eoc., Hung.; $\times 0.7$ (184).

Martinezicancer VAN STRAELLEN, 1939 [**M. schenki*; OD]. Carapace 0.3 wider than long, front narrow, supraorbital margin with 1 small spine; 2 antero- and 2 posterolateral teeth; regions well marked and tuberculated. *Paleoc., USA*(Calif.).

Pilumnoplax STIMPSON, 1858 [**P. sulcatifrons*; SD RATHBUN, 1918]. Carapace hexagonal, depressed; front straight; fronto-orbital border 0.7 width of carapace; anterolateral margin dentate; chelipeds massive; legs slender. *Eoc.-Oligo., W.N.Am.; Eoc., Spain; Rec., IndoPac.-W.Afr.-W.Indies.*—FIG. 333,2. *P. urpiniana* VIA, *M.Eoc., Spain*; $\times 1$ (314).

?**Tehuacana** STENZEL, 1944 [**T. tehuacana*; OD]. Carapace square, convex, front 0.3 width of carapace, fronto-orbital border 0.7 width of carapace, anterolateral margin short, arcuate, with 4 teeth, posterolateral margins converging, orbits medium-sized; regions well marked; sternum narrow, 5th somite almost hidden by male abdomen. *Paleoc., USA*(Tex.)—FIG. 333,9. **T. tehuacana*; *9a,b*, dorsal, ventral, $\times 3$ (281).

Subfamily PRIONOPLACINAE Alcock, 1900

Differs from Carcinoplacinae in third abdominal segment of males not filling space between fifth pereopods; greatest width of carapace not between extraorbital teeth. [According to BALSS (1957), this subfamily includes *Pseudorhombila*, the nominate genus of a subfamily which ALCOCK substituted for Carcinoplacinae MIERS.] *Oligo.-Rec.*

Prionoplax H. MILNE-EDWARDS, 1852 [**P. spinicarpus*; OD]. Carapace broadly trapezoidal, front about 0.3 width of carapace, anterolateral margins dentate, continuous with converging posterolateral margins; antennary flagellum in orbital hiatus; chelipeds subequal; somites 3 to 5 of male abdomen fused. *Rec., W.Indies-Panama-Ecuador.*

Euryplax STIMPSON, 1859 [**E. nitida*; OD]. Carapace broadly trapezoidal, front nearly 0.5 width of carapace, anterolateral margin short, dentate, chelae massive, almost isochelous, propodus short; all somites of male abdomen distinct. *Oligo., Panama; Rec., Gulf Mexico-W.Indies-Panama.*

Pseudorhombila H. MILNE-EDWARDS, 1834 [**Melia quadridentata* LATREILLE, 1828; OD]. Carapace wider than long, convex longitudinally, fronto-orbital margin 0.5 width of carapace, anterolateral borders arcuate, dentate, front straight, notched;

supraorbital margin with 2 fissures; regions partially indicated; antennules folded transversely; chelipeds massive, heterochelous; male abdominal somites 3 to 5 fused. *Mio., S.Am.*(Arg.); *Rec., W. Indies.*—FIG. 335,4. *P. patagonica* GLAESSNER, *Mio., Arg.; FO*, fronto-orbital margin; *F*, front, $\times 1$ (113).

Subfamily HEXAPODINAE Miers, 1886

Carapace wider than long, lateral margins rounded, front narrow, fifth pereopods absent; male abdomen not filling space between bases of fourth pereopods, male gonoducts open on sternum. ?*U.Cret., Eoc.-Rec.*

Hexapus DE HAAN, 1833 [**Cancer sexpes* FABRICIUS, 1798; OD]. Carapace small, smooth, quadrilateral, widening posteriorly, front 0.25 width of carapace, deflexed, notched; orbits small, anterolateral angles rounded, chelipeds small, 2nd to 4th pereopods nearly equal in size. *Mio., Japan; Rec., IndoPac.*

Gonicypoda H. WOODWARD, 1867 [**G. edwardsi*; OD]. Carapace subrectangular, front narrow, supraorbital margins long, ending in small projecting extraorbital teeth; regions generally not well marked; 2nd to 4th pereopods subequal. ?*U.Cret.*(Maastricht.), *W.Afr.; Eoc., Eu.-Egypt-India.*—FIG. 335,3. **G. edwardsi*, *L.Eoc., S.Eng.*; $\times 2$ (329); published figure has "outlines of absent limbs," including 5th pereopod, added without justification).

Thaumastoplax MIERS, 1881 [**T. anomalipes*; OD]. Differs from *Hexapus* in 3rd pereopods being stronger than 2nd to 4th ones, from *Gonicypoda* in wider front and smaller orbits. *Eoc., Peru; Oligo., Panama; Rec., W.Afr.-Thailand-Japan.*—FIG. 335,1. *T. prima* RATHBUN, *Oligo., Panama*; carapace, $\times 0.7$ (234).

Subfamily UNCERTAIN

Styrioplax GLAESSNER, herein [*nom. nov. pro Microplax* GLAESSNER, 1928 (*non* FIEBER, 1861; *nec* LILLJENBORG, 1865)] [**Microplax exiguus* GLAESSNER, 1928; OD]. Carapace small, square; frontal margin straight, deflexed, notched; orbits small; anterolateral angles rounded; male abdomen narrow; chelae heterochelous, 2nd to 5th pereopods long and slender, 5th being longest. *Mio., Eu.*(Aus.)—FIG. 335,2. **S. exiguus* (GLAESSNER); $\times 2$ (106).

Family PINNOTHERIDAE de Haan, 1833

Carapace soft, regions indistinct, front and orbits small; buccal cavity wide; merus of third maxillipeds wide, with rounded

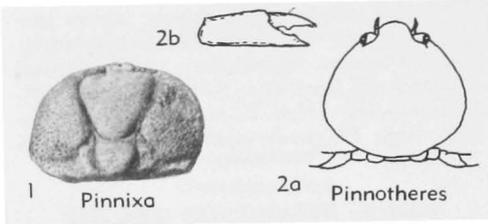


FIG. 336. Pinnotheridae (p. R528).

Parapinnixa HOLMES, 1894 [**Pinnixa? nitida* LOCKINGTON, 1877; OD]. Carapace calcified, much broader than long, anterior margin straight; orbits nearly round; 2nd pereiopod largest, 5th very small. *Mio.*, USA (Calif.); *Rec.*, Japan-N.Am.-(W. coast)-W.Indies.

Pinnixa WHITE, 1846 [**Pinnotheres cylindricum* SAY, 1818; OD]. Carapace much wider than long, calcified; front narrow, medially grooved; orbits broadly ovate to circular; chelipeds of moderate size, 4th pereiopods larger than 2nd and 3rd and much larger than 5th pereiopod; abdomen narrow. *Eoc.*, USA (Wash.); *Oligo.*, C.Asia; *Mio.*, USA (Calif.); *Rec.*, N.Am.(coasts)-S.Am.(coasts)-Japan-China.—FIG. 336,1. *P. eocenica* RATHBUN, *Eoc.*, USA (Wash.); carapace, $\times 2$ (238).

angles and palp not at antero-internal angle; male abdomen very narrow. [Five subfamilies are currently recognized.] *Eoc.-Rec.*

Pinnotheres BOSCH, 1802 [**Cancer pisum* LINNÉ, 1767; SD LATREILLE, 1810]. Carapace transversely oval to circular, smooth; chelipeds isochelous; pereiopods stout, of moderate length. *?Mio.*, Eu.-S.Am.; *Rec.*, cosmop. in warm seas.—FIG. 336,2. **P. pisum* (LINNÉ), *Rec.*; 2a, carapace and part of sternum (*st5*) and last legs (*coxa-co5*); 2b, right chela, $\times 3$ (52).

Family GRAPSIDAE Macleay, 1838

Carapace quadrangular, with straight or convex lateral margins; orbits at or near anterolateral angles; front wide; interantennular septum very wide; buccal frame

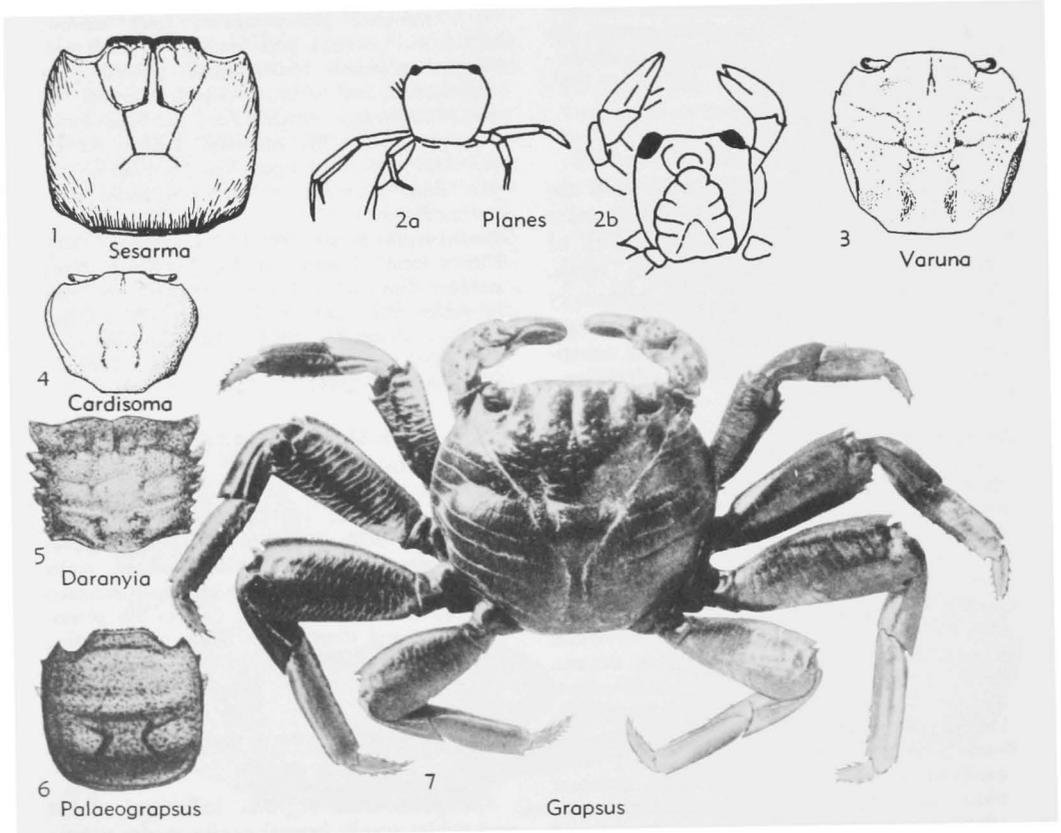


FIG. 337. Grapsidae (Grapsinae) (2,7), (Varuninae) (3), (Sesarminae) (1), (Subfamily Uncertain) (5,6); Gecarcinidae (4) (p. R529-R530).

square; mandibular palp articulating on external angle of merus or in middle of its anterior margin; male gonoducts open sternally. [The subfamily Plagusiinae, with deeply lobed front, is not represented by fossils.] *M.Eoc.-Rec.*

Subfamily GRAPSINAE Macleay, 1838

Front deflected; wide space between third maxillipeds; male abdomen filling entire space between fifth pereopods. *Oligo.-Rec.*

Grapsus LAMARCK, 1801 [**Cancer grapsus* LINNÉ, 1758; OD]. Carapace little broader than long, flat; regions well defined, branchial regions with parallel, oblique ridges; front strongly deflexed; orbits deep; chelipeds subequal, legs broad and compressed. *Rec.*, cosmop. in warm seas.—FIG. 337,7. **G. grapsus* (LINNÉ); male, dorsal view, $\times 0.5$ (234).

Planes BOWDITCH, 1825 [**P. clypeatus*; OD] [= *Nautilograpsus* H. MILNE-EDWARDS, 1837 (obj.); *Nautilograpsoides* SMIRNOV, 1929 (no type-species)]. Carapace quadrate to oval, as long as wide, convex; anterolateral angle sharp, with notch behind; front about 0.5 width of carapace, gently deflected; legs flattened. *Oligo.*, N.Caucasus; *Rec.*, cosmop.—FIG. 337,2. *P. prior* (SMIRNOV), *Oligo.*, N.Caucasus; 2*a,b*, dorsal, ventral, $\times 0.7$ (277, re-drawn).

Subfamily VARUNINAE H. Milne-Edwards, 1852

Front not deflected or not strongly so; space between third maxillipeds moderately wide; abdomen rarely covering entire space between fifth pereopods. ?*M.Eoc.*, *U.Eoc.-Rec.*

Varuna H. MILNE-EDWARDS, 1830 [**Cancer litteratus* FABRICIUS, 1798; OD] [= *Telphusograpsus* LÖRENTHEY, 1902 (type, *T. laevis*)]. Carapace about as wide as long, flat, with sharp edges; front slightly more than 0.3 of its width, straight, little deflected; orbits small, supraorbital margin notched; lateral margins convex, with 3 anterolateral teeth (including extraorbital); branchio- and gastrocardiac grooves marked; chelipeds equal, massive in males; 2nd to 5th pereopods with last segments flattened; abdomen with 7 somites. ?*M.Eoc.*, C.Am.; *U.Eoc.*, Rumania; *Rec.*, IndoPac.—FIG. 337,3. **V. litterata* (FABRICIUS), *Rec.*; carapace, $\times 0.7$ (15).

Brachynotus DE HAAN, 1833 [**Goneplax sexdentatus* RISSO, 1827] [= *Hemigrapsus* DANA, 1857 (type, *H. crassimanus*)]. Carapace broader than long, with 3 anterolateral teeth (including extraorbital); front less than 0.5 width of carapace, little deflected, mesogastric region marked anteriorly and posteriorly; chelipeds subequal; 2nd to 5th

pereopods not strongly compressed, smooth. ?*Plio.*, *Pleist.*, N.Am.; *Rec.*, coasts of Atl.-Pac.-Medit.

Utica WHITE, 1847 [**U. gracilipes*; OD]. Carapace octagonal, flat, frontal margin straight, anterolateral margins divergent, with 3 teeth; posterolateral margin straight; strong ridge transversely crossing cardiac and branchial regions; chelipeds small, 2nd to 5th pereopods long. *Pleist.* (*Sub-recent*), Australia; *Rec.*, W.Pac.-SW.Pac.

Subfamily SESARMINAE Dana, 1852

Front strongly deflected; third maxillipeds widely separated and with oblique ridge across ischium and merus; male abdomen filling space between fifth pereopods completely or almost completely. *U.Oligo.* or *L.Mio.-Rec.*

Sesarma SAY, 1817 [**Ocylope reticulatus*; OD]. Carapace square, sides straight and parallel or convex, surface flattened, gastric region well marked and subdivided; front 0.5 length of anterior margin or more, deflected; orbits deep, oval; chelipeds subequal, 2nd to 5th pereopods subequal in length; abdomen with 7 somites. *U. Oligo.* or *L.Mio.*, Brazil; *Pleist.* (*Sub-recent*), Australia; *Rec.*, cosmop. in warm waters.—FIG. 337,1. *S. paraensis* BEURLEN, *U.Oligo.* or *L.Mio.*, Brazil; carapace, $\times 1$ (32).

