

PART P  
ARTHROPODA 2

CHELICERATA  
WITH SECTIONS ON PYCNOGONIDA  
AND PALAEOISOPUS

BY LEIF STØRMER, ALEXANDER PETRUNKEVITCH, AND JOEL W. HEDGPETH

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CHELICERATA

By LEIF STØRMER

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**Subphylum CHELICERATA**  
**Heymons 1901**

Terrestrial and aquatic arthropods with pair of preoral appendages developed as 2-, 3-, and ?4-jointed chelicerae or pincers; next following pair of appendages (pedipalps) primarily ambulatory, secondarily modified into prehensile, sensory, or masticatory organs. Body divided into a prosoma (cephalothorax) with 6 postoral segments in addition to the preoral portion, and an opisthosoma (abdomen) of primarily ?12 segments, the 1st (comprising 7th somite) commonly reduced. Genital ducts open in the 8th postoral somite. *Cam.-Rec.*

**GROUPS AND THEIR OCCURRENCE**

The subphylum comprises the classes Merostomata and Arachnida. The Pantopoda (Pycnogonida) have also been in-

cluded in the Chelicerata but may belong to a separate group.

Whereas the merostomes are aquatic forms, the arachnids are confined to land, except for a few forms which are secondarily adapted to living in water. The different mode of life has influenced the development of several morphological structures, especially the appendages and respiratory organs (gills, lungs). In spite of this, other structures have been kept nearly unaltered in all members of the Chelicerata. Fig. 1 indicates the main ventral structure in a generalized chelicerate. The secondarily preoral position of the chelicerae is demonstrated in the ontogeny. The conservatism of the chelicerae is expressed in the eurypterid *Pterygotus*, where it has retained its general structure even though the pincers are enormously developed.

[P1]

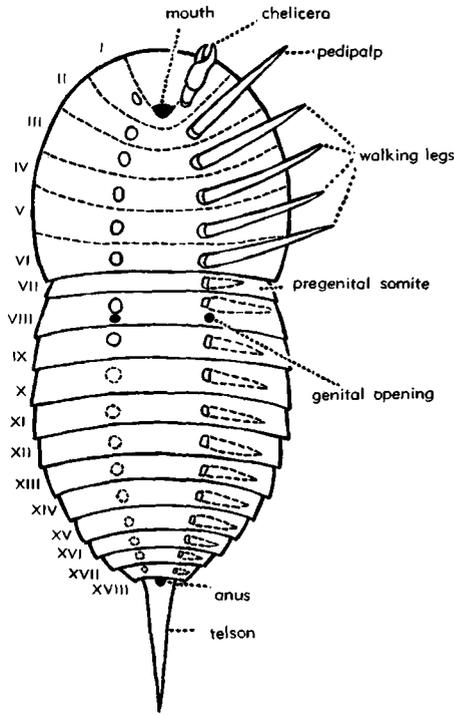


FIG. 1. Generalized chelicerate showing main morphological features of ventral side, diagrammatic.

Since fossil chelicerates are comparatively rare, our knowledge of the vertical and horizontal distribution of species is fairly limited. The vertical distribution of the orders is shown in Fig. 2. As for horizontal distribution, merostomes are known from North and South America, Europe, Africa, Asia and Australia, and are more frequent in the northern than in the southern hemisphere. Up to now fossil arachnids have been found almost exclusively in Europe and North America.

## CLASSIFICATION

A tabular summary showing main divisions of the chelicerates as generally recognized and adopted in organizing the *Treatise* follows. The arrangement of merostomes is by Størmer, of arachnids by Petrunkevitch, and of pycnogonids by Hedgpeth.

### Main Divisions of Chelicerata and Pycnogonida

- Chelicerata (*subphylum*), *L.Cam.-Rec.*
- Merostomata (*class*), *L.Cam.-Rec.*
- Xiphosura (*subclass*), *L.Cam.-Rec.*
- Aglaspida (*order*), *L.Cam.-U.Ord.*
- Xiphosurida, *Sil.-Rec.*
- Eurypterida (*subclass*), *M.Ord.-Perm.*
- Arachnida (*class*), *Sil.-Rec.*
- Latigastra (*subclass*), *Sil.-Rec.*
- Scorpionida (*order*), *Sil.-Rec.*
- Pseudoscorpionida, *Oligo.-Rec.*
- Phalangida, *Penn.-Rec.*
- Architarbida, *Carb.*
- Acarida, *Dev.-Rec.*
- Stethostomata (*subclass*), *Carb.*
- Haptopodida (*order*), *Carb.*
- Anthracomartida, *Carb.*
- Soluta (*subclass*), *Dev.-Carb.*
- Trigonotarbida (*order*), *Dev.-Carb.*
- Caulogastra (*subclass*), *?Dev., Carb.-Rec.*
- Latisterna (*superorder*), *Jur.-Rec.*
- Palpigradida (*order*), *Jur.-Rec.*
- Camarostomata (*superorder*), *Carb.-Rec.*
- Thelyphonida (*order*), *Carb.-Rec.*
- Schizomida, *?Plio.-Rec.*
- Kustarachnida, *Penn.*
- Labellata (*superorder*), *?Dev., Carb.-Rec.*
- Phrynichida (*order*), *Carb.-Rec.*
- Araneida, *?Dev., Carb.-Rec.*
- Rostrata (*superorder*), *Carb.-Rec.*
- Solpugida (*order*), *Carb.-Rec.*
- Podogona (*superorder*), *Carb.-Rec.*
- Ricinuuleida (*order*), *Carb.-Rec.*
- Pycnogonida (*subphylum*), *L.Dev.-Rec.*
- Pantopoda (*order*), *Rec.*
- Palaeopantopoda, *L.Dev.*

FIG. 2. Diagram showing known stratigraphic distribution of main divisions of the Chelicerata and inferred phylogenetic relationships. The oldest discovered representatives of the Arachnida, consisting of Silurian scorpionids, are so strongly differentiated that divergence of the arachnid subclasses and orders is inferred to belong in the pre-Silurian part of early Palaeozoic time. Probably, also, the merostomes and arachnids comprised distinct stocks before the earliest Cambrian. The abrupt appearance of so many orders of Arachnida in the Late Carboniferous clearly reflects conditions affecting preservation of these arthropods, rather than origin in the latter part of the Paleozoic era.

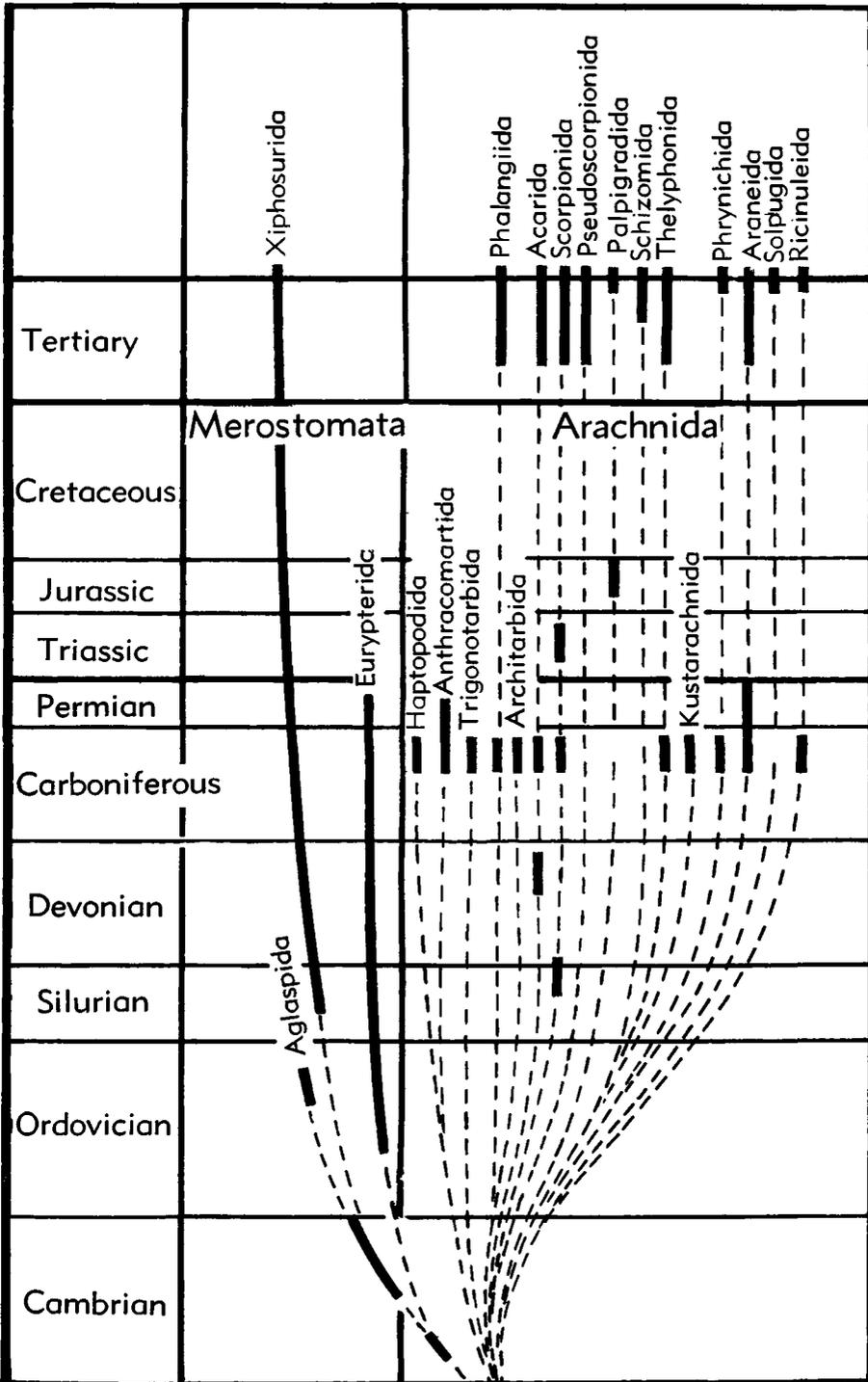


FIG. 2. (See facing page.)

# MEROSTOMATA

By LEIF STØRMER

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### Class MEROSTOMATA Dana, 1852

[=Poecilopoda M'COY, 1849 (*non* LATREILLE, 1817);  
Palacostraca GROBEN, 1905]

Aquatic Chelicerata of widely varying size, with body divided into a prosoma or cephalothorax and opisthosoma or abdomen (thoracetron) with a powerful, mostly styli-form telson. Prosoma with median ocelli and compound eyes (if not reduced), 6 pairs of prosomal appendages, the frontal one secondarily preoral, developed as 3- (or ?4-) jointed pincer-bearing limbs (cheliceræ); other prosomal appendages serving mainly as walking legs, with proximal seg-

ments (coxae) acting partly as jaws. Opisthosomal segments varying in number, free or ankylosed into a continuous shield. Appendages of the 1st, partly reduced opisthosomal segment situated below the prosoma, form the chilaria or a single plate (metastoma); other opisthosomal appendages plate-shaped and biramous, each consisting of a considerably reduced median branch and a lateral broad, strongly flattened branch carrying the gills; instead of the 1st pair of appendages below the abdomen (belonging to the 8th somite), is an operculum which contains openings of the genital ducts. *Cam.-Rec.*

[P4]

### MORPHOLOGY OF LIVING MEROSTOMES

The largest of the Recent forms may attain a length of about 60 cm. The body is covered by a stout exoskeleton, of which the expanded dorsal portion forms an excellent protection for structures underneath. The body (Fig. 3) is divided into 3 parts, the **prosoma** or cephalothorax, the **opisthosoma** or abdomen (thoracetron), and the **telson**. The semicircular strongly vaulted prosoma has a median **cardiac lobe** with a median crest, provided with 3 spines in young specimens. The **axial furrows** bordering the cardiac lobe converge slightly forward and become obsolete. In front of the cardiac lobe lie the **median ocelli**. A longitudinal ridge extending forward and back-

ward from each of the lateral compound eyes is called **ophthalmic ridge**. In young specimens each ridge bears 2 spines. The space between the ridges is termed the **cardiophthalmic region**, and that between the cardiac lobe and the ophthalmic ridges may be called the **interophthalmic region**. Here, and to some extent on the cardiac lobe, muscle markings suggest the segmentation.

The prosoma is separated from the opisthosoma by a transverse joint or hinge line. Embryological studies based on *Tachyplesus gigas* (MÜLLER) by IVANOV (11) show the joint line to cross the primary segmentation (Fig. 4A). The transverse joint line cuts through the 6th and 7th segments, the latter being reduced greatly. The broad steep rim surrounding the cardiophthalmic

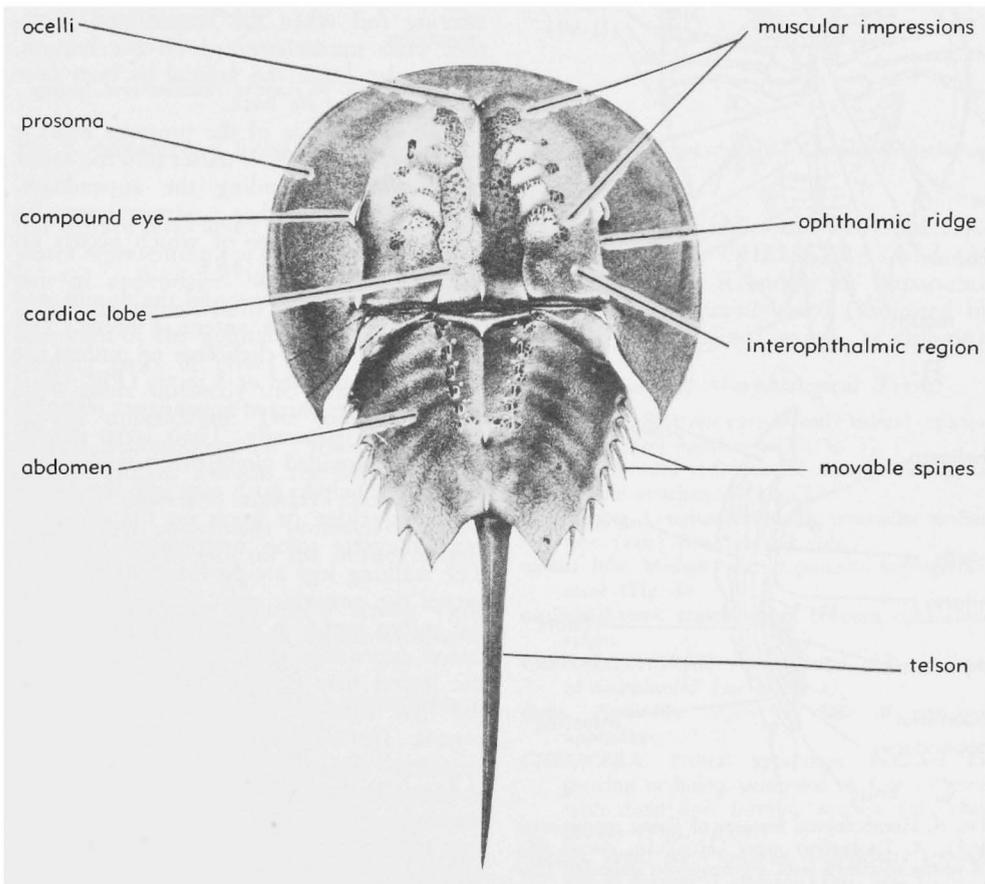


FIG. 3. Living merostome, the horseshoe crab, *Limulus polyphemus* (LINNÉ); dorsal view of a half-grown specimen,  $\times 0.5$  (56).

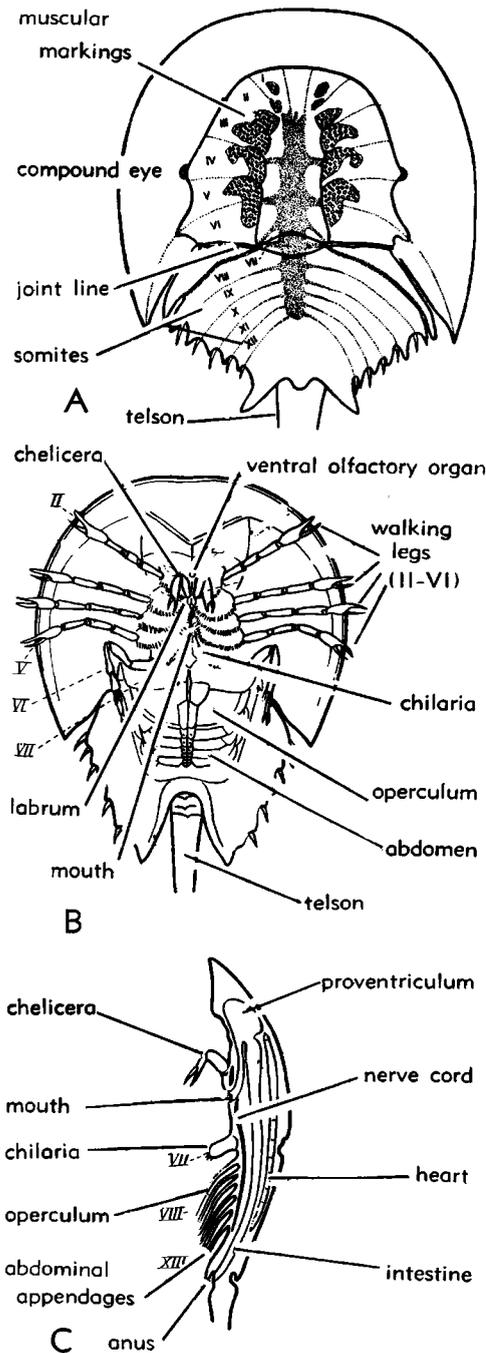


FIG. 4. Morphological features of living merostomes (64). A, *Tachypleus gigas* (MÜLLER), dorsal side of young specimen with segmentation indicated (enlarged). B,C, *Limulus polyphemus* (LINNÉ), ventral view and longitudinal section (much reduced) (64).

region and prolonged backward on each side may belong to an anterior segment of the prosoma.

The opisthosoma or abdomen forms a continuous, moderately vaulted shield. The serrate lateral margins, converging backward toward the telson, have intercalated movable spines. A trilobation of the abdomen is indicated by the axial furrows in which 6 pairs of invaginations, forming structures for muscle attachment (**apodemes**), may be distinguished. Embryological studies indicate existence of several rudimentary segments behind the segments with apodemes. The long styliform telson, articulating by a special T-shaped process to the abdomen, evidently represents tergal outgrowth from the posterior rudimentary segments. The telson is able to move in any direction and serves apparently as a steering rod when the streamlined horse-shoe crab moves forward on the bottom, and it also helps the animal to turn over when lying on its back.

The ventral side of the prosoma bears a broad doublure, which passes into the softer integument surrounding the appendages. The central mouth has a narrow upper lip (**labrum**) at the base of which occurs an olfactory organ (Fig. 4B).

