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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

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PART R

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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.]

CONTENTS

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 characteristic 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 Permotrias 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**

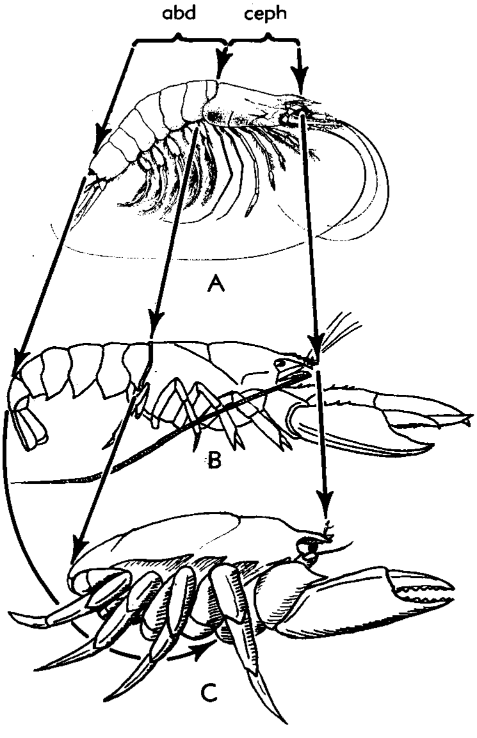


FIG. 217. Main divisions of the body in representative decapods (118).——*A. Penaeopsis.*——*B. Homarus.*——*C. Carcinus.* [EXPLANATION: *abd,* abdomen; *ceph,* cephalothorax (not to scale).]

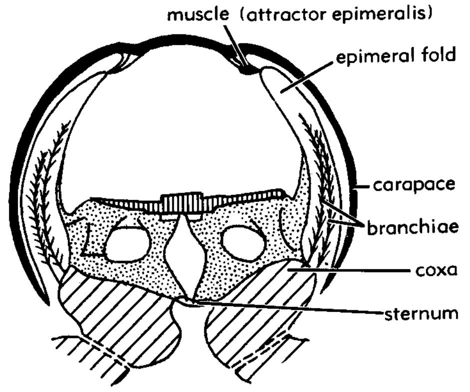


FIG. 218. Diagrammatic cross section of cephalothorax of reptantian decapod (118).

(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

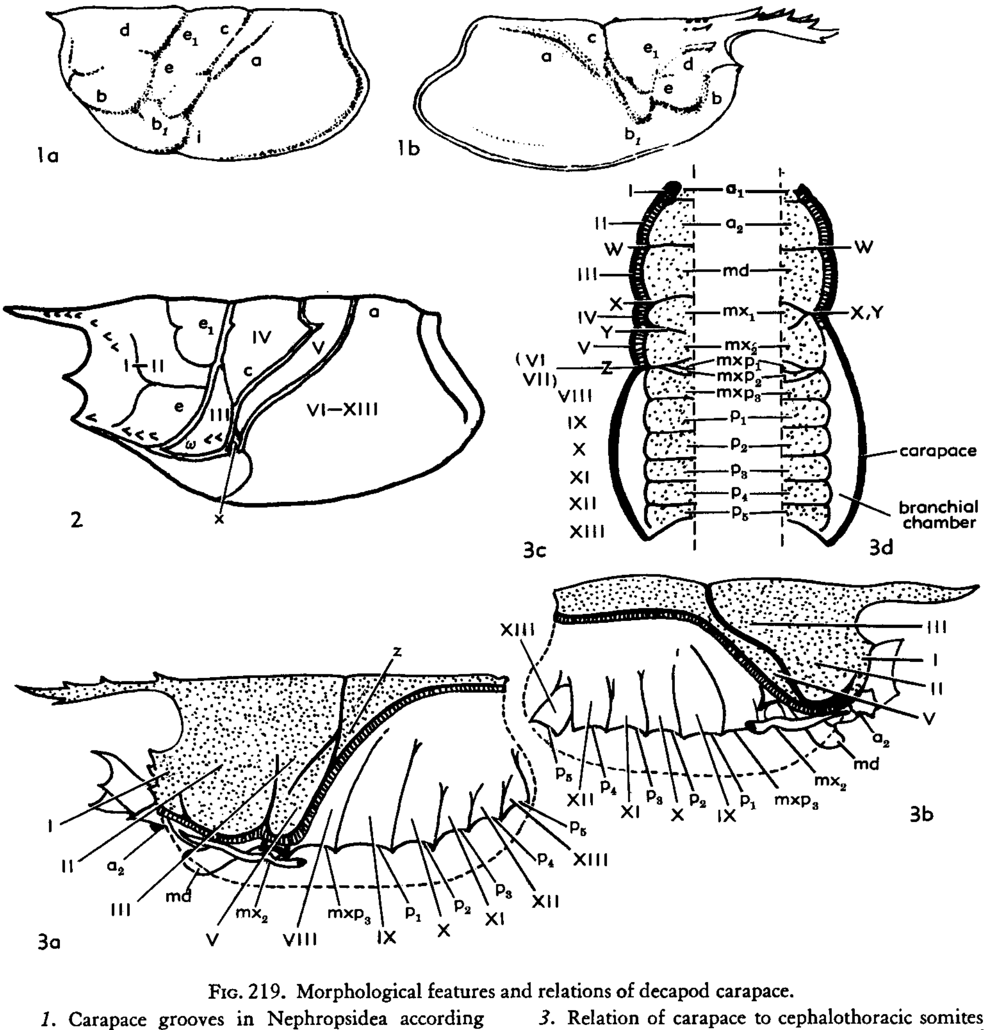


FIG. 219. Morphological features and relations of decapod carapace.

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,* pereiopodal (p_{1-5}); 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 *II/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

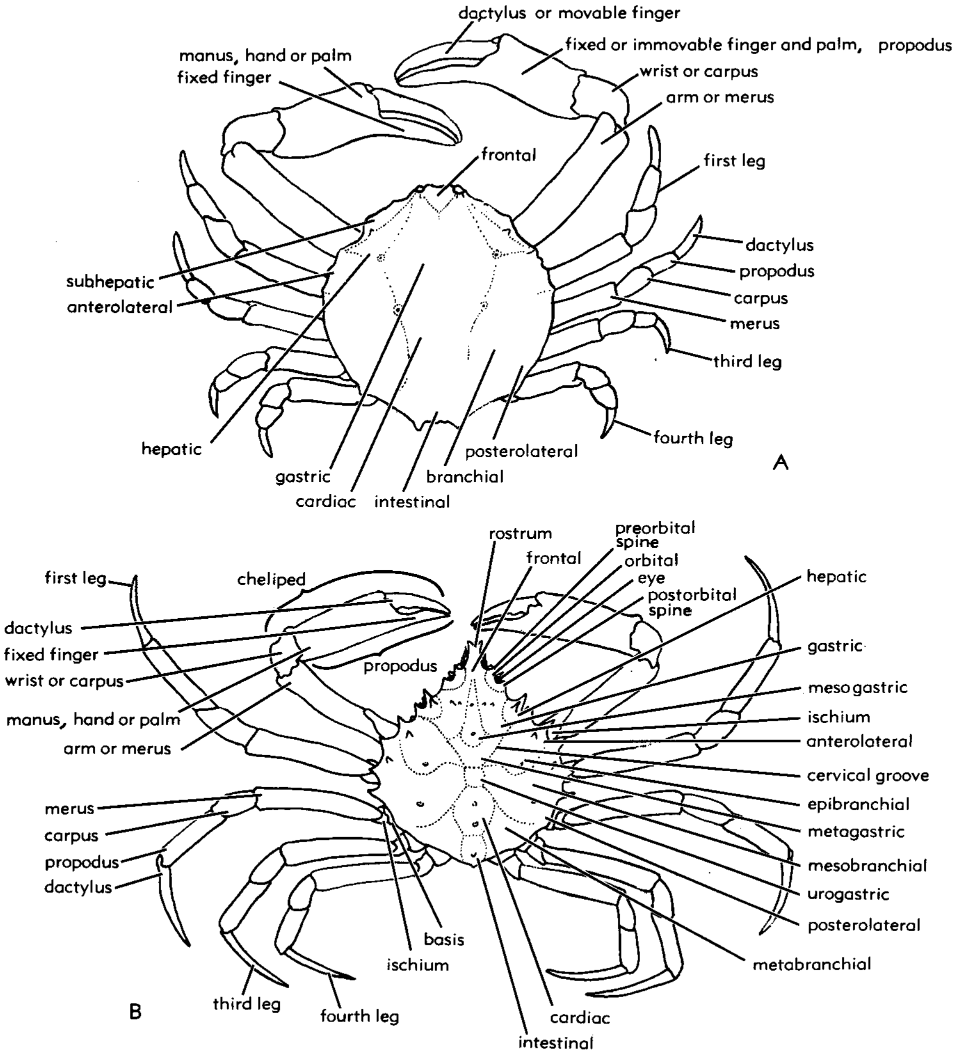


FIG. 220. Descriptive terminology of carapace regions and legs in crabs (redrawn from Rathbun, 234, 237, 243, 245).——*A*. Oxystomata (Leucosiidae).——*B*. Oxyrhyncha (Majidae).——*C*. Brachyrhyncha (Portunidae).——*D*. Brachyrhyncha (Grapsidae).

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-e_1 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

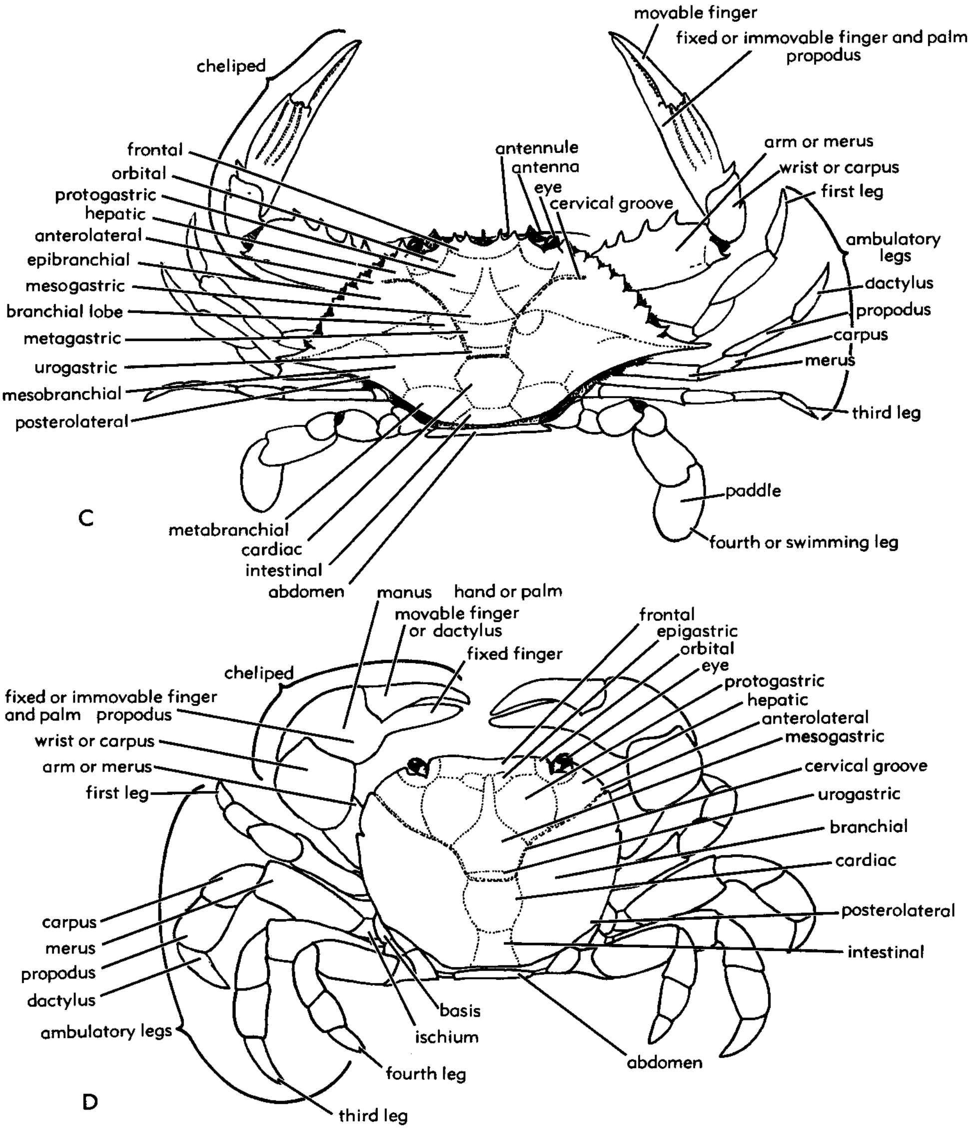


Fig. 220 (continued). *See facing page.*

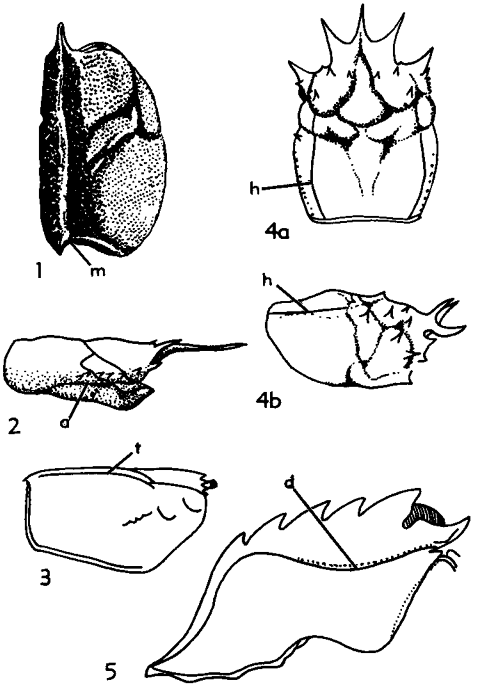


Fig. 221. Positions of lineae on decapod carapace. ——*1. Klytia ventrosa* von Meyer (*m*, median line).——*2. Munida bamffia* Pennant (*a*, linea anomurica).——*3. Thalassina anomala* (Herbst) (*t*, linea thalassinica).——*4. Paromola cuvieri* (Risso); *4a,b*, dorsal and lateral views (*h*, linea homolica).——*5. 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 **metabranchial 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 Thalassinoidea 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

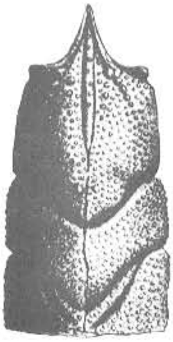


FIG. 222. Dorsal plate of *Klytia greppini* (OPPEL), M.Jur., Ger. (after Oppel, 219).

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 hepatical 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 Galatheidae 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

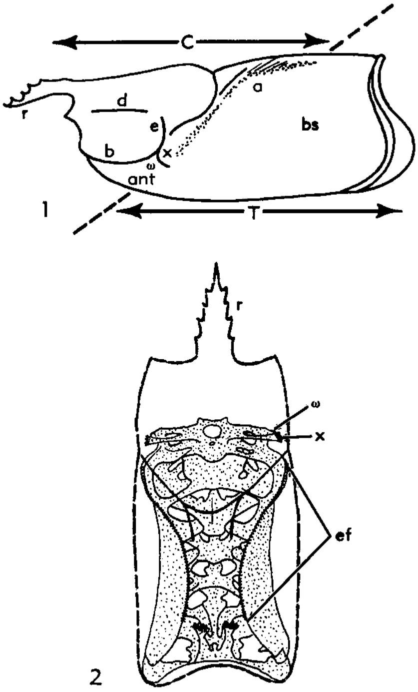


FIG. 223. Relations of carapace and internal skeleton in the lobster (*Homarus vulgaris*) (after Glaessner, 118).——*1*. Carapace, lateral view.——*2*. Diagrammatic dorsal view of internal skeleton (outline of carapace shown by broken lines). [EXPLANATION: *C*, cephalic portion; *T*, thoracic portion; *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

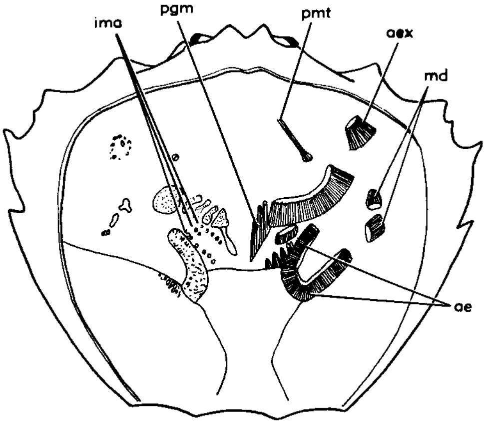


FIG. 224. Carapace of *Dromia personata* (LINNÉ) (middle part drawn as seen from inside, muscle attachments shown in left half, cut muscle in right half) (mod. after Abrahamczik-Scanzoni, 2). [EXPLANATION: *ae*, attractor epimeralis muscle; *aex*, antennar extensor muscle; *ima*, internal mandible adductor muscle; *md*, median dorsoventral muscle (attached to roof of branchial chamber); *pgm*, posterior gastric muscles (median part attached to apodeme); *pmt*, posterior mandible tendon.]

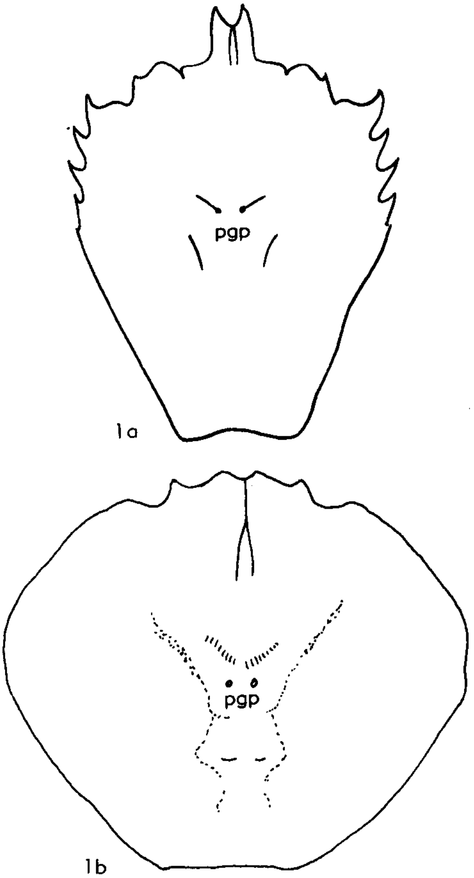


FIG. 225. Dorsal views of carapaces of *(1a) Notopocorystes (Cretacoranina) fritschi* GLAESSNER and *(1b) Zanthopsis bittneri* LÖRENTHEY showing posterior gastric pits *(pgp)* (109, 184).

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 maxillular 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 metagastric 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

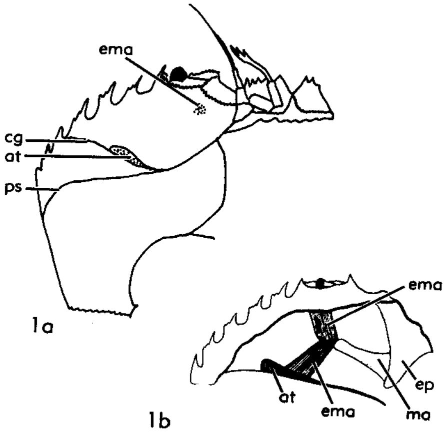


FIG. 226. Muscle insertions on anteroventral portion of carapace of *Eriphia spinifrons* HERBST; *1a*, external ventral view; *1b*, internal dorsal view with carapace opened (mod. from Abrahamczik-Scanzoni, 2). [EXPLANATION: *at*, adductor testis ("tensor of branchial chamber roof"); *cg*, cervical groove; *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 bedelta* (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. *Hoploparia longimana* (Sowerby). Cretaceous. After Woods.
7. *Paraclytia boetticheri* Mertin. Cretaceous. After Mertin.
8. *Palaeohomarus hemprichi* Mertin. Cretaceous. After Mertin.
9. *Homarus vulgaris* H. Milne Edwards. Recent. Original drawing.
10. *Nephrops norvegicus* L. Recent. Original drawing.
11. *Astacus fluviatilis* Fabricius. Recent. Original drawing.

Fam. Erymaidae: 1–4. Fam. Nephropsidae: 5–10. Fam. Astacidae: 11.

B. Evolution of the carapace in other reptantian decapods.

1. *Pseudoglyphea spinosa* (Assmann). Triassic. After Assmann.
2. *Litogaster tiefenbachensis* Assmann. Triassic. After Assmann.

3a. *Pseudopemphix albertii* (H. v. Meyer). Triassic. After Glaessner.
3b. *Pseudopemphix fritschi* Wüst. Triassic. After Scheffen.
4a, b. *Pemphix sueuri* (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. *Paraglyphea prestwichi* (Carter MS, Woods). Jurassic. After Woods.
8. *Glypheopsis cretacea* (McCoy). Cretaceous. After Woods.
9. *Magila latimana* Oppel. Jurassic. After Oppel.
10. *Schlueteria tetracheles* Fritsch. Cretaceous. Reconstruction, from holotype.
11. *Gebicula exigua* Alcock. Recent. After Alcock.
12. *Alpheus malleodigitatus* Bate. Recent. After Coutière.
13. *Coenobita perlata* H. Milne Edwards. Recent.
14a, b. *Eocarcinus praecursor* Withers. Jurassic. After Withers.
15a, b. *Prosopon mamillatum* H. Woodward. Jurassic. After Withers.
16. *Homolopsis edwardsi* Bell. Cretaceous. Reconstruction, from topotype.
17. *Dromiopsis rugosa* (Schlotheim). Danian. From topotype.
18. *Tetrachela raiblana* Glaessner. Triassic. After Glaessner.
19. *Eryon* sp. Jurassic. After Woods.
20. *Polycheles andamanensis* Alcock. Recent. After de Man, from van Straelen.
21. *Palaeopalinurus glaessneri* Bachmayer. Jurassic. Reconstruction, from holotype and paratype specimens. The unornamented areas believed to represent carapace furrows are marked by stippling.
22a, b. *Palinurus vulgaris* Latreille. Recent. Original drawings.

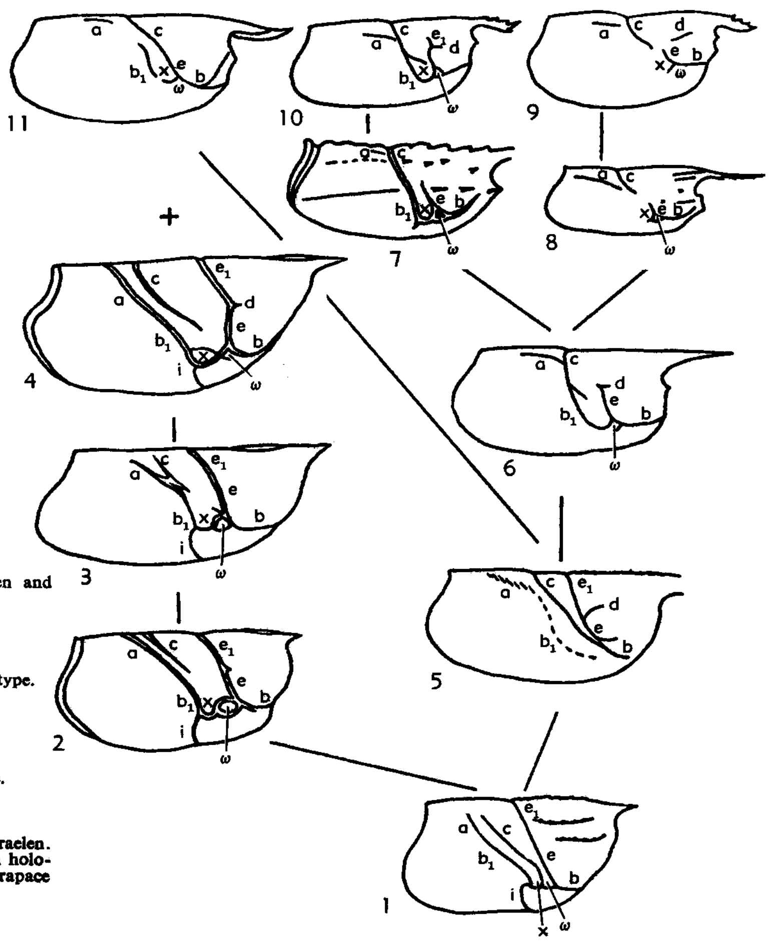


Fig. 227. Evolution of carapace in Decapoda (Glaessner, 118). [Explanation as in Fig. 219.]
[For Erymaidae, read Erymidae; for *Glypheopsis*, *Trachysoma*; for Nephropsidae, Nephropidae; for *Paraclytia*, *Paraclythia*; for *Paraglyphea*, *Glyphea*.]

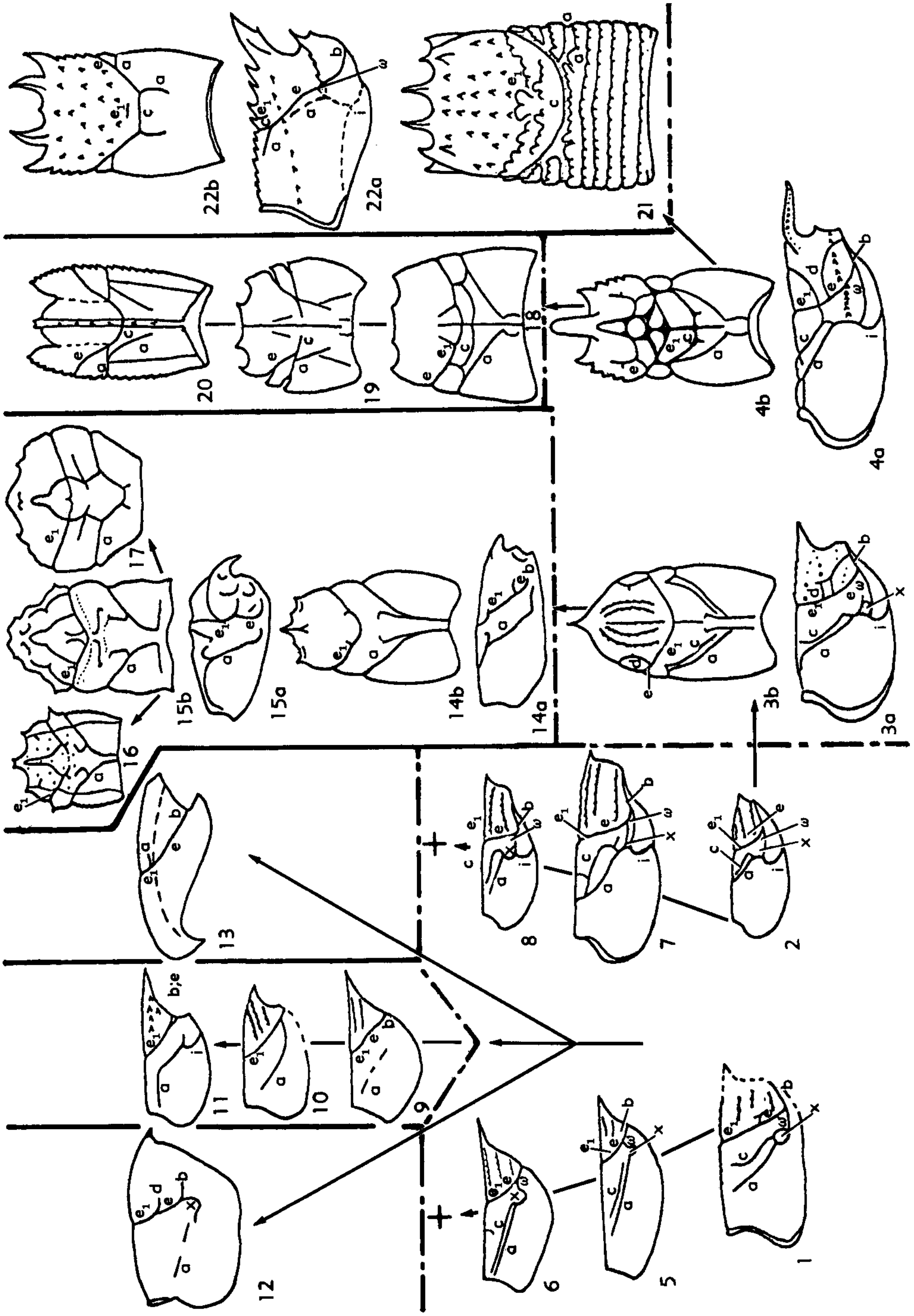


Fig. 227 *(continued, see facing page).*

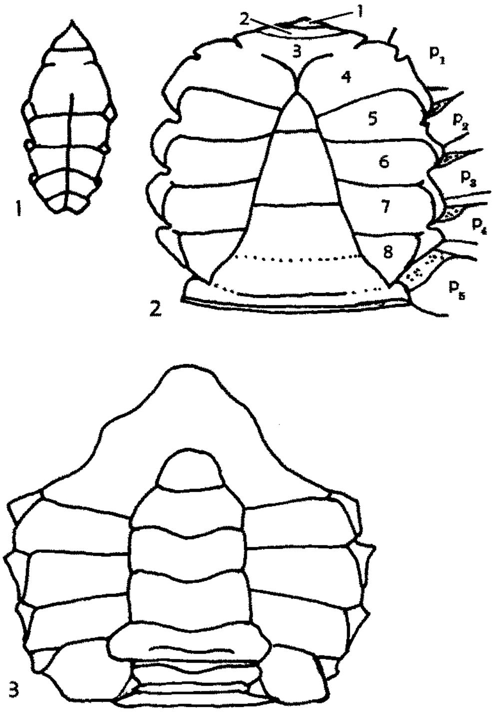


Fig. 228. Sternum and (in part) abdomen of some Recent male decapods.——*1. Corystes cassivelaunus* (Pennant) (after Balss, 13).——*2. Portunus pelagicus* (Linné) (Glaessner, n).——*3. Macrophthalmus latreillei* (Desmarest) (after Reuss, 250). [Explanation: *1-8,* thoracic sternites; p_1-p_5, coxae of successive pereiopods.]

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 Homolodromiinae and Homolidae, with sutured connections. Finally, in Palinuridae, Lithodidae, advanced Galatheoidea, and Brachy-

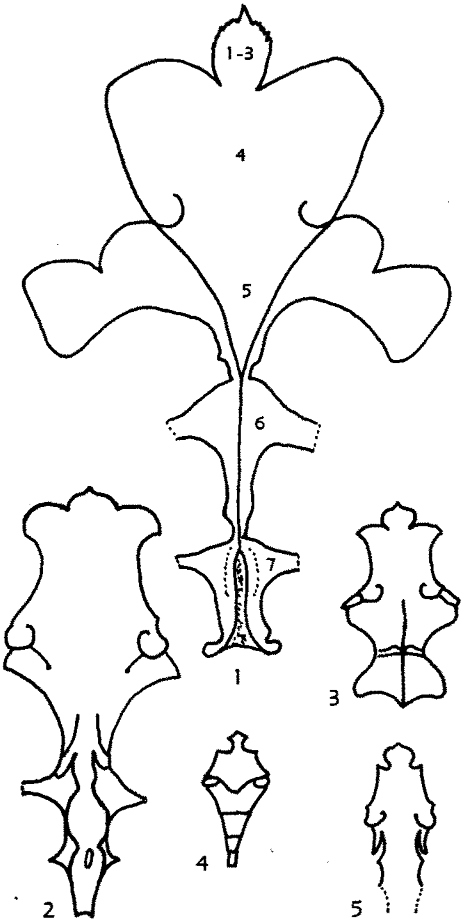


Fig. 229. Form of sternum in Raninidae.——*1. Ranina (Ranina) ranina* (Linné) (after Gordon, 123).——*2. Lyreidus fossor* Bennett (after Bennett, 20).——*3. Laeviranina ovalis* (Rathbun) (after Rathbun, 244).——*4. Notopocorystes (Cretacoranina) schloenbachi* (Schlüter) (after Mertin, 193).——*5. N. (N.) 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 **proepistome** 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 pereiopods becomes shieldlike (Fig. 229). An anteromedian triangular projection of this shield, wrongly named episternum by Van Straelen, is interpreted as fused thoracic sterna *1* to *3* (corresponding to maxillipeds *1* to *3*). The term **episternum** is applied to 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 pereiopods (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.

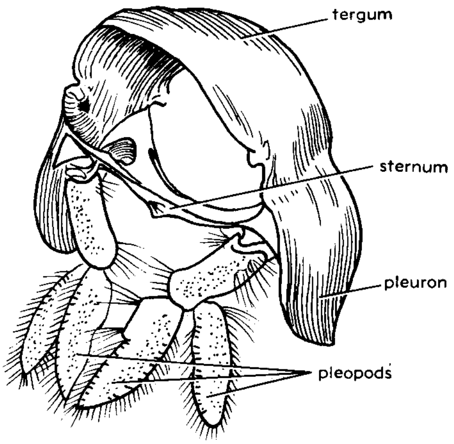


Fig. 230. Abdominal segment and attached appendages in Astacidea (from McGraw-Hill Encyclopedia of Science and Technology, p. 564, Crustacea section, by W. L. Schmidt, by permission of McGraw-Hill Book Company).

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

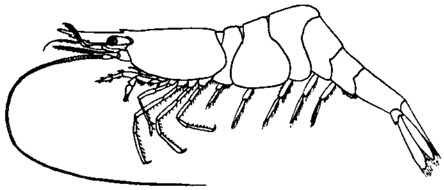


FIG. 231. Side view of caridean, *Hippolyte varians* LEACH, showing expanded second abdominal pleura (after Balss from Beurlen, 27).

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 Thalassinoidea, 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 crablike 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-

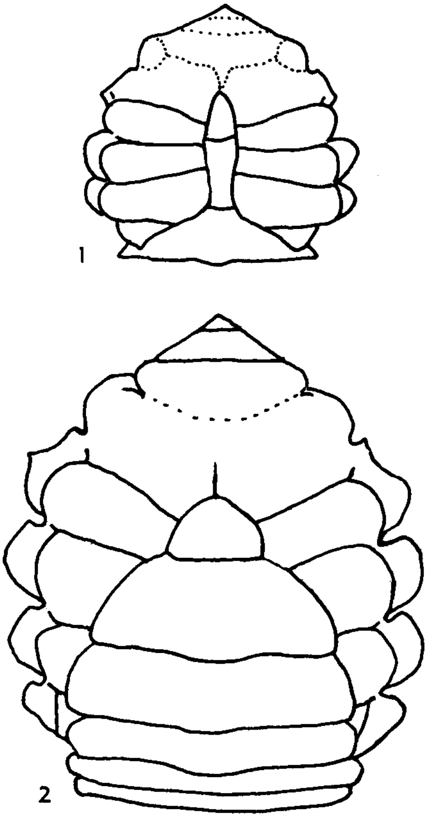


FIG. 232. Ventral views of crab abdomens.——*1*. *Callinectes sapidus* RATHBUN, male (mod. from Rathbun, 243).——*2*. *Scylla serrata* (FORSKÅL), female (mod. from A. Milne-Edwards, 198).

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).

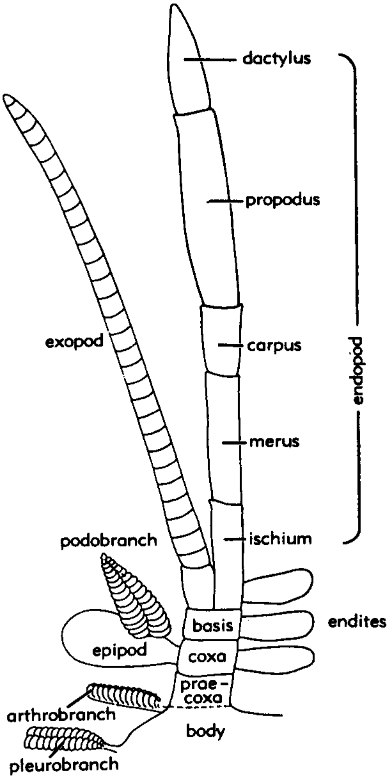


FIG. 233. Thoracopod podomeres in Decapoda, showing relations of exopod, endopod, endites, and gills (podobranch, arthrobranch, pleurobranch) (after Holthuis, 149).

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., 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 Penaeidea, 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-

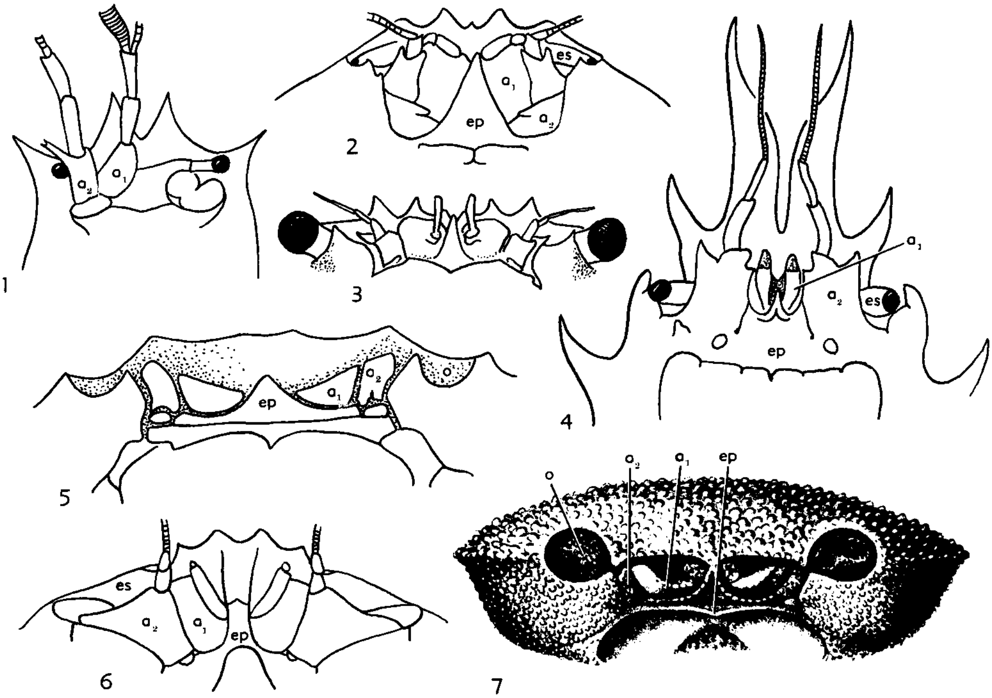


FIG. 234. Antennoorbital region in Brachyura shown in ventral *(1-6)* and frontal *(7)* views.——*1. Homolodromia paradoxa* A. MILNE-EDWARDS, with left a_1 and a_2 removed (52).——*2. Dromia* sp. (156).——*3. Portunus pelagicus* (LINNÉ) (15).——*4. Pisa tetraodon* (PENNANT) (52).——*5. Harpactocarcinus punctulatus* (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, obliquely, 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 protopodite (coxa, basis) and a three-segmented endopodite (corresponding to **ischium, merus, carpus**), ending in an annulated **flagellum.** The first segment of the protopodite 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 *Cancrinos* 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 pereiopods. 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 **pereiopods** *(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 pereiopod *5* in all living forms. It is present on periopod *4* of some natantians, Palinura, Astacidea, some Thalassinoidea, 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 pereiopods 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 pereiopod *1*, commonly on *2*, and in other families on other pereiopods. In the Penaeidea, Stenopodidea, and Astacidea the first three pereiopods are chelate. The

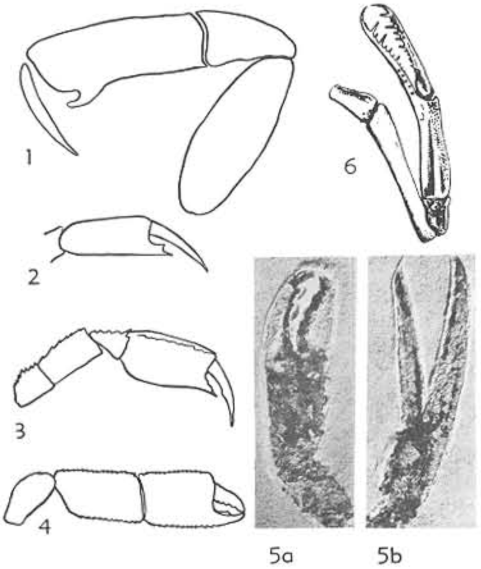


FIG. 235. Subchelae *(1-3)* and chelae *(4-6)* of first pereiopod in decapods.——*1. Glyphea udressieri* VON MEYER (34).——*2. Etallonia longimana* (MÜNSTER) (34).——*3. Thalassina anomala* (HERBST) (34).——*4. Axius* sp. (34).——*5. Homarus hakelensis* (FRAAS); *5a,b,* right and left chelae (115, 219).——*6. Palaeopentacheles roettenbacheri* (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 Thalassinoidea and Galatheoidea, 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 Hexapodinae 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

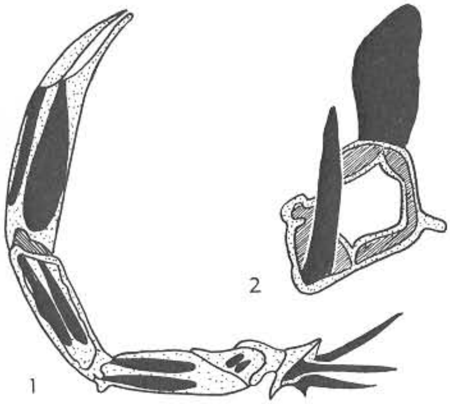


Fig. 236. Cheliped tendons in crab, *Maja verrucosa* H. Milne-Edwards; *1,* entire cheliped; *2,* proximal view of coxa showing flexor (above), extensor (below), articulations appearing as right and left projections, and articulations of basiischium appearing as upper and lower projections of internal 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. *R*408).

NERVOUS SYSTEM

The nervous system comprises the supraesophageal ganglion (syncerebrum), the

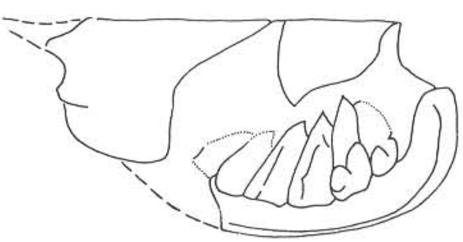


Fig. 237. Broken cephalothorax of *Oncopareia muncki* (Pelseneer) with partly preserved branchiae (podobranchs) in exposed branchial chamber, U.Cret., Belg. (mod. from Pelseneer, 227).

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. *R*432) 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)

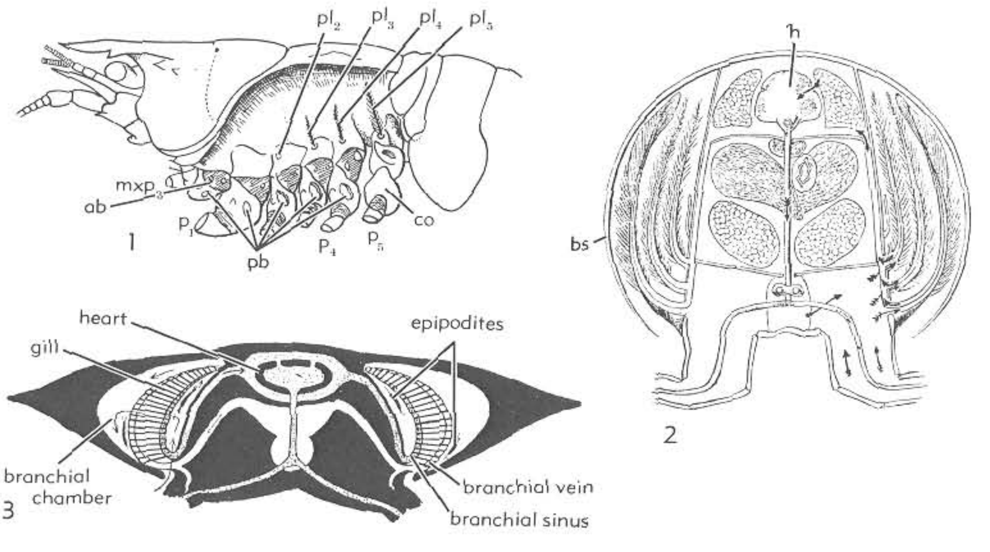


FIG. 238. Gill positions in decapods.——*1. Astacus pallipes* LEREBOULLET, showing left side of cephalothorax (branchiostegite removed) and anterior abdominal somites (mod. from Bouvier, 52).——*2. A. astacus* LINNÉ, diagrammatic cross section, arrows indicating direction of blood flow (mod. from Huxley, 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 arthrodial membrane of 3rd maxilliped (mxp_3) and 1st to 4th pereiopods (p_1 to p_4); *bs,* branchiostegite; *co,* coxa; *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 *Benthesicymus* (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 Stenopodidea, Astacidea, Palinura, Thalassinoidea, primitive Paguroidea, Galatheoidea, and Homolodromiinae. Dendrobranchs characterize the Penaeidea exclusively. Phyllobranchs are found in Caridea, most Paguroidea and Galatheoidea, all Hippoidea, and most Brachyura (13).

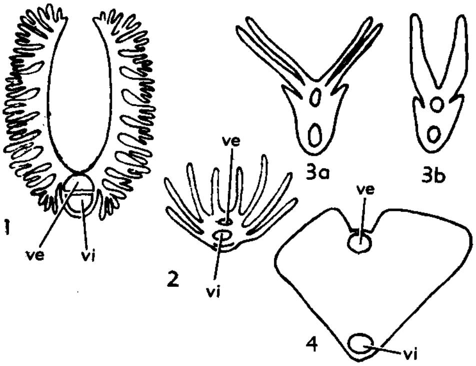


FIG. 239. Types of decapod branchial structures illustrated by cross sections (after Bouvier, 52). ——*1. Penaeus,* dendrobranch.——*2, 3a,b. Astacus, Dicranodromia,* trichobranch.——*4. Carcinus,* phyllobranch. [EXPLANATION: *ve, vi,* blood vessels.]

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 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 spermothecal 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 **protozoea** 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, protozoea, 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 pereiopods 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. *R*431). "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-

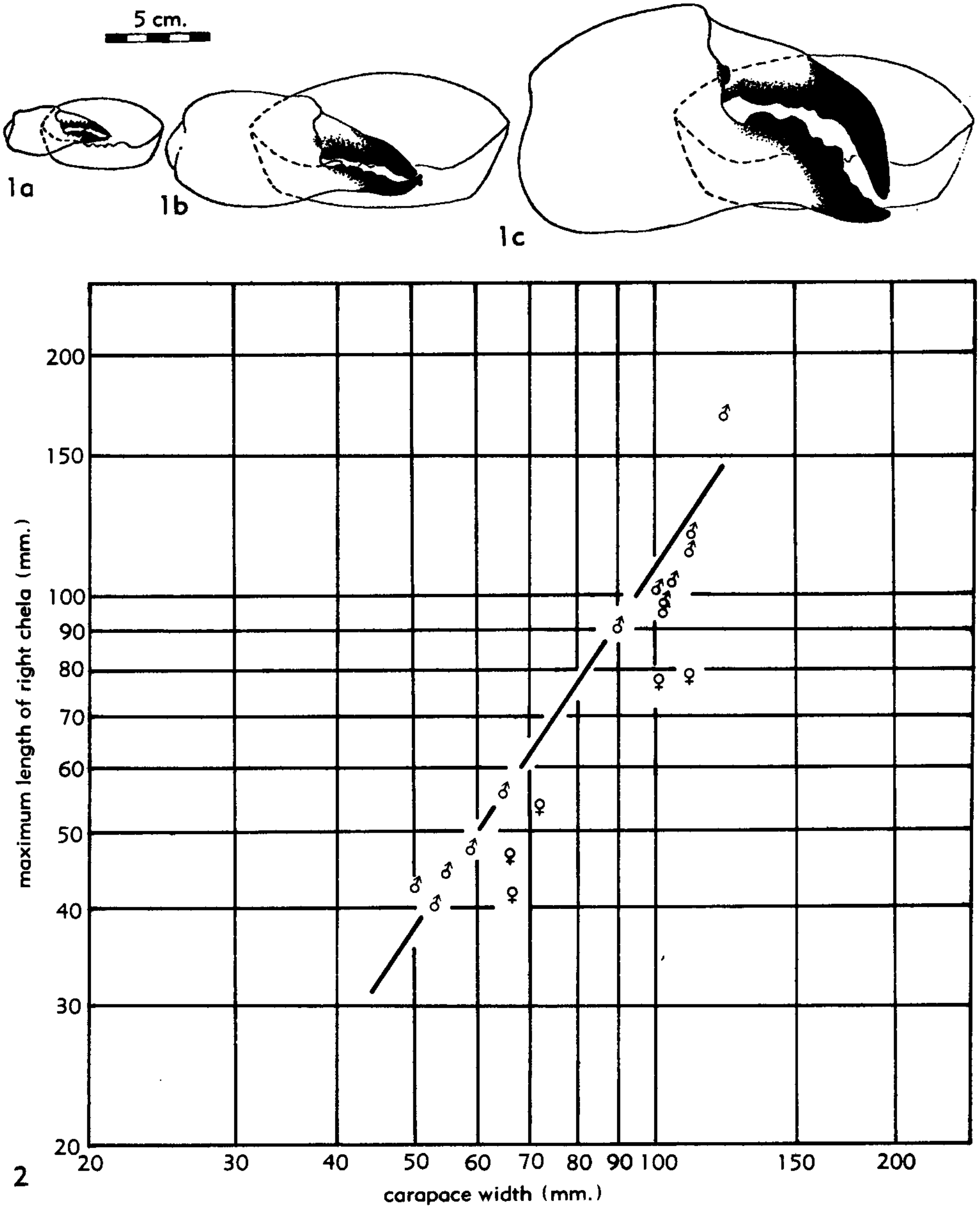


FIG. 240. Allometric growth of right chela of the crab *Tumidocarcinus giganteus* GLAESSNER, Mio., N.Z. (after Fleming, 93).——*1a-c.* Outlines of carapace and right chela of males.——*2.* Graph showing positive allometric growth of chela in males (each symbol representing one measured individual).

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 Balss (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 environment. 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 H_2S (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 *Thalassina 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 Faxe (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 Glypheoidea 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.

Table 1. *Assemblages of Decapod Crustacea from Calcareous Shales and Thin-bedded Limestones*

Age	Depressiform benthonic reptantians	Natantians	
		Penaeidea	Caridea
Early Tertiary	*Ibacus* *Palinurus(?)*		*Palaemon*
Late Cretaceous	*Eurycarpus* *Ibacus*	*Penaeus* *Benthesicymus* *Acanthochirana* *Carpopenaeus*	*"Palaemon"* *Oplophorus*
Middle and Late Jurassic	*Eryon* *Cycleryon* *Coleia* etc.	*Antrimpos* *Aeger* *Acanthochirana* *Bombur* etc.	*Udora* *Udorella* *Hefriga* *Blaculla*
Early Jurassic	*Coleia* *Proeryon*	*Antrimpos* *Aeger*	*Uncina(?)* Caridea indet.(?)
Late Triassic	*Tetrachela*	*Antrimpos* *Aeger* *Bombur*	

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*), Galatheidae, 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, Dromiacea, 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 pereiopods, particularly dactyli of the fifth pereiopods, 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 pereiopods 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 swimming 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, Thalassinoidea, 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

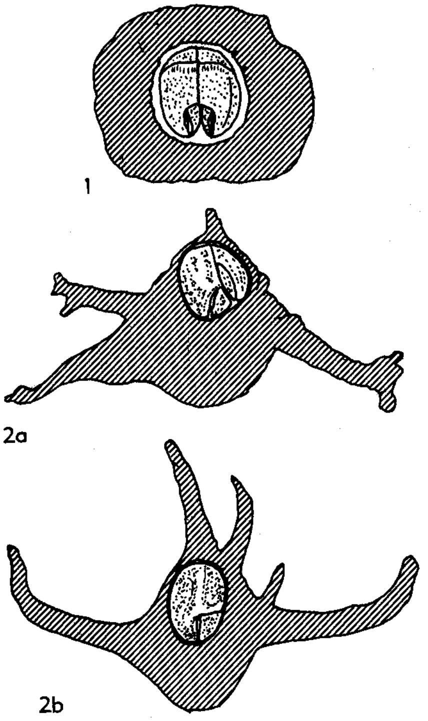


FIG. 241. Adaptation of chelipeds in Paguroidea (various sources).——*1. Pylocheles agassizi* A. MILNE-EDWARDS with 2 symmetrical chelae closing hole in rock.——*2. Pagurus* with chelae closing hole in shell overgrown by bryozoans; *2a, P. alcocki* (BALSS) with 2 heterochelous chelae; *2b, P. varians* (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.

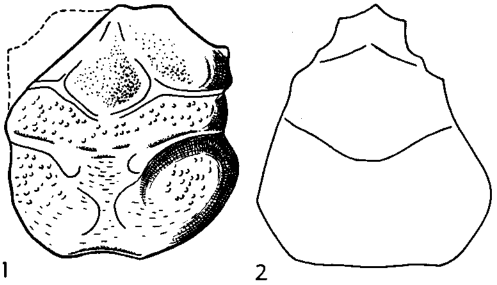


FIG. 242. Distortion of branchial chamber of Jurassic decapods owing to growth of parasites (after Houša, 153).——*1. Pithonoton marginatum* VON MEYER.——*2. Mesogalathea striata* (REMEŠ).

Common commensal natantians are Palaemonidae 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 epizoan 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 (Galatheidae, 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

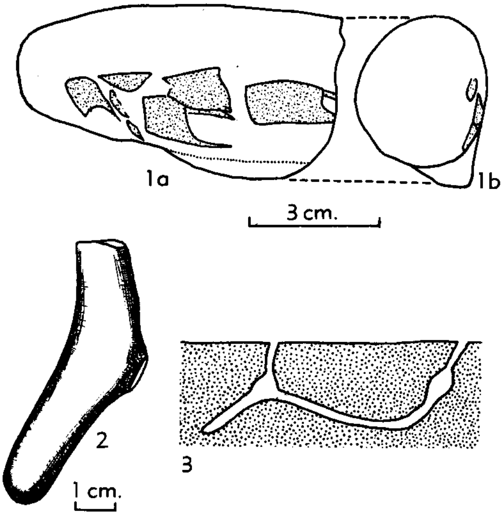


FIG. 243. Burrows of Callianassidae.——*1.* Burrow cast containing remains of *Protocallianassa* sp., U.Cret., Ger.; *1a,b,* side and end views (after Mertin, 193).—*2.* Burrow cast of *Callianassa* sp., Paleoc., Australia (after Glaessner, 116).——*3.* Burrow of *C. californiensis* (after MacGinitie from Mertin, 193).

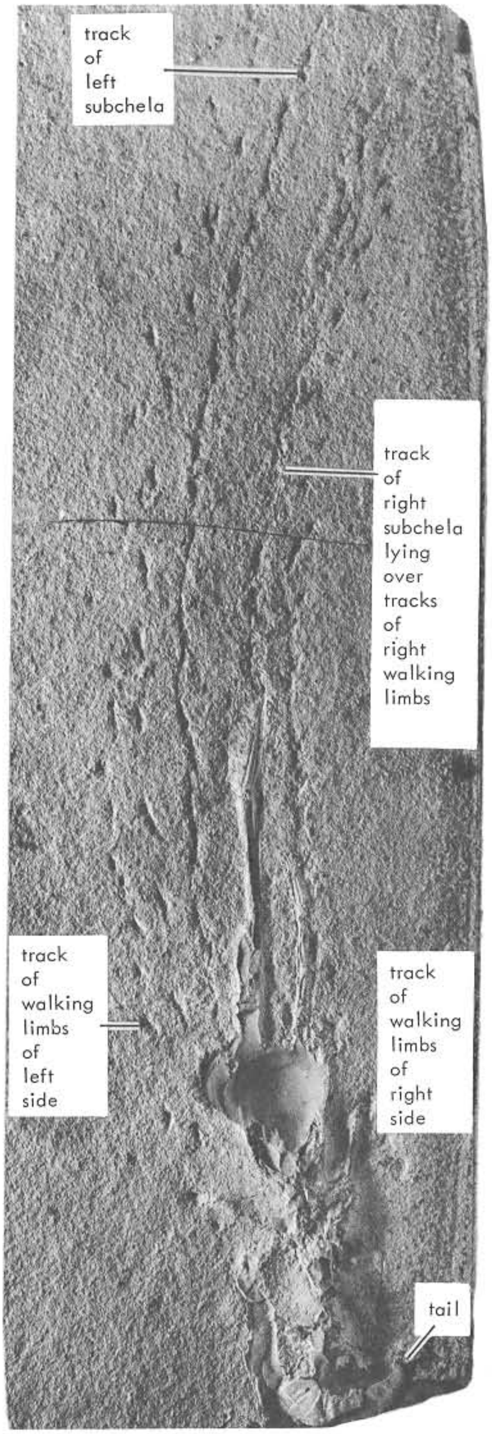


FIG. 243A. *Mecochirus longimanatus* (SCHLOTHEIM), with walking track, U.Jur., Ger. (343a).

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 Thalassinoidea 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.

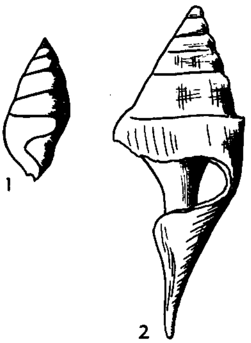


FIG. 244. Fossil gastropod shells damaged by pagurids (after Zapfe in Papp *et al.*, 224).——*1. Euthria intermedia* (regenerated), Mio., Austria. ——*2. Clavilithes parisiensis*, Eoc., Fr.

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. Decalcification 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.

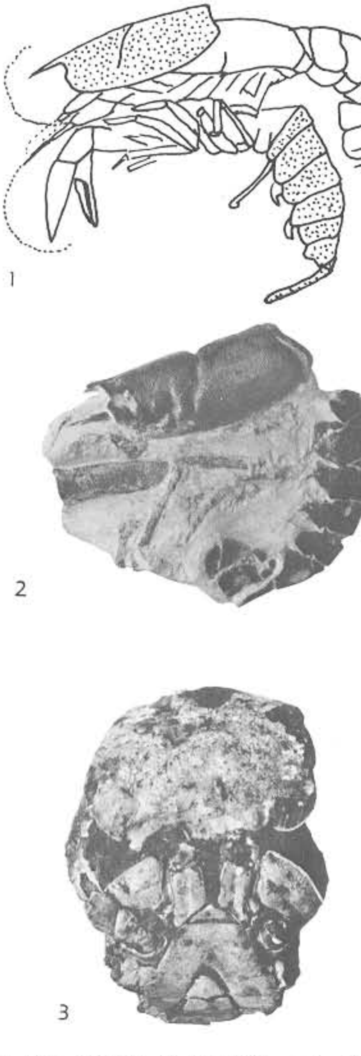


FIG. 245. Molting in decapods.——*1.* Fresh-water crayfish, *Parachaeraps* (Parastacidae), in process of molting (carapace and abdomen of shed exoskeleton, stippled) (redrawn from Hale, 139).——*2.* Molting position of *Hoploparia gammaroides* M'COY, L.Eoc., Eng. (after Glaessner, 107).——*3.* Molting position of *Potamon quenstedti* (ZITTEL), enclosed in fresh-water limestone, U.Mio., Ger.; frontal view showing opening of pleural suture (from Glaessner, 107).

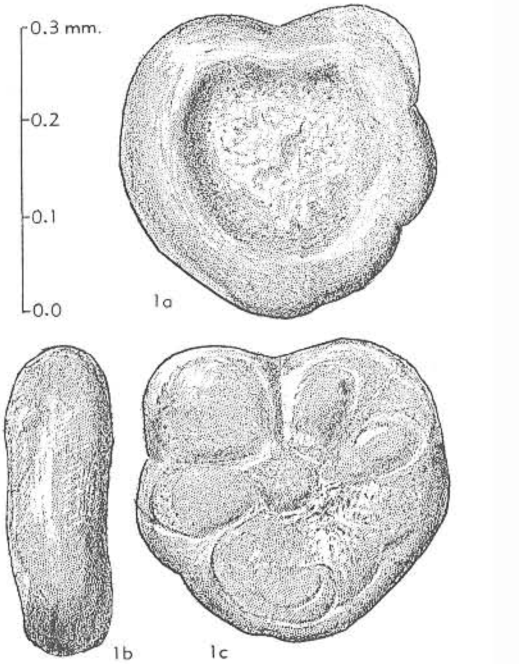


FIG. 246. Presumed gastrolith of larval nephropsidean, *Wechesia pontis* FRIZZELL & EXLINE, M.Eoc., USA(Tex.); *1a-c,* int., lat., ext. views (from Frizzell & Exline, 99).

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

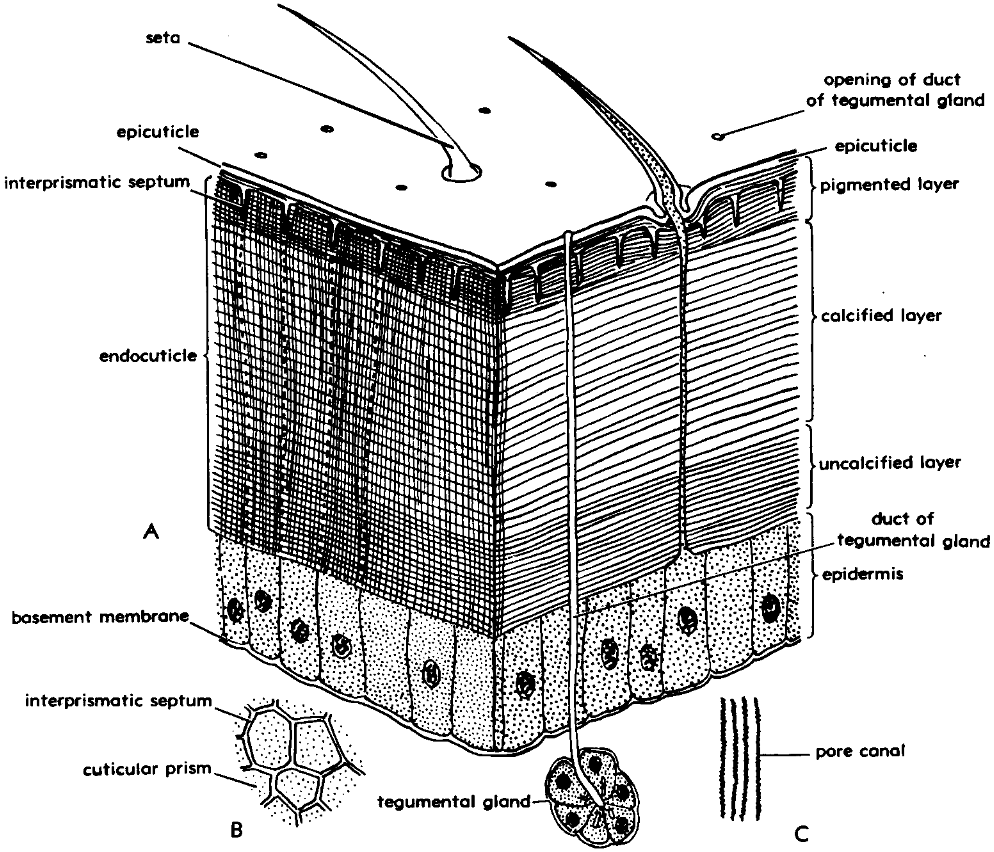


FIG. 247. Structure of decapod cuticle (from Dennell in Waterman, "The Physiology of the Crustacea," 316, by permission of Academic Press, Inc.). *A.* Diagram illustrating structure seen in vertical sections. ——*B.* Pigmented layer of endocuticle in horizontal section.——*C.* Pore canals in vertical section 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 (BUDDENBROCK 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 PELSENEER, 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 distintegrate 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 antiqua* 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, Lower 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 Decapoda 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 remains 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," Xanthilithes*).

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 Permotriassic Penaeidea (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

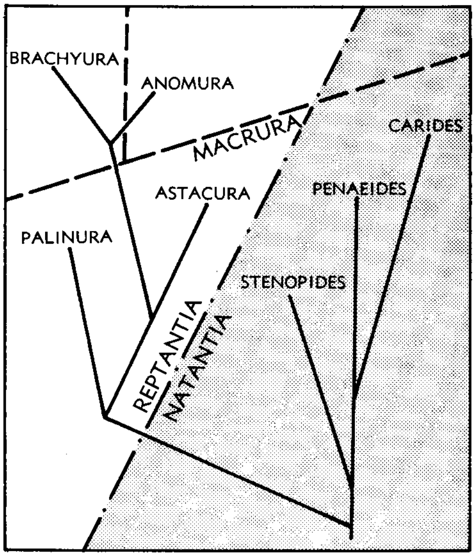


FIG. 248. Phylogeny of Decapoda inferred by BORRADAILE and BOUVIER (after Borradaile, 48, Bouvier, 1917).

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-interna-bearing." 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 Thalassinoidea, 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 Thalassinoidea 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 Glypheoidea 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-

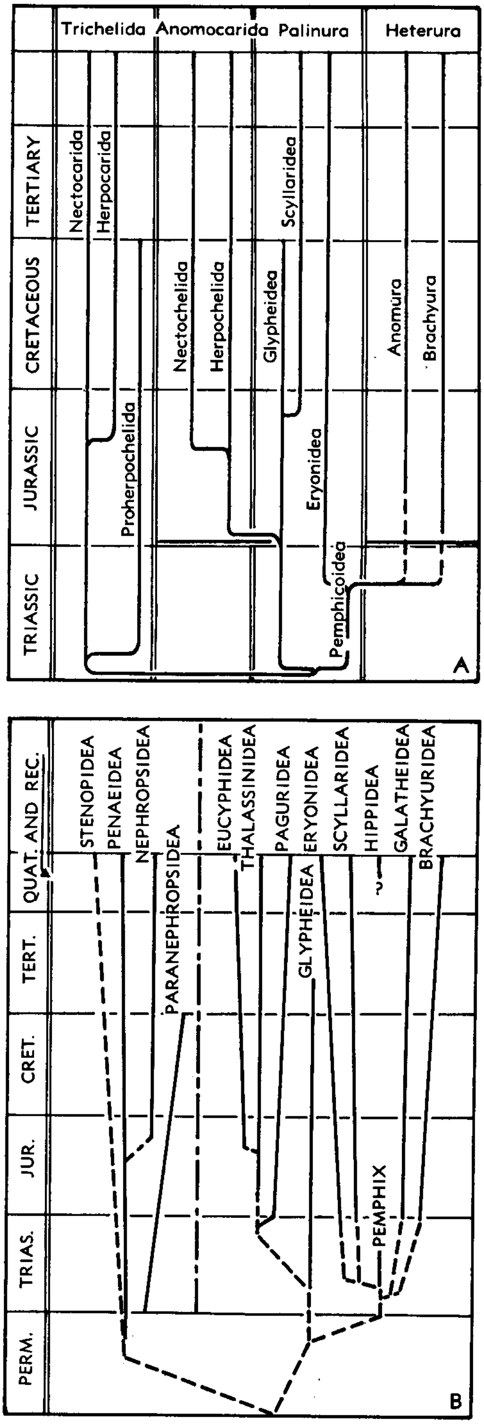


Fig. 249. Phylogeny of Decapoda *(A)* inferred by Beurlen (1930) (27) and *(B)* inferred by Beurlen & Glaessner (1930) (34).

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. *R*410), a critical survey of the evolution of the eucarids 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, Galatheoidea, 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

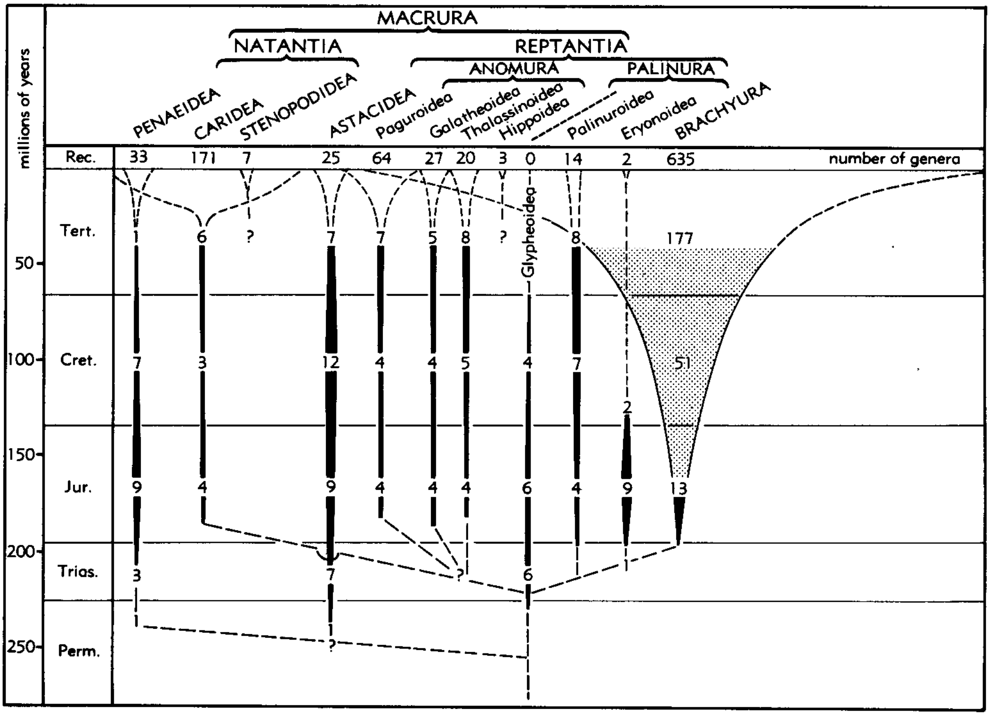


FIG. 250. Phylogeny and stratigraphic distribution of Decapoda. The numbers of pre-Quaternary genera are indicated approximately for each period. Numbers of Recent genera after CHACE (1951) (Glaessner, n).

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. BEURLEN (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 Cancridea from a form like the Upper Cretaceous *Avitelmessus* (Dakoticancridae, 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 (*Enoplonotus*). The Cretaceous Carcineretidae are unlike typical xanthids. They have a number of advanced portunoid characters, such as adaptation of the fifth pereiopod (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, Glyphythyreus*). 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 Ocypodoidea, 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 Ocypodoida. 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 Ocypodoidea 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, Thaumastochelidae)
  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 (Cancridea), Catometopa (Ocypodoidea), 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 (Erymaidae [Erymidae], Stenochiridae)
  - Division Herpochelida B. & G.
    - Tribe Nephropsidea (Nephropsidae, Potamobiidae, 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 Portunoidea, 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 Brachyura 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 *(senso 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 Thalassinoidea, 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 pereiopods or pereiopods *2* to *5* with seven segments; pereiopods *1* to *3* chelate, with the dactylus placed medially. Pleopods well developed, without stylamblys. Antennal stalk always with scaphocerite. Mandible undivided. First maxillipid without caridean expansion ("Eucyphidenanhang"); maxilliped *3* mostly seven-jointed, resembling pereiopod. 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.