Subfamily UNCERTAIN

Daranyia LÖRENTHEY, 1901 [**D. granulata*; OD]. Lateral margins of carapace converging posteriorly, with teeth decreasing in size; gastro- and cardio-branchial grooves weakly marked; fronto-orbital margin wide, sinuous, with median sulcus; orbits large. *M.Eoc.*, Sicily; *U.Eoc.*, Hung.—FIG. 337,5. **D. granulata*, *U.Eoc.*, Hung.; $\times 1$ (184).

Palaeograpsus BITTNER, 1875 [**P. inflatus*; SD GLAESSNER, 1929]. Carapace rectangular, about as wide as long, convex, finely granulate; front wide, lateral margins convex, with small teeth. *M.Eoc.*, Egypt; *M.Eoc.-U.Eoc.*, ?*Oligo.*, Eu.—FIG. 337,6. **P. inflatus*, *U.Eoc.*, Hung.; $\times 1$ (184).

Family GECARCINIDAE Macleay, 1838

Carapace transversely oval, anterolateral margins strongly arcuate; fronto-orbital margin much shorter than greatest width of carapace; front moderately wide, deflected; antennular grooves narrow; male gonoducts opening sternally. *Plio.-Rec.*

Gecarcinus LEACH, 1814 [**Cancer ruricola* LINNÉ, 1758; SD H. MILNE-EDWARDS, 1837]. Carapace convex, heart-shaped; fronto-orbital margin 0.5 greatest width of carapace or less, 0.12 to 0.2 of carapace width; chelipeds massive, legs stout. *Rec.*, C.Am.-Mex.-Colombia-W.Afr., Ascension Is.

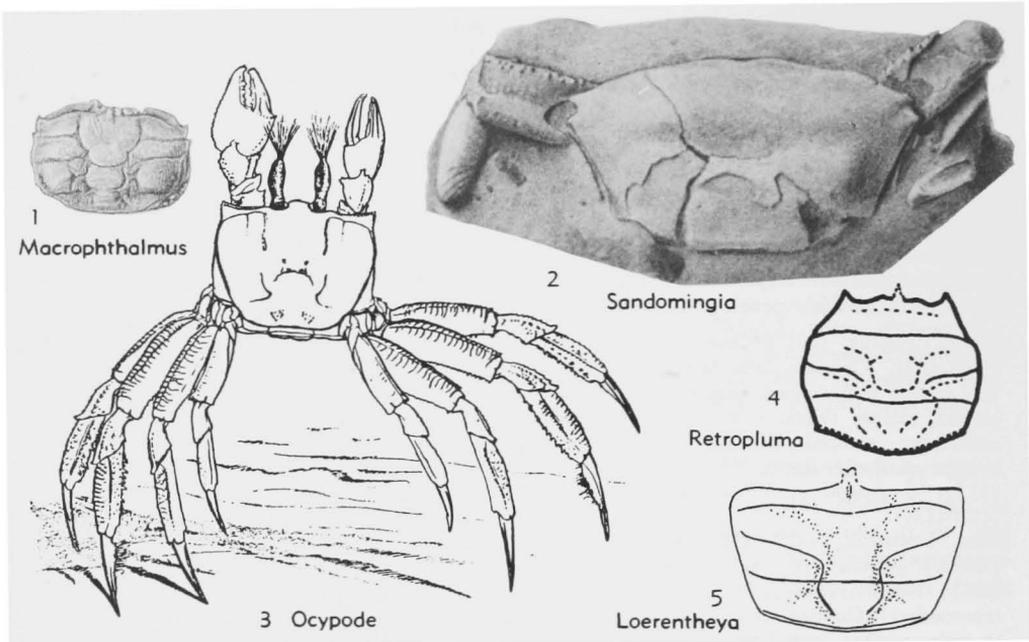


FIG. 338. Ocypodidae (Ocypodinae) (3), (Macrophthalminae) (1), (Subfamily Uncertain) (2,5); Retroplumidae (4) (p. R530-R531).

Cardisoma LATREILLE, 1825 [*C. guanhumi*; SD H. MILNE-EDWARDS, 1837]. Differing from *Gecarcinus* in fronto-orbital margin being much wider than 0.5 of greatest width of carapace and straight front about 0.25 of same; chelipeds unequal. *Plio.*, Fiji; *Rec.*, Gulf Mex.-Brazil-W. Mex.-Peru-W. Afr.-IndoPac.—FIG. 337,4. *C. carnifex* (HERBST), *Rec.*; $\times 0.5$ (15).

Superfamily OCYPODOIDEA Rafinesque, 1815

[*nom. transl.* GLAESSNER, herein (ex Ocypodidae RAFINESQUE, 1815)] [=subtribe Ocypodoida BEURLEN, 1930]

Carapace rectangular, wider than long; front small, projecting; orbits (where present) developed as long grooves for elongate eye stalks; antennules without fossae, small; antennae small; sternal plate wide; gonoducts open on sternum. *M.Eoc.-Rec.*

Family OCYPODIDAE Rafinesque, 1815

Carapace quadrilateral, convex longitudinally, front narrow, eye stalks long, fronto-orbital margin long, buccal frame narrowed anteriorly; male gonoducts opening sternally, male abdomen narrow. *M. Eoc., Mio.-Rec.*

Subfamily OCYPODINAE Rafinesque, 1815

[*nom. transl.* DANA, 1852 (ex Ocypodidae RAFINESQUE, 1815)]

Carapace with regions indistinct; front narrow, deflexed; antennules infolded obliquely or longitudinally; chelipeds heterochelous at least in males. *Plio.-Rec.*

Ocyopode WEBER, 1795 [*Cancer ceratophthalmus* PALLAS, 1772; SD] [= *Ocyopoda* LAMARCK, 1801 (obj.)]. Carapace square, little broader than long, convex, granulate; orbits large, shallow; chelae heterochelous, 2nd to 4th pereiopods long, 5th shorter; male abdomen narrow. *Pleist.*, USA (Fla.); *Rec.*, IndoPac.-Medit.-W. Afr.-N. Am. (coasts)-S. Am. (coasts).—FIG. 338,3. *O. cursor* (LINNÉ), *Rec.*; in running position, $\times 0.7$ (52, after Gravier).

Uca LEACH, 1814 [*Cancer vocans major* HERBST, 1782; OD] [= *Gelasimus* LATREILLE, 1817 (type, *Ocyopoda maracoani* LATREILLE, 1802)]. Carapace subquadrilateral, broader than long, with anterolateral angles produced and acute; lateral margins converging; female chelipeds equal, short; male chelipeds extremely heterochelous, one with manus commonly as big as rest of animal; legs stout. *Plio.-Pleist.*, N. Am.-Panama-E. Indies; *Rec.*, cosmop. on coasts of warm seas.

Subfamily MACROPHTHALMINAE Dana, 1852

Carapace rectangular, wider than long, regions well marked; front not very wide; eye stalks long; antennules infolded transversely. *Mio.-Rec.*

Macrophthalmus DESMAREST, 1823 [*Gonoplax transversus* LATREILLE, 1817; SD H. MILNE-ED-

WARDS, 1837]. Carapace moderately convex, front narrow, orbits and eye stalks very long, chelae long and slender. *Mio.*, Eu.; *Pleist.-Rec.*, Indo-Pac.—FIG. 338,1. *M. vindobonensis* GLAESSNER, *Mio.*, Austria; carapace, $\times 1$ (357a).

Hemiplax HELLER, 1865 [**Metaplax hirtipes* HELLER, 1862; OD (=?*Cleistostoma hirtipes* JACQUINOT & LUCAS, 1853)]. Differs from *Macrophthalmus* in wider front which equals 0.25 width of carapace; fixed fingers of chelae deflected. ?*Plio.*, N.Z.; *Pleist.-Rec.*, Australia-N.Z.

Subfamily UNCERTAIN

Loerentheyia BEURLEN, 1929 [**L. carinata*; OD]. Carapace trapezoidal, wider than long, front very narrow, supraorbital margins long, lateral margins convergent, posterior margin long, slightly convex; surface with gastrocercal grooves, 2 transverse keels and pair of oblique sinuous ridges. *M.Eoc.*, Hung.—FIG. 338,5. **L. carinata*; $\times 0.7$ (184).

Sandomingia RATHBUN, 1919 [**S. yaquiensis*; OD]. Carapace wide, anterior margin arcuate, anterolateral angle with extraorbital and lateral teeth, lateral margins converging; orbits long, shallow, extending whole width of carapace from front which is 0.85 width of carapace; chelipeds large, equal. *L.Mio.*, W.Indies.—FIG. 338,2. **S. yaquiensis*, San Domingo; dorsal, $\times 1$ (236).

Family RETROPLUMIDAE Gill, 1894

[=Ptenoplacidae ALCOCK, 1900]

Carapace transversely oval, flat, with two transverse crests, front narrow, little deflected; interantennular septum thin, no

distinct antennular fossae; orbits incomplete below; antennal flagella long; third maxillipeds slender, subpediform; sternal plate wide, male abdomen narrow, male gonoducts open on coxae of fifth pereopods, with sternal ducts; female gonoducts open on sternum of third pereopods; sternum of fifth pereopod reduced, and this pereopod rudimentary, close-set, subdorsal. *M.Eoc.-Rec.*

Retropluma GILL, 1894 [**Archaeoplax notopus* ALCOCK & ANDERSON, 1894; OD] [=*Archaeoplax* ALCOCK & ANDERSON, 1894 (*non* STIMPSON, 1863); *Ptenoplax* ALCOCK & ANDERSON, 1895 (type, *Archaeoplax notopus* ALCOCK & ANDERSON, 1894)]. Characters of family. *M.Eoc.*, Spain; *Plio.*, Italy; *Rec.*, IndoPac.—FIG. 338,4. *R. eocenica* VIA, *M.Eoc.*, Spain; carapace, $\times 1.5$ (314).

Superfamily UNCERTAIN

Family PALICIDAE Bouvier, 1898

[=Cymopoliidae FAXON, 1895]

Carapace subquadrilateral, wider than long, front notched, dentate, orbits and eyes large; anterolateral margins dentate, diverging posteriorly, buccal cavity quadrate, third maxillipeds not covering it; chelipeds moderate in size; second to fourth pereopods long, slender, fifth commonly short, subdorsal. Female genital openings between coxae of second pereopods, male openings sternal; sternal plate wide, abdomen narrow. [Family placed near Dorippidae by FAXON (1895) and BOUVIER (1897).] ?*L. Cret.-?U.Cret.*, ?*M.Eoc.*, *Rec.*

Palicus PHILIPPI, 1838 [**P. granulatus* (=Cymopolia *caronii* ROUX, 1828); OD] [=Cymopolia ROUX, 1828 (type, *C. caronii*) (*non* Cymopolia LAMOUROUX, 1816, subsequently transferred to plants)]. Carapace depressed, with 3 to 5 anterolateral teeth, surface granulate and tuberculate with pronounced transverse sculpture; supra- and infraorbital margins with fissures; antennules transverse; interantennular septum narrow; basal segment of antenna enlarged, in orbital hiatus; cheliped short, 5th pereopods subdorsal, may be filiform. *Rec.*, Medit.-Atl.-Pac.—FIG. 339,3. *P. cristatipes* (A. MILNE-EDWARDS); $\times 1.5$ (234).

?**Actaeopsis** CARTER, 1898 [**A. wiltshirei*; OD]. Carapace subhexagonal, slightly convex, wider than long, orbitofrontal margin 0.5 width of carapace, anterolateral margins arcuate, dentate; front large, sulcate, supraorbital margins with 2 fissures; cer-

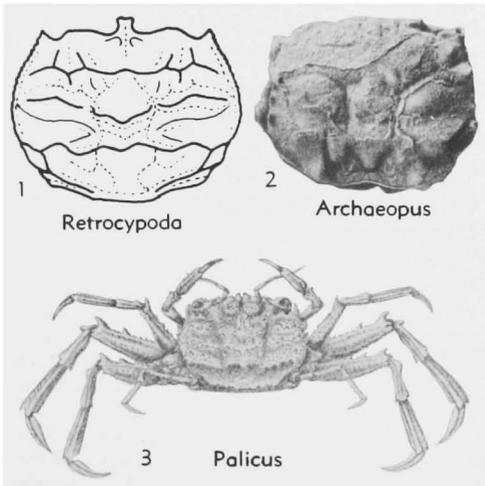


FIG. 339. Palicidae (p. R531-R532).

vical groove and gastric regions well marked, regions granulate. [This incompletely known and poorly figured genus seems to resemble also *Polycnemidium* REUSS.] *L.Cret.* (*Alb.*), Eng.

?*Archaeopus* RATHBUN, 1908 [**A. antennatus*; OD]. Carapace subrectangular, wider than long, flat; front straight, each orbit 0.25 length of anterior margin, with supraorbital, infraorbital, and strong extraorbital teeth; lateral margins slightly diverging posteriorly, denticulate; cervical groove distinct, regions well marked, tuberculated and granulated; basal segment of antennules large; buccal cavity and sternal plate wide; chelae slender, fingers ridged; 5th pereopods probably subdorsal. [Placed by RATHBUN in the Ocypodidae, by GLAESSNER (1929) in the "Cymopoliidae," and by BEURLEN in the Retroplumidae. Similarities with *Actaeopsis* CARTER, *Ophthalmoplax* RATHBUN, and *Retrocyropa* VIA need evaluation.] *U. Cret.*, USA (Calif.).—FIG. 339,2. **A. antennatus*; dorsal view of carapace, $\times 1$ (328).

?*Retrocyropa* VIA, 1957 [**R. almelai*; OD]. Carapace subquadrilateral, wider than long; front narrow, bilobed, deflexed; orbits long, deep; supraorbital margin sinuous, with extraorbital tooth; lateral margins convex, denticulate anteriorly; regions highly differentiated, with transverse gastrohepatic, gastrobranchial, and cardiobranchial crests; sternal plate and abdomen ridged, abdomen covering last sternite; chelae heterochelous, large in males; 5th pereopods subdorsal, reduced. *M.Eoc.*, Spain.—FIG. 339,1. **R. almelai*; carapace, $\times 0.7$ (314).

BRACHYURA

of uncertain systematic position or status

Anaglyptus A. MILNE-EDWARDS, 1873 [**A. delfortrei*; OD] [*non* MULSANT, 1839]. An insufficiently described unfigured leucosiid. *Oligo.*, SW. Fr.

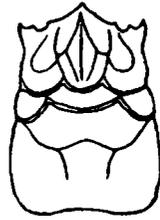
Cyphoplax HAIME, 1855 [**Goneplax impressa* DESMAREST, 1822; OD]. Based on a poorly preserved specimen said to be from Pliocene of Italy and on an unlabeled specimen believed to be from the Mio.-Plio. of the Balearic Islands, both resembling Ocypodidae, subfam. Macropluminae.

Lambropsis LÖRENTHEY, 1909 [**L. wanneri*; OD]. Carapace small, oval; front projecting, orbits with 2 supraorbital fissures, fronto-orbital margin more than 0.5 width of carapace; regions well marked, cardiac and branchial regions with transverse sculpture. [Assigned by LÖRENTHEY to Parthenopidae, by BEURLEN to Xanthidae; also resembling *Pseudodromilites* BEURLEN.] *M.Eoc.*, Egypt.