The appendages surround the mouth. No multijointed preoral antennae occur. The secondarily preoral **chelicerae** or pincers are small and composed of 3 joints (Fig. 4B,C; 5). The 5 other pairs of appendages resemble one another generally. Their large oblong **coxae** are provided along the mid-line with spines that help to push prey into the gullet. A strong ridge or knob on the posterior coxa suggests some masticatory function. The walking legs are provided with **chela**, except the posterior pair, which has several flat spines useful in digging. An unjointed lateral appendage (**flabellum**) is attached to the lateral base of the coxa. In the male, the first legs are modified into clasping organs. The mouth is bordered posteriorly by a small internal plate (**endostoma**). Two short vertical plates (**chilaria**) behind the mouth represent the rudimentary appendages of the pregenital (7th) segment (Figs. 4B, C; 5).

The opisthosomal shield has a broad doublure, but the major portion of the ven-

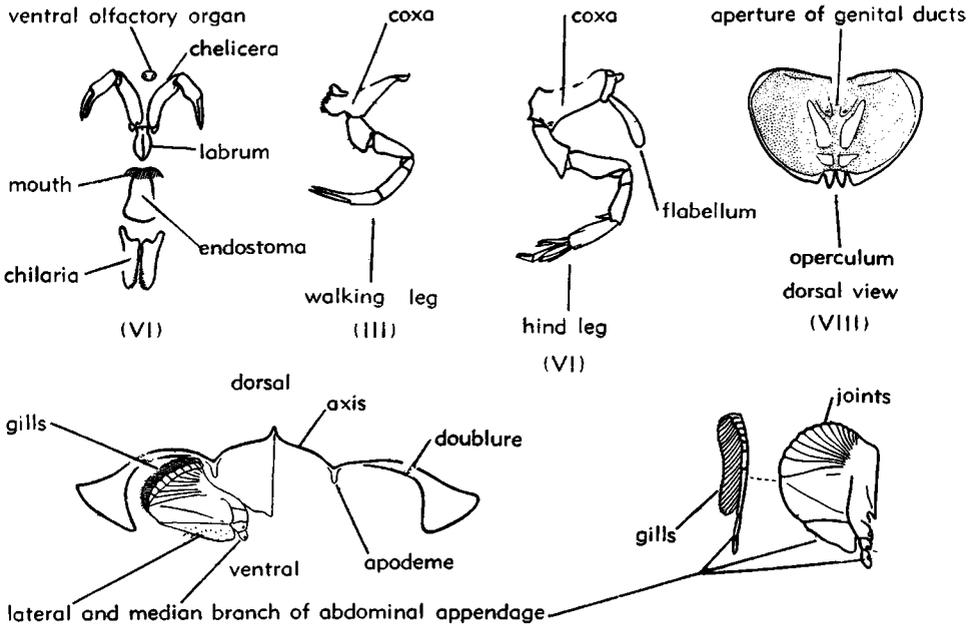


FIG. 5. Appendages of living xiphosurans; prosomal and abdominal appendages of *Limulus polyphemus* (LINNÉ) (much reduced) (64).

tral surface is occupied by the 6 overlapping plates representing the appendages. The first pair of appendages belong to the genital (8th) somite and form the **operculum** with openings of the genital ducts. The 5 succeeding pairs of plates (**gill appendages**) show more distinctly the biramous nature of the appendages. The jointed median branch, representing the "walking leg," is much reduced, whereas the lateral branch forms a powerful strongly flattened and multijointed appendage provided with the numerous book gills on the inner (dorsal) side (Fig. 5).

Internal organs include a strong "gizzard" and well-developed intestinal diverticula.

#### MORPHOLOGICAL TERMS APPLIED TO MEROSTOMES

The following alphabetically arranged glossary of morphological terms applied to merostomes is intended to give conveniently findable explanations of terms which may be unfamiliar to nonspecialists. Classification of the terms is indicated typographically so as to distinguish (1) those most

commonly used (indicated by boldface capitalized words, as **CHELICERA**) and (2) those ranked as secondary in importance because less frequently used (indicated by boldface uncanceled words, as **chilaria**).

#### Glossary of Morphological Terms

- ABDOMEN.** Posterior part of body behind cephalothorax (see opisthosoma) (Fig. 3).
- apodeme.** Inward deflection of sclerite serving for muscle attachment (Fig. 5).
- axial furrow.** Longitudinal groove separating median lobe (axis) from pleural area.
- cardiac lobe.** Median lobe of prosoma and opisthosoma (Fig. 3).
- cardiophthalmic region.** Space between ophthalmic ridges.
- CEPHALOTHORAX.** Fore part of body in front of opisthosoma (see prosoma).
- chela.** Pincer-like organ or claw of prosomal appendage.
- CHELICERA.** Preoral appendage modified for piercing or biting, composed of 3 or ?4 joints with distal ones forming a chela (pl., chelicerae) (Figs. 4B,C).
- chilaria.** Small plate forming rudimentary appendage of pregenital segment (Figs. 4B,C).
- COMPOUND EYE.** Lateral eye composed of many facets (Fig. 3).

- coxa.** Proximal (basal) joint of thoracic appendage, directly attached to body (Fig. 5).
- doublure.** Inwardly deflected marginal part of dorsal exoskeleton (Figs. 5, 18).
- endostoma.** Small plate on ventral side of body at posterior end of mouth (Fig. 5).
- epicoxite.** Small plate attached to median part of coxa (Fig. 18).
- epimer.** Lateral (pleural) expansion of tergite.
- epistoma.** Median plate on doublure in front of mouth (Fig. 7, 4b).
- epistomal suture.** Longitudinal suture bordering epistoma.
- exoskeleton.** External more or less mineralized chitinous covering of body.
- femur.** Joint belonging to proximal part of prosomal appendage.
- flabellum.** Joint attached to lateral border of coxa (Fig. 5).
- genal angle.** Posterolateral corner of prosoma.
- gill appendage.** Opisthosomal appendage bearing respiratory organ (Figs. 5, 17).
- glabellar area.** Elevated part of prosoma between compound eyes, corresponding to interophthalmic region.
- intercardiophthalmic region.** Small rectangular area of prosoma embracing cardiac lobe and minor part of interophthalmic region.
- interophthalmic region.** Space between cardiac lobe and ophthalmic ridge (Fig. 3).
- labrum.** Upper lip, just in front of mouth (Figs. 4B, 5).
- marginal suture.** Ecdysial junction between exoskeletal elements at prosomal margin.
- median suture.** Longitudinal suture on doublure in front of mouth (Fig. 18).
- MESOSOMA.** Anterior part of opisthosoma (abdomen) carrying appendages.
- METASOMA.** Posterior part of opisthosoma (abdomen) lacking appendages.
- METASTOMA.** Plate at posterior edge of mouth (Figs. 17, 18).
- ocellus.** Median visual organ located on prosoma (Fig. 3).
- occipital band.** Rim along posterior border of prosoma.
- occipital furrow.** Groove in front of occipital band.
- OPERCULUM.** Plate adjoining appendages of genital segment (Figs. 4B,C; 17).
- OPHTHALMIC RIDGE.** Longitudinal ridge above compound eye and extending forward and backward from it (Fig. 3).
- OPISTHOSOMA.** Posterior part of body behind prosoma (same as abdomen).
- PADDLE.** Flat distal portion of last prosomal appendage (toward rear) (Fig. 17).
- patella.** Joint forming knee in prosomal appendage.
- pleura.** Lateral part of opisthosoma.
- pleural furrow.** Groove crossing pleura.
- postabdomen.** Narrow posterior part of opisthosoma (abdomen) (Fig. 17).
- postventral plate.** Plate below posterior part of abdomen.
- preabdomen.** Broad anterior part of opisthosoma (abdomen) (Fig. 17).
- prefemur.** Joint proximal to femur in prosomal appendage.
- pretarsus.** Joint distal to tarsus in prosomal appendage.
- pretelson.** Opisthosomal segment anterior to telson (Fig. 17B).
- procephalic lobe.** Anterior (preoral) part of embryo.
- PROSOMA.** Fore part of body in front of abdomen (same as cephalothorax).
- proventriculum.** Anterior part of intestine (Fig. 4C).
- sclerite.** Chitinized cover of body segment forming part of exoskeleton.
- somite.** Body segment.
- STERNITE.** Plate forming ventral cover of somite (Fig. 17B).
- SWIMMING LEG.** Hindmost prosomal appendage serving as swimming organ (Fig. 17A).
- tarsus.** Joint of distal part of prosomal appendage.
- TELSON.** Postanal spine or plate (Figs. 1, 17).
- TERGITE.** Plate forming dorsal cover of somite (Fig. 17A).
- thoracetron.** Opisthosoma or abdomen.
- tibia.** Joint of distal part of prosomal appendage.
- trochanter.** Joint of proximal part of prosomal appendage.
- WALKING LEG.** Prosomal appendage serving for walking.

## CLASSIFICATION

Merostomes are divisible into 2 main groups which appropriately are ranked as subclasses; these are Xiphosura or horseshoe crabs, which are represented by modern *Limulus*, and the extinct Eurypterida. Classification of the Xiphosura is discussed in a recent paper (30) which explains considerations leading to recognition of 2 orders (Aglaspida, Xiphosurida), one without defined suborders and the other containing 2 suborders (Synziphosurina, Limulina). Families of the Limulina are grouped in 3 superfamilies. A tabulation of suprageneric units, showing the number of described genera and subgenera in each, follows.

### *Suprageneric Divisions of Merostomata*

(First figures in parentheses indicate number of genera and second the number of subgenera.)

- Xiphosura (*subclass*) (64; 3), *L.Cam.-Rec.*  
 Aglaspida (*order*) (12), *L.Cam.-U.Ord.*  
 Aglaspidae (8), *U.Cam.*  
 Strabopidae (2), *U.Cam.-U.Ord.*  
 Beckwithiidae (1), *M.Cam.*

- Xiphosurida (order) (27), *Sil.-Rec.*  
 Synziphosurina (suborder) (9), *U.Sil.-L.Dev.*  
   Limuloididae (1), *U.Sil.*  
   Bunodidae (3), *U.Sil.*  
   Neolimulidae (1), *U.Sil.-L.Dev.*  
   Pseudoniscidae (3), *U.Sil.*  
   Weinberginidae (1), *L.Dev.*  
 Limulina (suborder) (18), *L.Dev.-Rec.*  
   Belinuracea (superfamily) (3), *Dev.-U.Carb.*  
     Belinuridae (3), *Dev.-U.Carb.*  
   Euproopacea (superfamily) (8), *L.Dev.-Perm.*  
     Euproopidae (4), *U.Carb.-Perm.*  
     Liomesaspidae (2), *Penn.-Perm.*  
     Elleriidae (1), *U.Dev.-Penn.*  
   Kiaeriidae (1), *?L.Dev.*  
   Limulacea (superfamily) (7), *Perm.-Rec.*  
     Paleolimulidae (1), *Perm.*  
     Mesolimulidae (3), *L.Trias.-Jur., ?Cret.*  
     Limulidae (3), *Rec.*  
       Limulinae (subfamily) (1), *Rec.*  
       Tachypleinae (2), *Rec.*  
   Uncertain superfamily and family (2), *U.Carb.-Perm.*  
 Eurypterida (subclass) (25; 3), *Ord.-Perm.*  
   Eurypteracea (superfamily) (14; 3), *Ord.-Perm.*  
     Hughmilleriidae (6), *Ord.-Perm.*  
     Pterygotidae (1; 3), *Ord.-Dev.*  
     Eurypteridae (3), *Ord.-U.Carb.*  
     Carcinosomatidae (1), *Ord.-Sil.*  
     Mixopteridae (1), *Sil.-L.Dev.*  
     Megalograptidae (2), *Ord.*

- Stylonuracea (superfamily) (11), *Ord.-L.Perm.*  
   Stylonuridae (7), *Ord.-L.Perm.*  
   Dolichopteridae (2), *Sil.-Dev.*  
   Rhenopteridae (1), *L.Dev.*  
   Mycteropidae (1), *U.Carb.*

ONTOGENY

The ontogeny of Recent limulids is of considerable interest in connection with study of the phylogeny of the Merostomata. The earliest stages (Fig. 6, 1a) indicate only 4 primary segments (as inferred in the cephalon of trilobites), but in later ontogeny the secondary segments and appendages develop. A dorsal organ, probably sensory in function, is found in the last embryonic stages. The 1st free larva (Fig. 6, 1c) has been called the trilobite stage because of its general resemblance to such forms. The prosoma has more segments than the trilobite cephalon, however, and all segments of the abdomen in *Limulus* are fused, being indicated only by rows of pigment. The 1st larva is more like the fossil Euproopacea.

During ecdysis (molting) the exoskeleton opens along a marginal suture on the prosoma. The animal creeps out and leaves the abandoned exoskeleton (exuvia) with a closed suture: this may be preserved in the sediment as a "complete" specimen.

OCCURRENCE

Although grown-up limulids are benthonic forms crawling and digging in the sand and mud, the young larvae (and to some extent the adults) are able to swim on their backs by rapid strokes of the abdominal appendages. The Recent representatives of the Merostomata are marine forms, but *Carcinoscorpius* is also able to endure brackish and fresh water of estuaries and rivers.

Inasmuch as most older-than-Recent merostomes are nonmarine forms, fossil remains of these arthropods are chiefly confined to the less common fresh-water and brackish-water sediments and are not common. Because of the rare and scattered finds, the number of species known is relatively small compared with the number of genera described.

The large majority of known species of merostomes occur in Paleozoic rocks and only a small group continues to Recent time.

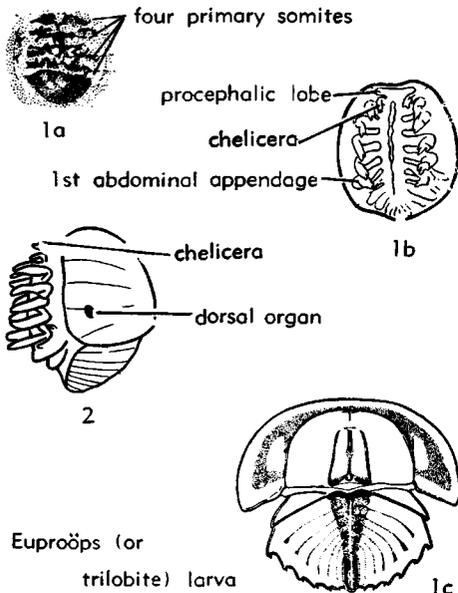


FIG. 6. Ontogeny of living xiphosurans. 1a-c, *Tachypleus gigas* (MÜLLER), (after IVANOV). 2, *Limulus polyphemus* (LINNÉ) (48).

The morphological changes that may be noticed during development of the Merostomata offer valuable information on the evolution of one arthropod group during the long time span from Cambrian to Recent. The living forms (horseshoe crabs or king crabs) are not much different from

their Mesozoic relatives and are thus excellent examples of persistent forms. The Recent forms, comprising 5 species previously referred to the genus *Limulus*, are bottom dwellers, inhabiting shallow water along the east coasts of North America and Asia.

## SYSTEMATIC DESCRIPTIONS

### Subclass XIPHOSURA Latreille, 1802

[*nom. correct.* STÖRMER, 1944 (*pro* Xiphosures LATREILLE, 1802)] [=Xyphosures LATREILLE, 1802 (*nom. neg.*); Gnathopoda STRAUS-DÜRKHEIM, 1829; Poccilopoda CLAUS, 1868 (*non* Poccilopes LATREILLE, 1817)]

Merostomata with trilobate dorsal shield. Prosoma large, abdomen with a variable number of segments and long styliform or lanceolate telson. Appendages of pregenital segment not ankylosed, abdominal appendages biramous with book gills. *L.Cam.-Rec.*

### Order AGLASPIDA Walcott, 1911

Xiphosura with elongate, more or less vaulted body. Prosoma with prominent compound eyes. Opisthosoma with 11 or 12 segments, all free, or the posterior ones ankylosed into a shield; trilobation absent or indistinct. Telson with broad, powerful basal portion. Postventral plates below the posterior portion of the abdomen. ?Chelicera 4-jointed, other 5 prosomal appendages, as well as abdominal appendages, developed as short walking legs. Exoskeleton phosphatic, outer surface with variable granulation. *L.Cam.-U.Ord.*

### DISCUSSION

*Morphological features.* The Aglaspida have an average length of 2 to 6 cm., but specimens longer than 21 cm. have been described. The subovate body has no true axial furrows, but a more or less distinct trilobation is suggested by different convexity of the axial and pleural regions. The comparatively large, mostly broad prosoma may have the genal angles prolonged into genal spines. The compound eyes generally have an antemedian position: ocelli may have been present but are not recognized surely. In some forms a glabellar area be-

tween the eyes and the posterior border, corresponding to the interophthalmic region in later forms, rises above the more flattened portion of the prosoma. The elevated glabellar area, which may be lobed (Fig. 7,1,2), has a subtriangular outline, the broadest part posterior.

The opisthosoma has 12 free articulating segments in the Paleomeridae and 11 in the Aglaspidae but 8 free anterior segments with ?3 ankylosed posterior segments in the Beckwithiidae. The pleurae, some with an anterior band or pleural furrow (or both) and mostly prolonged into pleural spines, overlap each other backwards. Their curved anterior border, not permitting a transverse straight joint line, suggests a somewhat imperfect articulation, the succeeding tergites sliding over each other. Inasmuch as only the 11th segment lacks pleurae in trilobed forms, no postabdomen is clearly demonstrated, except in the Beckwithiidae, where it forms the posterior shield.

The powerful telson has a broad basal portion, which is possibly a separate 12th segment united with the telson, as suggested by RAASCH (20). In *Beckwithia* (Fig. 9, 1), the posterior abdominal shield seemingly has a powerful but short dorsal spine rising in the middle. A telson may have been present at the terminal margin.

On the ventral side, behind the doublure, a 4-sided plate possibly may be interpreted as an epistoma (Fig. 7, 4b). Below the last abdominal segments and the base of the telson, the Aglaspidae have characteristic postventral plates (Fig. 7, 3). The plates evidently give support to powerful muscles leading from the telson.

The appendages are known to a certain extent in *Aglaspis* (Fig. 15, 4ab). The 1st pair seem to have 4-jointed chelicerae,

whereas other prosomal appendages are developed as single walking legs, of which 4 joints have been noticed. The same kind of legs have been found on the abdomen. This suggests primitive features compared with later Xiphosura and Eurypterida, in which the abdominal walking legs are much reduced.

The exoskeleton of the Aglaspidae has proved to be phosphatic, but whether this is characteristic of all members of the order is not certain. The ornamentation is char-

acteristic, consisting particularly of pustules, tubercles, and puncta.

*Ecology.* The Aglaspida were marine animals, for they occur together with trilobites and brachiopods. The sediments in which they are found suggest a quiet and fairly shallow marine environment.