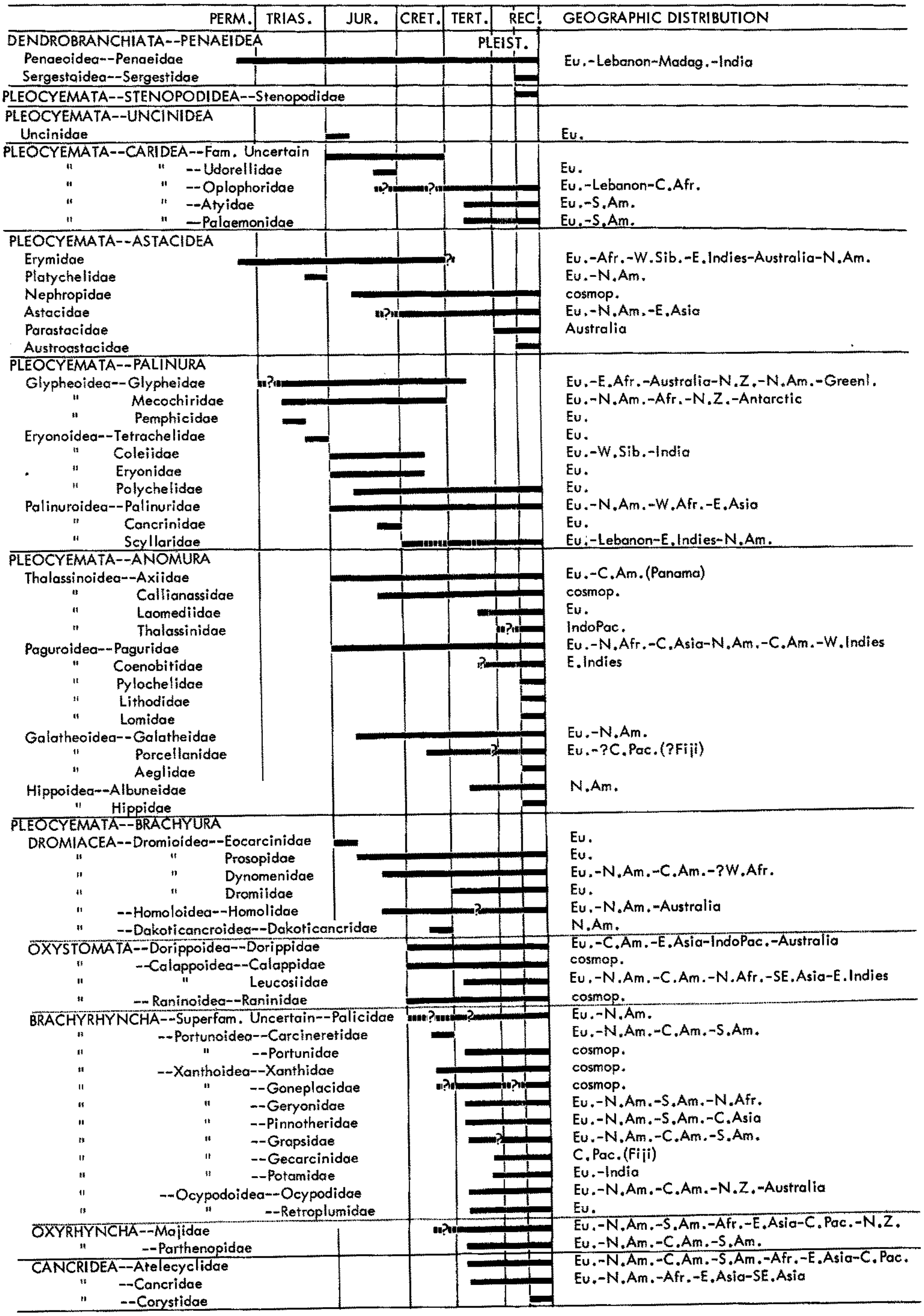


FIG. 251. Stratigraphic and geographic distribution of suprageneric taxa of Decapoda (Glaessner, n).

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+Eukyphida) 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 Dromiacea
        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 *R*114-116. 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 pereiopods chelate; eggs not carried by females, hatched as nauplius. *Permotrias.-Rec.*

Infraorder PENAEIDEA 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 pereiopods 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 Peneidia Rafinesque, 1815, =Penaeidae Rafinesque, 1815, ICZN)]

Third pereiopods 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 Peneidia Rafinesque, 1815) (Penaeidae on official list, ICZN)] [=Peneidea Dana, 1852]

Rostrum laterally compressed and well developed so that it overlaps ocular segment, pereiopods 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 Holthuis, who divides the Penaeidae into Penaeinae and Haliporinae, the Aristaeidae into Aristaeinae and Benthesicyminae, 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* (Kishinouye), Rec.; ×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 pereiopod shorter than others, with spinose merus and carpus, 3rd pereiopod longest; 3rd maxilliped as in *Aeger,* spinose. *U.Jur.,* Ger.; *U.Cret.(Cenoman.),* Lebanon.——Fig. 253,*1*. **A. cordata* (Münster), U.Jur., S.Ger.; ×0.7 (219).

Aeger Münster, 1839 [**Macrourites tipularius* von Schlotheim, 1822; SD Woods, 1925]. Rostrum long, sides granulate; 3rd maxilliped with thin long multiple spines; pereiopods *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., ×0.5 (11).

Antrimpos Münster, 1839 [**A. speciosus*; SD Woods, 1925] [=*Kölga* Münster, 1839 (no type)]. Antennules very short, antennae to twice length of body; rostrum dentate, carapace smooth, thin; length of pereiopods 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.; ×0.7 (219).——Fig. 252,*1*. *A. kiliani* (Van Straelen), U.Jur., Fr.; reconstr., ×1 (296).

Benthesicymus 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; pereiopods 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., ×0.5 (115).

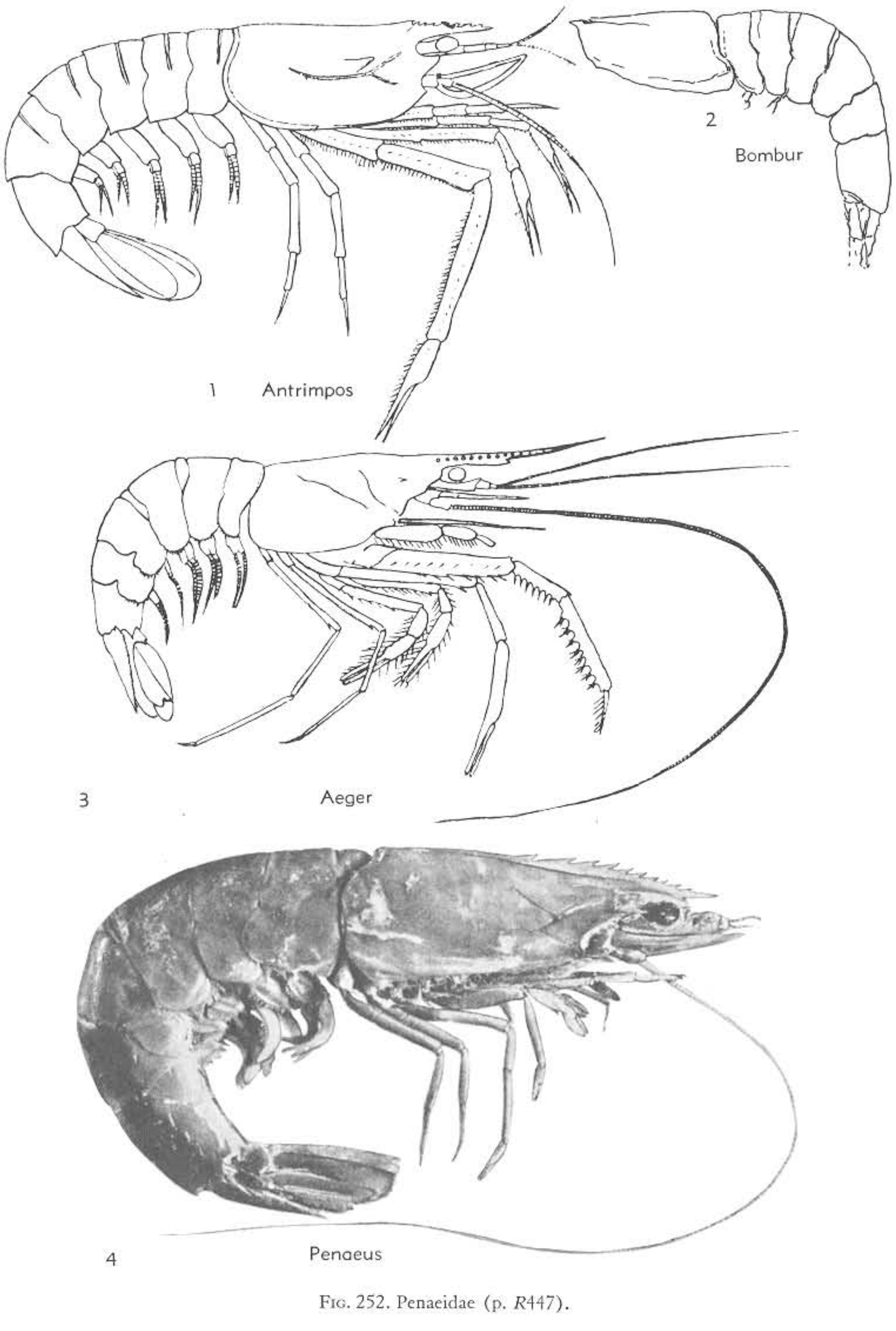


FIG. 252. Penaeidae (p. R447).

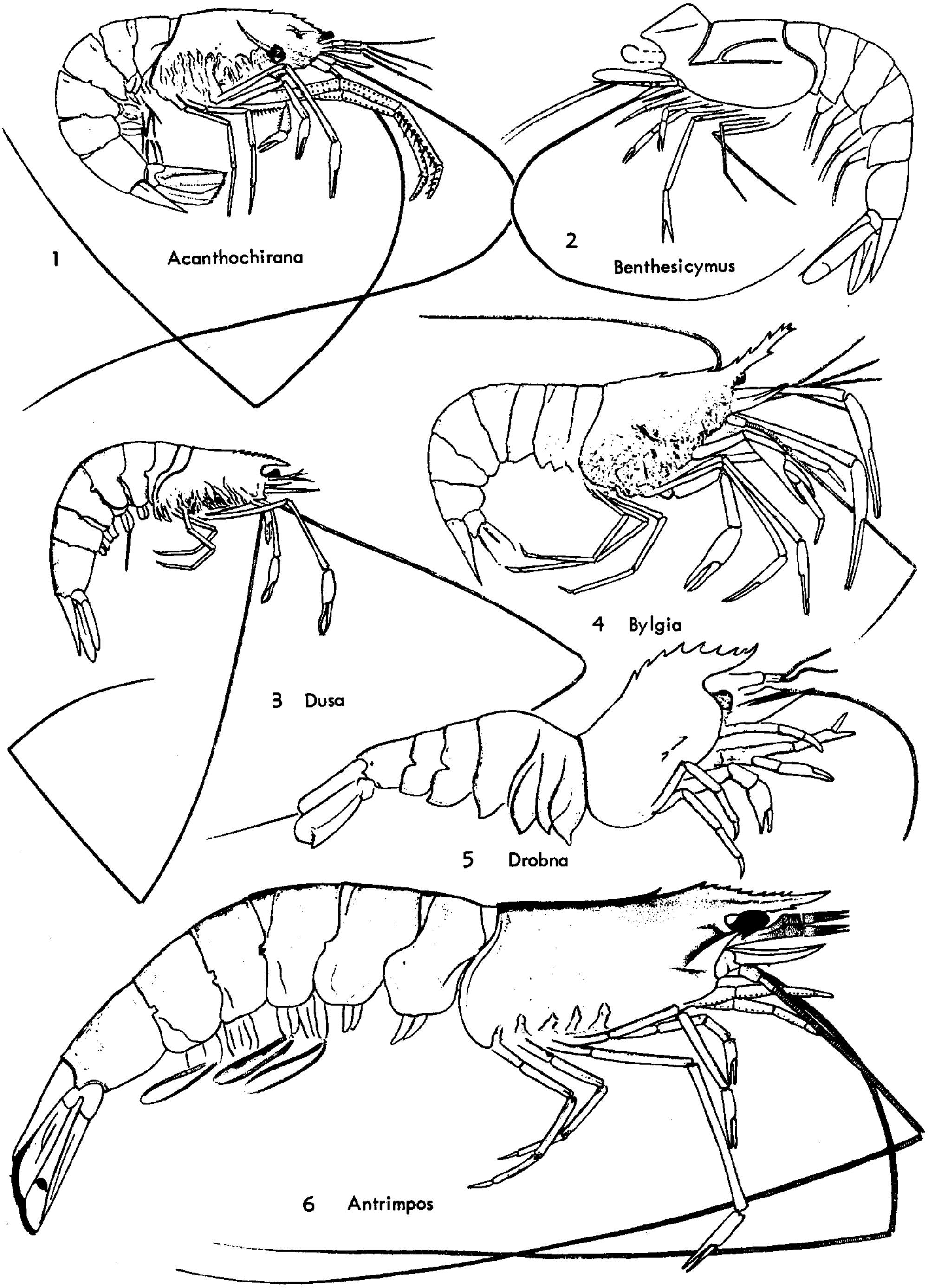


FIG. 253. Penaeidae (p. *R*447, *R*450).

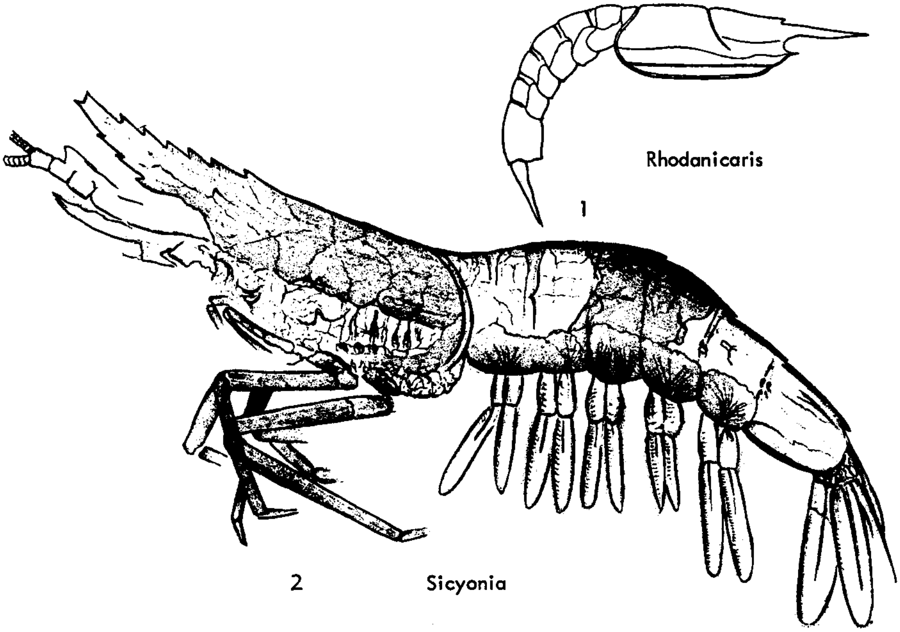


Fig. 254. Penaeidae (p. *R*450).

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.; ×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 pereiopods. *U.Jur.*, S.Ger.——Fig. 253,*4*. **B. spinosa*; ×0.7 (219).

Drobna Münster, 1839 [**D. deformis*; SD Glaessner, 1929]. Antennae long; rostral keel strongly curved and dentate, 3rd maxilliped thick, 1st pereiopod short and thick, abdomen curved, 3rd somite large. *U.Jur.*, S.Ger.——Fig. 253,*5*. **D. deformis*; ×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 pereiopods with wide propodus and curved fingers; abdomen as in *Penaeus* and *Antrimpos*. *U.Jur.*, S.Ger.——Fig. 253,*3*. **D. monocera*; ×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.), ×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 periopods short, pleopods very short. [Littoral, warm seas.] *U.Cret.*, Ger.; *Rec.*——Fig. 254,*2*. *S.? roemeri* (von der Marck), Senon., N.Ger.; ×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*; ×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 pereiopods *2* and *3* multiarticulate as in some Caridea; telson lanceolate. *U.Cret. (Cenoman.)*, Lebanon.——Fig. 255,*2*. **C. callirostris*; reconstr., ×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, strong and spinose, with elongate carpus and propodus and strong curved fingers; pereiopods *2* and *3* with small chelae; uropods without diaeresis. *L.Jur.*

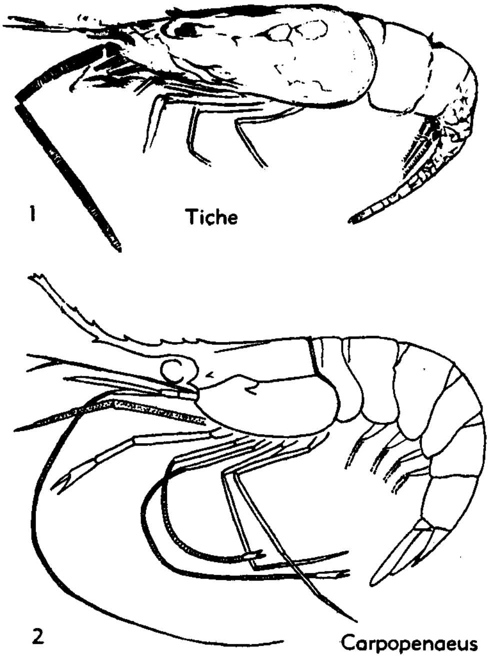


FIG. 255. Family Uncertain (p. R450).

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.; ×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

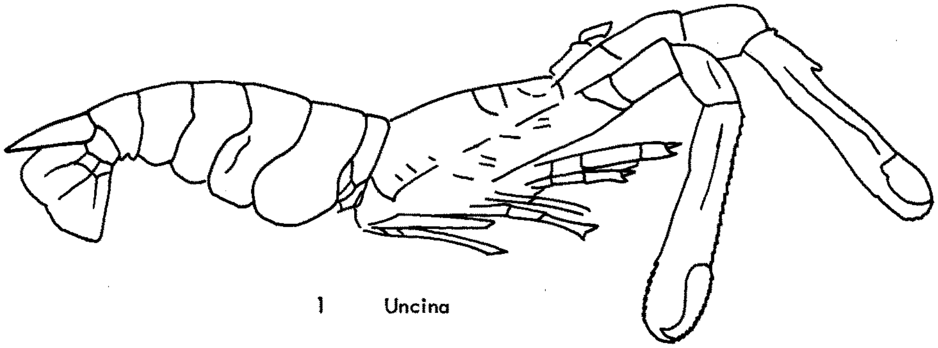


FIG. 255A. Uncinidae (p. R451).

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 Atyadea DE HAAN, 1849)]

Rostrum compressed; first two pereiopods subequal, chelate, all pereiopods may bear exopods. [Fresh-water.] *Tert.-Rec.*

Atya LEACH, 1816 [**Atys scaber* LEACH, 1815; OD] [=*Atyoida* RANDALL, 1839 (type, *A. bisulcata*)]. Rostrum not compressed; carpus of 2nd pereiopod very short, anteriorly deeply excavated, chelae divided to base; 3rd pereiopod 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.; ×0.7 (149, from Bouvier).

Caridina H. MILNE-EDWARDS, 1837 [**C. typus*; OD]. Rostrum generally compressed, smooth or serrate; carpus of 2nd pereiopod hardly excavated anteriorly; no exopods on pereiopods. *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 pereiopods 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.; ×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; ×2 (255).

Family PALAEMONIDAE Rafinesque, 1815

Antennules mostly three-flagellate, chelae of second pereiopod stronger than those of first, all pereiopods lacking exopods. [Marine and fresh water.] *Tert.-Rec.*

Palaemon WEBER, 1795 [**P. adspersus* 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.; ×0.7 (149).

Bechleja HOUŠA, 1956 [**B. inopinata;* OD]. Rostrum dentate, pereiopod *1* with small chela, pereiopod *2* with large chela, pereiopods *3* to *5* equal in length; telson little shorter than uropods; an-

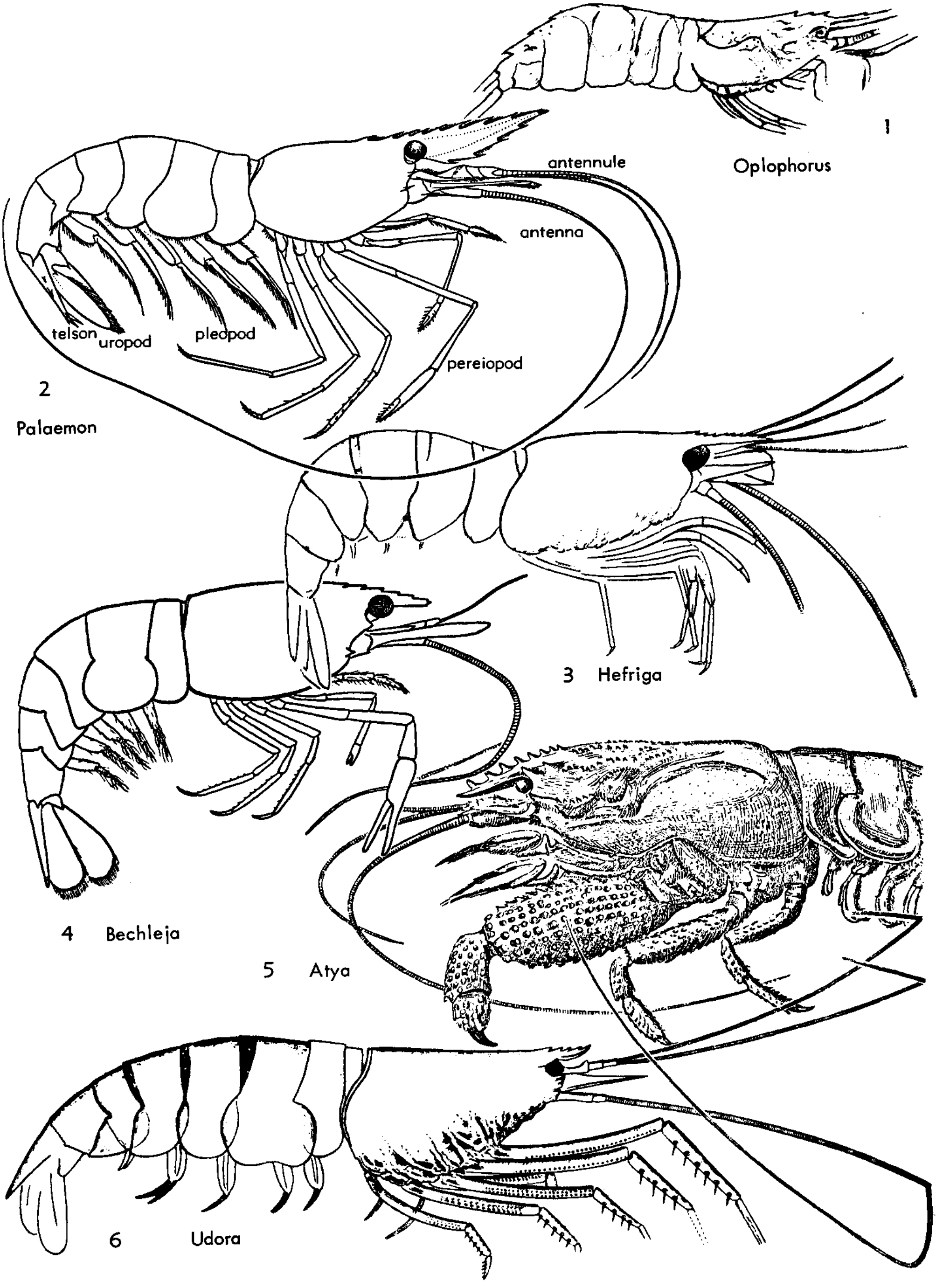


FIG. 256. Atyidae *(5)*; Oplophoridae *(1)*; Palaemonidae *(2,4)*; Family Uncertain *(3,6)* (p. *R*452, *R*454-*R*455).

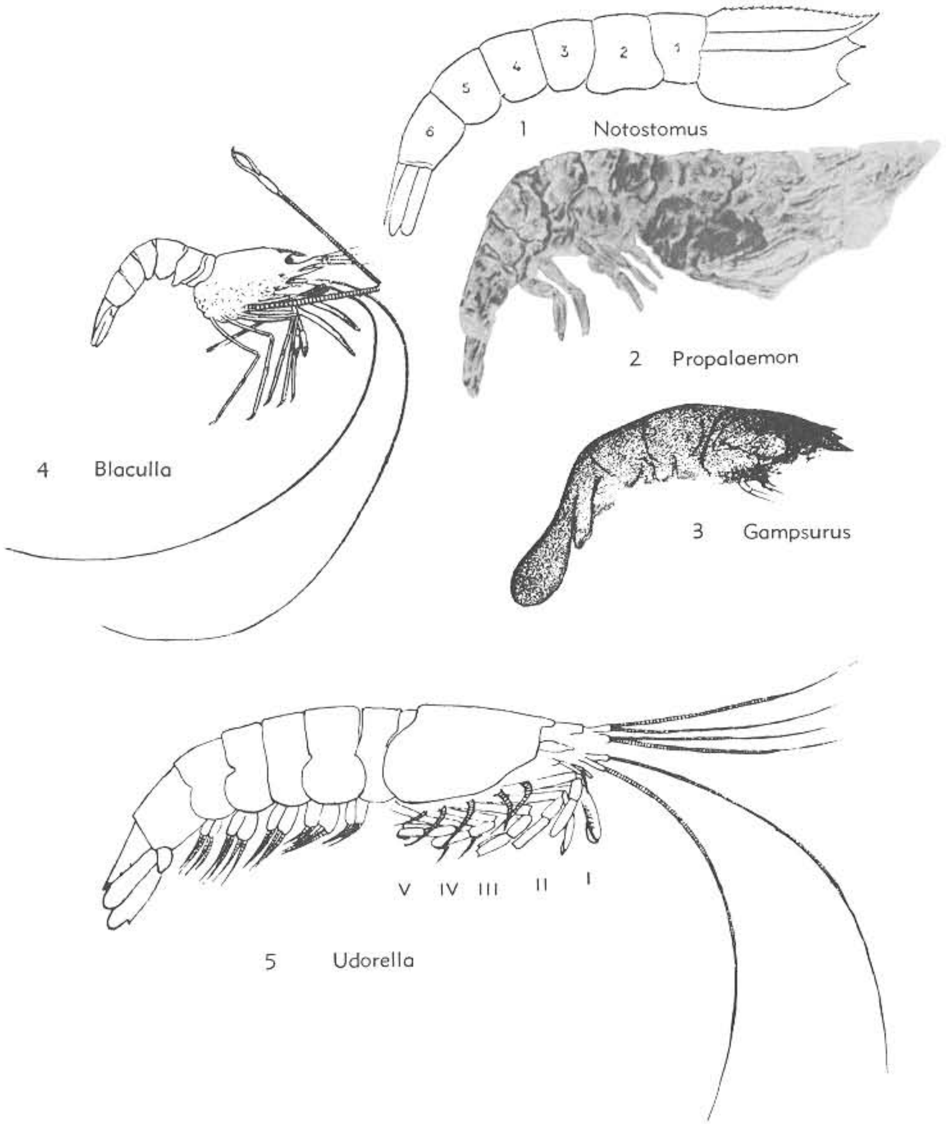


FIG. 257. Oplophoridae *(1)*; Palaemonidae *(2)*; Udorellidae *(5)*; Family Uncertain *(3,4)* (p. *R*455).

tennae 1.5 times length of cephalothorax. *U. Oligo.* or *L.Mio.*, Czech.——FIG. 256,*4*. **B. inopinata*, reconstr.; ×3 (152).

?**Homelys** VON MEYER, 1862 [**H. minor;* OD]. *U.Mio.*, Eu.

?**Micropsalis** VON MEYER, 1859 [**M. papyracea;* OD]. Rostrum smooth, 1st pereiopod with long chelae, antennae 3 times length of cephalothorax. *Oligo.*, Eu.

Propalaemon WOODWARD, 1903 [**P. osborniensis*; SD WOODS, 1925]. Rostrum serrate; pereiopods long and slender, pleopods long. *L.Oligo.*, Eng. ——FIG. 257,*2*. **P. osborniensis*; ×1 (326).

Family UDORELLIDAE Van Straelen, 1924

Third maxilliped ending in long thin terminal segment and finely spinose; pereiopods 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, pereiopods *1* to *5*), ×1 (11).

Family UNCERTAIN

Blaculla Münster, 1839 [**B. nicoides;* OD, M]. Rostrum denticulate, 1st pereiopod chelate, 2nd annulate, ending in small chela, left much shorter than right, pereiopods *3* to *5* without chelae; telson pointed, uropods with diaeresis. *U.Jur.*, S.Ger. ——Fig. 257,*4*. *B. sieboldi* Oppel, ×1 (219).

Hefriga Münster, 1839 [**H. serrata*; OD, M]. Rostrum denticulate, 1st 2 pereiopods with chelae, 3rd pereiopod longest. *U.Jur.*, S.Ger.——Fig. 256, *3*. **H. serrata*; ×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*; ×1 (191).

Udora Münster, 1839 [**U. brevispina*; OD, M]. Antennae long, rostrum denticulate, 2nd abdominal somite largest; 1st pereiopod chelate, all pereiopods spinose. *M.Jur.-U.Jur.*, Eu.——Fig. 256,*6*. **U. brevispina,* U.Jur., Ger.; ×1.3 (219).

Infraorder ASTACIDEA Latreille, 1803

[=Astacura Borradaile, 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 pereiopods chelate, chelae of third pereiopods largest; abdominal pleura well developed; uropods with diaeresis; genital openings coxal. *Permotrias.-Rec.*

Family ERYMIDAE Van Straelen, 1924

[*nom. correct.* Glaessner, 1929 (*pro* Erymaidae 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. *R*626.)

Subfamily ERYMINAE Van Straelen, 1924

[*nom. transl. et correct.* Beurlen, 1927 (*ex* Erymaidae Van Straelen, 1924)]

Carapace with median suture and intercalated plate; chelae of first pereiopods 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 *ω* 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.; ×2 (219).——Fig. 259,*3*. *E. bedelta* (Quenstedt), M.Jur., Eng.; ×0.7 (326).

Enoploclytia M'Coy, 1849 [**Astacus leachi* Mantell, 1822; OD]. Carapace and 1st pereiopods 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, ×0.7 (326). ——Fig. 258,*2*. *E. (E.) leachi granulicauda* (Schlüter), U.Cret., Ger.; carapace, ×0.7 (193).

E. (Palaeastacus) Bell, 1850 [**P. dixoni* 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; ×0.5 (326).

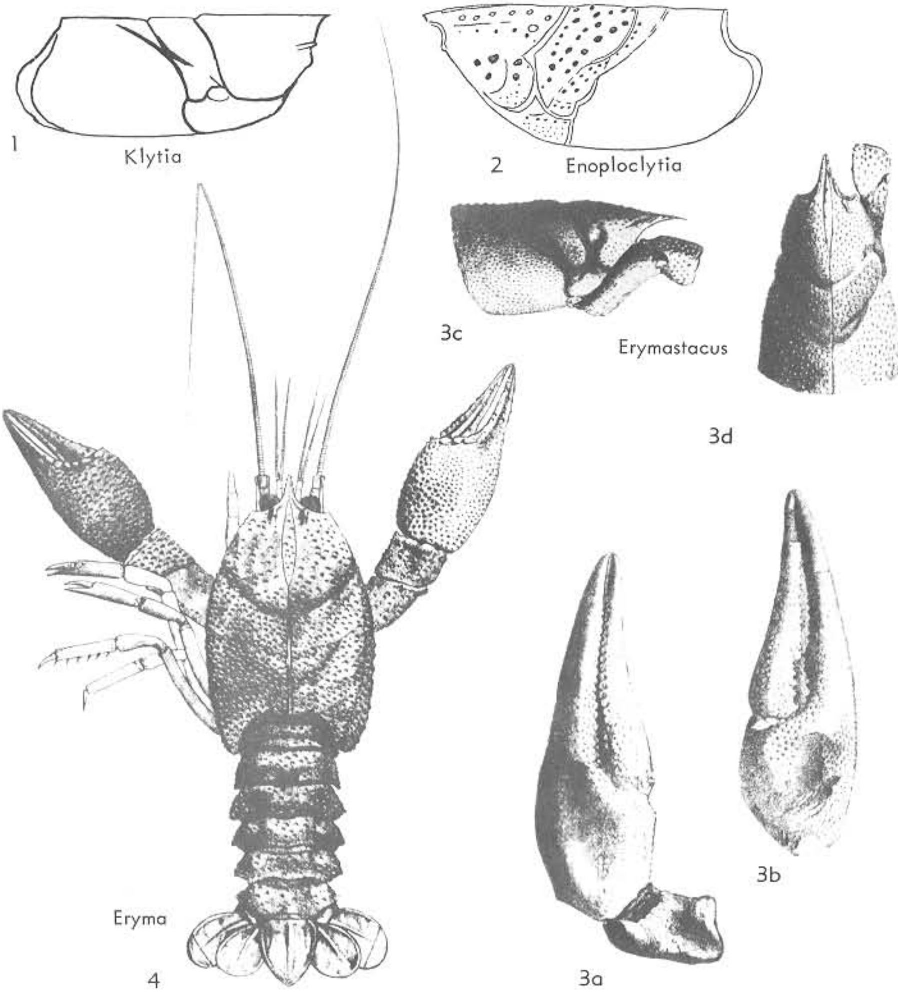


FIG. 258. Erymidae (Eryminae) (p. *R*455-*R*456).

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, ×0.7 (219).

Klytia VON MEYER, 1840 [**Glyphea ventrosa* VON MEYER, 1835]. Carapace with cervical groove deep, sinuous, inclined, but less sloping than postcervical 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, ×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, ×2 (39).

Clytiella GLAESSNER, 1931 [**C. spinifera*; OD]. Carapace wtih closely granulate surface and with

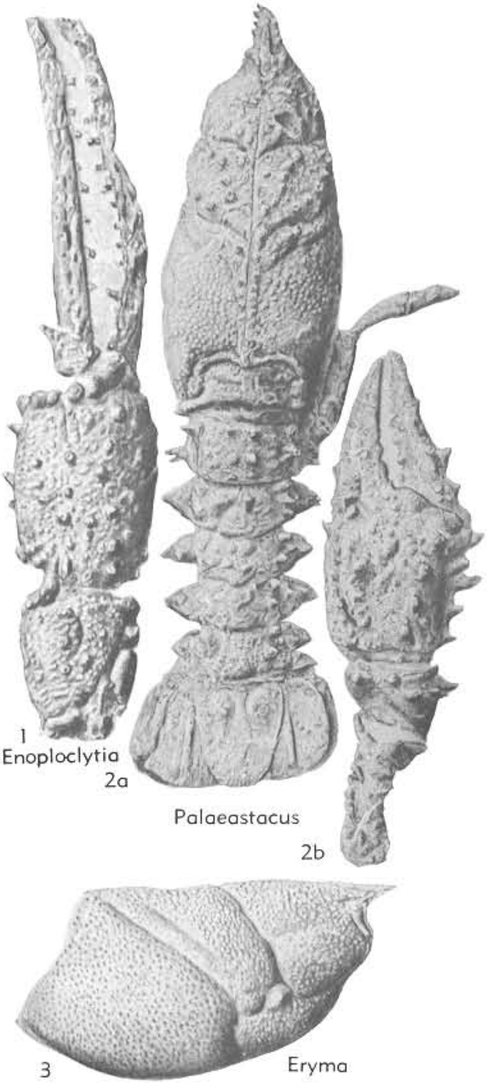


FIG. 259. Erymidae (Eryminae) (p. *R*455).

median keel bearing row of curved sharp spines; 1st pereiopods with massive chelae, fingers short. *U.Trias.*, Aus.——FIG. 261,*1*. **C. spinifera*; holotype, ×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, ×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 postcervical grooves parallel; branchiocardiac groove weak, sigmoidal; chelae long, with long denticulate fingers. *M.Trias.*, Eu.——FIG. 261,*3*. **L. silesiaca*; carapace and chela, ×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, ×1.5 (221).

?**Protoclytiopsis** BIRSHTEYN, 1958 [**P. antiqua;* OD]. Possibly synonym of *Lissocardia* from which it differs only in apparent absence of anterolateral

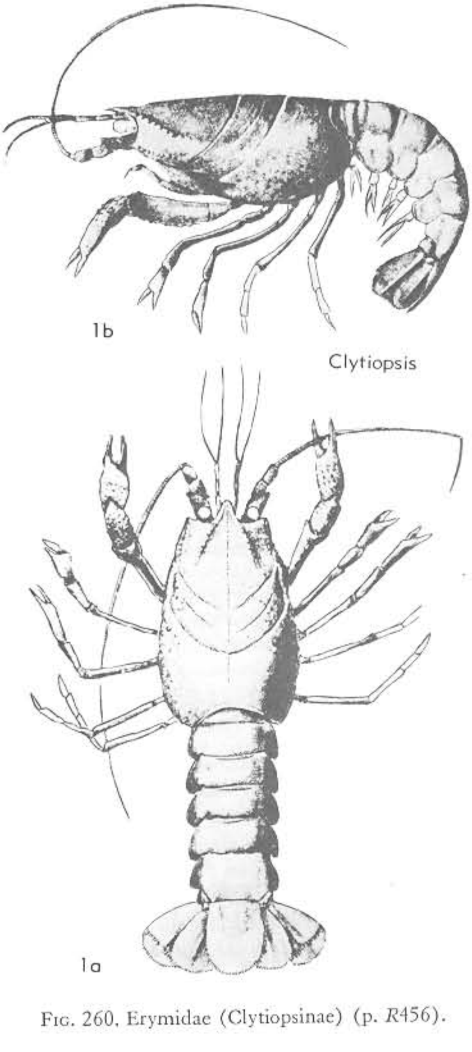


FIG. 260. Erymidae (Clytiopsinae) (p. *R*456).

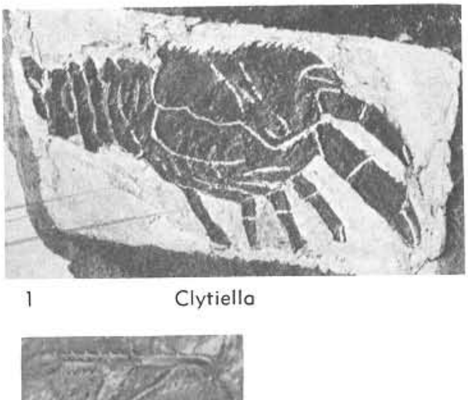


FIG. 261. Erymidae (Clytiopsinae) (p. *R*456-*R*458).

("gastral") ridges. [The name is spelled *Protoclutiopsis*, 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 pereiopods long and slender, second chelae smaller by about one-half, third chelae very small. *U.Trias.*

Platychela GLAESSNER, 1931 [**P. trauthi*; OD]. Characters of family. *U.Trias.*, Aus.——FIG. 263,*1*. **P. trauthi;* reconstr., ×0.7 (111).

?Platypleon VAN STRAELEN, 1936 [**P. nevadense*; OD]. Fragmentary abdomen resembling *Platychela*; 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 BEURLEN, 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.

Palaeonephrops 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, ×1 (193).

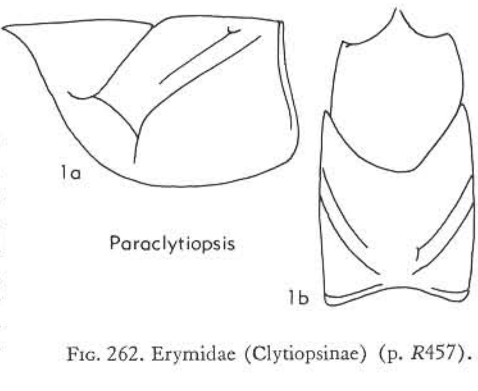


FIG. 262. Erymidae (Clytiopsinae) (p. *R*457).

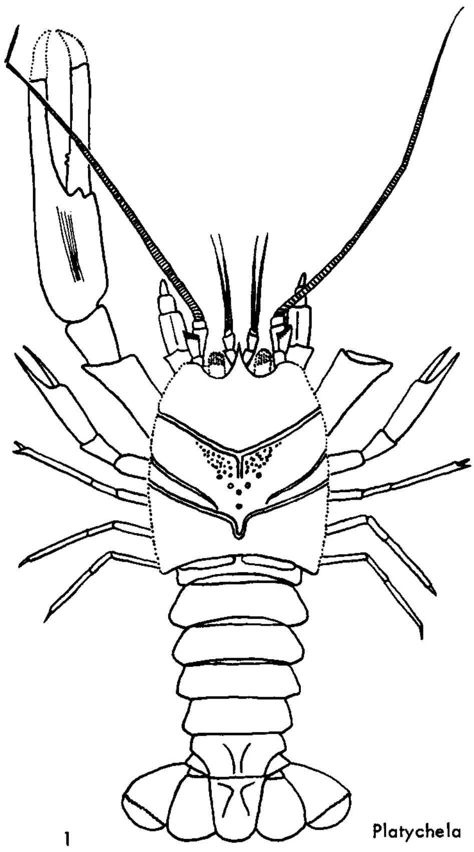


FIG. 263. Platychelidae (p. *R*458).

Paraclythia FRITSCH, 1877 [**P. nephropica*; OD] [=*Paraclytia* 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., ×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.; ×0.2 (341a).——FIG. 265,*1b*. *H. americanus* H. MILNE-EDWARDS, Rec.; carapace (*r,* rostrum; *1-3,* rostral spines; *α*, supraorbital spine; *β*, suborbital spine; *γ*, antennal spine; *c-e,* postcervical groove; *a,* branchiocardiac groove), ×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, ×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.; ×0.7 (326).——FIG. 265,*4b,c*. *H. stokesi* (WELLER), U.Cret. (Campan.), Antarctic; reconstr., *4b,* female, *4c,* abdominal somites 2-5 of ?male, ×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); *?Stenocheles* 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 pereiopods 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., ×0.7 (orig., after 193).

Subfamily NEOPHOBERINAE Glaessner, n. subfam.

[=Phoberinae MERTIN, 1941]

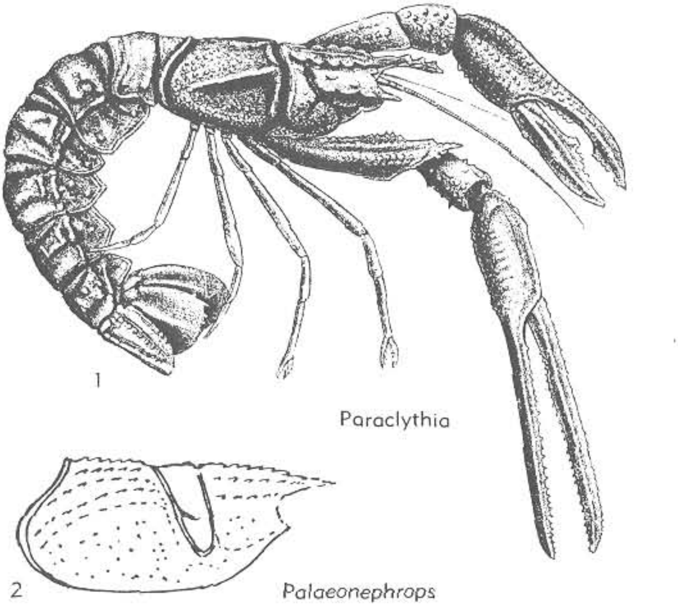


FIG. 264. Nephropidae (Nephropinae) (p. *R*458-*R*459).

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.; ×0.2 (112).

Palaeophoberus GLAESSNER, 1932 [**Stenochirus suevicus* QUENSTEDT, 1867; OD]. Carapace spinose, with distinct cervical and postvervical 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., ×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,* ×*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.; ×1 (219).

?Stenochirus OPPEL, 1861 [**S. meyeri* OPPEL, 1862; SD GLAESSNER, 1929]. Small; antennal flagella long, 1st pereiopods 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*; ×1 (219).

Family ASTACIDAE Latreille, 1802

[*nom. correct.* SAMOUELLE, 1819 (*pro* Astacini LATREILLE, 1802)] [=Potamobiidae HUXLEY, 1878]

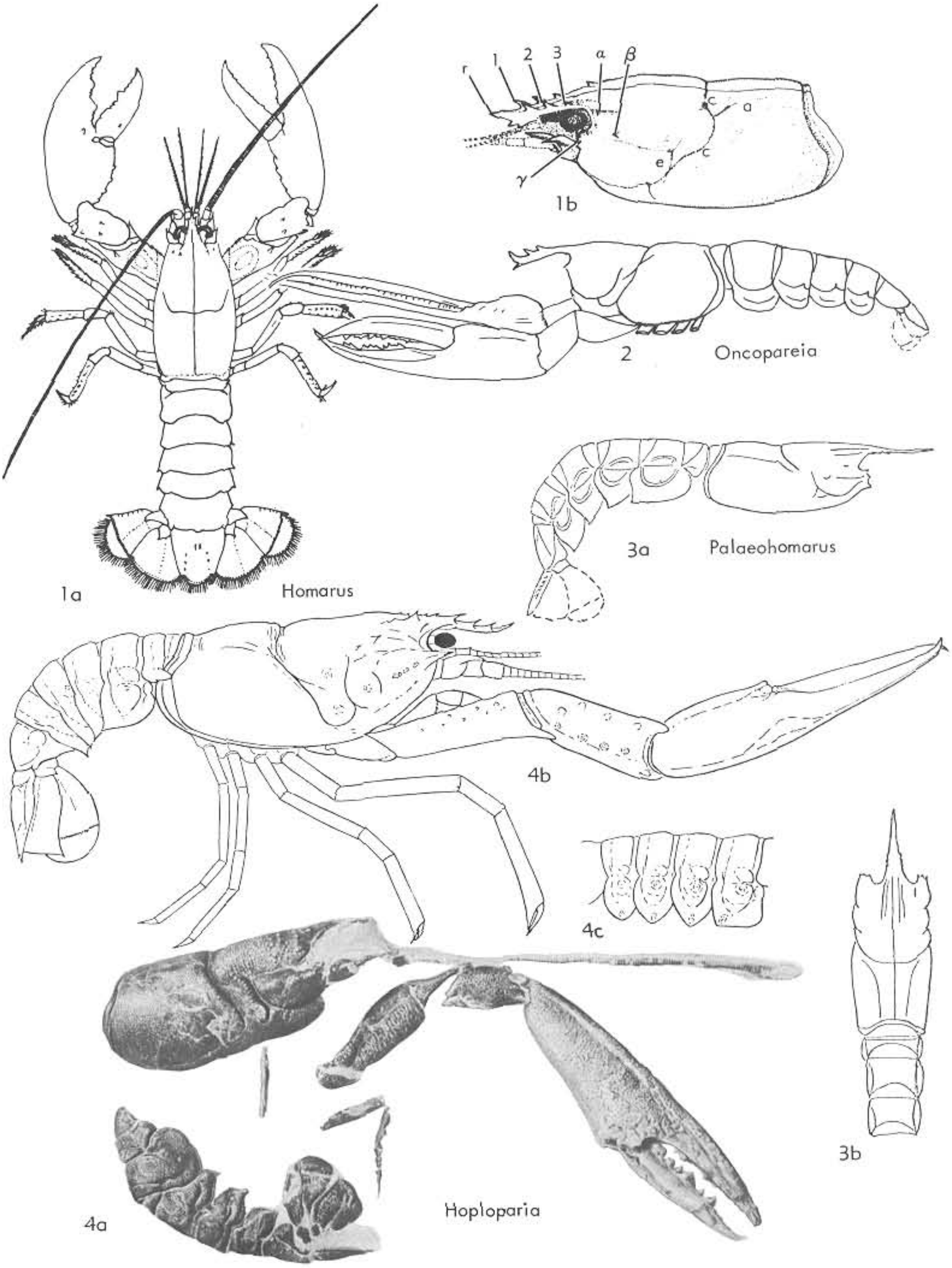


FIG. 265. Nephropidae (Homarinae) (p. *R*459).

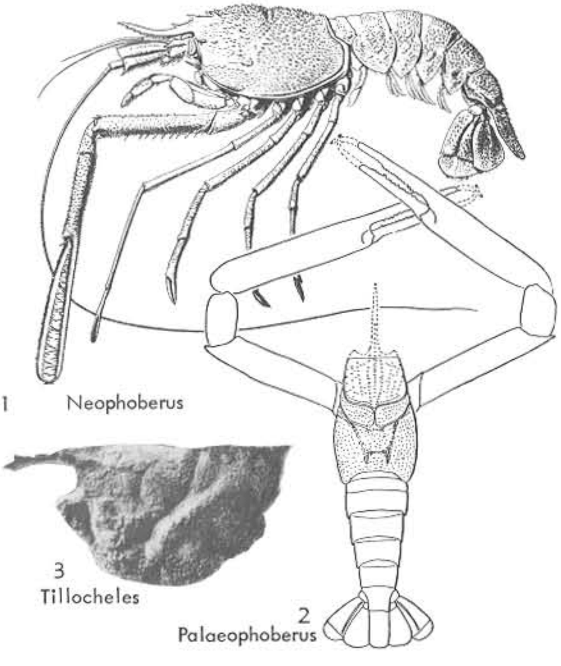


FIG. 266. Nephropidae (Neophoberinae) (p. *R*460).

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 pereiopods 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 postorbital ridges, one behind other; males without hooks on ischium of pereiopods, 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.; ×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 pereiopods *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

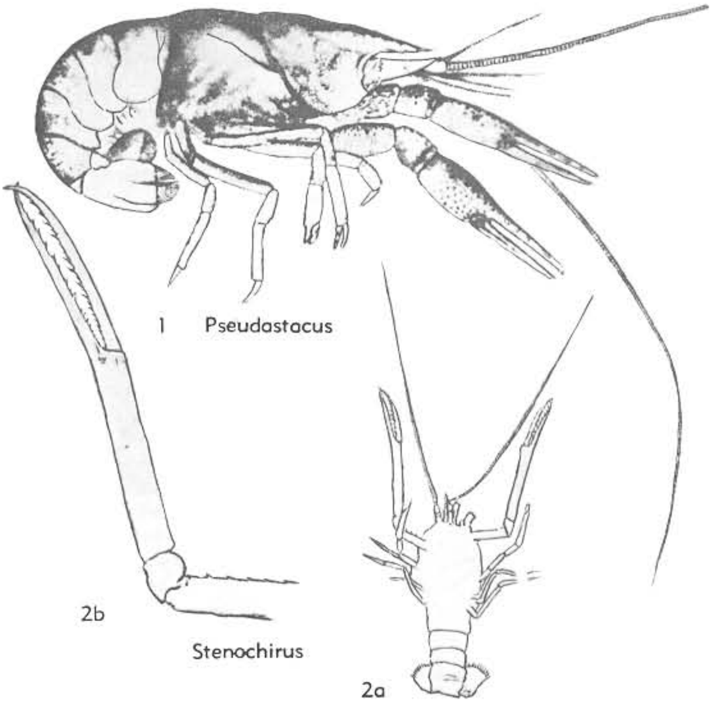


FIG. 267. Nephropidae (Subfamily Uncertain), (p. *R*460).

more than terminal and 1 pair of lateral spines or tubercles; telson without transverse suture. *Pleist.,* SE.Australia, *Rec.,* Tasmania.

Family AUSTROASTACIDAE 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, *Macrourites pseudoscyllarus* VON SCHLOTHEIM, 1820); *Brisa* MÜNSTER, 1839 (type, *B. lucida*); *?Selenisca* VON MEYER, 1847 (type, *S. gratiosa*); *Paraglyphea* BEURLEN, 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 branchiocardiac grooves very oblique, joined medially and laterally and in some species at additional points;

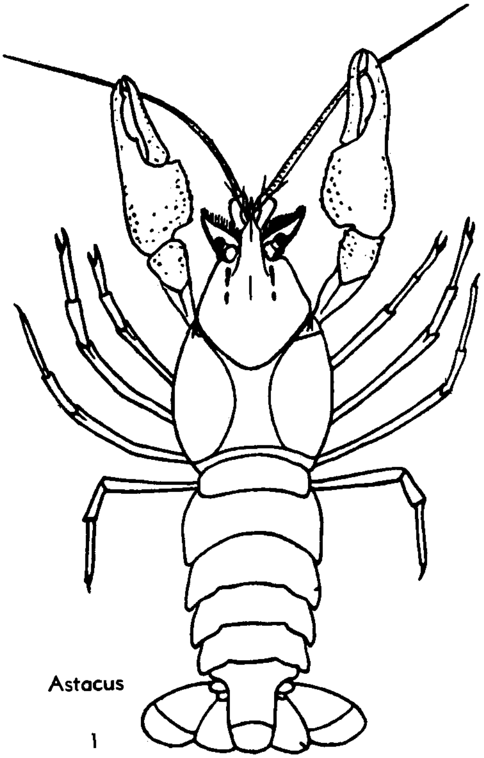


FIG. 268. Astacidae (p. R462).

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 pereiopods 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.; ×1 (219). ——FIG. 269,*3b. G. (G.) prestwichi* WOODS, L. Jur., Eng.; ×1 (326).

G. (Squamosoglyphea) BEURLEN, 1930 [**G. udressieri* VON MEYER, 1840; OD]. Carapace with scalelike sculpture. *U.Jur.,* Eu.——FIG. 269,*4.* **G. (S.) udressieri* (VON MEYER), Fr.; ×1 (219).

Litogaster VON MEYER, 1847 [*nom. subst. pro Liogaster* 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 distinguishable 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 pereiopod, ×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, ×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 pereiopods 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 pereiopods 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 pereiopods very long, slender, subchelate, 2nd pereiopods subchelate. *L.Jur.-U.Jur.,* Eu.-N.Z.——FIG. 270,*1.* **M. longimanatus* (SCHLOTHEIM), U. Jur., Ger.; ×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 pereiopods not exceeding body length, 1st abdominal somites reduced. *L.Cret.-*

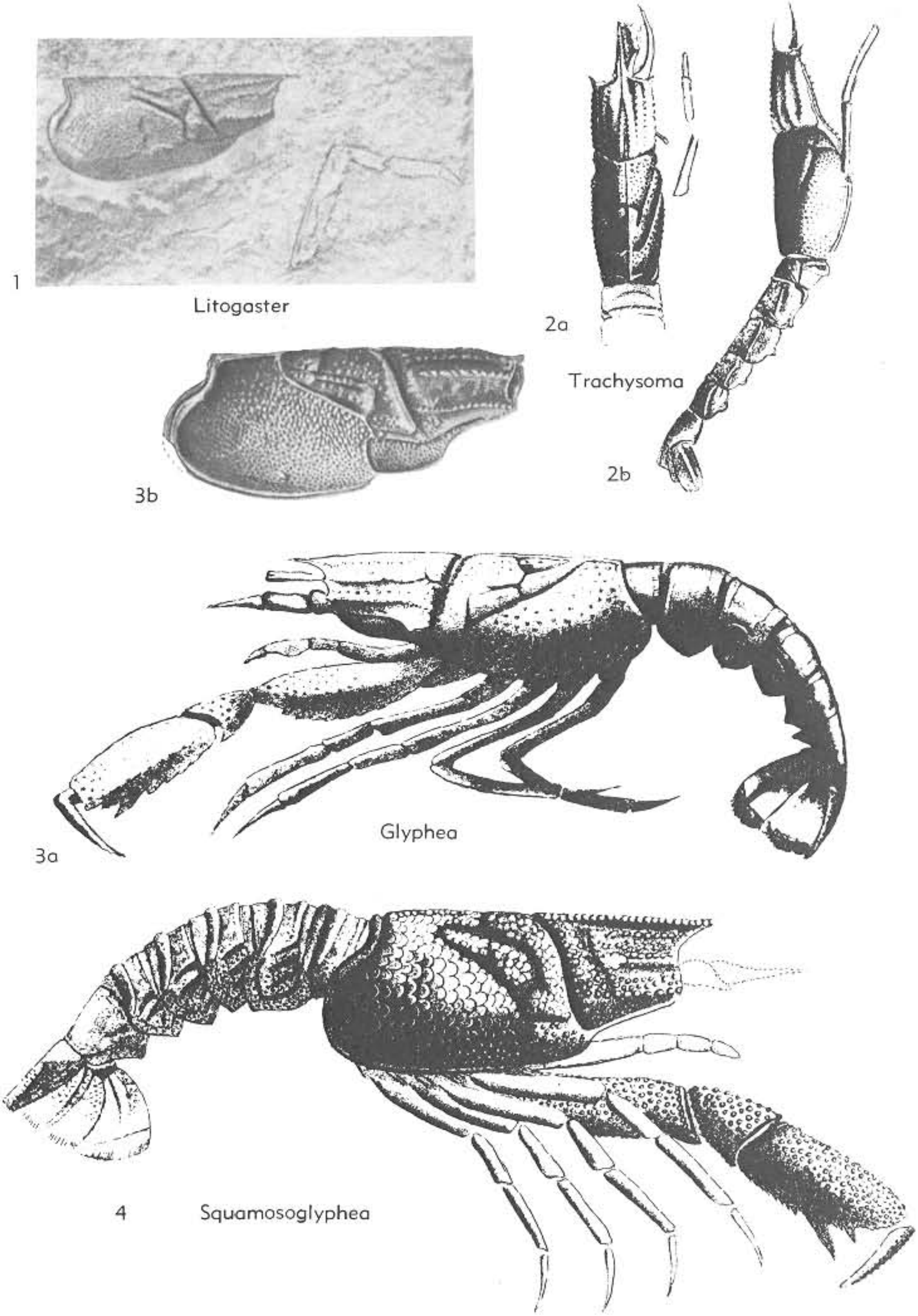


FIG. 269. Glypheidae (p. *R*463-*R*464).

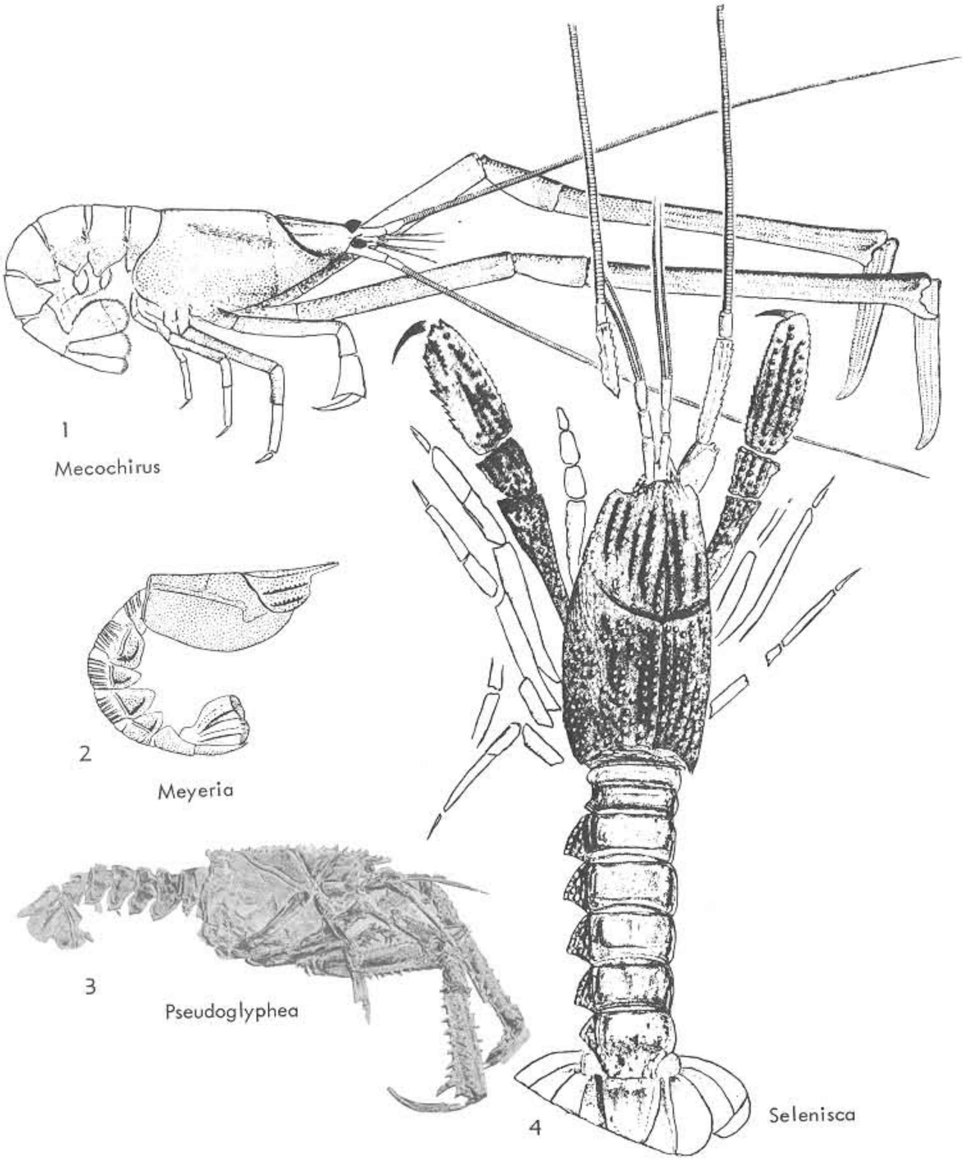


Fig. 270. Mecochiridae (p. *R*464-*R*466).

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.; ×0.7 (326).

?**Praeatya** Woodward, 1868 [**P. scabrosa*; OD]. Carapace with short rostrum, 1st 2 pereiopods not chelate. [Incompletely known.] *L.Jur.,* Eng.

Pseudoglyphea Oppel, 1861 [**Glyphea grandis* von Meyer, 1837; OD] [=*Scapheus* Woodward, 1863 (type, *S. ancylochelis*); *Heteroglyphea* Colosi, 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 pereiopods long, uropods with diaeresis. [Beurlen (1930) reinstated *Eumorphia* von Meyer, 1847 (type, *E. socialis*) for several species which other authors include in *Pseudo-*

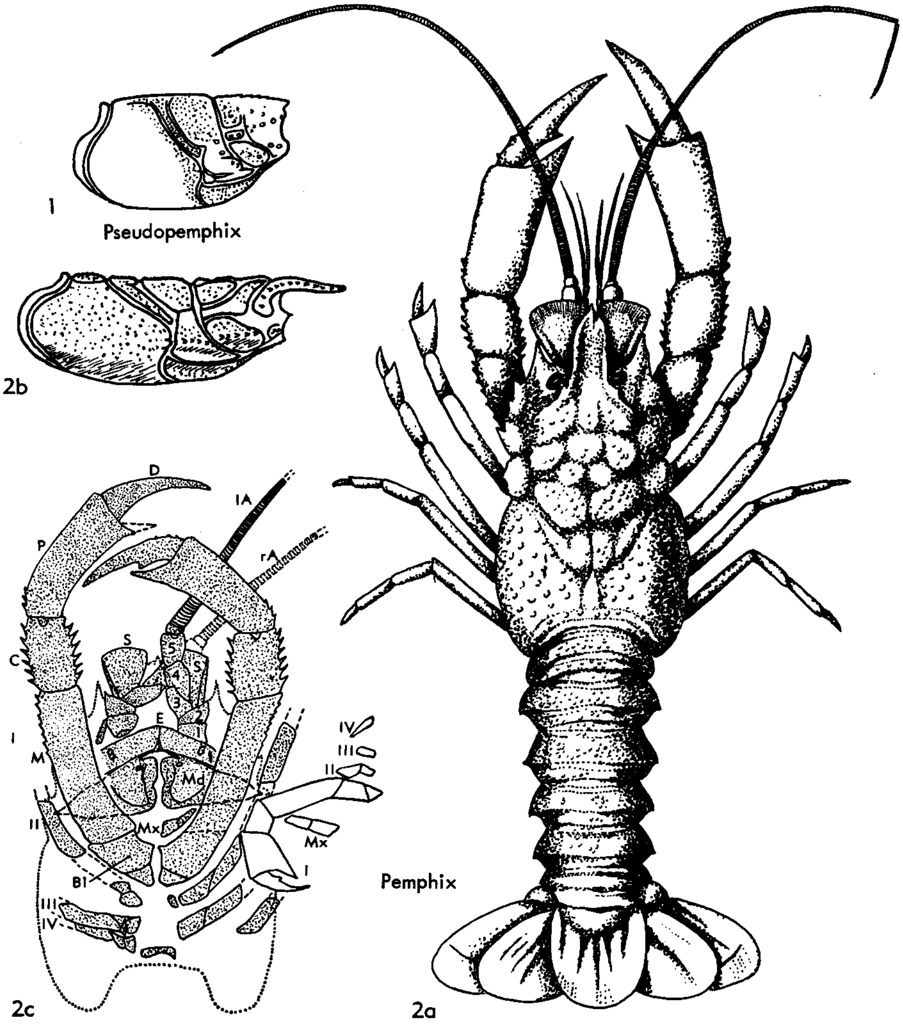


FIG. 271. Pemphicidae (p. *R*467-*R*468).

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. ancylochelis* (WOODWARD), Lias., Eng.; ×0.3 (326).

?**Selenisca** VON MEYER, 1847 [**S. gratiosa*; OD]. Carapace and 1st pereiopods covered with tubercles in longitudinal rows. [Based on a single specimen which OPPEL and VAN STRAELEN placed in *Glyphea,* whereas BEURLEN included it in the Mecochiridae.] *U.Jur.,* Ger.——FIG. 270,*4*. **S. gratiosa*; ×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 wtih longitudinal ridges; first three pereiopods subchelate; telson rounded. *M.Trias.*

Pemphix VON MEYER, 1840 [**Palinurus sueurii* DESMAREST, 1822; OD]. Carapace cylindrical,

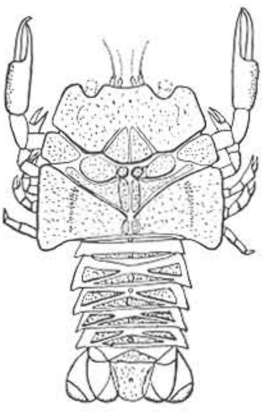


FIG. 272. Tetrachelidae (p. R468-R470).

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 pereiopods subchelate, strong, 2nd to 5th pereiopods equal; abdomen strong, transversely grooved, with pointed pleura; uropods with diaeresis. *M.Trias.*, Eu.——FIG. 271,*2*. **P. sueuri* (DESMAREST); *2a*, reconstr., ×0.7 (after Assmann, 1927, and Glaessner, 1932); *2b*, carapace, lat. view, ×0.7 (Glaessner, 1932); *2c*, ventral view, ×0.5 [I-IV, pereiopods *1-4*; *lA*, left antenna; *rA*, right antenna; *S*, antennal scale; *1-5*, antennal stalk; *E*, epistome; *Md*, mandible; *Mx*, maxilliped *3*; *B1*, basis; *M*, merus; *C*, carpus; *P*, propodus; *D*, dactylus of *P1*]. First 4 pereiopods 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 pereiopods almost chelate. *M.Trias.*, Eu.——FIG. 271,*1*. **P. albertii* (VON MEYER); carapace, lat. view, ×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 pereiopods chelate, dactylus 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.

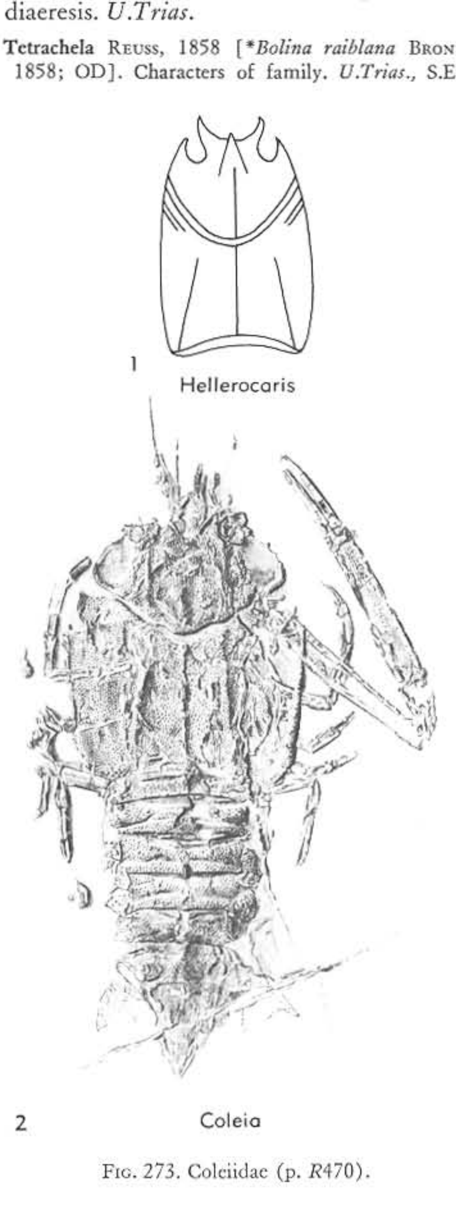


FIG. 273. Coleiidae (p. R470).

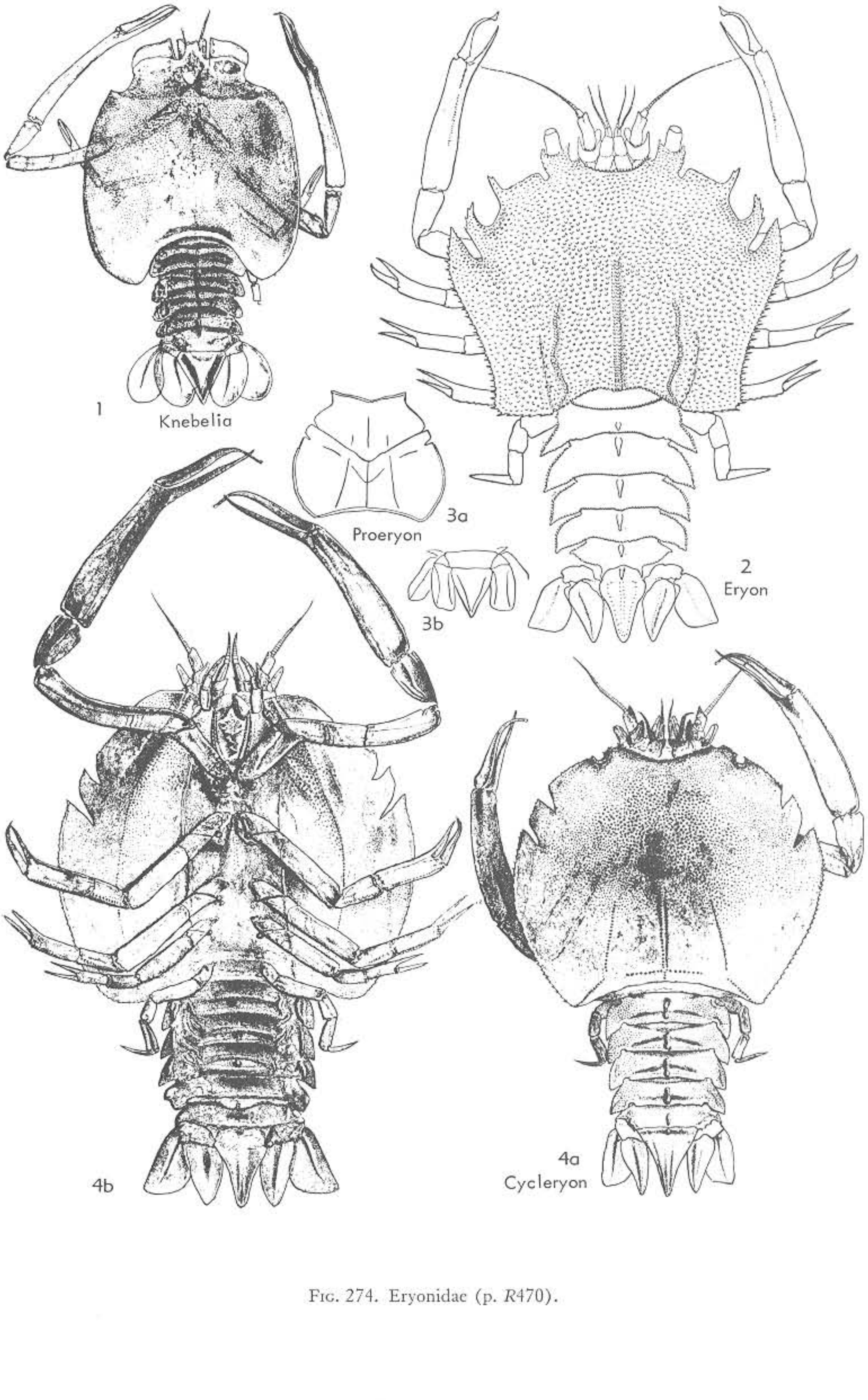
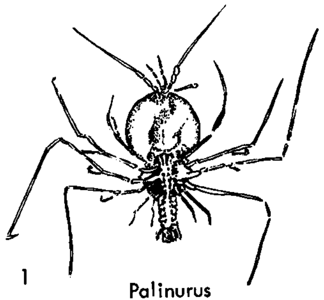
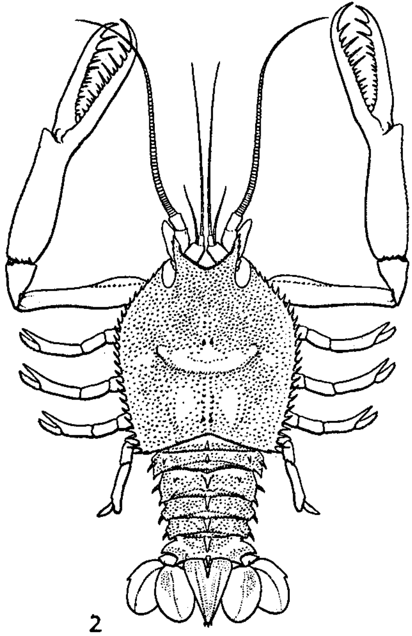


FIG. 274. Eryonidae (p. *R*470).