Lissopsis FRITSCH, 1887 [**L. transiens*; OD]. *U. Cret.*, Czech.

Martinocarcinus BÖHM, 1922 [**M. ickeae*; OD]. *U.Eoc.*, Java.

Microcorystes LÖRENTHEY, 1928 [*non* FRITSCH,



Charassocarcinus

FIG. 340. Family Uncertain (p. R532).

1893] [**M. latifrons*; OD]. Based on a single, small, incomplete carapace which was lost. *U. Mio.*, Hung.

Oedisoma BELL, 1858 [**O. ambiguum*; OD]. Carapace small, ovoid, convex, smooth, with rounded lateral margins, posterior margin deeply concave; orbits large, gastric regions distinct, branchial regions inflated. *L.Eoc.*, Eng.

Palaeoplax A. MILNE-EDWARDS & BROCCHI, 1879 [**Goneplax incerta* DESMAREST, 1822; OD]. Based on single worn specimen. *Subrec.*, IndoPac.

Psammograpsus A. MILNE-EDWARDS, 1860 (*nom. nud.*) [**P. parisiensis* (*nom. nud.*)]. *U.Eoc.*, N. Fr.

Pseudomicippe PELSENEER, 1886 (*non* HELLER, 1861) [**P. granulosa*; OD]. Unrecognizable fragment. *U.Senon.*, Neth.

Semiranina BACHMAYER, 1954 [**S. oroszyi*; OD]. Described as small raninid carapace; affinities uncertain. *U.Mio.*, Aus.

Vanua RATHBUN, 1945 [**V. linearius*; OD]. *Plio.*, Fiji.

DECAPODA

of uncertain systematic position or validity

Brome VON MÜNSTER, 1839 [**B. ventrosa*; SD GLAESSNER, herein]. Unrecognizable. *U.Jur.*, Ger.

*Charassocarcinus*¹ VAN STRAELEN, 1925 [**Stenochirus? mayalis* E. EUDES-DESLONGCHAMPS, 1877]. Carapace elongate, widening posteriorly; rostrum broadly triangular, with median keel at its base; orbits semicircular, with extraorbital teeth; cervical, postcervical and branchiocardiac grooves well developed, with additional furrows joining the branchiocardiac grooves, and also on anterior part; surface tuberculate. [Considered by EUDES-DESLONGCHAMPS as a macruran, by VAN STRAELEN provisionally as a brachyuran of the Homolodromiidae, by GLAESSNER (1933) as a galatheid. It is insufficiently known but appears to have either galatheid or palinurid affinities.] *M.Jur.* (*Bajoc.*), N.Fr.—FIG. 340,1. **C. mayalis* (EUDES-DESLONGCHAMPS); carapace, dorsal, $\times 1$ (re-drawn from 296). [This genus now is judged to belong in Tanaidacea.]

¹ See page R628.

Lupeites FRITSCH, 1887 [**L. granulatus*; OD]. Unrecognizable fragment. *U.Cret.*, Czech.

Olinacaris VAN STRAELEN, 1925 [**O. carinatus*; OD]. Carapace small, with median ridge anteriorly; rostrum wide at base, medially grooved; cervical and branchiocardiac grooves V-shaped; posterior margin concave. [Placed by its author in the Erymidae, by GLAESSNER (1929) in the Galatheidae. Also resembles *Gastrodorus*.] *M.Jur.* (*Bajoc.*), Fr.

GENERA QUESTIONABLY

ASSIGNED TO THE DECAPODA

Liocaris VAN STRAELEN, 1925 [**L. quadratus*; OD]. Carapace smooth, convex, 2 mm. long, with small

rostrum, median groove, and transverse groove behind first $\frac{1}{3}$ of its length. *M.Jur.* (*Bajoc.*), Fr.

Tropifer GOULD, 1857 [**T. laevis*; OD]. Carapace smooth, elongate, 6 mm. long, lateral margins carinate, parallel; posterior margins concave; rostrum short, blunt, eyes at anterolateral angles, large; surface with median and lateral longitudinal carinae; these cross cervical groove; abdomen medially keeled, with pleura. [WOODS (1925) placed this genus in the Eryonidea but it could belong to the Mysidacea (Lophogastridae).] *U. Trias.* (*Rhaet.*), Eng.

ADDENDUM TO DECAPODA

Information received too late for placement here is given on page R626.

HOPLOCARIDA

By R. C. MOORE

Superorder HOPLOCARIDA Calman, 1904

[Diagnosis (mainly based on CALMAN, 1909, p. 149)]

Head with two movable anterior somites bearing pedunculate eyes and triramous antennules; antennae with protopod of two segments; mandible without lacinia mobilis. Cephalothorax partly covered by well-developed carapace, at least four thoracic somites distinctly visible behind it; first five pairs of thoracopods subchelate, second to fifth pairs subequal or with second pair developed as powerful raptorial claws and distinctly larger than others, posterior thoracopods with protopod of three segments (relation of anterior thoracopod segments to those of other limbs doubtful). Abdomen bearing pleopods with appendix interna; telson with fixed median spine, and with or without styliform furca or broad carinate tailpiece lacking fixed spine and furca. Heart much elongated, extend-

ing through thoracic and abdominal regions; hepatic caeca highly ramified; spermatozoa spherical; development with metamorphosis, free-swimming nauplius stage not present. [Marine.] *L.Carb.-Rec.*

The Hoplocarida are represented mainly by the Stomatopoda, known from Jurassic to Recent, but they include also a small antecedent group of much importance named Palaeostomatopoda, which are known from late Paleozoic (Carboniferous) fossils. The palaeostomatopods are less specialized than the stomatopods and are inferred to be the ancestral stock of the Hoplocarida, or at least a closely related derivative of it.

The Hoplocarida differ especially from the Peracarida in better development of the carapace and in various features of their appendages. The Eucarida differ in having a large carapace fused to the cephalothorax and covering all this part of the body.

PALAEOSTOMATOPODA

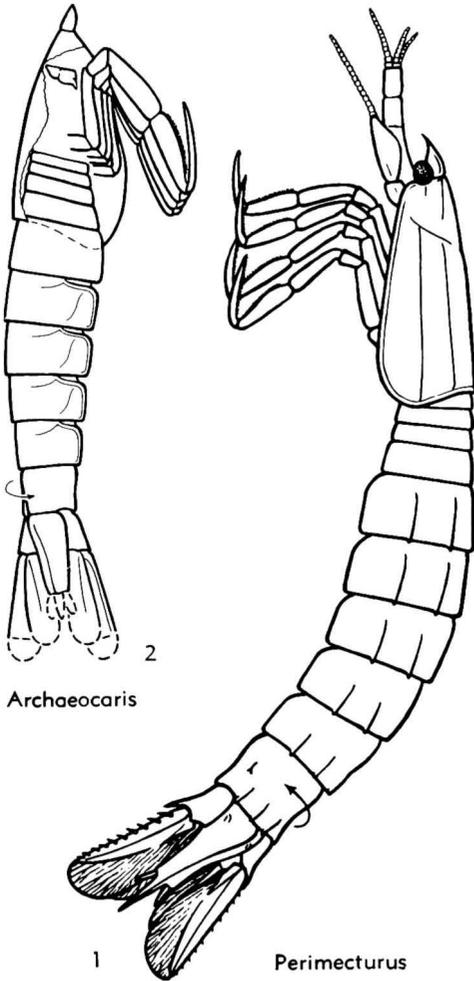
By H. K. BROOKS

[University of Florida]
[Chapter submitted August, 1964]

Extinct hoplocarids grouped in the order Palaeostomatopoda are distinguished by having the subchelate thoracic appendages (second to fifth pairs) of subequal size and

the telson with a fixed median spine and styliform furca.

These forms originally were classified by PEACH (1908) with the Mysidacea on the



absence of a marsupium and the presence of triramous antennules. Thus these fossils actually belong to the ancestral hoplocarid stock.

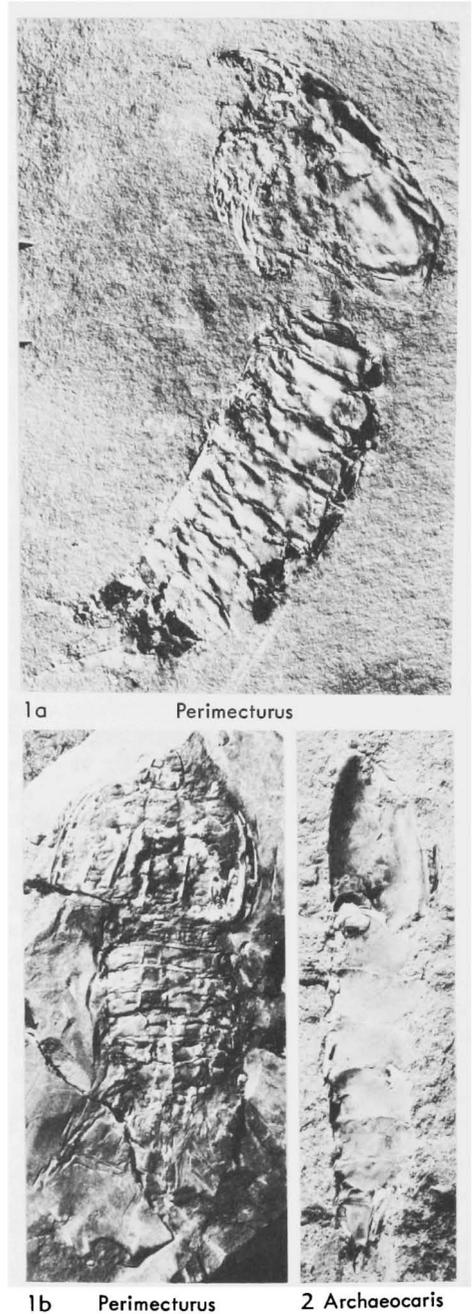


FIG. 341. Reconstruction of Palaeostomatopoda.—
1. *Perimecturus elegans* PEACH, L.Carb., Scot.; $\times 1.3$.
—2. *Archaeocaris vermiformis* MEEK, Miss., USA (Ky.); $\times 3$.

presumption that *Perimecturus* possessed a marsupium. Subchelate appendages were discovered (BROOKS, 1962) on *Archaeocaris* (Fig. 341,2) and subsequently have been seen on specimens of *Perimecturus* (Fig. 341,1) (e.g., *P. fraiponti* VAN STRAELEN, 1922).

The questionable marsupium and the biramous antennules portrayed by PEACH (226) led BROOKS (55) to refer these fossils to the superorder Eocarida. Restudy of European specimens by him has proved the

FIG. 342. Palaeostomatopoda, Perimecturidae (p. R534).

Order PALAEOSTOMATOPODA Brooks, 1962

Thoracopods subchelate, second to fifth pairs subequal, telson with fixed median spine and styliform furca. *L.Carb.(Miss.)-U.Carb.*

Family PERIMECTURIDAE Peach, 1908

Characters of order. *L.Carb.(Miss.)-U.Carb.*

Perimecturus PEACH, 1908, p. 39 [**Anthrapalaemon parki* PEACH, 1882, p. 78; OD] [= *Anthracomysis*

VAN STRAELEN, 1922, p. 39 (type, *A. rostrata*; OD, = *Anthrapalaemon parki*) (obj.)]. Carapace not covering last 4 thoracic somites; protopod of uropod with strong lateral spine; exopod with heavily chitinized outer margin and inner lobe membranous, with reticulate pattern; endopod of uropod reduced. *L.Carb.-U.Carb.*, Eu. (Scot.-Belg.). —FIG. 342,1a. *P. elegans* PEACH, *L.Carb.*, Scot.; $\times 1.3$ (55). —FIG. 342,1b. **P. parki* (PEACH), *L.Carb.*, Scot.; $\times 0.7$ (55).

Archaeocaris MEEK, 1872, p. 335 [**A. vermiformis*; OD]. Carapace smooth, covering all thoracic somites; uropods with lobate rami. *Miss.*, N.Am. (Ky.-Okla.). —FIG. 342,2. **A. vermiformis*, USA(Ky.); $\times 3$ (55).

STOMATOPODA

By L. B. HOLTHUIS¹ and RAYMOND B. MANNING²

[¹Rijksmuseum van Natuurlijke Historie, Leiden; ²United States National Museum (Contribution from The Marine Laboratory, Institute of Marine Science, University of Miami; stomatopod studies supported by NSF Grants G-11235 and GB-389)]
[Chapter submitted September, 1963]

MORPHOLOGY

BODY

The body of the Stomatopoda, like that of most Malacostraca, is divided into three sections: cephalon, thorax, and abdomen. The cephalon consists of an acron and five body somites; the thorax is formed of eight somites and the abdomen of six somites and a telson (Fig. 343).

Each somite is enclosed in a chitinous calcified exoskeleton. The dorsal part of

the exoskeleton of each somite is named tergite, the two lateral parts pleurites, and the ventral part sternite. The tergites of all somites together form the tergum and the sternites together comprise the sternum. The pleurites are usually indicated with the name pleura (sing., pleuron). Usually no distinct lines of separation are visible between the tergite, sternite, and pleurites of one somite.