*Affinities.* In general shape of the body, the Aglaspida recall the Trilobita and particularly some of the Merostomoidea (*Leancoilia*, *Emeraldella*) of the Middle Cambrian. In the forms mentioned, however,

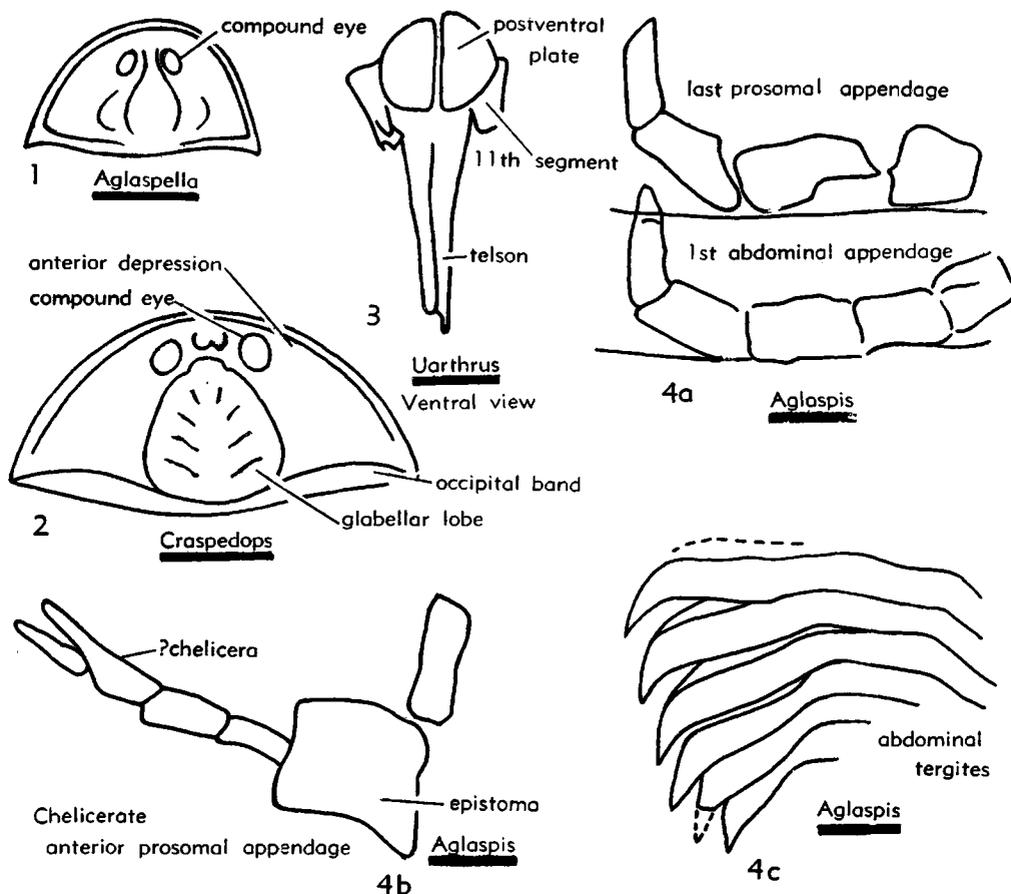


FIG. 7. Morphological features of aglaspids, U.Cam., Wis. (59) (p. P12-P14).

- 1, *Aglaspella eatoni* (WHITFIELD), prosoma (reconstr.),  $\times 1$ .
- 2, *Craspedops modesta* RAASCH, prosoma, showing anteriorly placed eyes and elevated glabellar area (reconstr.),  $\times 2$ .
- 3, *Uarthrus instabilis* RAASCH, posterior extremity from ventral side,  $\times 2$ .
- 4a-c, *Aglaspis spinifer* (RAASCH); 4a, last prosomal and 1st abdominal appendage; 4b, chelicerate anterior prosomal appendage with epistoma; 4c, freely articulating abdominal segments with laterally extended pleurae; all  $\times 1.3$ .

the cephalon has only 4 appendages behind the mouth, as compared with ?6 in the Aglaspidia; also antennae, such as possessed by Trilobita and Merostomoidea, are lacking in the Aglaspidia. The Synziphosurina have much in common with the Aglaspidia. Particularly, the Pseudoniscacea have a very similar body, differing mainly in possession of a large prosoma without compound eyes and an abdomen of 10 segments only. In the elongate nature of their body, the Aglaspidia resemble the Eurypterida. One of the aglaspids from Upper Cambrian rocks (*Strabops*, Fig. 9,2) actually was interpreted as a primitive eurypterid by CLARKE & RUEDEMANN (5), partly on the basis of erroneous assumption that the abdomen contains 12 segments, as in the Eurypterida. On the other hand, the genus *Paleomerus* (Fig. 8), from the Lower Cambrian, seems to represent a transition between the Xiphosura of aglaspid form and the Eurypterida, for the body shape and presence of compound eyes correspond to both the Aglaspidia and eurypterids such as *Hughmilleria* (Fig. 21,1); also, the seemingly loose articulation of the tergites in *Paleomerus* suggests the aglaspids, whereas the presence of 12 abdominal segments is a eurypterid character. The exact taxonomic placement of *Paleomerus* is uncertain because the nature of the appendages is unknown, but provisionally it is assigned to the Aglaspidia.

#### Family PALEOMERIDAE Størmer, 1955

Exoskeleton of medium size; opisthosoma with 12 free segments, the 12th trapezoid; telson unknown. *L.Cam.*

*Paleomerus* STØRMER, 1955 [*\*P. hamiltoni*]. Body (exclusive of telson) ovate, strongly vaulted; prosoma short, with antemedian compound eyes; 12th segment long, trapezoid (31). *L.Cam.*, Sweden. —FIG. 8,1. *\*P. hamiltoni*; 1a,b, side and dorsal views (reconstr.),  $\times 0.8$  (64n).

#### Family AGLASPIDIDAE Miller, 1877

[*nom. correct.* STØRMER, herein (pro Aglaspidac MILLER, 1877)]

Medium-size forms with 11 free abdominal segments, abdomen moderately elongate. *U.Cam.*

*Aglaspis* HALL, 1862 [*\*A. barrandeii*]. Dorsal shield pustulose; eyes submedian; prosoma with conspicuous rim, occipital band, and interophthalmic

region set off by relative convexity, occipital band, and tergites bearing paired postaxial nodes (20). *U.Cam.*, N.Am.—FIG. 7,4; 9,5a. *A. spinifera* RAASCH, Trempeal., Wis.; 7,4a, prosomal appendages,  $\times 2$ ; 7,4b, last prosomal and 1st abdominal appendage,  $\times 2$ ; 7,4c, abdominal segments,  $\times 0.5$ ; 9,5a, prosoma,  $\times 0.7$  (59). —FIG. 9,5b. *A. simplex* RAASCH, Trempeal., Wis.; dorsal side,  $\times 0.7$  (59).

*Aglaspella* RAASCH, 1939 [*\*A. granulifera*]. Like *Aglaspis* but with smaller, more elevated eyes; no marginal rim on prosoma and no postaxial nodes (20). *U.Cam.*, N.Am.—FIG. 7,1. *A. eatoni* (WHITF.), Trempeal., Wis.; prosoma (reconstr.),  $\times 1$  (64).

*Glypharthrus* RAASCH, 1939 [*\*Eurypterus thomasi* WALTER, 1924]. Dorsal shield smooth or pitted; eyes large, subcentral; marginal rim present, occipital and pleural furrows distinct; telson slender (20). *U.Cam.*, N.Am.—FIG. 9,3. *\*G. thomasi* (WALTER), Trempeal., Wis.; dorsal side,  $\times 2$  (59).

*Aglaspoides* RAASCH, 1939 [*\*A. sculpilis*]. Dorsal shield striated, pitted, or smooth; prosoma flat, without rim and occipital furrows; large subcentral convex eyes; no pleural furrows (20). *U.Cam.*, N.Am.—FIG. 9,6. *\*A. sculpilis*, Trempeal., Wis.; telson,  $\times 3$  (59).

*Uarthrus* RAASCH, 1939 [as *U. arthrus*] [*\*U. instabilis*]. Dorsal shield obscurely pitted; prosoma convex, without rim or occipital furrow; large

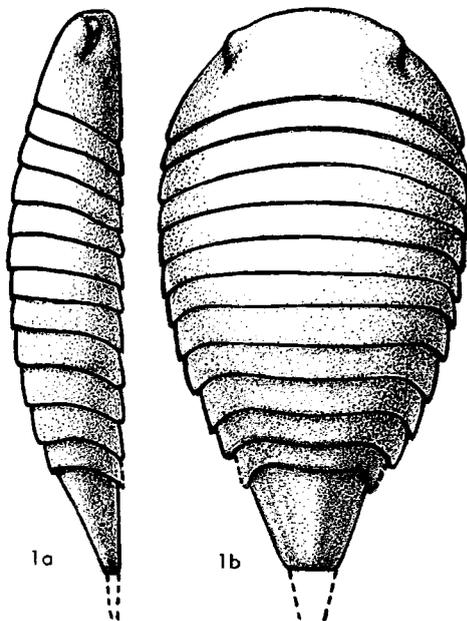


FIG. 8. *Paleomerus hamiltoni* STØRMER, from Lower Cambrian of Sweden; reconstr., side and dorsal views,  $\times 0.8$  (64 n) (p. P12).

close-set eyes near anterior margin; 11th segment U-shaped (20). *U.Cam.*, N.Am.—FIG. 7,3; 9,4. \**U. instabilis*, Trempeal., Wis.; 7,3, ventral view of 11th segment with telson,  $\times 2$ ; 9,4, prosoma,  $\times 3$  (59).

*Cyclopites* RAASCH, 1952 [pro *Cyclopina* RAASCH, 1939 (non AGASSIZ, 1846; nec CLAUS, 1862; nec BRADY, 1872)] [\**Cyclopina vulgaris* RAASCH,

1939]. Dorsal shield pitted; prosoma strongly convex; anterior very close-set eyes forming bilobed node; rim and occipital furrow absent; pleura with furrow near anterior margin (20). *U.Cam.*, N.Am.—FIG. 9,7. \**C. vulgaris* (RAASCH), Trempeal., Wis.; prosoma,  $\times 1.3$  (59).

*Craspedops* RAASCH, 1939 [\**C. modesta*]. Dorsal shield nearly smooth; prosoma moderately convex;

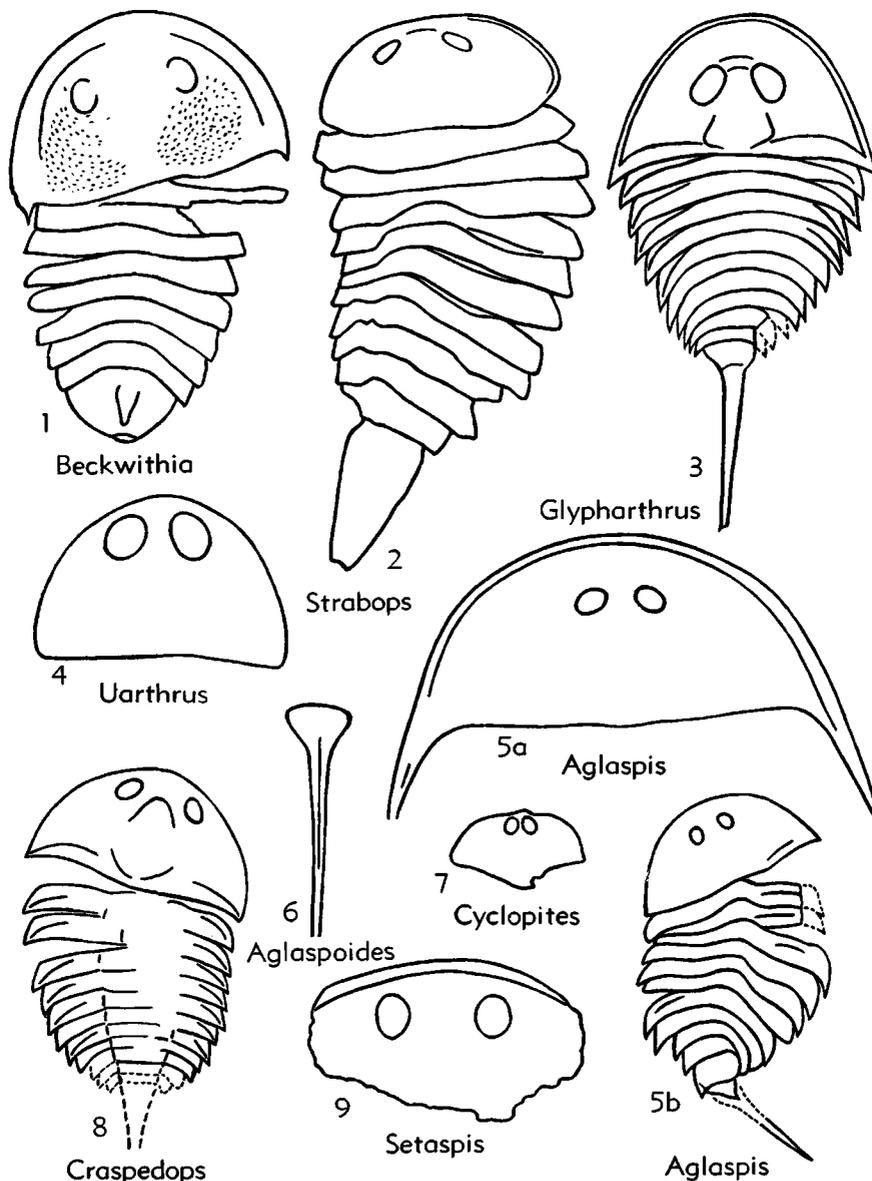


FIG. 9. Aglaspida (p. P12-P14).

eyes large, anterior, moderately far apart; occipital band present; interophthalmic region distinct, elevated lobate; pleural furrows on abdominal tergites (20). *U.Cam.*, N.Am.—FIG. 7,2; 9,8. \**C. modesta*, Trempeal., Wis.; 7,2, prosoma (reconstr.)  $\times 2$ ; 9,8, dorsal side,  $\times 3$  (59).

*Setaspis* RAASCH, 1939 [\**S. spinulosa*]. Dorsal shield pustulose; eyes large, widely separated, near anterior marginal rim; no occipital furrow (20). *U.Cam.*, N.Am.—FIG. 9,9. \**S. spinulosa*, Trempeal., Wis.; anterior part of prosoma,  $\times 0.7$  (59).

### Family STRABOPIDAE Gerhardt, 1932

[*nom. correct.* STØRMER, herein (pro Strabopidae GERHARDT, 1932)]

Medium-size forms with 11 free abdominal segments; prosoma short, elliptical; eyes antemedian; abdomen elongate or ovate; no pleural spines; telson broad. *U.Cam.-U.Ord.*

*Strabops* BEECHER, 1901 [*non* JORDAN, 1904] [\**S. thacheri*]. Dorsal shield with indication of scales near posterior border of abdominal segments; body elongate. *U.Cam.*, N.Am.—FIG. 9,2. \**S. thacheri*, Mo.;  $\times 0.7$  (34).

*Neostrabops* CASTER & MACKE, 1952 [\**N. martini*]. Dorsal shield seemingly smooth; body ovate; prosoma with quadrate glabellar elevation and occipital furrow (4). *U.Ord.*, N.Am.—FIG. 10. \**N. martini*, Ohio;  $\times 1.5$  (36).

### Family BECKWITHIIDAE Raasch, 1939

Aglaspidia with some posterior abdominal segments ankylosed. *M.Cam.*

*Beckwithia* RESSER, 1931 [\**B. typha*]. Dorsal shield pustulose; prosoma large, with flattened rim; eyes situated about midway between center and margin; 8 free abdominal segments; posterior triangular shield with dorsal spines; telson probably styliform. *M.Cam.*, N.Am.—FIG. 9,1. \**B. typha*, Utah;  $\times 1$  (61).

## Order XIPHOSURIDA Latreille, 1802

[*nom. correct.* STØRMER, 1952 (pro Xiphosures LATREILLE, 1802)] [=Xiphosures LATREILLE, 1802; Xiphosura STØRMER, 1944]

Xiphosura with a subovate to subcircular, flat or vaulted body and styliform telson; prosoma generally with a distinct cardiac lobe and ophthalmic region bordered by ridges; abdomen with 10 or fewer segments, all free, or some or all ankylosed. Chelicerae 3-jointed, abdominal appendage seemingly plate-shaped. *Sil.-Rec.*

### DISCUSSION

The Synziphosurina and Limulina, comprising the present order, have generally

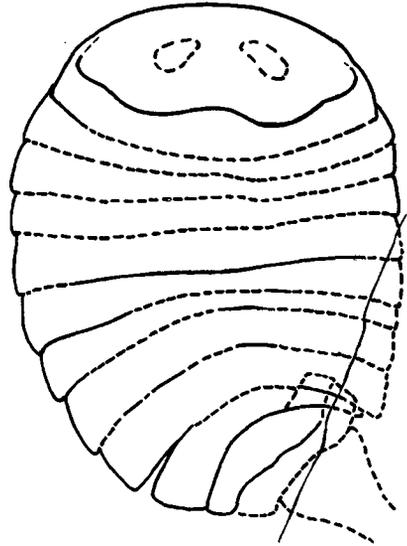


FIG. 10. *Neostrabops martini* CASTER & MACKE, *U.Ord.*, Ohio,  $\times 1$  (36) (p. P14).

been regarded as separate orders (Synziphosura and Limulida, 22, 28), presumed to have taxonomic rank equal to the Aglaspidia. Present knowledge of the Xiphosurida, however, indicates that the Synziphosurina and Xiphosurina are linked more intimately, whereas connection with the Aglaspidia is somewhat remote. For these reasons, the Synziphosurina and Limulina are here regarded as suborders of the Xiphosurida and together ranked as coordinate with the Aglaspidia.

## Suborder SYNZIPHOSURINA Packard, 1886

[*nom. correct.* STØRMER, 1952 (pro Synziphosura, PACKARD, 1886)] [=Bunodomorpha ZITTEL-E., 1913]

Xiphosurida with a medium to large prosoma, lacking distinct traces of compound eyes, cardiac lobe present or absent; abdomen with 9 to 10 segments, of which all may be free, or the 6th and 7th ankylosed; appendages (as far as known) with flattened distal spines instead of chelae. *U. Sil.-L.Dev.*

### DISCUSSION

The Synziphosurina form a small group of Xiphosura that are found associated with eurypterids and primitive vertebrates in the

Upper Silurian and Lower Devonian strata of several continents. They are small forms, measuring generally about 5 cm. in length (telson included).

**Morphological features.** The body (telson excluded) is subcircular to subovate. As shown in *Pseudoniscus*, the Synziphosurina were able to roll up. The large prosoma is semicircular to semielliptical in outline, the genal angles being slightly prolonged in certain forms. The prosoma is fairly large and smooth in *Pseudoniscus* (Fig. 11, 3) and *Weinbergina* (Fig. 11, 9), but smaller and more vaulted and sculptured in other genera. A cardiac lobe is distinct in *Bunodes*, *Bunaia*, and *Neolimulus* (Fig. 11, 2, 4, 10), in particular. The lobe has an anterior swelling in the 2 former genera. In

*Limuloides* and *Neolimulus* (Fig. 11, 1, 2) ophthalmic ridges enclosing a cardiophthalmic region are indicated, features similar to those found in more recent forms. A segmentation of the area outside the cardiac lobe is suggested by the radial furrows in *Bunodes* and *Bunaia* and by the radial ridges in *Limuloides*. In *Bunodes*, the marginal portion of the prosoma is very steep. Differences in character of the prosoma of *Pseudoniscus* and *Weinbergina* on one side and remaining known genera on the other suggest recognition of 2 superfamilies, but such division probably should await more evidence.