1

Palinurus



2

Palaeopentacheles

FIG. 275. Polychelidae *(2)*; Palinuridae *(1)* (p. *R*471, *R*473).

——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. artiformis* (SCHLOTHEIM), U.Jur., Ger.; reconstr., ×0.7 (11).

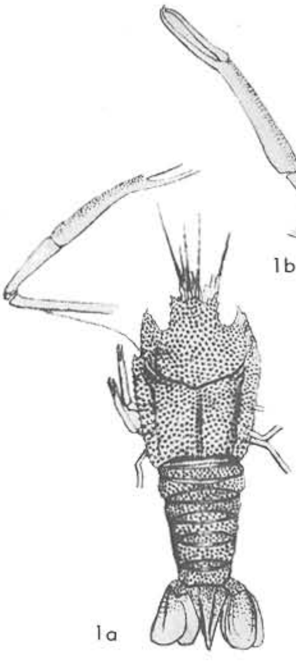
Cycleryon [*nom. subst.* GLAESSNER, 1965 (*pro Cyclocaris* BEURLEN & GLAESSNER, 1930, *non Cyclocaris* STEBBING, 1888)] [**Macrourites propinquus* VON SCHLOTHEIM, 1822; OD]. Carapace subcircular, frontal margin wide, eyes in small semicircular orbital indentations. *Jur.*, Eu.——FIG. 274,*4*. **C. propinquus* (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).

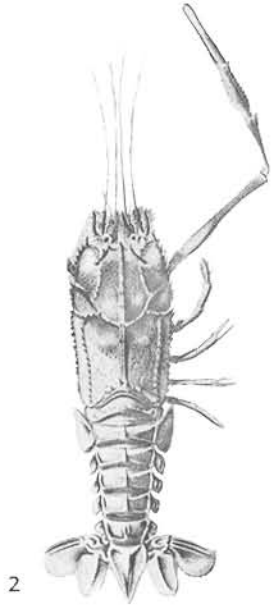
Knebelia VAN STRAELEN, 1922 [**Eryon bilobatus* MÜNSTER, 1839; OD, M] [=*Muensteria* KNEBEL, 1907 (*non* STERNBERG, 1838)]. Carapace with oval outline, without marginal indentations; telson large, uropods rounded. *U.Jur.*, S.Ger.——FIG. 274,*1*. **K. bilobata* (MÜNSTER); ×0.7 (219).

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.*



Palaeopolycheles



Polycheles

FIG. 276. Polychelidae (p. *R*471).

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 pereiopods slender; uropods rounded; postlarval stage with ovoid inflated carapace. [Abyssal and subabyssal.] *Rec.*, cosmop.——Fig. 276,2. **P. typhlops*, Rec.; ×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 pereiopods long and robust. *U.Jur.*, S.Ger.——Fig. 275,2. **P. roettenbacheri* (Münster); reconstr., ×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 pereiopods with long merus and carpus. *U.Jur.*, S.Ger.——Fig. 276,*1*. **P. longipes* (Fraas); *1a*, dorsal view, *1b*, cheliped, ×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 pereiopods 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

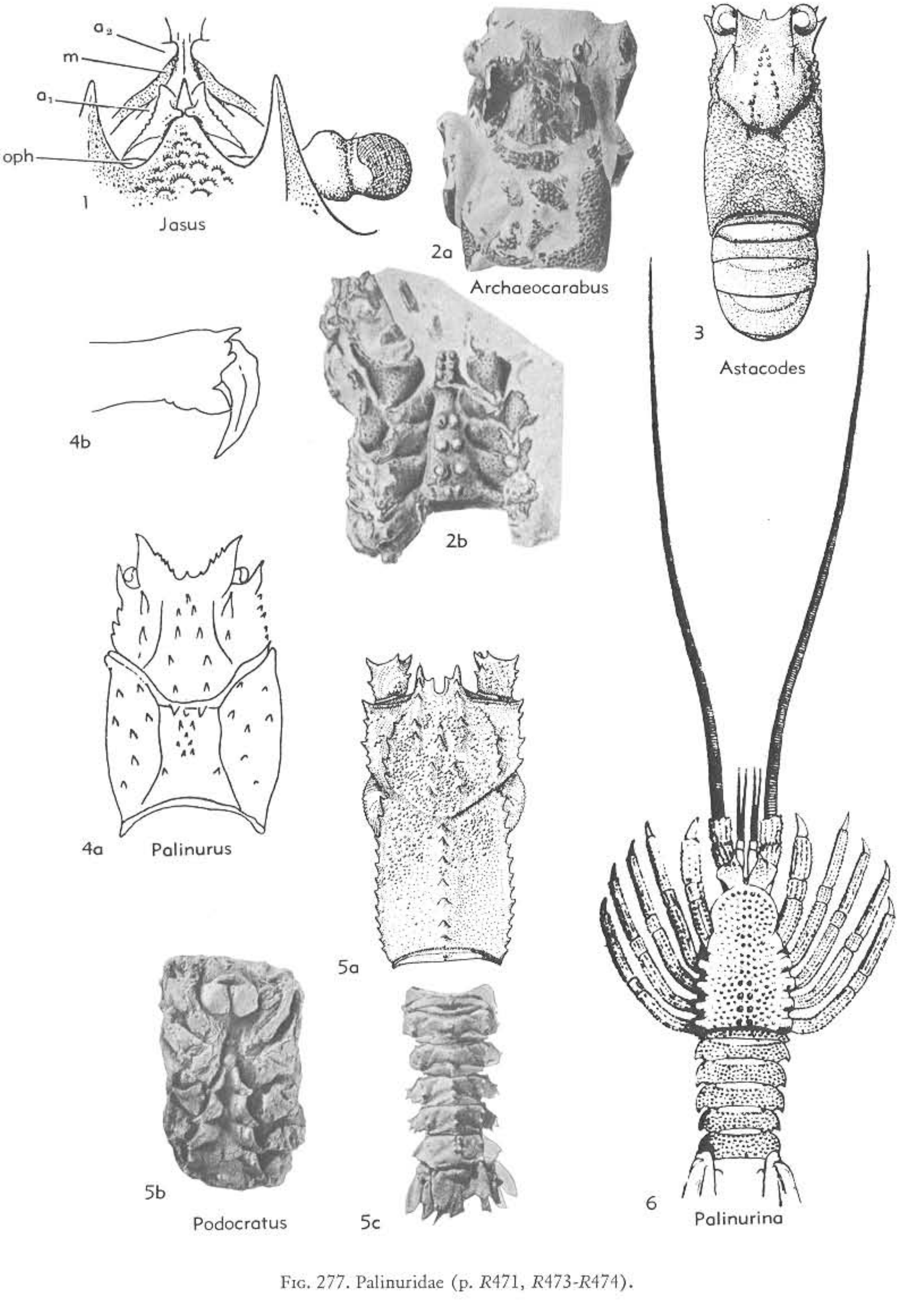


FIG. 277. Palinuridae (p. *R*471, *R*473-*R*474).

FIG. 278. Palinuridae (p. *R*473).

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 pereiopod *1,* ×0.1 (52).——FIG. 275,*1*. *Phyllosoma* larva of *P. elephas* (FABRICIUS), Rec.; ×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, ×1, *2b,* ventral view, ×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., ×0.5 (283).

Eurycarpus SCHLÜTER, 1868 [**E. nanodactylus*; OD]. Antennular stalks long, antennal stalks strong and spiny, pereiopods 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 (*a_2,* base of antenna; *m,* articulating membrane; *a_1,* antennular base; *oph,* eye stalk), ×1 (15).——FIG. 278, *1*. *J. flemingi* GLAESSNER, Oligo., N.Z.; ×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*

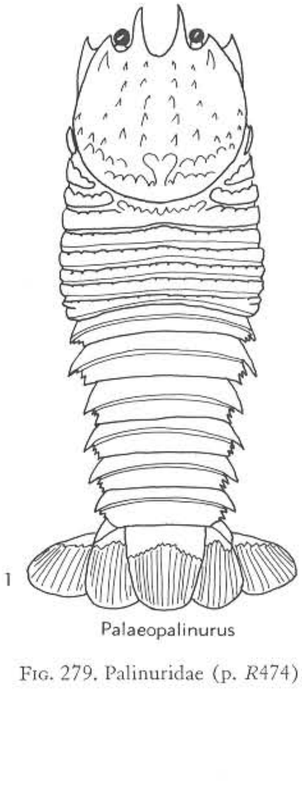


FIG. 279. Palinuridae (p. *R*474).

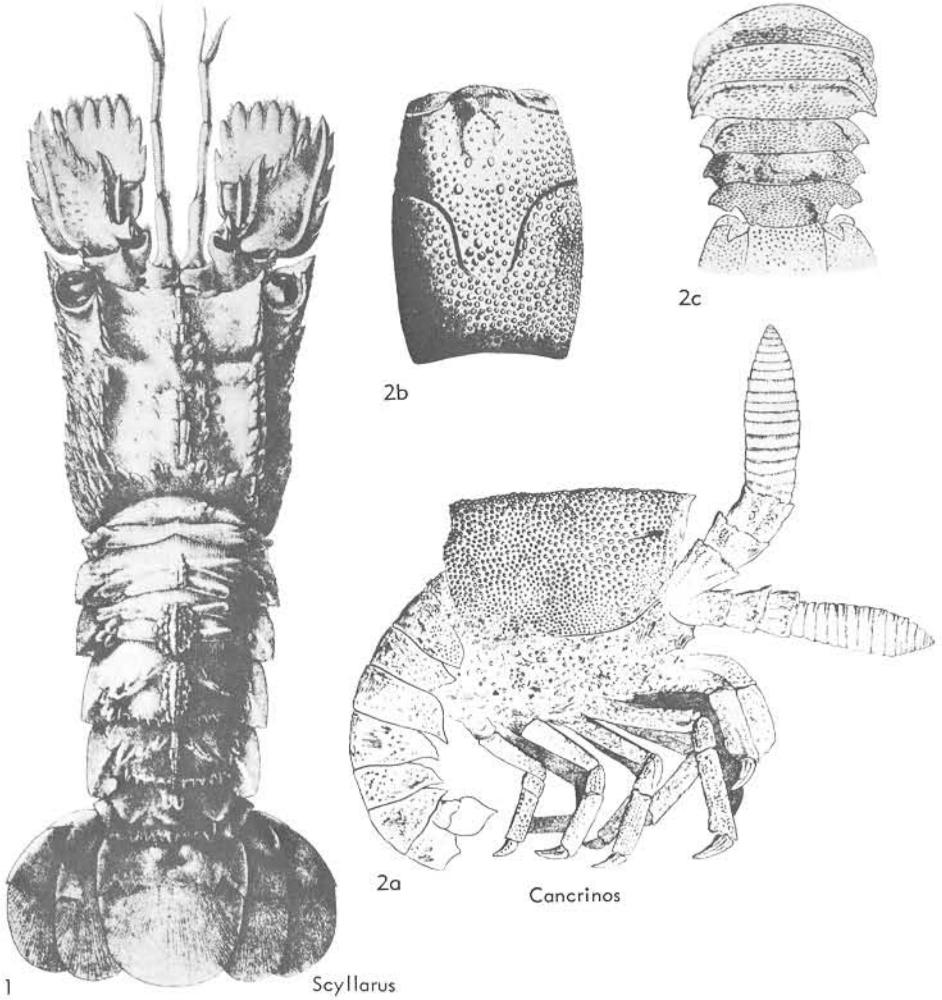


Fig. 280. Cancrinidae *(2);* Scyllaridae *(1)* (p. *R*475).

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 pereiopods *1-5, 5c,* abdomen, ×1 (283).

Palaeopalinurus Bachmayer, 1954 [**P. glaessneri;* OD]. Carapace cylindrical, with distinct postcervical groove, anterior portion with large supraorbital and other spines, posterior part transversely grooved and ridged. *U.Jur.,* Eu.——Fig. 279,*1*. **P. glaessneri;* reconstr., ×0.5 (Glaessner, n).

Palinurina Münster, 1839 [**P. longipes;* SD Woods, 1926]. Antennae thick and long, with setae, on strong short stalks; 1st pereiopods shorter than others; carapace and abdomen incompletely known. *L.Jur.,* Eng.; *U.Jur.,* Ger.——Fig. 277,*6*. **P. longipes,* U.Jur., S.Ger.; reconstr., ×1 [according 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.*

Cancrinos 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, ×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.; ×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, ×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, ×1.5 (244).

Scyllarides GILL, 1898 [**Scyllarus aequinoctialis* LUND, 1793; OD] [?=*Scyllaridia* BELL, 1858 (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.; ×1 (326).

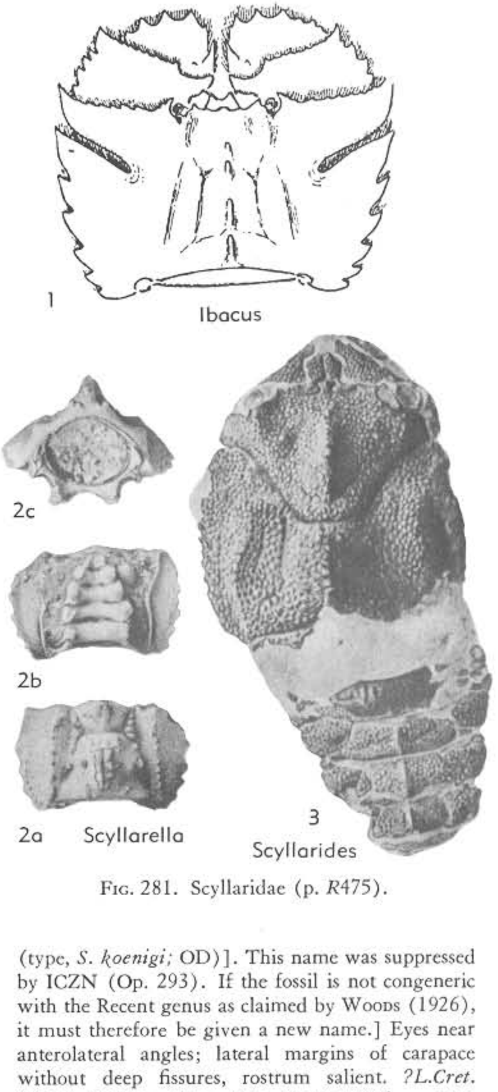


FIG. 281. Scyllaridae (p. *R*475).

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.*

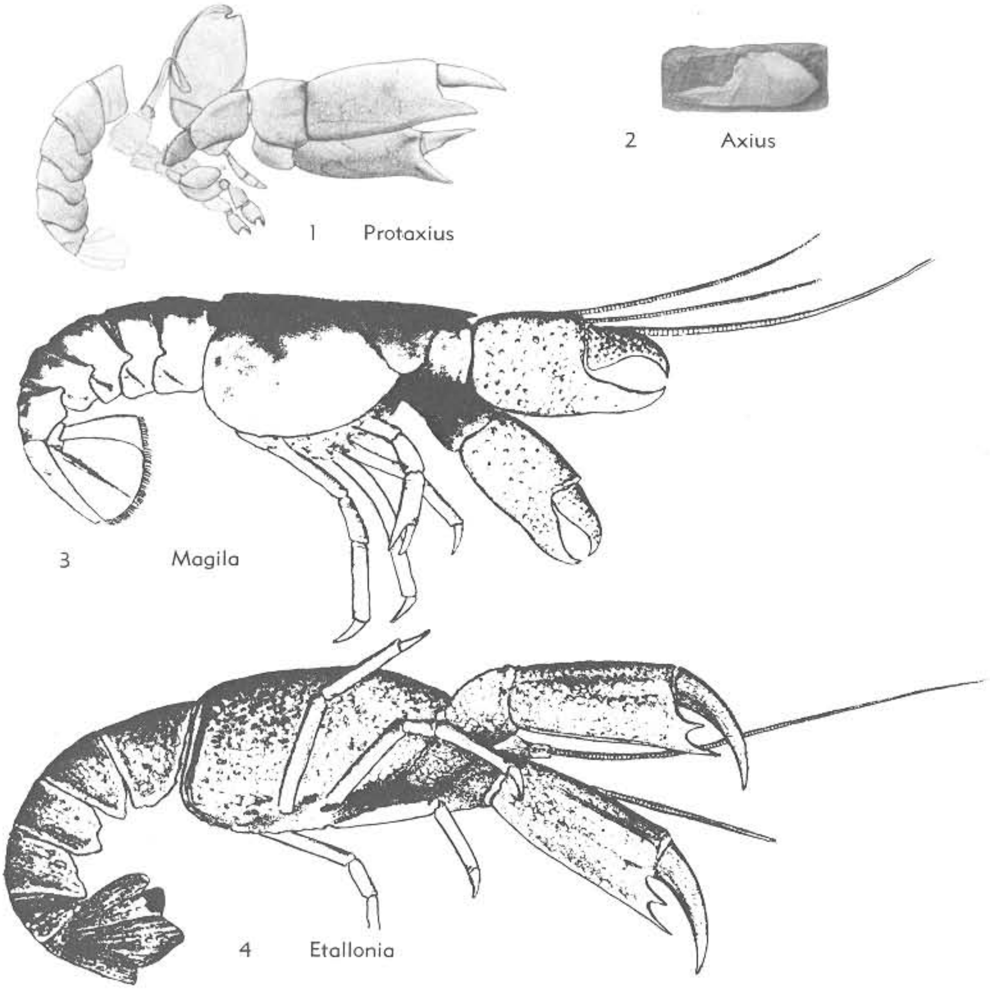


FIG. 282. Axiidae (p. *R477*).

Superfamily THALASSINOIDEA Latreille, 1831

[*nom. transl.* DANA, 1852 (*ex* family Thalassinides LATREILLE, 1831)]

Abdomen well developed but pleura more or less reduced; first pereiopods 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 pereiopods 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-

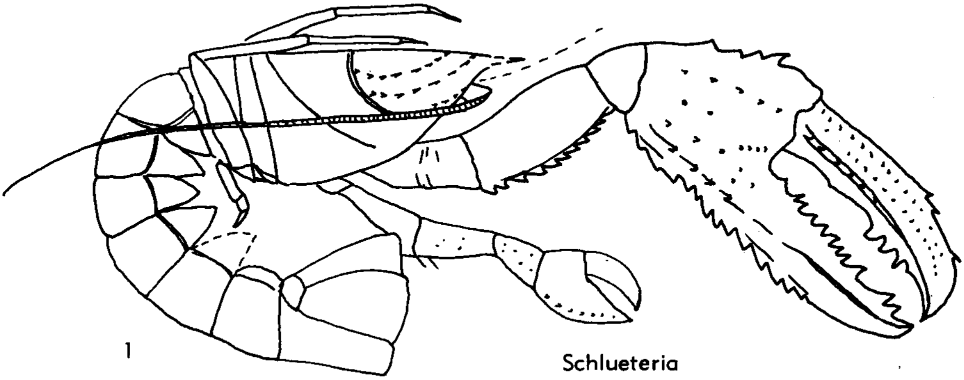


FIG. 283. Axiidae (p. R477).

lar flagella well developed; first pereiopods with large chelae, second pereiopods 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 pereiopod, ×1.5 (234).

Etallonia OPPEL, 1861 [**Magila longimana* MÜNSTER, 1839; OD] 1st pereiopods subchelate, with long rectangular manus and curved dactylus; abdominal pleura pointed. *U.Jur.*, S.Ger.——FIG. 282,*4*. **E. longimana* (MÜNSTER); ×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., ×3 (219).

Protaxius BEURLEN, 1930 [**Callianassa isochela* WOODWARD, 1876; OD]. First pereiopods with large chelae differing slightly in size only, with long manus and short dactylus; 2nd pereiopods 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.; ×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 pereiopods long, with very large spiny chelae; 2nd pereiopods flattened, chelate; 3rd and 4th pereiopods slender; 5th pereiopod reduced. *U.Cret.(Turon.-L.Senon.)*, Eu. ——FIG. 283,*1*. **S. tetracheles*, Czech.; reconstr., ×0.8 (Glaessner, n, mod. from 98).

Family LAOMEDIIDAE Borradaile, 1903

Rostrum well developed, linea thalassinica present, antennular flagella short; first pereiopods large, chelate or subchelate, isochelous; abdominal pleura well developed. *Mio.-Rec.*

Laomedia DE HAAN, 1841 [**L. astacina*; OD]. First pereiopods with stout chelae, subequal; 2nd pereiopods with simple dactylus. *Rec.*, Japan.

Jaxea NARDO, 1847 [**J. nocturna*; OD]. Chelae of 1st pereiopods slender, elongate, with long fingers; 2nd pereiopods 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, ×3 (8).

Family CALLIANASSIDAE Dana, 1852

Carapace weakly calcified, mostly with linea thalassinica, with cervical groove; antennular flagella short to medium in length; first pereiopods 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 pereiopods chelate, heterochelous; second pereiopods isochelous. *U.Cret.-Rec.*

Callianassa LEACH, 1814 [**Cancer (Astacus) subterraneus* MONTAGU, 1808; OD]. Carapace with cervical groove extended far back medially; 1st

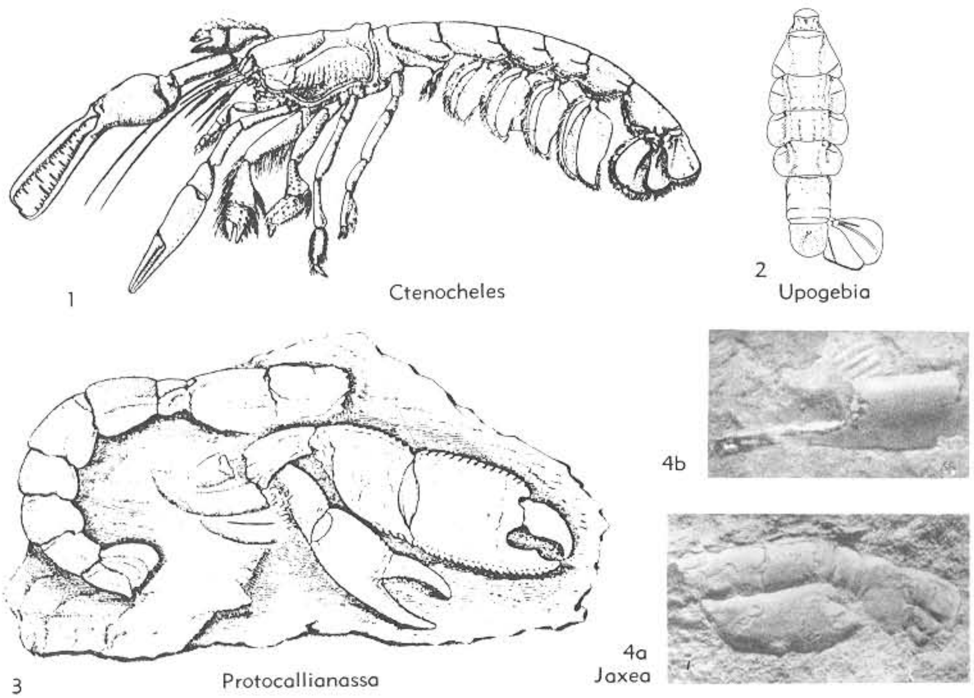


FIG. 284. Laomediidae *(4)*; Callianassidae (Callianassinae) *(1)*, (Protocallianassinae) *(3)*, Upogebiinae *(2)* (p. *R*477-*R*479).

pereiopods 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), ×0.7 (Glaessner, n).

Ctenocheles KISHINOUYE, 1926 [**C. balssi*; OD]. Differs from *Callianassa* in larger chela of 1st pereiopods 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 PELSENEER as *Ischnodactylus* (see p. *R*459) *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.; ×0.7 (362a).

Subfamily PROTOCALLIANASSINAE Beurlen, 1930

Carapace with linea thalassinica; first pereiopods 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.; ×1 (197).

Subfamily UPOGEBIINAE Borradaile, 1903

Carapace with well-developed rostrum, cervical and branchiocardiac grooves, and linea thalassinica; first pereiopods 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 pereiopods with strong propodus and short fixed finger, dactylus strong, gently curved; telson square, uropods wtihout 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,

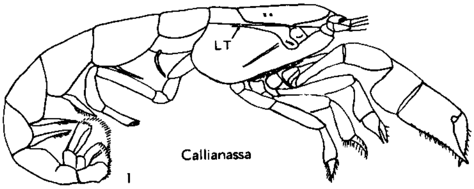


Fig. 285. Callianassidae (Callianassinae) (p. *R*477-*R*478).

×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 pereiopods 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 pereiopods 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)]

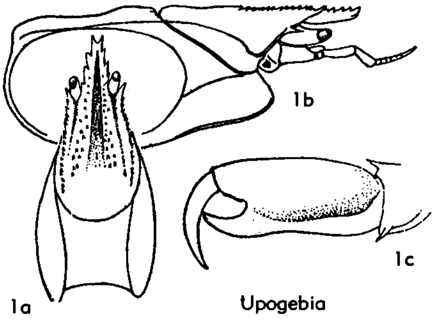


Fig. 286. Callianassidae (Upogebiinae) (p. *R*478-*R*479).

Carapace elongate, widened and weakly calcified posteriorly, rostrum very short, abdomen uncalcified and coiled or secondarily symmetrical externally; first pereiopods with chelae which are more or less heterochelous; second and third pereiopods elongate and ambulatory, fourth and fifth pereiopods 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 pereiopods 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 pereiopods 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).

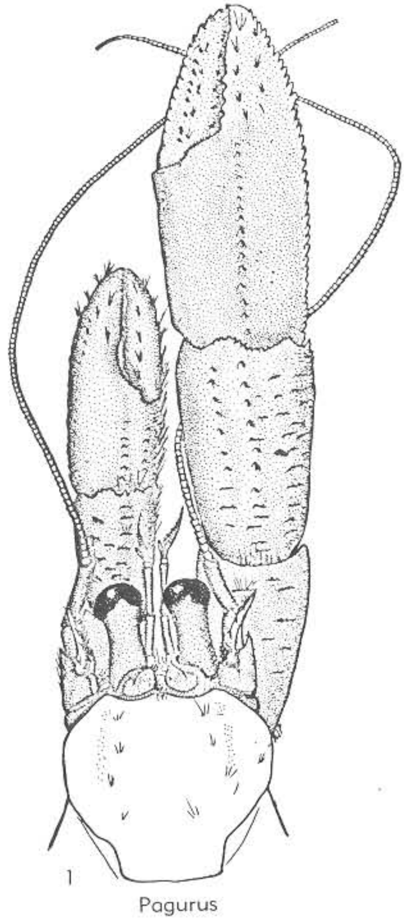


Fig. 287. Paguridae (Pagurinae) (p. *R*479).

Dardanus Paulson, 1875 [**D. hellerii*; OD (on official list, ICZN)] [=*Pagurites (Propagurites)* Beurlen, 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, ×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, ×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.

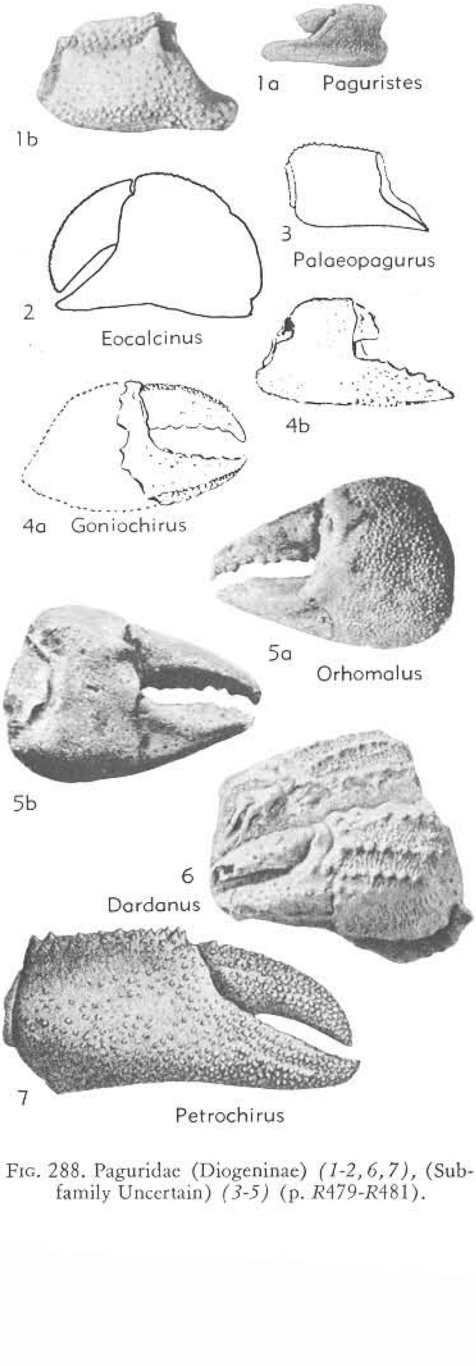


Fig. 288. Paguridae (Diogeninae) *(1-2,6,7)*, (Subfamily Uncertain) *(3-5)* (p. *R*479-*R*481).

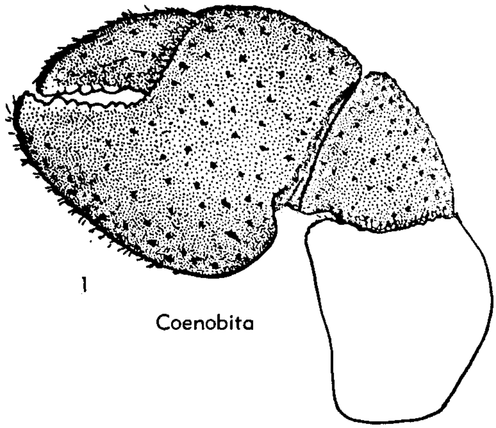


FIG. 289. Coenobitidae (p. *R*481).

P. priscus (Brocchi), *Mio.*, Hung.; right chela, ×1 (184).

Subfamily UNCERTAIN

Goniochirus Étallon, 1861 [**G. babeaui*; 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, ×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. deslongchampsi* Hée, U.Jur., Fr.; *5a,b*, outer and inner sides of left chela, ×1 (296).

Palaeopagurus Van Straelen, 1925 [**P. deslongchampsi;* 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. deslongchampsi*, Lias., Fr.; right chela, ×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 pereiopods 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.; ×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 pereiopod larger than left, fifth pereiopods 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 pereiopods 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; pereiopods with six segments, first pereiopods with well-developed chelae, fifth pereiopods 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.*

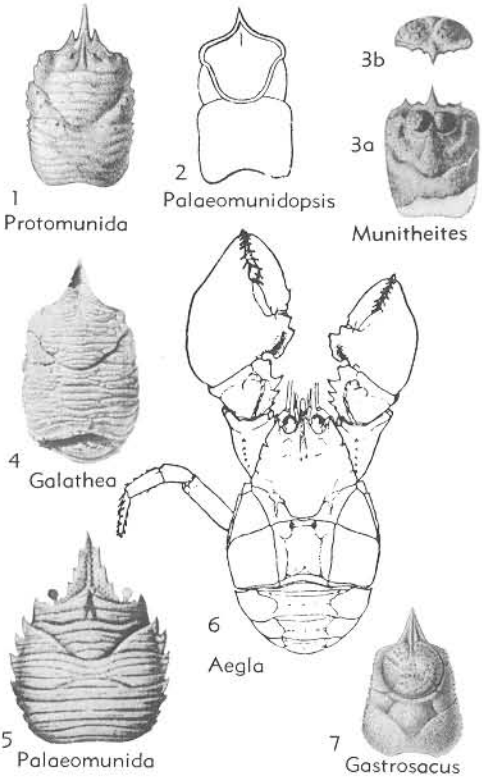


FIG. 290. Galatheidae (Galatheinae) *(1,4-5)*, (Subfamily Uncertain) *(2-3,7)*; Aeglidae *(6)* (p. R482-R483).

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, ×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. bamffia tenuimana* Sars, Rec.; ×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.; ×1 (184).

Protomunida Beurlen, 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.; ×3 (333).

Subfamily MUNIDOPSINAE Ortmann, 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. Beurlen (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.; ×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, ×1 (184).

Palaeomunidopsis Van Straelen, 1925 [**Gastrosacus moutieri* Van Straelen, 1923; OD]. Cara-

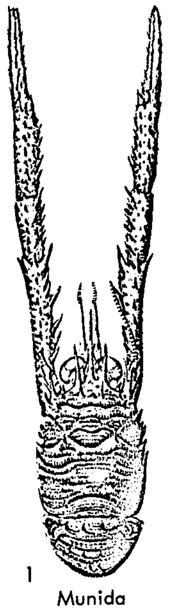


FIG. 291. Galatheidae (Galatheinae) (p. *R*482).

pace flat, sides parallel, rostrum narrowly triangular, gastric region raised. *M.Jur.*, Fr.——FIG. 290,*2*. *P. moutieri* (VAN STRAELEN); ×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); ×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 pereiopods 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, heterochelous 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 pereiopods with or without chelae, fifth pereiopods reduced. *Tert.-Rec.*

Family ALBUNEIDAE Stimpson, 1858

[*nom. correct.* ORTMANN, 1896 (*pro* Albuniidae STIMPSON, 1858)]

Carapace subquadrangular, without posterolateral extensions; first pereiopods 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.]

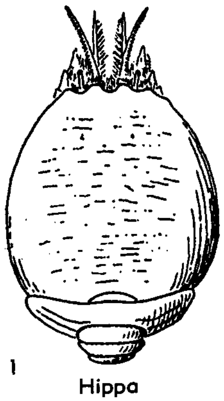


FIG. 292. Hippidae (p. *R*484).

Family HIPPIDAE Latreille, 1825

[*nom. correct.* BORRADAILE, 1907 (*pro* Hippides LATREILLE, 1825)]

Carapace ovoid, with posterolateral extensions covering posterior pereiopods, 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*; ×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 pereiopods 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 pereiopods chelate, fifth ones in dorsal position and tending to be reduced, fourth and fifth pereiopods commonly similar. Abdomen wide in both sexes, commonly with seven somites. Seminal ducts perforate coxa of fifth pereiopods, oviducts open in coxa of third pereiopods. *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 pereiopods 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 pereiopods with long chelae, 4th and 5th pereiopods probably elevated on back. *L.Lias.*, Eng.——FIG. 293,*7*. **E. praecursor*; *7a,b,* dorsal and side views of carapace (reconstr.), ×1 (321).

Family PROSOPIDAE von Meyer, 1860

[*nom. correct.* GLAESSNER, herein (*pro* Prosoponidae VON MEYER, 1860)]

Carapace mostly cylindrical, elongate, without or with incomplete lateral margin; without orbits but commonly with elongate orbital grooves; srong 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.; ×1.3 (367).——FIG. 293,*1*. *P. mamillatum* H. WOODWARD; *1a,* female abdomen, ×0.5; *1b-d,* dorsal, lat., and frontal views of carapace (reconstr.), ×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.; ×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.; ×3 (367).

Nodoprosopon BEURLEN, 1928 [**Prosopon ornatum* VON MEYER, 1860; OD]. Carapace elongate, rostrum bilobed, branchial regions inflated, posterior

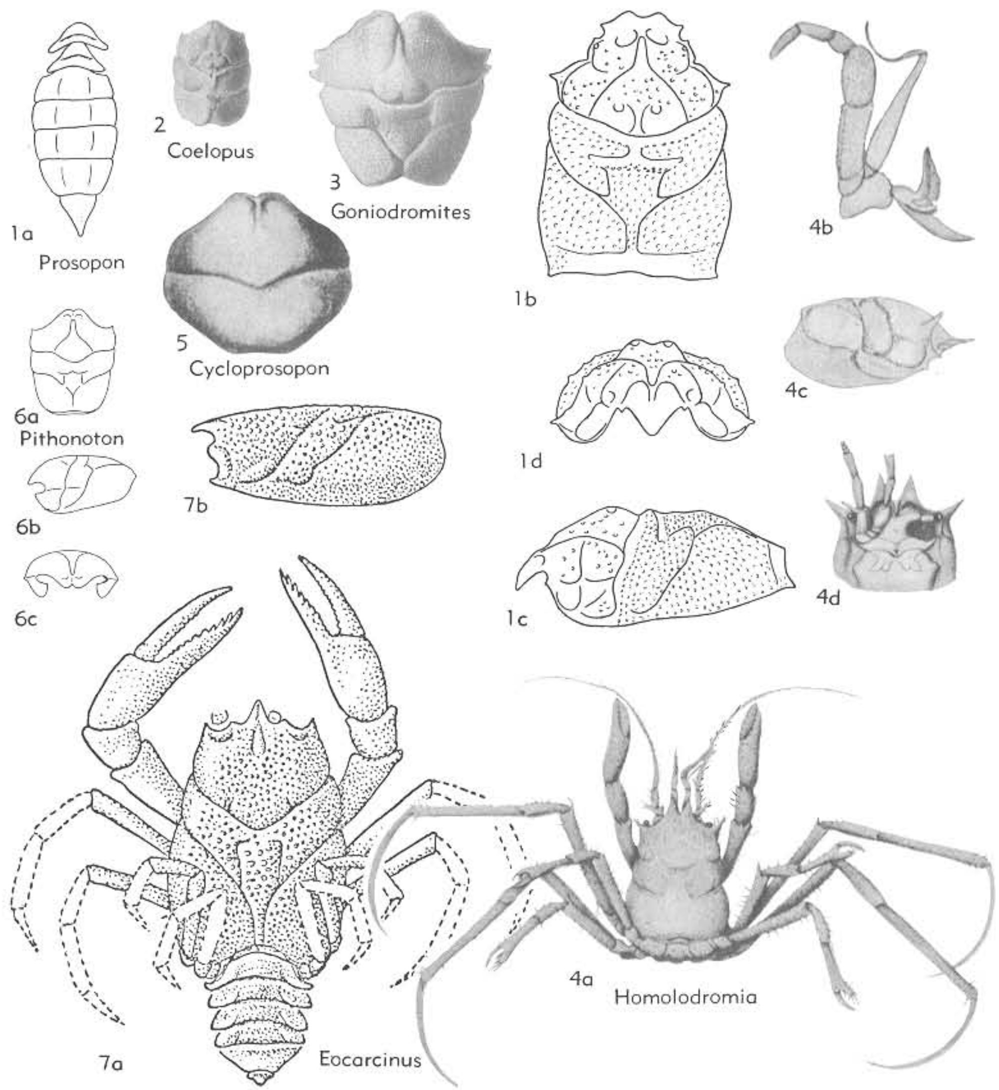


FIG. 293. Eocarcinidae *(7)*; Prosopidae (Prosopinae) *(1)*, (Pithonotinae) *(2-3,5-6)*, (Homolodromiinae) *(4)* p. *R*484-*R*486).

margin narrow. *U.Jur.*, Eu.——FIG. 294,*3*. **N. ornatum* (VON MEYER), Ger.; ×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. *R*627.]

Pithonoton VON MEYER, 1842 [**P. marginatum*; SD BEURLEN, 1928]. Carapace convex transversely and longitudinally; cervical and branchiocardiac 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 branchiocardiac furrows equally strong. *M.Jur.-U.Jur.*, Eu.——FIG. 293,*6*. **P. (P.) marginatum*, Tithon., Moravia; *6a-c*, dorsal, lat., and frontal views, ×1 (324).

P. (Cycloprosopon) LÖRENTHEY, 1928 [**C. typi-*

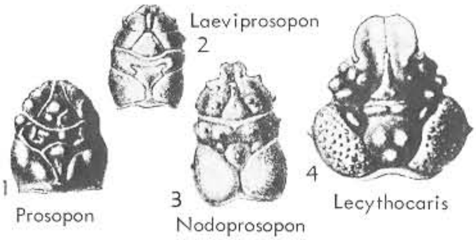


FIG. 294. Prosopidae (Prosopinae) (p. *R*484-*R*485).

cum; OD]. Carapace gently convex, wider than long, well-developed lateral margins, no anterolateral angle. Surface smooth, with cervical groove. *U.Jur.*, Eu.——FIG. 293,5. **P. (C.) typicum* (LÖRENTHEY), Tithon., Hung.; ×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; ×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; ×1 (250).

Iberihomola VAN STRAELEN, 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, ×1.5 (332).

Microcorystes 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;* ×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, ×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 BALSS to the Dromiidae.] *L.Cret.(L.Apt.)*, Eng.——FIG. 296,1. **V. wrighti*; *1a-c,* dorsal, frontal, and lat. views, ×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 pereiopods 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 pereiopods subdorsal, subchelate. *Rec.*, W.Ind.-E.Afr.——FIG. 293,4. **H. paradoxa*; *4a,* dorsal view of male, ×1; *4b,* left maxilliped, enlarged; *4c,* right lat. view of carapace, ×1; *4d,* ant. part of ventral surface, ×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 pereiopods with strong chelae, fourth and fifth ones reduced, subdorsal. Sternum of female with grooves;

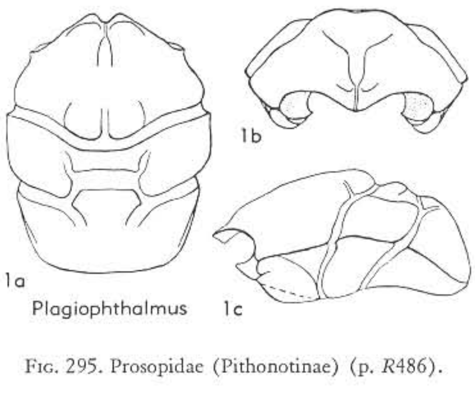


FIG. 295. Prosopidae (Pithonotinae) (p. *R*486).

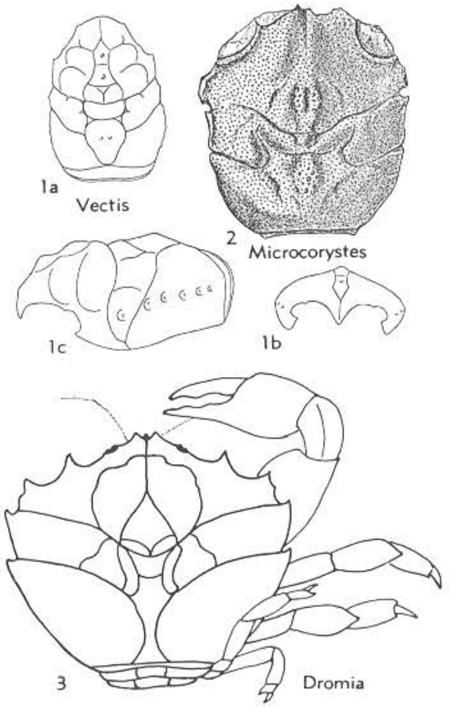


FIG. 296. Prosopidae (Pithonotinae) *(1,2)*; Dromiidae *(3)* (p. *R*486-*R*487).

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 pereiopods, 4th and 5th pereiopods subchelate. *Eoc., Pleist.,* Eu.; *Plio.,* Fiji; *Rec.,* Medit.-W.Afr.-W.Atl.-IndoPac.——Fig. 296,*3*. **D. personata* (Linné), Rec., E.Atl.-Medit.; diagrammatic, ×0.5 (Glaessner, n).

Dromilites H. Milne-Edwards, 1837 [**Dromia bucklandi*; OD] [=*Pseudodromilites* Beurlen, 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, ×1 (19).

Noetlingia Beurlen, 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., ×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 pereiopods 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-

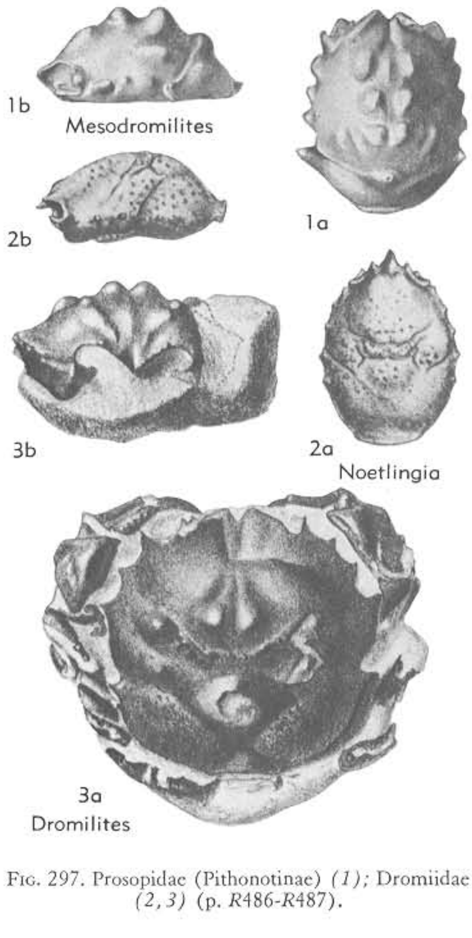


FIG. 297. Prosopidae (Pithonotinae) *(1)*; Dromiidae *(2,3)* (p. *R*486-*R*487).

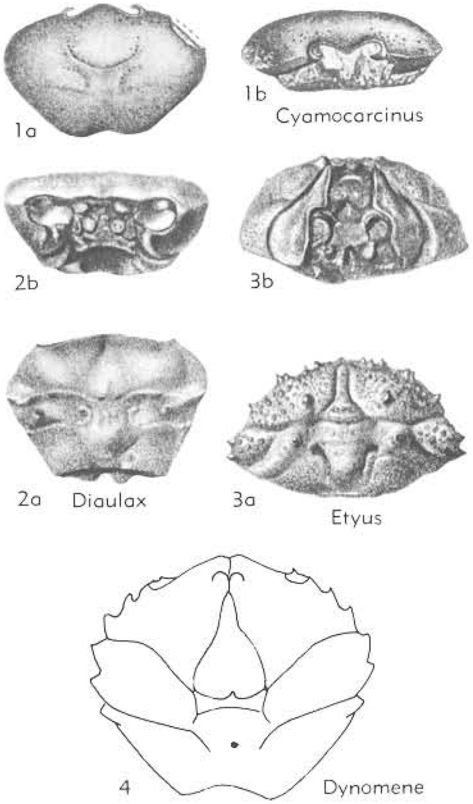


FIG. 298. Dynomenidae (p. *R*487-*R*488).

Pac.-N.Am.(W.coast).——FIG. 298,*4*. *D. filholi* BOUVIER, Pac. (tropic); carapace, ×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, ×1 (183).

Cyclothyreus 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, ×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, ×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, ×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, ×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, ×1 (344).

Gemmellarocarcinus 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, ×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, ×3 (282).

Family UNCERTAIN

Mithracites GOULD, 1859 [**M. vectensis*; OD]. Carapace elongate, lateral margins distinct, diverg-

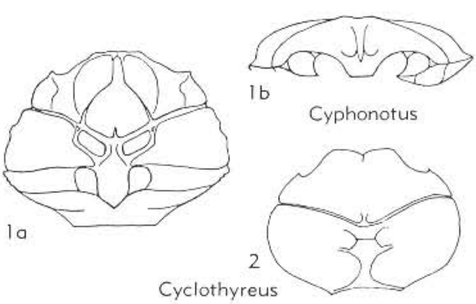


FIG. 299. Dynomenidae (p. *R*488).

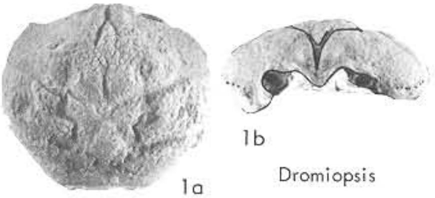


FIG. 300. Dynomenidae (p. *R*488).

ing, posterior margin wide, orbits large; 5th pereiopods reduced, dorsal. *L.Cret.(Apt.),* Eng.——FIG. 301,7. **M. vectensis*; carapace (reconstr.), ×1 (324).

Oxythyreus 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, ×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.; ×2 (283).

Stephanometopon BOSQUET, 1854 [**S. granulatum*; 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*; ×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, ×1 (344).——FIG. 301,*1c*. *X. wintoni* RATHBUN, Alb., Tex.; ant. view showing antennular bases, ×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 pereiopods dorsal, reduced. *U.Jur.-Rec.*

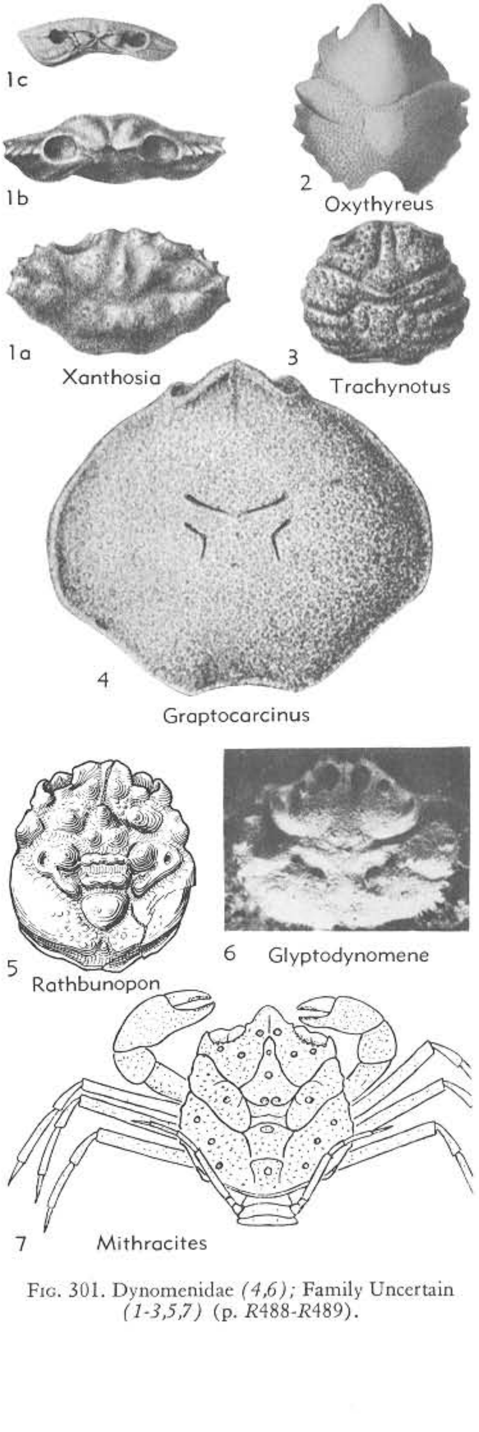


FIG. 301. Dynomenidae *(4,6)*; Family Uncertain *(1-3,5,7)* (p. *R*488-*R*489).

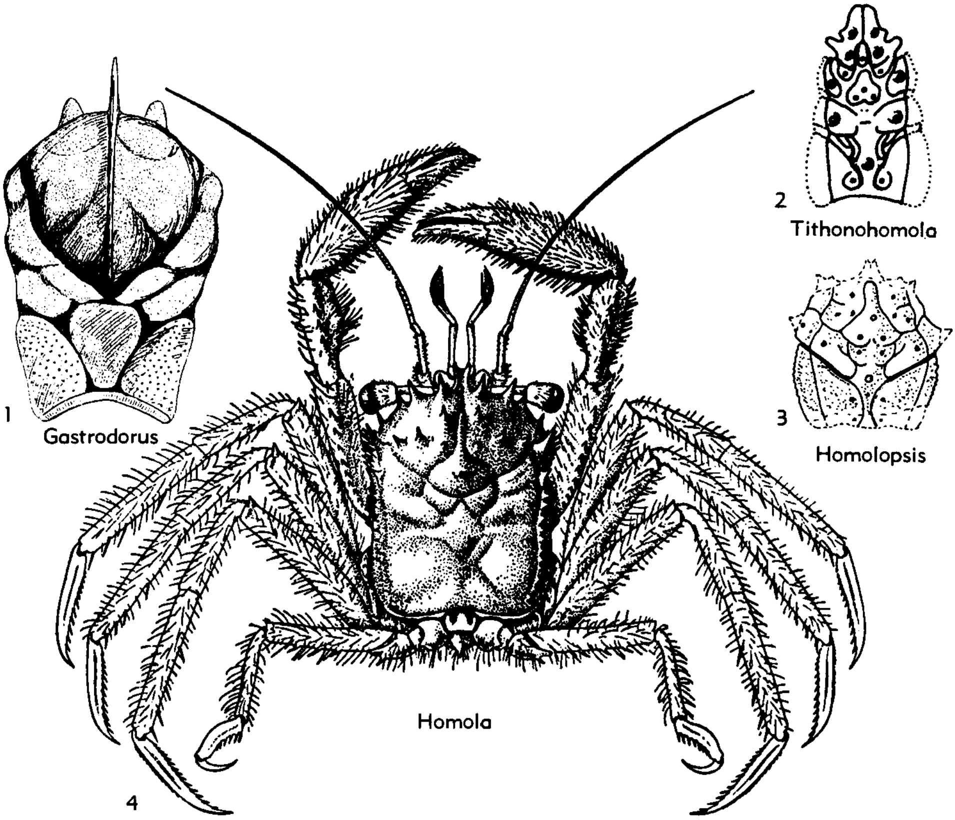


FIG. 302. Homolidae (p. *R*490-*R*491).

Family HOMOLIDAE White, 1847

[=Thelxiopeidae 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] [=*Thelxiope* RAFINESQUE, 1814 (type, *T. palpigera*, =*Cancer barbatus* FABRICIUS, 1793)]. Carapace elongate, subrectangular, cervical groove distinct, lineae distinct and dorsal, 5th pereiopods subchelate. *Rec.*, IndoPac.-Medit.-W.Afr.-N.Am.(E. coast-W. coast).——FIG. 302,*4*. **H. barbata* (FABRICIUS); dorsal view of male, ×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, ×7.5 (24).

Homolopsis BELL, 1863 [**H. edwardsi*; OD] [=*Hoplitocarcinus* BEURLEN, 1928 (type, *H. johboehmi*)]. 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.), ×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.), ×2 (Glaessner, n).

Superfamily DAKOTICANCROIDEA 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 pereiopods 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, ×1.5 (Rathbun, 1917).——FIG. 303,*2b*. *D. overanus australis* RATHBUN, Senon., USA(Miss.); dorsal side, ×1.5 (244).

Avitelmessus RATHBUN, 1923 [**A. grapsoideus*; OD]. Carapace with rounded outline, not strongly grooved, orbits wide, second to fourth pereiopods flattened. *U.Cret.(Senon.)*, N.Am.(N.Car.-Tenn.-Ala.-Miss.).——FIG. 303,*3*. **A. grapsoideus*, U.Senon., Tenn.; *3a,b*, dorsal and ventral surface of male; *3c*, left chela, *3d*, female abdomen; all ×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.); ×2 (244).

Section OXYSTOMATA H. Milne-Edwards, 1834

Buccal cavity elongate, subtriangular, antennules folded mostly longitudinally or obliquely; gonoducts coxal or sternal, fourth pereiopods normal or subdorsal. *L.Cret.(Alb.)-Rec.*

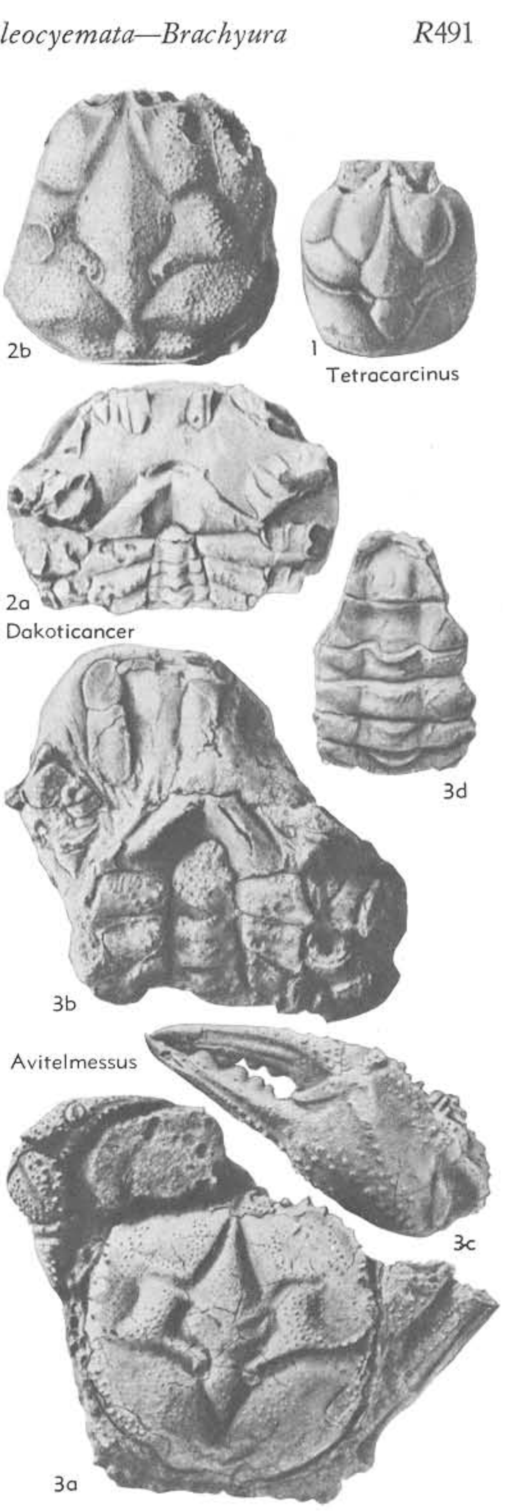


FIG. 303. Dakoticancridae (p. R491).

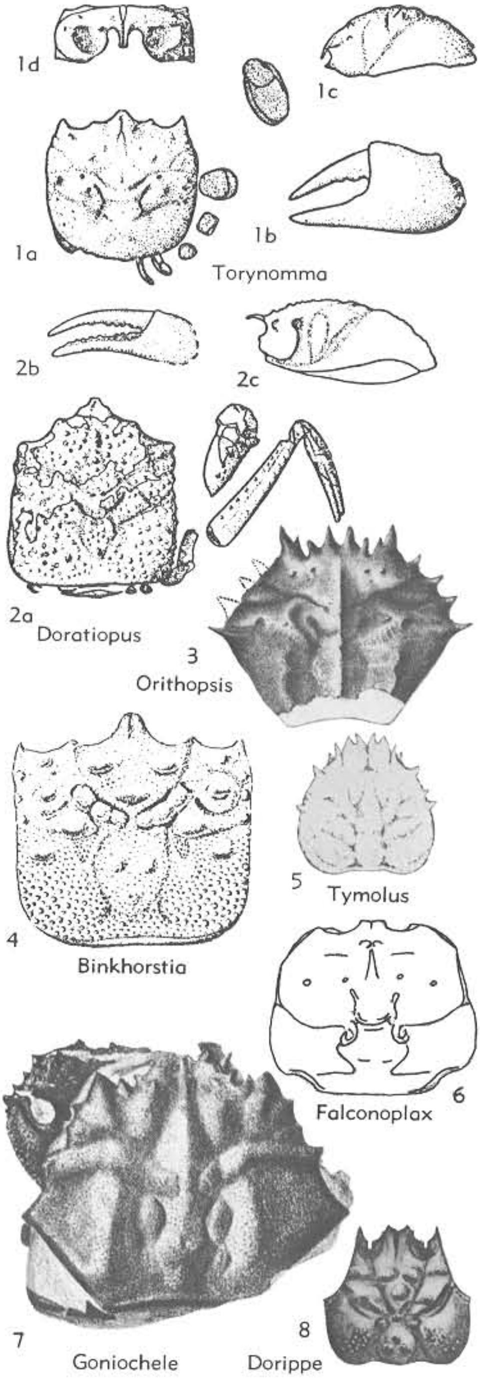


FIG. 304. Dorippidae (Dorippinae) *(3,7-8)*, (Tymolinae) *(1-2,4-6)* (p. *R*492-*R*493).

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 pereiopods 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. frascone* HERBST, 1785); SD LATREILLE, 1810]. Carapace flat, with anterolateral spines, widest in posterior 3rd, regions well marked, chelae small, 2nd and 3rd pereiopods 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, ×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.; ×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, ×0.7 (69).

Subfamily TYMOLINAE Alcock, 1896

Third maxillipeds covering buccal area completely. Oviducts opening in coxa of third pereiopods. 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, ×1 (157, after Sakai).

Binkhorstia NOETLING, 1881 [**Dromilites ubaghsi* BINKHORST, 1857; OD]. Carapace outline square, orbital margins long, transverse. *U.Cret.(U.Senon.)*,

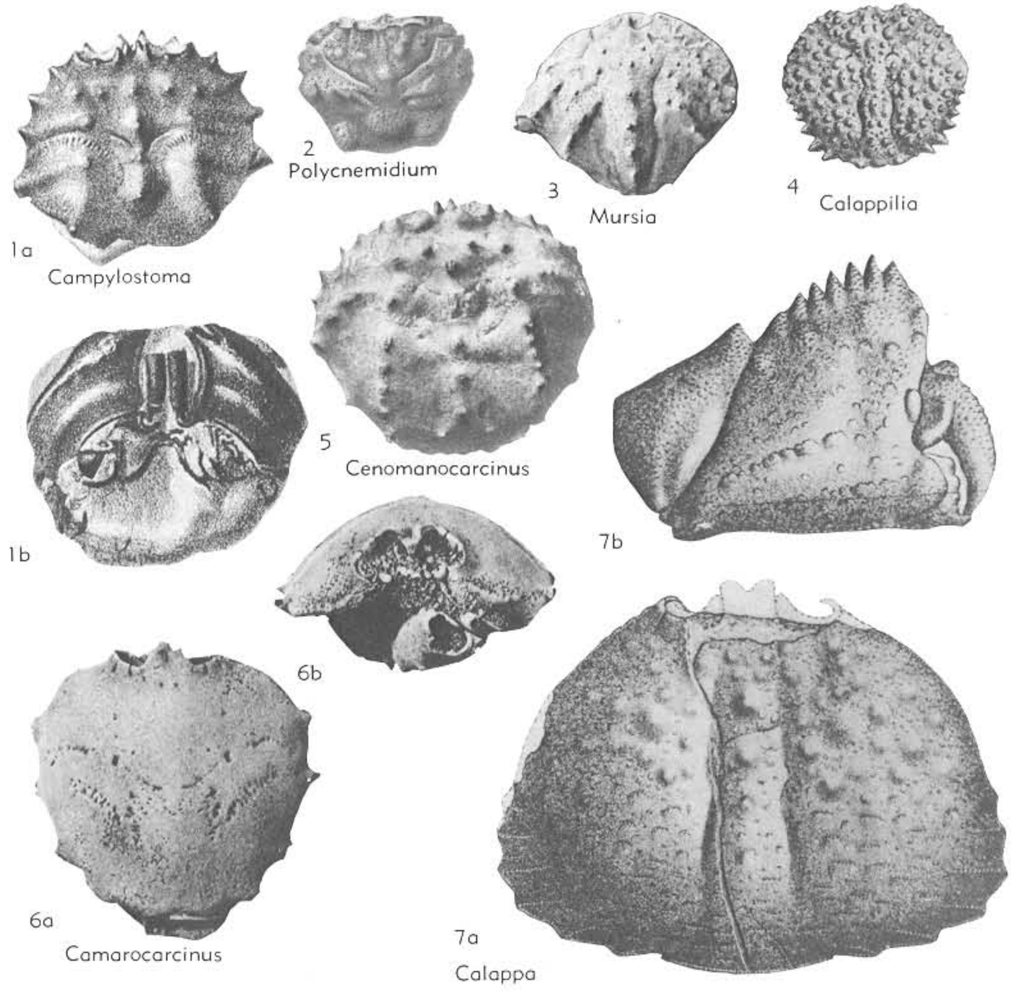


FIG. 305. Calappidae (Calappinae) (p. *R*494-*R*495).

Eu.——FIG. 304,*4*. **B. ubaghsi* (BINKHORST), Neth.; dorsal view of carapace, ×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, ×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 pereiopod coxae of females, abdominal depression deep. *U.Eoc.,* Venez.——FIG. 304,*6*. **F. kugleri*; carapace drawn from int. mold, ×1 (Glaessner, n).

Torynomma WOODS, 1953 [**T. quadrata*; OD]. Carapace subquadrate, widest anteriorly, orbital grooves large, rostrum narrow, oviduct opening on coxa of 3rd pereiopods. *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, ×1 (327).

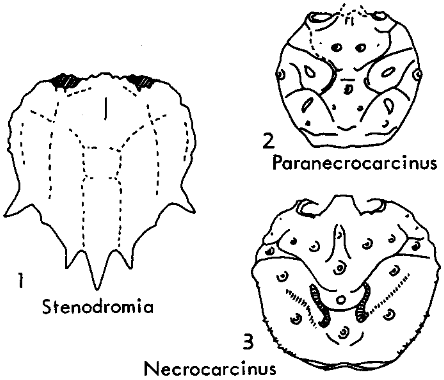


FIG. 306. Calappidae (Calappinae) (p. R495).

Superfamily CALAPPOIDEA de Haan, 1833

[*nom. transl.* BEURLEN, 1930 (*ex* Calappidea DE HAAN, 1883)] [="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, ×1 (184). [=*Aparnocondylus* 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, ×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, ×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, ×1 (19).

Cenomanocarcinus VAN STRAELEN, 1936 [**C. inflatus* (=*Neocrocarcinus inflatus* A. MILNE-EDWARDS in A. GUILLIER, 1886, *nom. nud.*); OD]. Differs from *Neocrocarcinus* 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, ×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.,* Atl.-Indo-Pac.-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, ×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, ×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, ×2 (after 306).

Polycnemidium 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, ×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, ×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* Farbicius, 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* (Brocchi), 1883 (*non* Miers, 1882)], Mio., Hung.; *2a,* dorsal view of carapace; *2b,* right chela, ×0.7 (184).

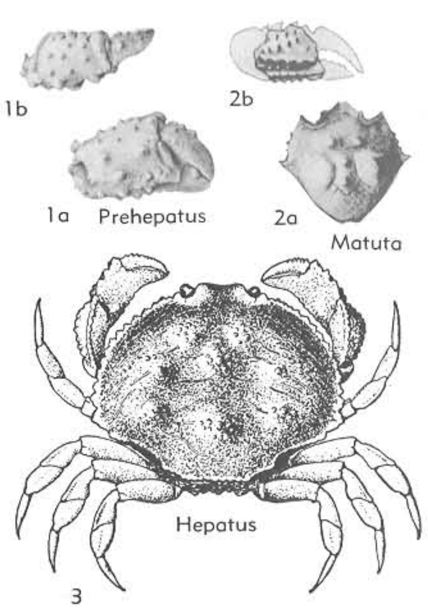


Fig. 307. Calappidae (Matutinae) (p. *R*495).

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, ×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, ×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

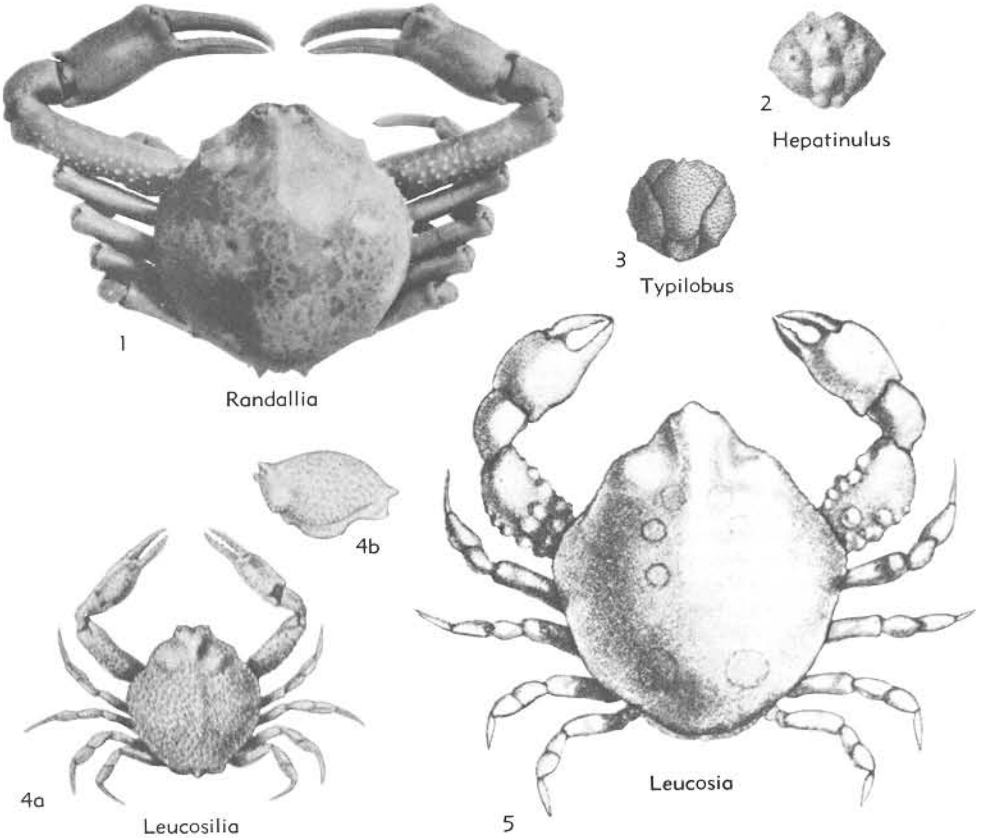


FIG. 308. Leucosiidae (p. *R*496-*R*498).

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.; ×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.; ×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.; ×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 pereiopods much shorter and decreasing in length. *?Eoc., Plio.,* Italy; *Rec.,* Medit.-W.Afr.——FIG. 310,*2*. **I. nucleus* (LINNÉ), Rec., Medit.; ×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, granulate, front narrow with median indentation, single posterior spine. *Mio.-Pleist.,* Panama; *Rec.,* Panama-Peru.——FIG. 308,*4*. **L. jurinei* (SAUSSURE), Rec.; *4a,b,* dorsal and lat. views of carapace, ×1 (245).

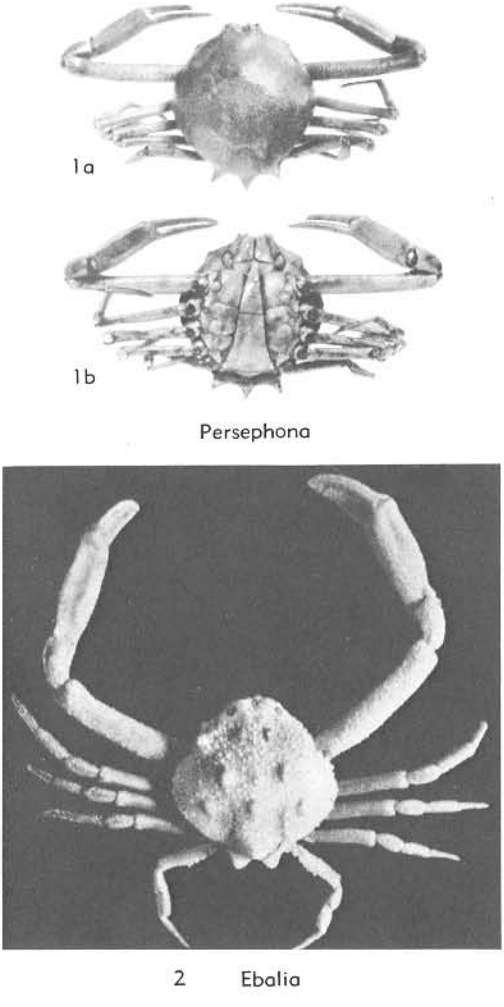


FIG. 309. Leucosiidae (p. *R*496, *R*498).