Each somite bears one pair of appendages which are implanted between the pleurite

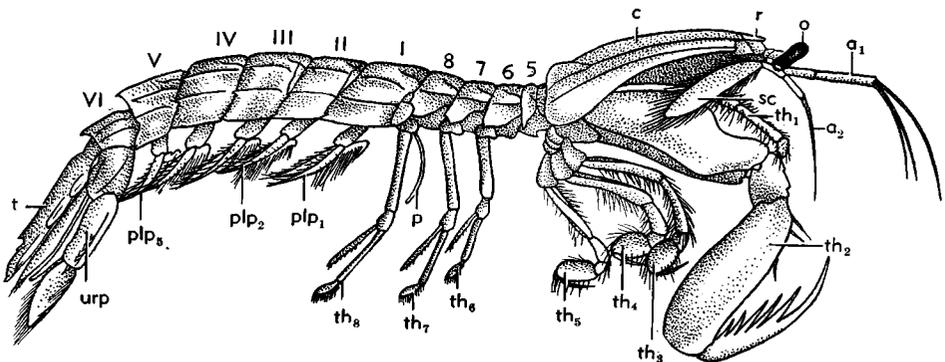


FIG. 343. *Squilla mantis*, ♂, Rec., Medit. (65). [Explanation: 5-8, fifth to eighth thoracic somites; I-VI, first to sixth abdominal somites; *a*₁, antennule; *a*₂, antenna; *c*, carapace; *o*, eye; *p*, penis; *plp*₁₋₃, first to fifth pleopods; *r*, rostrum; *sc*, scaphocerite; *t*, telson; *th*₁₋₈, first to eighth thoracopods; *urp*, uropod.]

and the sternite. The appendages consist of a single **protopod**, which bifurcates distally in branches termed **exopod** and **endopod** (Fig. 344,C). The protopod is composed of three segments (precoxa, coxa, and

basis, the first being mostly fused with the body). The endopod is formed by five segments (ischium, merus, carpus, propodus, dactylus) (Fig. 344,B). The exopod may consist of a number of segments, but

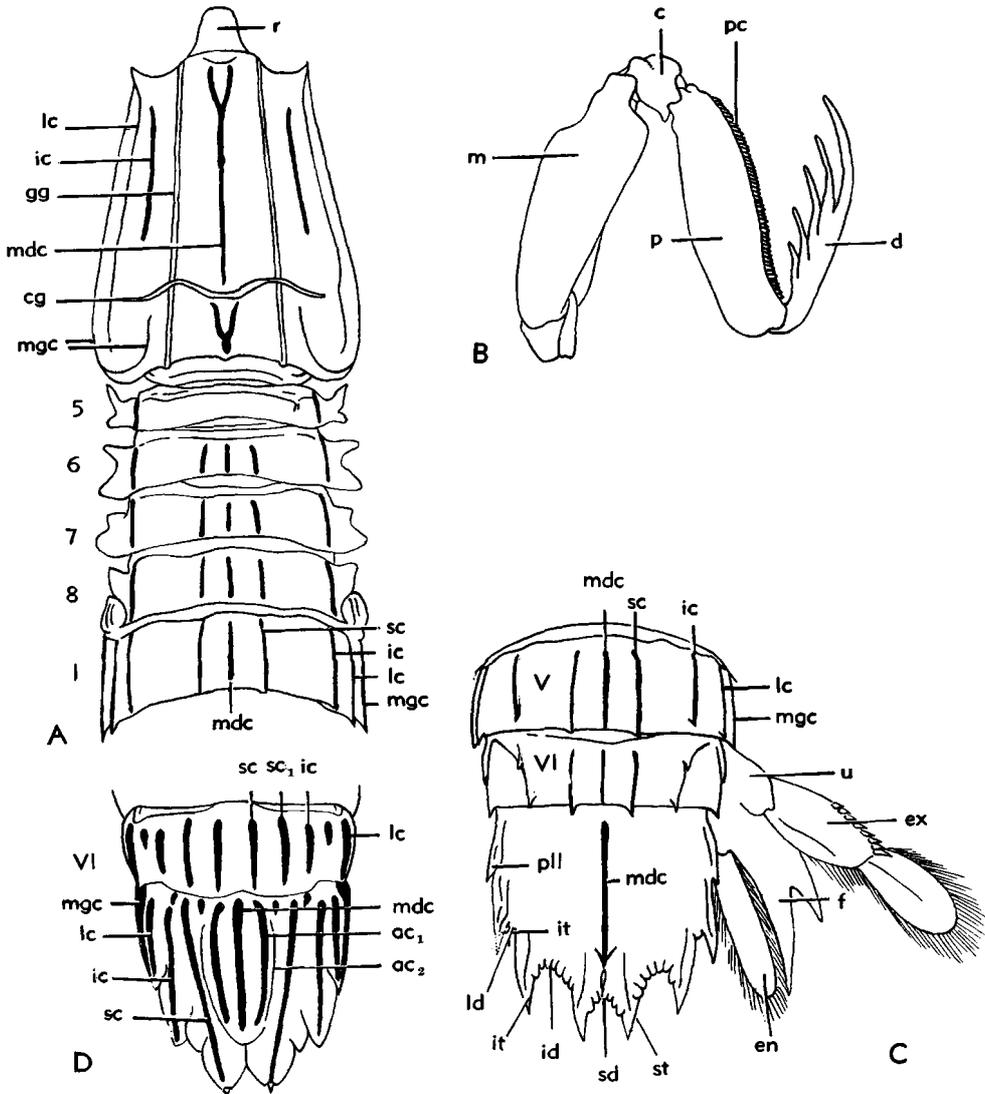


FIG. 344. *Squilla* sp. (A-C); *Odontodactylus* sp. (D).—A, thorax and first abdominal somite, dorsal; B, raptorial claw (second thoracopod); C, telson and last two abdominal somites, dorsal; D, telson and sixth abdominal somite (45). [Explanation: 5-8, fifth to eighth thoracic somites; I, V, VI, first, fifth and sixth abdominal somites; ac₁-ac₂, first and second accessory median carinae; c, carpus; cg, cervical groove; d, dactylus; en, endopod; ex, exopod; f, forked process; gg, gastric groove; ic, intermediate carina; id, intermediate denticle; it, intermediate tooth; lc, lateral carina; ld, lateral denticle; lt, lateral tooth; m, (ischio-) merus; mdc, median carina; mgc, marginal carina; p, propodus; pc, pectination of propodus; pl, prelateral lobe; r, rostrum; sc, submedian carina; sc₁, accessory submedian carina; sd, submedian denticle; st, submedian tooth; u, uropod (164).

commonly is reduced or entirely absent. The coxa may be provided on its outer margin with an appendage (**epipod**). **Endites** may be present on the inner margin of the coxa, basis, and ischium.

The acron (also named ophthalmic somite) and the antennular (=first cephalic) somite are not covered by the carapace. The other cephalic somites (second to fifth) and the first four thoracic somites are more or less distinctly fused and covered by the carapace. The carapace is a large unsegmented dorsal shield which covers the above-mentioned fused somites and overhangs (but does not enclose) the bases of the first five thoracopods (Fig. 343). Anteriorly it bears a flattened median rostrum, with which it is articulated. The rostrum is a small, usually triangular plate, which partly or entirely covers the ophthalmic and antennular somites; in some forms it ends in one or more spines.

The outer surface of the carapace is marked by two distinct longitudinal grooves (gastric grooves) which start on either side of the base of the rostrum and extend to the posterior margin of the carapace. A usually very distinct transverse **cervical groove** is visible in the posterior half of the carapace. Apart from these grooves, the upper surface of the carapace may be ornamented with a number of longitudinal **carinae**: a median carina, which may bifurcate anteriorly, before and behind the cervical groove; two lateral carinae, which extend backward from the anterolateral angle of the carapace nearly to the posterior margin; two intermediate carinae in the anterior part of the carapace between the **gastric groove** and the lateral carinae; and two marginal carinae which extend along the lateral margin of the carapace and may curve inward and forward near their posterior end, forming a loop around the end of the lateral carina (Fig. 344, *A*). Gastric grooves are present in all Stomatopoda but the cervical groove and carinae may be indistinct or even partly or entirely absent.

The last four thoracic somites (fifth to eighth) are free and not covered by the carapace; in some, parts of the fused thoracic somites are also visible behind the carapace. All six abdominal somites are free and well developed (Fig. 343). The

free thoracic and the first five abdominal somites may show eight longitudinal carinae (two submedian, two intermediate, two lateral, and two marginal); the sixth abdominal somite usually has but six carinae (Fig. 344, *D*). These carinae may end in posterior spines. Part or all of the carinae may be absent, while in some species secondary ridges are placed between the original eight carinae.

The telson is well developed; in some it is fused with the sixth abdominal somite. As a rule it shows six large teeth along its margin (two submedian, two intermediate, and two lateral); anterior to each lateral tooth the margin may show a prelateral lobe. Some forms possess denticles between the marginal large teeth; those between the submedian teeth are called submedian denticles; intermediate denticles are placed between the submedian and intermediate teeth; usually a single lateral denticle is found between the intermediate and lateral teeth (Fig. 344, *D*). The tips of the submedian teeth may bear a movable spinule. In the genus *Scudda* the margin of the telson is provided with movable spines. The telson may show several longitudinal carinae (one median, one or more pairs of submedians, one pair of intermediates, one pair of laterals, and one pair of marginals); additional longitudinal or irregular carinae may be present. In some forms the telson is ornamented with spines, bosses, or grooves, or may have a quite aberrant form.

APPENDAGES

The eyes, which are placed on the acron (ophthalmic somite) are well developed and stalked; their cornea may be very wide, so that the eyes are T-shaped, but also they may be strongly reduced.

The antennules consist of a three-segmented peduncle and two flagella, the ventral one of which is deeply cleft and divided into two slender branches, so that three flagella actually occur (Fig. 343).

The antennae have a two-segmented peduncle and a two-segmented exopod; the first segment of the exopod is short, the second large, flat and oval, forming the so-called antennal scale or scaphocerite. The

endopod consists of a peduncle of three segments and a many-jointed flagellum.

The mandibles are borne by the third cephalic somite. They are heavy and calcareous and consist of a basal pars molaris and a toothed pars incisiva; a palp may be present or absent.

The maxillules (also known as first maxillae) are carried by the fourth cephalic somite. They consist of two segments (coxa and basis), each with a distinct endite; an exopod is absent, while the endopod is visible as an unsegmented short palp.

The appendages of the fifth cephalic somite are the maxillae (or second maxillae). They consist of four segments, the first of which is more or less cylindrical and the others flattened; the first and second segments are each provided with an endite, that of the second segment being bilobed.

Appendages of the first five thoracic somites are commonly named maxillipeds, but it seems better to use the term thoracopods in order to avoid confusion. The thoracopods consist of seven segments designated as precoxa, coxa, basis, ischimerus (fused ischium and merus forming a single segment usually named merus), carpus, propodus, and dactylus. No exopod occurs, except in some early larvae. An epipod may be present at the outside of the base of these legs. In all first five thoracopods the dactylus and propodus together form a subchela.

The first thoracopods are very slender and their subchelae very short and small.

The second thoracopods are the strongest of all, forming powerful raptorial claws which are the main offensive and defensive weapons of the animal (Fig. 343). Their dactylus is elongate, commonly armed with teeth on the side that closes against the propodus, which is heavy and may also be provided with spines or teeth on the side turned toward the dactylus. The teeth of the propodus may be of two kinds—well-spaced, slender and sharp, or short and blunt, placed so close together that no interspaces are left. Strong and sharp movable spines may be present also on the basal part of the inner surface of the pro-

podus. Prey is caught between the dactylus and propodus, which come together like a pocket-knife (similar to the raptorial claw of a praying-mantis); the teeth and spines help to get a better hold of the captured animal. The carpus is short but the ischimerus is elongate and heavy.

The third, fourth, and fifth pairs of thoracopods are very similar, being more robust than the first but very much shorter and less powerful than the second. They are used for breaking up food and for bringing it to the mouth.

The last three thoracopods (sixth to eighth) are of an entirely different shape and completely lack subchelae. Their protopod consists of three cylindrical segments, of which the second is longer and more slender than the other two; the exopod consists of two segments and the endopod of one or two segments. The segments of the exopod are elongate, being stronger and longer than those of the endopod, the first of which is very short, the second narrow and slender or oval in shape.

In males a long tube-shaped copulatory organ protrudes from the inner side of the basal segment of the protopod of the last thoracopod.

The appendages of the first five abdominal somites (pleopods) are laminar (Fig. 343). Their protopod consists of a single segment, while the exo- and endopods also consist of a single flat segment. The endopod bears an appendix on the inner margin (appendix interna or stylamblys); at the end of this appendix are some retinacula with which the left appendix can attach itself to the right. The exopods bear the branchiae, which are implanted in the basal part of their anterior surface.

In males the endopod of the first pleopods is somewhat modified for copulation. Its modifications include a large appendix interna with retinacula, a hook-shaped process and a tube-shaped process. The exopod of the second pleopod of the males shows an incision in the distal margin, while a strong rib extends from this incision proximally.

The appendages of the sixth abdominal somite, termed uropods, together with the

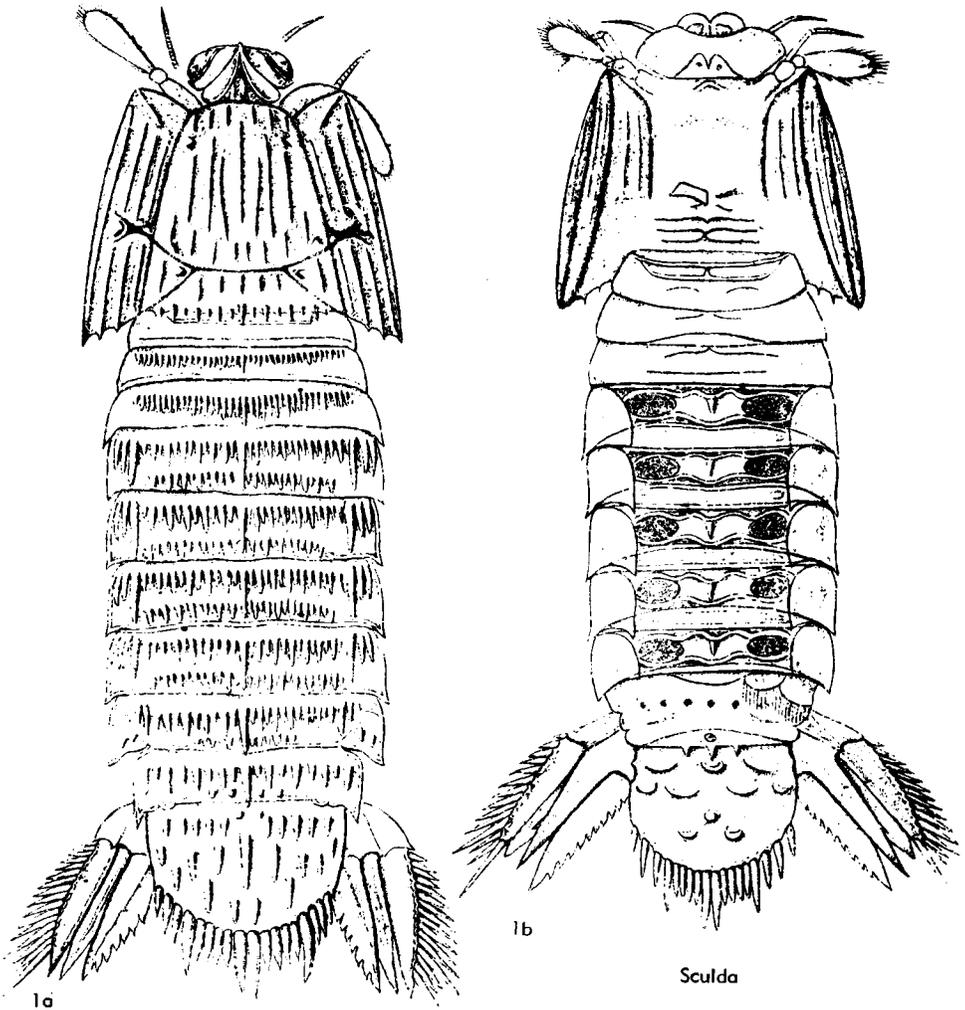
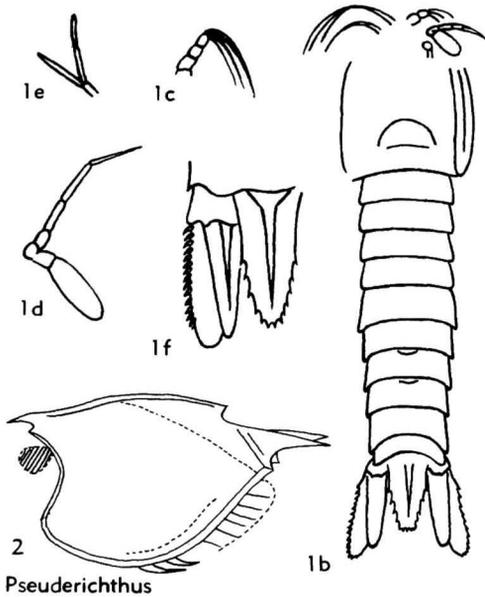


FIG. 345. Sculdidae (p. R546).