Most genera lack lateral eyes. Possible traces of eyes have been described in *Neolimulus* and *Pseudoniscus*. Early reconstruc-

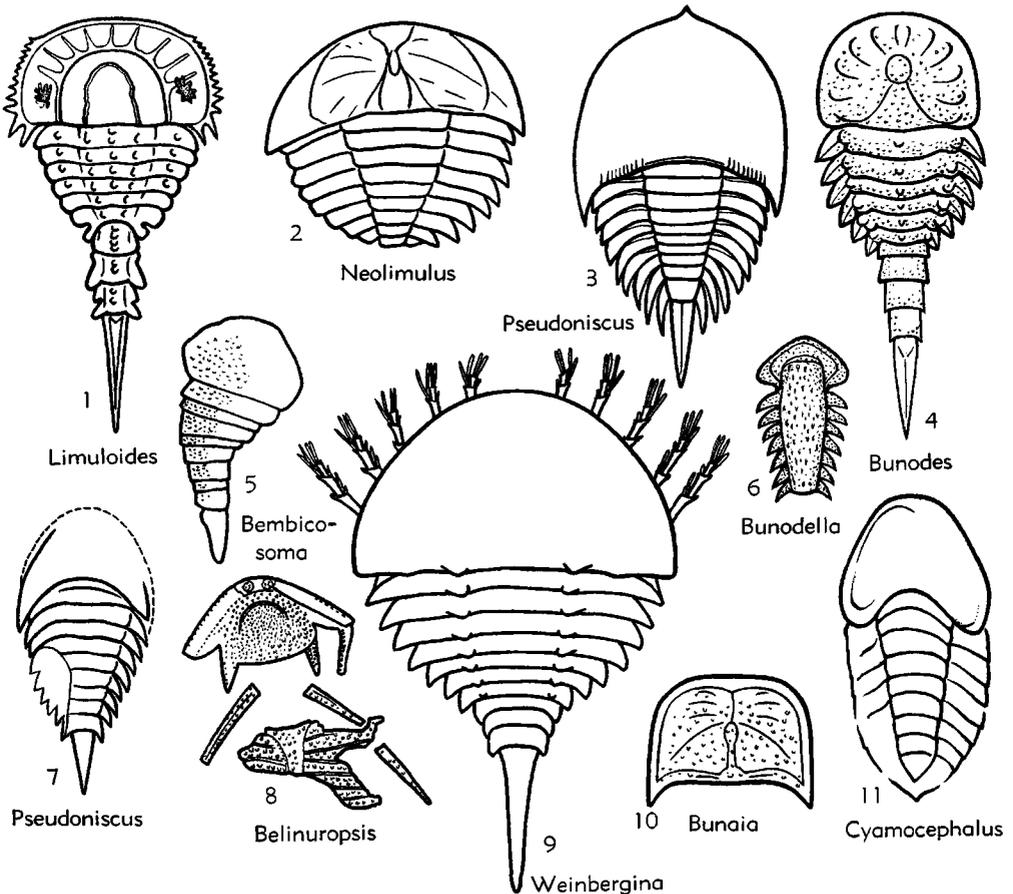


FIG. 11. Synziphosurina (p. P16-P17, P41).

tions of a Baltic species of *Pseudoniscus* indicated large eyes, but CLARKE found no trace of eyes in an American species, although RUEDEMANN has described certain structures that he interprets as small compound eyes and facial sutures. Because specimens commonly are somewhat crushed in the shale, it is difficult to be certain of the structures. A small stellate ornamentation outside the ophthalmic ridges in *Limuloides* (Fig. 11, 1) may be explained as a sensory organ seemingly homologous with the dorsal organ in the embryo of Recent Xiphosura (Fig. 6, 2).

The abdomen has 9 or 10 tergites, 10 segments being distinct in *Weinbergina* and assumed in *Pseudoniscus*. In *Limuloides* and *Bunodes*, there are 9 (fewer in an Australian species seemingly due to poor preservation), but here the 6th seems to be double, formed by fusion of the 6th and 7th. A trilobation is very distinct in *Pseudoniscus*, but may also be recognized in other genera having no axial (dorsal) furrows. The pleurae may be grooved and prolonged into short pleural spines. A postabdomen of 3 segments without pleurae is more or less conspicuous in some genera. In *Bunodes*, the 7th segment of the ankylosed 6th-7th segment may be included in the postabdomen. The telson is lanceolate.

Appendages are known only in *Weinbergina* (Figs. 11, 9, 15A). The 5 pairs of legs attached to the prosoma (cheliceræ not known) closely resemble the posterior legs of Recent Limulina; the peculiar spines on the distal joints are very similar. The lack of traces of abdominal appendages in a well-preserved specimen might suggest the presence of plate-shaped appendages, such as in Limulina and Eurypterida.

The exoskeleton of the Synziphosurina is smooth (*Pseudoniscus*) or more or less strongly ornamented (*Bunodes*, *Bunaia*).

**Ecology.** The probably benthonic Synziphosurina are not constituents of typical marine faunas. All the Silurian-Downtonian species belong to the eurypterid faunas probably inhabiting brackish or fresh water. The only known Lower Devonian genus (*Weinbergina*) occurs in the Hunsrück fauna, which also includes marine forms such as trilobites.

**Affinities.** In general shape of the body, the Synziphosurina have much in common with the antecedent Aglaspida. Both have a prominent abdomen with free tergites. On the other hand, the presence of a cardiac lobe in *Bunodes*, *Bunaia*, and *Neolimulus*, and also of ophthalmic ridges in the last, points strongly toward the Limulida. In fact, it may be somewhat difficult to draw a distinct line between these groups. The appendages of *Weinbergina* also indicate relationship with the more recent Xiphosura.

#### Family LIMULOIDIDAE Størmer, 1952

[=Hemiaspididae ZITTEL, 1881 (*nom. correct.* STØRMER, here in, *pro* Hemiaspididae ZITTEL, 1881)]

Small forms with cardiac lobe, ophthalmic ridges, radial ridges and marginal spines on the prosoma. Abdomen with broad axis, 9 free segments, of which the 6th is possibly double. Postabdomen 3-segmented without pleurae. *U.Sil.*

*Limuloides* STØRMER, 1952 [*pro* *Hemiaspis* WOODWARD, 1864 (*non* FITZINGER, 1861)] [*\*Hemiaspis limuloides* WOODW.] (30). *U.Sil.*, Eu.—FIG. 11,1. *\*L. limuloides* (WOODW.), Eng.;  $\times 1$  (67).

#### Family BUNODIDAE Packard, 1886

Synziphosura with vaulted and radially lobed prosoma; abdomen with cardiac lobe forming broad axis, 9 free segments, of which the 6th seems to be double; narrow postabdomen of 3 to 4 circular segments. *U.Sil.*

*Bunodes* EICHW., 1859 [*\*B. lunula*] [= *Exapinurus* NIESZKOWSKI, 1859]. Dorsal shield granulated, strongly vaulted; prosoma distinctly lobed radially, without genal spines. *U.Sil.*?*L.Dev.* (Downton.), Balt.-Norway.—FIG. 11,4. *\*B. lunula*, *U.Sil.*, Balt.; reconstr.,  $\times 1.3$  (64).

*Bunaia* CLARKE, 1919 [*\*B. woodwardia*]. Dorsal shield smooth or granulated; prosoma with narrow cardiac lobe, marginal rim, and genal spines. *L.Dev.* (Downton.), N.Am.-Spitzb.—FIG. 11,10. *B. heintzi* STØRMER, Spitzb.;  $\times 1$  (64).

*Bembicosoma* LAURIE, 1899 [*\*B. pomphicus*]. Dorsal shield granulated; cardiac lobe not known; postabdomen indistinct. May be eurypterid larva or related to *Bunodes* (16). *U.Sil.*, Eu.—FIG. 11,5. *\*B. pomphicus*, Scot.;  $\times 0.7$  (53).

#### Family NEOLIMULIDAE Packard, 1886

Small forms with broad prosoma having cardiac lobe, ophthalmic ridges uniting in front, with acute genal spines; abdomen

broad, with axial furrows, no postabdomen recognized. *U.Sil.-L.Dev.*

*Neolimulus* WOODWARD, 1868 [*\*N. falcatus*]. *U.Sil.-L.Dev.*, Eu.—FIG. 11,2. *\*N. falcatus*, Scot.;  $\times 3$  (64).

#### Family PSEUDONISCIDAE Packard, 1886

Small forms with large, somewhat flat smooth prosoma; abdomen with distinct axial furrows, 9 to 10 free segments prolonged laterally into pleural spines; no post-abdomen recognized. *U.Sil.*

*Pseudoniscus* NIESZKOWSKI, 1859 [*non* Costa, 1882] [*\*P. aculeatus*]. Sixth and 7th abdominal segments possibly ankylosed (5). *U.Sil.*, Eu.-N.Am.—FIG. 11,7. *\*P. aculeatus*, Balt.;  $\times 1.3$  (63).—FIG. 11,3. *P. roosevelti* CLARKE, N.Y.;  $\times 2$  (39).  
 ?*Cyamocephalus* CURRIE, 1927 [*\*C. loganensis*]. Prosoma with rounded genal angles; abdomen

with axial furrows, probably 10 segments. *U.Sil.*, Eu.—FIG. 11,11. *\*C. loganensis*, Scot.;  $\times 0.7$  (41).

*Bunodella* MATTHEW, 1889 [*non* PFEFFER, 1889; *nec* VERRILL, 1889] [*\*B. horrida*]. Abdomen elongate as in Pseudoniscidae but prosomal features and ornamentation different. *U.Sil.*, N.Am.—FIG. 11,6. *\*B. horrida*, Can.;  $\times 0.7$  (54).

#### Family WEINBERGINIDAE Richter & Richter, 1929

Medium-size forms with large semicircular smooth prosoma and short 10-segmented trilobate abdomen, with last 3 segments forming postabdomen; ?chelicerae and 5 pairs of walking legs with spines. *L.Dev.*

*Weinbergina* RICHTER-R., 1929 [*\*W. opitzi*] (22). *L.Dev.*, Eu.—FIG. 11,9; 15A. *\*W. opitzi*, Ger.; 11,9, dorsal side (reconstr.),  $\times 0.7$ ; 15A, prosomal appendages,  $\times 0.7$  (62).

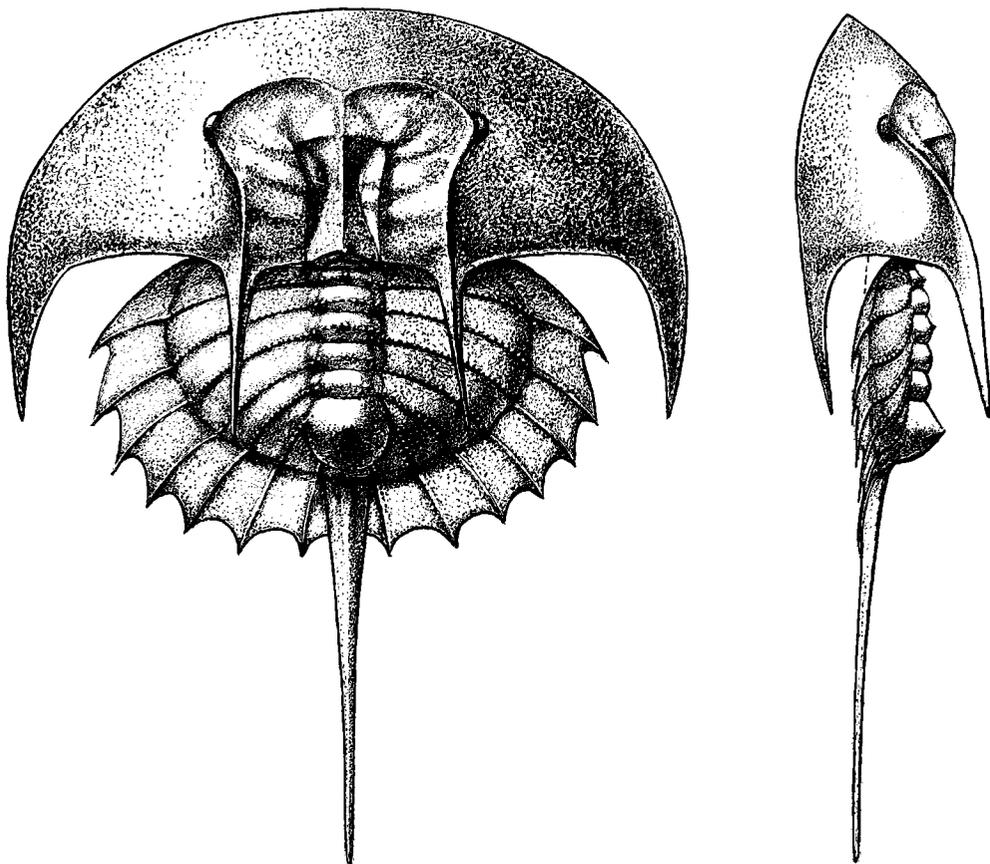


FIG. 12. *Euproops rotundatus* (PRESTWICH), U.Carb., Eng.; side and dorsal views (reconstr.),  $\times 2.5$  (64 n).

### Suborder LIMULINA Richter & Richter, 1929

[*nom. correct. et transl.* STÖRMER, 1952 (ex *Limulida* RICHTER & RICHTER, 1929)] [= *Limulada* RAYMOND, 1944]

Prosoma large, bearing cardiac lobe, ophthalmic ridges, ocelli, and lateral eyes; abdomen with as many as 9 well-developed segments, posterior ones or all of them ankylosed, or all free; telson styliform, longer than rest of abdomen (22). ?*L.Dev.* (*Downton.*)-*Rec.*

#### DISCUSSION

*Morphological features.* The basic, characteristic morphological features of this suborder were established already in the oldest known representatives, the Recent ones representing true persistent forms.

Whereas most Paleozoic *Limulina* were small forms, measuring about 3 to 5 cm. in length, Mesozoic ones are medium-sized, and Cenozoic species are large, measuring 30 to 60 cm. In general, the size of adult individuals belonging to the *Limulina* increases during development of the suborder.

The *Limulina* (Figs. 3, 12, 13, 16) have a large semicircular prosoma, generally prolonged into genal spines. The wedge-shaped, commonly keeled cardiac lobe, which may bear an anterior boss or node, extends forward to a re-entrant of the confluent ophthalmic ridges. These ridges run laterally from the re-entrant, turn posteriorly above lateral eyes forming strong keels which generally terminate in ophthalmic spines at the posterior margin of the prosoma. The cardiophthalmic region may have interophthalmic ridges bordering a rectangular intercardiophthalmic area which embraces the cardiac lobe and a narrow tract on either side of it (Fig. 12). Where interophthalmic ridges are present, the cardiophthalmic region is divided into 5 parts instead of 3. The 5-fold division is significant in forms which have been referred to *Prestwicianella* (now provisionally considered to be a synonym of *Euproops*, because the same structure seemingly occurs in the type species of the latter) (Figs. 12; 13, 3), as suggested by STUBBLEFIELD in 1947. The previous reconstruction of *Prestwicianella* (Fig. 13, 3, designated as *Euproops*) was based on a badly preserved specimen; a new reconstruction (Fig. 12) based on English

specimens, shows typical characters of *Euproops*.

The opisthosoma has a semicircular, subtriangular, or irregular hexagonal outline. The larvae of certain species at least were able to roll up. The abdomen is commonly more or less ankylosed into one continuous shield. *Neobelinuropsis* (Dev.) (Fig. 14) seems to have 8 free segments in front of the telson, the last segment probably double. In most species of *Belinurus* (Fig. 13, 1a, c, d) the 2 to 3 posterior segments probably are ankylosed. In almost all Euproopacea and Limulacea, all abdominal tergites are ankylosed into one continuous shield. The segmentation is suggested by annulation of the axis and in Paleozoic forms by pleural ridges prolonged into spines along the margin. Intercalated movable spines are present in members of the Limulacea. In certain genera, such as *Kiaeria*, *Elleria*, and *Paleolimulus*, one or more free segments evidently were present between the telson and the abdominal shield in front (21). In genera of the Euproopacea the annulated axis of the abdomen terminates in a broad segment and is provided with a conical spine at the top (Fig. 12).

Prosomal appendages are known in *Euproops* (Fig. 15B), *Paleolimulus* (Fig. 15C) and certain Mesozoic Limulacea. The appendages seem to be strikingly like those of Recent *Limulus*. In *Paleolimulus* the chelicerae are small and the walking legs slender and chelate, except the last pair, which have a whorl of spines; even a flabellum and plate-shaped abdominal appendages are demonstrated. Upper Devonian trails (named *Paramphibius*) have been referred to *Belinurus*-like forms, possibly *Protolimulus* (1).

The exoskeleton is very thin and but slightly impregnated with calcium carbonate in the Euproopidae (21). The surface of the shell is smooth (tuberculated in the doubtful genus *Bunodella*).

Little is known of the larvae of fossil *Limulina*. Possibly some of the smaller species described represent larvae of larger forms. The larvae seem to have been more spinous than the adults.

*Ecology.* The habitat of the *Limulina* changed between Devonian and Recent time. The Devonian species were almost

confined to marine waters probably outside deltaic deposits, but *Belinurus kiltorkensis* occurs in the Old Red Sandstone, suggesting that some species were able to invade brackish or fresh waters. With few exceptions the many species of Carboniferous-Permian time evidently were fresh-water forms. In the Triassic, a few specimens from the Zechstein suggest marine conditions, whereas the rest belong to brackish- or fresh-water faunas. The common *Mesolimulus walchi* from the Jurassic of Germany inhabited marine coastal waters, and a Liassic specimen from Scania suggests a brackish- or fresh-water environment. *Tachypleus decheni* of the Miocene lignite beds of Germany may have lived in brackish waters.

The Limulina were bottom-dwellers. Like Recent larvae of *Limulus*, some small

species of *Belinurus* possibly were swimmers. The dorsal shield of the Limulina is well adapted (streamlined) for crawling rapidly through the water on the bottom. The telson chiefly served as a steering-rod.

The taxonomy of the Limulina is based mainly on development of the ophthalmic ridges and general structure of the abdomen.