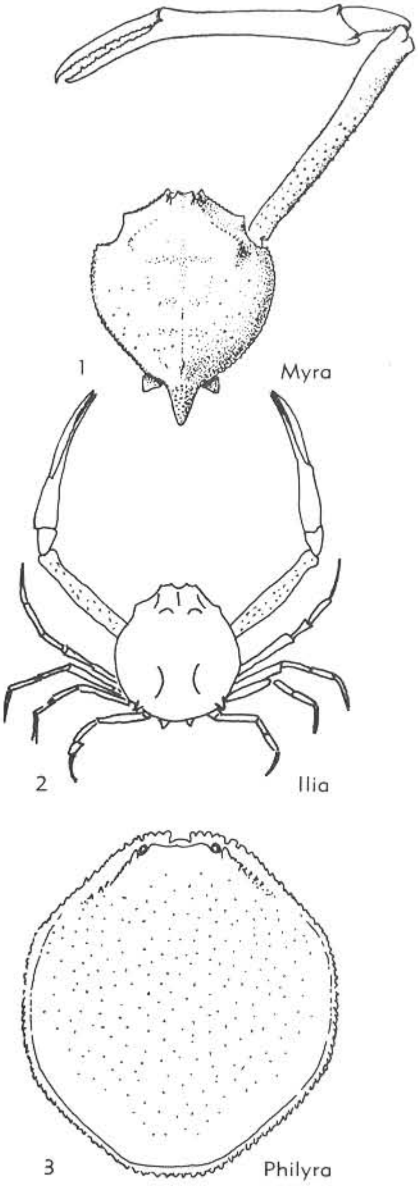


FIG. 310. Leucosiidae (p. *R*496-*R*498).

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.; ×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, ×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.; ×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.; ×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.; ×1 (184).

Superfamily RANINOIDEA de Haan, 1841

[*nom. transl.* 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 posteriorly, chelae flat, with fixed finger more or less deflected; oviducts opening in coxae of third pereiopods, 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 pereiopods, 5th pereiopods 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, ×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, ×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, ×1 (41). [According to PELSENEER, 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 pereiopods equally wide. *U.Cret. (Cenoman.)*, Eng.——FIG. 311,*4*. **H. cunningtoni*; frontal view, ×1 (344).

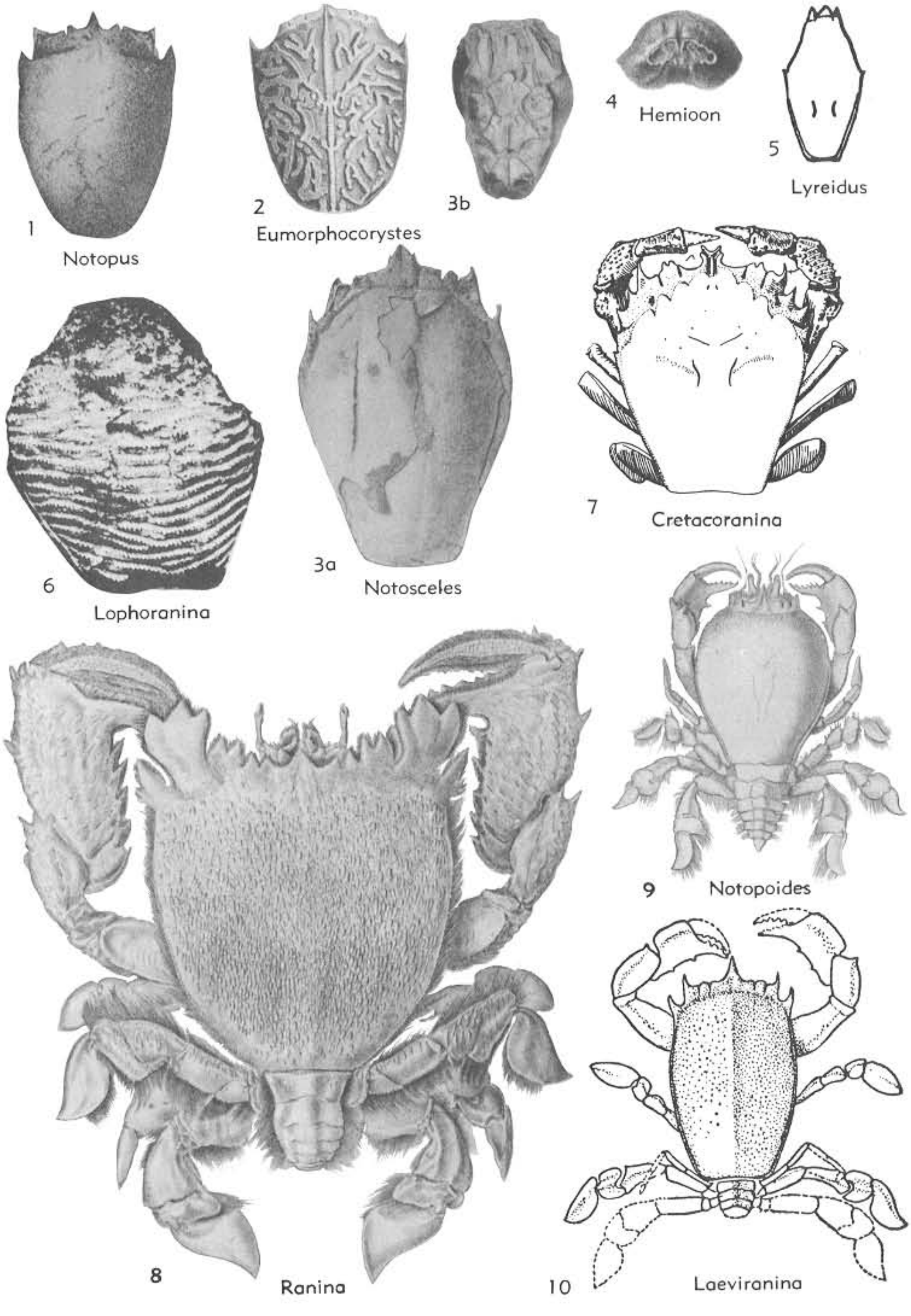


Fig. 311. Raninidae (p. *R*498, *R*500).

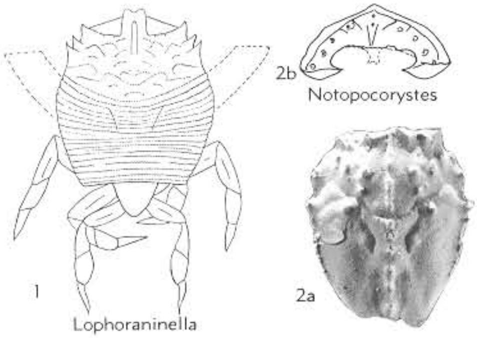


FIG. 312. Raninidae (p. *R*500).

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.), ×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.), ×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 pereiopod bases; 5th pereiopods 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, ×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 pereiopods 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, ×1 (Glaessner, n).

N. (Cretacoranina) 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.), ×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 pereiopods and widened again towards bases of 3rd pereiopods, 3rd to 5th ones similar in size and shape. *Mio.,* Java; *Rec.,* E.Indies.——Fig. 311,*9*. **N. latus,* Rec.; ×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.; ×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 pereiopods raised. *U.Cret.,* USA (Tex.); *Paleoc.,* USA(Tex.-Ark.-Ala.); *Rec.,* Indo-Pac.——Fig. 311,*3*. *N. bournei* (Rathbun), Paleoc., Tex.; *3a,* carapace, ×2; *3b,* ventral view, ×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 extraorbital 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 (Cretacoranina)*.] *U.Cret.(Senon.),* Eu.; *?Eoc.,* Borneo.——Fig. 313, *4*. **P. muelleri* (Binkhorst), U.Senon., Neth.; *4a,* carapace, dorsal view, ×1 [according to Pel-

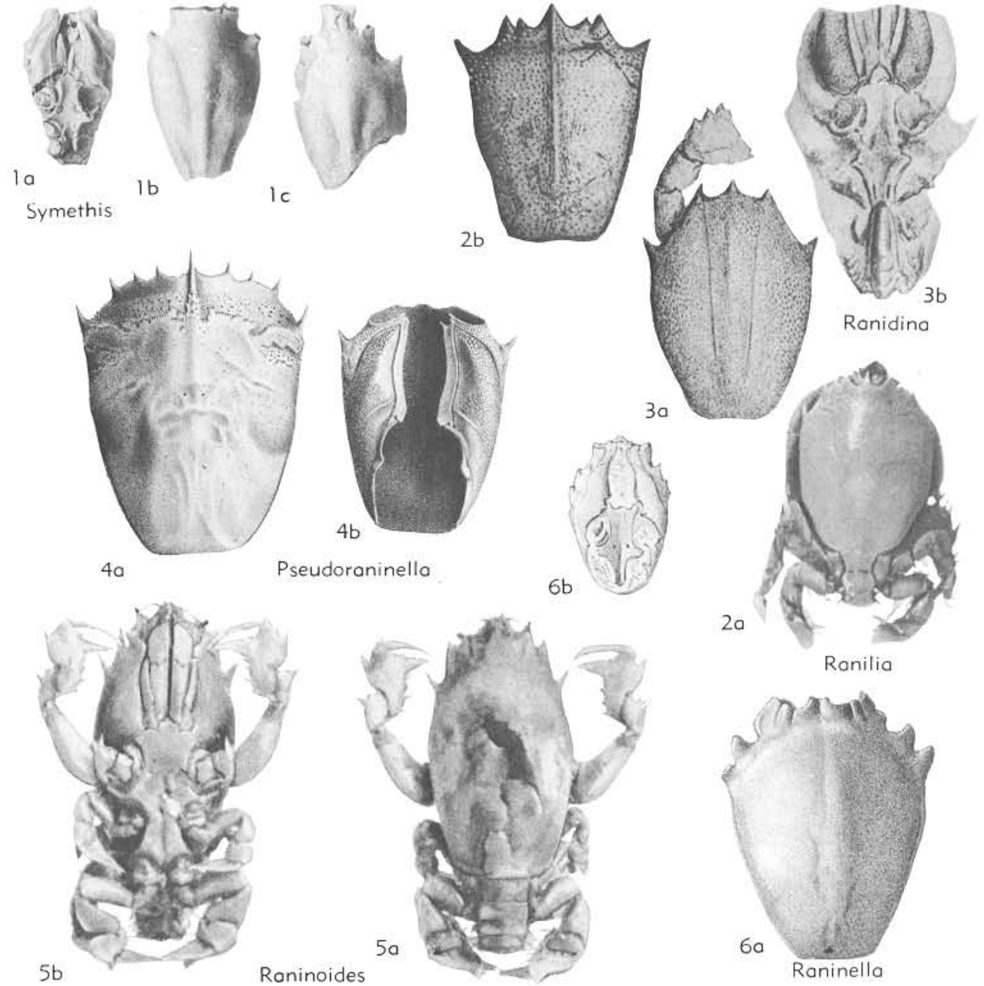


FIG. 313. Raninidae (p. *R*501).

SENEER (1886) the drawing is incorrect since the spines are flattened teeth, those nearest the rostrum being longer than outer ones], *4b*, ventral view, ×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 pereiopods. *Oligo.*, N.Am.; *Mio.*, Aus.-Hung.——FIG. 313,*3*. **R. rosaliae*, Mio., Aus.; *3a,b*, dorsal, ventral, ×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 pereiopods, 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.; ×1 (245).——FIG 313,*2b*. *R. vareolata* (LÖRENTHEY), Eoc., Hung.; dorsal view of carapace, ×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 pereiopods; buccal frame long and narrow. *U.Cret.*, Eu.; *?Paleoc.*, USA(Ala.).——FIG. 313,*6*. **R. trigeri*, Cenoman., Fr.; *6a,* dorsal, ×0.7 (53); *6b,* ventral view of smaller specimen (described as *R. elongata*), ×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 pereiopods, narrow between bases of 3rd pereiopods, 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, ×1 (after 245).

Symethis Weber, 1795 [**Hippa variolosa* Fabricius, 1793; OD] [=*Zanclifer* Henderson, 1888 (type, *Eryon caribensis* de Freminville, 1832)]. Fronto-orbital margin very narrow, front trilobate, produced; sternum linear between 2nd pereiopods, 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, ×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* Maiadae Samouelle, 1819)]

Chelipeds not much longer than second and third pereiopods; 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.; ×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.; ×1 (118).

Micromithrax Noetling, 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*; ×0.7 (214).

Periacanthus 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 Periacanthidae, 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.; ×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 preorbital spine; chelipeds long; fingers spoon-shaped, gaping in adult. *?Plio.,* Fiji; *Rec.,* USA(Fla.)-Mexico-Panama.

Subfamily MICROMAIINAE 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.*

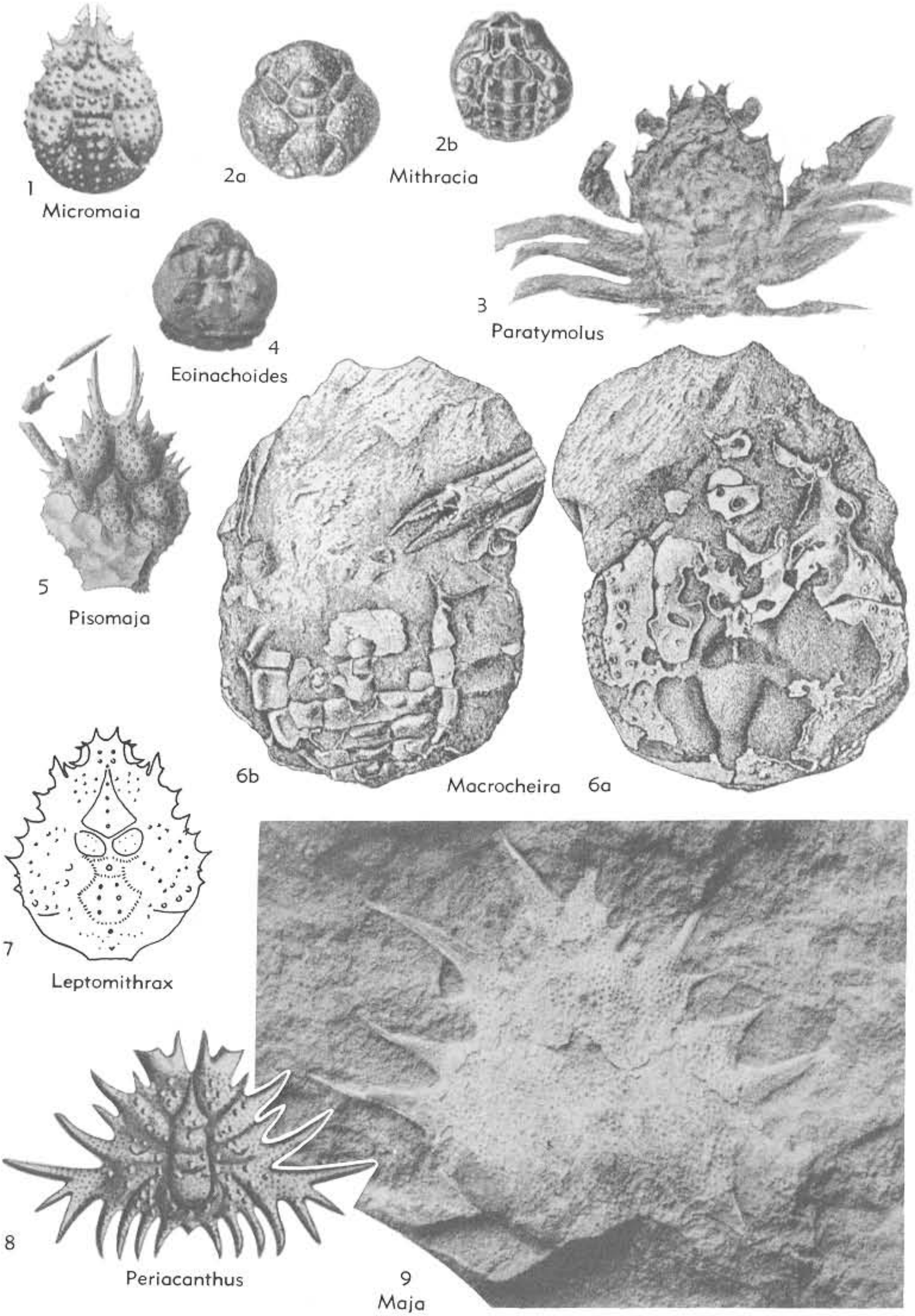


FIG. 314. Majidae (Majinae) *(7-9)*, (Micromaiinae) *(1-2, 5)*, (Inachinae) *(3-4, 6)* (p. *R*502-*R*504).

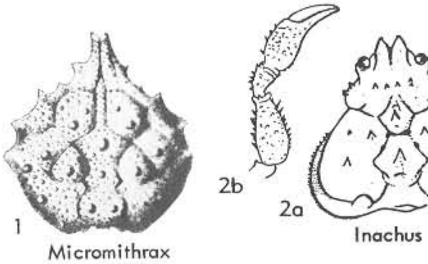


FIG. 315. Majidae (Majinae) *(1)*, (Inachinae) *(2)* (p. *R*502, *R*504).

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.; ×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, ×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;* ×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 pereiopods long. *Oligo.*, Eu.(USSR); *Plio.*, Eng.; *Rec.*, E.Atl.-Medit.——FIG. 315,*2*. **I. dorsettensis* (PENNANT), Rec.; *2a*, left part of carapace, ×1, *2b*, male right cheliped, ×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*; ×1.5 (300).

Euprognatha STIMPSON, 1871 [**E. rastellifera*; OD]. Carapace pyriform, rostrum short, with 2 small teeth; chelipeds with palms dilated, 2nd pereiopods 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, ×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, ×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 pereiopods 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, pereiopods subcylindrical. *Mio.*, Eu.-Japan; *Plio.*, N.Afr.; *Pleist.*, Eu.; *Rec.*, N.Pac.-N.Atl.——FIG. 316,*1*. **H. araneus* (LINNÉ), Rec.; male, dorsal view, ×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, ×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, ×0.5 (238).

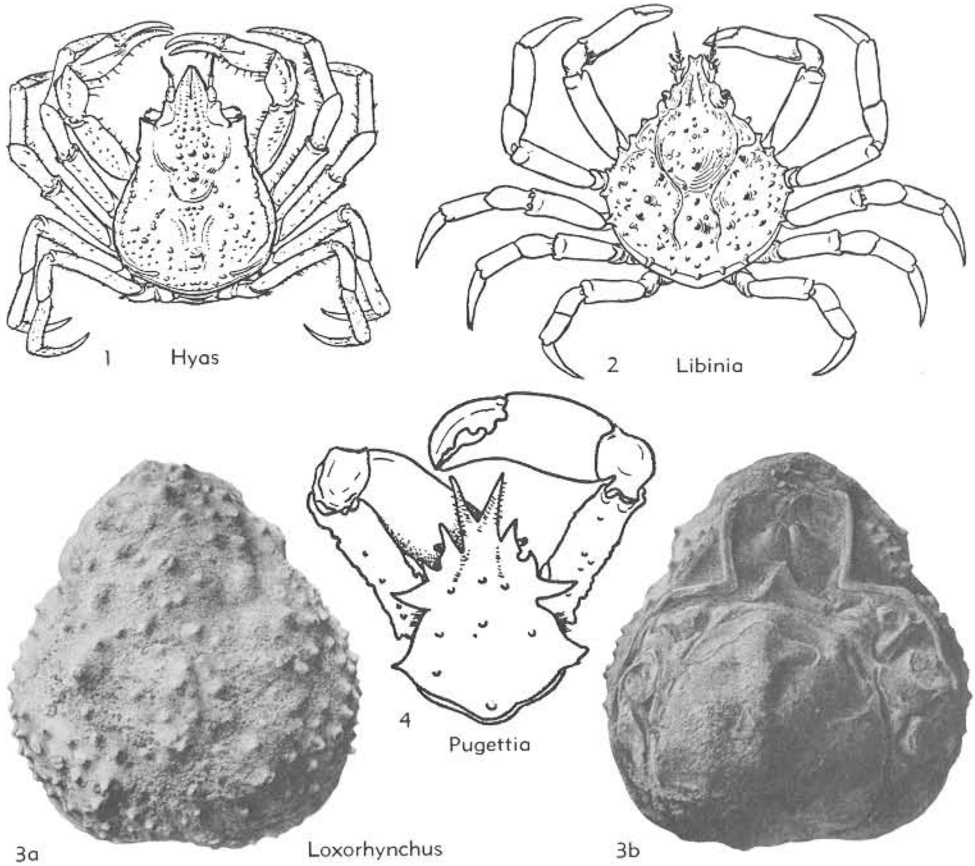


FIG. 316. Majidae (Pisinae) *(1-3)*, (Acanthonychinae) *(4)* (p. *R*504-*R*505).

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 eave 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, ×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-

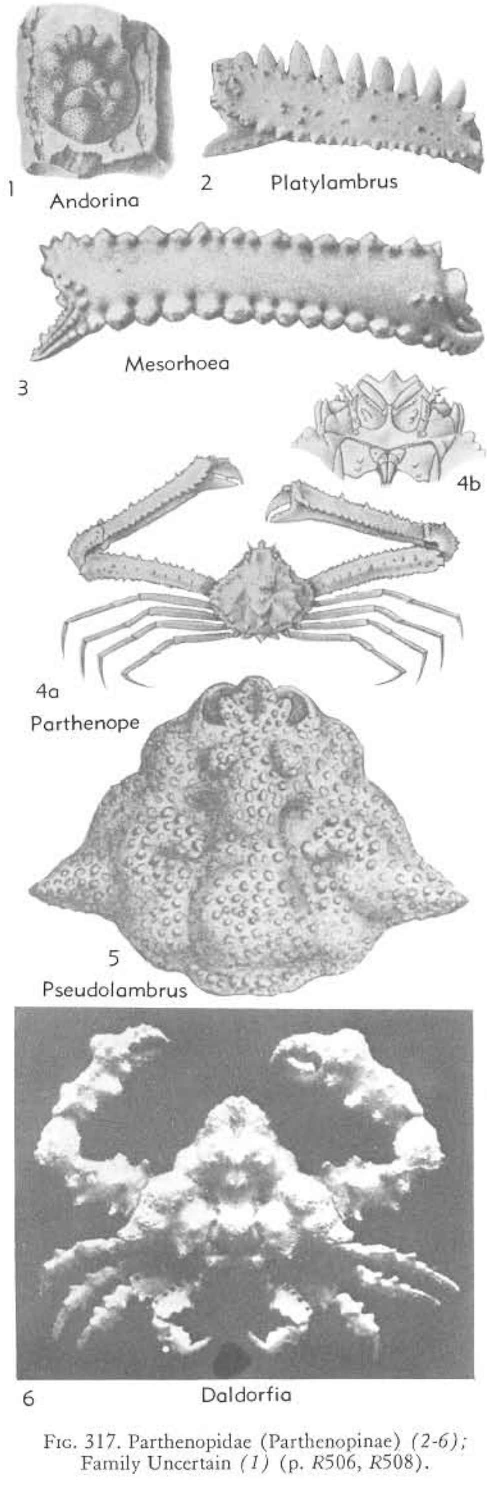


Fig. 317. Parthenopidae (Parthenopinae) *(2-6)*; Family Uncertain *(1)* (p. *R*506, *R*508).

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, ×1; *4b,* ventral view of anterior part, ×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, ×1 (244).

P. (Pseudolambrus) Paulson, 1875 [**Lambrus calappoides* Adams & White, 1848; OD] [=*Parthenolambrus* A. Milne-Edwards, 1878 (type, *Lambrus tarpeius* Adams & White, 1850); =*Phrynolambrus* 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; ×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-

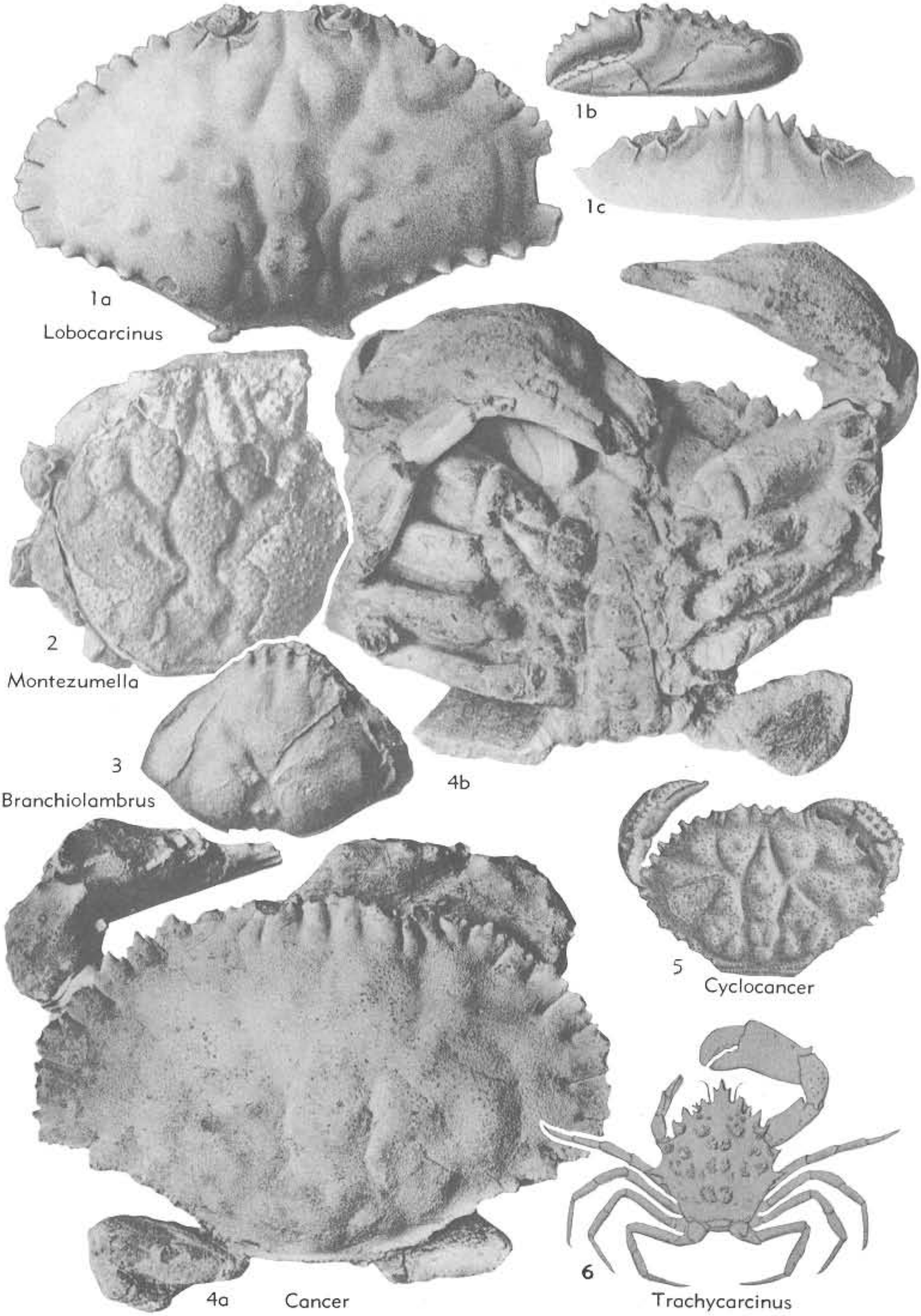


FIG. 318. Atelecyclidae *(2,5-6)*; Cancridae (Cancrinae) *(3-4)*, (Lobocarcininae) *(1)* (p. *R*508-*R*510).

ward. *Rec.,* IndoPac.-Cape Verde Is.——Fig. 317, *6.* **D. horrida* (Linné), male, ×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).

Mesorhoea 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, ×1 (238).

Subfamily EUMEDONINAE Miers, 1879

Carapace pentagonal or rhomboidal, front two- or four-lobed, first pereiopods 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 infraorbital 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;* ×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 pereiopods with pointed short dactyls. *Rec.,* Medit.-E.Atl.

Family ATELECYCLIDAE Ortmann, 1893

Carapace suboval to pentagonal, slightly elongate, front dentate, buccal frame elongate; antennulae infolded longitudinally. [Subfamilies Thiinae Alcock (1899) and Acanthocyclinae 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.; ×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.; ×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.; ×0.7 (243, after Faxon).

Family CANCRIDAE Latreille, 1803

[*nom. correct.* Dana, 1852 (*pro* Cancerides 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.*

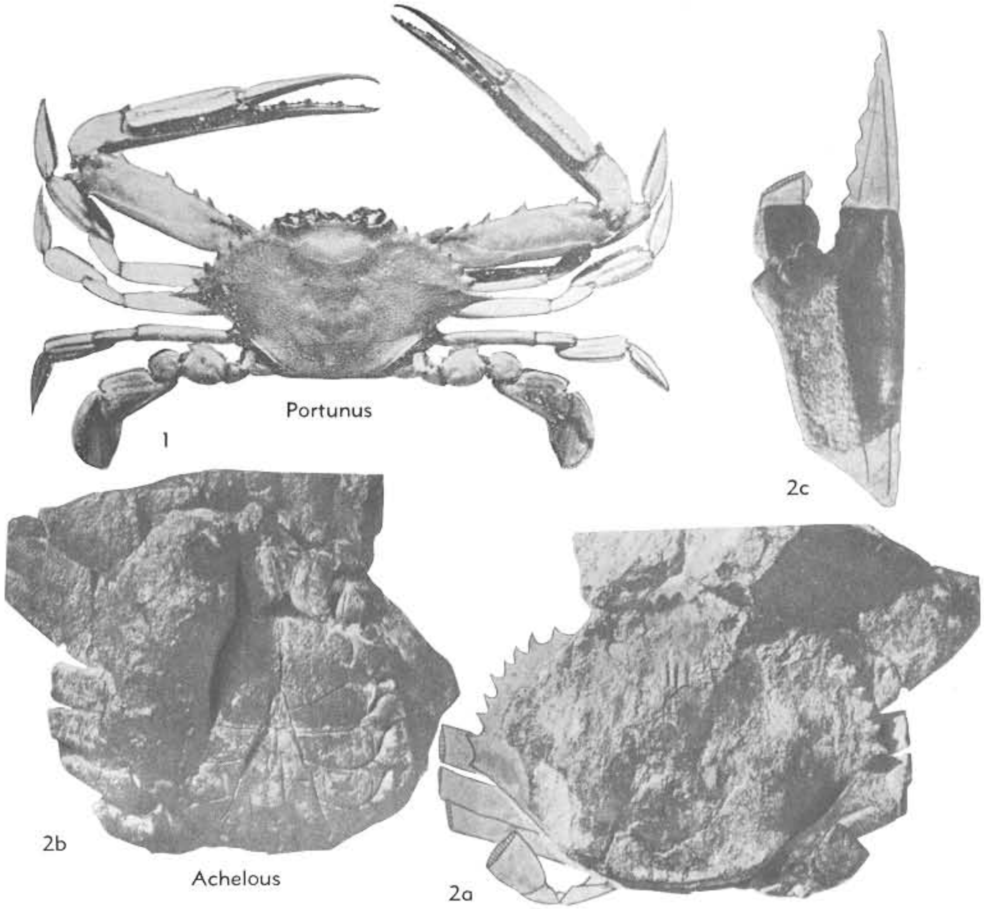


FIG. 319. Portunidae (Portuninae) (p. *R*510).

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; gastrocardiac 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; *4a,b,* dorsal, ventral, ×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, ×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, ×0.7; *1b,* chela, ×0.7; *1c,* fronto-orbital margin, ×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 BEURLEN, 1930]

Carapace flat, square or oval, with front narrow or wide, dentate or lobed; surface mostly with transverse ridges; chelae ridged; fifth pereiopods 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 pereiopods 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 pereiopods 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 pereiopods 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-Iran-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, ×0.25 (139).

P. (Achelous) 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. (Achelous) withersi* GLAESSNER, Mio., Iran; *2a,b,* dorsal, ventral, ×0.7; *2c,* right chela, ×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

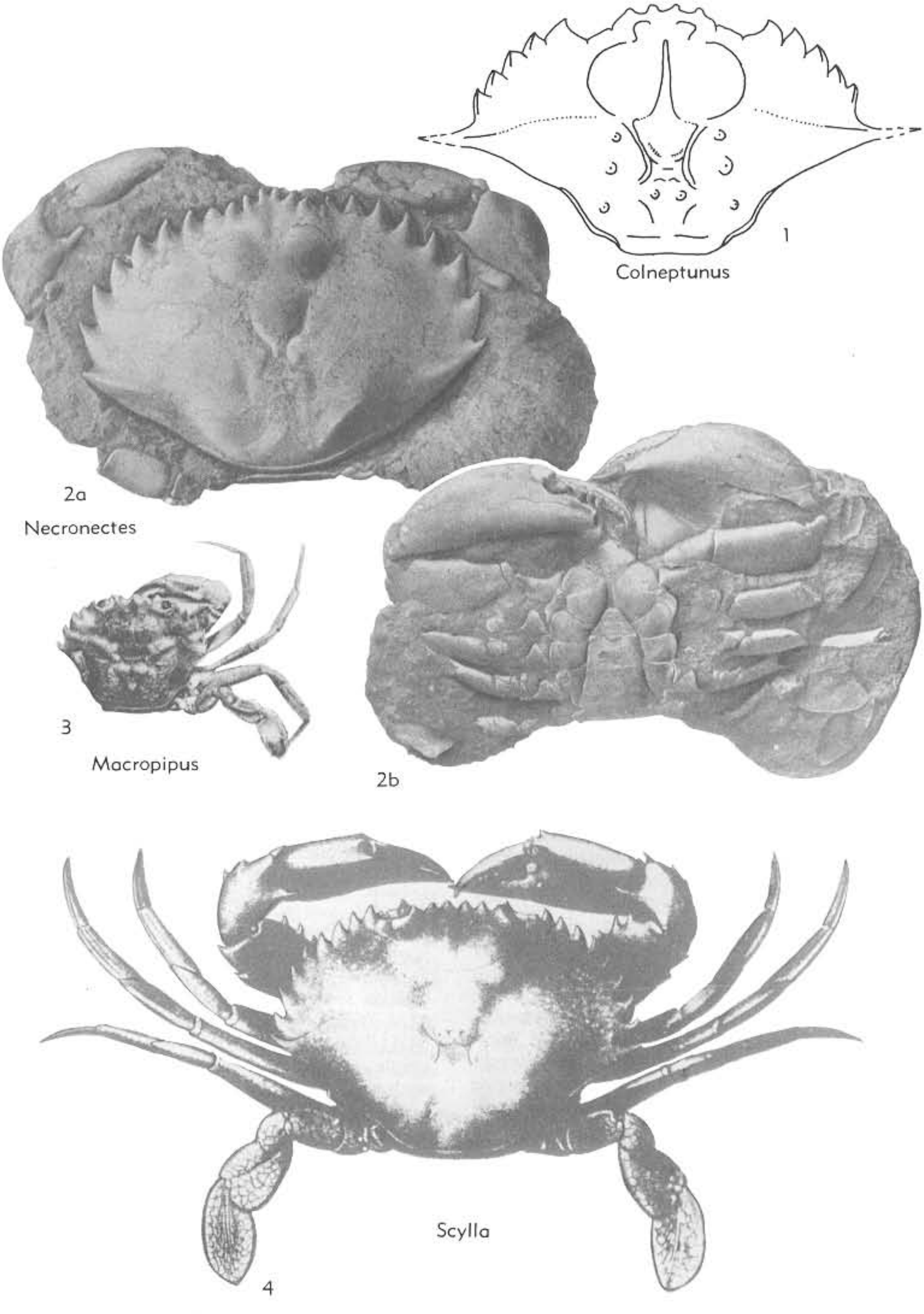


FIG. 320. Portunidae (Portuninae) *(1-2,4)*, (Macropipinae) *(3)* (p. *R*510, *R*512).

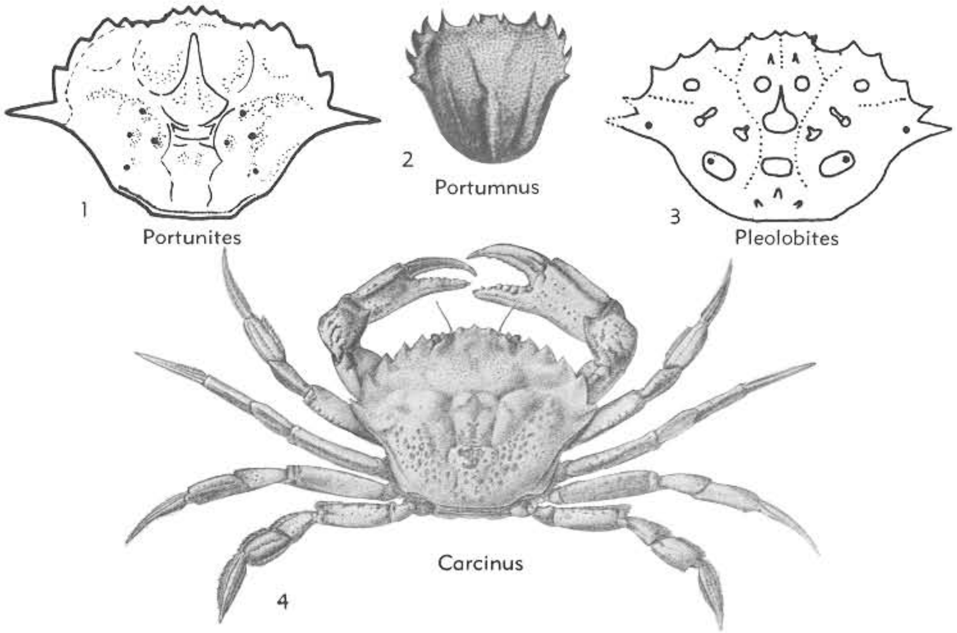


FIG. 321. Portunidae (Carcininae) (p. *R*513).

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, ×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, ×0.5; *2b,* chelipeds, frontal view, ×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.; ×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. *R*627.]

Macropipus Prestandrea, 1833 [**Portunus macropipus* Prestandrea, 1833; OD] [=*Portunus* Fabricius, 1798 (*non* Weber, 1795)] [ICZN Opinion 394]; *Liocarcinus* Stimpson & Pourtalès, 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.; ×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 pereiopods similar, rather stout, fifth pereiopods 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.; ×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 pereiopods flattened, said to be without "palette natatoire." [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, ×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, ×1 (184).

Portunites Bell, 1858 [**P. incertus*; OD] [=*Leiochilus* Reuss, 1859 (type, *L. morrisi*)]. 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; gastrocardiac regions well marked; arcuate ridge extending from lateral teeth to their sides; 5th pereiopods not flattened. *Eoc.*, Eu.-N.Am.-N.Z.; *Oligo.*, N.Am.; *Mio.*, Japan-Chile.——Fig. 321,*1*. *P. granulifer* Glaessner, Eoc., N.Z.; carapace (reconstr.), ×0.7 (118).

Subfamily PSAMMOCARCININAE Beurlen, 1930

Carapace subhexagonal, with anterolateral teeth, last being greatly elongated and modified. *L.Eoc.-L.Oligo.*

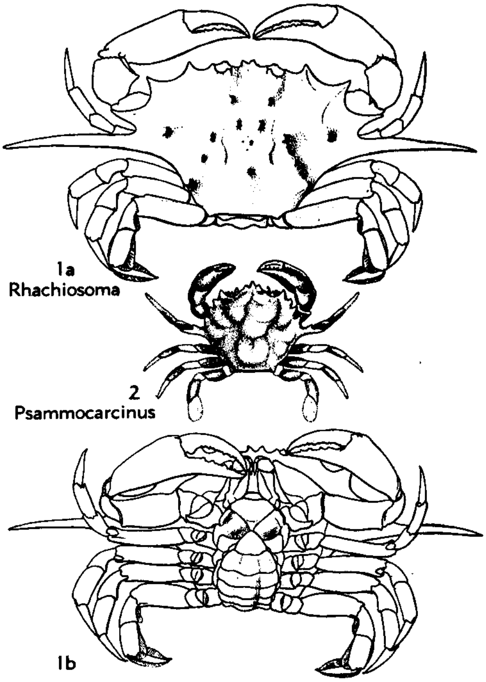


Fig. 322. Portunidae (Psammocarcininae) (p. *R*513).

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 pereiopods compressed. *Eoc.-L.Oligo.*, Eu.——Fig. 322,*2*. **P. hericarti* (Desmarest), Eoc., Fr.; carapace (reconstr.), ×1 (196).

Enoplonotus 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, ×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 (♀) (reconstr.), ×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*

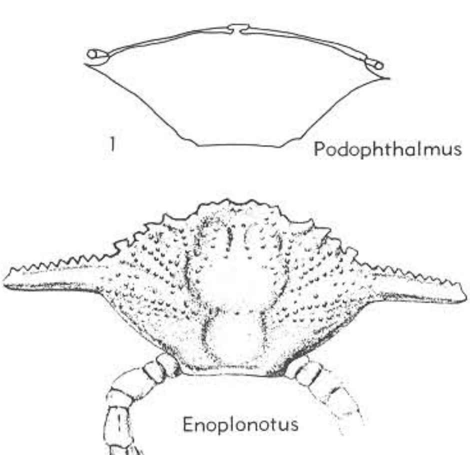


FIG 323. Portunidae (Psammocarcininae) *(2)*, (Podophthalminae) *(1-3)* (p. *R*513-*R*514).

(=**Portunus vigil* FARBICIUS, 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, ×0.5 (after 379a).

Euphylax 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, ×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 pereiopods with flattened propodus and oval dactylus. *U.Cret.*, Jamaica.——FIG. 324, *3*. **C. woolacotti*; dorsal, ×1.6 (319).

Cancrixantho VAN STRAELEN, 1934 [**C. pyrenaicus*; 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. pyrenaicus;* carapace and eye stalks, ×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; pereiopods 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 pereiopods with flat and wide propodus and dactylus (portunoid). *U.Cret. (Maastricht.)*, USA(Gulf Coast)-Brazil.——FIG. 324,*1*. **O. stephensoni*, USA(Tex.); carapace, ×0.4 (284).

Woodbinax STENZEL, 1953 [**W. texanus*; OD]. Front with 4 teeth, equal in width to orbits;

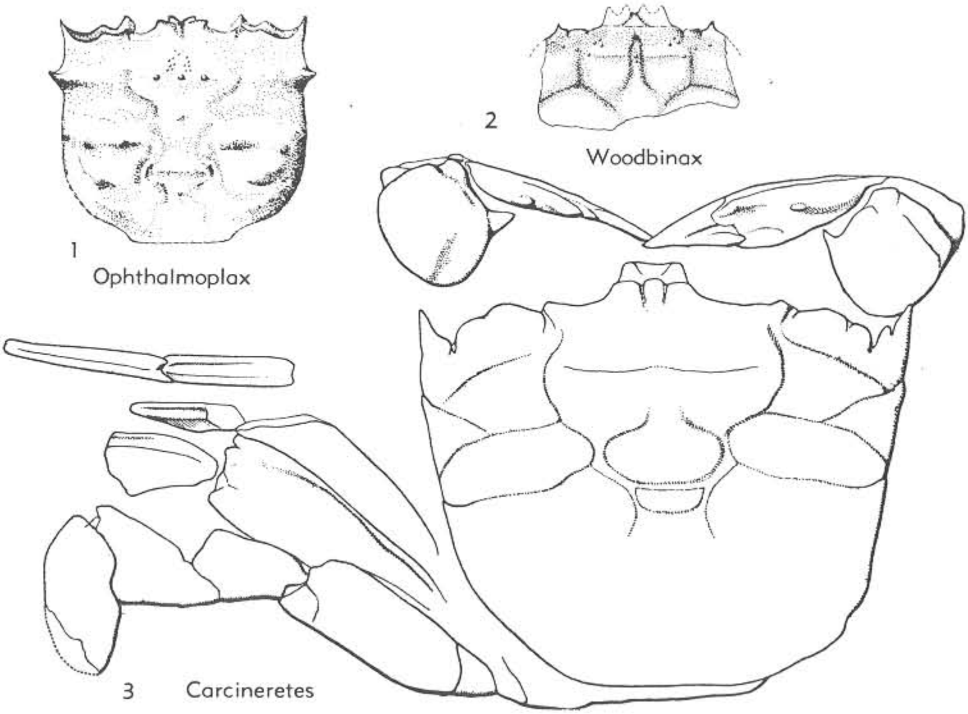


FIG. 324. Carcineretidae (p. *R*514-*R*515).

regions well marked, protogastric region with transverse ridge. *U.Cret.(Cenoman.)*, USA(Tex.). ——FIG. 324,2. **W. texanus*; anteromedian part of carapace, ×1.2 (284).

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 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.*

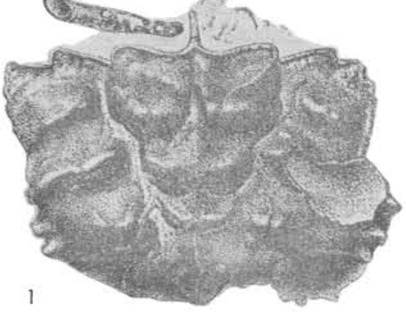


FIG. 325. Carcineretidae (p. *R*514).

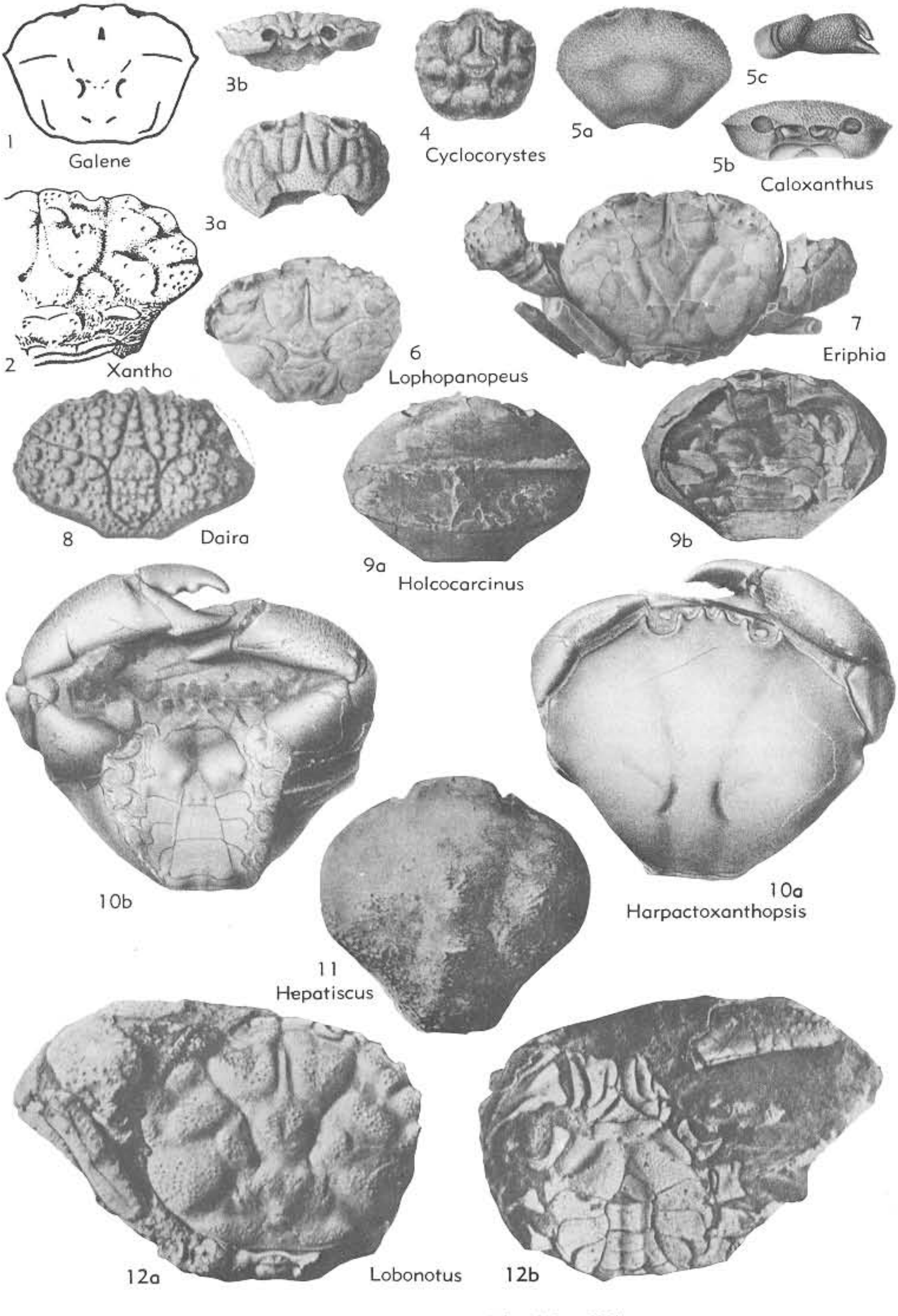


FIG. 326. Xanthidae (p. R517-R518, R520).

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, ×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, ×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 supraorbital 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, ×2; *5c*, cheliped, ×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* Rueppel, 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. bowerbankii*)]. 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, ×1 (19).

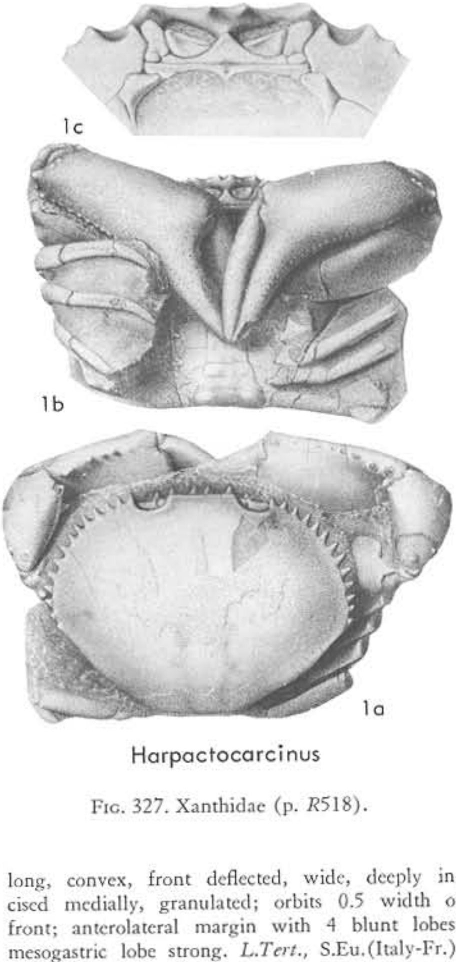
Cycloxanthops Rathbun, 1897 [*nom. subst. pro Cycloxanthus* A. Milne-Edwards, 1863 *(non* H. Milne-Edwards, 1850)] [**Xantho sexdecimdentatus* A. Milne-Edwards & Lucas, 1844; OD]. Carapace ovoid, front horizontal, prominent, medially notched; orbits small; anterolateral borders long, curved, with denticulation 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.; ×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; ×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



Harpactocarcinus

Fig. 327. Xanthidae (p. _R_518).

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. fittonii,_ =_Gecarcinus trispinosus_ Desmarest, 1822)]. Carapace subquadrilateral, 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), ×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, ×0.5; _1c,_ fronto-orbital region, ventral view, ×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, ×0.5 (198).

Hepatiscus 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; ×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 pereiopods 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, ×2 (320).

Lipaesthesius Rathbun, 1898 [*_L. leeanus_; OD]. Anterior portion of carapace very broad, posterior fourth very narrow; anterolateral margin arcuate, front deflexed, medially grooved; orbits small, subcircular; 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 supraorbital fissures, antennal base joined to front, antennular fossa transversely elongate. _?Eoc.,_

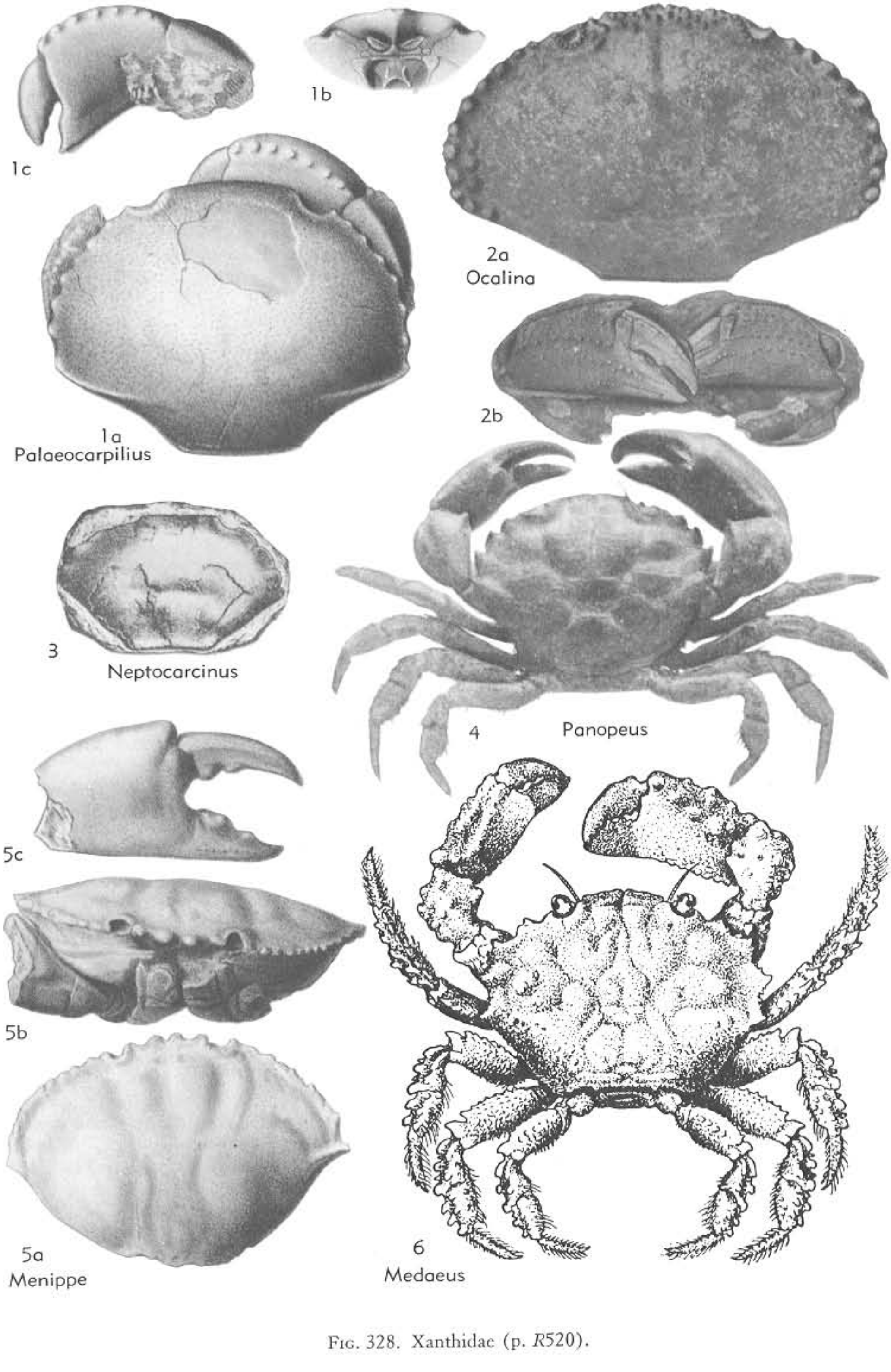


Fig. 328. Xanthidae (p. *R*520).

Borneo; *M.Eoc.*, USA(Tex.); *U.Eoc.*, Mex.; *Oligo.*, W.Indies.——Fig. 326,*12*. *L. mexicanus* Rathbun, U.Eoc., Mex.; *12a,b,* dorsal, ventral, ×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; ×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.; ×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.; *5a,b,* dorsal, frontal, ×0.5; *5c,* right chela, ×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*; ×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*; *2a,* carapace, ×0.5; *2b,* chelae, ×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; *1a,* dorsal view, ×0.7; *1b,* ventral view of frontal region, ×0.7; *1c,* internal view of right cheliped, ×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, ×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.; ×1 (243).

Phlyctenodes A. Milne-Edwards, 1862 [**P. tuberculosus*; 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. tuberculosus*; L.Tert., Fr.; ×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 spiniform 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.; ×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.

Simonellia VINASSA DE REGNY, 1897 [**S. quiricensis*; OD]. Carapace oval, slightly wider than long, flat and smooth; front short, wide; anterolateral margins with single tooth; lateral margins convex, posterior margin wide; sternal plate wide;

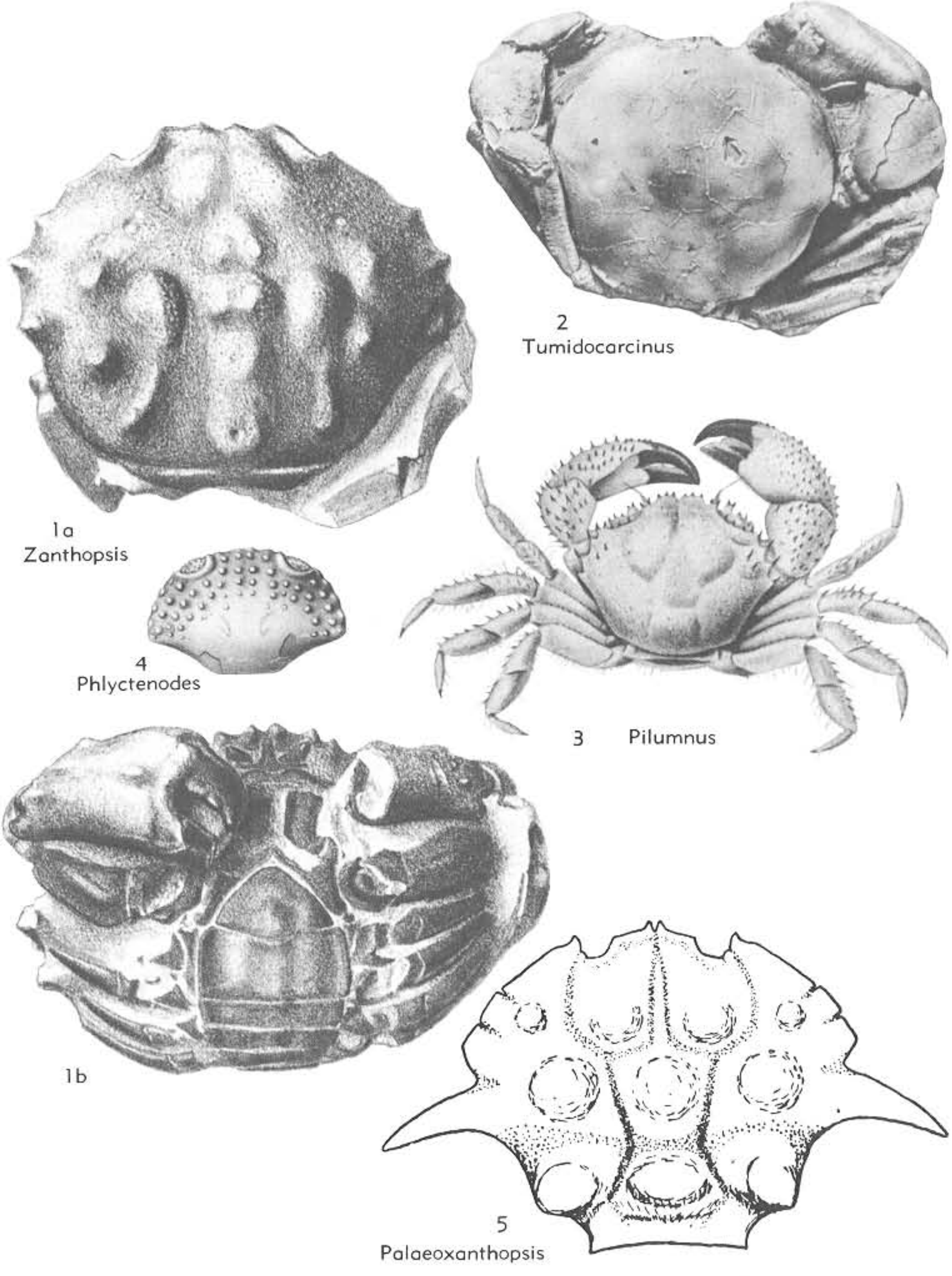


FIG. 329. Xanthidae (p. *R*520-*R*522).

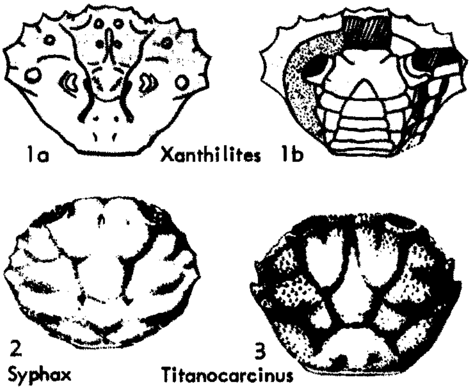


Fig. 330. Xanthidae (p. *R*522).

male abdomen triangular, narrowly pointed; right cheliped large, with long dactylus; pereiopods 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, X1.3 (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.; X2 (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.; X0.5 (118).

Xanthias Rathbun, 1897 [**Xanthodes granosomanus* Dana, 1852 (=*Xantho lamarckii* H. Milne-Edwards, 1834); OD] [=*Xanthodes* Dana, May, 1852 (*non* Guénee, 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, X0.4 (110).

Xanthodius Stimpson, 1859 [**X. sternbergnii*; 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 leachii* 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. [Vía (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 ♂ and ventral view ♀, X1 (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;

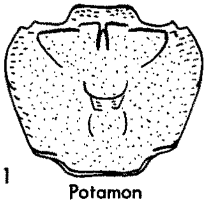


Fig. 331. Potamidae (p. *R*524).

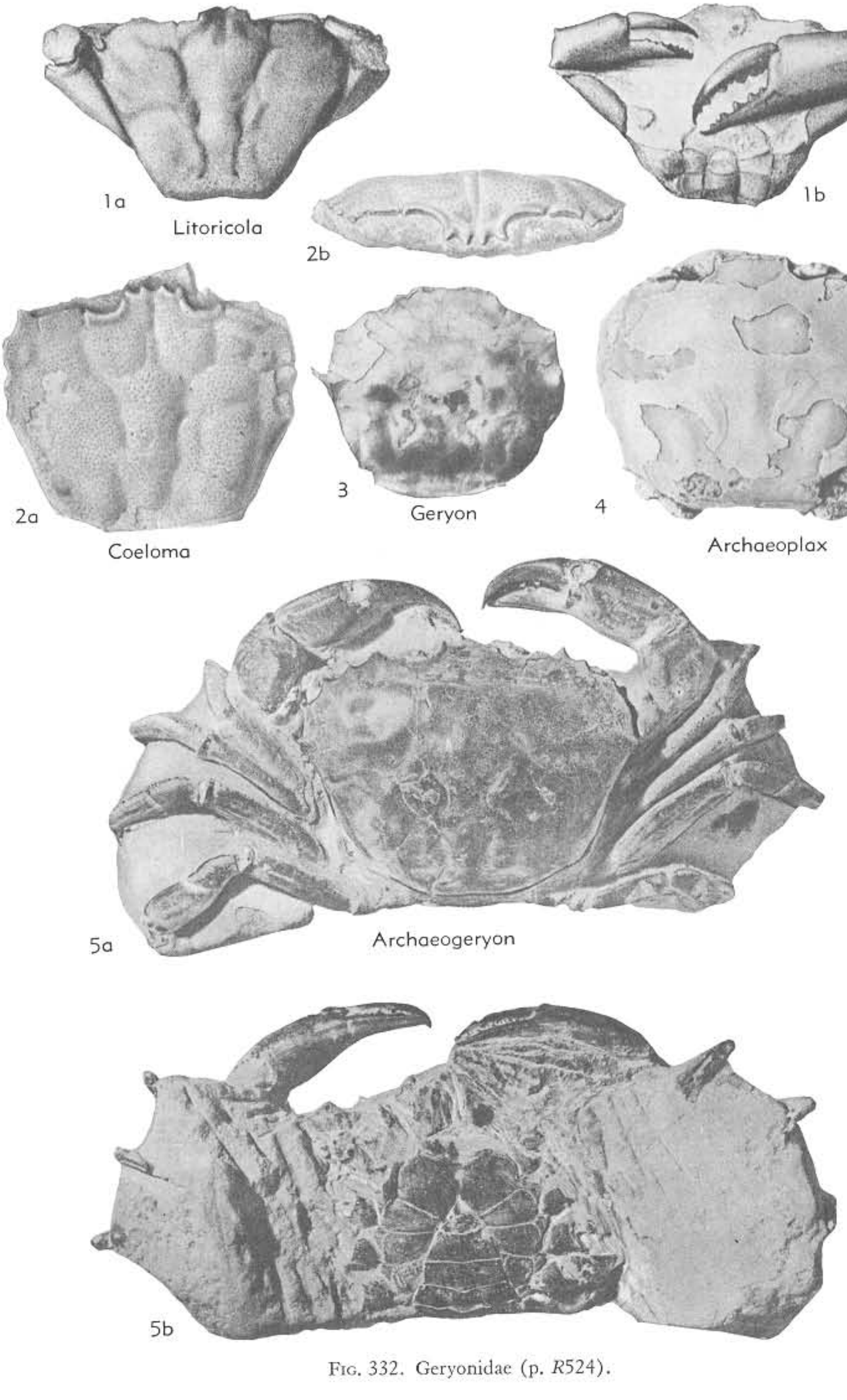


FIG. 332. Geryonidae (p. *R*524).

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 pereiopods 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 protogastric 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, ×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.; ×0.7 (303).

Archaeogeryon Colosi, 1924 [**A. fuegianus*; OD]. Differs from *Geryon* in flattened carpus, propodus, and dactylus of 5th pereiopods 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, ×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*; ×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, ×0.7 (198).

C. (Paracoeloma) Beurlen, 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, ×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, ×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*; ×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, ×0.7 (118).

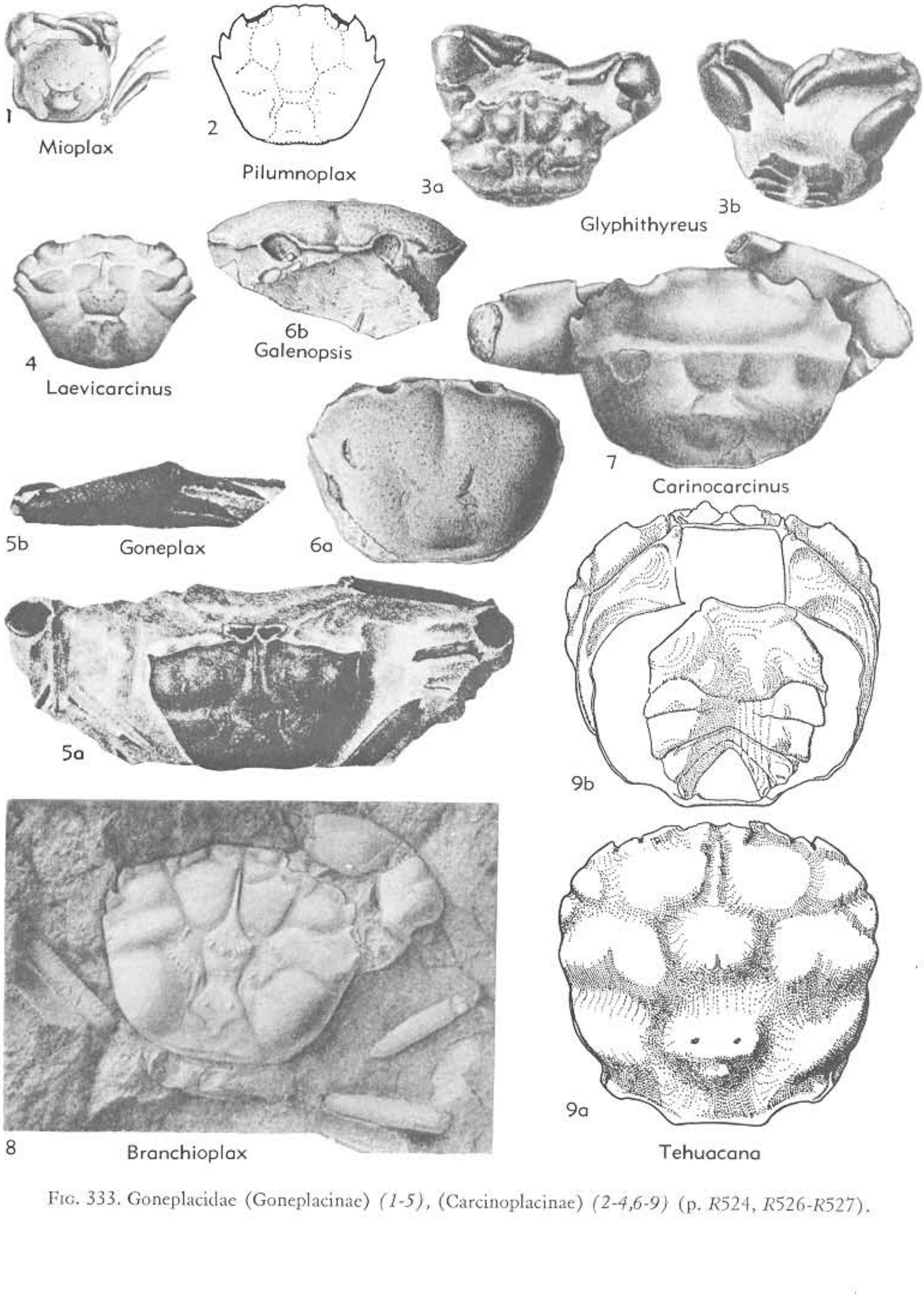


Fig. 333. Goneplacidae (Goneplacinae) *(1-5)*, (Carcinoplacinae) *(2-4,6-9)* (p. *R*524, *R*526-*R*527).

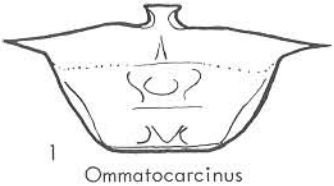


FIG. 334. Goneplacidae (Goneplacinae) (p. *R*525).

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 pereiopods. *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; ×1 (238).

Carcinoplacoides 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*; ×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, ×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, ×1 (19).

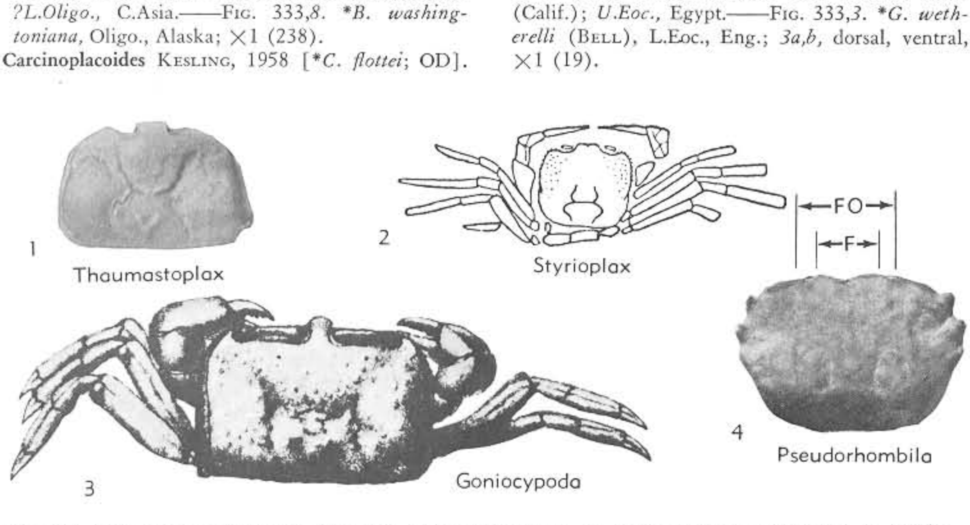


FIG. 335. Goneplacidae (Prionoplacinae) *(4)*, (Hexapodinae) *(1,3)*, (Subfamily Uncertain) *(2)* (p. *R*527).