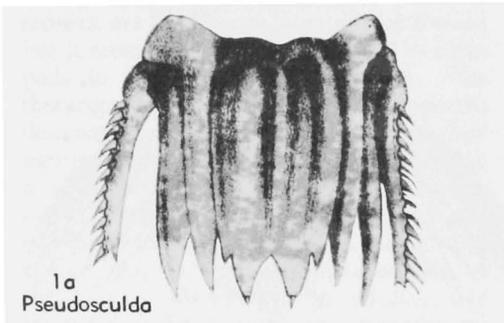
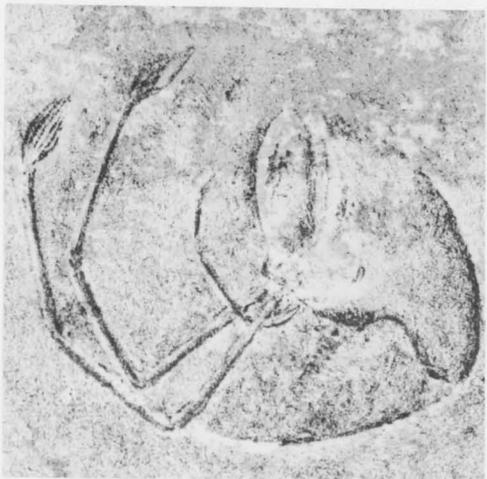
telson form the tail fan (Fig. 343; 344,C,D). The protopod consists of one segment and the endopod also is one-segmented; the exopod is formed of one (Sculdidae) or two segments (Squillidae). The protopod is ventrally prolonged between the bases of the exo- and endopod into a process which may end in two sharp teeth, but may also have a different shape. The basal segment of the exopod is armed on its outer margin with movable teeth, which may be blunt; the second segment of the exopod, as well as the endopod, are unarmed.

SIZE

Representatives of the fossil family Sculdidae are small to medium-sized. Species of *Sculda* may attain a length of 46 mm. and specimens of *Pseudosculda* 55 mm. in length are known; the "larval" genera *Pseuderichthus* and *Clausia* are respectively up to 24 and 50 mm. long. The smallest squillid is *Hoplosquilla acanthurus* (TATTERSALL), which is 10 to 11.5 mm. long, and the largest are species of *Harpiosquilla* and *Lysiosquilla*, which may become more than 300 mm. in length.



Pseuderichthus

1a
Pseudosculda

3

Clausia

FIG. 346. Scudidae (p. R546).

ONTOGENY

The Stomatopoda are oviparous. The eggs, which are carried between the third and fifth thoracopods, hatch either in the antizoea or in the pseudozoea stages, and pass through a number of pelagic stages before attaining the first postlarval (or littoral) stage. The larvae are of various types and so strongly different from the adults that they have been described as distinct genera (*Erichthus*, *Alima*, *Smerdis*, etc.) and even considered to represent a distinct family (Erichthidae). The entire development is known for only a few species of stomatopods; most described "larval species" have not yet been assigned to corresponding adult species. Some fossils have been interpreted as stomatopod larvae (*Protozoea*, *Clausia*, *Pseuderichthus*), but their status remains doubtful. VAN STRAELEN (1938) has reported on fossils from the Upper Cretaceous of Lebanon identified only as stomatopod larvae.

HABITAT AND DISTRIBUTION

Stomatopods are almost exclusively marine. A few species have been reported from brackish water, but these are exceptions. Most of them inhabit shallow water, but deep-sea forms are known; the greatest known depth from which a living stomatopod has been taken is 500-520 fathoms (900-936 m.), viz., *Bathysquilla microps*.

Stomatopods are practically restricted to tropical and subtropical seas, in which they are found all over the world. A few species extend into temperate seas (*Squilla desmarestii*, found northward into the southern North Sea; *S. empusa* and *Nannosquilla grayi* north to Massachusetts, USA; *S. oratoria*, as far north as Hokkaido, Japan; *Pseudosquillaopsis lessonii* and *Hemisquilla ensigera*, as far north as southern California). Southward the range of the Stomatopoda extends to South Australia, South Africa, and the Cape Horn region.

GEOLOGICAL DISTRIBUTION

Fossil remains of stomatopods are scarce and usually very imperfectly preserved. The oldest finds which can be identified with

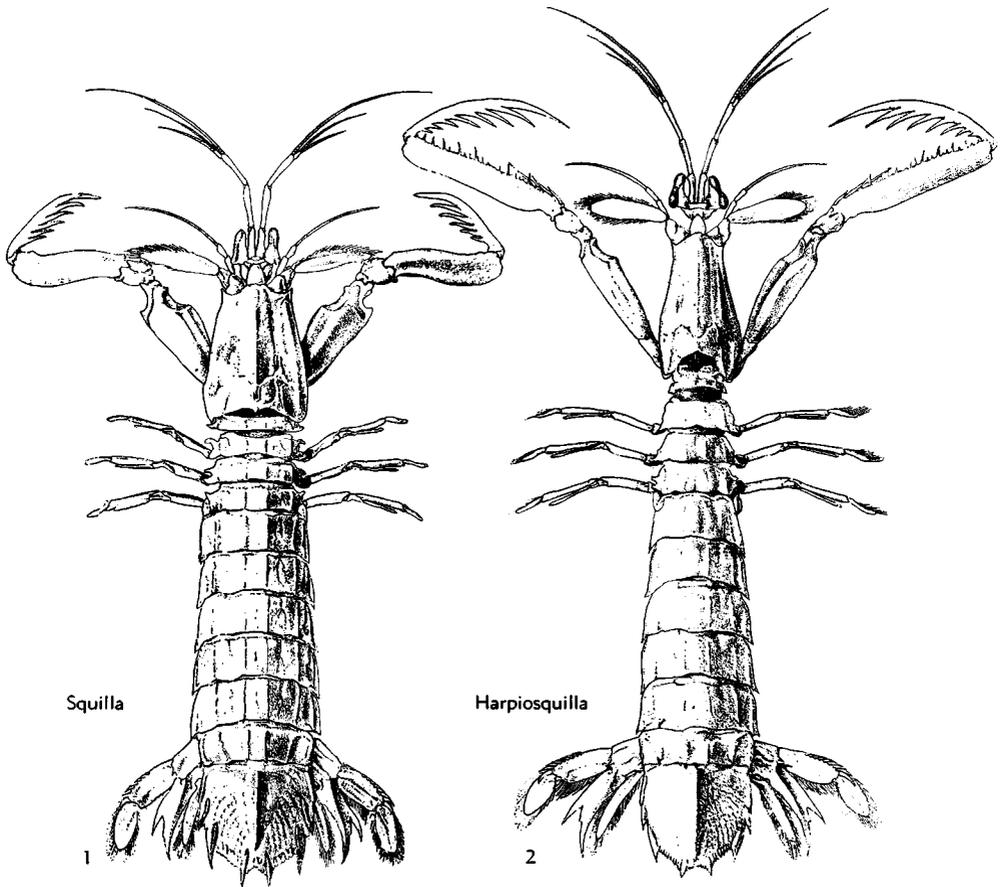


FIG. 347. Squillidae (p. R546-R549).

certainty as belonging to this group are from the Upper Jurassic, three species of *Sculda* having been found in the lithographic limestone of Solenhofen, Bavaria. The genus *Sculda* is found in the Cretaceous, where *Pseudosculda* also made appearance. True Squillidae also are known from the Upper Cretaceous, for BERRY (22) has described from beds of this age in Angola a squillid named *Chloridella angolia*, which may belong to the genus *Squilla*. REMY & AVNIMELECH (249) described a new species, *Eryon yehoachi*, from the Upper Cretaceous (Campanian) of Israel. As pointed out by Dr. M. F. GLAESSNER (in litt.), the figure shows that the specimen is not an eryonid but a stomatopod, of which only the telson and part of the sixth abdominal somite are preserved. The specimen may well belong

to the genus *Squilla*, but it is too incomplete for certain identification.

Fossils described as *Squilla cretacea* (SCHLÜTER, 1868), from the Cretaceous of West Germany, and *S. antiqua* (MÜNSTER, 1842), from the Eocene of northern Italy, certainly do not represent *Squilla* but may belong to the Sculdidae; the available evidence is insufficient to decide this with certainty. *Squilla wetherelli* (WOODWARD, 1879), from the Eocene of England, and *Chloridella sonomana* (RATHBUN, 1926), probably from the Pliocene of California, may belong to *Squilla*. *Squilla*, *Hemisquilla*, and *Gonodactylus*, all of which contain extant species, are represented by Tertiary fossils. As stated above, the true identity of *Squilla antiqua* MÜNSTER from the Eocene is unknown. *Squilla miocenica*

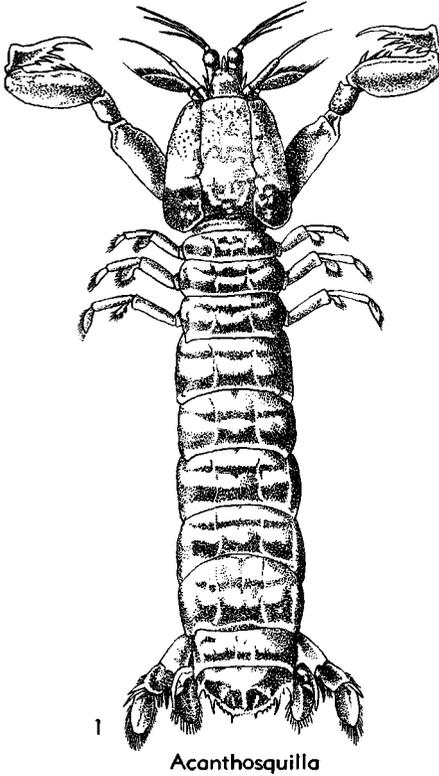


FIG. 348. Squillidae (p. R548).

LOVISATO, 1894, from the Miocene of Sardinia and Catalonia (Spain), is only known from raptorial dactyli and its generic identity is uncertain.

CLASSIFICATION

LINNÉ (1758) placed the Stomatopoda, together with the Decapoda and some other groups, in the genus *Cancer*. FABRICIUS (1775) first removed them, together with the macrurous Decapoda, to the genus *Astacus* and later (1781) erected the genus *Squilla* to contain all stomatopods known at that time. LATREILLE (1802-03) was the first to separate the Stomatopoda from the Decapoda as a distinct group; he divided the Malacostraca into two orders, which he designated as Decapoda and Branchiogastra. The latter contained families named Squillares [Stomatopoda, Mysidacea] and

Gammarinae [Amphipoda]. In 1817 LATREILLE erected the order Stomapodes which he restricted essentially to Stomatopoda as recognized today, for he transferred the mysids to his section Schizopodes of the order Decapoda. In 1819 LATREILLE also placed the genus *Phyllosoma* in the Stomatopoda [sic] and in 1825 divided this order into two families, Unipeltata [containing true Stomatopoda] and Bipeltata [*Phyllosoma*]. H. MILNE-EDWARDS (1837) divided the "famille des Unicuirassés" (=Unipeltata) in tribes named Erichthiens (containing three genera of larval stomatopods—*Squillerichthus*, *Alima*, *Erichthus*) and Squilliens (containing three genera of adult

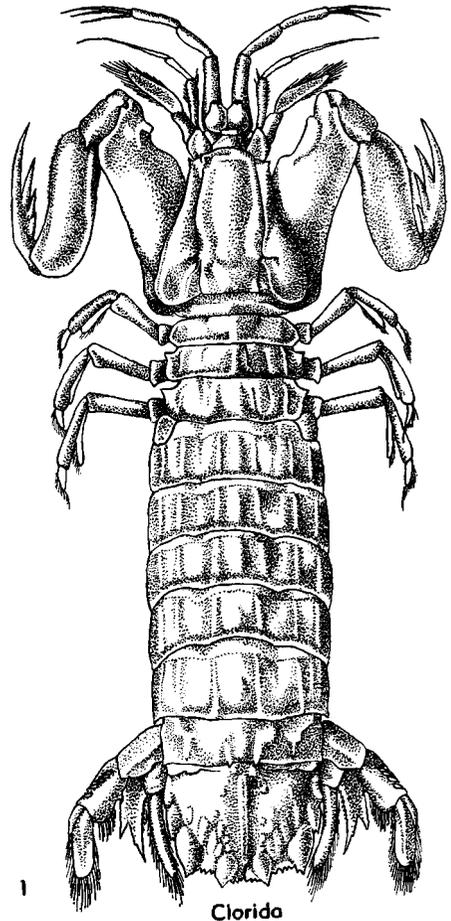


FIG. 349. Squillidae (p. R548).

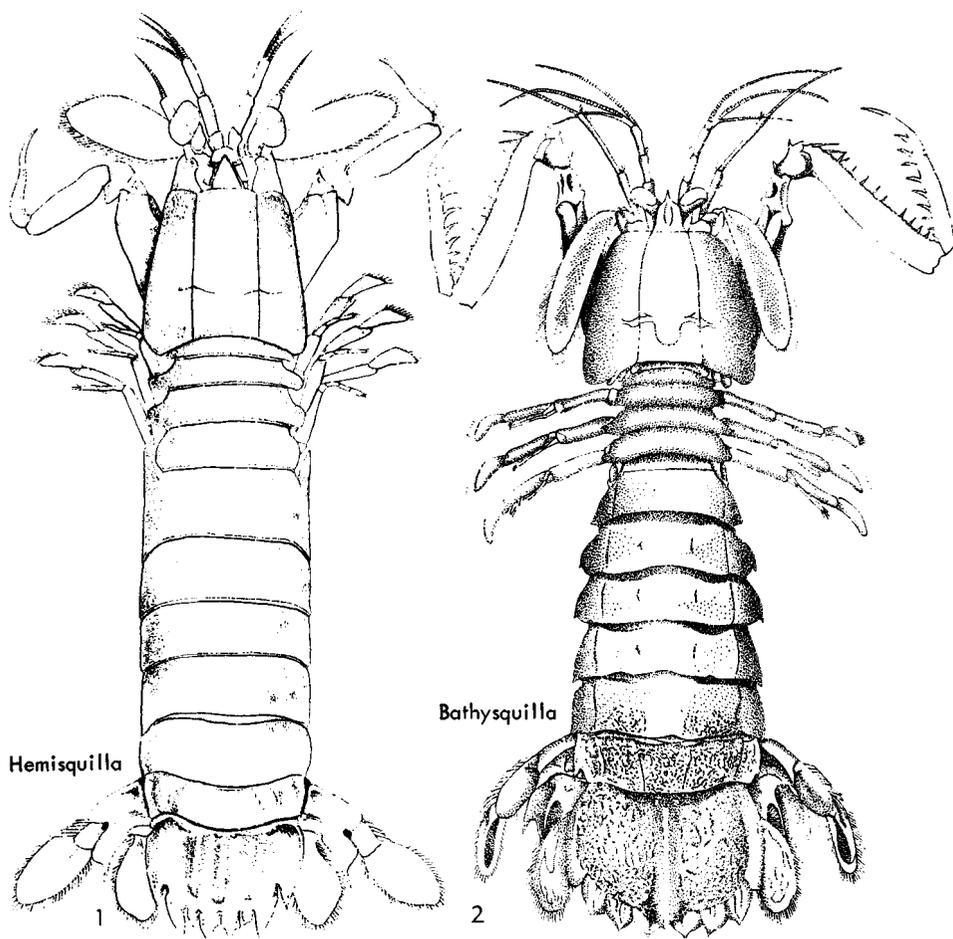


FIG. 350. Squillidae (p. R548-R550).

stomatopods—*Squilla*, *Gonodactylus*, *Coronis*). Later MILNE-EDWARDS (1852) restricted the order Stomatopoda [*sic*] to the true stomatopods. Since that time the order has been recognized by most carcinologists in its modern sense (i.e., as a separate taxon equal in rank to the Decapoda). In 1904 CALMAN divided the crustacean “series” Eumalacostraca into four “divisions,” one of which he named Hoplocarida, which contained the Stomatopoda as its only order; in this way CALMAN quite correctly emphasized the independence of the order and its great difference from the other crustacean orders.