*Phylogeny.* The fossil record permits us to follow evolution of the Limulina from Paleozoic to Recent time. The line of development may be traced from the Silurian *Neolimulus* (placed in the Synziphosurina) through *Belinurus* to the Euproopacea, and further to the Limulacea of Mesozoic and Cenozoic time. Characteristic of the phylogenetic development is shortening of the abdomen and gradual fusion of the abdominal segments. Gradual increase in size also

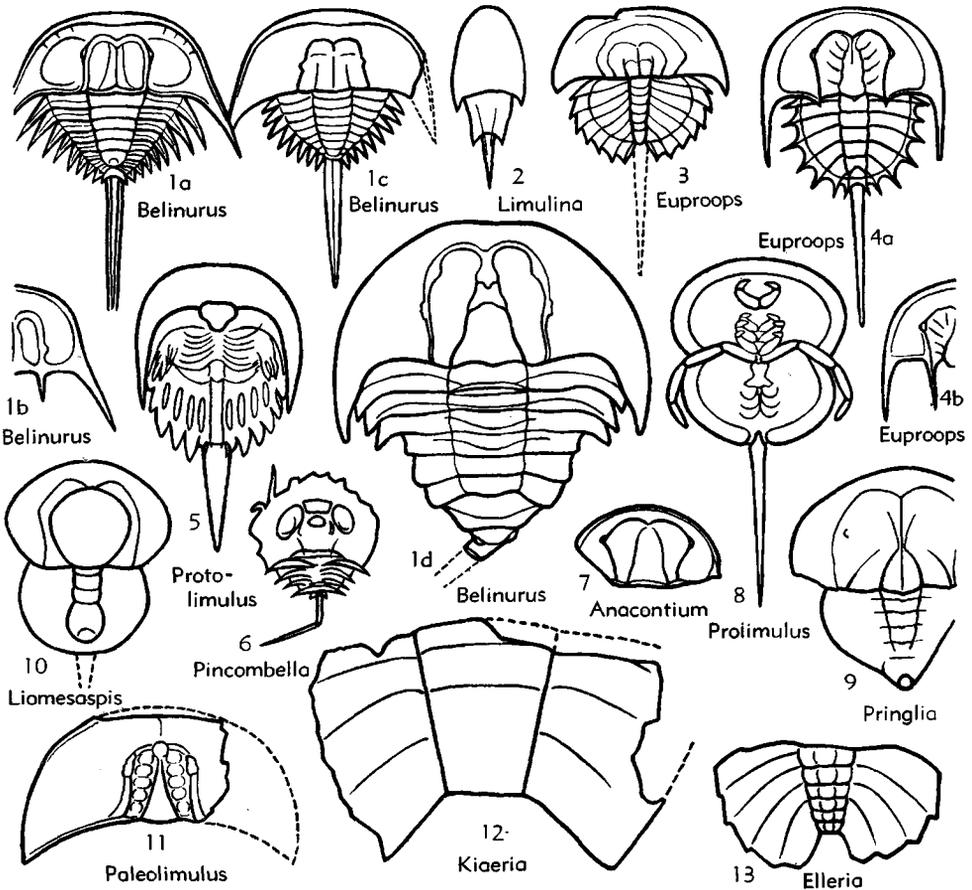


FIG. 13. Limulina (p. P20-P23).

is suggested. *Kiaeria* and *Elleria* seem to form a special line of development. The former probably had free segments in the posterior portion of the abdomen, a tendency also demonstrated in *Paleolimulus*.

### Superfamily BELINURACEA Zittel & Eastman, 1913

[*nom. transl.* RAYMOND, 1944 (ex Belinuridae ZITTEL-E., 1913)]

Anterior abdominal segments (or possibly all) movable but 2 or more posterior ones may be ankylosed. *M.Dev.-U.Carb.*

#### Family BELINURIDAE, Zittel & Eastman, 1913

[=Bellinuridae PACKARD, 1886]

Characters of superfamily. *M.Dev.-U.Carb.*

**Belinurus** KÖNIG, 1820 [*\*B. bellulus*] [=Bellinurus MEEK & WORTHEN, 1865; *Koenigiella* RAYMOND, 1944]. Small to medium in size, prosoma with genal spines and cardiac lobe of variable width (21). *U.Dev.-U.Carb.*, Eu.-N.Am.—FIG. 13,1a. *B. regina* BAILY, *U.Carb.*, Ire.; dorsal side,  $\times 2$  (67).—FIG. 13,1b. *B. arcuatus* BAILEY, *U.Carb.*, Ire.; part of prosoma,  $\times 3$  (67).—FIG. 13,1c. *B. baldwini* WOODWARD, *U.Carb.*, Eng.; dorsal side,  $\times 2$  (67).—FIG. 13,1d. *B. alleganyensis* ELLER, *U.Dev.*, N.Y.; dorsal side,  $\times 1$  (44).

**Neobelinuroopsis** ELLER, 1938 [*\*Bellinuroopsis rossicus* TSCHERNYSCHEW, 1933] [=Bellinuroopsis TSCHERN., 1933]. Medium in size, prosoma with

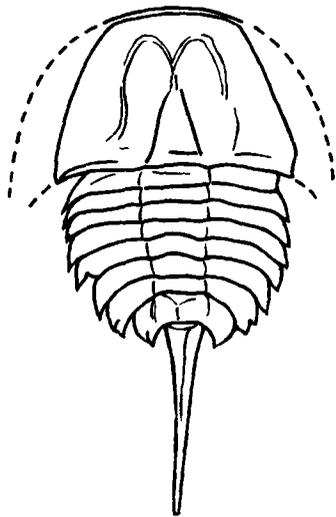


FIG. 14. *Neobelinuroopsis rossicus* (TSCHERNYSCHEW), *U.Dev.*, Russ.,  $\times 0.5$  (65).

distinct wedge-shaped cardiac lobe; rounded abdomen with 8 movable segments, the last one seemingly double, pleural spines present. *U.Dev.*, Russ.—FIG. 14. *\*B. rossicus* (TSCHERN.); dorsal side,  $\times 0.5$  (65).

**Protolimulus** PACKARD, 1886 [*\*Prestwichia eriensis* WILLIAMS, 1885]. Small, only ventral surface known; abdominal segments terminating in blunt spines; telson broad and short (17). *M.Dev.*, N.Am.—FIG. 13,5. *\*P. eriensis* (WILLIAMS), N.Y.; ventral side,  $\times 0.3$  (66).

### Superfamily EUPROPACEA Eller, 1938

[*nom. transl.* RAYMOND, 1944, ex Euproopidae ELLER, 1938)]

Cardiophthalmic area well marked, ophthalmic ridges converging backward from eyes; abdomen broad and rounded, composed of 6 or 7 ankylosed segments, with or without lateral spines. ?*L.Dev.* (Downton).-*Perm.*

#### Family EUPROPIDAE Eller, 1938

Small forms with wedge-shaped cardiac lobe bordered by distinct axial furrows, abdominal shield with annulated axis bearing a high boss on last segment. *U.Carb.-Perm.*

**Euproops** MEEK, 1867 [*\*Bellinurus danae* MEEK & WORTHEN, 1865] [=Anthracopeltis BOULAY, 1880; *Prestwichianella* WOODWARD, 1918 (pro *Prestwichia* WOODW., 1867; non LUBBOCK, 1863)]. Prosoma with flat genal spines and carinate ophthalmic spines; cardiophthalmic region with or without intercardiophthalmic area; abdomen with raised pleural ridges that cross flattened rim and are prolonged as marginal spines; annulated axis with knob on 1st and 3rd segments and elevated boss or short spine on hindmost segment; telson long. *U.Carb.-Perm.*—FIG. 13,4. *E. thompsoni* RAYMOND, Penn., Ill.; 4a, dorsal side,  $\times 1$ ; 4b, part of prosoma showing genal and ophthalmic spines,  $\times 1$  (60).—FIG. 15B. *\*E. danae* (MEEK-W.), Penn., Ill.; ventral view showing remnants of prosomal legs,  $\times 1.6$  (55).—FIGS. 12; 13,3. *E. rotundatus* (PRESTWICH), *U.Carb.*, Eng.; 12, dorsal and side views, new reconstr. based on better-preserved specimen than available to WOODWARD,  $\times 2.5$  (64n); 13,3, old reconstr. referred to *Prestwichianella* by WOODWARD,  $\times 0.5$  (67).

**Pringlia** RAYMOND, 1944 [*\*Prestwichia birtwelli* WOODWARD, 1872]. Genal spines vestigial or lacking, cardiophthalmic region tripartite, abdomen triangular, with faint axial furrows, high posterior boss or spine on axis, seemingly no raised pleural ridges and probably no marginal spines. *U.Carb.*, N.Am.-Eu.—FIG. 13,9. *\*P. birtwelli* (WOODW.), Eng.; dorsal side,  $\times 2$  (67).

**Anacontium** RAYMOND, 1944 [*\*A. carpenteri*]. Genal spines vestigial, no ophthalmic spines, cardiophthalmic region tripartite. *Perm.*, N.Am.—FIG. 13,7. *\*A. carpenteri*, Okla.; dorsal side of prosoma,  $\times 3$  (60).

### Family LIOMESASPIDIDAE Raymond, 1944

[*nom. correct.* STØRMER, herein (*pro* Liomesaspidae RAYMOND, 1944)]

Prosomal cardiac lobe bulbous; adult lacking genal spines; abdomen without marginal spines and raised pleural ridges; posterior axial segment with high boss (21). *Penn.-Perm.*

**Liomesaspis** RAYMOND, 1944 [*\*L. laevis*] (21). *Penn.*, N.Am.—FIG. 13,10. *\*L. laevis*, Ill.; dorsal side,  $\times 1.7$  (60).

**Prolimulus** FRITSCH, 1899 [*\*P. woodwardi*]. Prosoma and abdomen broad, well rounded, both without marginal spines. *Perm.*, Eu.—FIG. 13,8. *\*P. woodwardi*, Czech.; ventral side,  $\times 2$  (45).

### Family ELLERIIDAE Raymond, 1944

[*nom. correct.* STØRMER, herein (*pro* Elleridae RAYMOND, 1944)]

Abdominal axis and pleural area distinctly segmented, no boss on posterior axis; posterior part of abdominal shield deeply indented; prosoma unknown. *U.Dev.-Penn.*

**Elleria** RAYMOND, 1944 [*\*Euproöps morani* ELLER, 1938]. *U.Dev.-Penn.*, N.Am.—FIG. 13,13. *\*E. morani*, U.S.A.; dorsal side of abdominal shield,  $\times 1$  (44).

### Family KIAERIIDAE Størmer, 1952

[*nom. correct.* STØRMER, herein (*pro* Kiaeridae STØRMER, 1952)]

Large abdominal shield with axial furrows; segmentation and broad posterior indentation suggest posterior free segments; prosoma unknown. *?L.Dev.*

**Kiaeria** STØRMER, 1934 [*\*K. limuloides*]. *?L.Dev.*, Eu.—FIG. 13,12. *\*K. limuloides*, ?Downton, Norway; dorsal side of abdominal shield,  $\times 0.5$  (64).

### Superfamily LIMULACEA Zittel, 1885

[*nom. transl.* RAYMOND, 1944 (*ex* Limulidae ZITTEL, 1885)]

Small to large forms with cardiophthalmic region not well defined, posterior branches of ophthalmic ridges parallel; abdomen mostly subtrapezoidal with movable marginal spines. (Because of mode of preservation, ventral structures are commonly

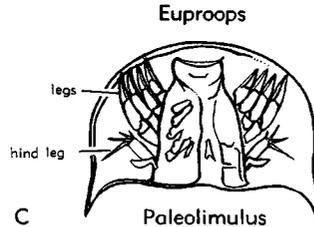
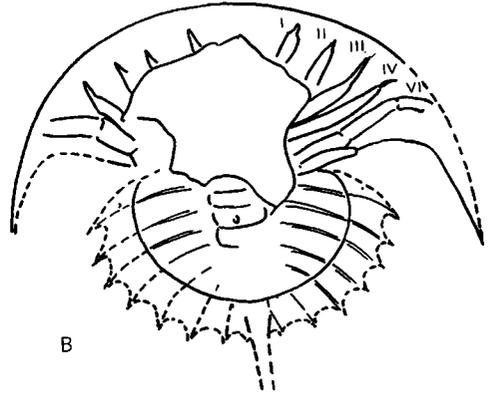
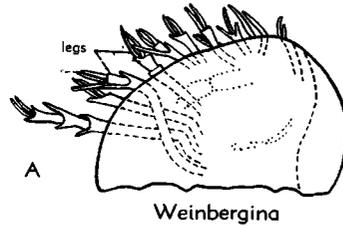


FIG. 15. Morphological features of Paleozoic xiphosurids. A, *Weinbergina opitzi* RICHTER & RICHTER, *L.Dev.*, Ger., showing nonchela legs,  $\times 0.6$  (62). B, *Euproöps anthrax* (WOODW.), *Carb.*, Eng., showing dorsal side of test and very slender legs,  $\times 0.7$  (67). C, *Paleolimulus avitus* DUNBAR, *Perm.*, Kans., showing chelicerae and chela legs,  $\times 1$  (43).

traced on dorsal surface, which has caused confusion.) *Perm.-Rec.*

### Family PALEOLIMULIDAE Raymond, 1944

Small forms with ophthalmic ridges meeting in front of cardiac lobe; abdominal axis distinctly annulated with movable segment in front of telson (21). *Perm.*

**Paleolimulus** DUNBAR, 1923 [*\*P. avitus*] (7). Interophthalmic area conspicuously lobed. *Carb.-Perm.*, Eu.-N.Am.—FIG. 15C; 16,1. *\*P. avitus*, *Perm.*, Kan.; 15C, ventral side of prosoma with

appendages,  $\times 1$ ; 16,1, dorsal side (reconstr.)  $\times 2$  (43).—FIG. 13,11. *P.?* *randalli* (BEECHER), U. Dev., Pa.;  $\times 1$  (34).

**Family MESOLIMULIDAE Størmer, 1952**

Small to medium in size; prosoma with ophthalmic ridges not meeting in front of cardiac lobe, genal angles moderately prolonged backwards; axial furrows distinct; no distinct annulation of abdominal axis, first pair of marginal spines within anterior third of abdomen. *L.Trias.-Jur., ?Cret.*

*Psammonlimulus* LANGE, 1923 [*\*P. gottingensis*]. Genal angles prolonged into blunt genal spines; abdomen narrow trapezoidal with postlateral prolongations. *L.Trias., Eu.*—FIG. 16,2. *\*P. gottingensis*; dorsal side,  $\times 0.7$  (52).

*Limulitella* STØRMER, 1952 [*pro Limulites* SCHIMPER, 1850 (*non* KRÜGER, 1823)] [*\*L. bronni* SCHIMPER, 1850]. Inner margin of genal angle forming a distinct angle with anterolateral margin of narrow subtriangular abdomen; axis may bear a median carina (30). *L.Trias.-U.Trias., Eu.-N.Am.*—FIG. 16,3. *\*L. bronni* (SCHIMPER), *L.Trias., Fr.*; dorsal side,  $\times 0.4$  (64).

*Mesolimulus* STØRMER, 1952 [*\*Limulus walchi*

Demarest, 1822]. Inner margin of genal angle more or less parallel to anterolateral margins of semi-circular to broad trapezoid abdomen, axis with median carina. *Jur., ?Cret., Eu.-?AsiaM.*—FIG. 16,4. *\*M. walchi* (DEMAREST), *Jur., Ger.*,  $\times 0.4$  (49).—FIG. 16,5. *M. syriacus* (H.WOODWARD), *Cret., Asia M.*;  $\times 0.2$  (67).

**Family LIMULIDAE Zittel, 1885**

[=Xiphosuridae Pocock, 1902]

Medium to large forms; prosoma with ophthalmic ridges not meeting in front of cardiac lobe, genal angles considerably prolonged backwards; abdomen subhexagonal, axial furrows indistinct, first pair of marginal spines about midway between anterior and posterior margin of abdomen. *Tert.-Rec.*

**Subfamily LIMULINAE Zittel, 1885**

[*nom. transl.* Pocock, 1902 (*ex* Limulidae ZITTEL, 1885)]

Prosoma vaulted; abdomen hexagonal with prominent posterior prolongations, movable lateral spines decreasing in length backwards. *Rec.*

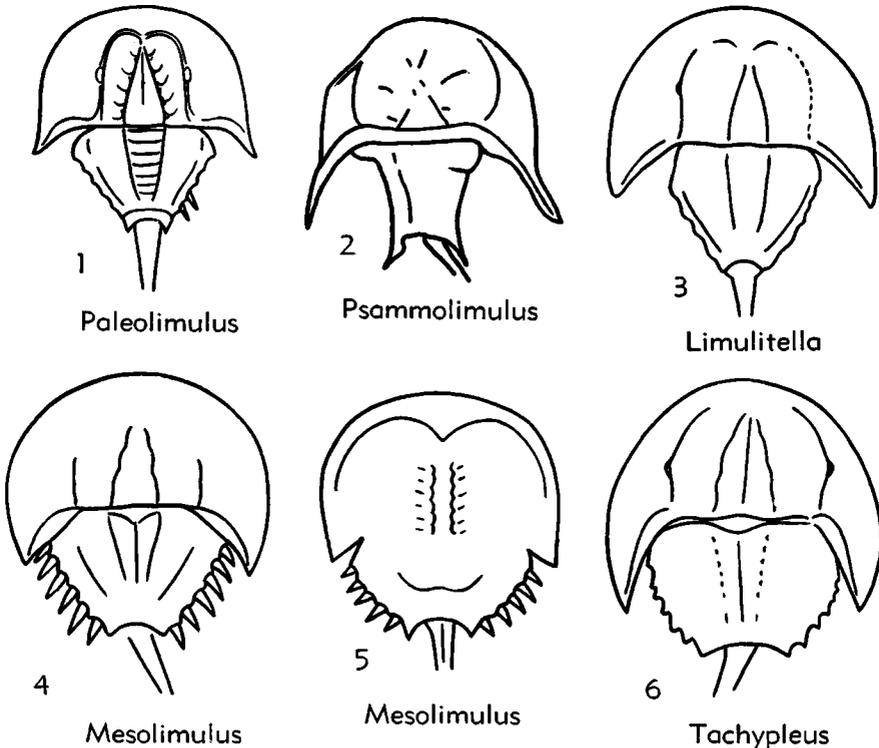


FIG. 16. Limulicæ (p. P21-P23).

*Limulus* MÜLLER, 1785 [pro *Xiphosura* BRÜNNICH, 1771; ICZN 1952] [\**Monolucus polyphemus* LINNÉ, 1758]. *Rec.*, E.N.Am.—FIGS. 3; 4B,C; 5; 6,2. \**L. polyphemus* (LINNÉ); 3, half-grown specimen, about  $\times 1$  (56); 4B,C, ventral side and long. sec.,  $\times 0.3$  (64); 5, prosomal appendages (64); 6,2, embryo, enlarged (48).