Laevicarcinus Lörenthey & Beurlen, 1929 [**L. egerensis*; SD Glaessner, 1929]. Carapace wider than long, flat; front medially notched, anterolateral 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.; ×0.7 (184).

Martinezicancer Van Straelen, 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; ×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, ×3 (281).

Subfamily PRIONOPLACINAE Alcock, 1900

Differs from Carcinoplacinae in third abdominal segment of males not filling space between fifth pereiopods; 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, ×1 (113).

Subfamily HEXAPODINAE Miers, 1886

Carapace wider than long, lateral margins rounded, front narrow, fifth pereiopods absent; male abdomen not filling space between bases of fourth pereiopods, 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 pereiopods nearly equal in size. *Mio.,* Japan; *Rec.,* IndoPac.

Goniocypoda 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 pereiopods subequal. *?U. Cret.(Maastricht.),* W.Afr.; *Eoc.,* Eu.-Egypt-India. ——Fig. 335,*3*. **G. edwardsi,* L.Eoc., S.Eng.; ×2 (329; published figure has "outlines of absent limbs," including 5th pereiopod, added without justification).

Thaumastoplax Miers, 1881 [**T. anomalipes*; OD]. Differs from *Hexapus* in 3rd pereiopods being stronger than 2nd to 4th ones, from *Goniocypoda* in wider front and smaller orbits. *Eoc.,* Peru; *Oligo.,* Panama; *Rec.,* W.Afr.-Thailand-Japan.——Fig. 335,*1*. *T. prima* Rathbun, *Oligo.,* Panama; carapace, ×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 pereiopods long and slender, 5th being longest. *Mio.,* Eu.(Aus.).——Fig. 335,*2*. **S. exiguus* (Glaessner); ×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

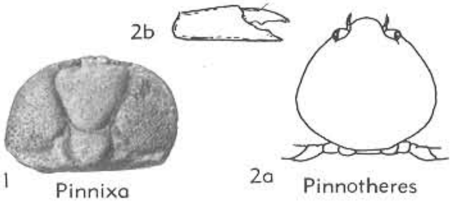


Fig. 336. Pinnotheridae (p. *R*528).

angles and palp not at antero-internal angle; male abdomen very narrow. [Five subfamilies are currently recognized.] *Eoc.-Rec.*

Pinnotheres Bosc, 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, ×3 (52).

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, ×2 (238).

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

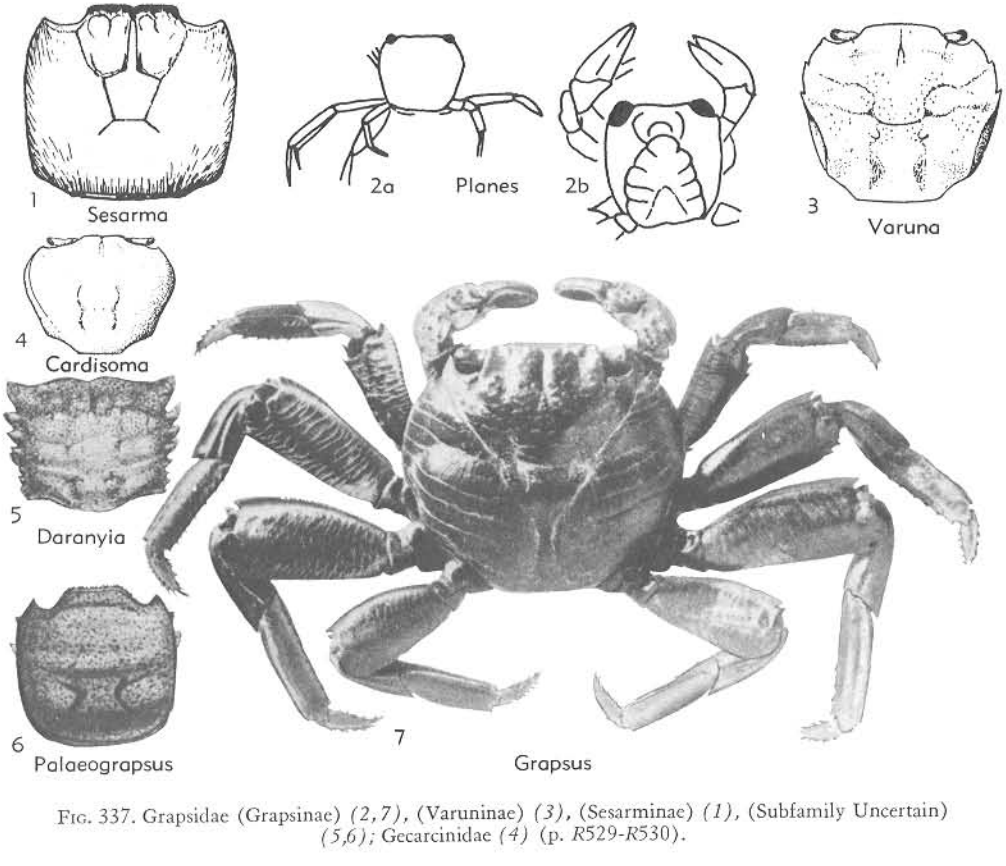


Fig. 337. Grapsidae (Grapsinae) *(2,7)*, (Varuninae) *(3)*, (Sesarminae) *(1)*, (Subfamily Uncertain) *(5,6)*; Gecarcinidae *(4)* (p. *R*529-*R*530).

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 pereiopods. *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, ×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; *2a,b,* dorsal, ventral, ×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 pereiopods. *?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 pereiopods 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, ×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 pereiopods 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 pereiopods long. *Pleist.(Subrecent),* 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 pereiopods completely or almost completely. *U.Oligo.-* or *L.Mio.-Rec.*

Sesarma Say, 1817 [**Ocypode 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 pereiopods subequal in length; abdomen wtih 7 somites. *U. Oligo.* or *L.Mio.,* Brazil; *Pleist.(Subrecent),* Australia; *Rec.,* cosmop. in warm waters.——Fig. 337,*1*. *S. paraensis* Beurlen, U.Oligo. or L.Mio., Brazil; carapace, ×1 (32).

Subfamily UNCERTAIN

Daranyia Lörenthey, 1901 [**D. granulata*; OD]. Lateral margins of carapace converging posteriorly, with teeth decreasing in size; gastro- and cardiobranchial 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.; ×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.; ×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.

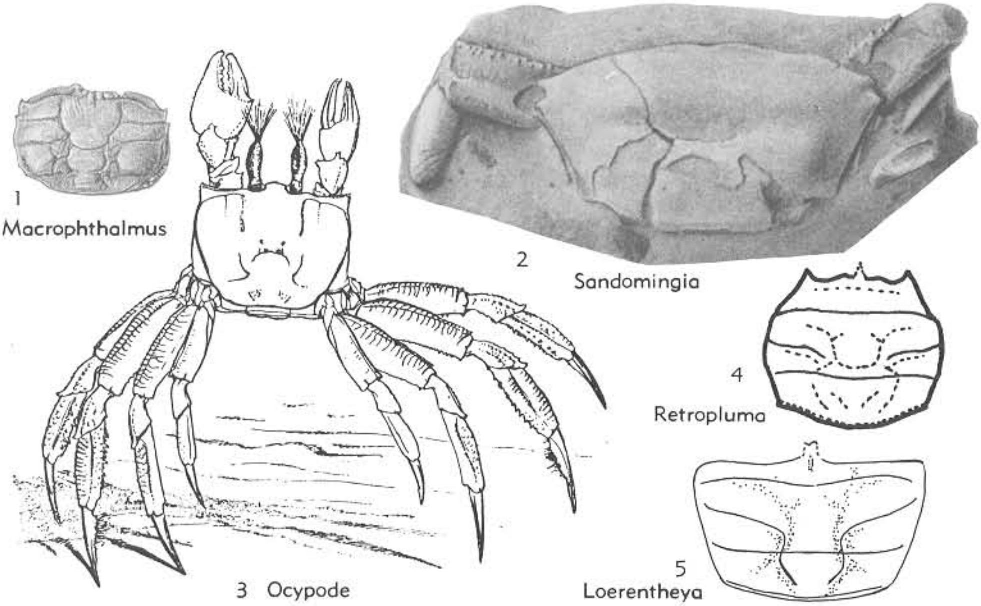


FIG. 338. Ocypodidae (Ocypodinae) *(3)*, (Macrophthalminae) *(1)*, (Subfamily Uncertain) *(2,5)*; Retroplumidae *(4)* (p. *R*530-*R*531).

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.; ×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.*

Ocypode WEBER, 1795 [**Cancer ceratophthalmus* PALLAS, 1772; SD] [=*Ocypoda* 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, ×0.7 (52, after Gravier).

Uca LEACH, 1814 [**Cancer vocans major* HERBST, 1782; OD] [=*Gelasimus* LATREILLE, 1817 (type, *Ocypoda 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, ×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

Loerentheya 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 gastrocardiac grooves, 2 transverse keels and pair of oblique sinuous ridges. *M.Eoc.,* Hung.——Fig. 338,*5*. **L. carinata*; ×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, ×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 pereiopods, with sternal ducts; female gonoducts open on sternum of third pereiopods; sternum of fifth pereiopod reduced, and this pereiopod rudimentary, close-set, subdorsal. *M.Eoc.-Rec.*

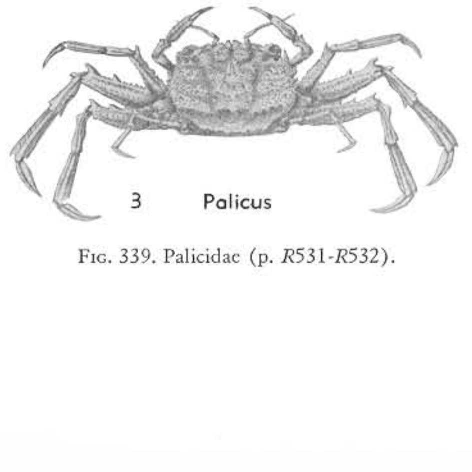


Fig. 339. Palicidae (p. *R*531-*R*532).

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, ×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 pereiopods long, slender, fifth commonly short, subdorsal. Female genital openings between coxae of second pereiopods, 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 pereiopods subdorsal, may be filiform. *Rec.,* Medit.-Atl.-Pac.——Fig. 339,*3*. *P. cristatipes* (A. Milne-Edwards); ×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; cervical 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 pereiopods 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 *Retrocypoda* Via need evaluation.] *U. Cret.,* USA(Calif.).——Fig. 339,*2*. **A. antennatus*; dorsal view of carapace, ×1 (328).

?**Retrocypoda** Vía, 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 pereiopods subdorsal, reduced. *M.Eoc.,* Spain.——Fig. 339,*1*. **R. almelai*; carapace, ×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. Macrophthalminae.

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, 1893] [**M. latifrons*; OD]. Based on a single, small, incomplete carapace which was lost. *U. Mio.,* Hung.

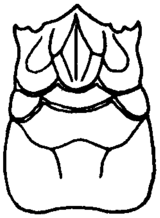


Fig. 340. Family Uncertain (p. R532).

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, ×1 (re-drawn from 296). [This genus now is judged to belong in Tanaidacea.]

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[1] See page R628.

Lupeites FRITSCH, 1887 [**L. granulatus*; OD]. Unrecognizable fragment. *U.Cret.*, Czech.

Olinaecaris 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 ⅓ 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 *R*626.

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, extending 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

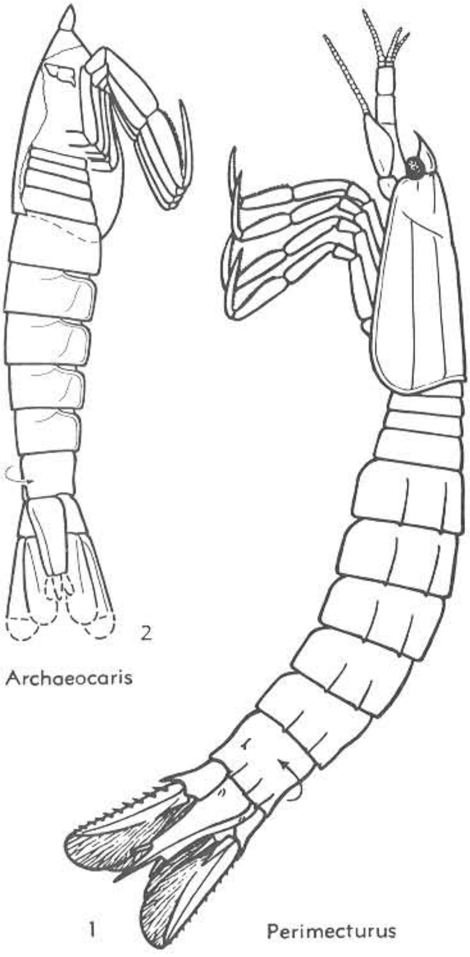
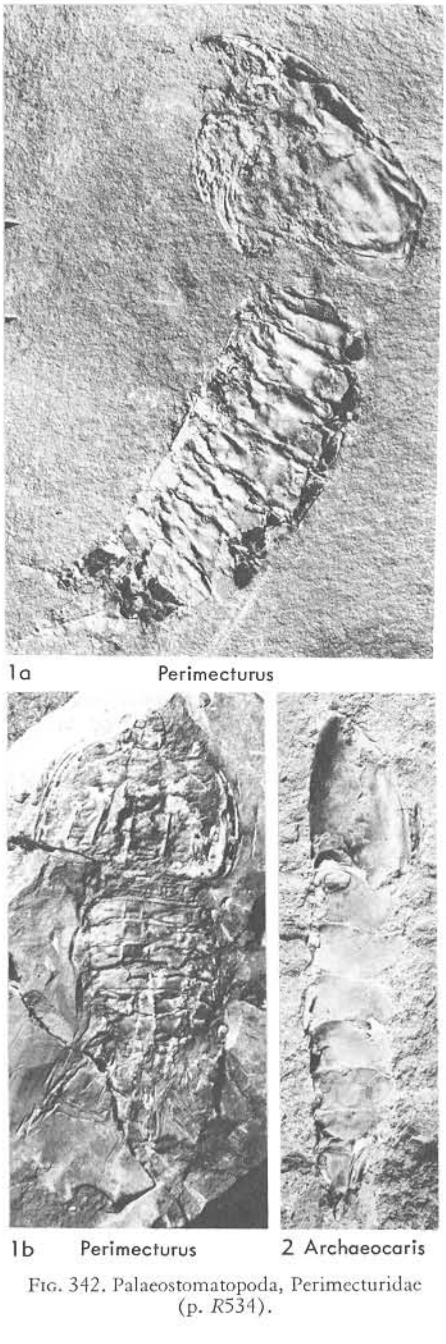


FIG. 341. Reconstruction of Palaeostomatopoda.——*1. Perimecturus elegans* PEACH, L.Carb., Scot.; ×1.3.——*2. Archaeocaris vermiformis* MEEK, Miss., USA (Ky.); ×3.

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 absence of a marsupium and the presence of triramous antennules. Thus these fossils actually belong to the ancestral hoplocarid stock.



1a Perimecturus

1b Perimecturus

2 Archaeocaris

FIG. 342. Palaeostomatopoda, Perimecturidae (p. *R*534).

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.; ×1.3 (55).——Fig. 342,*1b*. **P. parki* (Peach), L.Carb., Scot.; ×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.); ×3 (55).

STOMATOPODA

By L. B. Holthuis[1] and Raymond B. Manning[2]

[[1]Rijksmuseum van Natuurlijke Historie, Leiden; [2]United 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

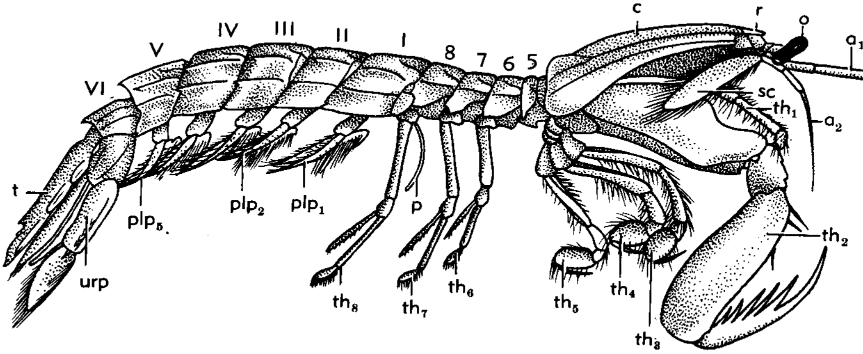


Fig. 343. *Squilla mantis*, ♂, Rec., Medit. (65). [Explanation: *5-8*, fifth to eighth thoracic somites; *I-VI*, first to sixth abdominal somites; a_1, antennule; a_2, antenna; *c*, carapace; *o*, eye; *p*, penis; plp_{1-5}, first to fifth pleopods; *r*, rostrum; *sc*, scaphocerite; *t*, telson; th_{1-8}, 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

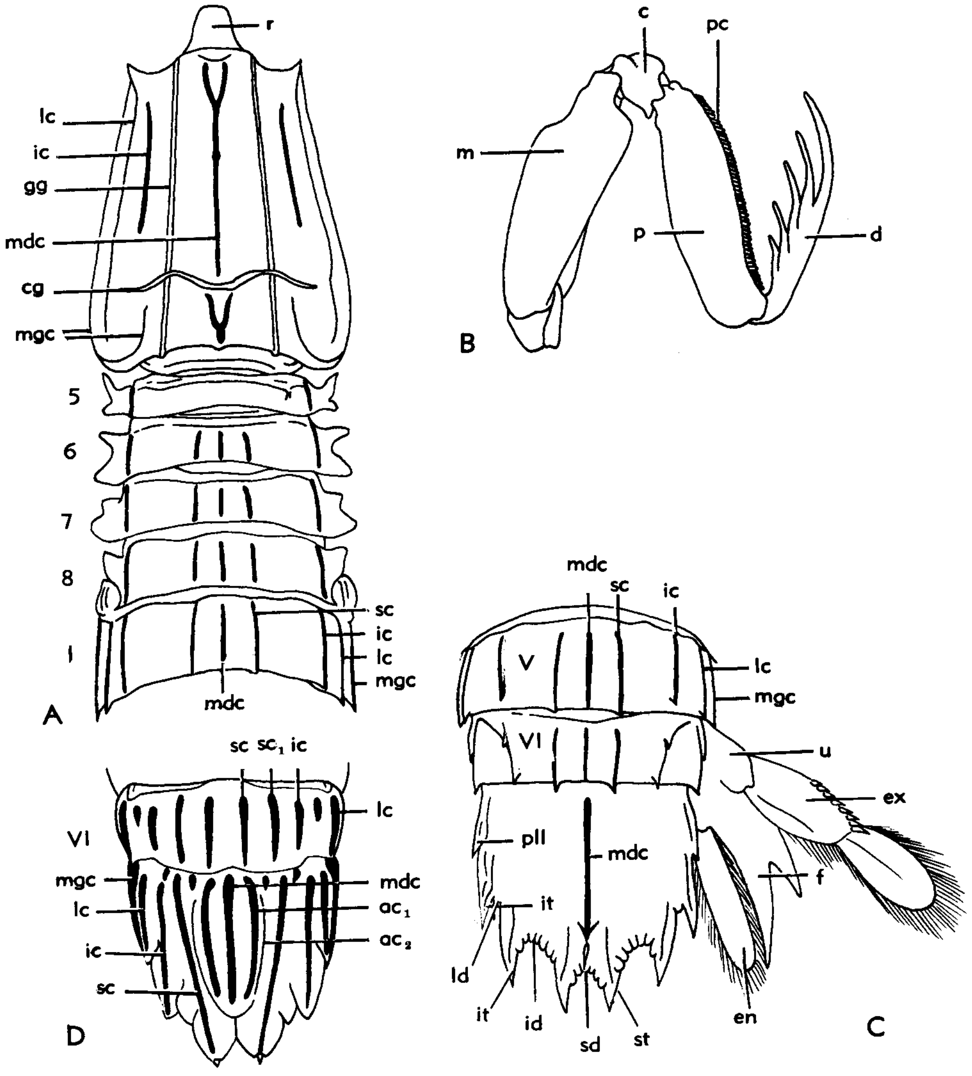


FIG. 344. *Squilla* sp. (*A-C*); *Odontodactylus* sp. (*D*).——*A*, thorax and first abdominal somite, dorsal; *B*, raptorial claw (second thoracopod); *C*, telson and last two abdominal somites, dorsal; *D*, telson and sixth abdominal somite (45). [Explanation: *5-8*, fifth to eighth thoracic somites; *I, V, VI*, first, fifth and sixth abdominal somites; ac_1-ac_2, 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*, pecination of propodus; *pll*, prelateral lobe; *r*, rostrum; *sc*, submedian carina; sc_1, 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 abovementioned 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 *Sculda* 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, ischiomerus (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 propodus. 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 ischiomerus 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

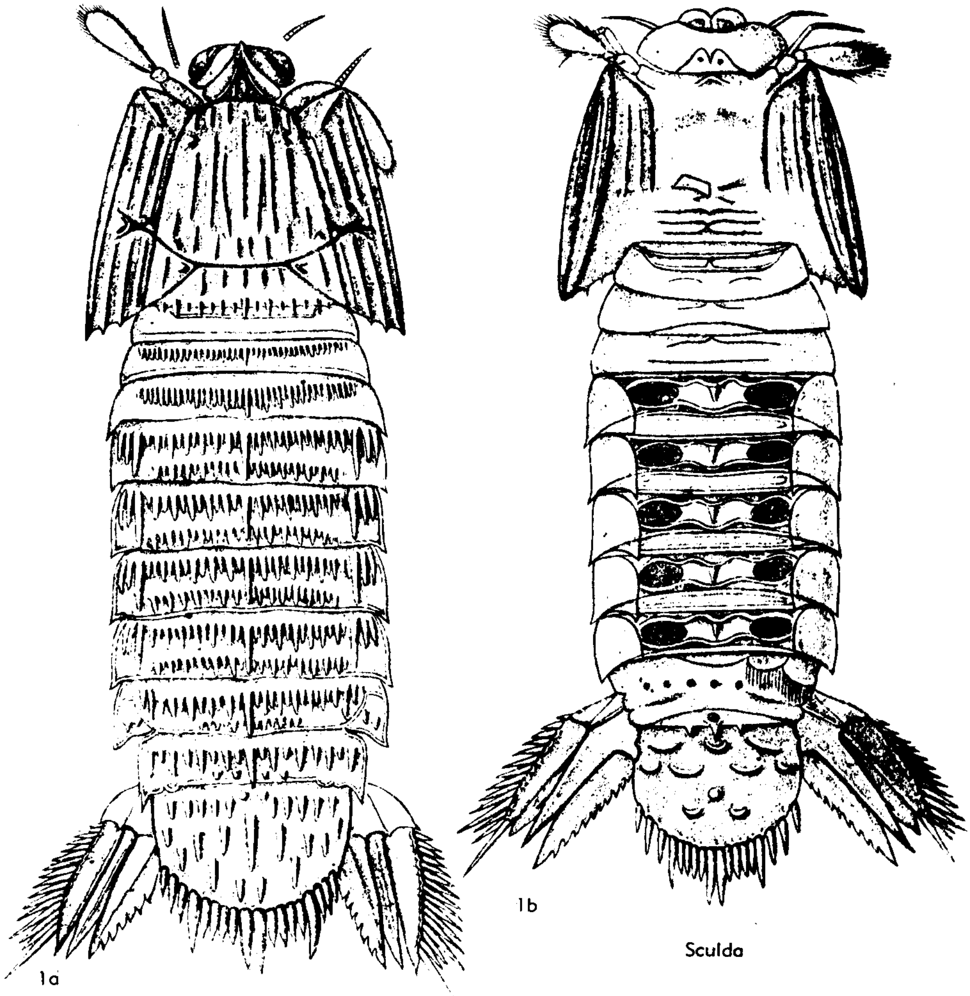


FIG. 345. Sculdidae (p. *R*546).

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.

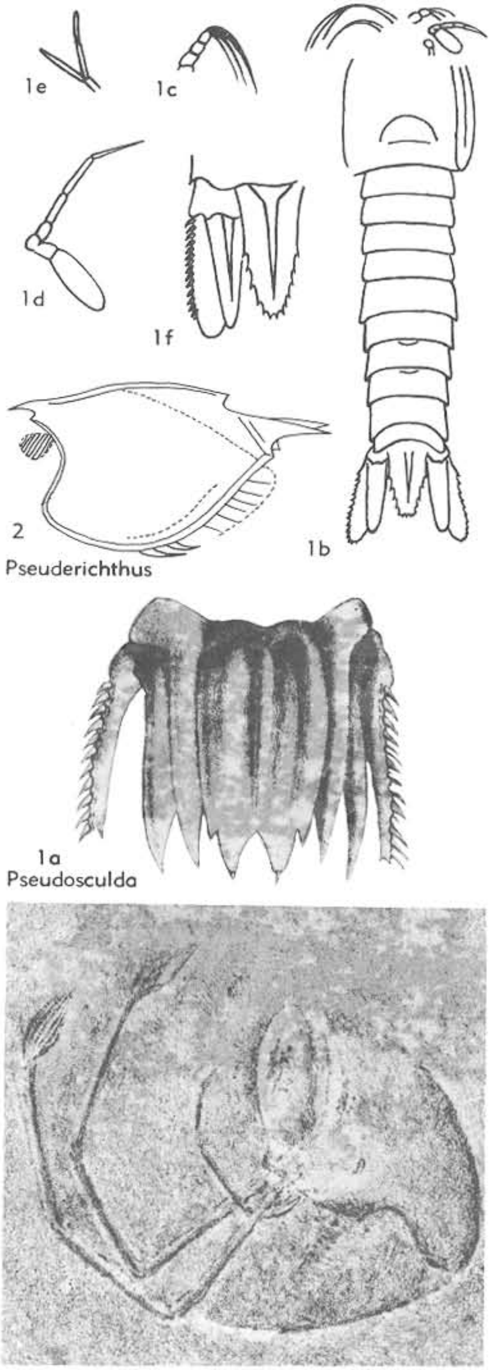


FIG. 346. Sculdidae (p. *R*546).

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; *Pseudosquillopsis 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

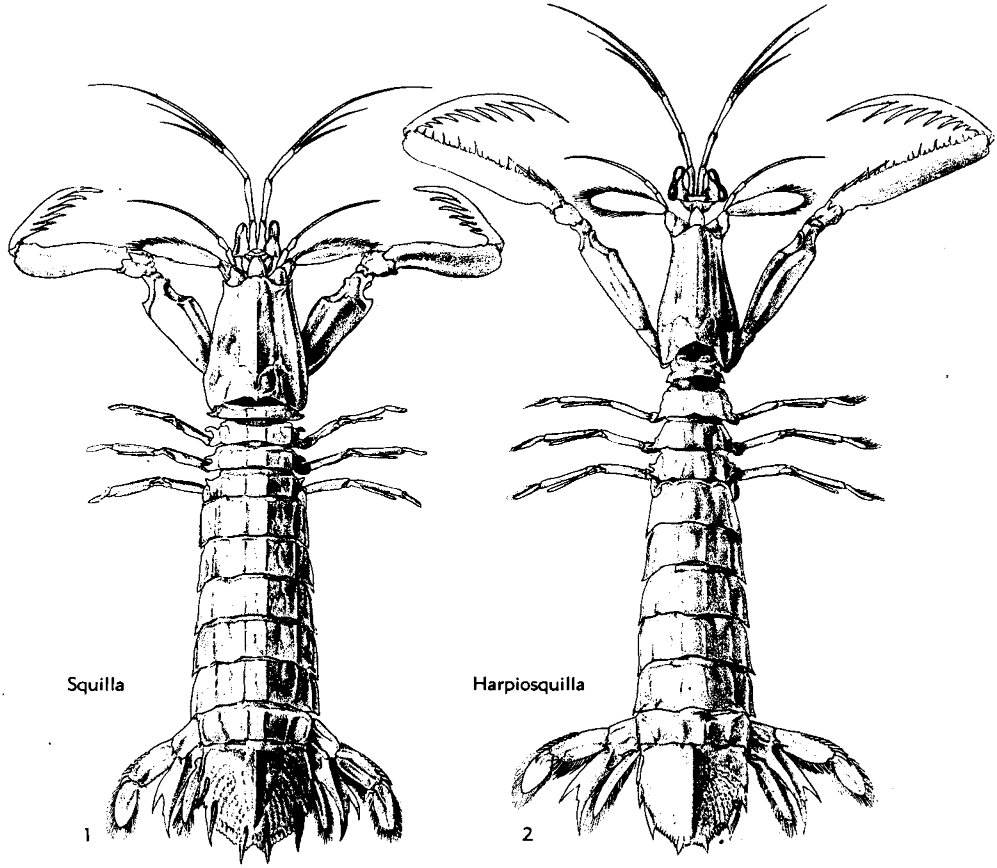


Fig. 347. Squillidae (p. *R*546-*R*549).

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*

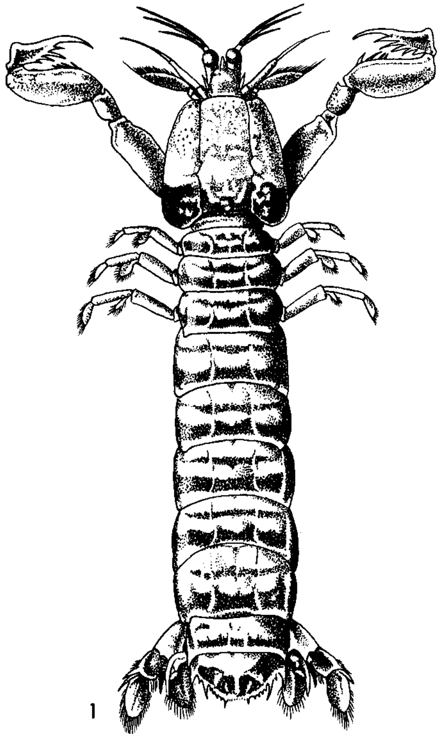


FIG. 348. Squillidae (p. R548).

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 Stomapoda [*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

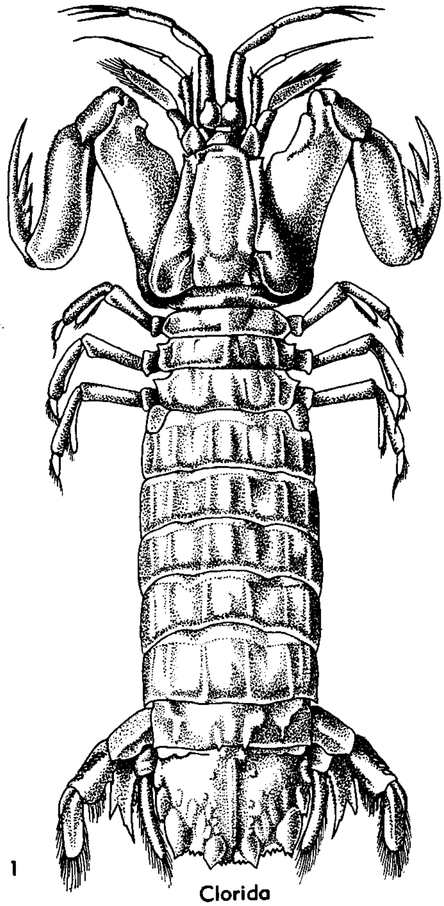


FIG. 349. Squillidae (p. R548).

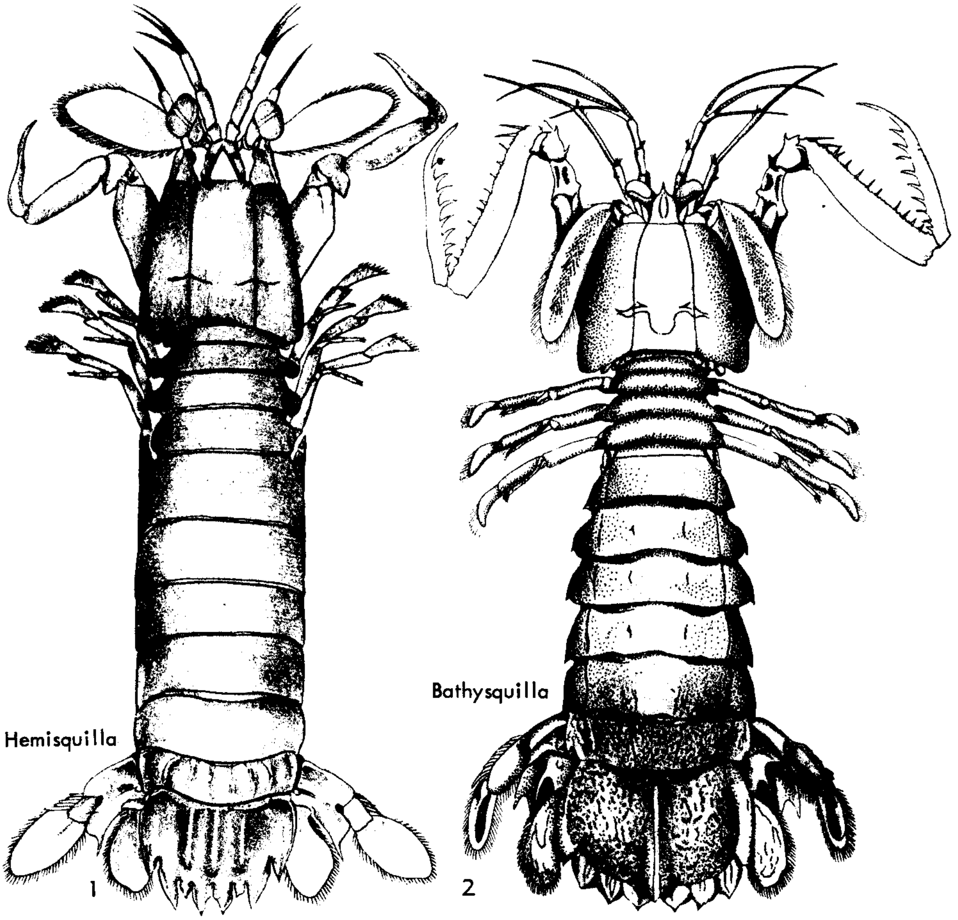


FIG. 350. Squillidae (p. *R*548-*R*550).

stomatopods—*Squilla, Gonodactylus, Coronis*). Later MILNE-EDWARDS (1852) restricted the order Stomapoda [*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 (SHIINO, 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,

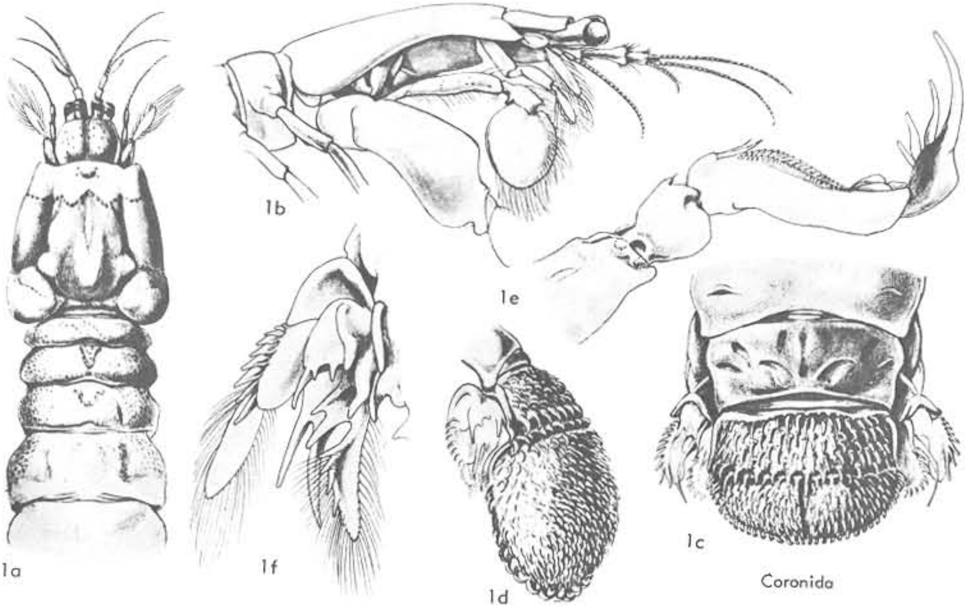


FIG. 351. Squillidae (p. R548).

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), *Protozoea* (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 *Protozoea* (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.

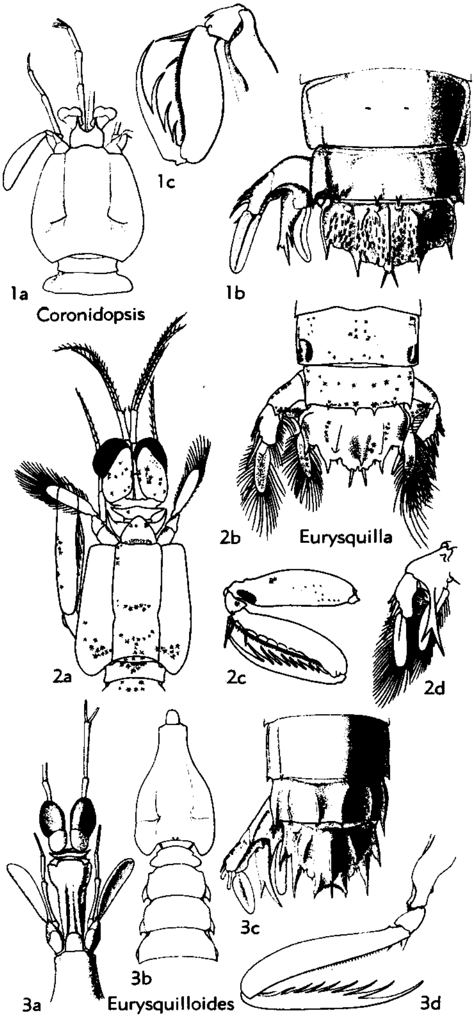


FIG. 352. Squillidae (p. *R*548-*R*549).

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.*

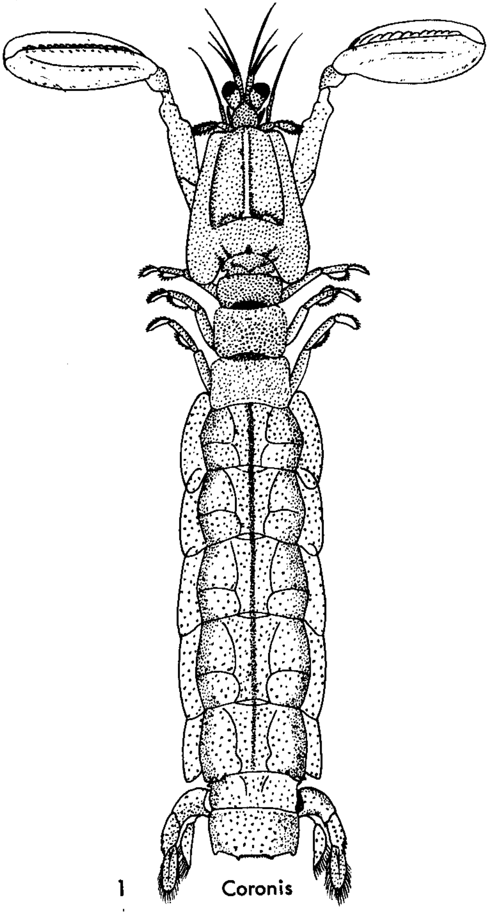


FIG. 353. Squillidae (p. *R*548).

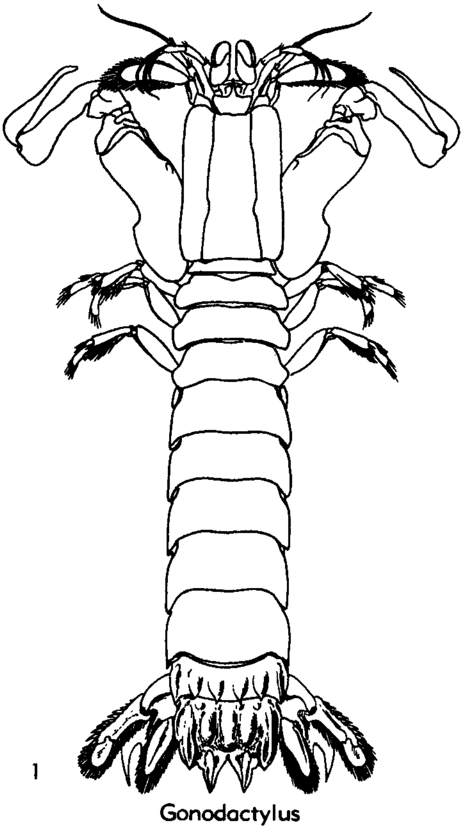


Fig. 354. Squillidae (p. *R*549).

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,*1*. **S. pennata*, U.Jur., Bavaria; *1a,b*, dorsal, ventral, approx. ×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. ×2 (220).

Pseuderichthus Dames, 1886, p. 571 [*non Pseuderichthus* 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, ×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* Gronovius, 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.*

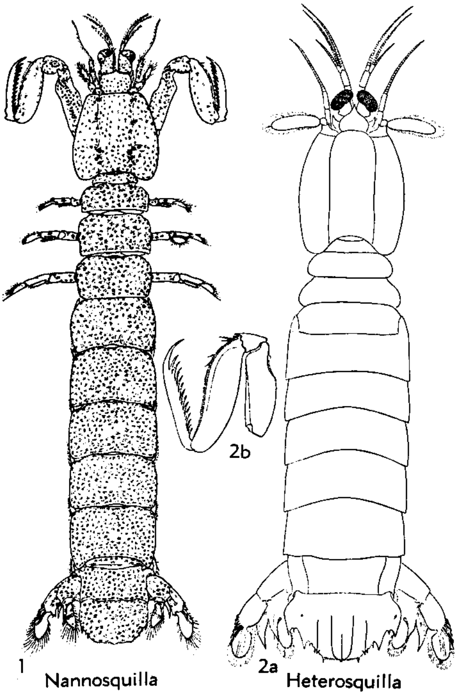


Fig. 355. Squillidae (p. *R*550-*R*551).

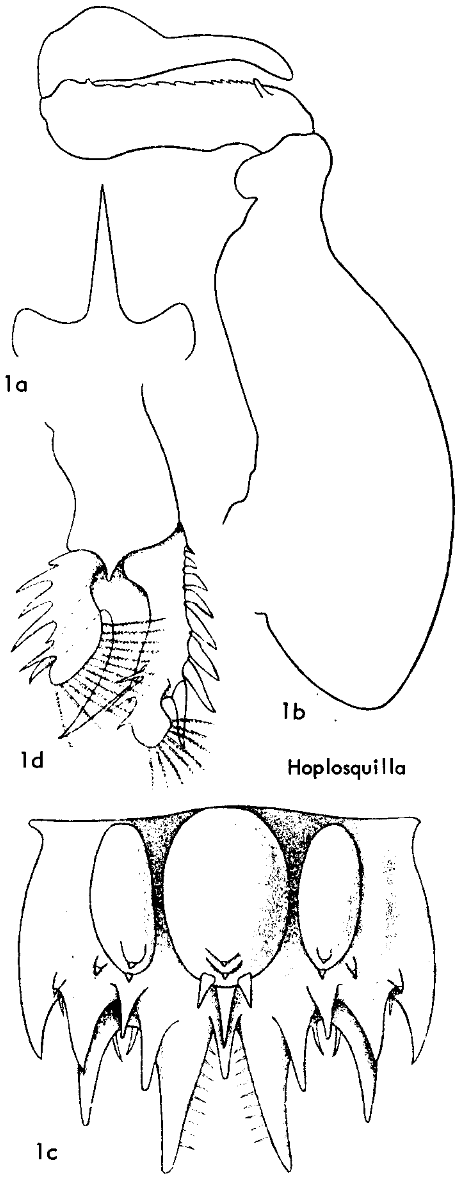


FIG. 356. Squillidae (p. *R*550-*R*551).

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*); *Halimonectes* 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. laticauda*)]. 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

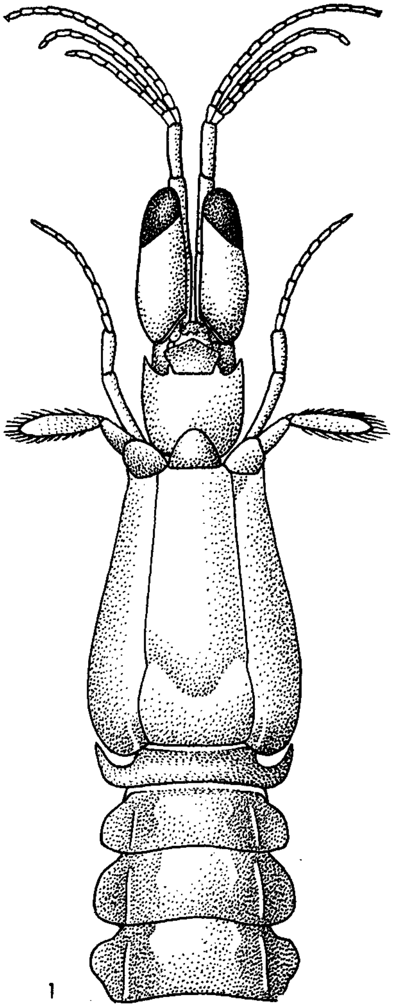


FIG. 357. Squillidae (p. *R*551).

animal, approx ×1 (65).——FIG. 347,*1*. *S. oratoria* DE HAAN, Rec., Japan; dorsal, approx. ×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,*1*. **A. multifasciata* (WOOD-MASON), India; dorsal, ×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, ×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, ×1.5 (325).

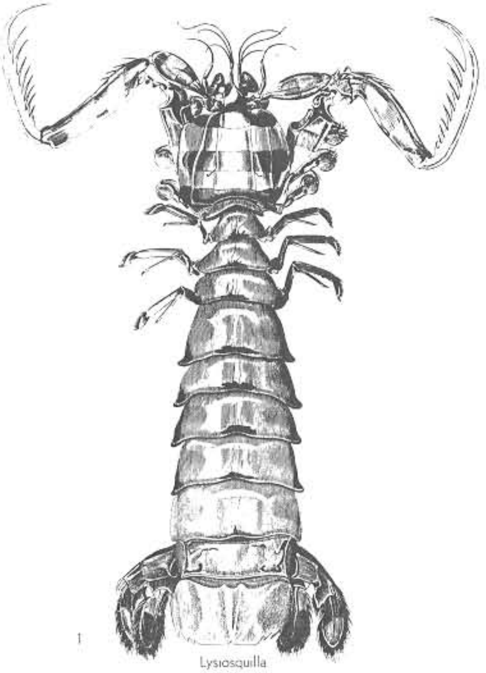


FIG. 358. Squillidae (p. *R*551).

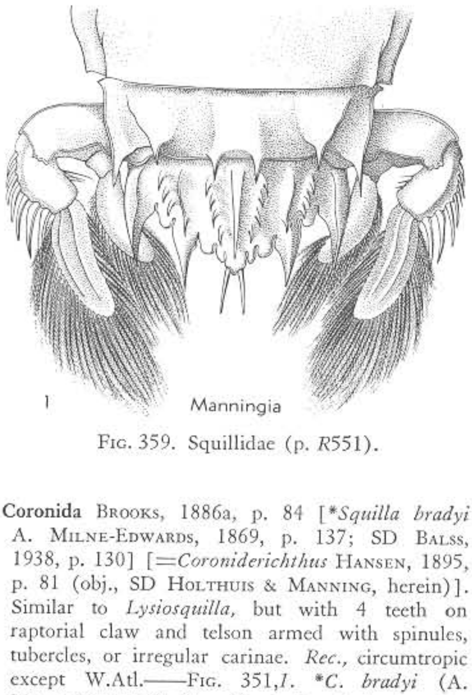


FIG. 359. Squillidae (p. *R*551).

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., ×8; *1c,d*, post. part of abdomen, dorsal, lat., ×8; *1e*, raptorial claw, ×10; *1f*, uropod, ventral, ×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. biscuspis*; *1a*, ant. part of body, ×3.5; *1b*, post. part of abdomen, ×4.5; *1c*, raptorial claw, ×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, ×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, ×11; *2b*, post. part of abdomen, dorsal, ×11; *2c*, raptorial claw, ×11; *2d*, uropod, ×11 (37).

Eurysquilloides MANNING, 1963, p. 315 [**Squilla*

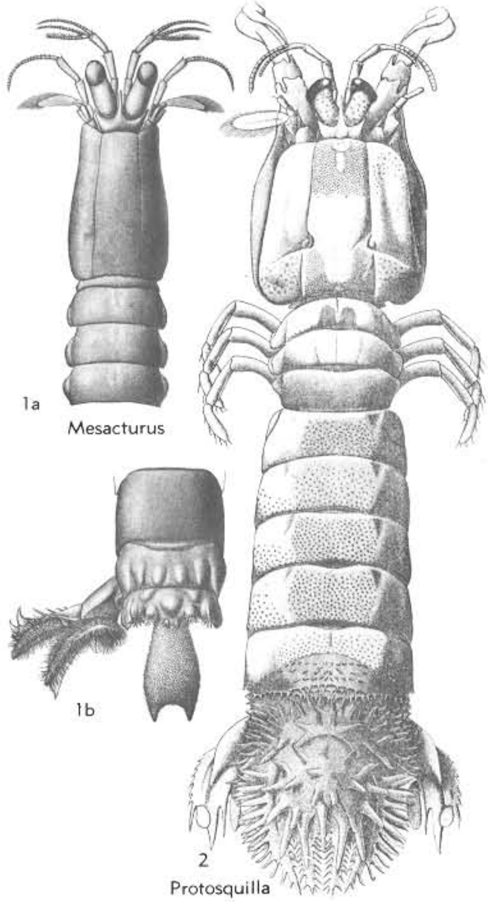


Fig. 360. Squillidae (p. *R*551-*R*552).

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, ×5; *3b,* thorax, dorsal, ×4; *3c,* post. part of abdomen, dorsal, ×4.2; *3d,* raptorial claw, ×4.5 (143).

Gonodactylus Berthold, 1827, p. 271 [**Squilla chiragra* Fabricius, 1781, p. 515; SD Holthuis & Manning, ICZN pend.] [=*Gonerichthus* 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, ×2 (37).

Harpiosquilla Holthuis, 1964, p. 140 [**Squilla harpax* de Haan, 1844, atlas, pl. li, fig. 1; OD] [=*Alimerichthus* Claus, 1871, p. 146 (*non Alimerichthus* 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 posterolateral 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. ×1 (137).

Hemisquilla Hansen, 1895, p. 72 [**Gonodactylus styliferus* H. Milne-Edwards, 1837, p. 530 (=*Gonodactylus ensiger* Owen, 1832, p. 6); OD, M]. Probably related to *Odontodactylus* and *Gonodactylus*; cornea subglobular; telson with

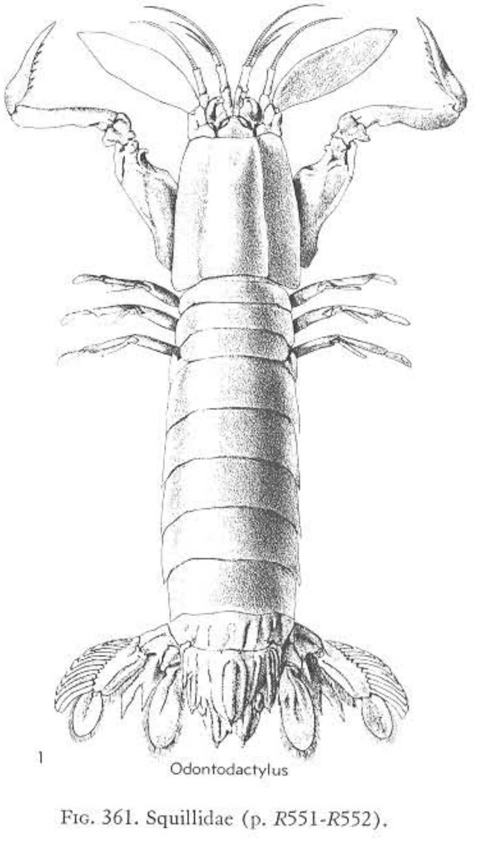
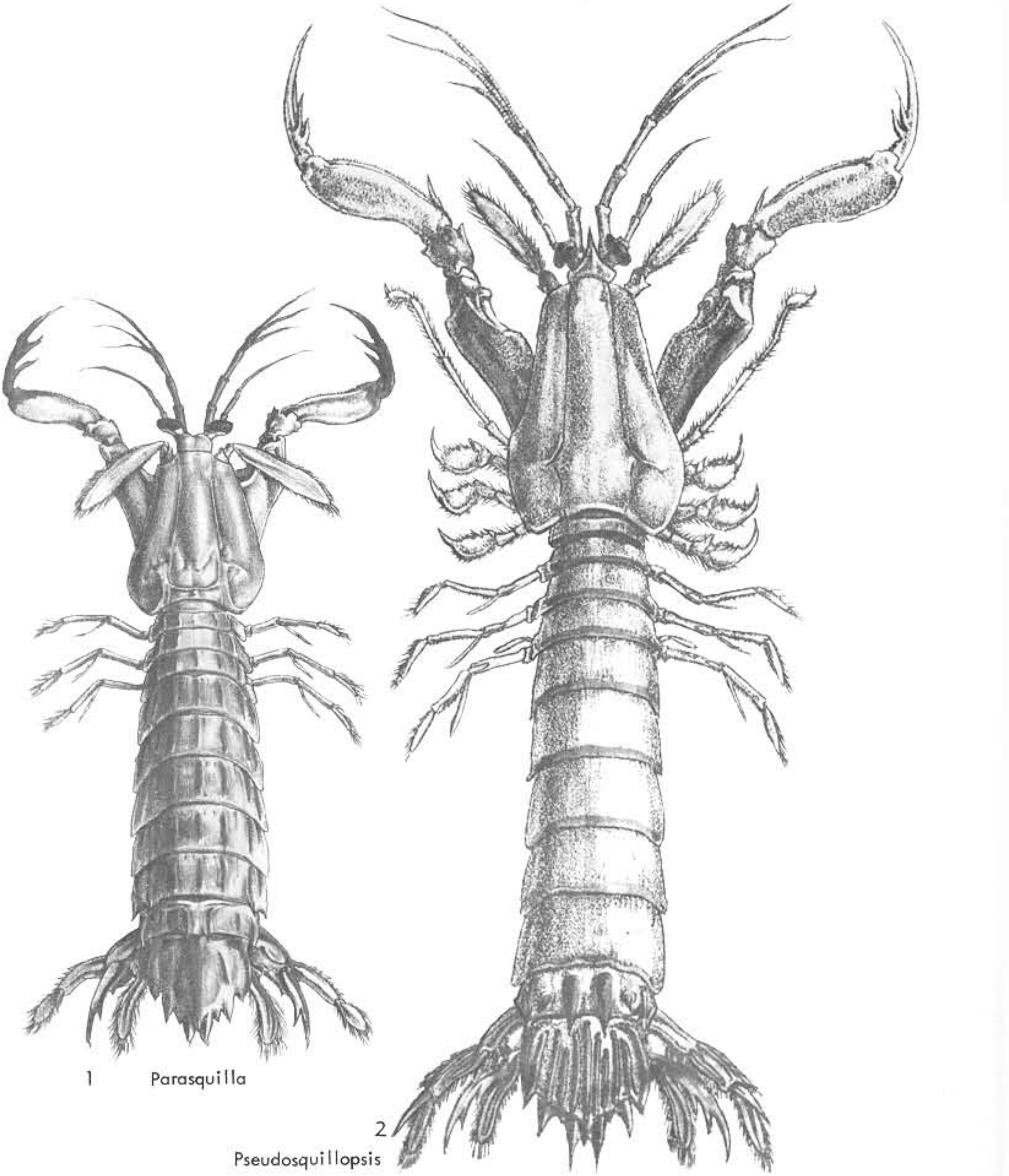


Fig. 361. Squillidae (p. *R*551-*R*552).

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, ×1 (208).

Heterosquilla MANNING, 1963, p. 320 [**Lysiosquilla platensis* BERG, 1900, p. 230; OD]. Closely resembling *Lysiosquilla* but telson with elevated median projection, variously armed. *Rec.*, circumtropic-subtropic.——FIG. 355,*2*. **H. platensis* (BERG), off Arg.; *2a*, dorsal, ×1.3; *2b*, raptorial claw, ×1.5 (225).

Hoplosquilla HOLTHUIS, 1964, p. 141 [**Gonodactylus acanthurus* TATTERSALL, 1906, p. 171; OD,



1 Parasquilla

2 Pseudosquillopsis

FIG. 362. Squillidae (p. *R*552).

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, ×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.); *Pontiobius* 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. ×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, ×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.——Fig. 360,*1.* *M. kempi* (Odhner), Ellice Is.; *1a,* ant. part of body, dorsal, mag. unknown; *1b,* post. part of abdomen, mag. unknown (218).

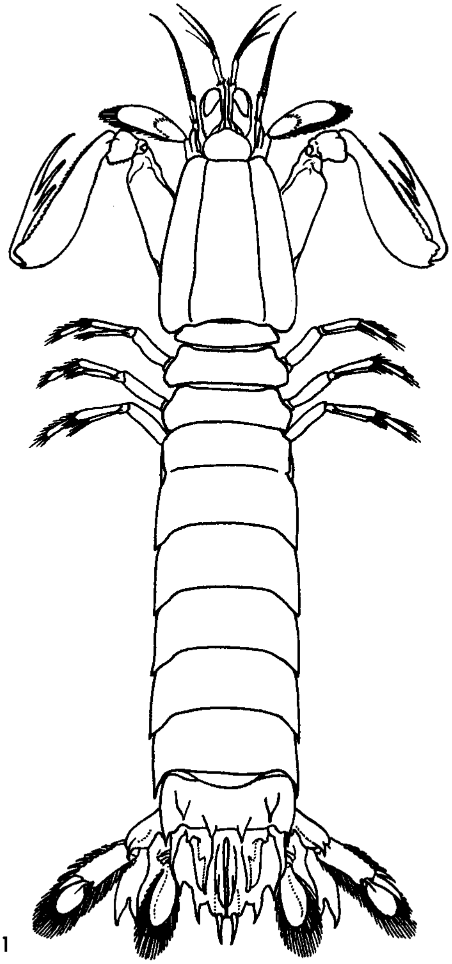


Fig. 363. Squillidae (p. *R*552).

Nannosquilla Manning, 1963, p. 318 [**Lysiosquilla grayi* Chace, 1958, p. 141; OD]. Size small; telson without median dorsal elevation but with marginal false eave under which true posterior armature is placed. *Rec.,* circumtropic-subtropic.——Fig. 355,*1.* **N. grayi* (Chace), off USA(Mass.); dorsal, ×3.75 (70).

Odontodactylus Bigelow, 1893, p. 100 [**Cancer scyllarus* Linné, 1758, p. 633; SD Bigelow, 1931, p. 144 (ICZN Official List, no. 731)] [=*Gamaris* H. S. (initials only), 1876, p. 275 (obj.; suppressed by ICZN, Official Index, no. 122); *Odontoerichthus* 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. ×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, ×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, ×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, ×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. ×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.(Tesnus F.),* USA(W.Tex.) *(Jour. Paleont.,* v. 29, p. 852-856, fig. 1-2, pl. 85-86). [Moore]

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CYCLOIDEA

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MORPHOLOGY

Carapace small, shieldlike, hemispherical, or helmet-shaped, truncated anteriorly; rounded, pointed or slightly indented posteriorly, calcified in many genera. Surface generally with a narrow median region delimited by grooves which converge posteriorly; one median and two or more lateral bosses in the frontal region; often with curved longitudinal or radial ridges and rows of granules on the surface.

The ventral surface is preserved only in Paleozoic forms. It shows a large triangular median plate which tapers posteriorly to a point about two-thirds of the length from the anterior end. Seven pairs of narrow, elongate, trapezoidal plates radiate from its sides (Fig. 363,A, *C*). It has been assumed that the trapezoidal plates represent the protopods of biramous legs (Fig. 363A,*A*). A pair of indistinct anteroventral structures or organs may correspond in subcircular shape and in position to a pair of bosses on the dorsal side. One pair of antennae (Fig. 363A,*B*) arises from the anterolateral angles of a truncated frontal margin. There is a lateral doublure of the carapace. No abdomen is known but short posteromedian appendages are interpreted as a telson and a pair of ovate furcal plates. Anterolateral circular orbits or compound eyes are found on some convex carapaces. In the shieldlike *Halicyne* an emargination of the anterior margin on either side of the frontal lobe may indicate the position of the eyes. The position of the mouth is not definitely known. According to Hopwood (1925) it was in front of the anterior edge of the large ventral median triangular plate and he interpreted a small anterior structure as a labrum and metastome.

Other authors consider the large plate as a labrum, and the small fusiform shield so interpreted by Hopwood could have been a rostral plate. Packard and Hopwood refer to a mud-infilled longitudinal tubular structure as possibly the alimentary canal.

The main distinctive characteristics are the small carapace which covers a head with one pair of antennae and in some forms sessile eyes; it is fused to a thorax with seven segments bearing legs which were probably biramous. Where present, the abdomen was reduced to a telson and a pair of furcal plates. The carapace is variously sculptured, mainly in the anterior re-

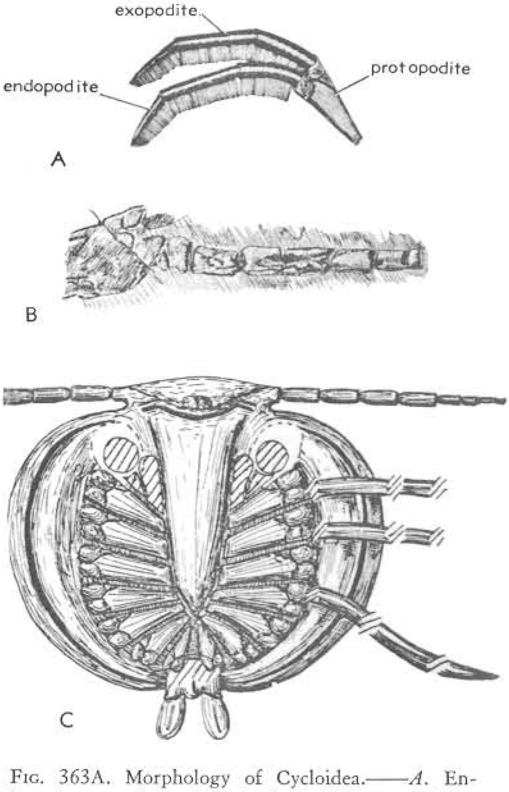

Fig. 363A. Morphology of Cycloidea.——*A*. Enlarged restoration of limb of Cycloidea, ×2.5(4).——*B*. *Cyclus (?) johnsoni* Woodward, base of antenna, ×2.5(4).——*C*. Reconstruction of the ventral side of Cycloidea, ×2 (referred to *Halicyne* by Hopwood) (4).

gion, and with the exception of a few almost evenly granulated forms, bears a median elevated region which tapers posteriorly.

AFFINITIES

The presence of antennae and the structure of the legs and caudal appendages (if interpreted correctly by HOPWOOD) suggest crustacean affinities but these small fossils cannot be assigned to any known group of Crustacea. Earlier investigators considered affinities with larval or adult Xiphosura or Eurypterida, which were suggested mainly by the radial arrangement of the ventral structures. Comparisons with trilobite larvae were also made and find some support in the presence of the glabella-like median elevation and the antennae, but fail in details. HOPWOOD concluded that *Cyclus* was to be included in the Branchiura but the resemblance of some of the flatter Cycloidea to the parasitic Branchiura is quite superficial and the presence of suction cups in the species described by him is unlikely. Closely related forms have a highly vaulted calcified carapace which does not suggest attached or parasitic habits. TRAUTH (1918) described Permian and Triassic forms as Decapoda Brachyura but they are clearly related to Cycloidea. GLAESSNER (1928) considered the possibility of their derivation from Phyllocarida as a result of benthonic (crablike) adaptation of these Malacostraca but the morphological similarities are only superficial. An origin from primitive swimming (possibly copepod-like) Crustacea through adaptation to benthonic life is perhaps more likely but fossil Copepoda of this age are unknown. The Cycloidea seem to have no known living or extinct relatives and their systematic position is uncertain.

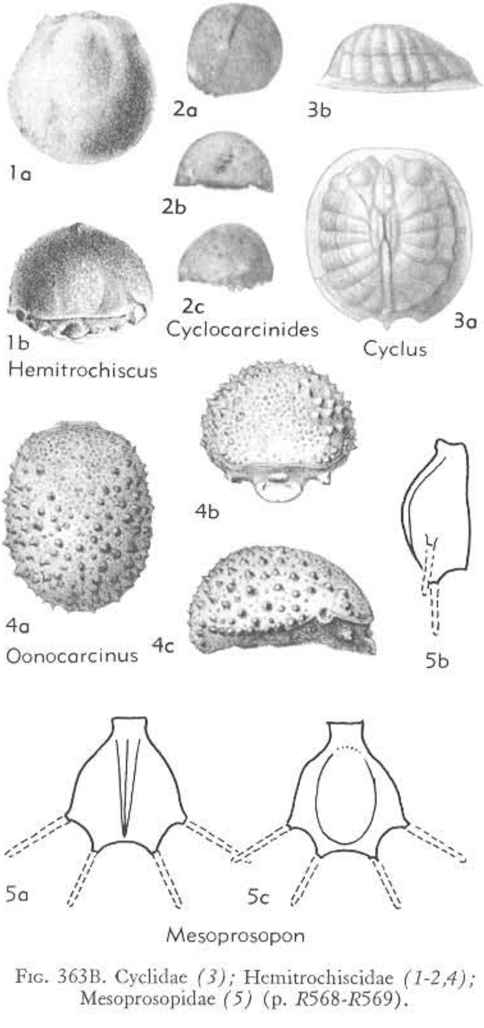

FIG. 363B. Cyclidae *(3)*; Hemitrochiscidae *(1-2,4)*; Mesoprosopidae *(5)* (p. R568-R569).

STRATIGRAPHIC AND GEOGRAPHIC DISTRIBUTION

The Cycloidea range from Lower Carboniferous to Upper Triassic. They are known from North America, Europe, and central Asia. They occur in marine and brackish-water sediments.

SYSTEMATIC DESCRIPTIONS

Class and Order UNCERTAIN

Superfamily CYCLOIDEA Glaessner, 1928

[*non* WHITEHOUSE, 1941]
[=Cyclina RICHTER, 1933 in DITTLER *et al.*]

Family CYCLIDAE Packard, 1885

Carapace small, outline circular or oval, dorsal surface shieldlike or highly convex,

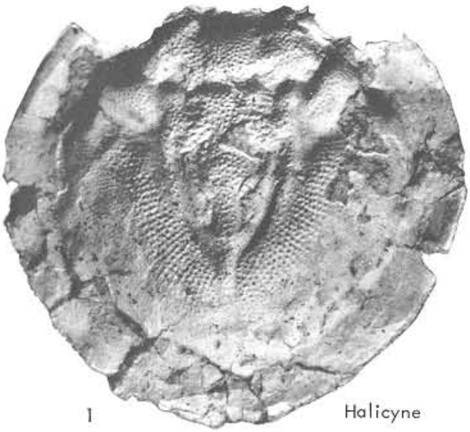

FIG. 363C. Cyclidae (p. *R*569).

with the highest point behind the center. A median region narrowed posteriorly, anteriorly there are a number of rounded bosses. Margin entire or denticulate. Lateral regions smooth, longitudinally keeled, or radially grooved. A single pair of transverse antennae attached laterally to the frontal region. Ventral side of cephalothorax with about seven radiating plates grouped around a large central plate which tapers posteriorly. [This is known only in few species]. *L.Carb.-U.Trias.*

Cyclus de Koninck, 1841 [**Agnostus ?radialis* Phillips, 1836; OD] [*non* Leach, 1815 (*err. pro Cyclas* Latreille, 1802), *nec* Jurine, 1817 *nec* Anton, 1837 (*err. pro Cyclas* Lamarck, 1798), *nec* Barrande, 1879] [=*Paraprosopon* Gemmellaro, 1890 (type, *P. reussi*)]. Carapace small, with oval or circular outline, cap- or helmet-shaped, with elevated median ridge narrowing posteriorly, and anterior and anterolateral bosses; with or without concentric and radial lateral ridges; surface finely granulated or smooth, margin smooth. Antennae attached laterally to frontal margin. Ventral side of cephalothorax with large median shield which tapers posteriorly, and ?7 pairs of radiating structures which may be bases of ?biramous legs. Small telson with lobate furcal appendages known in one species. [The flattened species formerly known as *Cyclus* were placed in *Halicyne* by Hopwood (1925); they do not conform with it and may have to be placed in a new genus.] *L.Carb.*, N.Eu.(Belg.-Eng.-Ire.-Ural)-C. Asia; *U.Carb.*, USA(Ill.-Kans.)-Eng.; *L.Perm.*, Eu.(Ural-Sicily).——FIG. 363B,*3*. **C. radialis* (Phillips), L.Carb., Belg.; *3a-b*, dorsal, lat. view, ×2 (8).

Carcinaspides Glaessner, herein [*nom. subst. pro Carcinaspis* Schafhäutl, 1863 (*non* Stimpson, 1858)] [**Carcinaspis pustulosus* Schafhäutl, 1863; OD]. Differing from *Halicyne* in pustulated surface and finely lobulate lateral and posterior margins of carapace. *U.Trias.*, Eu.(Alps).

Halicyne von Meyer, 1844 [**Limulus agnotus* von Meyer, 1838; OD]. Carapace moderately convex, shield- to helmet-shaped, outline truncated anteriorly and rounded posteriorly, with a posteromedian projecting point. Anterior part and median ridge with elevated bosses; surface smooth or granulated. Front truncated. Lateral margins sharp, smooth. *L.Trias.-U.Trias.*, C.Eu.-USA (Utah).——FIG. 363C,*1*. *H. ornata* Trümpy, M.Trias., Ger.; ×2 (7).

Family HEMITROCHISCIDAE Trauth, 1918

Carapace convex, with orbits and deflexed rostral plate. Surface sculpture consisting of granulation and denticulation, particularly on lateral margins, and weak grooves. *Perm.-Trias.*

Hemitrochiscus Schauroth, 1854 [**H. paradoxus;* OD]. Carapace very small, hemispherical, surface finely granulate, with weak median keel and demarcation of anterior regions. Frontal region marked off by transverse orbitofrontal line. Line of fine pointed granules follows lower margin. *U.Perm.*, Eu.(Ger.).——FIG. 363B,*1*. **H. paradoxus*, U.Perm., Ger.; *1a,b*, ×1 (1).

Cyclocarcinides Glaessner, herein [*nom. subst. pro Cyclocarcinus* Stolley, 1914 (*non* Guérin-Méneville in Duperry, 1838)] [**Cyclocarcinus serratus* Stolley, 1914; OD]. Carapace small, hemispherical, surface finely granulate, regions not or very faintly marked. Front and orbits as in related genera. Lateral and posterior margins denticulate. *U.Trias.*, Eu.(Alps-Carpath.-Bosnia).——FIG. 363B,*2*. **C. serratus* (Stolley), U. Trias., Alps; *2a-c*, dorsal, ant., left lat. view, ×2 (6).

Oonocarcinus Gemmellaro, 1890 [**O. insignis;* SD Glaessner, herein]. Carapace up to 33 mm. long, ovoid. Surface with weakly delimited median and anterior regions and granulated sculpture. Orbitofrontal line and lateral denticulate keels well developed. Front deflexed, with lateral projections, orbits circular. *Perm.*, Eu.(Sicily); *U. Trias.*, Eu.(Alps-Carpath.).——FIG. 363B,*4*. **O. insignis*, Perm., Sicily; *4a-c*, dors., ant., right lat. view, ×1 (2).