Recent studies on the embryology (SHIHO, 1942) and internal morphology (SIEWING,

1956) of the Stomatopoda seem to indicate that they arose as an offshoot of the main malacostracan line sometime after the Nebaliacea.

Classification of the Stomatopoda is rather simple. The first attempt to divide the group was made by H. MILNE-EDWARDS (1837) when he recognized the tribes called Erichthiens and Squilliens. When it was found that the Erichthiens were merely the larvae of Squilliens, only one family, Squillidae, was recognized among Recent stomatopods, a situation which exists at present. DAMES (1886) erected the families Sculdidae and Pseudosculdidae for fossil stomatopods. KEMP (1913), in his important monograph of the Indo-West Pacific stomatopods,

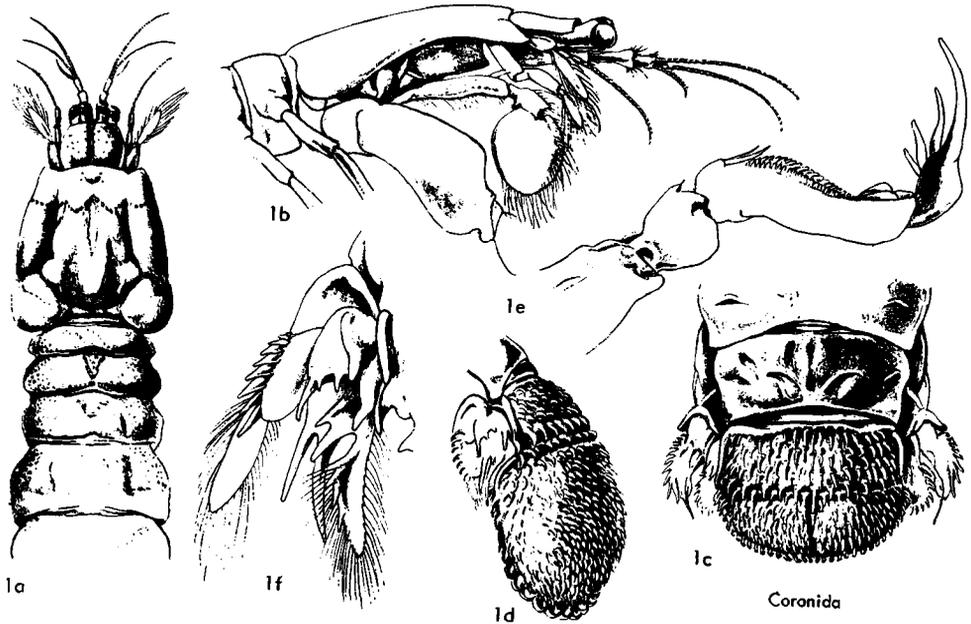


FIG. 351. Squillidae (p. R548).

recognized the Squillidae and Sculdidae, but ignored the Pseudosculdidae. Differences considered by some to distinguish the Sculdidae and Pseudosculdidae now are thought to be based on misinterpretation of fossil material, and thus evidence for keeping these families separate is insufficient.

The number of genera of Stomatopoda is limited. In all, only eight genera of fossil Stomatopoda have been proposed—*Sculda* (MÜNSTER, 1840), *Buria* (GIEBEL, 1857), *Necroscilla* (WOODWARD, 1879), *Pseudosculda* (DAMES, 1886), *Pseuderichthus* (DAMES, 1886), *Protozoa* (DAMES, 1886), *Clausia* (OPPENHEIM, 1888), and *Squillites* (SCOTT, 1938). Three of these have been removed subsequently from the Stomatopoda. GLAESSNER (1957, p. 178) and H. K. BROOKS (1962) have shown that *Necroscilla* is a synonym of *Pygocephalus* (HUXLEY, 1857), and BROOKS has demonstrated that *Squillites* is a syncarid. ROGER (1946) indicated that *Protozoa* (spelled by him incorrectly as *Protozoe*) is not a stomatopod but a branchiopod. *Buria* is a synonym of

Sculda. *Pseuderichthus* is of uncertain status and may be the larva of either *Sculda* or *Pseudosculda*, or for that matter, of another genus. *Clausia* is considered by some authors as possibly a sculdid larva, while others refuse to recognize it as a stomatopod; its status is highly dubious.

As to Recent Stomatopoda, 17 genera have been described on larval forms and 29 on adults. Until very lately the number of stomatopod genera recognized by carcinologists was about eight, but there is now a tendency to split the old, rather unwieldy genera, which often are assemblages of several not very closely related groups (SERÈNE, 269; MANNING, 190). In this chapter of the *Treatise* the most recent taxonomic partitions have been taken into account, and a total of 24 genera (including fossil and Recent) are recognized.

A tabulation of suprageneric divisions of the Stomatopoda showing their stratigraphic occurrence and numbers of contained genera is given on page R116.

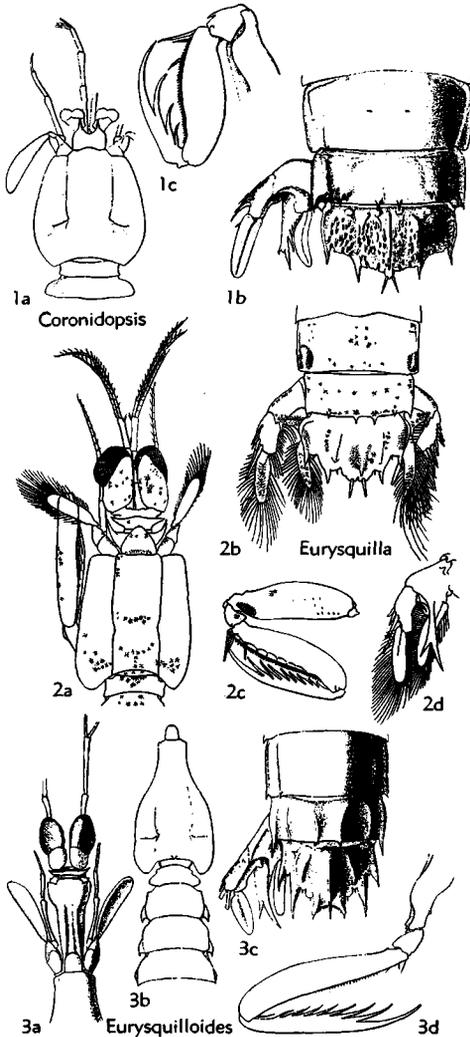


FIG. 352. Squillidae (p. R548-R549).

SYSTEMATIC DESCRIPTIONS

Order STOMATOPODA

Latreille, 1817

[*nom. correct.* VOIGT, 1836, p. 188 (*pro* Stomapodes LATREILLE, 1817, p. 40)] [=Unipeltata LATREILLE, 1825, p. 283; Squilloidea DANA, 1852, p. 614; Squillacea, BOAS, 1883, p. 488]

Cephalothorax partly covered by well-developed carapace, both acron and antennular somite as well as four posterior thoracic somites being free, not covered by carapace; movable rostrum present; eyes

stalked. Protopods of antennae each composed of two segments and exopods likewise two-segmented; first five thoracopods subchelate, uniramous, second very strong, forming powerful raptorial claw, last three biramous and not chelate; thoracopods with protopod consisting of three segments. First five abdominal somites each bearing pair of pleopods which carry branchiae; each pleopod provided with appendix interna. [Stomatopods are oviparous. After oviposition the eggs are not fastened to the body, but carried between the third to fifth thoracopods or deposited in burrows made by these animals. Larval development includes a number of pelagic stages.] *Jur.-Rec.*

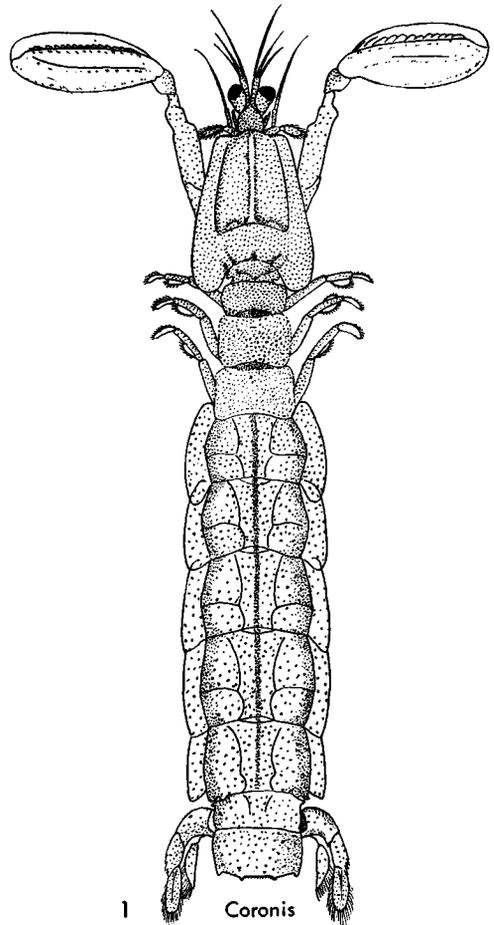
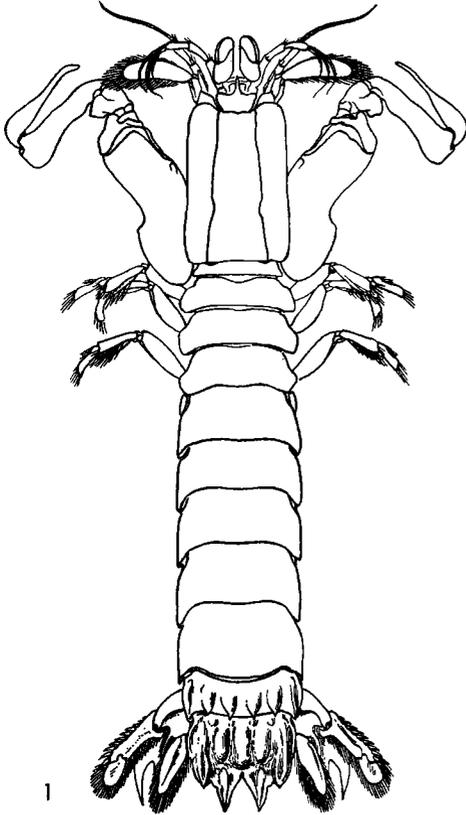


FIG. 353. Squillidae (p. R548).



Gonodactylus

FIG. 354. Squillidae (p. R549).

Family SCULDIDAE Dames, 1886

[Sculdidae DAMES, 1886, p. 565] [=Pseudosculdidae DAMES, 1886, p. 567]

Exopod of uropod consisting of single segment, with numerous movable spines on outer margin. *Jur.-Cret.*

Sculda MÜNSTER, 1840, p. 19 [**S. pennata*; OD, M] [=*Buria* GIEBEL, 1857, p. 382 (type, *B. rugosa*)]. Telson wider than long, margin lacking teeth but with numerous movable spines; inner margin of uropodal exopod with teeth. *U. Jur.-U. Cret.*, Bavaria-Lebanon.—FIG. 345, *I*. **S. pennata*, *U. Jur.*, Bavaria; *1a, b*, dorsal, ventral, approx. $\times 3$ (169).

?*Clausia* OPPENHEIM, 1888, p. 713 [non *Clausia* CLAPARÈDE, 1863] [**C. lithographica*; OD, M]. Larval stage of uncertain status. [Possibly not even a stomatopod.] *U. Jur.*, Bavaria.—FIG. 346, *3*. **C. lithographica*; side view, approx. $\times 2$ (220).

Pseudericthus DAMES, 1886, p. 571 [non *Pseu-*

derichthus BROOKS, 1886 (which has priority)] [**P. cretaceus*; OD, M]. Larval stage, probably of one of foregoing genera. *U. Cret.*, Lebanon.—FIG. 346, *2*. **P. cretaceus*; side view, $\times 1.3$ (255). *Pseudosculda* DAMES, 1886, p. 566 [**Sculda laevis* SCHLÜTER, 1872, p. 195; OD, M]. Telson longer than wide, with fixed teeth; inner margin of uropodal exopod without teeth. *Cret.*, Lebanon.—FIG. 346, *1*. **P. laevis* (SCHLÜTER); *1a, f*, tail fan, enl. (255, 265); *1b*, animal, dorsal view, enl. (255); *1c*, antennule, enl. (255); *1d*, antenna, enl. (255); *1e*, 6th thoracopod, enl. (255).

Family SQUILLIDAE Latreille, 1803

[*nom. correct.* WHITE, 1847, p. 83 (pro *Squillares* LATREILLE, 1803, p. 36)] [=Saonides BILLBERG, 1820, p. 13; Erichthidae WHITE, 1847, p. 82; Chloridellidae RATHBUN, 1900, p. 155; Squillinae + Lysiosquillinae + Gonodactylinae GIESBRECHT, 1910, p. 148; Saoidae POULSEN, 1956, p. 133]

Exopod of uropod consisting of two segments, basal one bearing movable spines on outer margin. *Cret.-Rec.*

Squilla FABRICIUS, 1787, p. 333 [non *Squilla* GRONOVIVS, 1760; O. F. MÜLLER, 1776; SCOPOLI, 1777; O. FABRICIUS, 1780 (all suppressed by ICZN)] [**Cancer mantis* LINNÉ, 1758, p. 633; SD LATREILLE, 1810, p. 422 (ICZN Official List, no. 619)] [=*Squilla* FABRICIUS, 1781, p. 514 (*nom.*

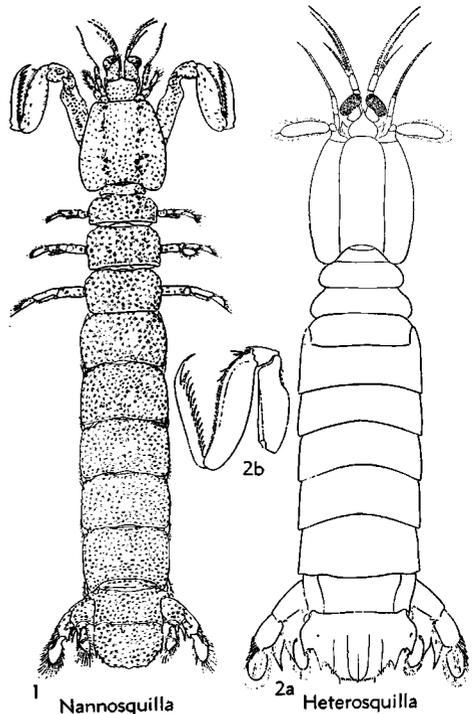


FIG. 355. Squillidae (p. R550-R551).