#### Subfamily TACHYPLEINAE Pocock, 1902

Prosoma less vaulted than in Limulinae; hexagonal abdomen with less prominent posterior prolongations, movable lateral spines not decreasing in length backwards. ?*Tert.*, *Rec.*

*Tachypleus* LEACH, 1819 [\**Limulus gigas* MÜLLER, 1785]. Movable lateral spines of abdomen different in sexes, long and equal in male and young female, posterior 3 short and apically acute in adult female. ?*Tert.*, *Rec.*, E.Asia?Eu.—FIG. 4A; 6,1. \**T. gigas* (MÜLLER), *Rec.*; 4A, young specimen with segments indicated; 6,1a,b, embryological stages; 6,1c, first free larva (IVANOV). —FIG. 16,6. *T. decheni* (ZINKEN), Mio., Ger.,  $\times 0.13$  (35).

*Carcinoscorpius* POCOCK, 1902 [\**Limulus rotundicaudatus* LATREILLE, 1802]. Movable spines of abdomen short, 2nd and 3rd longest, others progressively decreasing backwards in male, becoming abruptly shorter in female. *Rec.*, E.Asia.

#### Superfamily and Family UNCERTAIN

*Pincombella* CHAPMAN, 1932 [\**P. belmontensis*]. Anterior margin of prosoma spinose, no true genal spines; abdomen with 5 transverse segments, all but last with marginal spines. *Perm.*, Austral.—FIG. 13,6. \**P. belmontensis*, N.S.W.,  $\times 1$  (38). Genus undet. Body narrow, abdominal shield without visible segmentation. *U.Carb.*, Eng.—FIG. 13,2. Gen. and sp. undet.,  $\times 2$  (42).

### Subclass EURYPTERIDA Burmeister, 1843

[=Gigantostroaca HAECKEL, 1896]

Small to very large merostomes with elongate lanceolate, rarely trilobed body; prosoma of moderate size; opisthosoma with 12 movable segments and styliform to spatulate telson, with division commonly into a 7-segmented preabdomen and 5-segmented postabdomen; prosomal appendages 6, comprising 3-jointed chelicerae, walking legs, the last pair commonly transformed into swimming legs. Mouth central, bordered posteriorly by endostoma and metastoma. Operculum with median genital appendage, abdominal appendages plate-shaped with nonlaminar gills. *Ord.-Perm.*

#### DISCUSSION

Like the Xiphosura, the Eurypterida are not typical marine forms. Their remains generally are confined to sediments deposited in brackish or fresh water and are not abundant.

Fragments of the giant *Pterygotus* in the Scottish Old Red Sandstone early attracted attention of workmen in the quarries and by reason of their characteristic sculpture were interpreted as petrified seraphim. Descriptions of the eurypterids were published first in America by DE KAY in 1825 and HARLAN in 1825, but more extensive knowledge of the group is obtained from publications by HALL in 1859, HUXLEY & SALTER in 1859 (10), and WOODWARD in 1866-78 (33). Important morphological details were described by SCHMIDT in 1883 (24), and LAURIE in 1892 (16), 1893, and 1898; by means of a special method, HOLM in 1898 (9) was able to isolate and study in minute details the excellently preserved exoskeletons of *Eurypterus fischeri* from Silurian rocks of the Baltic. Knowledge of American eurypterids was considerably extended by CLARKE & RUEDEMANN in 1912 (5).

In spite of considerable variation in development of the exoskeleton, particularly the prosomal appendages, the Eurypterida exhibit a very definite plan of construction, thus forming a well-defined group.

*Morphological features.* The length of the eurypterid body generally ranges from 10 to 20 cm., but very large forms occur also in each geological system from Ordovician to Carboniferous. *Megalograptus walchi* MILLER and *Echinognathus clevelandi* (WALC.), from the Ordovician, *Eurypterus pustulosus* HALL and *Slimonia acuminata* (SALTER), from the Silurian, and *Tarsopterella scoticus* (WOODW.), from the Devonian, attained a length of at least 100 cm.; *Ctenopterus? lacoana* (CLAYPOLE), Devonian, probably 140 cm., and large species of *Pterygotus* at least 180 cm., this being the largest arthropod known.

The body is covered by a chitinous exoskeleton of variable thickness. Most "complete specimens" probably represent cast exuviae from the ecdysis. Besides the more solid exoskeleton of the body and appendages, parts of the softer integument, such as

intersegmental membranes, may be preserved (*Eurypterus*, *Rhenopterus*). The soft integument is provided with numerous hairs (Fig. 17C), and the presence of tactile hairs also on the more solid test is indicated by numerous pores, particularly in the doublure of the abdominal plate-shaped appendage (Fig. 22, 3f).

A distinct ornamentation is characteristic of the exoskeleton of the Eurypterida. The surface may be smooth or provided with scales, tubercles, knobs, or spines of different kinds. In *Hughmilleria* (Fig. 21, 1) numerous parallel integumental folds ("teraced lines") are found on the anterior portions of prosoma and tergites. This is apparently the more primitive ornamentation (not unlike structures in trilobites), which develops into rows of scales or tubercles. The scales may be crescentic, as in *Pterygotus* (Fig. 20, 2a,c; 22, 3f) and to some extent in *Eurypterus* (Fig. 17A,B); or tongue-shaped, as in *Echinognathus* (Fig. 29, 5d); or acute, as in *Lepidoderma* (Fig. 21, 3a) and *Campylocephalus* (Fig. 29, 8). The scales tend to develop into round or oblong raised tubercles, as in *Carcinosoma* (Fig. 23; 29, 3c), *Ctenopterus* (Fig. 27, 4b), and *Tarsopterella* (Fig. 27, 6b), or undulating as in *Tylopterella* (Fig. 29, 4a). The scales and tubercles may be closely set or scattered, and commonly are confined to distinct parts of the body. Prominent knots tend to occur along the posterior margins of the prosoma and tergites, as in *Tarsopterella* (Fig. 27, 6a), or *Rhenopterus* (Fig. 27, 5a). A peculiar, reticulate ornamentation is found in *Mycterops* (Fig. 30). A color pattern is noticed in *Megalograptus*.

The elongate, mostly lanceolate body may have a scorpion-like appearance, a feature particularly characteristic of the Carcinomatidae (Fig. 23) and Mixopteridae (Fig. 25). The body is divided into a prosoma or cephalothorax, and an opisthosoma comprising 12 movable segments and a telson. The abdomen of many eurypterids is divided into a broader preabdomen of 7 segments and a narrower nearly cylindrical postabdomen of 5 segments. When the term opisthosoma is applied, one may distinguish the limb-bearing mesosoma of 6 segments from the 6-segmented mesosoma without ventral appendages.

The prosoma is moderately convex, with a subquadratic, subtriangular to semicircular outline. A pair of median ocelli, which may be mounted on a node (Fig. 19, 3d; 21, 1a; 29, 3a), is generally situated on the highest part of the prosoma.

The lateral compound eyes have a marginal to subcentral or anterior position. The eyes vary considerably in size and shape. The large eyes of the Pterygotidae (Fig. 19, 2; 22, 1a, 2a, 3a) have an elliptical outline. In most eurypterids, the eyes are kidney-shaped, and in some strongly curved (*Stylonuracea*, Fig. 27, 1, 2b, 3a, 4a, 6b, 7b), with the more or less steep visual surface facing outward and forward. Small eyes are found in *Mixopterus* (Fig. 25A). The visual surface is composed of numerous closely set pits representing the individual facets, visible in *Pterygotus* (Fig. 19, 2) and some species of *Hughmilleria*.

The margin of the prosoma is inflected, forming a broad doublure that passes into the more flexible softer integument surrounding the appendages and the mouth. A marginal suture (or line of weakness), which opens during ecdysis, is characteristic of the Eurypterida. The doublure is traversed by one or more sutures. One median suture, which may be more or less obsolete, is characteristic of *Eurypterus* (Fig. 17) and *Rhenopterus* (Fig. 27, 5b). In most eurypterids, however, a median epistoma is bordered by a pair of epistomal sutures (Fig. 22, 3c). Possibly one extra pair of sutures crosses the doublure in *Hughmilleria* (Fig. 19, 1a; 21, 1g). Inasmuch as a small narrow epistoma is found in *Lepidoderma* and the plate seems to be reduced in *Rhenopterus*, a tendency toward reduction of the epistoma in evolution of the Eurypterida is suggested.

No separate labrum is developed among eurypterids. Impressions near the posterior border of the epistoma possibly may represent traces of an olfactory organ, such as in Recent Xiphosura (Fig. 19, 1a).

The abdomen is attached to the prosoma by a special articulation formed by the doublure of the prosoma and 1st tergite. This is characteristic of *Eurypterus*, but may be found in all eurypterids. The preabdomen has a moderately vaulted median (axial) portion and a flattened or slightly concave pleural portion. A distinct triloba-

tion is found in *Mixopterus* (Fig. 25A) and *Megalograptus* (Fig. 24). The first tergite is generally shorter than the others. Probably, it represents the 7th (pregenital) segment, which is reduced in most arachnids.

As an exception, the large 1st (and possibly 2nd) tergite in *Mycterops* (Fig. 29, 1; 30) should be mentioned. The 1st to 6th tergites have a more or less rectangular outline, and the 7th or last preabdominal

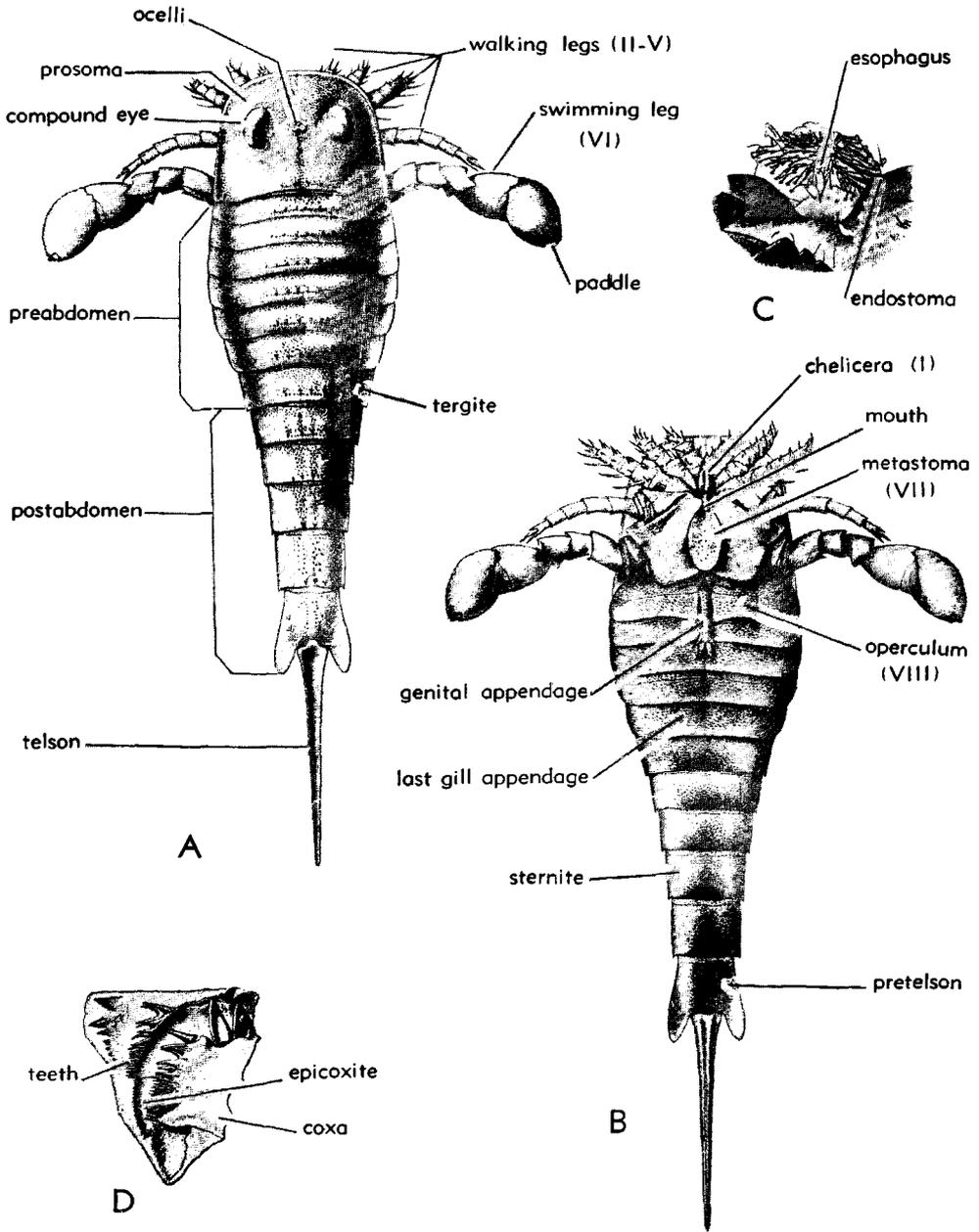


FIG. 17. Morphological features of eurypterids as shown by *Eurypterus fischeri* Eichw., M.Sil., Balt. (47). A, B, Dorsal and ventral views of entire specimen (reconstr.),  $\times 0.5$ . C, Gullet,  $\times 13$ . D, Coxae around mouth, showing denticulate margins,  $\times 6$  (47).

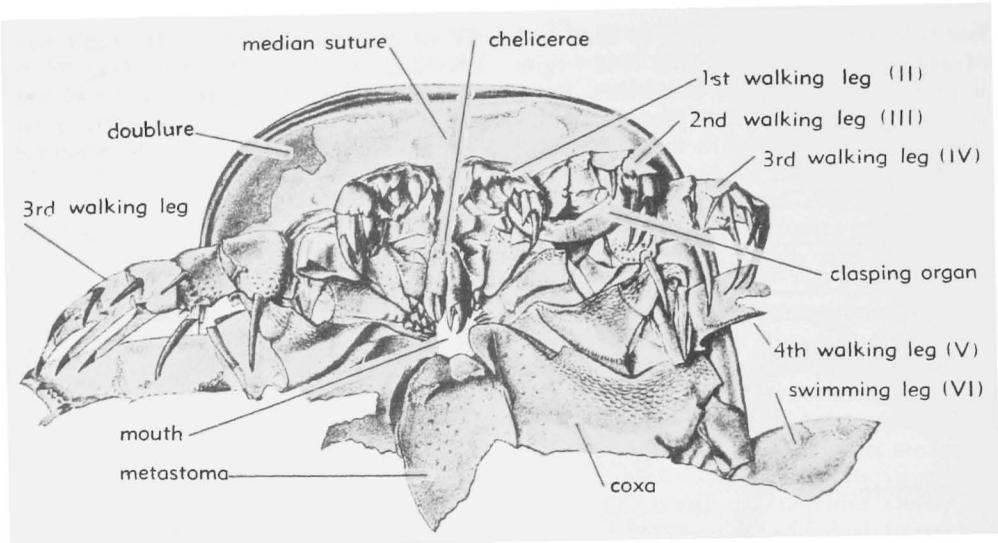


FIG. 18. Ventral surface of prosoxa of *Eurypterus fisheri* EICHW., Sil., Balt., showing well-preserved appendages of etched-out specimen,  $\times 1.3$  (47).

tergite may have postlateral fins or spurs. Each tergite is attached to the one in front by means of an intersegmental membrane attached to the anterior and posterior doublure.

Because of the powerful plate-shaped appendages on the first 6 segments of the abdomen, corresponding powerful sternites are not developed. Such sternites, on the other hand, are developed on the posterior 6 segments and are fused with the tergites on the dorsal surface, forming cylindrical rings telescopically inserted into each other. Lateral spurs or fins may be present on the postabdominal segments (*Lepidoderma*, Fig. 21, 3a; *Tarsopterella*, Fig. 27, 6a). The 12th segment, or **pretelson**, may differ somewhat from the other abdominal segments (*Eurypterus*, Figs. 17, 18; *Pterygotus*, Fig. 22, 1a,b, 2a, 3a; *Megalograptus*, Fig. 24). In *Megalograptus* a peculiar pair of flat ?cerci are developed.

A powerful telson articulates with the last abdominal segment. The most primitive type seems to be a lanceolate telson with a flat ventral surface and a median dorsal keel (*Hughmilleria*, Fig. 21, 1a,b). From this type the longer styliiform telson of *Lepidoderma* was possibly developed (Fig. 21, 3a), and similarly that of certain stylonurids (Fig. 27, 4a), and the curved, possibly poisonous tail-spines of *Carcinosoma*

(Fig. 23) and *Mixopterus* (Fig. 25). Another line of development possibly led to the telsons of *Slimonia* (Fig. 21, 2a) and *Salteropterus* (Fig. 21, 5a,b), in which the lanceolate telson bears lateral fins. In *Pterygotus* (Fig. 22, 1a,b, 2a, 3a), nothing is left of the lanceolate telson. The telson forms a broad tail-fin or horizontal rudder, which in *Pterygotus* (*Pterygotus*) (Fig. 22, 2a) may have a raised median keel, probably serving also as a competent vertical rudder.

Appendages are attached to the ventral surface of the prosoxa and preabdomen. Below the prosoxa, the 6 pairs of appendages are radially arranged around the central mouth. The first pair of appendages is invariably developed as 3-jointed chelicerae (Fig. 19, 3a), in which the 3rd joint forms the opposing movable finger. In most forms the chelicerae are very small, but in the Hughmilleriidae (Fig. 21, 1b) and the Stylonuracea (Fig. 27), they are somewhat larger, and in the Pterygotidae (Fig. 22, 1a-c, 2a,b, 3a,b), they are enormously developed, the basal joint being greatly prolonged and the inside of the chelae being provided with small and large striated teeth, the large ones measuring several cm. in length. Studies of the brain in recent Chelicerata indicate the chelicerae to be innervated from the tritocerebrum, thus representing the

first postoral segment, the actual preoral position of the chelicera being a secondary phenomenon due to a posterior migration of the mouth in the early ontogenetic stages.

The 2nd to 5th pairs of appendages are generally developed as walking legs, more or less alike and increasing in size backward (Fig. 18; 19, 3*b,c*). Each walking leg has an elongate, subtriangular flat coxa with a small epicoxite (Fig. 17; 19, 3*b,c*) at the base of the serrate oral margin. The 5th coxa of *Eurypterus* (Fig. 19, 3*c*) has a small circular foramen, possibly covered by a thin membrane and functioning as an auditory organ. The walking leg attached to the distal portion of the coxa has 7 to 8 joints, 8 when a double trochanter is present in the 5th leg. In *Megalograptus* (Fig. 24) 8 joints seem to be present in the 2nd walking leg,

owing to addition of an extra segment between the 2nd and 3rd. The joints of the walking legs have been interpreted as trochanter (1-2), prefemur, femur, patella, tibia, tarsus, and pretarsus. The more or less cylindrical joints generally are inserted telescopically into each other. Each joint is provided with fixed (or rarely movable) primarily ventral spines. In less primitive legs, the spines may be absent, as in the 5th walking leg ("balancing leg") of *Eurypterus* (Fig. 19, 3*c*) and *Megalograptus* (Fig. 24) and in other legs of *Pterygotus* (Fig. 22, 1*a, 3a, 3g*) and stylonurids (Fig. 27, 1, 2*c, 4a, 5a,b, 7a*); or the spines may be strongly developed and specialized, as in *Carcinosoma* (Fig. 23), *Mixopterus* (Fig. 25), *Megalograptus* (Fig. 24), and the 1st and 2nd pairs of legs in *Ctenopterus* (Fig. 27, 4*a*).