Family MESOPROSOPIDAE Glaessner, 1928

[*nom. correct.* Glaessner, herein (*pro* Mesoprosoponidae Glaessner, 1928)]

Carapace pear-shaped in outline, narrow in front, widening posteriorly, with paired posterior and posterolateral spines. *Trias.*

Mesoprosopon Stolley, 1914 [**M. triasinum;* OD]. Characters of family. *U.Trias.(Nor.),* Eu.(Aus.).——Fig. 363B,*5*. **M. triasinum,* U.Trias., Aus.; *5a-c,* dorsal, right lat., ventral view, ×2 (6).

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See Addendum to Cycloidea (p. *R*629).

BOSTRICHOPODIDA

By Gerhard Hahn

[Freie Universität, Berlin, West Germany] [Materials for this order prepared by Gerhard Hahn, submitted December, 1965, revised October, 1967]

Class and Order UNCERTAIN

Order BOSTRICHOPODIDA Hahn, 1967

[*nom. correct.* Hahn, herein (*pro* Bostrichopida Hahn, 1967)] [=Mastigomyrii Steinmann, 1929 *(partim)*]

Bostrichopus (the only known genus) shows the features of a metanauplius larva: body divided in a nonsegmented cephalon with three pairs of appendages (antennules, antennae, mandibles), and a short segmented pereion without observed appendages. Cephalon with large triangular, apically situated, serrate-edged rostrum, two deep, crescentic grooves unknown as to function, and insertions of paired appendages. Antennules (visible only on negative impression of single known specimen) short, uniramous, with paired, leaflike terminal segments. Antennae biramous, with medium-sized pro-

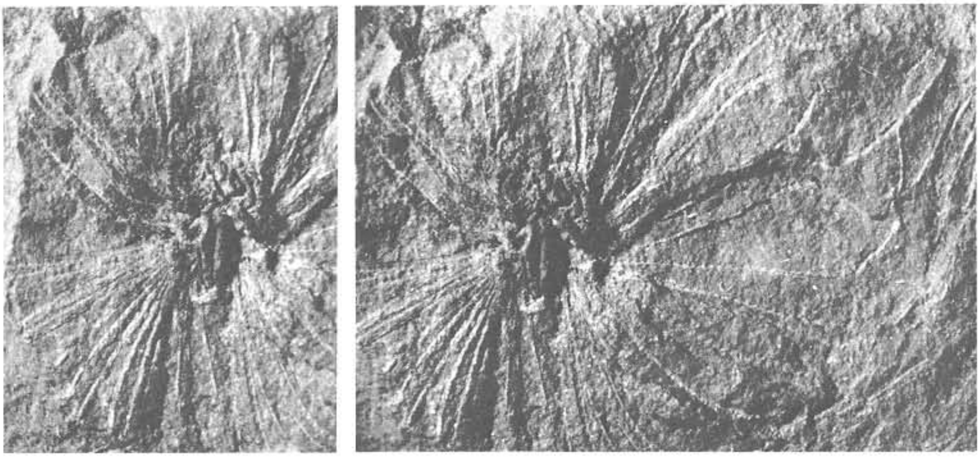

FIG. 363D. Bostrichopodidae (p. *R*571).

topodite, long forward-bent exopodite, and short endopodite; exopodite with about ten long, segmented, whiplike appendages (three times as long as body), which are attached serially; endopodite with two similarly constructed appendages. Mandibles with stout base (possibly divided into exopodite and endopodite) and bearing about 20 appendages, which are attached side by side. Pereion with five or six somites, interpreted to be first thoracomeres split off by the nauplius-body. [Only the ventral side of *Bostrichopus* is known.] *L.Carb.*

Bostrichopus antiquus is a very unique little arthropod (length of body, 3.3 mm.; total length with appendages, 13.0 mm.). Its long, flexible appendages separate this arthropod from most other known crustaceans; its short, scarcely segmented body accentuates this exceptional position. Therefore, in the first-published description (Goldfuss, 1838) *Bostrichopus* was interpreted as a crustacean of unknown systematic position, perhaps belonging to the Cirripedia. In decades subsequent to 1838 many authors discussed the systematic placement of the genus, postulating its inclusion among crustaceans, chelicerates, annelids, or representing an entirely new class of arthropods. All used the old, partly incorrect figures given by Goldfuss.

In 1929 Steinmann revised *Bostrichopus* and gave a new interpretation of it as a forerunner of some myriapods. He classified it with Notostigmophora in the "Stamm Mastigomyrii," which is a complete misinterpretation. *Bostrichopus* shows no affinities with any myriapods and the group "Mastigomyrii" is an unnatural unit which cannot be used in systematics. The revision by Hahn (1967) showed that *Bostrichopus* can be understood best as a larval crustacean. It is either a real metanauplius larva of an unknown adult or a neotenic form which failed to complete its transformation. Placement among the Malacostraca is indicated by the divided terminal segments of the antennules, for such divided antennules are found in some other malacostracan groups.

Comparable fossils are *Marria* Ruedemann, 1931, and *Paramarria* Wells, 1944, the first tending to be a metanauplius and the second a nauplius. Other than the common metanauplius features no close relations between *Bostrichopus* and *Marria* can be discerned, because *Marria* shows neither antennules nor rostrum, nor crescentic grooves, and the appendages are differently constructed in the two genera. A detailed description and interpretation of *Bostrichopus* has been given by Hahn (1967).

Family BOSTRICHOPODIDAE Hahn, 1967

[*nom. correct.* Hahn, herein (*pro* Bostrichopidae Hahn, 1967)]

Characters of order. *L.Carb.*

Bostrichopus Goldfuss, 1838, p. 27 [**B. antiquus;* M]. Characters of family. [*Bostrichopus* is known only from the type species and from a single specimen of it which shows the ventral side of the

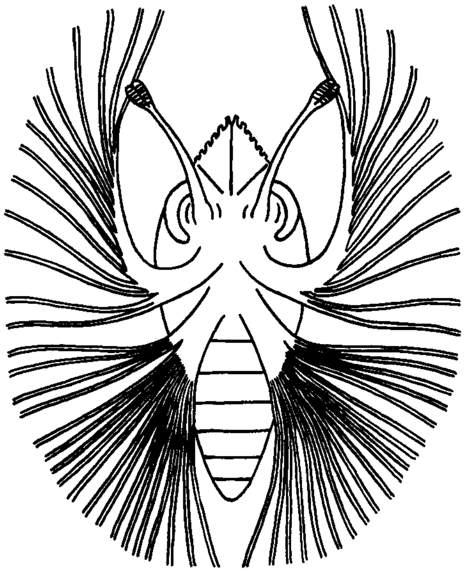

FIG. 363E. Bostrichopodidae (p. *R*572).

animal in positive and negative impressions, produced by splitting the slab. The specimen is kept in the Paleontological Institute at the University of Bonn, Germany.]——FIG. 363D-E. **B. antiquus;* 363D, stereoscopic view of ventral side, positive slab, ×7; 363E, ventral view of body and proximal part of appendages (reconstr.), ×15 (both Hahn, 1967).

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MYRIAPODA, EXCLUSIVE OF INSECTA

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[Chapter submitted July, 1965]

CONTENTS

INTRODUCTION

Species of the group Myriapoda are terrestrial, in part fossorial arthropods, and are only rarely recovered as recognizable fossils. Moreover, since modern systems of classification rely heavily upon configuration of the mouth parts and sperm transfer apparatus of the males, it is not surprising that our knowledge of extinct forms (particularly those of the Paleozoic) is unusually deficient. The following account of the myriapods can be represented only as an introduction to the state of our ignorance of the subject.

Even Recent species are perhaps less known than any other group of animals of comparable size. Most myriapods are of little or no economic importance; they tend to be cryptic in habits and are rarely seen; and most of them adhere closely to a few basic characteristic plans of body form. Taxonomic characters in all of the groups are subtle and subjective. For these reasons, only a handful of systematists have worked extensively on myriapods, with the result that the classification, even of higher categories, is far from satisfactorily arranged.

Numerous classifications of the Arthropoda proposed in recent years offer arrangements of the various classes to suit almost any taste. The first "modern" system of myriapodous forms was published by R. I. POCOCK in 1893, and has not been much improved upon subsequently. Prior to POCOCK's time (and again more recently) the name Myriapoda was used as a category of rank equal to the Insecta, Crustacea, and Arachnida, and was therefore involved in an unwarranted separation of the myriapodous and hexapodous arthropods. POCOCK recognized five classes of these animals grouped in two higher-rank assemblages, as follows:

Major Divisions of Myriapoda according to Pocock, 1893

PROGONEATA
  Class Pauropoda
  Class Diplopoda
  Class Symphyla

OPISTHOGONEATA
  Class Chilopoda
  Class Insecta

The primary basis for this dichotomy, which was the nature of the opening of the reproductive system, has come under attack in recent decades, chiefly in papers by TIEGS and SNODGRASS, who consider this character to have only secondary importance. Although much of the disagreement is well justified, it should not be overlooked that the Progoneata and Opisthogoneata of POCOCK do associate classes that appear to be closely related on grounds of overall basic morphological similarity. [Few well-informed students of the arthropods will deny that chilopods are more similar to primitive insects than either is to diplopods, and I can find no justification for recognition of a group Myriapoda that excludes the six-legged forms.]

On the basis of his studies of the embryogeny of pauropods, symphylans, and insects, TIEGS (1947) proposed that myriapodous arthropods be grouped on the basis of mouthpart structures, particularly the number of gnathal segments involved in the head. His arrangement of assemblages is as follows.

Major Divisions of Myriapoda according to Tiegs, 1947

MONOGNATHA [hypothetical grade
  (no known representatives)]
DIGNATHA
  Pauropoda
  Diplopoda
TRIGNATHA
  Chilopoda
  Labiata (Symphyla+Insecta)

Aside from altered position of the Symphyla, this grouping does not differ radically from that of POCOCK, and may seem to be satisfactory in its inclusion of Chilopoda and Insecta in a common group. However, other varieties of arrangement can be achieved by the selection of other characters for primary emphasis. A recent paper by HUBERT FECHTER (1963) advocates the following dichotomy based on characters of the preoral (buccal) cavity.

Clearly, a satisfactory arrangement of the various myriapod classes cannot be based upon the evaluation of a single character, but needs to take account of all structural features considered collectively.

Major Divisions of Myriapoda according to Fechter, 1963

PREORAL CAVITY WITH SINGLE PAIR OF MOUTH PARTS
  Diplopoda
  Pauropoda
  Chilopoda
PREORAL CAVITY WITH TWO PAIRS OF MOUTH PARTS
  Symphyla
  Insecta

The two groups named Diplopoda and Chilopoda have long been known. Members of both were included by LINNÉ (1758) in his "order" Insecta aptera. The name Myriapoda was proposed by LATREILLE (1796) as an order of the Insecta, and it included not only myriapods as currently known, but also isopod crustaceans that bear a superficial resemblance to various Diplopoda. In 1800, CUVIER divided the previously distinguished group of "Insecta" into Insecta and Crustacea; in the following year LAMARCK added the class Arachnida, of correlative rank. LATREILLE in 1802 recognized the Myriapoda as a subclass which included the orders Chilognatha (=Diplopoda) and Syngnatha (=Chilopoda), as well as the Crustacea. In 1814, W. E. LEACH elevated the Myriapoda to the rank of class, corresponding to the assemblages called Crustacea, Arachnida, and Insecta by earlier French specialists, and this concept of the myriapods persisted until 1887, when it was dismembered by POCOCK.

Symphylids were known scientifically as early as 1839, but they suffered a long obscurity in the status of aberrant chilopods and were not accorded ordinal rank until 1880, by J. A. RYDER. Pauropods were quite unknown until 1865, and were given ordinal status (by implication at least) by their discoverer, Sir John LUBBOCK, in 1866. Members of these two groups are among the smallest of the Arthropoda and are known so far only from Recent species.

As the fossil records of all myriapod groups are still so deficient, any speculation concerning their mutual phylogenies must be based upon knowledge of living forms.

This area has provided a fertile field for investigation, and is treated elsewhere in this volume (MANTON, p. *R*42). For present purposes it seems sufficient to remark that two main groups can be recognized—one progoneate, with members basically vegetarian, and the other mostly opisthogoneate, with more primitive members at least tending to be carnivorous. Of the latter group, the similarity of symphylans to japygid insects is notable, and the mouth parts of all chilopods, symphylans, and primitive insects are formed upon a basically similar plan. The evolution of these myriapodous groups must have occurred with astonishing rapidity during the Early Devonian, probably contemporaneously with development of the primitive land plants.

Virtually the sum of our present knowledge of fossil myriapods stems from the early work of S. H. SCUDDER during the 1880's and of ANTON FRITSCH about a decade later. Both of these workers were competent paleontologists; SCUDDER, in addition, was an authority on many orders of extant insects. Neither, however, can be considered very conversant with the classification of Recent myriapods. Many reconstructions of fossil forms published by SCUDDER and FRITSCH are more conjectural, in my opinion, than the material available to them can justify. An attempt has been made by VERHOEFF (1926) to integrate the work of FRITSCH into classification of Recent forms, but VERHOEFF did not restudy any fossil material, and his new names and groups are therefore no better than accounts in the original literature. Clearly nothing very satisfactory will ever be done until some specialists on living forms can restudy the old collections and also a large amount of new specimens in better condition than usual. Most of the known fossil species derive from Upper Carboniferous beds of Late Pennsylvanian age, but a fair number have been found also in the Baltic amber. So far as I know, no discoveries of Mesozoic myriapod species have been reported. The scattering of Devonian specimens suggests diplopod-like creatures at that age, but they are so poorly preserved that it is difficult to determine any critical characters.

Generic names incorrectly referred to the Myriapoda and invalidly proposed family-group names for myriapods are cited at the end of this chapter.

GENERAL CHARACTERS OF MYRIAPODA

The myriapods are exclusively terrestrial arthropods distinguished by division of the body into a head and trunk, with the head bearing a single pair of antennae and the trunk showing apparent gradation of components from a series of similar metameres at one extreme to a well-separated trisegmented thorax and multisegmented abdomen. The appendages are uniramous at all stages of growth and evolution, primitive forms generally having coxae with endite lobes. Respiration is by means of trachea or in small forms by exchange of gas directly through the body wall.

Specialists concerned with study of the Arthropoda now are mostly agreed that members of this assemblage are divisible into two divergent groups. This is now evident enough to lead to an attack on the homogeneity of the so-called phylum and renewal of spirited controversy such as occurred in the late 1890's. There is indeed reason to suspect that the so-called "chelicerates" and "mandibulates" may not have had a common arthropodan ancestral form, and those who insist upon phylogenetic purity may wish to dismember the arthropods into two phyla of similar features but separate ancestry. The proposal and acceptance of such an arrangement would of course affect the grades of classification within each phylum to some extent. My own inclination at the present is to regard the myriapodous arthropods as a superclass of the subphylum Mandibulata equivalent in rank to the Crustacea, giving the following arrangement of major categories.

Major Divisions of Arthropoda

- Subphylum MANDIBULATA
  - Superclass Crustacea (or Branchiata)
  - Superclass Myriapoda
    - Class Archipolypoda
    - Class Diplopoda
    - Class Pauropoda

Class Symphyla
Class Chilopoda
Class Insecta (or Hexapoda)
Subphylum CHELICERATA (accorded this rank in *Treatise* Part P)

The occasion is taken here to express disagreement with a recently published proposal (VANDEL, 1949) to combine all of the nonhexapodous groups into a single class Myriapoda, the Insecta being regarded as a separate group of equivalent rank.

Restoration of an Upper Carboniferous assemblage of myriapods from Bohemia is given in Figure 385, p. *R*605.

CLASSIFICATION

In the systematic treatment to follow, only groupings having pre-Pleistocene representation are included. Although considerable disagreement currently exists among specialists concerning Recent orders and their limits, I offer an overall classification of the main groups of myriapods carried as far as orders. This shows an arrangement of the Diplopoda that differs from earlier classifications in placing greater emphasis on certain groups and considerably less weight on others.

A discussion of various ordinal classification of the Diplopoda has recently been published by CHAMBERLIN & HOFFMAN (1958), who introduced a new set of names. So many different ordinal names have been proposed for the same groups of animals that adoption of a uniform ending seemed to be the best solution. In general, the proposal of "-ida" endings for diplopod orders has been accepted by the majority of students of this class. Extension of the arrangement into the Chilopoda has met with less approval, partly because of a smaller multiplicity of alternative names applied to orders of this class.

The following list is noteworthy for its lack of such categories as suborders, superfamilies, and the like. Study of the classification of "myriapods" is yet in its infancy, and many years will pass before an adequate system can be worked out.

Major Divisions of Myriapoda

- MYRIAPODA *(superclass). U.Sil.-Rec.*
  - ARCHIPOLYPODA *(class). U.Sil.-Penn.*
    - Euphoberiida *(order). U.Sil.-Penn.*
  - DIPLOPODA *(class). Penn.-Rec.*
    - Penicillata *(subclass). Oligo.-Rec.*
      - Polyxenida *(order). Oligo.-Rec.*
    - Pentazonia *(subclass). Penn.-Rec.*
      - Glomeridesmida *(order). Rec.*
      - Glomerida *(order). Oligo.-Rec.*
      - Amynilyspedida *(order). Penn.*
    - Helminthomorpha *(subclass). U.Penn.-Rec.*
      - Spirobolida *(order). U.Penn.-Rec.*
      - Stemmiulida *(order). Rec.*
      - Polyzoniida *(order). Oligo.-Rec.*
      - Siphonophorida *(order). Rec.*
      - Julida *(order). ?Eoc., Oligo.-Rec.*
      - Spirostreptida *(order). ?Penn., Rec.*
      - Callipodida *(order). Oligo.-Rec.*
      - Platydesmida *(order). Rec.*
      - Chordeumida *(order). Oligo.-Rec.*
      - Polydesmida *(order). Oligo.-Rec.*
  - PAUROPODA *(class). Rec.*
    - Pauropodida *(order). Rec.*
  - SYMPHYLA *(class). Oligo.-Rec.*
    - Scolopendrellida *(order). Oligo.-Rec.*
  - CHILOPODA *(class). Cret.-Rec.*
    - Anamorpha *(subclass). Oligo.-Rec.*
      - Scutigerida *(order). Oligo.-Rec.*
      - Lithobiida *(order). Oligo.-Rec.*
    - Epimorpha *(subclass). Cret.-Rec.*
      - Geophilida *(order). Cret.-Rec.*
      - Scolopendrida *(order). Oligo.-Rec.*
  - INSECTA *(class).*

SYSTEMATIC DESCRIPTIONS

Superclass MYRIAPODA Latreille, 1796

Mandibulate terrestrial arthropods with body divided into head and trunk, latter showing all gradations from series of similar metameres to distinction into trisegmented thorax and multisegmented abdomen. Single pair of antennae; appendages uniramous at all stages, usually with coxal endite lobes in the primitive forms. Gas exchange by trachea or in small forms directly through the body wall. *U.Sil.-Rec.*

Class ARCHIPOLYPODA Scudder, 1882

[=Macrosterni FRITSCH, 1899; Palaeocoxopleura VERHOEFF, 1928]

Extinct Paleozoic myriapods apparently similar to Diplopoda but with segmental elements much less coalesced, prozonites retaining medially divided sternum with pair of legs. Head apparently larger than body segments, and provided with large compound eyes. Characters of mouth parts and location of gonopore unknown. *U.Sil.-Penn.*

Our knowledge of the morphology of this group is very deficient, yet collectively the scraps of information seem to indicate animals of a nature quite different from the Diplopoda. There is some reason to suspect that at least several of the species may have been aquatic or semiaquatic. The larger forms of *Acantherpestes* are commonly used in textbooks to illustrate "giant, spined, Paleozoic myriapods" and in his 1882 monograph, SCUDDER provided an impressive, if conjectural, life-size reconstruction of a specimen crawling up a plant stem. Most if not all of the American material comes from ironstone nodules of the Mazon Creek beds (M. Penn.) of Illinois. I have reexamined many of SCUDDER's original specimens (now in the Harvard University Museum of Comparative Zoology), and have been unable to see very much in the way of detailed structure. FRITSCH's specimens in carbonaceous shale apparently are in much better condition and should be restudied. In proposing the name Palaeocoxopleura for this group, VERHOEFF (1928) suggested that the broad sterna might be due to a fusion of the sternites with pleurites. It seems equally reasonable to postulate fusion of pleurites with tergites, a common condition among diplopods.

Probably more than one family should be recognized for genera referred here to this class and order. There is some doubt that the genus *Palaeosoma* belongs here, for the allocation merely follows the original placement of its type-species in *Acantherpestes.*

SCUDDER originally included three families (Archidesmidae, Euphoberidae, Archijulidae) in the Archipolypoda. Of these, I cannot allocate the Archidesmidae with confidence to either to Archipolypoda or Diplopoda, and prefer temporarily a status of "*incertae sedis*" for its two genera. The Archijulidae (the type genus of which was spelled "*Archiulus*") seems to me to represent perfectly typical juliform Diplopoda. Finally, a part of SCUDDER's original Euphoberiidae has been removed to the diplopod subclass Pentazonia, making up there the order Amynilyspedida.

Unquestionably, thorough revision of the Archipolypoda is one of the most urgently needed tasks remaining in arthropod paleontology, as these forms stand at the base of the radiation of terrestrial mandibulates.

Order EUPHOBERIIDA Hoffman, new order

[*nom. correct.* HOFFMAN, herein (*pro* Euphoberidae SCUDDER, 1882)]

Characters of class. *U.Sil.-Penn.*

Family EUPHOBERIIDAE Scudder, 1882

Head wide, with large oval ocellaria composed of many small ocelli; collum segment presumably present; first three body segments very short, each with single pair of legs; following segments seemingly diplosomites with single dorsal tergite, but with separate pleural and sternal elements on prozonites and metazonites, both subsegments with pair of legs; tergites with prominent erect spines, commonly forked. *U.Carb.(Penn.)*

Euphoberia MEEK & WORTHEN, 1868, p. 26 [**E. armigera*; OD]. Metatergal spines slender, curved, simple or irregularly forked; sternal spines simple; legs not distally compressed; prosterna short, without stigmata, metasterna longer and with stigmata present; coxae apparently without exsertile coxal sacs. *U.Carb.*, Eu.(Czech.); *Penn.*, N.Am.——FIG. 364,*1*. *E. histrix* FRITSCH, Czech.; diplosegment (reconstr.), ×4 (after Fritsch).

Acantherpestes MEEK & WORTHEN, 1868, p. 559 [**A. major*; OD, M]. Terga with 2 or 3 rows of stout, regularly forked spines; exsertile coxal sacs apparently present; some posterior legs said to be strongly compressed and laminate. *Penn.*, N.Am.-Eu.——FIG. 365,*1*. **A. major*, USA(Ill.); *1a*, entire animal, ×0.5; *1b,c*, ventral side of segmental fragment and spine, ×2 (after Scudder).——FIG. 365,*2*. *A. gigas* FRITSCH, Czech.; head and anterior segments, dorsal view (reconstr.), ×1 (after Fritsch).

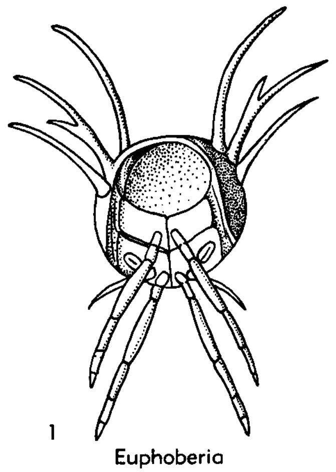


FIG. 364. Euphoberiidae (p. *R*577).

Chonionotus JORDAN, 1854, p. 12 [**C. lithanthraca*; OD, M]. [Apparently similar to *Acantherpestes*, but I have been unable to consult the original description and can give no diagnosis. If SCUDDER (1885, p. 729) is correct in suspecting the names to be synonyms, *Chonionotus* has 14 years priority over *Acantherpestes*.] *Penn.*, N.Am.

Palaeosoma JACKSON & BRADE-BIRKS, 1919, p. 410 [**Acantherpestes giganteus* BALDWIN, 1911; OD]. Segments numerous, flattened dorsally, with lateral expansions and bearing lateral spines; sternites large, prozonite distinctly shorter element; 2 pleurites on each side of segments. *U.Carb.*, Eu.

Family UNCERTAIN

The following four genera, all but one described by PEACH from Upper Silurian and Lower Devonian strata of Scotland, are presumably referable to the Archipolypoda. PEACH (1882) set up a family Archidesmidae for *Archidesmus* and *Kampecaris*, which, if correctly founded, may include also the somewhat later *Anthracodesmus*. *Pattonia* appears to be distinctly different, but the structural details of all these nominal genera are not very well preserved and revision of the available material is much needed.

Anthracodesmus PEACH, 1898, p. 121 [**A. macconochiei*; OD, M]. *L.Dev.*, Eu.(Scot.).

Archidesmus PEACH, 1882, p. 182 [**A. macnicoli*; OD, M]. *U.Sil.-L.Dev.*, Eu.(Scot.).

Kampecaris PAGE, 1856, p. 135 [**K. forfarensis*; OD, M]. *L.Dev.*, Eu.(Scot.).

Pattonia PEACH, 1898, p. 115 [**P. couttsi*; OD, M]. *L.Dev.*, Eu.(Scot.).

Class DIPLOPODA Gervais, 1844

[=Chilognatha LATREILLE, 1802]

Terrestrial, tracheate, oviparous, anamorphic Arthropoda characterized by development of compact head with pair of short, simple, eight-jointed antennae, powerful mandibles, and subbuccal gnathochilarium formed from embryonic maxillary elements. Head followed by variable number of postcephalic segments, without distinct separation into thorax and abdomen, each segment appearing to be an anatomical diplosomite, composed of two embryonic somites almost completely fused during ontogeny, most diplosomites retaining two pairs of seg-

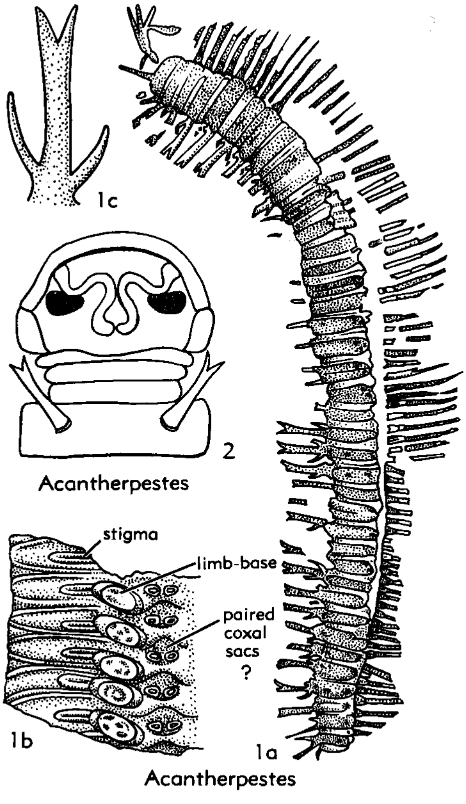


FIG. 365. Euphoberiidae (p. *R*577-*R*578).

mented appendages, except for those immediately behind head where anterior pair of each segment may be completely suppressed except for remnants of its internal musculature. Body wall typically impregnated with calcium carbonate, except during and following molting; segments composed of variable number and arrangement of sclerites (tergites, pleurites, sternites) as discussed below, primitive condition marked by retention of sclerites separated by flexible sutures or open membraneous areas. Most species adapted for rolling into spiral or flat coil or compact sphere, dorsal areas of segments therefore almost universally much longer than ventral; anterior third or half of each segment normally telescoped into posterior part of preceding segment. Typically each abdominal segment containing pair of complex glands that secrete volatile poisonous liquid. *Penn.-Rec.*

Respiration in the Diplopoda occurs by means of a system of profuse fine tracheae opening through stigmata near bases of the legs.

Nutrition basically is by the ingestion of dead vegetable material, but rarely animal food may be taken. The digestive tube is essentially straight and unmodified, beginning with a preoral buccal cavity, followed by an esophagus opening into the mid-gut, into which the Malpighian tubules discharge. The hind-gut is set off by a prominent sphincter-type valve and consists of two subdivisions with highly convoluted linings. The mid-gut alone is derived from endoderm, the esophagus and pharynx being stomodeal in origin and the hind-gut proctodeal. In species of the subclass Pentazonia the gut may be looped into an S- or N-shaped coil. The anal opening is located in the terminal segment and closed by two tightly fitting anal valves or periprocts.

Reproduction is by external development of internally fertilized eggs. The sexes are separate and the opening of the reproductive systems is located in or just behind the coxae of the second pair of legs in both males and females. Mating is achieved by prolonged clasping of the female, and apparently no courtship behavior has been developed in the class. Spermatic masses are extruded beforehand from the male seminal openings onto the gonopods (modified appendages from the seventh segment) from which spermatic material is then transferred into seminal receptacles in the cyphopods (specialized structures terminating outer ends of the oviducts). In pentazonoid forms, the gonopods are not developed, and the male achieves spermatophore transfer with his mouth parts. Eggs vary greatly in size and number, and are accorded different treatment in various groups; they may be laid in clusters and brooded by one of the parents, scattered singly in humus environments, or enclosed in an igloo-shaped mud nest built by the mother. The young usually hatch with three pairs of legs, and pass through anamorphic growth stages (usually seven), with segments and legs added at each molt (number depending upon the species). Segmentation is teloblastic, the proliferation zone being located in the penultimate segment. Development is gradual, hemimetabolous in nature, without major changes in structure or appearance, and may require a year or more for maturity. Mating usually takes place shortly after the final molt into sexual maturity. Neoteny is unknown, and seems improbable in the group, although males of several families alternate mature, reproductive phases with periods of apparent regression into an immature condition.

EXTERNAL CHARACTERS

In Diplopoda the head is normally a solid, compact capsule composed of five or six embryonic somites (the number still not finally established) closed laterally by large and powerful mandibles and ventrally by a **gnathochilarium** formed by the fusion of various maxillary elements. The head contains a pair of simple antennae and usually photoreceptor structures in the form of ocelli that may be single or grouped into an ocellarium on each side of the head. The rear of the head capsule usually is partly closed on each side by occipital processes for muscle attachment. Diplopods are normally hypognathous, with the head directed ventrally.

Usually no definite subdivisions of the cranium can be distinguished, but topographically a number of regions are referred to (Fig. 366,*1*). The ventralmost front edge, called the labrum, usually is notched medially and provided with a submarginal row of labral setae; in some species the labrum may be elevated or of a different texture from the remainder of the head. Also, in some forms a median vertical suture in the labral region is the external reflection of the epipharynx within. Just dorsal to the labrum a surface referred to as the clypeus extends upward as far as the antennal sockets in front and laterally from the labrum one can distinguish the subantennal genae. Some writers set off the upper half of the clypeus as the frons, but the division is highly subjective. The topmost area of the head, termed the epicranium, normally carries a definite median epicranial suture that extends down to a point between the antennae; this suture is the external reflection of a median internal septum upon which the mandibular muscles originate.

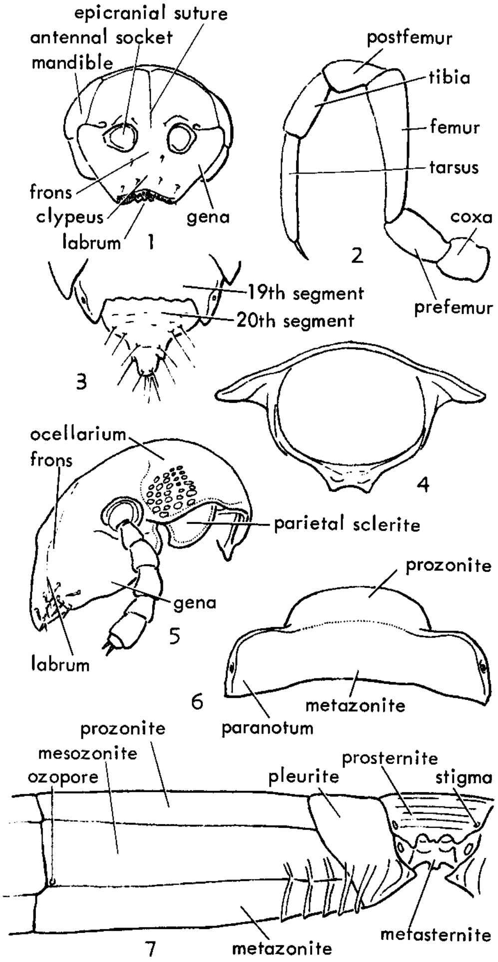


FIG. 366. External structural features used in classification of Diplopoda (Hoffman, n).——*1*. Head of generalized polydesmoid, anterior aspect, ×7.——*2*. Ambulatory leg of generalized polydesmoid, ×7.——*3*. Ultimate and penultimate segments of polydesmoid, dorsal aspect, showing modification of 20th segment into triangular epiproct, ×7.——*4*. Mid-body segment of polydesmoid, posterior aspect, legs omitted, showing lateral projection of pleurotergite into paranota, ×8.——*5*. Cranium of spiroboloid, appendages removed, oblique anterior-lateral aspect, ×8.——*6*. Mid-body segment of polydesmoid, dorsal aspect, ×8.——*7*. Mid-body segment of spiroboloid, tergal sclerites represented as flattened, showing characteristic arrangement of 3 tergal bands with a single pleurite on each side and 2 imbricate sternites, ×5.

The lateral edges of the cranium are notched on each side next to the antennal sockets for reception of outer ends of the suspensors of the internal "tentorium." In the order Polydesmida, these notches are very deep and the suspensors are thus isolated from the cranial margin; for many years they have been misinterpreted as sensory organs. In some orders, just behind the suspensorial notch is a distinctly marked element named the parietal sclerite which perhaps may represent a pleural remnant of one of the cranial somites. In most diplopods the parietal sclerite is present only as a lateral lobe of the surface.

True sensory organs occur in several orders (Chordeumida, Callipodida, Stemmiulida) as distinct, convex, pearl-like structures located near the true ocelli. In the Pentazonia, a prominent, deep, horseshoe-shaped sensory organ typically occurs lateral to the antennal sockets (Fig. 366, *1, 5*); both of the described types have been identified as the "Tömösvary organ," such as occurs also in chilopods, but the structure seems so utterly different that I doubt the homology to be a correct one.

In diplopods generally, the antennae are composed of eight segments or antennomeres, which are generally similar in appearance except for differences in relative length and width. The seventh usually is shortest and the eighth is sunk into its distal end. The eighth antennomere bears a variable number of small conical sensory structures, presumably olfactory in nature, the customary number being four but in some 20 or more. In cursorial, quick-moving forms the antennae are always much longer and more slender than in fossorial or slow-moving species. In many the distalmost antennomeres may be specially thickened or provided with sensory trichobothria or sensory pits or both.

Light-sensitive structures are limited to simple convex or nearly flat ocelli, usually pigmented, located on the sides of the epicranium. Ocelli are present in most diplopod orders but are absent altogether from the largest (Polydesmida) and may be randomly suppressed in cavernicolous or subterranean species in other orders. When present, they may be arranged in a single row or in a cluster of variable size and shape (but usually ovoid or subreniform) containing up to 50 or 60 ocelli; for such a composite feature the name "ocellarium" has been proposed as a substitute for the incorrect but transition "eye." Whether such structures are capable of forming an image is doubtful, although in certain quick-moving Chordeumida the ocellarium is very prominently convex and perhaps is able to detect motion.

The mouth parts are dominated by the normally large, robust mandibles, originating from the second postoral cephalic somite. In the majority of Diplopoda the mandibles are superficially three-jointed; actually, the large basal segment (coxopodite of SNODGRASS) is divided into a proximal cardine and a distal stipe by a rigid suture. The distalmost segment (*Praemandibel* of ATTEMS, lacinia of SNODGRASS) attached by a movable hinge joint bears at its distal end one or more strong rasping "teeth" subtended on the inner surface by several rows of pectinate lamellae; still more proximally on the inner side may be an area modified by ridges or flutings into a grinding surface. Basally, the premandible is produced into a long apodeme to which flexor muscles are attached; these muscles originate on the epicranium or on the internal epicranial septum. The mandibles may be drastically suppressed in various groups, particularly the subclass Pselaphognatha and the helminthomorph orders Polyzoniida and Siphonophorida, the last two groups suspected of being suctorial in feeding behavior.

The ventral side of the head capsule in Diplopoda is closed by a flattened plate, the gnathochilarium, formed from the first maxillae and therefore an appendage of the third postoral cephalic somite. Essentially, this plate consists of a median basal element, the mentum, which commonly is divided transversely to set off an anterior or distal promentum. Proximal from the mentum are the elongated lingual lamellae, each of which bears a distal olfactory cone; laterally from the lamellae and commonly from the mentum also are the stipes, each of which carries two distal sensory cones. The stipes may be subtended basally by smaller random cardines and the mentum may rest upon a thin transverse sclerite, the prementum. Located at the base of the gnathochilarium is a large transverse plate, the gula (hypostoma of LATZEL), which is the sternal remnant of the second maxillary elements and thus not a part of the gnathochilarium in the strict sense.

The gnathochilarium tends to be characteristic in form and shape for each order of the Diplopoda. In some orders it is invariable, whereas in others random subdivision, fusion, or suppression of the various parts may occur, or even sexual dimorphism within a single species. In older literature the form of the structure is accorded preeminence in schemes of classification.

The size of the first body segment is strongly reduced in accordance with the adaptation for recurving the head and anterior segments, and it consists chiefly of a transverse tergite commonly called the collum. The form of the collum varies greatly. Normally it is smaller than the head or the second tergite and in some it may be flabellately broadened to cover the head completely like a broad-brimmed hat, or it may be strongly depressed laterally to form a sort of hood over all or most of the head capsule. In some diplopod orders the collum has no appendages, but in others the first pair of legs is clearly attached by muscles to the inside of the collum.

The composition of the body segments is extremely varied (as discussed under the heading "Subclass Helminthomorpha"). Each segment is composed of two fused somites, and in some forms the external sclerites reflect this relationship. In many orders we can distinguish two subsegments, the prozonite and metazonite, which may be separated only by a suture or by a distinct waistlike constriction, the stricture, that usually includes the suture or lies just behind it (Fig. 366,*6*). In some orders, notably the juliform groups, three transverse sclerites are discriminated, but there are only two sternites and one pleurite on each side (Fig. 366,*7*); obviously some secondary division, perhaps of the metazonite, has occurred here. In the extinct order Amynilyspedida, some fossils show the presence of two pleurites on each side, corresponding with two tergites, and this condition may still be observed in newly molted specimens of the orders Polydesmida and Chordeumida; clearly this is the primitive arrangement. In many groups the tergites are divided into two halves by a mid-dorsal longitudinal suture, the orders so represented forming a natural group on the basis of other characters and perhaps worthy of a superordinal rank. The surface of the body segments may be entirely smooth, coriaceously wrinkled, granulose, tuberculate, spinose, or showing various combinations of these conditions. In many forms the metazonites are produced laterally into paranota that impart a broad compact appearance. The paranota, when present, may be strongly depressed (common in forms which roll into a ball) or horizontal or even strongly elevated; their edges may be entire or deeply notched or strongly dentate. The metazonites of most diplopods carry a pair of defensive glands opening laterally, in some on all segments from the fifth to the penultimate (primitive condition), but in many orders an abbreviated sequence is common and in several groups there are no glands whatever. In most Recent species the glands open to the exterior through small ozopores, usually flush with the segmental surface but in a few on special elevated areas or through elongated erect stalks. Even in fossil imprints on a fine-grained matrix (black carboniferous shale) I could not be sure of the presence of ozopores in Upper Pennsylvanian specimens of *Xyloiulus* recently studied. Drawings of Paleozoic millipeds with large, prominent pits indicated as "repugnatorial pores" must be regarded with some skepticism.

The terminal segment of the body is composed of a dorsal tergite, the telson (or epiproct), anal valves (periprocts), and a sternite (or hypoproct) (Fig. 366,*3*). Sometimes, as in Pentazonia, these elements are found attached to each other by connective tissue only; more usually the last segment is a solid ring enclosing the two periprocts. The epiproct may or may not be extended as a caudal projection.

The configuration of the sternal elements varies greatly among the different orders. Basically, the generalized sternum is a broad, flat plate with coxal sockets, a pair of stigmata, and internal projections of the latter that function for muscle attachment. Probably a wide sternum is the primitive condition from which most diplopods have departed, but within the single family Platydesmidae one finds genera with widely separated legs closely related in other respects to those in which the coxae are in contact. Such taxonomic names as "Macrosterni" and "Eurysterna" seem grossly to overemphasize the relative systematic importance of sternal width. Normally the sterna in diplopods are associated with the metazonites, where both pairs of appendages are localized, and the prozonites are thus either open ventrally (Chordeumida) or closed by the ventral fusion of the pleurotergites. In primitive groups the sterna remain essentially free from the pleurotergites; the gradual fusion of these, as well as other segmental elements, is clearly an evolutionary adaptation to a burrowing mode of life. In all groups the sterna of the first pair of appendages remain free and movable at least. In the Pentazonia, the sterna are medially divided into two halves widely separated by the coxae between them. This appears to be a secondary or derived condition associated in some way with ability to roll into a sphere.

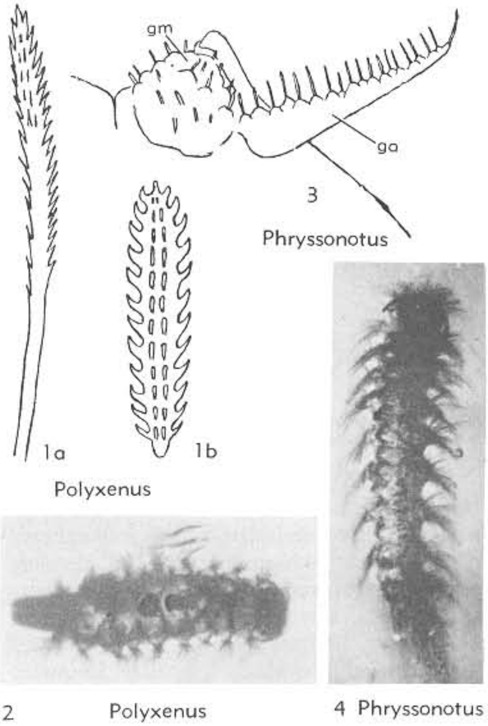


FIG. 367. Synxenidae *(3,4)*; Polyxenidae *(1,2)* (p. *R*583-*R*584).

Subclass PENICILLATA Latreille, 1827

[=Pselaphognatha LATZEL, 1884]

Minute, highly disjunct diplopods probably worthy of separate class status. Body wall soft, without carbonate impregnation, with lateral clusters of modified trichomes and transverse rows of clavate setae; head followed by 11 to 13 body segments, with 13 to 17 pairs of legs, none modified for sperm transfer or for clasping. Head with transverse suture between antennae and ocellus clusters; mouth parts reduced from normal diplopod form, particularly gnathochilarium in which mental elements are not evident, but stipital palps are hypertrophied. *Oligo.-Rec.*

Members of this group are essentially tropical or subtropical in their distribution; they appear to be definitely colonial and partial to dry situations. At first glance they are strikingly similar to the larvae of dermestid beetles, and are capable of very agile movement. Several dozen Recent species are known, and two forms have been recorded from Oligocene amber deposits. Penicillates are separated on the basis of extremely subtle chaetotactic characters, requiring high magnification.

Order POLYXENIDA Chamberlin & Hoffman, 1958

[=Ancyrotricha COOK, 1895; Schizocephala VERHOEFF, 1928]

Characters of subclass. *Oligo.-Rec.*

Family SYNXENIDAE Silvestri, 1923

Adults with 12 body segments and 17 pairs of legs; tarsal claws of last 2 pairs of legs modified into pubescent laminae; tergites with 2 transverse rows of clavate setae. *Oligo.-Rec.*

Phryssonotus SCUDDER, 1885, p. 73 [**Lophonotus hystrix* MENGE, 1854, p. 12; OD, M] [=*Lophonotus* MENGE, 1854 (*non* STEPHENS, 1829); *Synxenus* SILVESTRI, 1900, p. 114; *Schindalmonotus* ATTEMS, 1926, p. 113; *Kubanus* ATTEMS, 1926, p. 113; *Koubanus* ATTEMS, 1928, p. 198]. Characters of family. *Oligo.*, Eu.-Burma; *Rec.*, S.Afr.——FIG. 367,*3,4*. *P. hystrix* (ATTEMS), *3*, Rec., S.Afr., gnathochilarium (*ga*, outer feeler; *gm*, middle feeler), ×? (not stated) (Attems); *4*, Oligo., Baltic amber, whole animal, ×7 (Bachofen von Echt).

[Some recent investigators have suggested that *Schindalmonotus hystrix* ATTEMS, 1928, from South Africa, is congeneric with the Oligocene species *Lophonotus hystrix* MENGE for which SCUDDER proposed the new generic name *Phryssonotus*. If this synonymy is proved correct, it will result in the anomaly of two synonymous generic names having been based upon an identical specific name, and it is likewise possible that ATTEMS' name *hystrix* is even a homonymous synonym of MENGE'S! But considering the extremely subtle microscopic characters now utilized in the definition of polyxenoid species, it seems unlikely that such a synonymy can be easily proved.]

Family POLYXENIDAE Gray, 1842

Adults with 11 segments and 13 pairs of legs; tarsal claws of various form but not modified as in Synxenidae; tergites with 2 rows of setae, terminal segment with two tufts of long, white, sericeous setae. [Numerous Recent genera, of which one is recorded from the Baltic amber.] *Oligo.-Rec.*

Polyxenus LATREILLE, 1802, p. 45 [**Scolopendra lagura* LINNÉ, 1758, p. 637; OD, M] [*nom. correct.* GOLDFUSS, 1820 (*pro Pollyxenus* LATREILLE, 1802)]. Ocelli present, terminal antennal segment smaller than penultimate; tarsal claws trilobed; tergites with 2 transverse rows of short, broad,

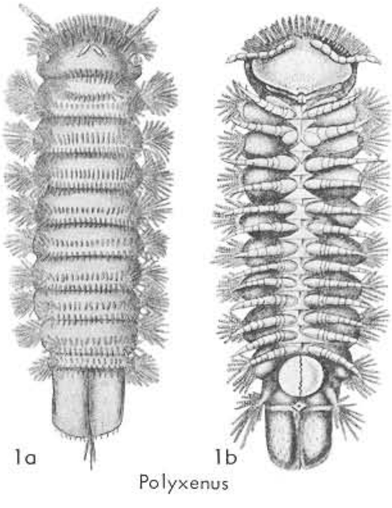


FIG. 368. Polyxenidae (p. *R*583-*R*584).

clavate setae along posterior border. *Oligo.*, Eu.; *Rec.*, Eu.-N.Am.——FIG. 367,*1*; 368,*1*. **P. lagurus* (LINNÉ), Rec., Eu.; 367,*1a,b*, tactile hairs of dorsal side, ×? (not stated); 368,*1a,b*, dorsal, ventral, ×2 (Attems).——FIG. 367,*2*. *P.* sp., Oligo., Baltic amber, ×9 (Bachofen von Echt).

[The validity of GOLDFUSS' emendation of LATREILLE's original orthography of this name has recently come under challenge by at least one worker who believes that the double "l" was not a *lapsus*. Those who follow this line of reasoning will prefer to alter the spelling of the family name also to Pollyxenidae. In my opinion, *Polyxenus* is a good Greek proper name signifying "stranger," and so entirely appropriate, whereas "Pollyxenus" is a misspelling in any language.]

Subclass PENTAZONIA Brandt, 1833

[=Oniscomorpha POCOCK, 1887; Opisthandria VERHOEFF, 1894]

Body form typically short and robust, segmental elements consisting of arched dorsal tergum, two ventrolateral pleura, and two paramedian sterna (latter separated by coxae), these sclerites joined by flexible sutures or by membrane (Fig. 369,*6*). None of anterior legs modified by sperm transfer, but last two pairs of legs of males form large forcipate clasping appendages (telopods) used to hold female during copulation. Head transversely broadened, with prominent horseshoe-shaped or rounded-oval sensory pit on each side lateral to antennae (Fig. 369,*5*). Head without epicranial suture; gnathochilarium modified from usual diplopod form by fusion of sclerites. Digestive tract looped or coiled. Tracheae dichotomously branched, radiating from internally enlarged stigmal pouches. *Penn.-Rec.*

Two Recent orders, somewhat dissimilar in external form, but united by the foregoing diagnosis, are represented in the Holarctic region, Indoaustralian area, and extreme South Africa. A third order, perhaps the ancestral group, is known only from the Upper Carboniferous of central Europe.

Order GLOMERIDESMIDA
Cook, 1895

[*nom. transl. et correct.* CHAMBERLIN & HOFFMAN, 1958 (*ex* suborder Glomeridesmoidea COOK, 1895] [=Limacomorpha POCOCK, 1894]

Body small, slender, flattened, somewhat elongated, composed of head and 22 body segments, not capable of rolling into sphere; ocelli absent; antennae short and slender, antennomeres similar in size and proportion. Females with enormously protrusible ovipositors, half as long as body. Sensory pit on head rounded. Lamellae linguales fused into single median plate, mentum reduced to transverse basal strip. *Rec.*

Order GLOMERIDA Cook, 1895

[*nom. correct.* CHAMBERLIN & HOFFMAN, 1958 (*pro* Glomeroidea COOK, 1895)] [=Oniscomorpha POCOCK, 1894; Plesiocerata VERHOEFF, 1910]

Small (6 mm.) to large (more than 120 mm.) forms capable of rolling into tight sphere; body composed of 14 to 16 segments covered with 11 to 13 tergites, some posterior segments having coalesced to form enlarged prominent pygidium. Females with 17 to 21 pairs of appendages, males with 19 to 23 pairs, of which last two or three are modified to serve in clasping female. Body form very broad and robust, terga highly arched, second very much enlarged laterally and usually with marginal groove into which fit tips of other tergites when animal is rolled up. Sensory pit on head large, horseshoe-shaped, located between the ocelli and antennal sockets. Gnathochilarium basically similar to that of Glomeridesmida in that fused lingual lamellae are dominant elements, with mentum reduced and displaced basally. In suborder Glomerididea (Fig. 369,*3*), stipes are sub-

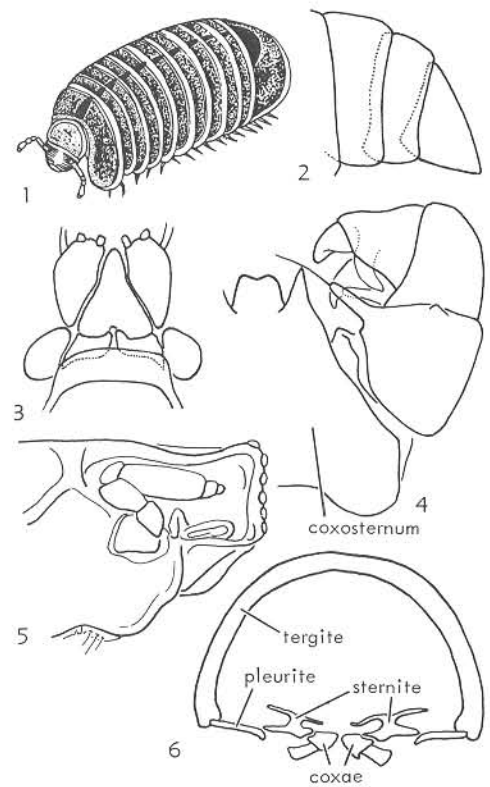


FIG. 369. External structural features used in classification of pentazoniate Diplopoda.——*1. Glomeris conspersa* (KOCH), lateral aspect of entire animal, ×3 (Koch).——*2*. Posterior segments of glomeroid, lateral aspect, ×10.——*3*. Generalized glomeroid gnathochilarium, ×18.——*4*. Pair of legs (18th) of *Onomeris australora* HOFFMAN, modified into telopods, anterior aspect, left side, ×30.——*5*. Front of head of *O. australora,* left side, ×25.——*6*. Generalized mid-body segment of pentazoniate diplopod showing paired sternites and pleurites and single tergite characteristic of this subclass, enl. (*2-6,* Hoffman, n).

tended by large and distinct cardines; in Sphaerotheridea latter elements are missing and stipes are considerably displaced distally. Oviducts terminate just behind coxae of second pair of legs and through cyphopod composed of three or four small sclerites. [Two suborders have been proposed—Sphaerotheridea with moderate to large species restricted to South Africa, India and Indo-Australian region and lacking fossil representation, and Glomeridea, which is widespread in Palearctic regions and extends also into the Malayan archipelago. It is represented by a few fossil forms in northern Europe.] *Oligo.-Rec.*

Family GLOMERIDIDAE Leach, 1815

[*nom. correct.* COOK, 1896 (*pro* Glomeridae LEACH, 1815)]

Body composed of collum, enlarged second tergite, and nine or ten more tergites, usually smooth and polished; females with 17 pairs of legs, males with last two or three pairs of legs modified as claspers. First tergite small, reniform, smaller than head; antennae moderately long, geniculate between third and fourth segments, sixth segment usually largest. *Oligo.-Rec.*

Glomeris LATREILLE, 1802, p. 44 [**Oniscus marginatus* VILLIERS, 1789; OD]. Genera of this family (only one here cited) are distinguished by technical characters of telopods, exposition of which would be too lengthy to be justifiable in this account. *Oligo.-Rec.,* Eu.——FIG. 369,*1*. *G. conspersa* KOCH, Rec.; entire animal, ×3 (after Koch).——FIG. 369,*2-6*. *G. australora* HOFFMAN, Rec.; *2,* posterior segments, ×10; *3,* gnathochilarium, ×18; *4,* telopods, ×30; *5,* front of head, ×25; *6,* midbody segment, diagrammatic, ×10 (Hoffman, n).

Order AMYNILYSPEDIDA Hoffman, new order

[=Palaeomorpha VERHOEFF, 1928]

Pentazonia of apparently primitive status, superficially resembling Recent Glomerida but differing in lacking terminal pygidium, in having two pairs of pleurites to each body segment at least in some forms, and in presence of erect spines upon segments. *Penn.*

The taxonomy and nomenclature of this group is in a state of particular confusion. Almost certainly several families are involved, but perhaps are best undefined until a restudy can be made. For the present I combine three genera under a single family name.

Family AMYNILYSPEDIDAE Hoffman, new name

[New name is replacement for invalid family-group names published by FRITSCH (1899) as follows: Proglomeridae (incl. only *Archiscudderia* FRITSCH, 1899), Sphaerherpestidae (incl. only *Glomeropsis* FRITSCH, 1899), Acroglomeridae (incl. only *Amynilyspes* SCUDDER, 1882)]

Characters of order. [A heterogeneous "family" with characters of the order. Prob-

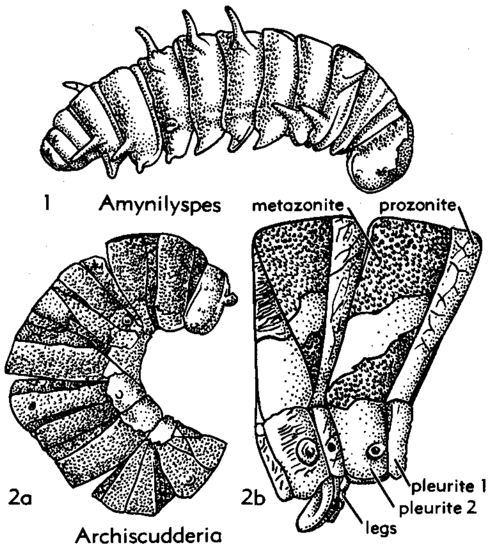


FIG. 370. Amynilyspedidae (p. *R*586).

ably each of the included genera represents a distinct family.] *Penn.*

Amynilyspes SCUDDER, 1882 [**A. wortheni*; OD, M]. Head large, rounded, with small "eyes"; trunk composed of 13 segments with lateral rows of erect spines. *U.Carb.*, N.Am.-Eu.——FIG. 370,*1*. *A. typicus* FRITSCH, Czech.; side view of entire animal, ×3 (after Fritsch). [=*Amynilispes* FRITSCH, 1901, p. 33 *(nom. null.)*]

Archiscudderia FRITSCH, 1899, p. 35 [**A. paupera;* SD HOFFMAN, herein]. Head with small, indistinct, laterally placed "eyes"; trunk segments about 15, with well-developed pleurites; dorsal spines not evident. *U.Carb.*, Eu.——FIG. 370,*2*. **A. paupera*, Czech.; *2a*, side view of animal, ×2; *2b*, 2 segments in lateral view showing details, ×6 (after Fritsch).

Glomeropsis FRITSCH, 1899, p. 38 [**G. ovalis*; OD, M]. Trunk with about 16 segments with well-developed pleurites and sternites; dorsal spines absent; "eyes" with up to about 600 ocelli. *U. Carb.*, Eu.(Czech.).

Subclass HELMINTHOMORPHA Pocock, 1887

[=Proterandria VERHOEFF, 1894; Eugnatha + Colobognatha ATTEMS, 1898]

Typical diplopods of elongate, usually slender body form. Body segments clearly diplosomatic in composition but somewhat variable in degree of sclerite fusion. Normally individual segments can be regarded as composed of anterior, telescoping prozonite that does not bear legs, and posterior larger metazonite which carries two pairs of legs and which may be variously extended laterally or surficially ornamented. In nearly all helminthomorphous diplopods pleural elements are associated with leg-bearing metazonites in varying degrees of coalescence, forming so-called "pleurotergites." [In a few primitive forms the pleurites may be attached to the sternite and metazonite only by a flexible membranous articulation, in others they may be firmly fused to the metatergite but remain loosely attached to the sternum. In the most advanced condition (Polydesmida) all of the metatergal elements are, in the adults, completely fused into a complete ring with no visible trace of the original sutures (the immature stages, particularly during molting, usually reflect the ancestral multiscleritic condition (Fig. 366,*4*). In some forms, especially the Juliformia, each segment appears to be formed of three subequal transverse rings, divided by longitudinal sutures at the mid-dorsal and mid-lateral lines, which share a common elongate pleurite on each side and a pair of imbricate sterna (Fig. 366,*7*). At least one pair of legs on seventh segment of males is modified into sperm-transfer organs (gonopods), in some both leg pairs of this segment so modified, few with adjoining legs on segments six and eight becoming involved in some way. Vasa deferentia open through coxae of second pair of legs in primitive forms, or they may open through paired or single sclerotized structures located just behind these coxae in more specialized members of subclass. Ambulatory legs essentially homogeneous in construction through group, consisting of coxa, prefemur, femur, postfemur, tibia, and tarsus, latter normally provided with acute distal pretarsus or claw (Fig. 366,*2*). [In a few Recent species an accessory false podomere is inserted between the coxa and prefemur, such an intercalary segment having no muscle origins or insertions. Eversible coxal sacs are frequent, particularly in more primitive groups, and in many forms the more distal podomeres (postfemora, tibiae,

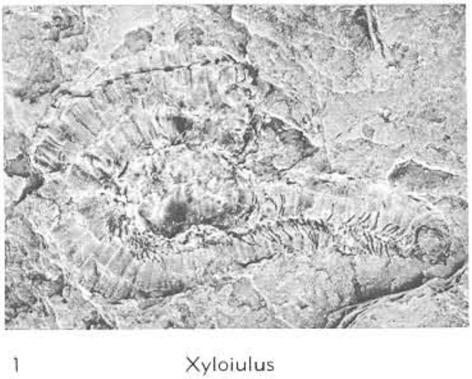


FIG. 371. Xyloiulidae (p. *R*587).

tarsi) may develop eversible cushions in the male sex.] Spiracular openings (stigmata) occur always in sterna, usually just lateral to coxal sockets; internal extensions of stigmal pouches usually elongated apodemes providing origins for many leg muscles. *U.Penn.-Rec.*

The number of orders referable to this subclass is currently still unsettled, as noted in the preceding remarks on classification. The fossils known from Tertiary formations are easily assignable to well-known Recent orders; those from the Paleozoic beds remain somewhat enigmatic since the characters required for a precise ordinal allocation seem rarely to be fossilized. Many Pennsylvanian species from coal beds of the Northern Hemisphere appear to be quite typically helminthomorph in external structure.

Order SPIROBOLIDA Cook, 1895

[*nom. transl. et correct.* CHAMBERLIN, 1938 (*ex* suborder Spiroboloidea COOK, 1895)] [=Spiroboloidea COOK, 1895; Anocheta COOK, 1895; ATTEMS, 1926]

Elongate, cylindrical Diplopoda with stipites of gnathochilarium widely separated proximally by large undivided triangular mentum; segments 1 to 5 each bearing single pair of legs, sixth with two pairs; vasa deferentia opening through simple median eversible membraneous tube behind coxae of second pair of legs; gonopods consisting of anterior pair of coleopods that completely enclose smaller posterior phallopods; both pairs are completely retracted within the body. *U.Penn.-Rec.*

Family SPIROBOLIDAE Bollman, 1893

Moderate to large-sized spiroboloids characterized particularly by configuration of male genitalia; externally family can be recognized by shape of first body segment (collum) which is laterally acutely angular and subtended by anteriorly projecting ventral part of following pleurotergite. *Pleist.-Rec.*

Hiltonius CHAMBERLIN, 1918, p. 166 [**H. pulchrus*; OD]. Distinguishable from other genera of the family only by characters of the male genitalia. [*Spirobolus australis* GRINNELL, Pleist., USA (Calif.), probably belongs here as a senior synonym of one of the several species of *Hiltonius* known to occur in southern California.] *Pleist.*, N.Am.; *Rec.*, N.Am.

Family XYLOIULIDAE Cook, 1895

Paleozoic ?Spirobolida characterized by the ornamentation of the pleurotergites with fine longitudinal or oblique ridges and grooves. Metazonites at most only slightly greater in diameter than prozonites. Body about ten times as long as broad. Length of legs about half body diameter. *U.Penn.*

Xyloiulus COOK, 1895, p. 3 [**Xylobius sigillariae* DAWSON, 1860, p. 271; OD] [=*Xylobius* DAWSON, 1860 (*non* LATREILLE, 1834; GUÉRIN, 1841); *Pylojulus* FRITSCH, 1899, p. 46]. Segments not distinctly divided into prozonite and metazonite of different diameters; longitudinal grooves numerous, mostly parallel to main body axis, continuous along entire length of segment. *U.Penn.*, N.Am.-Eu.——FIG. 371,*1*. *X. bairdi* HOFFMAN; USA(Ohio); external mold of ventral surface, ×3 (Hoffman, 1963).

Family NYRANIIDAE Hoffman, new family

Large (diameter up to 10 mm.) xyloiuloids in which diameter of metazonites is distinctly greater than that of prozonites and ornamentation of two subsegments is different; grooving of prozonite finer and more closely spaced, that of metazonite larger and farther apart. *U.Carb.*

Nyranius HOFFMAN, 1963, p. 172 [**Julus costulatus* FRITSCH, 1883; OD]. Characters of family. [Two known species from the Gaskohle Formation of Nyrany, Czechoslovakia.] *U.Penn.*, Eu. ——FIG. 372,*1*. **N. costulatus* (FRITSCH); side view of entire specimen, ×1 (after Fritsch, 1899).

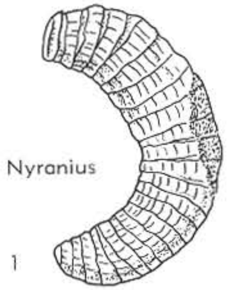


FIG. 372. Nyraniidae (p. *R*587-*R*588).

Family PLAGIASCETIDAE Hoffman, new family

Small xyloiulids in which longitudinal grooving is distinctly oblique and restricted to ventrolateral surfaces of the metazonite of each segment; prozonite smooth and unmodified. *U.Penn.*

Plagiascetus HOFFMAN, 1963, p. 172 [**P. lateralis*, OD]. Characters of family. [One species known from the Allegheny Series just below the Freeport Coal beds.] *U.Penn.*, N.Am.——FIG. 373,*1*. **P. lateralis* HOFFMAN, USA(Ohio); mold of lateral surface, anterior third of body, ×5 (Hoffman, 1963).

Family ANTHRACOJULIDAE Hoffman, new family

Spiroboloid? diplopods apparently similar in segmental form to Recent species in that segments appear to be composed of three transverse pleurotergal sclerites and rectangular pleurite on each side, but differing by broadened sterna, which are as wide as half of leg length. *U.Carb.*

Anthracojulus FRITSCH, 1899, p. 29 [**A. pictus*; OD, M] [=*Anthracoiulus* VERHOEFF, 1928 (obj.)]. With characters of family. *U.Carb.*, Eu. ——FIG. 374,*1*. **A. pictus*, Czech.; mid-body segment (reconstr.), anterior aspect, ×1.3 (after Fritsch).

Order STEMMIULIDA Cook, 1895

[*nom. correct. et transl.* CHAMBERLIN & HOFFMAN, 1958 (*ex* suborder Stemmatoiuloidea COOK, 1895)] [=Monocheta COOK, 1895 (*partim*)]

Disjunct tropical cursorial millipeds of small to moderate size, combining facies of juloid and chordeumoid forms. Body fusiform, laterally compressed, with prominent mid-dorsal longitudinal suture on each segment; sides of segments obliquely striate; sternites entirely free from pleurites and of two different shapes. Antennae long and slender, one or two large convex ocelli on each side of head; gnathochilarium basically of typical helminthomorph structure but may be sexually dimorphic, lingual lamellae much longer in males than in females of same species and almost completely obliterating mentum. Anterior legs commonly enlarged, almost invariably with plumose setae, pencils of long hairs, or other modifications; vasa deferentia opening through eversible median projection just behind second pair of legs; anterior gonopods well developed and complex, posterior gonopods wanting or represented only by minute rudiments. Telson small, distally truncate, with several pairs of spinnerets. Ozopores present in continuous sequence. *Rec.*

This singular order, despite the occurrence of spinnerets on the last segment and

FIG. 373. Plagiascetidae (p. *R*588).

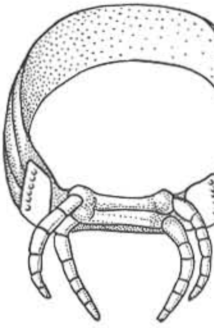


FIG. 374. Anthracojulidae (p. R588).

mid-dorsal segmental sutures, appears to be only distantly related to the chordeumoids, with which group it has often been united as a suborder. I judge the stemmiulids to represent survivors of a very primitive milliped stock which probably had most in common with ancestral spiroboloids. The living species are of course highly specialized in several characters, such as sexual dimorphism and modification of the male anterior legs.

O. F. COOK discovered that the young of *Diopsiulus bellus*, a West African species, emerge from the egg with as many as 35 body segments, in contrast to the seven-segmented condition of the first instar of all other helminthomorphs.

The group is known from the single family Stemmiulidae with five genera occurring in the neotropical region, western Africa, Kenya, and southern India. COOK believed that the Pennsylvanian xyloiulids were closely related to stemmiulids and groups both forms in a single order "Monocheta." I have recently published (HOFFMAN, 1963) an alternative suggestion that xyloiulids are perhaps more related to the spiroboloids.

Order POLYZONIIDA Cook, 1895

[*nom. transl. et correct.* CHAMBERLIN & HOFFMAN, 1958 (*ex* suborder Polyzonoidea COOK, 1895] [=Ommatophora BRANDT, 1841; Orthozonia VERHOEFF, 1940]

Small diplopods with reduced mouth parts, mandibles very small, probably not used for chewing; gnathochilarial elements reduced and fused, mostly no longer recognizable; head small and usually conical, with two or three pairs of ocelli; antennae short and thick. Segments composed of broad tergites lacking median dorsal suture, separate pleurites on each side, and usually narrow sternites. Gonopore of males opening behind coxae of second pair of legs, usually through two membraneous penes; eight pairs of legs in front of gonopods; latter still evidently leglike, small, incurved, consisting of a normal sternum and six or seven jointed appendages. *Oligo.-Rec.*

A basically Holarctic group most abundant today in western North America and east Asia; one family (Siphonotidae), however, is confined to the southern Hemisphere. One genus is known from the Baltic amber; this genus and probably the same species is still found in the same part of northern Europe.

Family POLYZONIIDAE Gervais, 1844

[*nom. correct.* WOOD, 1865 (*pro* Polyzonidae GERVAIS, 1844)]

Characters of order. [Distinguishable from other polyzonioid families only by microscopic characters of the male genitalia, mouth parts, gonopore opening, and related subtle characters.] *Oligo.-Rec.*

Polyzonium BRANDT, 1837 [**P. germanicum*; OD, M]. Small, compact polished diplopods with small, largely concealed head and short antennae, body relatively broad and concealing the legs. *Oligo.*, Eu.; *Rec.*, Eu.-N.Am.——FIG. 375,*1*. *P.* sp. (probably *germanicum*), Baltic amber, entire animal, dorsal aspect, ×8 (after Bachofen von Echt).

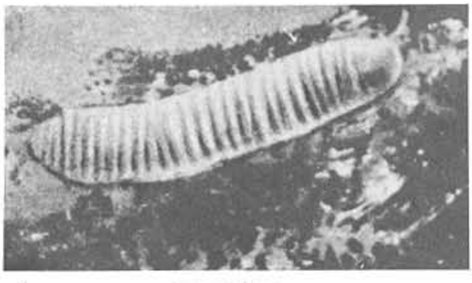


FIG. 375. Polyzoniidae (p. R589).

Order SIPHONOPHORIDA Cook, 1895

[*nom. transl.* CHAMBERLIN & HOFFMAN, 1958 (*ex* suborder Siphonophoroidae COOK, 1895)] [=Heterozonia VERHOEFF, 1940]

Minute to small tropical millipeds with two pairs of leglike gonopods similar to those of Polyzoniida, but characterized by striking reduction of head and mouth parts, elongation of body, and difference between diameters of prozonites and metazonites. Head small, conic in outline, commonly prolonged into long slender "beak"; ocelli absent; antennae enlarged and clavate, with two articles bearing distinct sensory pits; gnathochilarium reduced to single elongate triangular plate without evidence of normal sclerites; mandibles acicular, possibly nonfunctional. Sternites free from pleurotergites, latter either smooth and polished or densely hirsute, without median dorsal suture; commonly produced into moderate paranota; ozopores present in continuous sequence from fifth to penultimate segments; gonopods small, leglike, with four to seven segments, anterior gonopods typically shortter and stouter, posterior ones usually with terminal article greatly elongated. *Rec.*

This order contains the large family Siphonophoridae and perhaps also the poorly known group Siphoniulidae. Owing to the basic similarity of the gonopods in most of the known forms, classification below the level of family is presently chaotic, with a large number of clearly superfluous generic names in existence. Siphonophorids are basically tropical animals, although extending northward in the Sonoran region of southwestern North America. They appear to be specialized members of a basically primitive group of millipeds.

Order JULIDA Brandt, 1833

[*nom. correct.* CHAMBERLIN, 1938 (*pro* Julidea BRANDT, 1833)] [=Zygochaeta COOK, 1896; Symphyognatha VERHOEFF, 1900]

Body composed of large and variable number of cylindrical segments (30 or more), sternites, pleurites, and tergites immovably fused except in few species; coxae of legs without eversible sacs; telson without spinnerets; vasa deferentia open through simple or double penis located medially in intersegmental membrane behind second pair of legs. Gnathochilarium of characteristic form, mentum being divided into small elongate promentum located between lingual lamellae, and transverse, medially divided secondary mentum at base of gnathochilarium, these two mental elements widely separated by stipes which are broadly in contact medially over basal half of structure. In several famiiles gnathochilarium may be somewhat different in form between sexes. Gonopods composed of two highly modified pairs of appendages of seventh segment, entirely or partially retracted into body cylinder; first and commonly also second pair of legs modified in males for clasping females. *?Eoc., Oligo.-Rec.*

Members of this order are at present almost exclusively Holarctic in distribution (a few species spill over into the upper part of the Oriental Region). The number of valid families is somewhat uncertain, but four now are recognized. Of these, one family (Paeromopodidae) is endemic in western United States and has no known fossil representation. The Julidae are exclusively Palearctic in distribution and occur also in Oligocene amber. The Parajulidae are now restricted to North America and eastern Asia, and without doubt the various records of "*Julus*" from the American Tertiary can be placed in this family. Finally, the ancient and now somewhat relict family Nemasomatidae has most of its species in Europe, a few being on record from Asia and North America. One member of the group has been reported from the Baltic amber.