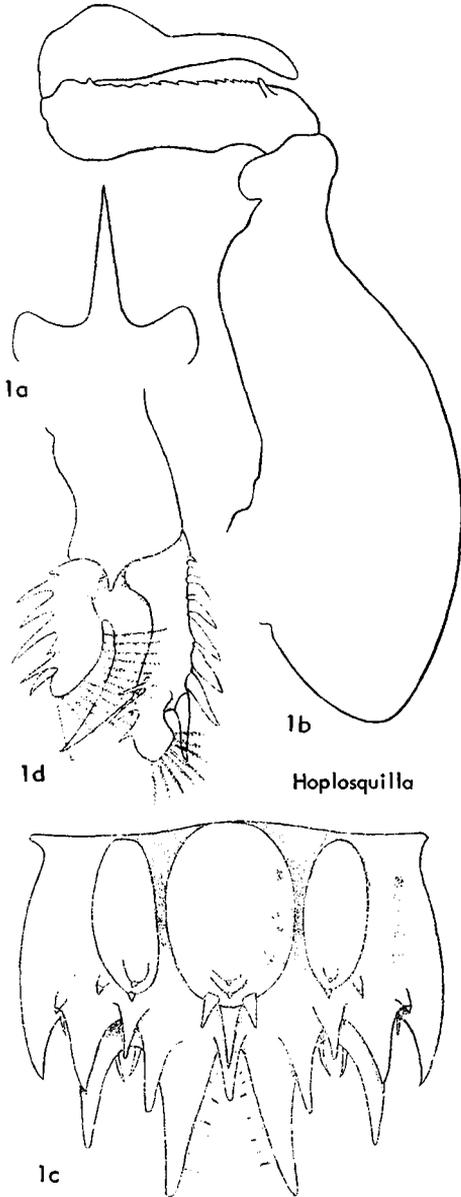


FIG. 356. Squillidae (p. R550-R551).

nud.) (obj.); *Entomon* LATREILLE, 1796, p. 197 (obj.); *Alima* LEACH in TUCKEY, 1817, unnumbered plate (type, *A. hyalina*); *Sao* BILLBERG, 1820, p. 135 (obj.); *Squillerichthus* H. MILNE-EDWARDS, 1837, p. 497 (type, *S. typus*); *Halmonectes* GUÉRIN in SAGRA, 1855, pl. 3, fig. 11 (type, *H. souleyetii*); *Hyalopelta* GUÉRIN in SAGRA, 1857, p. lxiv (type, *Alima tetracanthura* GUÉRIN,

1830, pl. 4; SD HOLTHUIS & MANNING, herein); *Pterygosquilla* HILGENDORF, 1890, p. 172 (type, *P. laicauda*)]. Cornea broader than eye stalk; rostrum trapezoidal or triangular, without spines; cervical groove distinct; abdomen with longitudinal carinae; telson with sharp median carina; tips of submedian teeth movable or fixed; submedian denticles present, usually more than 4 intermediate denticles present; dactylus of raptorial claw with more than 3 teeth (including terminal one), upper margin of propodus with even pectination of closely placed, short, blunt spinules. ?*Cret.*, *Rec.*, cosmop. (tropical-temperate).—FIG. 343. **S. mantis* (LINNÉ), *Rec.*, E.Atl.; lat. view, entire

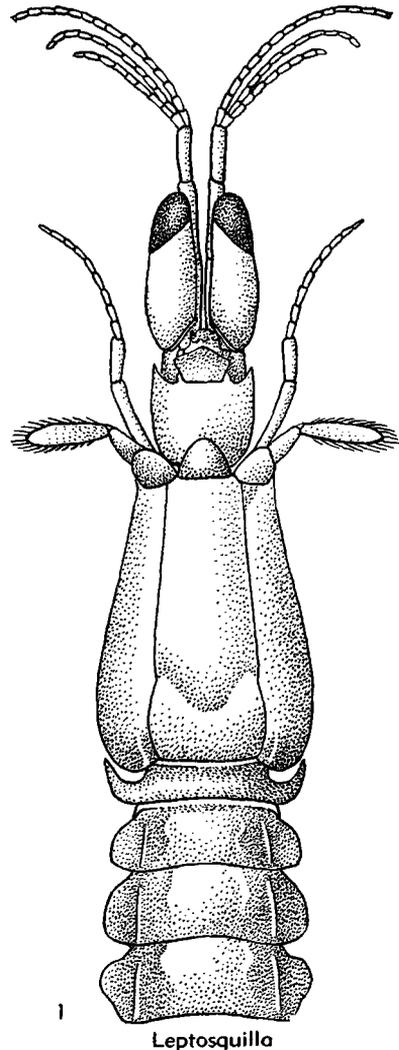


FIG. 357. Squillidae (p. R551).

animal, approx $\times 1$ (65).—FIG. 347, *I. S. oratoria* DE HAAN, Rec., Japan; dorsal, approx. $\times 1$ (137).

Acanthosquilla MANNING, 1963, p. 319 [**Lysiosquilla multifasciata* WOOD-MASON, 1895, p. 1; OD]. Similar to *Nannosquilla* but telson with dorsal row of 5 or more spines above posterior margin. Rec., circumtropic.—FIG. 348, *I. *A. multifasciata* (WOOD-MASON), India; dorsal, $\times 2$ (325).

Bathysquilla MANNING, 1963, p. 323 [**Lysiosquilla microps* MANNING, 1961, p. 693; OD]. Position uncertain; telson with blunt median carina and all 4 pairs of marginal teeth with movable apices. Rec., W.Atl.-Indo-W.Pac.—FIG. 350, *2. B. crassispinosa* (FUKUDA), Japan; dorsal, $\times 0.45$ (102).

Clorida EYDOUX & SOULEYET, 1842, p. 264 [**C. latreillii*; SD FOWLER, 1912, p. 302] [= *Chloridus* DANA, 1852, p. 615 (*nom. null.*); *Chlorida* MIERS, 1880, p. 13 (*non* AUDINET-SERVILLE, 1834) (*nom. null.*); *Chloridella* MIERS, 1880, p. 13 (*nom. van.*) (obj.)]. Related to *Squilla* but distinguished by having eyes with stalk broader than cornea in combination with movable apices of submedian teeth of telson. Rec., Indo.-W.Pac.—FIG. 349, *1. *C. latreillii* EYDOUX & SOULEYET, India; dorsal, $\times 1.5$ (325).

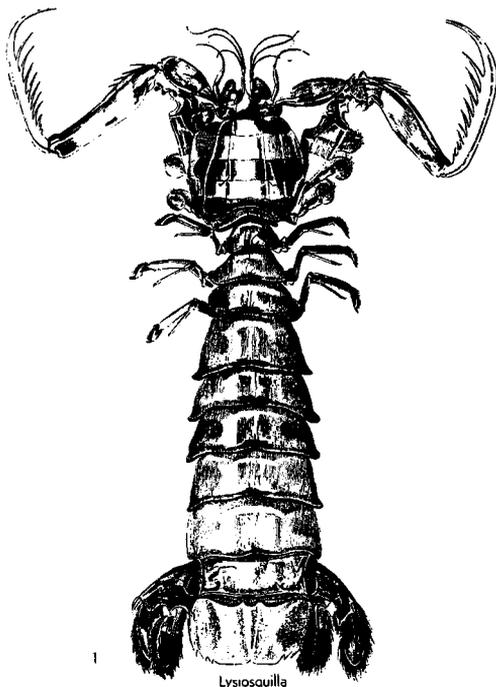


FIG. 358. Squillidae (p. R551).

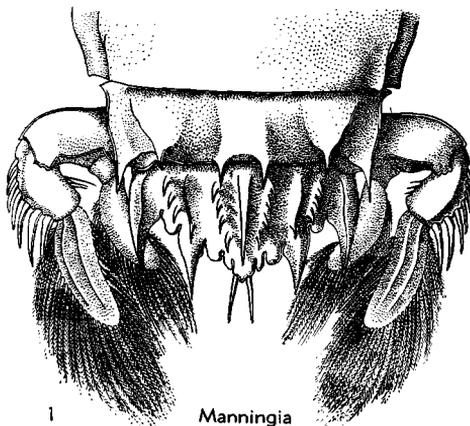


FIG. 359. Squillidae (p. R551).

Coronida BROOKS, 1886a, p. 84 [**Squilla bradyi* A. MILNE-EDWARDS, 1869, p. 137; SD BALSS, 1938, p. 130] [= *Coroniderichthus* HANSEN, 1895, p. 81 (obj.), SD HOLTHUIS & MANNING, herein]. Similar to *Lysiosquilla*, but with 4 teeth on raptorial claw and telson armed with spinules, tubercles, or irregular carinae. Rec., circumtropic except W.Atl.—FIG. 351, *1. *C. bradyi* (A. MILNE-EDWARDS), Cape Verde Is.; *1a, b*, ant. part of body, dorsal, lat., $\times 8$; *1c, d*, post. part of abdomen, dorsal, lat., $\times 8$; *1e*, raptorial claw, $\times 10$; *1f*, uropod, ventral, $\times 13$ (125).

Coronidopsis HANSEN, 1926, p. 19 [**C. bicuspis*; OD, M]. Similar to *Manningia* but rostrum with 2 apical spines. Rec., Indonesia.—FIG. 352, *1. *C. bicuspis*; *1a*, ant. part of body, $\times 3.5$; *1b*, post. part of abdomen, $\times 4.5$; *1c*, raptorial claw, $\times 4$ (143).

Coronis DESMAREST, 1823, p. 345 [**C. scolopendra* LATREILLE, 1828, p. 474; SM LATREILLE, 1828, p. 474]. As in *Nannosquilla* but telson without posterior false eave. Rec., W.Atl.—FIG. 353, *1. C. excavatrix* (BROOKS), off USA (N. Car.); dorsal, $\times 2$ (60).

?**Erichthalima** BROOKS, 1886, p. 83 [**E. synthetica* BROOKS, 1886, p. 111; SM]. Based on larval stage of doubtful affinity. Rec., Atl.

Eurysquilla MANNING, 1963, p. 314 [**Lysiosquilla plumata* BIGELOW, 1901, p. 156; OD]. Like *Squilla* in having sharp median carina on telson but with less than 4 intermediate marginal denticles; also similar to *Manningia* but rostrum with at most single apical spine and dactylus of raptorial claw with more than 7 teeth. Rec., W.Atl.-E.Pac.-Gulf of Aden.—FIG. 352, *2. *E. plumata* (BIGELOW), Puerto Rico; *2a*, ant. part of body, $\times 11$; *2b*, post. part of abdomen, dorsal, $\times 11$; *2c*, raptorial claw, $\times 11$; *2d*, uropod, $\times 11$ (37). **Eurysquilloides** MANNING, 1963, p. 315 [**Squilla*

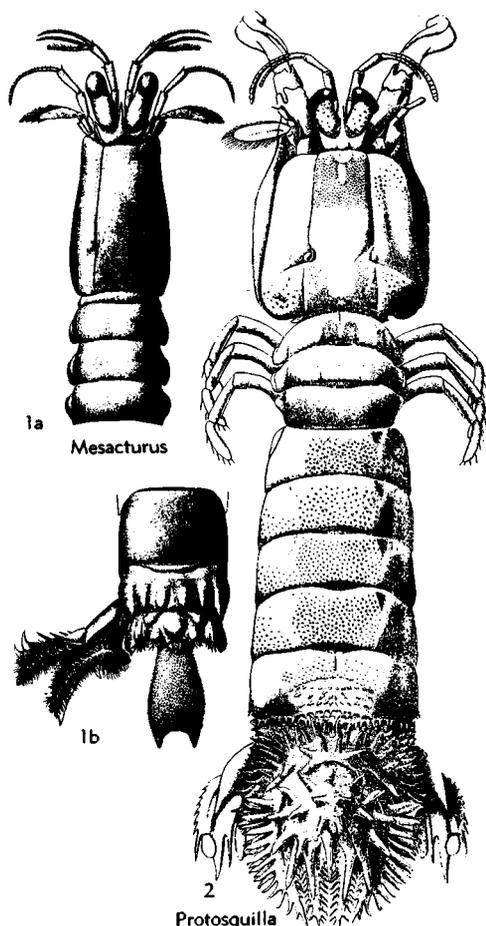


FIG. 360. Squillidae (p. R551-R552).

sibogae HANSEN, 1926, p. 15; OD, M]. Similar to *Eurysquilla* but with abdomen partially carinate and antennular somite very elongate. *Rec.*, Indonesia.—FIG. 352,3. **E. sibogae* (HANSEN); 3a, ant. part of body, dorsal, $\times 5$; 3b, thorax, dorsal, $\times 4$; 3c, post. part of abdomen, dorsal, $\times 4.2$; 3d, raptorial claw, $\times 4.5$ (143).

Gonodactylus BERTHOLD, 1827, p. 271 [**Squilla chiragra* FABRICIUS, 1781, p. 515; SD HOLTHUIS & MANNING, ICZN pend.] [= *Gonerichthys* BROOKS, 1886, p. 83 (type, *Squilla chiragra* FABRICIUS, 1781; SD HOLTHUIS & MANNING, herein) (obj.)]. Related to *Mesacturus*, *Protosquilla*, and *Hoplosquilla*, previously classed as "groups" within *Gonodactylus*; cornea cylindrical or somewhat rounded; anterolateral angles of carapace in advance of rostral base; 6th abdominal somite not fused with telson, which has median carina

and 1 or 2 pairs of additional carinae; uropodal endopod laminate; dactylus of raptorial claw basally swollen, unarmed on inner margin. *U.Mio.*, USA (N.Car.); *Rec.*, W.Atl.-E.Pac.-Indo-W.Pac.—FIG. 354,1. *G. oerstedii* HANSEN, *Rec.*, Puerto Rico; dorsal, $\times 2$ (37).

Harpiosquilla HOLTHUIS, 1964, p. 140 [**Squilla harpax* DE HAAN, 1844, atlas, pl. li, fig. 1; OD] [= *Alimerichthys* CLAUS, 1871, p. 146 (non *Alimerichthys* GUÉRIN in SAGRA, 1855) (type, *A. pyramidalis* LANCHESTER in GARDINER, 1903, p. 457; SD HOLTHUIS & MANNING, herein)]. Closely resembling *Squilla* but distinguished by presence of triangular lobes in front of postero-lateral angles of carapace and spaced, spiniform teeth on upper margin of propodus of raptorial claw. *Rec.*, Indo.-W.Pac.—FIG. 347,2. **H. harpax* (DE HAAN), Japan; dorsal, approx. $\times 1$ (137). *Hemisquilla* HANSEN, 1895, p. 72 [**Gonodactylus styliiferus* H. MILNE-EDWARDS, 1837, p. 530 (= *Gonodactylus ensiger* OWEN, 1832, p. 6); OD, M]. Probably related to *Odontodactylus* and *Gonodactylus*; cornea subglobular; telson with

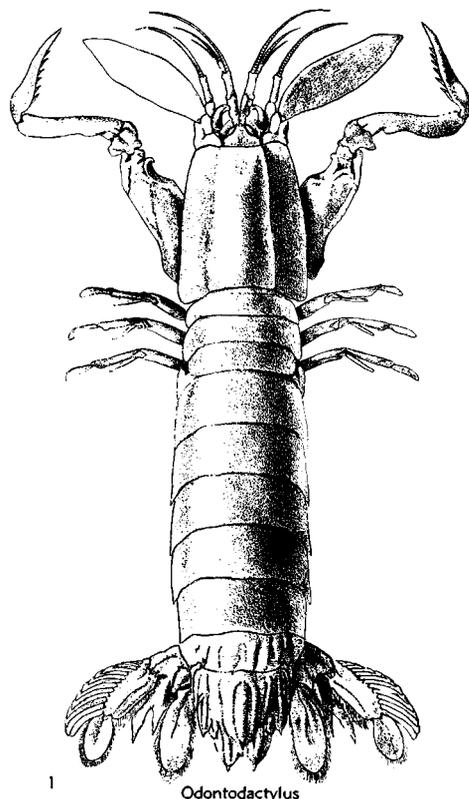


FIG. 361. Squillidae (p. R551-R552).

median carina and pair of additional carinae; dactylus of raptorial claw unarmed. *M.Mio.*, USA (Calif.); *Rec.*, W. Atl.-E. Pac.-Australia. — FIG. 349, 1. *H. braziliensis* (MOREIRA), *Rec.*, Brazil; dorsal, $\times 1$ (208).