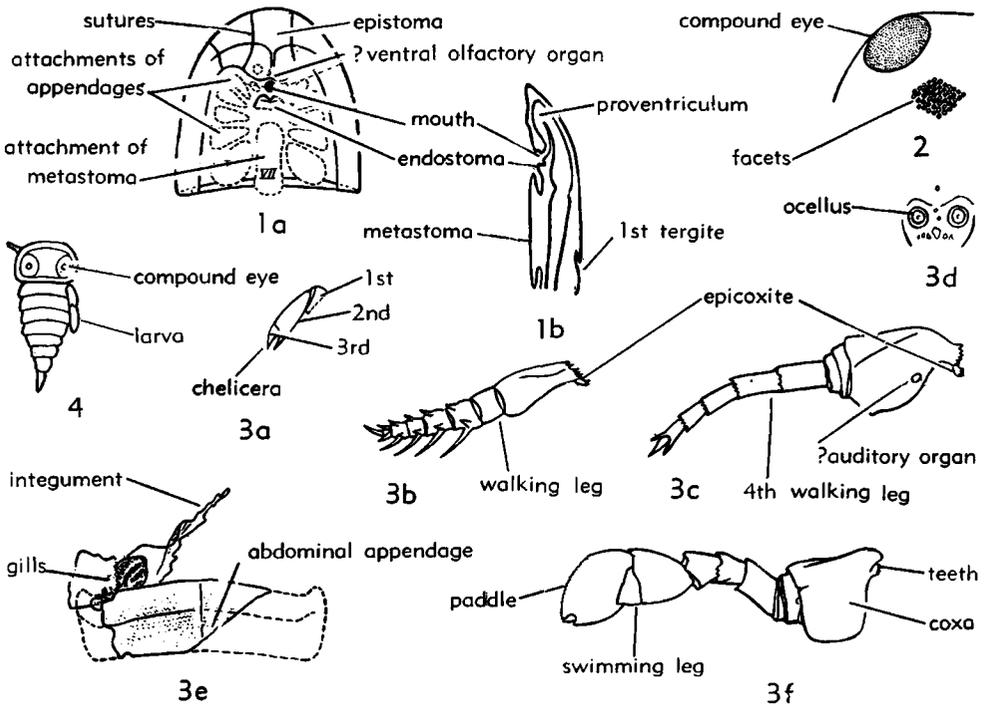


FIG. 19. Morphological features of eurypterids.

1*a,b*, *Hughmilleria*, L.Dev., Norway; 1*a*, ventral side of prosoma with appendages removed; 1*b*, longitudinal section; both  $\times 1$  (64).

2, *Pterygotus* sp., Sil., Balt., showing compound eye and enlarged view of eye facets (47).

3*a-f*, *Eurypterus fischeri* Eichw., Sil., Balt.; 3*a*, chelicera; 3*b*, walking leg; 3*c*, last walking leg ("balance leg"); 3*d*, median ocelli,  $\times 4$ ; 3*e*, abdominal plate-shaped appendage with gills; 3*f*, swimming legs; all except 3*d*,  $\times 1$  (47).

4, *Stylonurus myops* Clarke, Sil., N.Y., young larva,  $\times 11$  (40).

Special lobes on the 1st and 2nd walking legs in *Eurypterus* (Fig. 18), *Mixopterus* (Fig. 25), and *Brachyopterus* (Fig. 26) are interpreted as sexual clasping organs.

The 5th pair of legs (6th pair of prosomal appendages) is either developed as walking legs (Stylonuracea) or converted into broad and flat swimming and balancing legs (Eurypteracea) (Fig. 19, 3f). The swimming legs of the Eurypteracea are formed by the strong expansion of the 2 penultimate joints into an oar-blade or paddle. Also, among the Stylonuracea certain forms show a tendency toward converting the last legs into swimming legs. In *Dolichopterus* (Fig. 27, 3a,b; 24, 1b), the ultimate joint takes part in the formation of the paddle. The coxae of the last pairs of legs are strongly developed as large plates, which cover half the ventral surface of the prosoma. The oral margin is provided with powerful teeth and knobs.

The mouth is bordered dorsoposteriorly by a short plate, cleft in front. This plate, called the endostoma (Figs. 17C; 19, 1a,b), is probably formed by prosomal sternites.

The metastoma is a larger plate covering (in ventral view) the endostoma and median portions of the posterior coxae (Figs. 14, 17B). The metastoma, attached at its dorsal surface, is probably homologous with the chilaria of Xiphosura and hence represents the fused and strongly modified appendages of the 7th (pregenital) somite. The metastoma thus actually belongs to the first segment of the abdomen. The plate is elliptical to trapezoid in outline, with a cleft or transverse anterior margin and a transverse or cleft (*Megalograptus*) posterior margin (Fig. 22, 1e, 3d; 25, 2b). Broader and narrower forms of one species may denote different sexes.

The operculum and 4 succeeding plate-shaped appendages (Fig. 19, 3e; 20, 1a,c) are built on the same plan. The appendages (not sternites) are attached along the anterior border and overlap each other backwards. The posterior plates are fused along the median line, transverse rows of pigmented scales suggesting a rudimentary segmentation. A broad posterior doubleure passes into a more flexible integument with elliptical branchial areas containing the gills (Fig. 19, 3e; 21, 1b,d). The nature of

the gills is uncertain, but unpublished plates by HOLM, based on specimens of *Eurypterus fischeri*, suggest minute tufts instead of book gills. In large forms, such as *Pterygotus* and *Slimonia*, more prominent leaflike appendages have been interpreted as gills.

The operculum (Fig. 17B; 20, 1a,b) represents appendages of the 8th (genital) segment corresponding to the 2nd abdominal tergite. Sexual dimorphism is expressed by 2 types of genital appendages (Fig. 20, 1a,b, 2a-d; 21, 1e,f, 2b,c). The appendage, which probably is formed by fusion of the inner branches of a primarily biramous appendage (as in *Limulus*), is either long and narrow (male) or short and broad (female). In *Pterygotus* (Fig. 20, 2a,b; 22, 2d), the pear-shaped median appendage shows traces of dorsal apertures (possibly female) of oviducts or a small combined aperture (possibly male) (Fig. 20, 2d). Both the female and male appendage has a hastate basal portion, generally with 3 separate joints. In *Eurypterus*, the median appendages of the 9th segment also take part in formation of the genital appendage (Fig. 20, 1c).

Remains of the intestine, reaching from the mouth backward to the base of the telson, were described in *Carcinosoma* by RUEDEMANN in 1921. Possible coprolites have been found in connection with *Megalograptus* by CASTER & KJELLESVIG-WAERING (1955).

*Ontogeny.* The smallest larva known (*Stylonurus*, Fig. 19, 4) measures 2 to 3 mm. in length. The specimen is not well preserved; but it deviates from the adult in having a smaller number of abdominal segments, and the compound eyes evidently are mounted on ovate nodes. In a specimen of *Eurypterus* 7 mm. long, the basal portion of the telson is much broader than in the adult.

*Ecology.* Eurypterid remains are scarce, and particularly so in marine faunas. Most described species belong to brackish- and fresh-water faunas. In general, one may say that the eurypterids inhabited fresh and brackish waters near the coast and occasionally visited the sea. With their well-protected gills, it is possible that the eurypterids were able to spend short intervals of time on land.

Most eurypterids were benthonic forms, crawling around on the bottom and digging in mud and sand. On the other hand, streamlined forms (as *Hughmilleria* and *Pterygotus*) probably belong to the nekton. The swimming was performed by means of the swimming legs and movements of the body, but it is also possible that a rapid shooting forward through the water may have been accomplished by powerful strokes of the abdominal appendages, as in early larvae of *Limulus*. In *Pterygotus*, the walking legs are developed only slightly, and swimming abilities are indicated by modification of the telson into a tail-fin and rudder.

Because of powerful teeth on the coxae and chelicerae of Pterygotidae, the eurypterids were probably able to feed on larger animals which possessed a solid exoskeleton, perhaps including primitive vertebrates, common in the same fossil faunas.

**Phylogeny.** The geological appearance of the Eurypterida gives little information on phylogeny of the group. The earliest known forms occur in Lower Ordovician (Deepkill) rocks, and the Ordovician species comprise representatives of most of the families. During evolution of different branches of the eurypterid stock, a tendency toward

increase in size and in elaboration of ornamentation may be noticed.

The genus *Hughmilleria*, with rather uniform walking legs and seemingly primitive ornamentation, probably occupies a central position in the eurypterid stock. In this and all other genera belonging to the superfamily Eurypteracea, the swimming legs are similarly developed. In the Stylonuracea, on the other hand, the last prosomal legs are still walking legs, although in some forms (Dolichopteridae) a tendency toward formation of swimming legs is demonstrated.

The ancestors of the Eurypterida are probably to be found in forms such as *Paleomerus* (Fig. 8) from Lower Cambrian deposits. As already mentioned this genus combines xiphosuran and eurypterid characters. The earliest eurypterids, possibly from Lower Cambrian (or perhaps Precambrian), probably had 5 pairs of simple walking legs. The main eurypterid branch developed characteristic swimming legs, and the further branching of this stock manifests itself in adaptations to different habitats. In another branch of the Eurypterida, the last walking legs were kept more or less unchanged in most forms and only a few developed some kind of swimming legs.

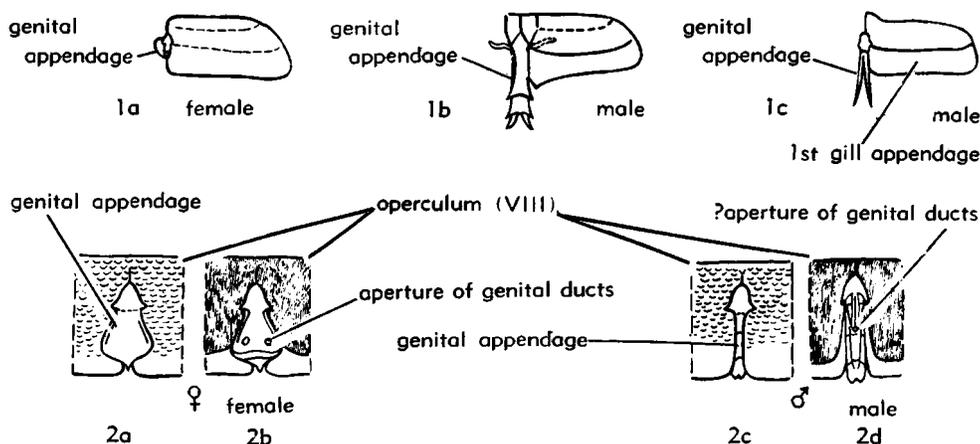


FIG. 20. Genital appendages of eurypterids.

1a-c, *Eurypterus fischeri* EICHW., Sil., Balt., from ventral side; 1a, female; 1b,c, male;  $\times 1$  (47).

2a-d, *Pterygotus (Pterygotus) rhenaniae* JAEKEL, Dev., Ger.; 2a,b, female, ventral and dorsal views; 2c,d, male, ventral and dorsal views (64).

## Superfamily EURYPTERACEA

## Burmeister, 1845

[*nom. transl.* STØRMER, 1951 (*ex* Eurypteridae BURMEISTER, 1845)]

Eurypterida with last prosomal appendages developed as swimming legs that carry paddles formed by expansion of the 2 penultimate joints. *Ord.-Perm.*

## Family HUGHMILLERIIDAE Kjellesvig-Waering, 1951

[*nom. correct.* STØRMER, herein (*pro* Hughmilleridae KJELLESVIG-WAERING, 1951)]

Small to large forms with outer surface smooth or partly provided with transverse integumental folds, or semilunar to pointed scales; compound eyes small, antelateral, marginal or subcentral; telson lanceolate or somewhat expanded; epistoma present; chelicerae small to medium, without teeth; walking legs stout, with spines or denticles; swimming paddles narrow; metastoma ovate to cordate; genital appendage of male narrow, without lateral points. *Ord.-Perm.*

**Hughmilleria** SARLE, 1902 [*\*H. socialis*]. Small to medium forms, with smooth surface or with transverse folds or semilunar scales; body lanceolate, with postlateral prolongations of first post-abdominal segment, and lanceolate telson; chelicerae medium-sized; metastoma ovate; genital appendage short and broad in female, long and narrow in male. *Ord.-Perm.*, Eu.-N.Am.—FIG. 19,1; 21,1a-g. *H. norvegica* (KIAER), ?L.Dev. (Downton.), Norway; 19,1a, ventral side of prosoma with appendages removed, attachments of appendages outlined; 19,1b, long. sec. of prosoma and 1st segment of abdomen, both about  $\times 1.3$ ; 21,1a, dorsal side; 21,1b, ventral side with branchial area outlined; 21,1c,d, sections of body; all  $\times 0.5$ ; 21,1e,f, median genital appendages of male and female,  $\times 1$ ; 21,1g, ventral doublure of prosoma,  $\times 0.8$  (all 64).—FIG. 21,1h. *H. bellistriata* KJELLESVIG-WAERING, Sil., Wis.; prosoma with sculpture,  $\times 0.7$  (50).

**Slimonia** PAGE, 1856 [*\*Himantopterus acuminatus* SALTER, 1856]. Large forms with smooth outer surface; prosoma quadratic, with small compound eyes at antelateral corners; postabdomen narrow, anterior half of telson strongly expanded; chelicerae small, walking legs with denticles but no spines; metastoma narrow cordate, genital appendages fairly long and narrow in both sexes. *U.Sil.*, Eu.—FIG. 21,2. *\*S. acuminata* (SALTER), Sil., Scot.; 2a, dorsal side,  $\times 0.1$ ; 2b, ?female genital appendage; 2c, ?male genital appendage, about  $\times 0.13$  (67).

**Salteropterus** KJELLESVIG-WAERING, 1951 [*\*Eurypterus abbreviatus* SALTER, 1859]. Small forms;

outer surface with pointed triangular scales; anterior part of carinate telson broadly trigonal with serrated posterior edges and followed by a long, flat median stem which expands into a flattened posterior end (13). *L.Dev.* (Downton.), Eng.—FIG. 21,5. *\*S. abbreviatus* (SALTER); anterior and posterior part of telson,  $\times 1$  (50).

**Grossopterus** STØRMER, 1934 [*\*Eurypterus? overathi* GROSS, 1933]. Medium forms; outer surface with minute semilunar scales; prosoma subquadratic with expanded, rounded antelateral corners, compound eyes small, intermarginal; walking legs powerful, with spines; genital appendage of male long lanceolate, with serrated margins (26). *L.Dev.-M.Dev.*, Eu.-N.Am.—FIG. 21,4. *\*G. overathi* (GROSS), *L.Dev.*, Ger.; 4a, dorsal side, about  $\times 0.25$ ; 4b, genital appendage of ?male,  $\times 0.3$  (64).

**Lepidoderma** REUSS, 1855 [*non* WATERHOUSE, 1875; *nec* ZELINKA, 1889] [*\*L. imhofi*] [= *Adelophthalmus* JORDAN & MEYER, 1856; *Anthraconectes* MEEK-W., 1868]. Small to medium forms; outer surfaces with pointed scales and striae; body elongate, with spurs, contracted postabdomen, and long and styliform telson; compound eyes intramarginal; walking legs mostly devoid of spines, genital appendage of male long, of female short, with spatulate lateral lobes (12). ?*U.Dev.*, *Carb.-M.Perm.*, Eu.-N.Am.-Asia.—FIG. 21,3a. *L. mansfieldi* (C. E. HALL), *Carb.*, Penn., U.S.A.; about  $\times 1.3$  (46).—FIG. 21,3b,c. *L. mazonense* (MEEK-W.), Penn., Ill.; about  $\times 1$ ; 3b, metastoma and swimming leg; 3c, female genital appendage (50). ?**Hastimima** WHITE, 1908 [*\*H. whitei*]. Large forms; test with scattered oblong scales or closely set mucrones; telson acute, hastate, with lateral expanded portion well separated from narrow median plate. *Carb.*, S.Am.-N.Am.—FIG. 21,6. *\*H. whitei*, Brazil; 6a, coxa with proximal joints; 6b, telson,  $\times 0.3$  (after CLARKE & RUEDEMANN).

## Family PTERYGOTIDAE Clarke &amp; Ruedemann, 1912

Small to very large exoskeleton with distinct semilunar scales; large marginal compound eyes; telson strongly expanded; epistoma present; chelicerae very large and long, provided with strong teeth in chelae; walking legs generally small, slender, without spines; metastoma subovate to cordate; genital appendage short and pear-shaped in female, somewhat short, narrow and blunt in male. *Ord.-Dev.*

**Pterygotus** AGASSIZ, 1839 [*\*P. problematicus*]. *Ord.-Dev.*, Eu.-Spitz.-N.Am.-Austral.

**P. (Pterygotus)** [= *Curviramus* RUEDEMANN, 1935]. Prosoma subtrapezoid; compound eyes adjoining antelateral margin; chelicerae with curved distal margin, coxae of swimming legs with 11 to 13

teeth; telson with pronounced median dorsal carina passing into short terminal spine. ?*Ord.*, *Dev.* Eu.-N.Am.—FIGS. 20,2; 22,2a-d. *P. (P.) rhenaniae* JAEKEL, L.Dev., Ger.; 20,2a,b, genital appendage of female, dorsal, ventral,  $\times 0.14$ ; 20,2c,d, genital appendage of male, dorsal, ventral,  $\times 0.14$ ; 22,2a, dorsal,  $\times 0.45$ ; 22,2b, chelicera,  $\times 0.7$ ; 22,2c,d, genital appendages, male, female,  $\times 0.2$  (64).—FIG. 22,2e. *P. (P.) anglicus* AGASSIZ, L.Dev.(Old Red Sandstone), Scot.; metastoma,  $\times 0.3$  (67).

**P. (Acutiramus) RUEDEMANN, 1935** [*Pterygotus buffaloensis* POHLMAN, 1881]. Prosoma subquadrate; compound eyes at antelateral margin; chelicerae with acute distal margin, the large tooth of chelae distally inclined, coxae of swimming legs with 13 to 15 teeth; telson with low median carina or row of knobs. ?*Ord.*, *Sil.-Dev.*, Eu.-N.Am.-?Austral.—FIG. 22,1a-e. \**P. (A.) buffaloensis* POHLMAN, Sil., N.Y.; 1a,b, dorsal, ventral,  $\times 0.045$ ; 1c, chelicera,  $\times 2$ ; 1d, swimming leg,  $\times 0.3$ ; 1e, metastoma,  $\times 0.3$ : (40).—FIG.

22,1f. *P. (A.) bohemicus* (BARRANDE), Dev., Czech., ?male genital appendage,  $\times 0.17$  (57).