Typical members of these four families are fairly characteristic in size and proportions, but all grades of intermediate forms exist, and the family characters are drawn largely from details of the mouth parts and secondary sexual characteristics of the males.

Family JULIDAE Meinert, 1868

Gonopods entirely concealed within body, posterior pair usually larger and with large prominent mesomerite lobe; telopod of anterior gonopods mostly absent or rudimentary; first pair of legs of males reduced in size, commonly to small uncate processes. *?Oligo., Mio.-Rec.*

A large number of genera are known from the Palearctic region, chiefly distinguishable by minutiae of the male genitalia. It is presently impossible to allocate any of the fossil records for *"Julus"* to the correct genus; in its current restricted sense *Julus* is a small genus of three or four species confined to northern Europe; it may have been present during the Oligocene or earlier. Insofar as I can determine, only one generic name has been based upon a fossil referable to this family: this name was obscurely proposed and was omitted from Neave's *Nomenclator Zoologicus.*

Bertkaupolypus VERHOEFF, 1926, p. 334 [*nom. subst. pro Pseudoiulus* VERHOEFF, 1897 (*non* BOLLMAN, 1893)] [**Julus antiquus* BERTKAU, 1878; OD]. In the original description of this form, BERTKAU cites the name as *"Julus antiquus* v. Heyd. *i.l."* suggesting that VON HEYDEN was the describer of the species, as subsequently has been assumed. However, it is by no means clear whether VON HEYDEN provided BERTKAU with the name or description, or both, and it seems preferable to settle for a certainty and credit the species to BERTKAU's authorship. The species certainly seems referable to the Julidae, but shows no specific characters whatever, and the generic name seems to have been based solely upon the geological age of the fossil. *Mio.*, Eu.(Ger.).

Family NEMASOMATIDAE Bollman, 1893

[*nom. correct.* HOFFMAN, 1961 (*pro* Nemasomidae SILVESTRI, 1896, *nom. transl. ex* Nemasominae BOLLMAN, 1893] [= Blaniulidae SINCLAIR, 1895; Isobatidae COOK, 1895; Protoiulidae VERHOEFF, 1896]

Small, slender juliform diplopods; gonopods partially exposed, usually composed of two separate pairs of appendages, telopods of at least anterior pair usually present and movable; first pair of legs of male usually reduced in size, strongly uncate in some forms, leglike in others. *Oligo.-Rec.*

The majority of the known nemasomatids occur in southern Europe, chiefly in the Pyrenees and Balkans; several other genera occur in eastern Asia. A few are found in central Asia, Europe, and western United States. The majority are at least partially cavernicolous; the surface forms are subboreal relict forms of an earlier Holarctic distribution. Clearly the family is now in a state of decline. One species recorded from the Baltic amber by MENGE is probably correctly allocated to the genus, since MENGE was reasonably competent in this group.

Blaniulus GERVAIS, 1836 [**Julus guttulatus* BOSC, 1791; OD, M]. Small, slender species (about 20 times as long as wide); ocelli absent; pleurotergites with transverse row of short setae on caudal margin; gonopods large and prominently projecting from body; first leg pair of males reduced but distally clavate. *Oligo.*, Eu.(Baltic region); *Rec.*, Eu.

Family PARAJULIDAE Bollman, 1893

[*nom. transl. et correct.* CHAMBERLIN, 1921 (*ex* Parajulinae BOLLMAN, 1893)] [=Paraiulidae COOK, 1895]

Small to moderate-sized julids; the male gonopods at least distally exposed, normally made up of two separate pairs of appendages; anterior gonopods with distinct, movable telopods; mandibles with ten pectinate lamellae; first pair of legs of males hypertrophied, prominently clavate; second pair reduced. *?Eoc., Mio.-Rec.*

The distribution of this family is exclusively Holarctic, the great majority of known genera and species occurring in North America. Two genera extend south into Mexico and Guatemala; several occur in Japan and adjacent Asia. Almost certainly all of the various Tertiary fossils described under the name *"Julus"* are in fact referable to this family instead of the Julidae. Since genera, as well as species, are distinguished almost exclusively upon details of the male genitalia, it seems unlikely that the collocation of fossil parajulids to a Recent genus can be made with any degree of certainty.

Parajulus HUMBERT & SAUSSURE, 1869 [**P. olmecus*; SD POCOCK, 1895] [In recent years this genus has been divided into about 15 genera on the basis of small details of the gonopods. The species *Parajulus cockerelli* MINER, from the Florissant Shales (Oligo., Colo.) is remarkably well preserved and shows an indication of gonopod form, but must be restudied before its correct position can be determined. It clearly is not congeneric with the Mexican species of *Parajulus* in the modern restricted sense. The still older form *"Julus telluster"* SCUDDER, from the Green River shales, is probably also referable to the Parajulidae.] *?Eoc.*, N.Am.; *Mio.*, N.Am.; *Pleist.-Rec.*, N.Am.-Asia.——FIG. 376,*1a,b*. *P. cockerelli*

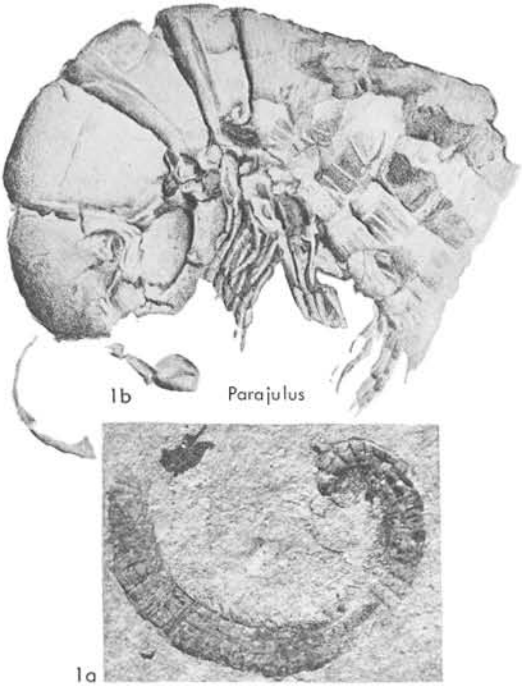


FIG. 376. Parajulidae (p. R591-R592).

MINER, Mio., USA(Colo.); *1a,* entire fossil, lat. view, ×2.5, *1b,* ant. end of fossil, lat. view, enl. (Miner, 1926).

Order SPIROSTREPTIDA
Cook, 1895

[*nom. correct.* CHAMBERLAIN, 1943 (*ex* Spirostreptoidea COOK, 1895)] [=Diplocheta COOK, 1895 (in part); Chorizognatha VERHOEFF, 1900 (in part)]

Large and diverse group of chiefly tropical millipeds, including some of largest known Recent members of the class. Pleurotergites and sternites firmly fused, latter typically quite small and obscured by coxae; no median longitudinal tergal suture. Body typically smooth and polished, although longitudinal carinae or crests occur sporadically among several subgroups. Head convex, elongate, with prominent transverse suture between frons and epicranium (usually visible between internal angles of characteristically subtriangular ocellaria). Antennae moderately long, distalmost articles often shorter and subovoid in outline, one or two with distinct sensory organ on outer surface. Collum large, extending downward and forward covering base of head and often also much of antennae and mouth parts, often sexually dimorphic and more strongly produced in males. Legs moderate to elongate, animals often capable of rapid crawling and considerable migration, in larger species many of the anterior legs of males are provided with permanent or eversible ventral pads presumably useful in copulation. Gonopods variable in form, one or two pairs may be developed, normally completely concealed within body or only apices visible. Vasa deferentia open through median, bilobed "pseudopenis" located behind coxosternum of second pair of legs. First pair of legs of males with prefemora often modified into small hooks that engage hypostomal plate of gnathochilarium. *?Penn., Rec.*

Spirostreptoids are at present divisible into three major subgroups although whether all are coordinate is disputed. The typical group contains three chiefly tropical families in which the anterior pair of gonopods is highly modified by elongation of the coxal elements into tubular structures sheathing the bases of the greatly attenuated, flagelliform telopodites; the posterior gonopods are rudimentary or wanting. A second group, likewise tropical, has the gonopods much less modified, and the posterior elements may be relatively conspicuous. The last group, at one time recognized as a separate order Cambalida, has two pairs of fully formed gonopods and a slightly different gnathochilarium pattern; its genera are somewhat more restricted to the temperate parts of the world at the present.

O. F. COOK (1895) has proposed that the genus *Archicambala* (based by him on the Pennsylvanian fossil *Xylobius dawsoni* SCUDDER) is referable to this third and last suborder of the Spirostreptida. This allocation must be verified by a restudy of the original material: SCUDDER's illustrations do not appear to be adequate for making such a placement.

Order CALLIPODIDA
Bollman, 1893

[=Monozonia BRANDT, 1833 (*partim*); Lysiopetaloidea CHAMBERLIN, 1943]

Small to large helminthomorph diplopods allied to Chordeumida and Polydesmida, pleurotergites commonly with elevated longitudinal ridges. Gonopores in males perforating coxae of second pair of legs; gonopods formed from only anterior pair of legs of seventh segment; epiproct with marginal row of six spinnerets. Antennae long and slender, epicranium of males commonly prominently impressed or concave; collum small, reniform, with prominent internal apodeme on anterior edge for attachment of head muscles. *Oligo.-Rec.*

The so-called "crested millipeds" are mostly active foragers well adapted for life in semiarid situations; many are often found in caves, several genera being troglobionts. Although basically vegetarian in habits, some species are carnivorous. The present-day stronghold of the order is in the eastern Mediterranean area, chiefly in the southern half of the Balkan peninsula; a second area of concentration is in southwestern United States, particularly in California. Three families are distinguished in the European fauna and apparently a fourth is isolated in northern Iran. The exact family status of the Nearctic forms has not yet been determined.

One callipodoid form has been recovered from Oligocene strata in France. This specimen, in relatively good condition, has been allocated to the family Dorypetalidae, but without examination of the gonopods any such family placement is only speculative.

?Family DORYPETALIDAE Verhoeff, 1900

Protosylvestria HANDSCHIN, 1944, p. 4 [**P. sculpta*; OD, M]. Metazonites with prominent and distinct longitudinal parallel ridges; gnathochilarium typical of order. *Oligo.*

Order PLATYDESMIDA Cook, 1895

[*nom. transl.* CHAMBERLIN & HOFFMAN, 1958 (*ex* suborder Platydesmoidea COOK, 1895)]

Small to moderate-sized helminthomorph diplopods of generalized structure; sternites entirely free and movable, either broad and flattened or narrow and having prominent median apophysis; pleurites also free in few genera, more commonly fused with tergites, in which case posterior half of resulting pleurotergite may be prominently extended laterally into paranota, all tergal elements having distinct longitudinal median suture. Gonopores in males perforate coxae of second pair of legs; eight pairs of legs in front of gonopods, which are small, with five to seven segments and scarcely modified from normal leg construction, their sterna identical with those of adjacent walking legs. Epiproct typically broadened, with up to six small conical projections of the caudal edge; pleurotergites of penultimate segment typically coalesced into complete ring; hypoproct may be present or absent; ozopores in continuous sequence from fifth to penultimate segment. Antennae typically rather short and robust; head small, usually with reduced mouth parts; ocellaria not developed. *Rec.*

Platydesmids at the present time constitute a small, basically subtropical group of primitive millipeds dispersed into three or four families. Most of the known species occur in the Mediterranean region, North America, and southeastern Asia. It seems likely that they represent a grade of organization approximating the common ancestor of the chordeumoid and polydesmoid groups.

Order CHORDEUMIDA Cook, 1895

[*nom. transl. et correct.* CHAMBERLIN, 1943 (*ex* suborder Chordeumoidea COOK, 1895)] [=Coelochaeta COOK, 1895; Ascospermophora VERHOEFF, 1913]

Small to moderate-sized helminthomorph diplopods; all of sterna free from pleurotergites, which lack ozopores and internal scent glands, but show median longitudinal suture in adults; gonopores of males opening through coxae of second pair of legs; epiproct with three pairs of marginal spinnerets. Collum small, ovoid, fitting usually into depression on rear side of head. Gonopods formed from appendages of seventh segment; commonly adjacent pairs of legs may be partially modified to aid in sperm transfer. Antennae usually long and slender. Agile, quick-moving forms in general; partial to cool climates and now virtually restricted to the Northern Hemisphere. *Oligo.-Rec.*

?Family CRASPEDOSOMATIDAE Cook, 1895

[=Craspedosomidae VERHOEFF, 1899]

Antennae long and slender; pleurotergites smooth, shining, metazonites produced lat-

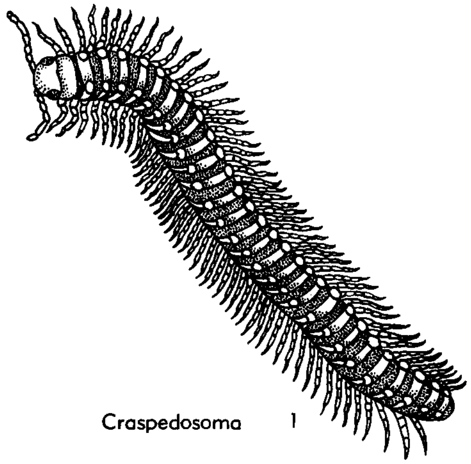


FIG. 377. Craspedosomatidae (p. *R*594).

erally into short paranotal swellings. Two pairs of legs behind gonopods with eversible coxal sacs. Peltogonopods without flagellum, but with "cheirite" formed by fusion of telopod with tracheal apodeme. *Oligo.-Rec.*

?**Craspedosoma** LEACH, 1815, p. 380 [**C. Rawlinsii*; OD]. Body with 30 segments; paranota represented as rounded lateral knobs; ocellaria large and prominent, subtriangular; front of head impressed in males, slightly convex in females; 1st and 2nd pairs of legs of males reduced in size, 3rd to 7th pairs larger than those following. Peltogonopods with prominent cheirites; gonopods reduced to broad, flattened sternum, with 6 erect conical processes, neither pair of gonopods with flagella. *Oligo.-Rec.*, Eu.——FIG. 377,*1*. *?C. angulatum* KOCH & BERENDT, *Oligo.* (Baltic amber), Baltoscandia; entire animal, ×4.5 (after Koch & Berendt).

[The foregoing allocation is made on the basis of external appearance only, as the form of the gonopods in *C. angulatum* are unknown. Placement of the species in *Craspedosoma* was, however, apparently acceptable to VERHOEFF, an outstanding authority on Palearctic diplopods.]

Atractosoma FANZAGO, 1876, p. 70 [**A. meridionale*; OD, M]. Metazonites with unusually broad paranota, giving animal polydesmoid appearance; collum wider than head; antennae about as long as greatest width of body; ocellaria prominent, each with about 25 to 30 ocelli. [If MENGE's identification of this genus in the Baltic amber is correct, it possibly provides an example of glacial displacement, since *Atractosoma* no longer occurs north of southern Germany.] *Oligo.*, Eu. (Baltic region); *Rec.*, Eu.(Italy-Aus.-Ger.).

Euzonus MENGE, 1854, p. 14 [**E. collulum*; OD, M]. Body fusiform, without paranota; antennae twice as long as width of body, its 3rd and 5th articles longest (*fide* SCUDDER, probably in fact 2nd and 4th); ocellaria semicircular, with about 20 ocelli in each. [The family position of this genus is not clear, but it may be retained provisionally in the Craspedosomatidae pending later study.] *Oligo.*, Eu.

Order POLYDESMIDA
Pocock, 1887

[*nom. correct.* CHAMBERLIN, 1938 (*pro* order Polydesmoidea POCOCK, 1887)] [=Merochaeta COOK, 1896; Proterospermophora VERHOEFF, 1900]

Helminthomorpha with 18 to 22 segments in adults, all segmental sclerites fused into compact rings that lack even sutures when fully calcified; ocelli absent from all species. Male genitalia formed from eighth pair of legs only, and in form of two prominent gonopods located in oval aperture in metasternum of seventh body segment. Gonopores of males open through small knobs on coxae of second pair of legs, and of females through modified bivalvate cyphopods located just behind sternum of second legs. *Oligo.-Rec.*

The Polydesmida is the largest order of diplopods and the most variable in body form. The size ranges from about two mm. to more than 120 mm. in length; in most species the metazonites are produced into broad paranota that are modified highly in different families; in some forms the paranota are secondarily suppressed. Gonopods usually consist of an enlarged coxa, commonly with a distinct sternal remnant attached, and a more slender distal telopod set usually at a right angle to the coxal axis; the telopod may be a single unjointed piece or in some groups may be divided by more or less distinct sutures into regions essentially homologous with the podomeres of ambulatory legs. In random specimens a genetic accident may result in the occurrence of a complex gonopod on one side of the body and a perfectly normal leg on the other.

The gnathochilarium is constant in form throughout the order, elongate rectangular in outline with a basal mentum and with no promentum set off; the lingual lamellae are in contact for most of their length.

Polydesmoids are most diverse and abundant in tropical regions; in many respects

Fig. 378. Polydesmidae (p. _R_595).

they appear to be a very old group and it is surprising that so far none have been discovered in Pennsylvanian coal bed deposits. At the present time some 30 to 40 families are recognized, but many of them will probably be degraded to subfamily status when better known. The species of the Oligocene Baltic amber appear to be about the same as those currently living in northern Europe. So far apparently only one family is known from fossils older than the Pleistocene.

Family POLYDESMIDAE Leach, 1815

Small to moderate-sized polydesmoids in which gonopod coxae are enlarged and in contact along their median edge, partly fused to each and each with prominent depression on ventral side into which telopod can be retracted; no sternal remnant between coxae. Telopod usually arcuate, with large internal chamber into which seminal groove discharges. Dorsum usually flattened, with several transverse rows of slightly raised polygonal areas. _Oligo.-Rec._

Polydesmus Latreille, 1802 [*_Julus complanatus_ Linné; OD, M]. Distinguishable from other genera of this family only by details of gonopod structure. Both sexes with 20 body segments. _Oligo.-Rec._, Eu.——Fig. 378,_1_. _P. laurae_ Pocock, _Rec._; entire animal, dorsal aspect, ×4.5 (after Attems).

Order and Family UNCERTAIN

The following generic names have been based upon fossil diplopods, apparently referable to the subclass Helminthomorpha, but at the present time they cannot be allocated to a particular order with any degree of certainty. All appear, however, to be referable to the so-called "juliform" group, comprising the orders Julida, Spirobolida, and Spirostreptida.

Archicambala Cook, 1895, p. 6 [*_Xylobius dawsoni_ Scudder; OD]. Genus proposed by Cook without diagnosis and placed by him with _Archiulus_ Scudder in family _Archiulidae_. This family-group in turn was aligned with several other families that make up the present suborder Cambalidea of the order Spirostreptida. Whether this placement is anywhere near being correct cannot even be guessed at present. _Oligo._, N.Am.

Archiulus Scudder, 1868, p. 496 [*_A. xylobioides_; OD, M]. The genus was based upon several species from the Pennsylvanian beds of North America, and subsequently recorded by Fritsch from the Gaskohle of Bohemia. Probably this is a composite genus, and may go into the vicinity of the Xyloiulidae when better known. _Penn._, N.Am.

Isojulus Fritsch, 1899, p. 25 [*_Julus constans_ Fritsch, 1879 (=_Archijulus constans_ Fritsch, 1894); SD Hoffman, herein]. _U.Carb._, Eu. (Czech.).

Pleurojulus Fritsch, 1899, p. 27 [*_P. biornatus_ Fritsch; SD Hoffman, herein] [=_Pleuroiulus_ Verhoeff, 1928]. Juliform group with rounded ocellaria and antennae similar to those of Recent spirobolids. So-called "pleurites" are clearly nothing more than fractured lower ends of pleurotergites broken when animal was flattened, not an uncommon occurrence.] _U.Carb._, Eu.——Fig. 379,_1_. _P. levis_ Fritsch, Czech.; entire animal, ×1.4 (from Müller).

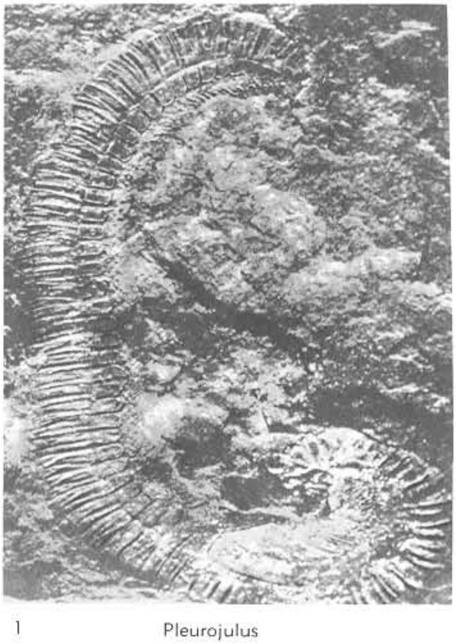


FIG. 379. Order and Family Uncertain (p. *R*595).

Class PAUROPODA Lubbock, 1866

[*nom. transl.* POCOCK, 1893 (*ex* order Pauropoda LUBBOCK, 1866)] [=Monopoda BOLLMAN, 1893; Heterognathes HUMBERT & SAUSSURE, 1872]

Minute progoneate myriapods with single pair of mandibles and pair of maxillae fused into subbuccal structure with poorly defined parts. Antennae singular in form, composed of basal four-jointed stalk that gives rise to two branches, one with long slender basal article and multiannulate flagellum composed of many tiny articles, other branch shorter and distally bearing two flagella and spherical sensory organ. Body composed of 11 segments and pygidium, bearing nine pairs of legs. Dorsum may have six to ten tergites. First pair of legs rudimentary. Gonopores open behind base of second pair of legs. Testes located on dorsal side of enteron, ovaries on ventral side. Body without tracheal and circulatory systems. Maximum size about two mm. No known fossil record (Fig. 380,*1*). *Rec.*

Since the first scientific record of this group was published in 1868, the pauropods have been studied by only a few competent students, particularly F. SILVESTRI and H. J. HANSEN in the last century and more recently PAUL REMY. So far little attempt has been made to define suprafamilial categories within the class; most workers heretofore have been content to recognize a single order bearing the same name and definition as the class. In 1896, the perspicacious O. F. COOK set up three orders—Cinona, Monona, and Lepona, each with a single family, but these names were never subsequently accepted (probably for the reason that each was monotypic). Since COOK's time a number of additional families have been defined and it will probably become desirable to arrange these groups in either ordinal or subordinal series. Since

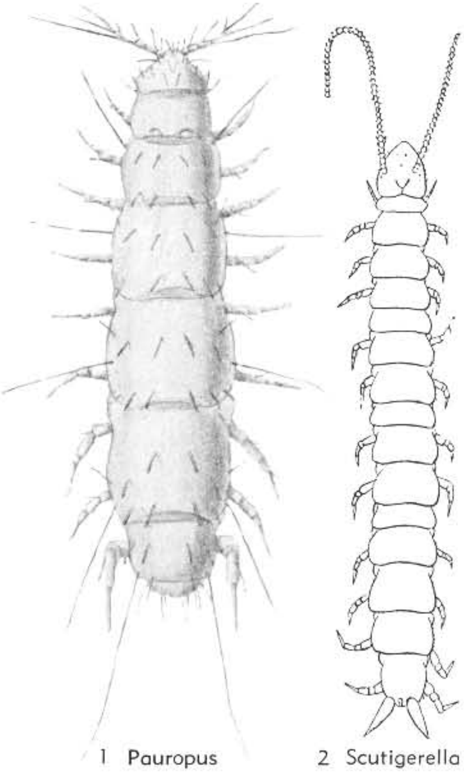


FIG. 380. Representatives of Pauropoda and Symphyla (Attems).——*1*. Pauropoda, Pauropodida, Pauropodidae, *Pauropus huxleyi* LUBBOCK, dorsal view of specimen, ×50.——*2*. Symphyla, Scolopendrellida, Scutigerellidae, *Scutigerella immaculata* (NEWPORT), dorsal view of specimen, ×15.

this type of work is best done by a specialist on the group, I here restrict my attention to the alteration of the existing ordinal name to conform with those used in other myriapod groups for the sake of uniformity.

Order PAUROPODIDA Lubbock, 1866

[*nom. correct.* HOFFMAN, herein (*ex* order Pauropoda LUBBOCK, 1866)]

Characters of class. *Rec.*

Class SYMPHYLA Ryder, 1880

[*nom. transl.* POCOCK, 1893 (*ex* order Symphyla RYDER, 1880)]

Small, fragile, pigmentless cryptic arthropods with prognathous head, bearing two simple multisegmented moniliform antennae, pair of mandibles, and two pairs of maxillae similar to those of insects, second pair fused into labium. Body with 12 leg-bearing segments, dorsally with 15 or 22 tergites (higher number apparently due to occurrence of intercalary tergites possibly corresponding to legless embryonic somites), and terminal segment behind last pair of legs giving rise to pair of large trichobothria and two large "cerci" (these last two pairs of appendages probably homologous to legs). Legs similar in shape, composed of five podomeres of which the basalmost (coxae), tend to form syncoxites or coxosternites by median fusion; this coxal region on all legs except first pair carries small lateral stylus and more median eversible coxal sac, presumably homologous to similar structures occurring in abdominal appendages of Thysanura. Legs terminate in paired claws. Body wall thin, flexible, without calcium carbonate impregnation or pigmentation cells. Tracheal system present, opening through two stigmata located just behind antennae. Dorsal circulatory vessel present. Gonads located ventral to gut, basically pair of organs but broadly fused or anastomosed, gametic ducts running anteriorly and fusing to common duct inside median, single gonopore located between second and third pairs of legs. No external sperm transfer appendages. Sexes always separate; females oviparous. Size ranging from about two to ten mm. (Fig. 380,2). [Symphylids live in moist localities, chiefly in forests, under stones or in humus. At the present time species of this class are known from all of the continents.] *Oligo.-Rec.*

FIG. 381. Scolopendrellidae (p. *R*597-*R*598).

So far only a single order has been recognized within this group, having the same name and characteristics. Of the three present families, two are somewhat closely related and the third is more disjunct. Perhaps at some future time it will become desirable to distinguish two orders. For the present I only alter the ordinal name into conformity with those of other myriapod classes. The symphylids are perhaps the least-studied of myriapods, and practically no systematic work has been done on the group since the early part of the present century.

Order SCOLOPENDRELLIDA Hoffman, new order

Characters of class. *Oligo.-Rec.*

Of the three currently recognized families, one has been recorded from Baltic amber of Oligocene age.

Family SCOLOPENDRELLIDAE Newport, 1845

Body with 15 tergites (thin intercalary tergite between each two primary tergites). Legs of first pair usually less than half as long as those of second pair. Coxal styli weak or indistinct. Caudolateral corners of tergites produced into triangular projections. Dorsal surface of last pair of legs with only few setae. Cerci usually with circularly set-off terminal area. *Oligo., Rec.*

Scolopendrella GERVAIS, 1836 [**S. notacantha*; OD, M]. First pair of legs about 0.7 as long as 2nd; posterior margin of each tergite with longitudinally striated groove between caudolateral projections; epicranial suture interrupted in front of middle and shortly branched. *Oligo., Rec.*, cosmop.——FIG. 381,*1*. ?*Scolopendrella* sp., Oligo. (Baltic amber), NW.Eu.; ×12 (after Bachofen von Echt, 1942).

Class CHILOPODA Latreille, 1817

[*nom. transl.* POCOCK, 1887 (*ex* order Chilopoda LATREILLE, 1817)] [=Syngnatha LATREILLE, 1802; BOLLMAN, 1893]

Terrestrial, tracheate, mandibulate, opisthogoneate arthropods characterized by numerous trunk segments, each with single pair of appendages (hence corresponding to embryonic somites), by modification of appendages of first trunk segment into pair of forcipulate poisonous prehensors; and by presence of pair of mandibles followed by two pairs of maxillae. Antennae simple, filiform, unbranched, composed of variable number of short unmodified articles; head strongly compressed dorsoventrally and covered by single cephalic plate. Photoreceptors absent, or present as small lateral cluster of ocelli on each side, or in form of large convex multifaceted "eyes" similar to those of insects. Body typically elongate, more or less flattened, body wall chitinous and flexible, without carbonate impregnation, each segment composed of tergite, sternite, and variable number of small pleural sclerites that vary in number and arrangement from one group to another. Trunk homonomous, no evidence of any distinction into thorax and abdomen. Growth either epimorphic and completed in egg stage or anamorphic and completed in series of postembryonic molts. In the latter condition, growth is teloblastic, with somite blocks originating in penultimate segment. *Cret.-Rec.*

So far as known, chilopods are exclusively carnivorous, as indicated by the universal presence of poison fangs and glands. The sexes are separate, although usually indistinguishable externally (in some forms the posteriormost legs of the males may be enlarged or modified); fertilization is internal, presumably by spermatophore introduction, and all species are oviparous. In the subclass Epimorpha, the females usually remain coiled around the egg cluster and afford some measure of protection to both eggs and the young chilopods after hatching.

To an even greater extent than in diplopods, members of this group are remarkably similar through the extent of a family or even an order; the distinction of genera and species is made on the basis of a number of cryptic features collectively. Formation of the mouth parts, number and dispersion of the pleurites, location and form of epidermal glands, and chaetotaxy of the limbs are all involved. Since there is considerable variation (ontogenetic, individual phenotypic, sexual, and geographic) within most species, the systematics of chilopods are exceptionally difficult, and only a few workers have ever achieved authoritative status concerning the Recent species.

Fossil chilopods extend back definitely to the Cretaceous, but the great majority of fossil records are from the Oligocene Baltic amber. A number of generic and specific names have been based upon upper Paleozoic "chilopods" but owing to the typically execrable preservation, it is very difficult to be sure that even the class has been accurately determined. The subtlety of most taxonomic characters utilized in the study of this group renders it unlikely that we will ever gain much insight into the morphology and diversity of pre-Tertiary chilopods.

CLASSIFICATION

It is generally agreed that four orders of living Chilopoda can be recognized. The arrangement of these orders into subclasses, however, is a matter of much dispute and hinges upon whether primary importance is attached to the method of body growth or construction of the tracheal system. The arrangement adopted here was proposed by ERICH HAASE in 1880 and subsequently accepted by the celebrated Viennese authority CARL ATTEMS. This system recognizes two subclasses, Epimorpha and Anamorpha, based upon details of embryonic metamerism; the first contains the scolopendrid and geophilid centipedes and the second the lithobiid and scutigerid forms.

In 1895 SILVESTRI set up a system of four groups defined on the basis of stigmal characters: (1) Pantastigmata, geophiloids; (2) Oligostigmata, scolopendroids; (3) Artiostigmata, lithobioids; (4) Anartiostigmata, scutigeroids. Later in the same year, R. I.

Pocock, giving more emphasis to the form of the tracheal system, recognized two subclasses: Anartiostigmata, for the new order Scutigeromorpha, and Artiostigmata, to include the new ordinal names Lithobiomorpha, Geophilomorpha, and Scolopendromorpha.

Verhoeff (1901) used the Pocock arrangement but altered the names of the subclasses to Notostigmophora (=Anartiostigmata) and Pleurostigmophora (=Artiostigmata). More recently, Wang (1951) changed the subclass names of Verhoeff to Notostomata and Pleurostomata.

From the standpoint of priority, the earliest available names for the two subclasses of the Pocock-Verhoeff system are Schizotarsia and Holotarsia, first used by Brandt in 1841. The still earlier names Inaequipedes and Aequipedes of Latreille (1827) are probably vernacular in nature, so that from the standpoint of priority alone, we should probably revert to Brandt's terminology, if this subclass dichotomy should ever be generally accepted by students of the Chilopoda. As an impartial observer I incline toward the Epimorpha-Anamorpha division of Haase.

The ordinal terminations "-omorpha" introduced by Pocock have been in vogue ever since 1895, and there is understandable reluctance on the part of current specialists to part with them. The newer endings "-ida" are employed here chiefly in order to achieve ordinal uniformity with the Diplopoda, in which group arbitrary "-ida" endings have served a long-needed purpose.

EXTERNAL CHARACTERS

To a very considerable extent, genera and families of chilopods are distinguished by the formation of the mouth parts, particularly the number and arrangement of the mandibular lamellae, the degree of coalescence of the several labral elements, and the configuration of the two pairs of maxillae. As it is extremely unlikely that such characters will be readily available even in well-preserved amber material, the following brief account of taxonomic characters is restricted largely to external features. It must be emphasized that in general chilopods are perhaps more variable than other kinds of myriapods, and the investigator must be alert for ontogenetic, sexual, geographic, and individual phenotypic variability within a single species. Sexual dimorphism is more pronounced in the specialized groups (Lithobiida, Geophilida); variation in meristic characters increases proportionately with the actual numerical status of the features involved (species with large number of body segments are more variable in this respect than those with reduced numbers). It must be recalled that chilopods are soft-bodied, muscular, and flexible animals, their proportions are thus a function of body condition; considerable telescoping usually accompanies preservation after death.

In general, each of the four orders has a definite and characteristic body form permitting instant recognition. Even body fragments may be identified as to order with considerable confidence. Beyond this, however, allocation of a specimen to family is more difficult. Within the Geophilida, particularly, families are difficult to distinguish externally, but a few details of body form are helpful: the Himantariidae include species in which the body is noticeably flattened and ribbon-like, with a rather small head; the Dignathodontidae are made up chiefly of attenuated creatures with unusually small heads, the body size becoming larger back to the posterior two-thirds of the length. In the Geophilidae, and many other related families, the head is the broadest part of the body, which tapers evenly back to the ultimate segment.

The antennae vary considerably and are useful in identification. In the Geophilidae the number of articles is fixed at 14, but the individual articles may be elongated, or very short, the terminal articles may be enlarged to form a distal club, or the entire structure may be compressed. In other orders the number of articles varies greatly, and is usually only a generic character, or in some only a specific one.

In earlier work the size and shape of the head plate was given much importance and provided the original basis for such names as *Mecistocephalus,* but the character is one subject to ontogenetic variability and has no real basic systematic value. The sides of the head may be set off by distinct submarginal rims or not, and paramedian sutures may be evident. Ocelli may be absent (all Geophilida, some Scolopendrida, random Lithobiida), or present as small lateral clusters behind the antennal sockets (most Scolopendrida and Lithobiida), or there may be two large, multifaceted "eyes" similar to those of insects (Scutigerida). The ventral side of the head is covered by large prehensors (modified appendages of the first body segment) that may extend well in front of the head, or may be visible beyond its sides when seen in dorsal aspect. These appendages (Fig. 382,*1*) consist of a large homogeneous coxosternum, the front edge of which may be medially diastemate, commonly with paramedian sets of acute projections; the prehensors themselves represent the telopods of the appendages and are usually heavy and powerful, with a prominent distal "claw" perforated for the release of venom produced in a basal gland located either within the prehensor itself or further back inside the body. The number of segments in the prehensor is variable owing to a general tendency for reduction and many of the segments are provided with a projection on the inner margin.

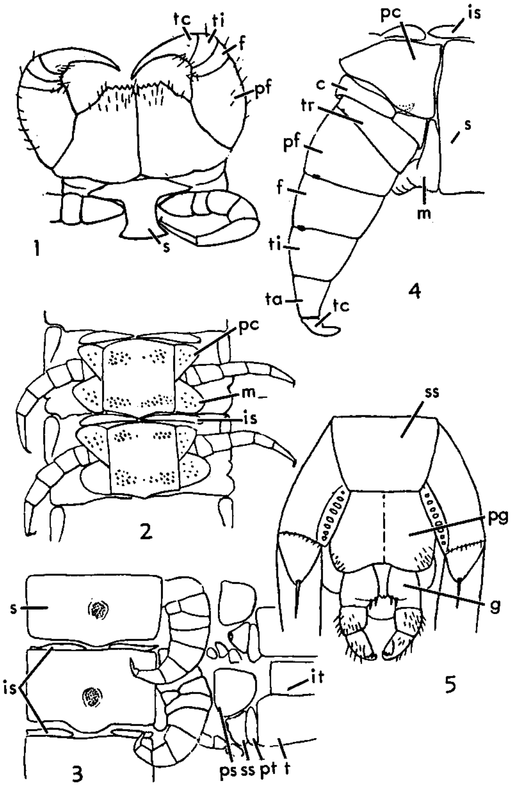


FIG. 382. External structural features used in classification of Chilopoda (Attems).——*1*. *Lithobius forficatus* (LINNÉ), prehensors and legs of 2nd body segment, ventral aspect, ×10.——*2*. *Pachymerium kervillei* ATTEMS, mid-body segments, ventral aspect, ×12.——*3*. *Himantarium gabrielis* (LINNÉ), mid-body segments cut mid-dorsally and flattened showing numerous pleural sclerites characteristic of most Geophilida, ×10.——*4*. *Meinertophilus superbus* (MEINERT), walking leg from middle of body, ×30.——*5*. *Lithobius forficatus* (LINNÉ), posterior end of body of female, ventral aspect, showing triarticulate female gonopods, ×10. [Explanation: *c*, coxa; *f*, femur; *g*, gonopod; *is*, intercalary sternite; *it*, intercalary tergite; *m*, metacoxa; *pc*, procoxa; *pf*, prefemur; *pg*, pregonopodal sternite; *ps*, prescutellar sclerite; *pt*, paratergite; *s*, sternite; *ss*, stigmal sclerite; *t*, tergite; *ta*, tarsus; *tc*, tarsal claw; *ti*, tibia; *tr*, trochanter.]

The body segments are composed of primary leg-bearing segments with alternating, much smaller, intercalary segments. The usual arrangement of sclerites is that of a single dorsal tergite, a variable number of smaller lateral pleurites and subcoxal elements, and a single sternite. The tergites are of variable form; some are appreciably larger than their neighbors, some may be strongly margined laterally, or produced into lateral expansions, and commonly median or paramedian sutures are evident. In the Lithobiida the caudolateral corners of many tergites are produced into triangular projections, providing what are commonly used as combinations to distinguish genera or subgenera.

The arrangement of pleural sclerites (Fig. 382,*2*,*3*) is different for each order, and within the Geophilida this provides differences between families and genera, or even specific differences. Basically there appear to be three rows of pleurites, as well as a dorsal row of "paratergites." Usually one of the pleurites contains the stigmal opening. In geophiloids most or all of the body segments carry a stigma on each side, but in the scolopendroids a reduction in number of stigmata is observed, and a count of the stigmatiferous segments provides formulas characteristic for certain genera. This reduction is considered to be a specialization of some sort, a departure from the primitive homonomous condition.

The sterna in most forms are provided with fields or areas of cuticular pores, capable often of secreting luminescent material. The shape and distribution of pore fields provides generic and specific characters. In geophiloids the anterior edge of many sternites is provided with a median paxilla that may or may not project into a depression (sacculus) on the rear of the preceding sternum.

The legs are typically composed of seven podomeres (Fig. 382,*4*); the coxa may be distinct and easily recognizable or partially involved in the pleural structure and difficult to distinguish clearly. The telopodal segments are the trochanter, prefemur, femur, postfemur, tibia, tarsus, and tarsal claw (or pretarsus). The tarsus may be divided into two segments, or, in the Scutigerida, into a great number of very small pseudotarsi. Aside from length and proportions, leg structure is essentially homogeneous within a given order. The terminal legs are commonly modified. In some scolopendroids they are enormously thickened and modified into a pair of pincers used in defense and perhaps also in the capture and holding of prey. In many geophiloids the ultimate pair of legs of the males are clavately enlarged and glandular; the same is often true in the Lithobiida where some of the podomeres are enlarged, or ornamented, or provided with deep cavities. In many of the latter order, the penultimate legs are involved in sexual modification, and in both sexes the two last pairs are normally much longer than others and usually carried above the ground when the animal is running. These legs have recently been distinguished as "tenacipeds" from the other 13 pairs of "cursipeds." In lithobioids and scutigeroids, the ultimate legs produce a type of viscid secretion that forms thin threads handled by the tenacipeds to entangle captured prey. In the Scutigerida a generic name *Lassophora* has been set up in recognition of this peculiarity. In some groups of chilopods, particularly geophiloids, the last pair of legs may be reduced in size and number of podomeres, and the terminal claw may be lost entirely.

The terminal end of the body, beyond the last pair of ambulatory legs, apparently derives from three embryonic somites; in the adult it forms a rather compact genitoanal region composed of two apparent segments with separate sternites and tergites. The genital segment is provided with small appendages composed of two or three segments and presumably homologous to the regular legs. These so-called gonopods are more prominent in the females (Fig. 382, *5*), and in the Lithobiida their form and basal spines provide specific characters.

The corresponding male structures are either small styliform remnants or absent; the penis is small, poorly sclerotized, and contained entirely within the body; it provides little in the way of systematic characters.

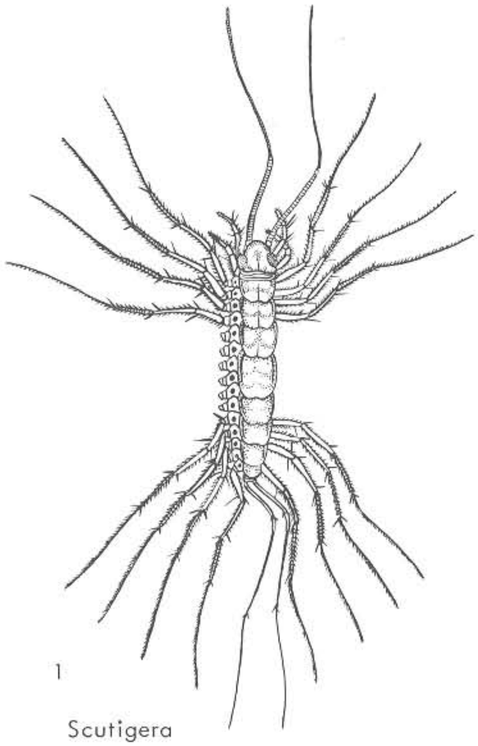
Chaetotaxy plays a very important role in the classification of many centipede groups, especially in the Lithobiida where the legs are provided with serially homologous, movable spurs on most or all segments. Several methods of presenting and evaluating variation in the leg spurs have been devised; probably the best is the so-called "Ribaut system." By this approach, each spur may be given a code designation that indicates its location on the leg; thus "VPA" means a spur on the ventral, anterior side of the prefemur. This spur can then be localized by providing the number of the legs on which it is found; thus "VPA *13-15*." A complete presentation of spur distribution can be achieved by the use of a table such as shown below in abbreviated form (dorsal setae only; for leg pairs *1, 2, 14,* and *15*. C=coxa; P=prefemur; F=femur; Ti=tibia; a, m, and p=anterior, median, and posterior):

Spur Distribution on Legs of Chilopoda

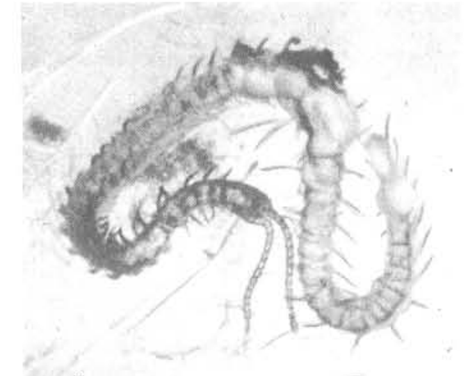
	C	P	F	Ti
1		p	a	a
2		p	ap	a
14	a	mp	p	
14	a	amp	p	

Subclass ANAMORPHA Haase, 1880

Development hemianamorphic, young with only seven pairs of legs when hatched from egg, then passing through four or



1 Scutigera



2 Geophilus

FIG. 383. Scutigeridae *(1)*; Geophilidae *(2)* (p. *R602-R603*).

five anamorphic stages in which body segments and legs are added and finally through several additional anamorphic stages to achieve maturity; eggs laid singly by female and never brooded. Body with 19 segments and 15 pairs of legs, segments usually displaying distinct alternation of large and small tergal plates; stigmata opening on segments *2, 4, 6, 9, 11, 13,* and *15,* but may be missing from one or more of them. *Oligo.-Rec.*

Order SCUTIGERIDA Pocock, 1895

[*nom. correct.* CHAMBERLIN, 1941 (*pro* Scutigeromorpha POCOCK, 1895)] [=Schizotarsia BRANDT, 1841; Anartiostigmata SILVESTRI, 1895]

Body composed of 15 leg-bearing segments, covered dorsally with eight distinct tergites that correspond to larger tergites of Lithobiida; tracheal system opening through dorsal, median, unpaired stomata located on posterior edge of tergites. Antennae extremely elongated, with as many as 400 tiny articles. First maxillae small and short, with prominent coxa, setose coxal lobe, and two-pointed telopod; second maxillae very long and slender, having greatly reduced sternum fused with coxa on each side, prefemur and femur with long slender macrosetae or bristles. Prehensors large, prominent, their sternum reduced or absent, coxae large, medially in contact but not fused, each with several long stout spurs on distal edge. Legs long, their basal articles with several long acicular setae, tarsi divided into great number of small secondary segments. Tergites usually invested by various spicules, setae, hairs, cones, and other modifications. [A highly specialized group of chilopods, now chiefly tropical in distribution, often placed in a subclass of its own. Several species of southeast Asia attain a body length of two or three inches.] *Oligo.-Rec.*

Family SCUTIGERIDAE Newport, 1844

Characters of order. [Two subfamilies and about 18 genera are recognized.] *Oligo.-Rec.*

Scutigera LAMARCK, 1801 [**Scolopendra coleoptrata* LINNÉ, 1758; OD, M] [=*Cermatia* ILLIGER, 1807; *Selista* RAFINESQUE, 1820; *Cryptomera* RAFINESQUE, 1820]. Basal podomeres with longitudinal keels or crests; antennal articles broader than long; tarsi of 6th to 14th pairs of legs with 2 distal spines; tergites with acute spinules. *Oligo.-Rec.,* Eu.-N.Afr.-Asia-C.Am.——FIG. 383,*1*. *S. leachi* KOCH & BERENDT, Oligo. (Baltic amber), NW.Eu.; entire animal, except legs of mid-region, ×3.6 (after Koch & Berendt).

Order LITHOBIIDA Pocock, 1895

[*nom. correct.* Chamberlin, 1941 (*pro* Lithobiomorpha Pocock, 1895)] [=Artiostigmata Silvestri, 1895; Unguipalpi Bollman, 1893]

Body composed of 15 segments having alternate large and small tergites (those of segments *1, 3, 5, 7, 10, 12, 14,* and *16* much smaller than others); stigmata on segments *2, 4, 6, 9, 11, 13,* and *15* or on reduced number of this series down to minimum of two segments. Antennae undifferentiated, filiform, with 13 to more than 100 articles. Ocelli present or absent. Mandible terminating in several strong teeth and accessory plumose setae. Sternum of first maxillae small, coxae essentially separated, telopods biarticulate; coxae and sterna of second maxillae fused, telopods with three or four segments, no palps present, terminal claws simple. Prehensors with large medially suturate coxosternum, its anterior edge dentate; telopod robust, uncate, with large distal segment. Coxae of ambulatory legs divided into four subsegments, each subtended by pleural procoxal sclerite; telopods normally with six podomeres, tarsus commonly divided into two or three subsegments. Legs of first to 13th pairs short and used for locomotion (cursipeds), last two pairs (14th, 15th) elongate and apparently used for mating or capture of prey or both (tenacipeds); podomeres of most legs provided with macrosetae or movable spurs in regular, serially homologous sequences. *Oligo.-Rec.*

The order is divided into several families with essentially separate present distributions. The Lithobiidae are basically Holarctic; the Gosibiidae are represented in Central America, southern United States, and eastern Asia; the Cermatobiidae and Henicopidae are chiefly confined to the Southern Hemisphere, although a few henicopid genera occur in North America. Undisputed fossils are known so far only from Baltic amber, the nominate genus *(Lithobius)* being still abundant in the same region at the present time.

Family LITHOBIIDAE Leach, 1814

Several posterior legs with coxal glands, most legs with macrosetae or spurs; pleura of prehensorial segments not in contact ventrally behind coxosternum; tibiae of legs without terminal triangular projection. Ocelli, when present, close to edge of cephalic plate. *Oligo.-Rec.*

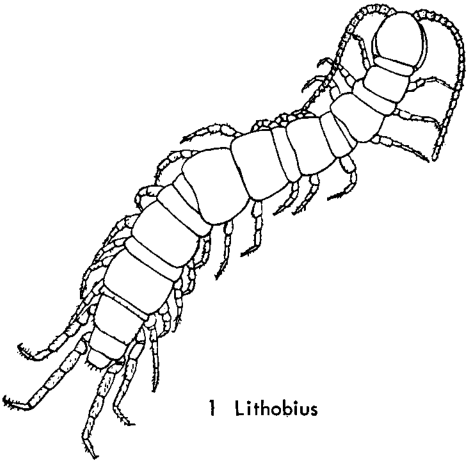


Fig. 384. Lithobiidae (p. *R*603).

Lithobius Leach, 1814, p. 408 [**Scolopendra forficata* Linné, 1758; OD, M]. Coxae of last 4 or 5 pairs of legs with only single row of gland pores on ventral side, 1st segment of female gonopods not modified along its inner margin. Antennae with more than 25 articles. All tarsi divided into 2 subsegments; tenacipeds of males unmodified; prosternum of prehensors with 2 or 3 marginal teeth. *Oligo.,* Eu.; *Rec.,* N.Am.-Eu.——Fig. 384,*1*. *L. tricalcaratus* (Attems), Rec., N.Am.; entire animal, dorsal aspect, ×10 (Attems).——Fig. 382, *1,5*. **L. forficatus* (Linné), *Rec.,* Eu.; *1,* prehensors, ventral aspect, enl.; *5,* post. end of body of female, ventral aspect (Attems).

Subclass EPIMORPHA Haase, 1880

Postembryonic development epimorphic, young leaving egg with complete complement of legs and segments; body with at least 25 segments, up to maximum of nearly 200. Eggs brooded by female parent. *Cret.-Rec.*

Order GEOPHILIDA Pocock, 1895

[*nom. correct.* Chamberlin, 1941 (*pro* Geophilomorpha Pocock, 1895)] [=Pantastigmata Silvestri, 1895]

Body very elongate, vermiform, with short legs and antennae; body segments ranging from 31 to nearly 200 (number rarely constant for given species); stigmata present on all segments from second to penultimate. Antennae with 14 articles, ocelli never present. Sterna commonly with pore fields; pleural sclerites may be numerous and in several longitudinal series. Legs short, never beset with stout movable spurs. *Cret.-Rec.*

This order of superficially very similar animals is divided into nearly a dozen families on the basis of mouth-part structure. The characters utilized are extremely subtle, and in the case of small species, must be determined from microscope-slide preparations studied with an oil-immersion lens. The family position of some individuals can be determined on the basis of their external form, but usually only by a specialist who is very familiar with the group. It is possible that specimens in amber can be identified correctly, but other fossils cannot be determined reliably.

Family GEOPHILIDAE Newport, 1844

Mandibles without dentate lamella, their margins with pectinate fringe; one or two clypeal areas behind bases of antennae, which are threadlike and only rarely thickened distally. Paratergites absent. Terminal legs six- or seven-jointed, usually with distal clawlike pretarsus. *Oligo.-Rec.*

Geophilus Leach, 1814 [**Scolopendra electrica* Linné, 1758; OD, M]. Body usually widest at head; no clypeal areas present. Coxae of 2nd maxillae fused into syncoxite; telopods of prehensors composed of 4 segments, prehensors usually not extending in front of the head. *Oligo.*, Eu. (Baltic Region); *Rec.*, Eu.-N.Am.——Fig. 383,2. *G.* sp., Oligo., Baltic amber; whole animal, ×12 (Bachofen von Echt).

Family UNCERTAIN

Calciphilus Chamberlin, 1949 [**C. abboti*; OD]. *Cret.*, USA(Ariz.).

Order SCOLOPENDRIDA Pocock, 1895

[*nom. correct.* Chamberlin, 1941 (*pro* Scolopendromorpha Pocock, 1895)] [=Oligostigmata Silvestri, 1895]

Small to huge chilopods which are voracious predatory animals. Body usually robust, with 25 or 27 segments bearing long legs and antennae; stigmata present on only about half of body segments. Antennae usually with 17 to 34 articles (number usually constant for species at lower end of range). Ocelli usually present, sporadically absent. Last pair of legs usually longest, commonly greatly modified (thickened, compressed), and minimally with stout spines on some or all podomeres. *Rec.*

The smallest species of this order are about 15 mm. in length, whereas the largest (*Scolopendra gigantea*) is nearly 270 mm. long, exceeding nearly all other terrestrial arthropods. The order is predominantly tropical or subtropical in its present distribution.

Family SCOLOPENDRIDAE Newport, 1844

Ocelli present, usually four on each side of head. Sternites with two paramedian longitudinal sutures or none, never with transverse sutures; each half of intercalary sternites divided, intercalary tergites usually poorly developed, often not visible. Tarsi always divided into two segments. [One species, of very dubious generic position, has been described from the Baltic amber. The following generic diagnosis applies to Recent species, and not necessarily to the single known fossil.] *Oligo.-Rec.*

Scolopendra Linné, 1758 [**S. forficata;* OD, M (but see Crabill, 1954, Bull. Zool. Nomencl., v. 11; p. 134, for proposed designation of *S. morsitans* Linné as type species in harmony with accustomed usage]. With 21 pairs of legs, all tarsi triarticulate; 9 pairs of spiracles; claw of maxillary palp dentate on inner edge. [One fossil species (*S. proavita* Menge) is assigned to this now dominantly tropical genus.] *Oligo.*, Eu.(Baltic region); *Rec.*, tropical and subtropical areas of all continents.

Class, Order, and Family UNCERTAIN

The following generic names have been based upon presumptive myriapod remains of late Paleozoic age, but in such condition as to make their reference to a particular class virtually impossible. The authors of the names referred them to the Chilopoda or Archipolypoda.

Eileticus Scudder, 1882, p. 178 [**E. anthracinus*; OD, M]. *Penn.*, USA(Ill.).

Hemiphoberia Fritsch, 1899, p. 40 [**H. alternans*; OD, M]. *U.Carb.*, Eu.(Czech.).

Heterovorhoeffia Fritsch, 1899, p. 42 [**H. crassa*; OD, M]. *U.Carb.*, Eu.(Czech.).

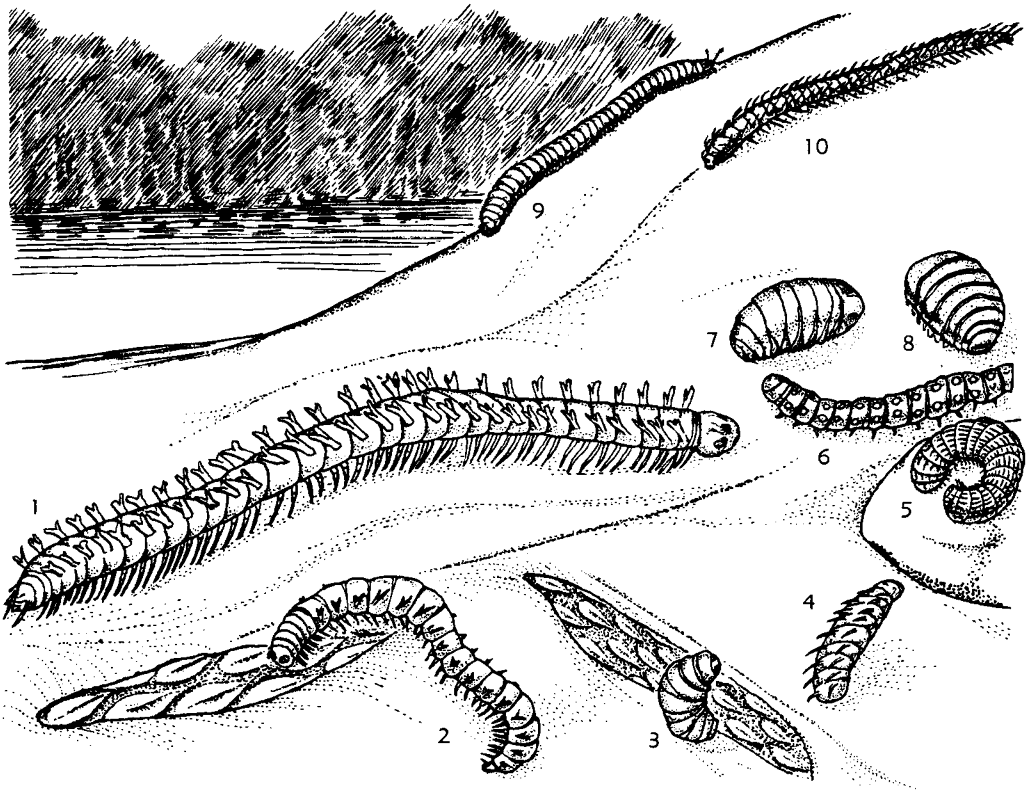


FIG. 385. Upper Carboniferous myriapod fauna from Bohemia (reconstr.), animals, ×0.7; (1) *Acantherpestes gigas;* (2) *Acantherpestes ornatus;* (3) *Archiscudderia paupera;* (4) *Amynilyspes typicus;* (5) *Xyloiulus pstrossi;* (6) *Sandtneria gemmata;* (7) *Glomeropsis ovalis;* (8) *Archiscudderia problematica;* (9) *Pleurojulus biornatus;* (10) *Euphoberia histrix* (after Fritsch).

Ilyodes SCUDDER, 1890, p. 442 [**I. divisa*; SD HOFFMAN, herein]. *Penn.*, USA(Ill.).

Latzelia SCUDDER, 1890, p. 418 [**L. primordialis*; OD, M]. *Penn.*, USA(Ill.).

Palenarthrus SCUDDER, 1890, p. 421 [**P. impressus*; OD, M]. *Penn.*, USA(Ill.).

Purkynia FRITSCH, 1899, p. 41 [**P. lata*; OD, M]. *U.Carb.*, Eu.(Czech.).

Sandtneria FRITSCH, 1899, p. 42 [**S. gemmata*; OD, M]. *U.Carb.*, Eu.(Czech.).

GENERIC NAMES INCORRECTLY REFERRED TO MYRIAPODA

Palaeocampa MEEK & WORTHEN, 1865, p. 52 [**P. anthrax*; OD, M]. This nominal genus was made the type of an order Protosyngnatha by SCUDDER, 1882; more recently *P. anthrax* has been regarded as a polychaete annelid. Whatever its correct position, *Palaeocampa* does not seem to be a myriapod.

Julopsis HEER, 1874, p. 120 [**J. cretacea*; OD, M]. The status of this form has not been challenged hitherto, but close examination by me of HEER's original figures (K. Svenska Vetenskaps. Akad., Handl., v. 12, no. 6, 1874) has failed to provide basis for distinguishing *J. cretacea* from any of the fern frond remains with which HEER's paper is concerned. *Julopsis* then may be construed as an available occupied generic name in botany.

Palaeojulus GEINITZ, 1873 [**P. dyadicus*; OD, M]. Based upon a fern frond, *Scolecopteris elegans.*

Trichiulus SCUDDER, 1884, p. 291 [**T. villosus*; SD HOFFMAN, herein]. This generic name was later discarded by SCUDDER himself as based upon a plant fragment.

INVALIDLY PROPOSED FAMILY-GROUP NAMES FOR MYRIAPODS

A number of family-group names were set up by FRITSCH (1899) for myriapods described from the Nyrany coal beds of Czechoslovakia and several by SCUDDER (1890) for American forms of similar age. Some of these names (listed below) are invalid, as they are not derived from the stem of any generic name originally assigned to them.

Acroglomeridae FRITSCH, 1899, p. 33. Name proposed for the single genus *Archiscudderia* FRITSCH, 1899 (pentazoniate diplopod now placed in Amynilyspedidae, order Amynilyspedida).

Eoscolopendridae SCUDDER, 1890, p. 419. Name proposed for the genera *Eileticus* SCUDDER, 1882, *Palenarthrus* SCUDDER, 1890, and *Ilyodes* SCUDDER, 1890 (myriapods of uncertain class, order and family).

Gerascutigeridae SCUDDER, 1890, p. 418. Name proposed for the genus *Latzelia* SCUDDER, 1890 (myriapods of uncertain class, order and family).

Proglomeridae FRITSCH, 1899, p. 35. Name proposed for the genus *Amynilyspes* SCUDDER, 1882 (pentazoniate diplopod, Amynilyspedidae).

Projuloidae FRITSCH, 1901, p. 25. Invalid name based on nonexistent genus proposed to include polydesmids *Isojulus* and *Pleurojulus* and spirobolids *Anthracojulus* and *Xylobius* (=*Xyloiulus*).

Sphaerherpestidae FRITSCH, 1899, p. 38. Name proposed for the genus *Glomeropsis* FRITSCH, 1899 (pentazoniate diplopod, Amynilyspedidae).

RESTORATION OF CARBONIFEROUS MYRIAPODS

In the nature of an afterthought summarizing features of various sorts of fossil myriapods, it seems appropriate to reproduce an assemblage of Upper Carboniferous fossils of this group as reconstructed by FRITSCH (Fig. 385).

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ARTHROPLEURIDA

By W. D. Ian Rolfe

[Hunterian Museum, University of Glasgow] [The writer is indebted to Dr. S. M. Manton, F.R.S., for helpful discussion of *Arthropleura* and living myriapods, and to Dr. J. K. Ingham for much assistance in reconstructing *Arthropleura*]

[Chapter submitted June, 1966]

CONTENTS

INTRODUCTION

The arthropleurids are an extinct group of rare gigantic centipede-like arthropods which inhabited coal swamps during Late Carboniferous times. The group, as here interpreted, is known with certainty to contain only the eponymous genus *Arthropleura,* although two other genera may be related, one of them even ancestral.

There has been much discussion of the affinities of *Arthropleura*: it has been referred to Chelicerata, Trilobitomorpha, Crustacea, Myriapoda, and Arthropoda *incertae sedis.* The Arthropleurida is here tentatively regarded as a unique class of myriapods, showing parallel evolutionary trends to the polydesmid diplopods, but differing from them in the number of segments in and structure of the limb, and in the gigantic length attained. Although arthropleurids are rare, their huge size makes them suitable for detailed study and the limb is as well known as that of any fossil arthropod. In terms of body size, *Arthropleura* can claim to be the largest terrestrial arthropod known.

MORPHOLOGY

The most striking feature of *Arthropleura* is its colossal size. The largest most complete specimen known *(7)* is two feet eight inches long (80 cm.), yet isolated segments and paratergal folds which have been found indicate that animals up to six feet (180 cm.) in length must have existed *(9).* Small individuals representing young instars are also known, however, and the most complete of these (described as the separate species *A. moyseyi* by Calman but subsequently regarded as a juvenile *A. armata*) is 65 mm. long (Fig. 386).

The cuticle seems to have been relatively thin for such a large arthropod: Waterlot states that its maximum thickness is 2 mm. Over the large rosette plate (shown on Figure 391,*C*) the space between internal and external molds measures less than 0.12 mm., indicating a cuticle of this thickness. In flattened, carbonized limbs, details of the morphology of one surface are commonly impressed through onto the other (*see* Fig. 389,*C*), as may also be details of the venation of underlying plant fragments. There is no indication that the cuticle was mineralized during life and it was probably only toughened by sclerotization.

The juvenile *Arthropleura armata* referred to above (Fig. 386) has the course of the intestine indicated in the hind two-thirds of the body by a zone of darker ironstone packed with plant fragments. It occupies just more than half the width of the axis and is confined to it, although secondarily pressed through the tergites.

FIG. 386. Rubber cast from external mold of almost complete juvenile *Arthropleura armata* JORDAN & MEYER (holotype of *A. moyseyi* CALMAN), head slightly displaced, dorsal, U.Carb., Eng., ×2 (Rolfe, n).

HEAD

The head is known from only one specimen (Fig. 386). It is poorly preserved, but can be seen to be broader than long and approximately one-third the greatest width of the body. The specimen shows the ventral surface of the head, with an anteriorly fimbriated, curved appendage forming the side of the head and thus resembling the myriapod mandible in position.

BODY

The body is elongate and of almost uniform width but tapers anteriorly and posteriorly (Fig. 387). It is longitudinally trilobed dorsally, forming a median **axis** with lateral **paratergal folds.** The tergites are dorsoventrally depressed and there is no reason to believe that they were much more convex in life.

The number of body somites is unknown; the two almost complete specimens described have 27 and 23 postcephalic somites preserved, but both specimens are somewhat disarticulated and these numbers are minimal. No telson has yet been observed.

Tergites of the somites vary in shape, size, and ornament according to their position on the body and according to the age of the individual. Anterior tergites are narrower, show more anteriorly oriented paratergal folds and bear fewer tubercles and spines than those in the central region of the body (Fig. 388); the first three tergites are also shorter than succeeding ones. Posteriorly the tergites gradually diminish in breadth and have the paratergal folds increasingly directed rearward. Each tergite overlaps the next somite behind by approximately one quarter of its length. This region of the tergite is only finely tuberculate and bears a transverse rib and furrow marking it off from the main area of the tergite.

The axial region of each tergite is rectangular and separated from the two lateral triangular paratergal folds by furrows. From this furrow and the frequent occurrence of paratergal folds isolated from axes most authors have deduced that the paratergal folds were movably articulated with the axis, and indeed the name *Arthropleura* refers to this feature. It is possible, however, that the split sometimes seen separating paratergal folds from the axis is due to flattening of the originally more convex segment and not to any original hinge structure.

Both axis and paratergal folds commonly bear all sizes of tubercles, grading from large, posteriorly directed, blunt conical spines to fine granules. Each paratergal fold also bears two recurved keels, the crests of which are serrate-tuberculate distally. The tuberculation pattern and direction of the prominent, main paratergal keel have been

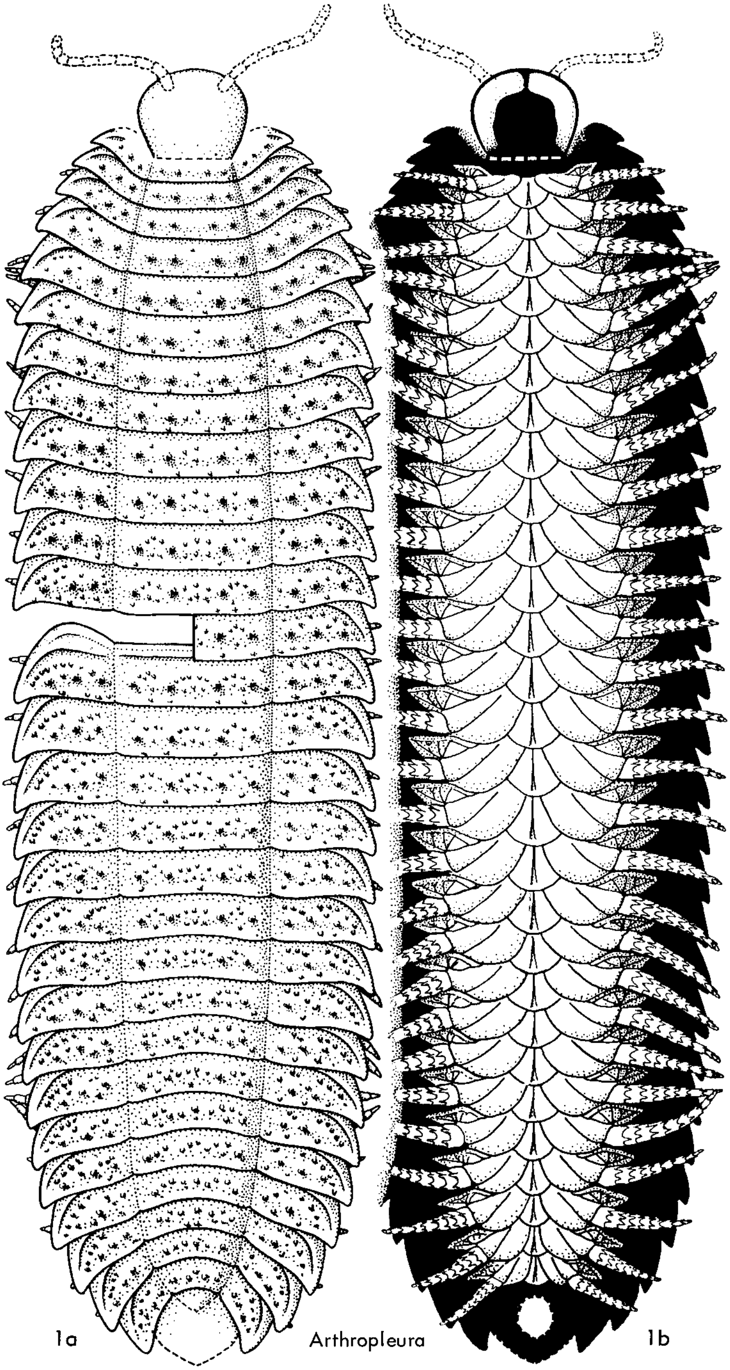

FIG. 387. Reconstruction of *Arthropleura armata* JORDAN & MEYER, dorsal, ventral. Half of one tergite removed to show anterior border of underlying tergite; no limbs shown on first trunk somite. Interrupted lines indicate restored regions of body, approx. ×0.1 *(16)*.

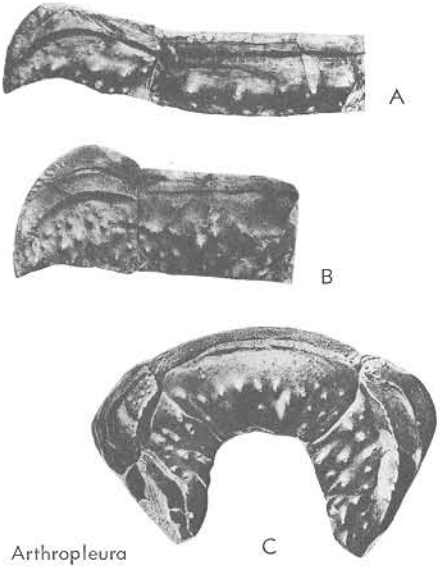

FIG. 388. Isolated tergites of *Arthropleura armata* Jordan & Meyer, dorsal, Carb., Saar, ×0.5.——*A*. Axis and left paratergal fold from anterior body somite showing anteriorly directed paratergal fold and sparse tuberculation *(19)*.——*B*. Axis and left paratergal fold from middle body somite *(19)*.——*C*. Complete last body somite (pretelson) *(1)*.

the two chief characters used in differentiating species of *Arthropleura,* although no statistical study of these highly variable characters is yet available.

The sternite is only seen preserved as a triangular area between the bases of the ventral limbs. It bears a shallow median longitudinal sulcus and has a convex posterior margin. According to Waterlot *(19),* the integument is either smooth or finely granulose. The pleuron immediately underneath the paratergal folds is finely pitted (or granulose?) and wrinkled, but otherwise featureless. Other structures which probably comprise the pleuron are dealt with in the following section.

LIMBS AND ASSOCIATED STRUCTURES

Each segment bears one pair of limbs ventrally inserted almost halfway between the mid-ventral line and tips of the paratergal folds. Prior to 1934 all authorities agreed that the limb of *Arthropleura* was uniramous. After a most exhaustive study of the available material Waterlot *(19)* concluded that the limb was biramous, comparable to that of the trilobite in basic structure yet even more primitive in that the two rami were identical in form. This interpretation was challenged by Størmer (1944), and subsequent study by Rolfe and Ingham *(16)* of largely uncrushed material (Fig. 389) vindicated Størmer's view that the limb is uniramous. A reconstruction of the limb is shown in Figure 390.