Heterosquilla MANNING, 1963, p. 320 [**Lysiosquilla platensis* BERG, 1900, p. 230; OD]. Closely re-

sembling *Lysiosquilla* but telson with elevated median projection, variously armed. *Rec.*, circumtropic-subtropic. — FIG. 355, 2. **H. platensis* (BERG), off Arg.; 2a, dorsal, $\times 1.3$; 2b, raptorial claw, $\times 1.5$ (225).

Hoplosquilla HOLTHUIS, 1964, p. 141 [**Gonodactylus acanthurus* TATTERSALL, 1906, p. 171; OD,

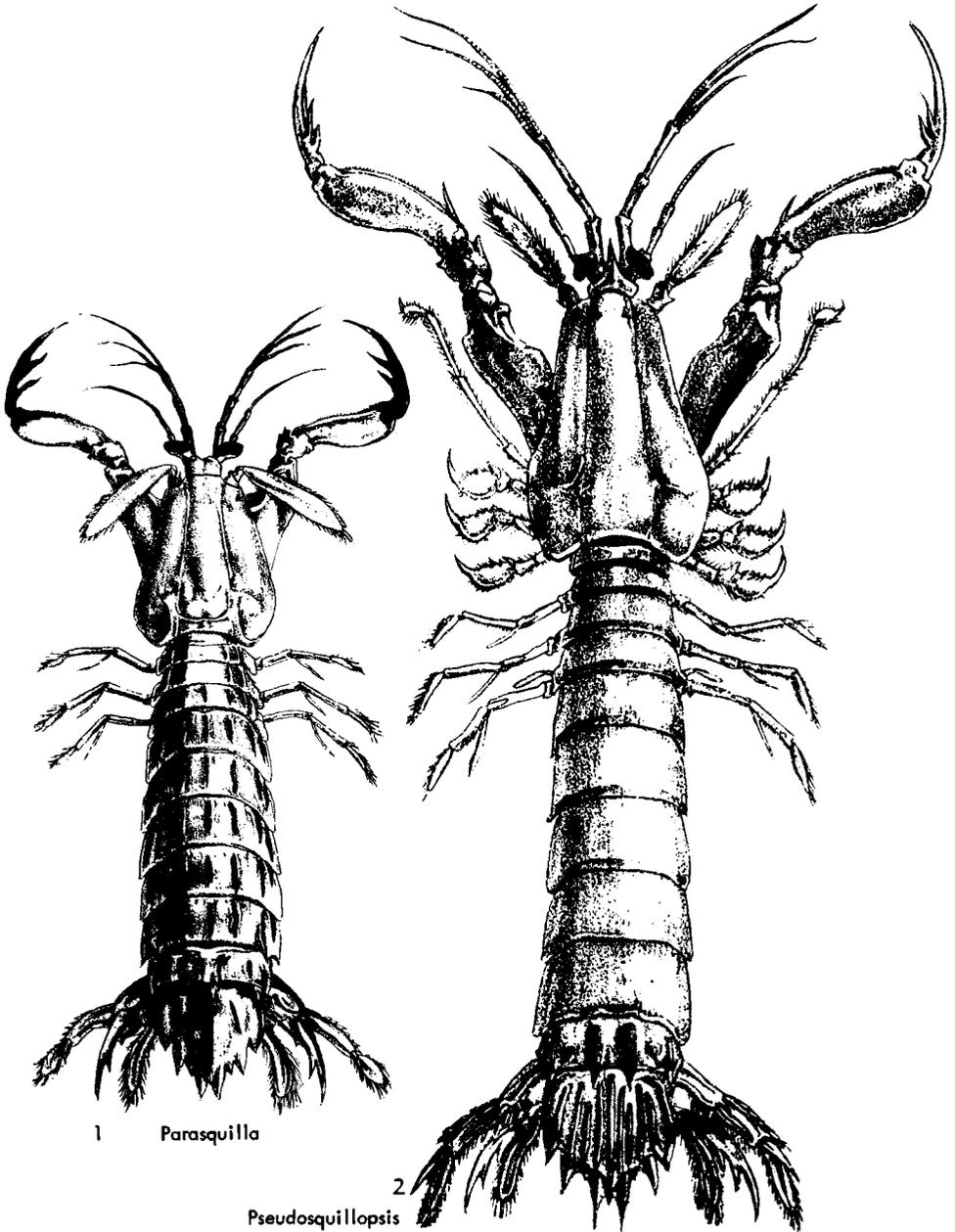


FIG. 362. Squillidae (p. R552).

M]. Resembling *Gonodactylus*, in which formerly it was included as "group"; anterolateral angles of carapace in advance of rostral base; uropods with inner margin of endopod and terminal segment of exopod with spines. *Rec.*, Ceylon.—FIG. 356, 1. **H. acanthurus* (TATTERSALL); 1a, rostrum, mag. unknown; 1b, raptorial claw, mag. unknown; 1c, telson, dorsal, mag. unknown; 1d, uropod, dorsal, mag. unknown (286).

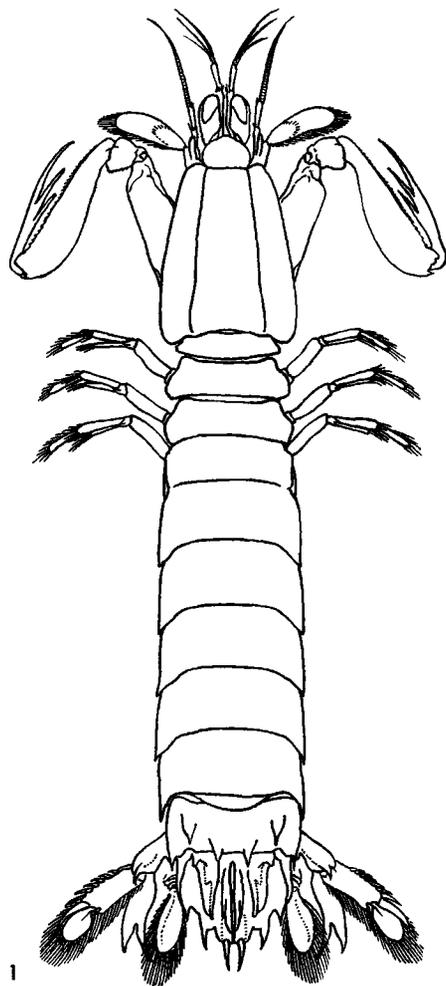
?*Lampropelta* GUÉRIN in SAGRA, 1857, p. lxvi [**L. duvaucellii* GUÉRIN in SAGRA, 1857, p. lxvi; OD, M]. Based on larval form of doubtful affinity. *Rec.*, Atl.

Leptosquilla MIERS, 1880, p. 12 [**Squilla schmeltzii* A. MILNE-EDWARDS, 1873, p. 87; OD, M]. Related to *Squilla* but distinguished by presence of cylindrical eyes, with cornea narrower than stalk, and elongate antennular somite. *Rec.*, Indo-W.Pac.—FIG. 357, 1. **L. schmeltzii* (A. MILNE-EDWARDS), India; ant. part of body, dorsal, $\times 16$ (164).

Lysiosquilla DANA, 1852, p. 615 [**L. inornata*; SD FOWLER, 1912, p. 539 (ICZN Official List, no. 730)] [= *Erichthus* LATREILLE, 1817, p. 43 (type, *Astacus vitreus* FABRICIUS, 1775, p. 417; suppressed by ICZN, Official Index, no. 121); *Smerdis* LEACH in TUCKEY, 1817, unnumbered plate (type, *S. vulgaris*; SD HOLTHUIS & MANNING, herein, suppression by ICZN pend.); *Pontioebius* GUÉRIN in SAGRA, 1857, p. lxiv (type, *Erichthus latreillii* GUÉRIN, 1830, p. 42; SD GURNEY, 1946, p. 166); *Erichthoidina* CLAUS, 1871, p. 120 (type, *E. armata*; SD HOLTHUIS & MANNING, herein); *Lysioerichthus* BROOKS, 1886, p. 83 [type, *Erichthus duvaucellii* GUÉRIN, 1844, pl. 24, fig. 3; SD HOLTHUIS & MANNING, herein]. Related to *Coronida*, *Coronis*, *Nannosquilla*, *Acanthosquilla*, and *Heterosquilla* but size much larger; telson without prominent dorsal elevation, posterior teeth and denticles usually fused. *Rec.*, circumtropic.—FIG. 358, 1. *L. maculata* (FABRICIUS), Indo-W.Pac.; dorsal, approx. $\times 1$ (175).

Manningia SERÈNE, 1962, p. 20 [**Pseudosquilla pilaensis* DE MAN, 1888, p. 296; OD, M]. Like *Squilla* in having sharp median carina on telson but with 5 pairs of additional carinae and less than 4 intermediate marginal denticles; body depressed; dactylus of raptorial claw with 4 teeth. *Rec.*, Indo-W.Pac.—FIG. 359, 1. **M. pilaensis* (DE MAN), Indo-China; post. part of abdomen, dorsal, $\times 14$ (126).

Mesacturus MIERS, 1880, p. 124 [**Gonodactylus furcicaudatus* MIERS, 1880, p. 124; OD, M]. Like *Gonodactylus*, in which it was formerly included as "group," in having anterolateral angles of carapace in advance of rostral base; telson with up to 5 pairs of carinae in addition to median; uropodal endopod not laminate, usually solid, curved, and covered with stiff hairs. *Rec.*, Indo-W.Pac.—



Pseudosquilla

FIG. 363. Squillidae (p. R552).

FIG. 360, 1. *M. kempi* (ODHNER), Ellice Is.; 1a, ant. part of body, dorsal, mag. unknown; 1b, post. part of abdomen, mag. unknown (218).
Nannosquilla MANNING, 1963, p. 318 [**Lysiosquilla grayi* CHACE, 1958, p. 141; OD]. Size small; telson without median dorsal elevation but with marginal false cove under which true posterior armature is placed. *Rec.*, circumtropic-subtropic.—FIG. 355, 1. **N. grayi* (CHACE), off USA (Mass.); dorsal, $\times 3.75$ (70).
Odontodactylus BIGELOW, 1893, p. 100 [**Cancer scyllarus* LINNÉ, 1758, p. 633; SD BIGELOW, 1931, p. 144 (ICZN Official List, no. 731)] [= *Gammaris* H. S. (initials only), 1876, p. 275 (obj.; sup-

pressed by ICZN, Official Index, no. 122); *Odon-toerichthus* BIGELOW, 1894, p. 543 (type, *O. tenuicornis* JURICH, 1904, p. 396; SM JURICH, 1904, p. 396)]. Cornea globular; telson with median carina and 1 to 3 pairs of additional carinae; dactylus of raptorial claw basally swollen, with 2 to 9 small, triangular teeth. *Rec.*, W. Atl.-Indo-W.Pac.—FIG. 361,1. *O. japonicus* (DE HAAN), Japan; dorsal, approx. $\times 2$ (137).

Parasquilla MANNING, 1961, p. 7 [**P. meridionalis*; OD] [= *Faughnia* SERÈNE, 1962, p. 17 (type, *Pseudosquilla haani* HOLTHUIS, 1959, p. 179; OD)]. Like *Squilla* in having sharp median carina on telson but with less than 4 intermediate marginal denticles; most closely related to *Pseudosquilla* and *Pseudosquillopsis* but differing from them in having cervical groove on carapace and carinae on abdomen. *Rec.*, E.Atl.-W.Atl.-Indo-W.Pac.—FIG. 362,1. *P. ferussacii* (ROUX), Sicily, dorsal, $\times 1.25$ (259).

Protosquilla BROOKS, 1886, p. 84 [**Gonodactylus folinii* A. MILNE-EDWARDS, 1868, p. 65; SD HOLTHUIS & MANNING, herein]. Anterolateral angles of carapace not in advance of rostral base; 6th abdominal somite fused with telson; telson

dorsally ornamented with carinae, bosses, or spines, or combinations of these. *Rec.*, W.Afr.-Indo-W.Pac.—FIG. 360,2. *P. guerinii* (WHITE), Hawaii; dorsal, $\times 7.5$ (60).

Pseudosquilla DANA, 1852, p. 615 [**Squilla ciliata* FABRICIUS, 1787, p. 333 (SD HOLTHUIS & MANNING, ICZN pend.)] [= *Alimerichthus* GUÉRIN, 1855, pl. 3, fig. 12 (type, *A. cylindricus*; OD,M); *Pseuderichthus* BROOKS, 1886a, p. 83 (obj.; SD MANNING, 1963, p. 310)]. Resembles both *Parasquilla* and *Pseudosquillopsis* in that body is semicylindrical but differs from both in lacking complete pectination of raptorial claw. [*Manningia*, *Coronidopsis*, *Eurysquilla*, and *Eurysquilloides*, are related but have depressed body and raptorial claw armed with more than 3 teeth.] *Rec.*, circumtropic.—FIG. 363,1. **P. ciliata* (FABRICIUS), Puerto Rico; dorsal, $\times 2$ (37).

Pseudosquillopsis SERÈNE, 1962, p. 12 [**Squilla cerisii* ROUX, 1828, p. unnumbered, pl. 5; OD]. Related to *Pseudosquilla* but with 5 pairs of carinae on telson in addition to median carina and with pectinate propodus on raptorial claw. *Rec.*, E.Atl.-E.Pac.-Japan.—FIG. 362,2. **P. cerisii* (ROUX), Corsica; dorsal, approx. $\times 2$ (259).

SUBCLASS, ORDER, AND FAMILY UNCERTAIN

Tesnusocaris BROOKS, 1955 [**T. goldichi*; OD]. Cephalon elongate (25 mm.) subtrapezoidal, chitinous, with large elliptical compound eyes near front edge, pair of long tapering antenniform appendages besides other short ones; elongate body

(50 mm.+) of nearly identical short somites, each bearing pair of limbs which widen distally. *L.Penn.(Tesusus F.)*, USA(W.Tex.) (*Jour. Paleont.*, v. 29, p. 852-856, fig. 1-2, pl. 85-86). [MOORE]

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