It is not yet known whether the limb comprises eight, nine or ten segments. The clawlike pretarsus numbered *10* may not be an independent segment and the posterior, incompletely preserved segment *1* may not be a limb segment but a subcoxal sclerite. Thus either it, or segment *2,* represents the coxa. Each segment bears distally a pair of stout outwardly and downwardly directed spines. Segment *8* is consistently longer than other segments, although one specimen (Fig. 389,*B*) is known in which a more proximal segment is longest, suggesting either that this limb is abnormal owing to regeneration after an injury, or that the segment number is not constant for all limbs. The anterior surface of the limb is smooth, whereas the posterior face bears tubercles, some of which show a terminal pore suggesting the original presence of a seta. Both surfaces of the limb show sharp linear invaginations of the cuticle, which on the proximal regions of the limb run obliquely across the segments. These form ridges on the inside of the limb, probably analogous to the *costae coxales* of Recent centipedes, and doubtless served both to strengthen the leg joints and to provide sites for the attachment of limb muscles. It was these ridges, and especially that on the proximal region of the posterior face of the limb, that Waterlot misinterpreted as the dorsal edge of one ramus of a biramous limb overlapping the other ramus. On the posterior face of the limb, the invaginations of segments *1, 2,* and *3* have a radial disposition (Fig. 390) and when found isolated these segments may be mistaken for a rosette plate and its associated anterior face of segment *2.*

The more proximal structures associated with the limb may be referred to as the **rosette plate, B plate** and **K plate.** The two

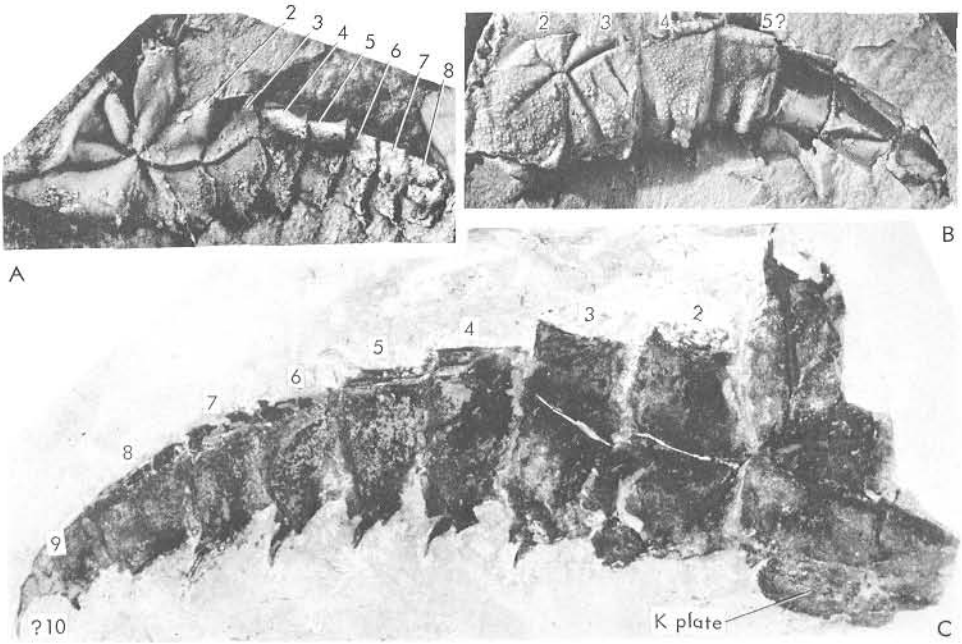

FIG. 389. Limbs of *Arthropleura*.——*A*. Rubber cast from external mold of anterior face of left leg of young individual showing *B* and rosette plates and segments *2-8*, Carb., Eng., ×2.3.——*B*. Right leg, showing internal mold of posterior face of segments *2-5?* and external mold of anterior and dorsal surface of distal segments (one segment lacking in this individual, possibly due to regeneration), Carb., Eng., ×2.3.——*C*. Complete flattened right leg, anterior view, but with features of posterior face of limb impressed through. Shows *K*, *B*, and rosette plates and segments *2-10*, Carb., Neth., ×1.1 *(16)*.

latter terms were introduced by KLIVER (1884) and ANDRÉE *(1)* to signify the basal segment and supposed gill lamella *(Kiemenblätter)* of the limb. All three structures are here interpreted as sclerotized regions of the body wall (*i.e.*, pleurites or subcoxal sclerites), as in living centipedes (MANTON 1965; SNODGRASS 1952), rather than true limb segments, although there must still be debate on this point as outlined below. Since the function of the rosette plate is only a passive one, therefore, it is suggested that the hitherto used term "rosette organ" be abandoned.

The rosette plate is an elongate, convex plate, bounded anteriorly and posteriorly by convex borders, and divided into a number of lobes by deep subradial sulci. WATERLOT *(19)* devised the notation given in Figure 390 for these lobes. Most of the lobes shown usually are present but in older individuals the number of adventitious lobes is greater and the lobes tend to be more irregular in form (Fig. 391). Several of the lobes bear mammiform tubercles with central pores which were originally setiferous. Young individuals lack this tuberculation, however (Fig. 389,*A*).

The *B* plate is a triangular convex posterior extension of the rosette plate, from which it is separated by a deep sulcus oriented almost perpendicular to the sagittal plane of the body (Fig. 392). Such a huge terrestrial creature as *Arthropleura* would need massive buttressing of the limb bases at their insertion on the body wall to enable limb movement to take place. It seems likely that the rosette and *B* plates provided such reinforcement of the pleuron, and their situation in front of the limb suggests that the limbs thrust backward and downward in normal locomotion.

In an attempted analogy with *Limulus*, WATERLOT *(19, 21)* regarded the *C* lobe of the rosette plate (Fig. 390) as a precoxal segment, which attached the limb to the

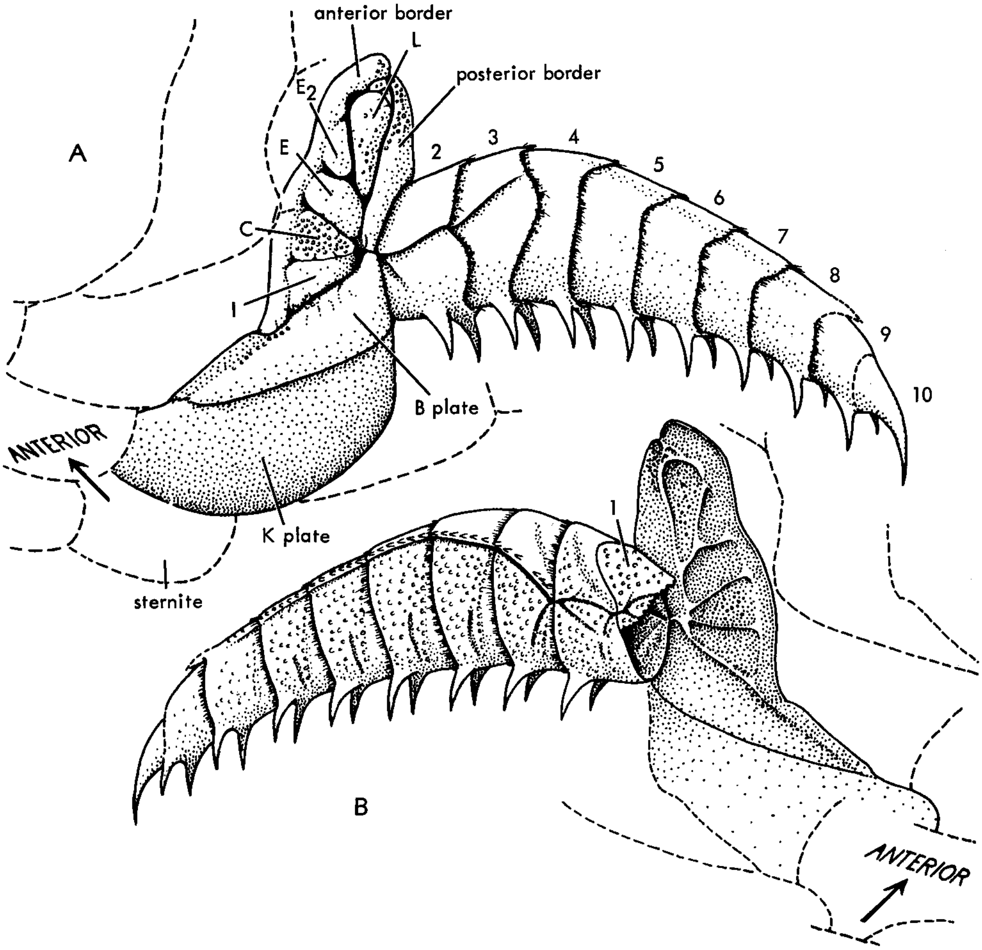

FIG. 390. Reconstruction of left leg of medium-sized adult *Arthropleura.* Both views are taken obliquely to emphasize the morphology and the limb is thus slightly foreshortened. Interrupted lines indicate most of sternite, *K, B,* and rosette plates of body somite immediately in front and posterior edge of *B* plate of somite immediately behind, and serve to orient the limb relative to the body wall. The letters show WATERLOT's notation for lobes of the rosette plate——*A.* Anteroventral view.——*B.* Posterodorsal view ×1 *(16).*

body wall and articulated with it by the insertion of the *C* lobe between the *I* and *E* lobes (supposedly evaginations of the sternum). As RICHARDSON *(14)* has pointed out, however, WATERLOT's schematic cross section of a limb-bearing somite (*19,* fig. 27; *21,* fig. 4) is misleading in showing a leg suspended wholly outside the body, with no provision for the passage of leg muscles into the body. Furthermore, to separate off the *C* lobe as a distinct limb segment is clearly unjustifiable. It is difficult to accept WATERLOT's interpretation of the homologies of the other basal limb structures which followed from his view. For example, it would be impossible to recognize as such a precoxa which articulated with the basis and yet not with the coxa, as WATERLOT's latest reconstruction *(21)* implies.

The frequent occurrence of isolated well-preserved rosette plates with their *B* plates attached implies that the surrounding pleuron consisted of unsclerotized integument, as must also the intersegmental mem-

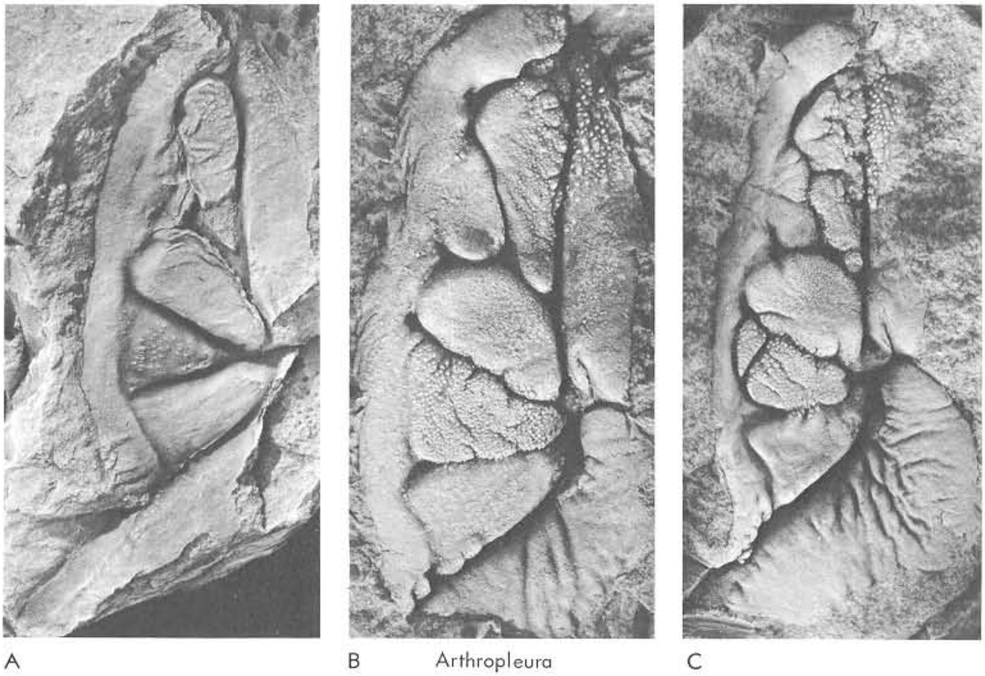

FIG. 391. Left rosette plates with portion of *B* plate attached of *Arthropleura* to show increase in tuberculation and number of adventitious lobes with size (i.e., age).——*A*. Westphal., Neth., ×1.8.——*B*. Penn., USA(Ill.), ×1.5.——*C*. Penn., USA(Ill.), ×1 (Rolfe, n).

brane between these plates and limb segment *2*.

The *K* plate ("ventral lobe" of STØRMER, 1944; "epipodite" or "gill plate" of other authors) is a thin plate, usually oval and irregularly wrinkled. In isolated limbs and limb fragments this plate appears pitted and commonly occurs with its anterior edge tucked under the incurved posterior edge of the *B* plate, but it may also overlap the same plate and WATERLOT has suggested that it is only attached by a small tongue to the "distal" end of the *B* plate; the variable position of the plate suggests that it is only attached by unsclerotized integument. The original position of the plate is therefore doubtful. If the pitting is regarded as the internal expression of tuberculation, then this plate would seem to be part of the posterior face of the limb, only secondarily shifted into an anterior position. The consistent position of the overlapping *K* plates preserved *in situ* on the flattened specimen shown in Figure 392 argues against this, however. Differences in appearance between *K* plates on isolated limbs and those *in situ* probably reflect their different attitudes during flattening. The *K* plate has only one surface and it is therefore difficult to interpret it as a lamellar gill, as originally suggested by KLIVER and accepted by subsequent authors. If the *K* plate could be shown to be a gill plate it would imply that the *B* and rosette plates were coxal structures. ANDRÉE *(1)* and PRUVOST (1919) thought that the *K* plates might represent oostegites. The *K* plate is here interpreted as a convex, less sclerotized area of the ventral integument. The function of the plate, if it is not just an intercalated sclerite, must remain doubtful until its structure and position on (or even within) the body are better known. It is tempting to regard it as homologous with either the coxal sac or eversible vesicle of modern myriapods; VERHOEFF suggested that the supposed coxal sacs of the Myriapoda Archipolypoda enabled their owner to respire on land and

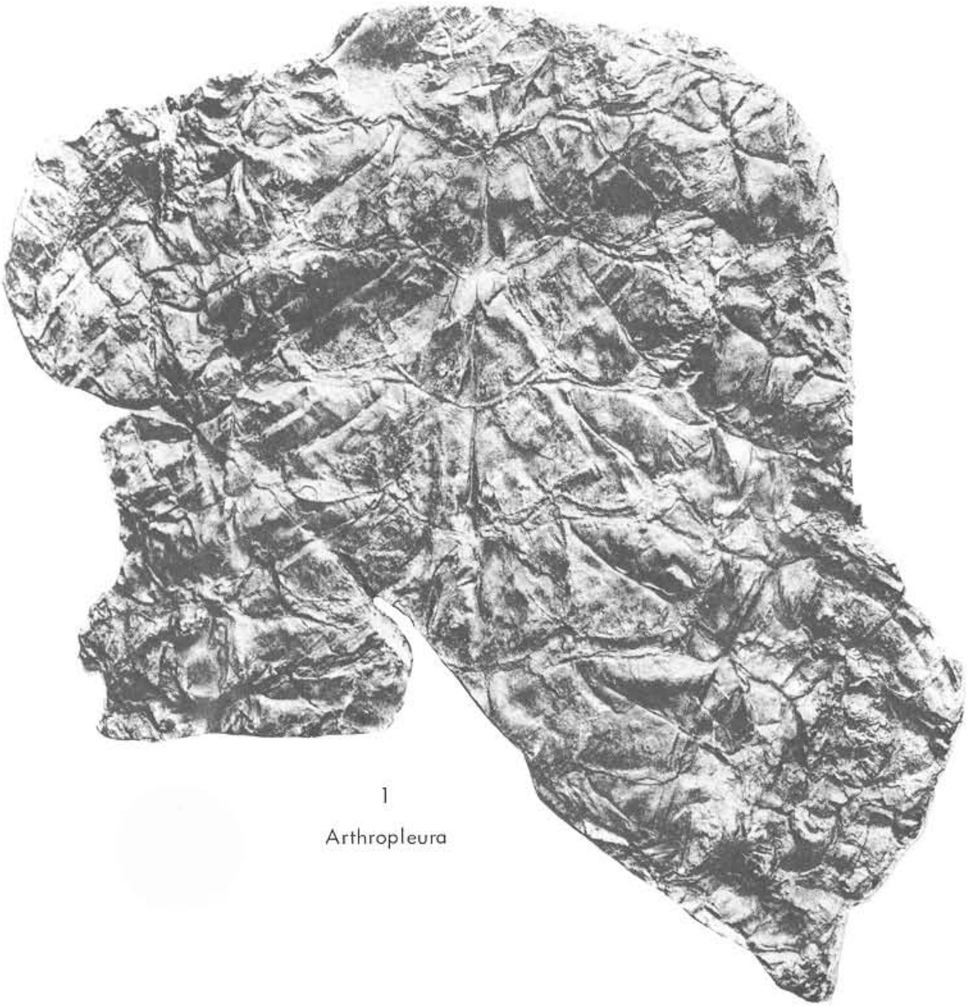

FIG. 392. Pedigerous ventral surface of small specimen of *Arthropleura armata* JORDAN & MEYER. This specimen, which is only half of an originally larger specimen, shows 7 pairs of limbs flattened *in situ* onto 6 sternites. Most of the rosette plates are concealed beneath limbs of the somite immediately in front, but one can be seen at the top right, Carb., Saar, ×1 *(19)*.

could be everted to function as gills when in water.

In 1947 WATERLOT *(20)* described two limb segments which he suggested belonged to a gnathobasic cephalic limb. Additional evidence is required before this view can be confirmed or denied.

PALEOECOLOGY

Most specimens of *Arthropleura* have been found either in nonmarine shales or clay ironstone concretions of the Coal Measures. The few which have been found in undoubted marine strata were probably washed in from nonmarine sources. Finds are characteristically associated with plants, the delicate fronds of which are so well preserved that WATERLOT *(19)* inferred that they could not have drifted far. This association with abundant plants, commonly in roofs of coal seams, suggests that both *Arthropleura* and vegetation were drowned by the submergence of the forest swamp at the initiation of another cyclothem. Furthermore, the most abundant finds of *Arthropleura* have been made in the limnic basin of the Saar, where there is a complete absence of marine fauna, the associated forms being chiefly insects and chelicerates, with a few nonmarine ostracodes, branchiopods, bivalves, fishes, *Spirorbis,* and a myriapod *(19).* The largest most complete specimens known come also from such intermontane limnic basins, whereas specimens from paralic deposits usually occur as detached paratergal folds, axes, sternites, limbs, limb fragments, or rosette plates (8). The ever-present problem of selective diagenesis must not be overlooked, however, and it is possible that any originally calcareous shelly fauna would be dissolved during the production of humic acids in peat formation. Similarly, the tenuous condition of the *Arthropleura* cuticle may only be a reflection of these conditions, mineralized layers in the cuticle being readily dissolved under these conditions and only sclerotized tissues remaining unattacked.

From their occurrence and morphology, WATERLOT *(19,21)* deduced that *Arthropleura* was amphibious. He suggested that it was predominantly a lacustrine creature, which moved slowly over the surface of marshy lake floors breathing by gill lamellae. He also envisaged that *Arthropleura* could climb out onto land and live in the undergrowth where the necessary humidity would be maintained to enable the gill plates to function. From the nature of the supposed cephalic limb, WATERLOT *(20)* inferred that *Arthropleura* was carnivorous and fed on small prey such as worms. Even if this limb is a gnathobasic maxilla, however, this need not imply a carnivorous owner, for such a large creature, if herbivorous, would also need powerful mouth parts to break and shred the large amount of vegetation required for sustenance. VAN DER HEIDE (*10;* 1956) questioned the aquatic habit, suggesting that the development of legs with pointed claws indicated that *Arthropleura* clambered among the plant debris of the boggy ground of the coal swamp.

Until the nature of the *K* plates is elucidated or spiracles are discovered, the exact way in which *Arthropleura* respired, and hence its habit, must remain obscure. However, comparison with the form and function of modern myriapods is fruitful, thanks to the valuable body of knowledge published by MANTON (1950-65). As KOMAREK *(17)* has pointed out, *Arthropleura* resembles such Recent diplopods as the Polydesmida in its general habitus. According to MANTON *(11,12):*

> These "flat-backed" millipedes live under dead leaves and loose damp material. The lateral projection of their legs restricts their burrowing, and they cannot force their way through soil as can the juliform types. Both spines and wings will direct flattish objects away from the body, so leaving an unimpeded space in which the legs may move. The animals are thus well suited to push into crevices which give way predominantly in one plane, as does the damp layered mass of semi-decayed leaves on a woodland floor, or the bark and wood of decaying logs. The push is applied mainly by the dorsal surface or "flat back," the keels when present providing both protection for the legs and a surface of application for the force.

Such a description might well be of the habit of *Arthropleura* which may be envisaged plowing through the surface layers of the forest peat of the typical coal swamp. It is therefore improbable that *Arthropleura* could burrow, as GARSTANG *(5)* seems to have been the first to suggest in his verse "The trilobites and after." *Arthropleura* probably had a sluggish but powerful gait, and it would have readily fallen prey to contemporary amphibians and reptiles, doubtless *Arthropleura's* only enemies.

The gut infilling preserved in the juvenile *Arthropleura armata* previously mentioned is packed with vegetable debris. Carbonized wood tracheids with scalariform pitting are visible and fragments of epidermis are recognizable. Mr. D. BRETT, of Glasgow University Botany Department, who kindly determined these elements, states that the fragments are of lycopods. This is direct evidence that *Arthropleura* was herbivorous, and not predominantly carnivorous as WATERLOT suggested, although it does not prevent it from being an omnivore *(16).*

In characters such as body shape, lateral projection of the paratergal folds, lateral insertion of limbs on the body wall, and herbivorous diet, *Arthropleura* does indeed resemble the polydesmid diplopods. It is suggested that these resemblances have been acquired by these two separate classes of myriapods as a result of parallel evolution.

The great size attained by *Arthropleura* was explained by ANDRÉE (1913) on HANDLIRSCH's theory for the giant size of Coal Measure insects. This theory suggests a correlation of such gigantism with tropical or subtropical climates, where growth is not interrupted by a pause during a cold season. MANTON *(12)* has stated that factors such as difficulties of molting and of tracheal respiration limit large size in arthropods, "but the power which can be put out by the legs is alone sufficient to restrict size increase in millipedes." These problems would doubtless be acute for *Arthropleura* but they can only be answered when the nature of the respiratory organs is known.

These giant arthropods were completely dependent upon the unusual environment of the Coal Measures swamp for their survival and their range in time and space coincides with that of the Euramerian floral belt, with the exception of one undescribed record from the west of the Angaran floral province *(13)*. Thus *Arthropleura* ranges from Westphalian A to Stephanian C; PŘIBYL (1960) has figured specimens from the Namurian A of Czechoslovakia but these are not certainly *Arthropleura*.

AFFINITIES AND CLASSIFICATION

In view of the conflicting opinions on the affinities of *Arthropleura*, a brief history of these views is desirable.

Prior to KLIVER's (1884) description of a specimen bearing 13 pedigerous sternites (Fig. 392), interpretations of the systematic position were understandably diverse. Thus JORDAN & MEYER (1853) originally suggested that *Arthropleura* was a decapod crustacean and later (1854) made comparisons with eurypterids and trilobites. KLIVER dissociated this arthropod from insects and arachnids and stated that it could not be a myriapod, although he presented no argument in support of this view. He regarded *Arthropleura* as a nondecapod crustacean and compared the appendages with those of the Branchiopoda. ZITTEL (1885) established the family Arthropleuridae and pointed out that the lack of tagmosis and nature of the ventral surface differentiated the family from Isopoda and Amphipoda. Since he could not classify the Arthropleuridae with any other crustacean group, however, he suggested that it formed a connecting link between Isopoda and Amphipoda. ANDRÉE (1910) suggested that this lack of tagmosis was primitive. He inferred that since gill plates were present on at least 11 segments, but only on the fewer somites of either thorax or abdomen of Recent amphipods or isopods, respectively, *Arthropleura* is closely related to the common ancestor of the Edriophthalma (*i.e.,* Amphipoda, Tanaidacea, and Isopoda). Later (1913) he concluded that it also formed a link between the Isopoda and Schizopoda (Euphausiacea and Mysidacea). The first to have listed *Arthropleura* among the myriapods were MOYSEY & WOODWARD (in MOYSEY, 1911).

CALMAN (1913, in BROILI, 1932) concluded that *Arthropleura* is "certainly not an isopod" and criticized ANDRÉE's views. If *Arthropleura* is a crustacean, in the view of CALMAN it is "of a type hitherto unknown," but it might "even be a very generalized and primitive kind of myriapod"; CALMAN therefore referred it to Arthropoda *incertae sedis*.

The next major change in the systematic position of the group was made by WATERLOT (1934) who founded the order Arthropleurida, ranked by him as having taxonomic status equal to the Trilobita within the crustacean subclass Archaeocrustacea (later, 1949, within the Trilobitomorpha). STØRMER (1944) challenged WATERLOT's reconstruction of a biramous trilobite-like limb for *Arthropleura*. He concluded that the limb was uniramous, having "little in common with the trilobite appendage," and judged that the only trilobitan feature of *Arthropleura* was the trilobation of the tergites. STØRMER therefore only referred the genus with doubt to the Arachnomorpha.

A posthumous note on KOMAREK's views of the systematic position of *Arthropleura* was published by SHAROV (1960), who denied that *Arthropleura* is related to the Trilobita and stated, without foundation, that it is a typical representative of the diplopod myriapod family Polydesmidae, both in leg morphology and in its paleoecology. Novozhilov (1962) accordingly referred the Arthropleuridae to the Diplopoda, *Ordo incertae sedis,* in the Russian "Osnovy paleontologii."

The present writer provisionally regards the Arthropleurida as a distinct class of myriapods. Evidence for this attribution to the Myriapoda is slender, and only amounts to the lack of tagmosis of the large number of somites, presence of uniramous limbs on all known somites, and the inferred terrestrial habit. The Arthropleurida differ from other myriapod classes in the large number of their leg segments and in the presence of the rosette plate. [The coxosternopleurites of the Archipolypoda probably served to strengthen the leg bases of these large myriapods and in this respect resemble the arthropleurid rosette plate. Details of the two plates are quite different, however, and such similarity of function is to be expected in both such unusually large arthropods. If the paratergal folds of *Arthropleura* are articulated with the axis, as has been suggested, then this would suggest comparison with the "Eurysterna."]

Further details of the morphology of *Arthropleura* are needed to verify its true position within the Arthropoda, and, if the current attribution proves to be correct, to deduce its relationship to other myriapod classes. Data are needed on such critical points as: nature of the respiratory structures (tracheal or branchial), number of antennae, nature and number of mouth parts, and position of genital openings. Should *Arthropleura* prove to have gill plates and lack spiracles, then of course it could not be a myriapod, and the Arthropleurida would need to be elevated to superclass rank. *Arthropleura* would then strikingly resemble Snodgrass' (1956, fig. 1C) hypothetical primitive walking arthropod, his "protarthropod" or even "protomandibulate." Such a gill plate would provide the only criterion for regarding *Arthropleura* as a crustacean. Although a similarly large number of trunk segments is found in the Branchiopoda, such numerous limb segments are unknown in the Crustacea, or indeed in any other arthropod group except Pycnogonida. There is thus little support at present for Guthörl's *(9)* view that *Arthropleura* occupied a position intermediate between the Crustacea and Myriapoda.

It is unwise to seek any fundamental phylogenetic significance in either the trilobed or onisciform habitus, since these features recur in widely separate arthropod groups and are clearly highly adaptive.

SYSTEMATIC DESCRIPTIONS

Class ARTHROPLEURIDA Waterlot, 1934

[*nom. transl.* Størmer, 1944 (*ex* order Arthropleurida Waterlot, 1934)] [=Gigantopleurida Guthörl, 1934]

Gigantic myriapods? with long body of more or less uniform width. Single pair of multiarticulate uniramous limbs borne by each somite, limbs characterized by numerous (8 to 10—number uncertain) of segments. Large, radially lobed subcoxal? sclerite (rosette plate) situated anterior to base of each limb. *U.Carb.*

Family ARTHROPLEURIDAE Zittel, 1885

Characters of class. *U.Carb.*

Arthropleura Jordan & Meyer in Meyer, 1853, p. 161 [**A. armata* (=*Halonia irregularis* Geinitz, 1855; *Macropteris punctata* Goldenberg, 1885; *Amynilyspes springhillensis* Copeland, 1957); M] [=*?Troxites* Goldenberg, 1854, p. 36 (type, *T. germari;* M); *?Troxitis* Scudder, 1879 *(nom. null.); Anthropleura* Geinitz, 1866 (*nom. null.); Arthropleuria* Boule, 1893 *(nom. null.); Athropleura* Guthörl, 1934 *(nom. null.); ?Branchipusites* Goldenberg, 1875, p. 23 (type, *B. anthracinus;* M); *?Branchiopusites* Goldenberg, 1877 *(nom. null.); ?Arthropleurion* Goldenberg, 1877, p. 48 (type, *A. inermis;* M); *?Athropleurion* Goldenberg, 1877 *(nom. neg.); ?Carcinochelus* Goldenberg, 1877, p. 34 (type, *C. anthracophilus;* M)]. Tergites dorsoventrally depressed, divided by 2 longitudinal axial furrows into 3 lobes, comprising central rectangular axis and 2 lateral subtriangular paratergal folds, all bearing prominent spines and tubercles. Probably 29 posteriorly imbricating postcephalic somites, excluding telson. Paratergal folds directed forward in anterior region of body and backward in posterior region. Head small, obovate, broader than long (poorly known). Telson unknown. Limbs inserted midway between ventral mid-line and tips of paratergal folds and separated by sternite. Each limb segment except 1st with pair of long distal spines; last segment? a claw; proximal segments with prominent ridges and grooves, anterior face smooth, posterior tuberculate. Rosette plate separated from posterior triangular *B* plate by sulcus. *K* plate thin, variable in position. *U.Carb.,* C. Eu.-NW. Eu.-USSR(Kazakh.)-N.Am.(Can.-Ill.).——Fig. 386,*1;* 387,*1.* **A. armata,* Eng.; 386,*1,* dorsal, ×2 (Rolfe, n); 387,*1a,b,* dorsal, ventral, ×0.1 *(16).* [See also Fig. 388-392.]

TAXA DOUBTFULLY CLASSIFIABLE AS ARTHROPLEURIDA

The following two rare genera show certain similarities to *Arthropleura* but are not known in sufficient detail to be more closely compared. *Camptophyllia* is known from six specimens in Coal Measure clay-ironstone concretions like those containing *Arthropleura* itself, whereas *Bundenbachiellus,* a possibly ancestral form, is known from two specimens from the marine Hunsrück Shale. From the intact preservation of the latter Broili *(3)* concluded that *Bundenbachiellus* was an amphibious form.

Bundenbachiellus Broili, 1930, p. 219 [*nom. subst. pro Megadactylus* Broili, 1929, p. 141 (*non* Fitzinger, 1843, *nec* Hitchcock, 1865)] [**Megadactylus giganteus* Broili, 1929; M]. Body elongate, with at least 8 somites; tergites broad, with longitudinal, posteriorly diverging, spined ridges; anterolateral edges of paratergal folds notched and setose; ?telson subcircular. At least 7 pairs of uniramous limbs emerging between somites, 1 pair per somite; limbs with at least 6 segments distally, last a claw. [Compared with Myriapoda, Isopoda and Syncarida by Broili *(2,3)* who concluded that if it was not a myriapod, then it represented an undescribed group of Crustacea. Prior to this, Hennig (1922, p. 144-145) had suggested a comparison with *Arthropleura.* Another specimen, described as *B? minor* by Broili *(3),* is even more myriapod-like in showing the head with a single pair of antennae (although a 2nd pair might also be present according to Broili), 12 body somites with large paratergal expansions, 1st 2 body somites smaller, 3rd and 4th larger than other somites; single pair of uniramous limbs per somite, 6- or 7-segmented, last digit clawlike. ?Telson semicircular.] *L.Dev.(Siegen.),* Eu.(Ger.).——Fig. 393,*1a-c.* **B. giganteus* (Broili), Hunsrück Sh.; *1a,* holotype, dors., ×0.5; *1b,c,* 2 tergites, dorsal, lat., spinules on longitudinal ridges not shown *(2).*——Fig. 393, *1d. B.? minor* Broili, Hunsrück Sh.; holotype, ventral, ×2.0 *(3).*

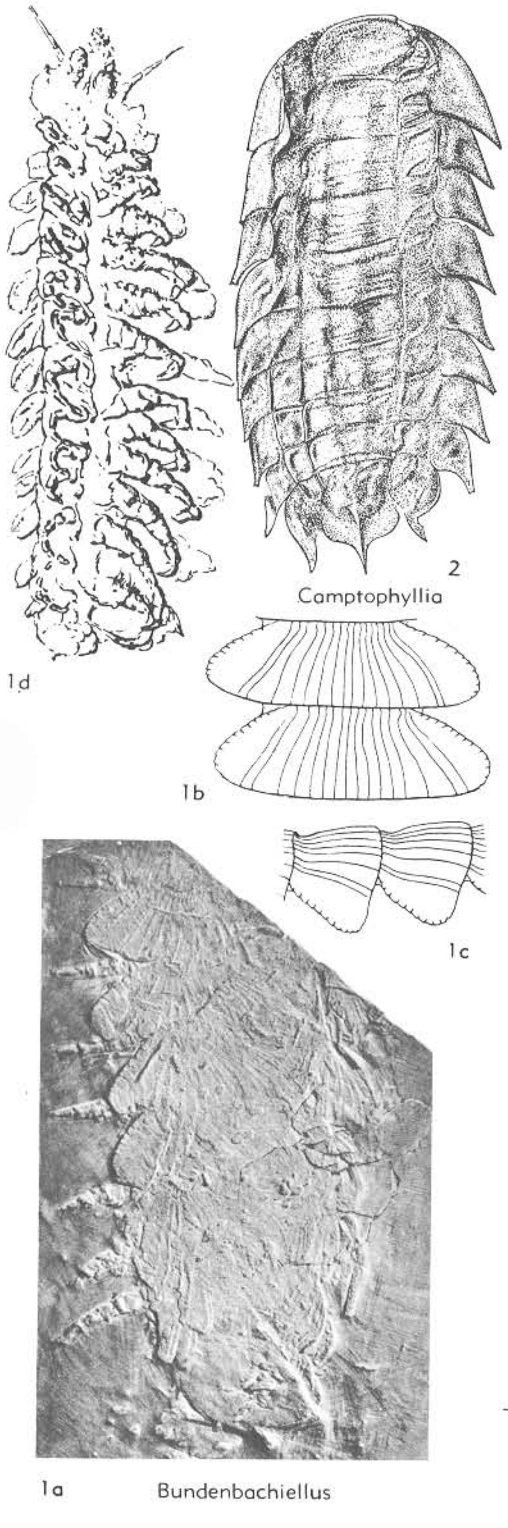

Fig. 393. Doubtful taxa, Arthropleurida (p. *R*618-*R*619).

Camptophyllia GILL, 1924, p. 466 [**C. eltringhami;* OD]. Body elongate, approximately twice as long as greatest breadth; slightly depressed, onisciform; of 10 posteriorly imbricating somites (telson excluded), bearing low, elongate granules; somites divided by 2 longitudinal axial furrows into 3 lobes, each somite with median axis and 2 lateral, posteriorly directed paratergal folds; 1st somite semicircular, paratergal folds extending posteriorly to cover 2nd somite laterally?; axis one-third width of body at center, narrowing anteriorly and more so posteriorly; with 1 median and 2 lateral, longitudinal, low ridges. Head unknown (probably concealed beneath 1st segment). Telson oval, posteriorly acuminate, with prominent dorsal keel or tubercle. [Originally described as Arthropoda *incertae sedis* and compared with Isopoda; PEACH regarded it as an "aberrant millipede." Referred conditionally to Arthropleurida by BROOKS (1962).] *U.Carb.(Westphal.B, similis-pulchra Zone),* Eng.(Durham-S.Staffs.).——FIG. 393,*2*. **C. eltringhami,* Durham; holotype, dorsal, post. border of 10th segment not shown, ×2 *(6)*.

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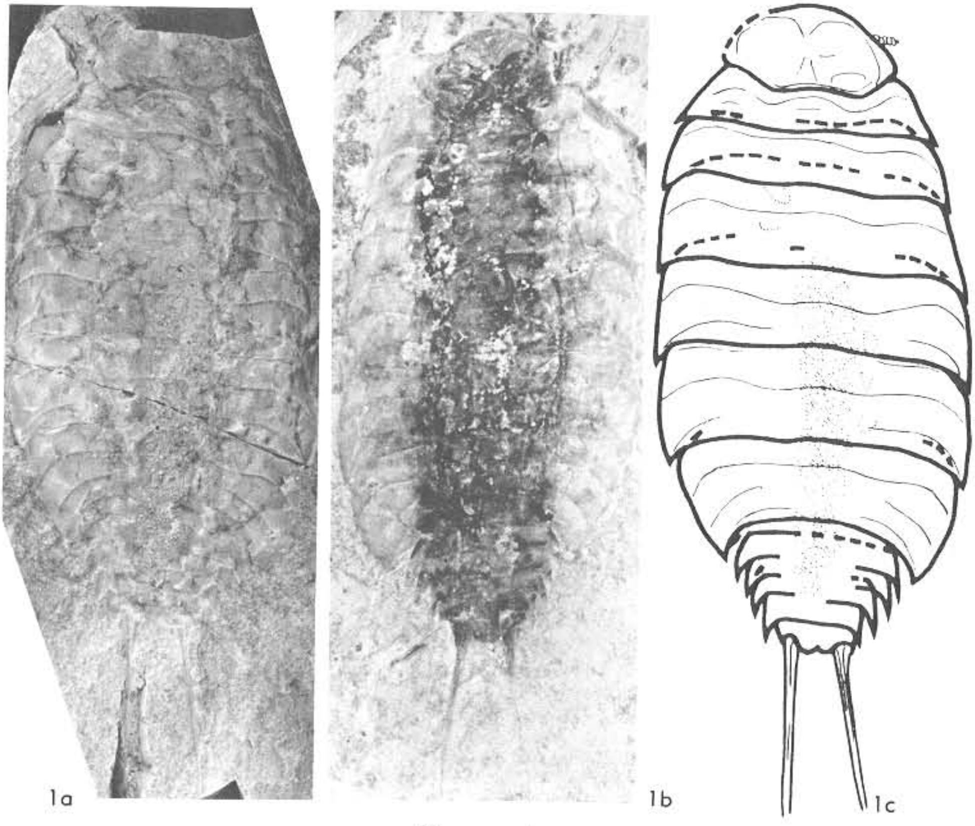
ARTHROPODA INCERTAE SEDIS

By W. D. Ian Rolfe
[Hunterian Museum, University of Glasgow]

This section deals with three categories of doubtful arthropods, but it does not claim to treat all Arthropoda *incertae sedis*. Although many of these taxa are based on inadequate material, it is probable that some represent unique extinct higher-rank groups. The problem of their classification is particularly difficult since the diagnostic morphological features required for comparison with extant Arthropoda are so frequently not seen in fossil arthropods.



Oxyuropoda

FIG. 394. Doubtful taxa formerly attributed to Arthropleurida (p. *R*621).

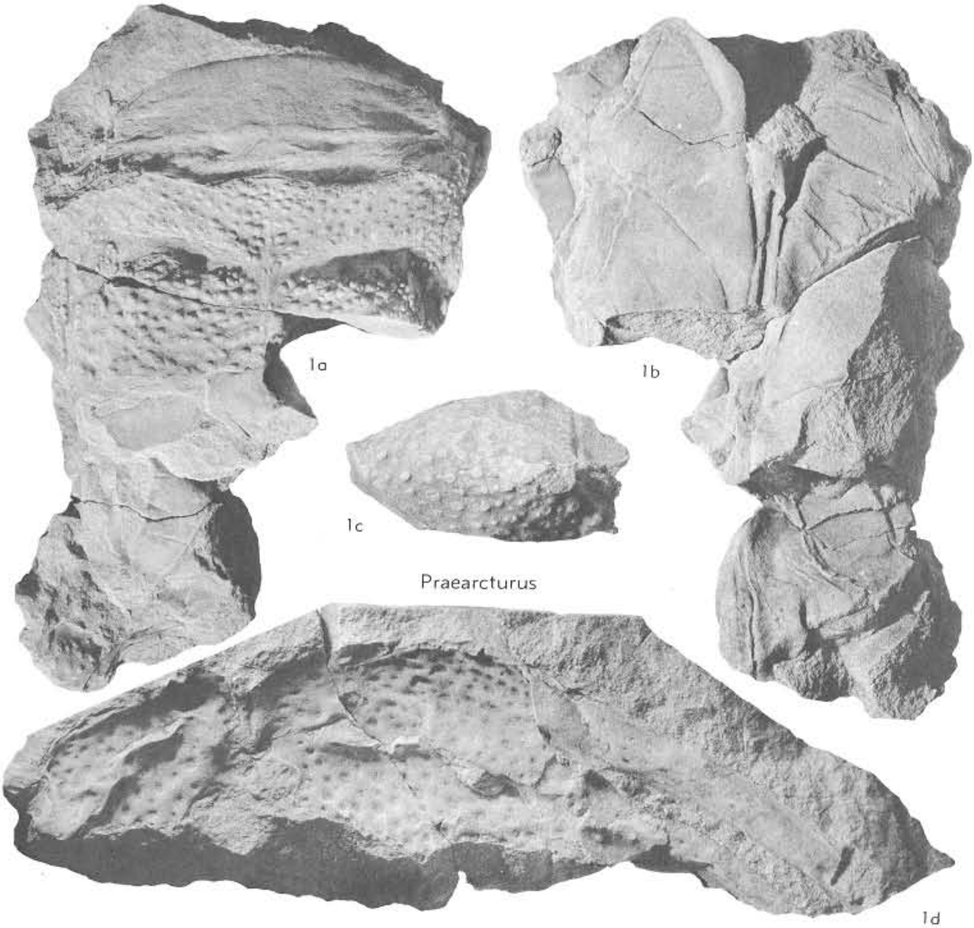


FIG. 395. Doubtful taxa formerly attributed to Arthropleurida (p. *R*622).

DOUBTFUL TAXA FORMERLY ATTRIBUTED TO ARTHROPLEURIDA

Oxyuropoda CARPENTER & SWAIN, 1908, p. 63 [**O. ligioides;* OD]. Body onisciform. Head small, broader than long, with antennae? Thorax long, of 6 somites, with longitudinal trilobation; somites with single transverse rib on anterior 3, 2 on 4th, and 3 on last 2 somites. Abdomen small, of 4 or 5 somites, paratergal folds produced into posteriorly directed processes. Telson small, posteriorly emarginate; caudal rami (or uropods?) long, slender, with 2 longitudinal ridges. [Cuticle preserved in green apatite. The "antenna" reported by CARPENTER & SWAIN is a plant fragment typical of many which lie on the slab; features supposed by them to be appendages could not be seen on the holotype, although an antenna may be present. Thought by original authors to have affinity with Tanaidacea and to link them with various suborders of Isopoda. They also compared *Oxyuropoda* with *Arthropleura,* a suggestion tentatively accepted by BROOKS (1962), but which, in view of the tagmosis of the former, seems improbable. A relationship to the Tanaidacea-Isopoda would still appear to be the best assignation, although critical features are lacking. CALMAN (1909) stated this form is an isopod although after study of *Arthropleura* he later (in BROILI, 1932) rejected this view and in agreement with BROILI associated it rather with *Cheloniellon.* Referred to Arachnomorpha by SCHULZE (1939); STØRMER (1944) accepted this with reservation and established for it the subclass? Oxyuropodida. There is no foundation for suggesting that *Oxyuropoda* is a phyllocarid, as by ROGER (in PIVETEAU, 1953).] *U. Dev. (Famenn.),* Ire. (Co. Kilkenny).——FIG. 394,*1.* **O. ligioides,* holotype; *1a,* part, whitened,

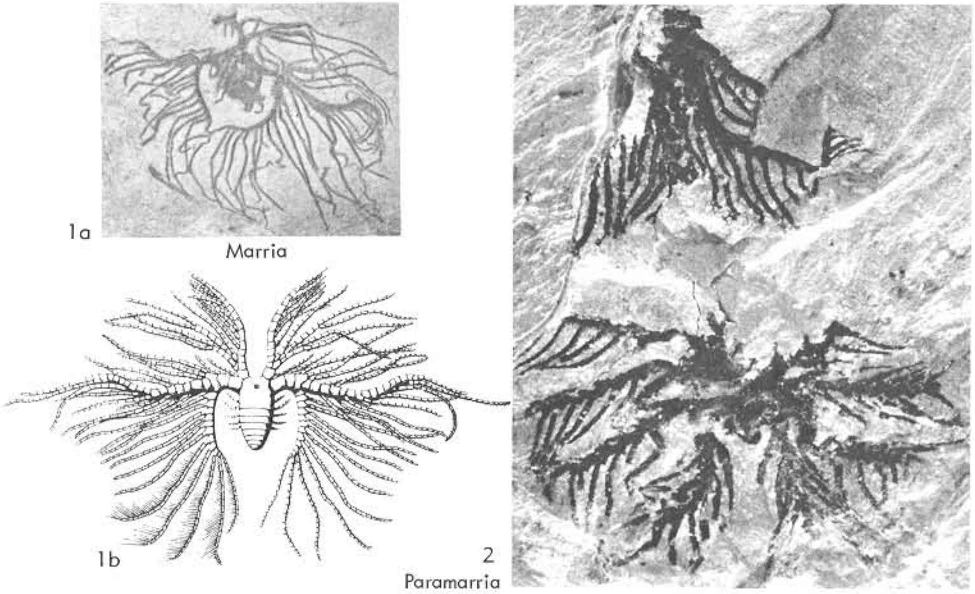


FIG. 396. "Marriocarida" (p. *R622-R623*).

×1.25; *1b,* counterpart, immersed in alcohol, ×1.25; *1c,* outline combining features seen on *1a* and *1b,* stippling marks area of mineral particles originally filling gut (interrupted lines indicate anterior edge of somites, impressed through adjacent cuticle, or restored boundaries; dotted lines mark cuticle-free areas which may represent sites of limb insertion), ×1.3 (Rolfe, n).

Praearcturus WOODWARD, 1871, p. 266 [**P. gigas;* M]. Tergite large; smooth anterior? semicircular articulating half ring; low median keel and pair of transverse lateral furrows, each furrow deepening to a pit under halfway from median keel to edge of tergite; covered with large rounded tubercles except in furrow. Limb bases deeply inserted on ventral surface, anteriorly? directed, separated by median, longitudinally grooved sternite. Each limb with subtriangular basal segment and up to 2 short segments preserved distally; dorsal surface tuberculate, ventral smooth. [Known only from specimen preserving one tergite with 2 pairs of ventral limb bases and from a number of isolated cheliform appendages. Supposed chelation of appendages may be due to fracture along deep invaginations of cuticle. Referred by WOODWARD to Isopoda and by ZITTEL (1885) to Arthropleuridae, although presence of 2 pairs of limbs per somite excludes it from either of these groups.] *L.Dev.(Gedinn.),* Eng.——FIG. 395,*1.* **P. gigas,* Ditton. (I_0), Hereford(Rowlstone); *1a,b,* lectotype, dorsal, ventral, ×0.54; *1c,d,* paralectotypes, fragments of supposed chelate appendages, ×0.54 *(10).*

"MARRIOCARIDA"

Marria RUEDEMANN, 1931, p. 4 [**M. walcotti;* M]. Ovoid "body" (?attachment disc or float) with 3 main branches (?stipes), each forking dichotomously to produce 6 main branches fringed with many lateral, denticulate (?thecae) branches. Dendroid graptolite or hydroid? [Described by RUEDEMANN *(5)* as a crustacean nauplius, with segmented body, antennae and mandibular limbs. SIMONETTA *(6)* compared features of the holotype and one paratype with those of Cambrian dendroid graptolites and suggested that 4 of the remaining 5 paratypes were poorly preserved sponge spicules, as WALCOTT had originally identified them. Prof. O. M. B. BULMAN has studied these 5 paratypes and confirms that they "afford no acceptable demonstration of the existence of graptolites or graptolite-like organisms in the Eldon Formation" (*in litt.* 26 April 1966). The "segmentation" resulted from splintery fracture of the Burgess Shale matrix. Features of the holotype as described by SIMONETTA correspond best with those of dendroid graptolites, and it is unfortunate that this author concluded by referring *Marria* to the Graptoloidea Dichograptidae, an Ordovician family. Type of Marriocaridae (*recte* Marriocarididae) RUEDEMANN, 1931, and suborder Marriocarida RUEDEMANN, 1931.] *M.Cam.,* Can.(B.C.).——FIG. 396, *1.* **M. walcotti,* Burgess Sh.; *1a,* holotype, ×1.3 *(5); 1b,* RUEDEMANN's "restoration" as a crustacean nauplius, ×1.3 *(11).*

Paramarria Wells, 1944, p. 437 [**P. galenensis;* M] [=*Paramaria* Sharov, 1965 *(nom. null.)*]. Central "body" (?attachment disc or float) with at least 8 branches (?stipes). Each main branch zigzagged owing to regularly alternate disposition of lateral branches. Possibly a hydroid or dendroid graptolite resembling *Ptilograptus.* [Referred by Wells *(9)* to Marriocarida Marriocaridae. No segmentation visible. Dr. D. Skevington, who has examined the holotype, noticed notching of minor branches suggestive of thecae, and agreed that *Paramarria* might possibly be a hydroid or dendroid similar to *Ptilograptus,* although it is impossible to be certain of the affinity of this fossil until better-preserved material is available.] *U.Ord.(Maquoketa Sh.),* USA(Ill.).——Fig. 396,2. **P. galenensis;* holotype (below) and associated fragment, ×5 (Rolfe, n).

MIMETASTER

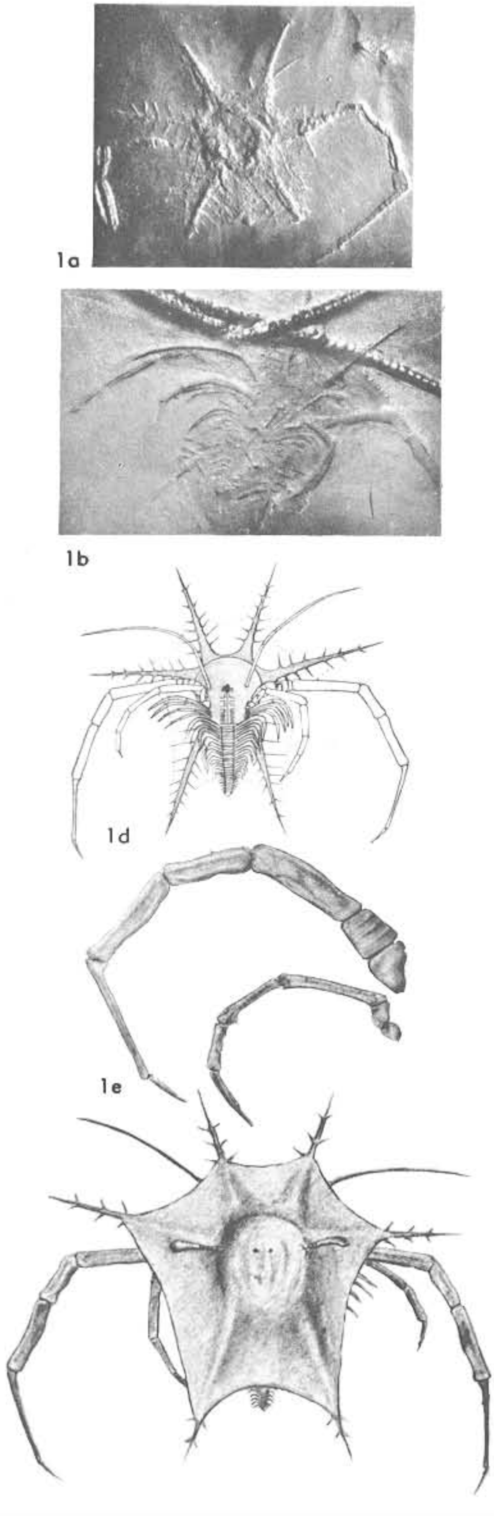
This remarkable arthropod was originally thought by Abel and Broili not to be a single animal but to comprise two symbionts. The six-rayed dorsal headshield has suggested a starfish body to all workers, and the name *Mimetaster* was given in the belief that this was an arthropod which mimetically resembled a starfish. Although the organism partly satisfies the conditions of protective mimicry in resembling its model (the starfish *Loriolaster mirabilis* according to Lehmann) and in being much less common than the model, the resemblance does not seem sufficiently striking to constitute true mimicry.

From the frequent occurrence of *Mimetaster* on slabs with the starfish *Furcaster* and from the presence of one specimen overlapping a *Furcaster* arm, Gürich *(1b)* argued that *Mimetaster* preyed on starfish. He claimed that the starfish was in an "agonized" position and that both creatures were obviously fighting before death. As Opitz *(3,4)* pointed out, however, these attitudes resulted from shifting of the specimens by postdepositional current action.

Although Gürich *(1b)* knew of the significance of prominently developed spines as an aid to floating in planktonic arthropods such as crustacean larvae, he preferred to regard *Mimetaster* as a benthonic form. The headshield of *Mimetaster* strikingly resembles that of the planktonic acanthosoma larva of sergestid decapods and the pelagic larvae of stomatopods. Beurlen, Størmer, and Sharov emphasized that the small size, relatively expanded headshield and presence of large anterior swimming appendages (antennae?) indicate that *Mimetaster* was a planktonic creature. This being so, it is difficult to envisage *Mimetaster* preying upon starfish living in or on the sea floor and to see any significance in the supposed resemblance to a starfish. For the same reason, it is impossible to accept Lehmann's *(2)* view that *Mimetaster* fed off the body fluids of starfish prey. The occurrence of both starfish and *Mimetaster* on the same slab may be explained by the sinking of dead *Mimetaster* to the sea floor to be buried along with the benthos.

The systematic position of *Mimetaster* is still problematic. All authors have noticed the similarity between *Mimetaster* and the Middle Cambrian trilobitoid *Marrella.* The presence of biramous limbs and of only two pairs of cephalic limbs in *Marrella (7)* suggests that *Mimetaster* cannot be placed in the Marrellomorpha, as Beurlen suggested. It may well be that the similarities of *Mimetaster* (and of *Marrella?*) to larvae are more than homeomorphic. On this interpretation, the large number of trunk segments would indicate either a trilobitan or branchiopod crustacean metanauplius. Although the head shield recalls such a trilobite as *Olenelloides,* the metamorphosis required to transform *Mimetaster* from such a "late meraspis" form into an adult of any of the five trilobite genera known from the Hunsrück Shale would be prohibitive, and necessitate a hitherto unknown diminution in the number of somites. The most likely crustacean in the Hunsrück fauna to regard as a suitable parent would be the branchiopod *Vachonisia.* This arthropod has five cephalic appendages, about 50 moniliform trunk appendages and lacks a caudal furca. Thus, during the metamorphosis from larva to adult, *Mimetaster* would need to lose one cephalic appendage and gain a large number of trunk appendages. Lehmann *(2)* has already noted the striking resemblance between the abdomina of both genera.

Mimetaster Gürich, 1932, p. 136 [*nom. subst. pro Mimaster* Gürich, 1931 (*non* Sladen, 1882)] [**Mimaster hexagonalis* Gürich, 1931, p. 236; M] [=*Mimeaster* Størmer, 1939 *(nom. null.)*].



Head shield flat, bilaterally symmetrical, with central, concave-sided thin disc (? of unsclerotized cuticle) produced distally into 6 prominent subradial processes, each process bearing several cross bars. Pair of widely spaced, dorsal, club-shaped prominences (?stalked eyes or dorsal organ) separated by pair of pits (?sessile eyes). Small subcentral mouth on ventral surface, bordered laterally by 2 crescentic elevations. Flat longitudinal ridge between posterior border of mouth and posterior border of ?cephalon, with 6 short transverse ridges, ?indicating segmentation; 7 pairs of uniramous ?cephalic appendages; preoral appendage (?antennule) long and slender; 1st postoral appendage (?antenna) large, longer than body, posteriorly recurved, of 7 segments; 2nd postoral appendage half length of 1st, of 7 segments; 4 remaining pairs of postoral ?cephalic appendages short. Trunk triangular, of approximately 24 somites, becoming smaller posteriorly, with longitudinal axis bounded by axial furrows; each somite with pair of small moniliform, uniramous, setose? appendages. Telson a small discoidal plate; furca absent. [Type of order Mimetasterida BEURLEN, 1934 *(nom. transl. et correct.* STØRMER, 1944, *ex* suborder Mimetastrida BEURLEN, 1934).] *L.Dev.(Siegen.),* Eu.(Ger.).——FIG. 397,*1*. **M. hexagonalis* (GÜRICH), Hunsrück Sh.; *1a,* dors., ×1 *(1b); 1b,* ventral, 2 arms of starfish *Furcaster* also visible, ×1; *1c,d,* dorsal, ventral views (reconstr.), ×1, ×0.7; *1e,* 1st (?antenna) and 2nd postoral cephalic? appendages, ×2 *(2).*

KABLIKIA

Kablikia GEINITZ, 1862, p. 138 [**K. dyadica* (=*K. silurica* GEINITZ, 1863, obj.); M]. Elongate, longitudinally trilobed, posteriorly tapering body comprising poorly preserved head followed by at least ?31 somites. Anterior 18 somites with pointed, anteriorly curved, paratergal folds; posterior somites ?lacking such folds. *L.Ord.(Llandeil.),* Eu. (Czech.).

[The unique specimen occurs on a slab with the equally unique *Dalmaniopsis ḳabliḳae* GEINITZ (p. *O*525); both specimens were destroyed in Dresden during the war on 13/14 February 1945. The slab did not come from the Semily Formation, Stephanian, Upper Carboniferous of Dolní Stěpanice, near Vrchlabi, Czechoslovakia, as originally recorded and subsequently cited (Richter & Richter, 1955; *Treatise,* p. *O*525), but from the Dobrotivá Shales, Osek and Kvan Beds, Llandeilian, Ordovician, as corrected by GEINITZ in 1863. *D. ḳabliḳae* was shown by GEINITZ (1863) (*cf.* Richter & Richter, 1955) to be a synonym of *Placoparia zippei* (BOECK). In the absence of any specimens, it is impossible to be sure of the affinities of *Kabliḳia,* but it may be a poorly preserved dalmanitid trilobite, possibly even *Ormathops* which is known from these beds.]

FIG. 397,*1*. *Mimetaster hexagonalis* (GÜRICH), L.Dev. (Hunsrück Sh.), Ger.; *1a-c,* ×1; *1d,* ×0.7; *1e,* ×2 (*1a, 1b; 1b-e,2*) (p. *R*623-*R*624).

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ADDITIONAL SOURCES OF ILLUSTRATIONS

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(11) **Ruedemann, R., 1934**

ADDENDUM TO DECAPODA

By M. F. GLAESSNER

Since the *Treatise* chapter on decapods was submitted for publication (1964) and set in type (precluding significant alterations), major work on fossil Decapoda has been published by FÖRSTER and SECRETAN, and C. W. WRIGHT has forwarded information on a revision of all British Cretaceous crabs which is in preparation.

FÖRSTER (1966, 1967) and SECRETAN (1964) have made noteworthy contributions to knowledge of general morphology and phylogeny of decapods, particularly of the Astacidea. They have clarified problems which are reviewed in the relevant paragraphs of this chapter, but these matters cannot be further discussed here. The most important taxonomic revisions made by the authors mentioned are listed below, in systematic order. Resulting revised diagnoses and diagnoses of new taxa recently proposed by other workers are included, and a correction is made to an entry under "Decapoda of uncertain systematic position or validity." A number of recent contributions to the knowledge of fossil burrows, some of which were probably made by decapod crustaceans are not included in the following list of additional references.

Infraorder CARIDEA Dana, 1852

Family UNCERTAIN

Hefriga MÜNSTER, 1839 [**H. serrata;* M] [=*Bombur* MÜNSTER, 1839 (type, *B. complicatus,* according to FÖRSTER (1967,4), but other specimens assigned to *Bombur* (Fig. 252,2), and particularly "*B.*" *aonis* BRONN (*U.Trias.,* Eu.), may be young *Antrimpos*)].

Infraorder ASTACIDEA Latreille, 1802

Family ERYMIDAE Van Straelen, 1924

Subfamily ERYMINAE Van Straelen, 1924

Protoclytiopsis BIRSHTEYN, 1958, which is not a synonym of *Lissocardia* as revised by FÖRSTER (1967), and *Clytiella* GLAESSNER are included in the Eryminae by FÖRSTER (1967).

Eryma VON MEYER, 1840 [**Macrourites modestiformis* VON SCHLOTHEIM, 1922; OD] [=*Erymastacus* BEURLEN, 1928; *Klytia* VON MEYER, 1840]. Rostrum moderately long, denticulate; cervical groove deep; gastro-orbital groove weak; postcervical and branchiocardiac grooves variably developed, subparallel or joined; sculpture weak; abdomen smooth; chelae stout or slender; fingers longer than propodus. *L.Jur.-L.Cret.,* Eu.; *M.Jur.-U.Jur.,* E.Afr.-Madag.-Indonesia. (Förster, 1966).

Enoploclytia M'COY, 1849 [**Astacus leachi* MANTELL, 1822; OD]. Gastro-orbital groove wide, deep, short; postcervical groove deep, joining groove *i;* branchiocardiac groove short; tubercle *ω* distinct; gastric and cardiac regions sculptured; chelae slender, fingers long. *L.Cret.(U.Alb.)-U.Cret., ?Paleoc.,* Eu.-W.Afr.-Madag.-N.Am.; *L.Cret.(Apt.),* E.Australia. (Förster, 1966).

Palaeastacus BELL, 1850 [**P. dixoni* (=*Astacus sussexiensis* MANTELL, 1833); OD]. Gastro-orbital groove weak; postcervical groove stronger than and separate from branchiocardiac groove; chelae short, spinose, with short fingers. *L.Jur.-U.Cret.(Cenoman.),* Eu.; *L.Cret.(Alb.)-U.Cret.,* N.Am.; *L.Cret.(Alb.),* E.Australia (Förster, 1966).

Phlyctisoma BELL, 1862 [**P. tuberculatum;* SD GLAESSNER, 1929]. Carapace inflated, gastro-orbital groove deep; postcervical groove joins *i;* branchiocardiac groove weak and short; sculpture coarse; chelae massive. *L.Jur.-L.Cret.(U.Alb.),* Eu.-Madag. (Förster, 1966).

Family PLATYCHELIDAE Glaessner

(see p. *R*458)

Work by FÖRSTER (1967) has shown that *Lissocardia* VON MEYER, 1851, does not belong to the Clytiopsinae. FÖRSTER considered *Platychela* and *Lissocardia* as of uncertain position in the classification. They could be tentatively included in one family. *Lissocardia* is considered as possibly close to a common origin of Pemphicidae, Glypheidae, and Erymidae.

Infraorder PALINURA Latreille, 1802

Family GLYPHEIDAE Winckler, 1883

Paralitogaster GLAESSNER, herein [*nom. subst. pro Aspidogaster* ASSMANN, 1927 (*non* BAER, 1826)] [**Litogaster limicola* KÖNIG, 1920; OD]. Resembles *Litogaster* but gastro-orbital groove weak, postcervical stronger than branchiocardiac groove;

gastral ridges strong, spinose, separated by smooth areas; spines on cardiac and dorsal branchial regions. *L.Trias.-M.Trias.*, Eu. [According to FÖRSTER (1967), *Pemphix meyeri* ALBERTI, the type species of *Seebachia* WÜST, 1903 (*non* NEUMAYR, 1882) belongs here rather than to *Pseudopemphix*.]

Family MECOCHIRIDAE Van Straelen, 1925

According to FÖRSTER (1967), *Triasiglyphea* VAN STRAELEN, 1936, is a synonym of *Pseudoglyphea* OPPEL, 1861. *Platypleon* VAN STRAELEN, 1936, is also tentatively included here.

Infraorder BRACHYURA Latreille, 1802

Superfamily DROMIOIDEA de Haan, 1833

Family PROSOPIDAE von Meyer, 1860

Subfamily GONIODROMITINAE Beurlen, 1932

[*nom. transl.* GLAESSNER herein (*ex* Goniodromitidae BEURLEN, 1932)] [=Pithonotinae GLAESSNER, 1933]

Subfamily PROSOPINAE von Meyer, 1860

WRIGHT & COLLINS (1968) place here *Mithracites* GOULD, 1859, *Rathbunopon* STENZEL, 1945, and *Vectis* WITHERS, 1945.

Family DROMIIDAE de Haan, 1833

WRIGHT & COLLINS (1968) place here *Mesodromilites* H. WOODWARD, 1900.

Kierionopsis DAVIDSON, 1966 [**K. nodosa;* OD]. Carapace subrectangular, inflated, with blunt pustule-bearing marginal spines, 4 median and several dorsolateral bosses and granulate posterobranchial regions. *Paleoc.*, USA(Tex.).

Family DYNOMENIDAE Ortmann, 1892

WRIGHT & COLLINS (1968) place here *Trachynotus* BELL, 1893, and *Xanthosia* BELL, 1863. This genus was also discussed by SECRETAN (1964).

Superfamily DORIPPOIDEA de Haan, 1841

Family CYMONOMIDAE Ihle, 1916

[*nom. correct.* WRIGHT & COLLINS, 1968 (*pro* Cymonomae IHLE, 1916); *nom. transl.* WRIGHT & COLLINS, 1968 (*ex* Cymonominae IHLE, 1916) (GORDON, 1963)]

WRIGHT & COLLINS (1968) place here *Doratiopus* WOODS, 1953, and *Torynomma* WOODS, 1953.

Superfamily CALAPPOIDEA de Haan, 1833

Family CALAPPIDAE de Haan, 1833

Necrocarcinus BELL, 1863 [**Orithya labeschei* DESLONGCHAMPS, 1835; SD GLAESSNER, 1929] [=*Orithopsis* CARTER, 1872 (type, *O. bonneyi*); *Neocarcinus* STOLICZKA, 1873 (erroneous spelling)]. [WRIGHT & COLLINS (1968) found *O. bonneyi* based on an insufficiently cleaned and erroneously figured specimen of *N. tricarinatus* BELL, 1863.]

Superfamily RANINOIDEA de Haan, 1841

Family RANINIDAE de Haan, 1841

Lophoranina FABIANI, 1910 [**Ranina marestiana* KÖNIG, 1825; OD]. [This is recognized as a genus by VÍA BOADA, 1966.]

Raninella A. MILNE-EDWARDS, 1862 [**R. trigeri*; OD] [=*Hemioon* BELL, 1863 (type, *H. cunningtoni*) which is based on young specimens of *R. elongata* A. MILNE-EDWARDS, according to WRIGHT & COLLINS.]

Superfamily PORTUNOIDEA Rafinesque, 1815

Family PORTUNIDAE Rafinesque, 1815

Subfamily POLYBIINAE Ortmann, 1893

[=Macropipinae STEPHENSON & CAMPBELL, 1960]

Polybius LEACH, 1820 [**P. henslowii;* M]. *Rec.*, Eu.

Superfamily XANTHOIDEA Dana, 1851

Family PINNOTHERIDAE de Haan, 1833

Pinnixa WHITE, 1846 [**Pinnotheres cylindricum* SAY, 1818; OD]. *Eoc.-Rec.*, N.Am.-Eu.-C.Asia-Indonesia.

P. (Pinnixa). Carapace much wider than long. *Oligo.*, C.Asia; *Mio.*, USA(Calif.); *Rec.*, N.Am.-Indonesia.

P. (Palaeopinnixa) VÍA BOADA, 1966 [**Pinnixa eocenica* RATHBUN, 1926; OD]. Carapace not much wider than long, outline semicircular, lateral borders of gastric and cardiac regions distinct. *Eoc.*, USA(Wash.); *Mio.*, Spain; *?Rec.*, Eu.

DECAPODA
of uncertain systematic position or validity

New discoveries of Mesozoic Tanaidacea have made it clear that the little-known genus *Charassocarcinus* Van Straelen, 1925 (p. *R*532), belongs to this order and not to the Decapoda.

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ADDENDUM TO CIRRIPEDIA

By W. A. Newman and V. A. Zullo

MORPHOLOGY OF THORACICA

(see p. *R*217)

In the only balanid with complemental males so far described, *Balanus masignotus (52),* an external pocket often forms below the sheath of the rostrum in which the males reside (Fig. 118). This pocket would be detectable in fossil material. It is not always developed in this species, however, and other Recent balanids known to have males display no obvious structural changes in the shell. Therefore, on the basis of this criterion, the existence of males in fossil forms might go undetected.

ADDITIONAL RHIZOCEPHALAN GENERA

(see p. *R*272)

PELTOGASTRIDAE

Angulosaccus, Boschmaia, Briarosaccus, Cyphosaccus, Dipterosaccus, Galatheascus, Peltogasterella (=Gemmosaccus, Chlorogaster, Ligella), Pterogaster, Septosaccus, Temnascus, Tortugaster, Trachelosaccus.

SACCULINIDAE

Drepanorchis, Heterosaccus, Loxothylacus, Ptychascus, Sesarmaxenos.

LERNAEODISCIDAE

Parthenopea, Septodiscus, Triangulopsis, Triangulus.

ADDITIONAL THORACICAN SUBGENUS (BALANIDAE)

(see p. *R*285)

Balanus (Actinobalanus) Moroni, 1967, p. 923 [**B. (Hesperibalanus?) actinomorphus* Moroni, 1952, p. 73; SD Moroni, 1967, p. 919]. *Balanus* with solid wall and porous basis. Primary denticles of basal margin of wall without secondary denticles. *Plio.-low.Pleist.,* N.Eu.-Medit. [Moroni, N. A., 1967, *Classificazione sottogenerica ed affinita di Balanus actinomorphus Moroni, 1952:* Rivista Italiana Paleont., v. 73, no. 3, p. 919-928].

ADDENDUM TO CYCLOIDEA

By M. F. GLAESSNER

A recent paper by GALL & GRAUVOGEL (*Faune du Buntsandstein. II.-Les Halicynes:* Ann. Paléontologie, v. 53, pt. 1, 14 p., 7 pl., 5 fig., 1967, Paris) adds significantly to the knowledge of *Halicyne* and the Cycloidea but still leaves much doubt on the morphology and affinities of *Halicyne.* A semicircular anteromedian plate seen in one specimen and designated as rostral is not easily explicable in terms of crustacean morphology. The presence of compound eyes in the anterolateral emarginations is confirmed; they are considered as stalked. Paired triangular "frontal horns" anterior to the eyes are unexplained; they may be appendages. This form has five pairs of stout, spinose, five-segmented legs, each with a strong, curved, anteriorly directed dactylus, giving the animal a chelicerate-like (rather than crustacean) habit. If the legs are biramous they are not similar to the limbs shown in HOPWOOD's reconstruction (Fig. 363A,*A*); annulated appendages interpreted as exopods now have been found in *Halicyne* but apparently only in positions behind the other legs. What has been termed endoskeleton could well be homologous to the ventral plates known in Paleozoic specimens; the presence of a carbonized alimentary canal is confirmed. Numerous close-set posterolateral vertical lamellae under the carapace may be gills, resembling those of some chelicerates.

Halicyne is still considered to represent Crustacea of unknown affinities. GALL & GRAUVOGEL (1967) propose a family Halicynae [*recte* Halicynidae] and a subclass Halicyna. Both taxa seem premature, pending a restudy of related Paleozoic fossils.

INDEX

Italicized names in the following index are considered to be invalid; those printed in roman type, including morphological terms, are accepted as valid. Suprafamilial names are distinguished by the use of full capitals and author's names are set in small capitals with an initial large capital. Page references having chief importance are in boldface type (as **R327**).