**P. (Erettopterus) SALTER, 1859** [*pro Himantopterus* SALTER, 1856 (non WESTMAIL, 1836)] [*\*Erettopterus bilobus*]. Prosoma semielliptical, compound eyes at antelateral margin; chelicerae with angular distal margin, coxae of swimming legs with 13 to 15 teeth, telson bilobed. *Sil.-Dev.*, Eu.-N.Am.—FIG. 22,3a-f. *P. (E.) osiliensis* SCHMIDT, Sil., Balt.; 3a, dorsal,  $\times 0.1$ ; 3b, chelicera, fixed joint,  $\times 0.3$ ; 3c, prosomal doublure with epistoma,  $\times 0.3$ ; 3d, metastoma,  $\times 0.2$ ; 3e, ?male genital appendage,  $\times 0.3$ ; 3f, ventral surface 1st postabdominal seg.,  $\times 0.7$  (63).—FIG. 22,3g, \**P. (E.) bilobus* (SALTER), Sil., Scot.; walking leg,  $\times 1$  (67).

### Family EURYPTERIDAE Burmeister, 1845

Small to large exoskeleton with inconspicuous, semilunar, tongue-shaped to

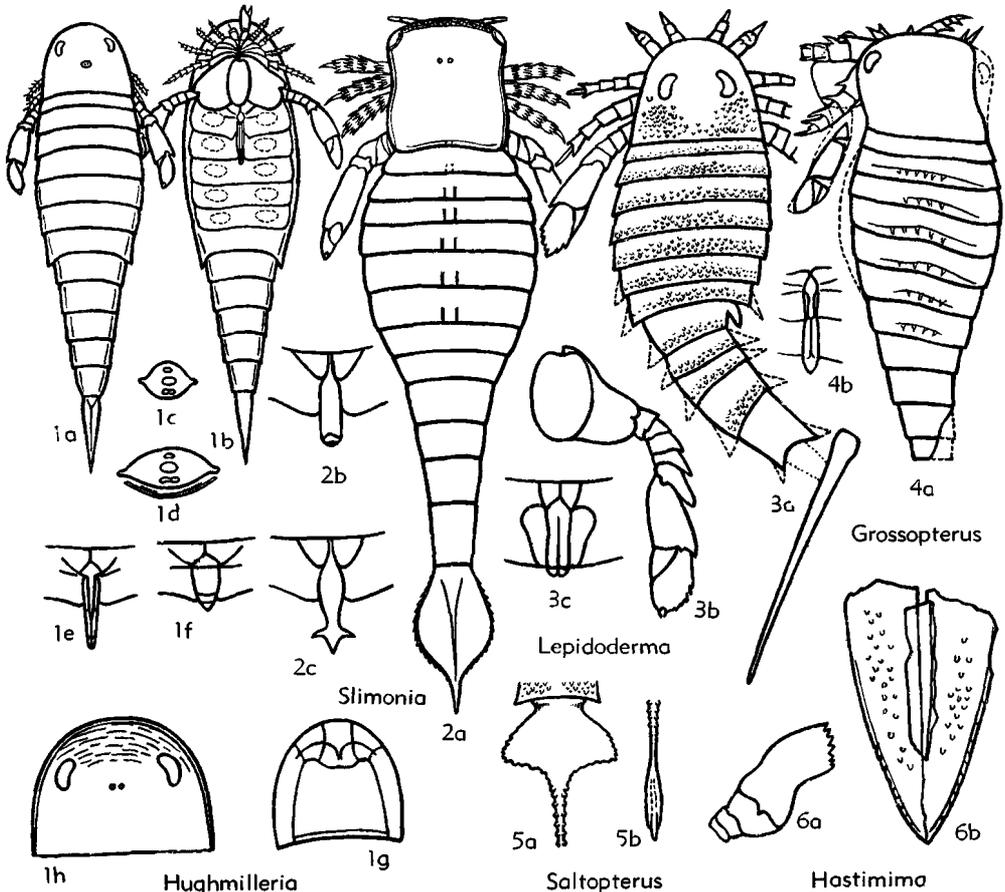
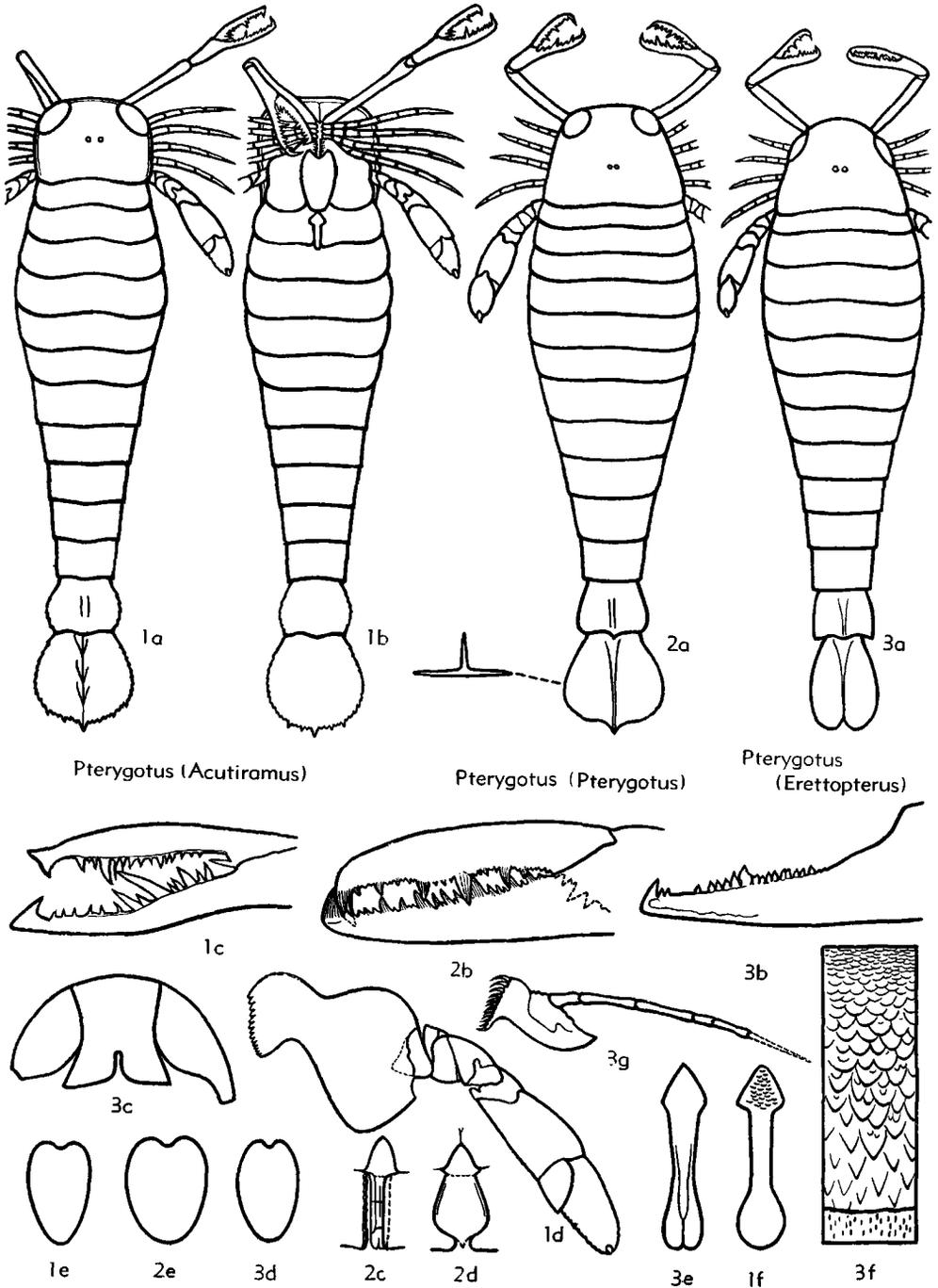


FIG. 21. Hughmilleriidae (p. P30).

pointed scales or curved ridges; prosoma subrectangular; telson styliform; compound eyes subcentral, slightly curved; no epi-

stoma; chelicerae small, walking legs mostly spinose; metastoma ovate, genital appendage very short with covered lateral lobes in



Pterygotus (Acutiramus)

Pterygotus (Pterygotus)

Pterygotus (Erettopterus)

FIG. 22. Pterygotidae (p. P30-P31).

female, but long, with diverging distal spines in male. *Ord.-U.Carb.*

*Eurypterus* DE KAY, 1825 [*non* MABILLE, 1877; *nec* SHARPE, 1896] [*\*E. remipes*]. Exoskeleton

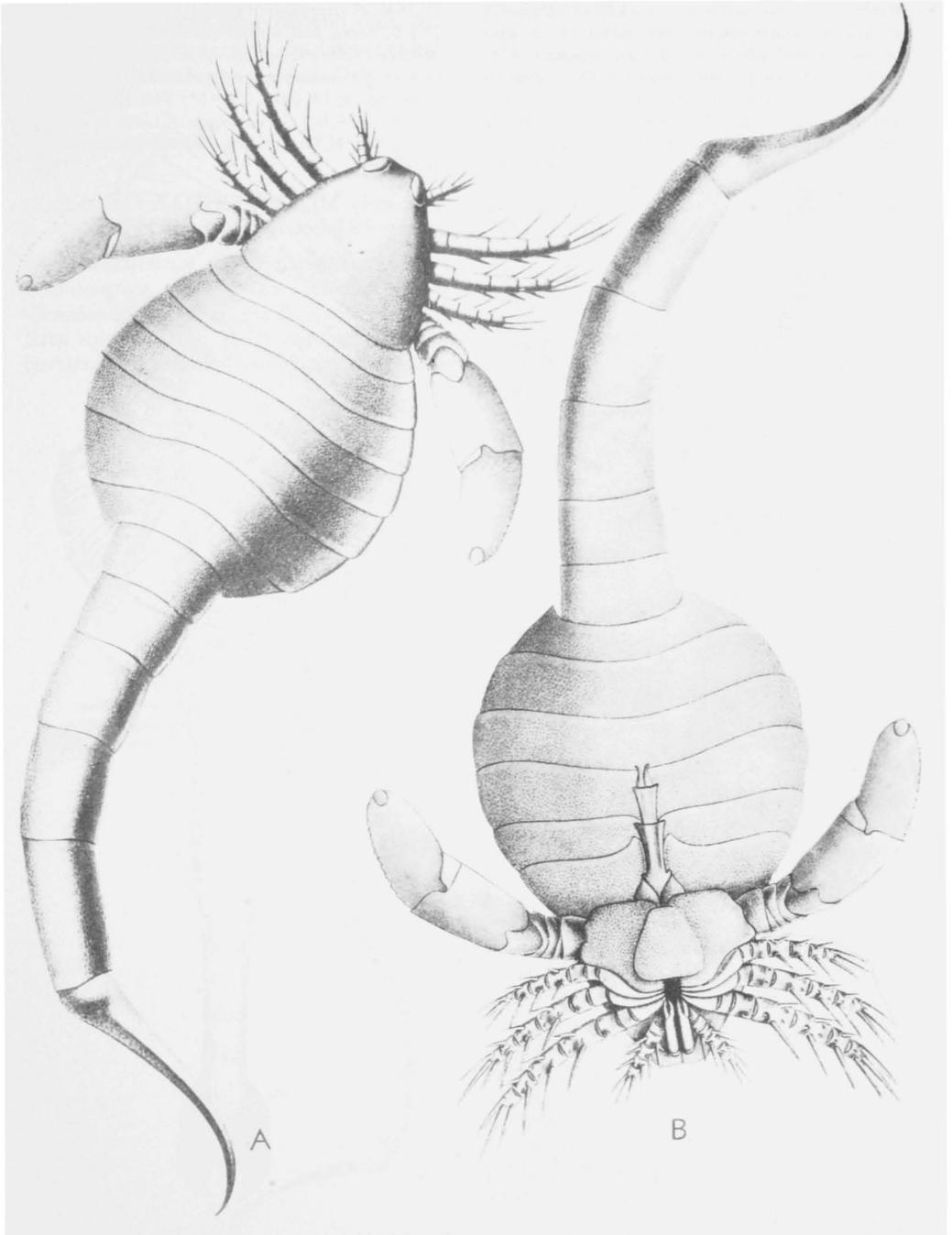


FIG. 23. *Carcinosoma scorpionis* (GROTE & PITT), Sil., N.Y. A,B, Dorsal and ventral views of male (reconstr.),  $\times 0.27$  (40).

locally provided with scales, metastoma not contracted, pretelson with postlateral prolongations; paddle of swimming leg strongly expanded. *Ord.-Carb.*, Eu.-N.Am.-Asia.—FIG. 17; 18; 19, *3a-c,e*, *f*; 20, *1*. *E. fischeri* EICHW., Sil., Balt.; 17*A,B*, dorsal and ventral side, about  $\times 0.5$  (reconstr.); 17*C*, gullet, with endostoma,  $\times 13$ ; 17*D*, denticular margin of coxae around mouth,  $\times 6$ ; 18, ventral side of prosoma of etched specimen, 2nd walking leg with clasping organ, probably female,  $\times 1.3$ ; 19, *3a*, chelicera; 19, *3b*, walking leg; 19, *3c*, 4th walking leg; 19, *3f*, swimming leg; 19, *3e*, abdominal appendages (plate), with gills; 20, *1a*, left half of operculum with median genital appendage of female; 20, *1b*, of male, 20, *1c*, median appendages of next abdominal appendages (plate), supporting male genital appendage of the operculum (all 47).

**Onychopterella** STØRMER, 1951 [*pro Onychopterus* CLARKE & RUEDEMANN, 1912 (*non* REICHENBACH, 1850)] [*\*Eurypterus kokomoensis* MILLER & GURLEY, 1896]. Medium size, outer surface with minute pointed scales; metastoma not contracted; last walking leg long, swimming leg with inconspicuous paddle ending in a spur (29). *Sil.*, N.Am.—FIG. 29, 2. *\*O. kokomoensis* (MILLER-G.), Ind.; 2*a*, ventral side,  $\times 0.5$ ; 2*b*, metastoma,  $\times 1$  (40).

**Tylopterella** STØRMER, 1951 [*pro Tylopterus* CLARKE & RUEDEMANN, 1912 (*non* CAPIOMONT, 1868; *nec* LECONTE, 1876)] [*\*Eurypterus boyli* WHITEAVES, 1884]. Small thick (partly calcareous) exoskeleton with curved ridges of confluent tubercles and large knobs near median line; prosoma with raised margin; metastoma contracted (29). *Sil.*, N.Am.—FIG. 29, 4. *\*T. boyli* (WHITEAVES), Ont.; 4*a*, dorsal side, about  $\times 0.17$ ; 4*b*, ornamentation, enlarged (40).

### Family CARCINOSOMATIDAE Størmer, 1934

[*nom. correct.* STØRMER, herein (*pro* Carcinosomidae STØRMER, 1934)]

Small to large exoskeleton with scattered minute tubercles or raised tongue-shaped scales; body scorpion-like, prosoma subtriangular, compound eyes small, intramarginal and antemedian; preabdomen broad, ovate, postabdomen narrow, cylindrical, with curved telsonic spine; epistoma short and narrow; chelicerae small, walking legs with long spines, 2nd pair of legs being the largest, swimming legs with long, slightly expanded 7th and 8th joints; metastoma subtriangular; genital appendage probably short and broad in female, long with distal spines in male. *Ord.-Sil.*

**Carcinoma** CLAYPOLE, 1890 [*pro Eurypterus* CLAYPOLE, 1890 (*non* KOCH, 1839; *nec* DUJARDIN, 1845;

*nec* GISTL, 1850)] [*\*Eurypterus newlini* CLAYPOLE, 1890] [= *Eusarcus* GROTE & PITT, 1875 (*non* PERTY, 1833)]. *Ord.-Sil.*, Eu.-N.Am.—FIG. 23; 29, *3b-d*. *C. scorpionis* (GROTE & PITT), Sil., N.Y.; 23*A,B*, dorsal and ventral side of male (reconstr.)  $\times 0.27$ ; 29, *3b*, metastoma,  $\times 3$ ; 29, *3c*, ornamentation of abdominal appendage,  $\times 2$ ; 29, *3d*, swimming leg,  $\times 0.4$  (FIG. 23, 40\*; FIG. 29, *3b-d*, 40). —FIG. 29, *3a*, *C. vaningeni* CLARK & RUEDEMANN, Sil., N.Y.; prosoma and opisthosoma, about  $\times 3$  (40).

### Family MIXOPTERIDAE Caster & Kjellesvig-Waering, 1955

Large exoskeleton with scattered tubercles or semicircular scales, body scorpion-like, prosoma subquadrate protruding antemedially; preabdomen fairly narrow, with axial furrows; postabdomen narrow, with curved

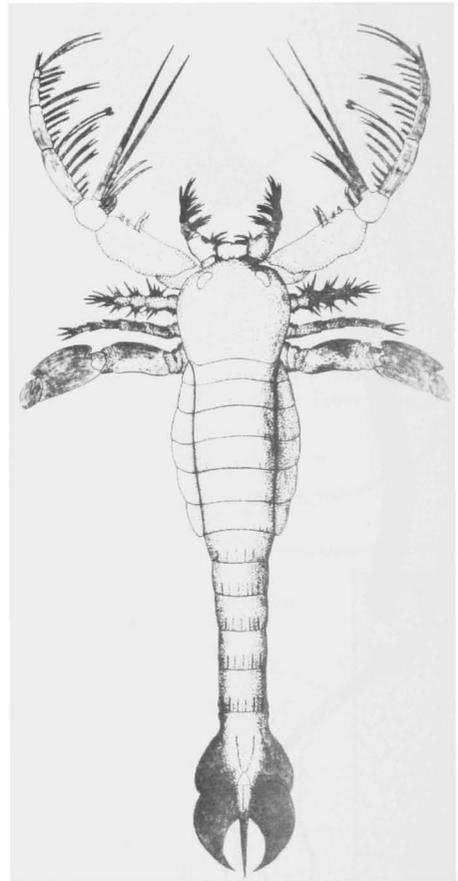


FIG. 24. *Megalograptus ohioensis* CASTER & KJELLESVIG-WAERING, U.Ord., Ohio, dorsal view (reconstr.),  $\times 0.12$  (37).

telsonic spine; 1st and 2nd walking legs strongly developed, with paired spines, 3rd and 4th moderate in size, with short spines, swimming legs with long 7th and short 8th joint; metastoma narrow cordate; genital appendage of male long. *Sil.-L.Dev.*

**Mixopterus** RUEDEMANN, 1921 [*\*Stylonurus (Ctenopterus) multispinosus* CLARKE-R., 1912] (33).  
 —FIG. 25; 29.6. *M. kjaeri* STØRMER, ?*L.Dev.* (Downton.), Norway; 25*A,B*, dorsal and ventral views of male (reconstr.), showing clasping organs on 1st walking legs,  $\times 0.17$  (64\*); 29.6*a,b*, metastoma and part of swimming leg,  $\times 0.3$  (64).

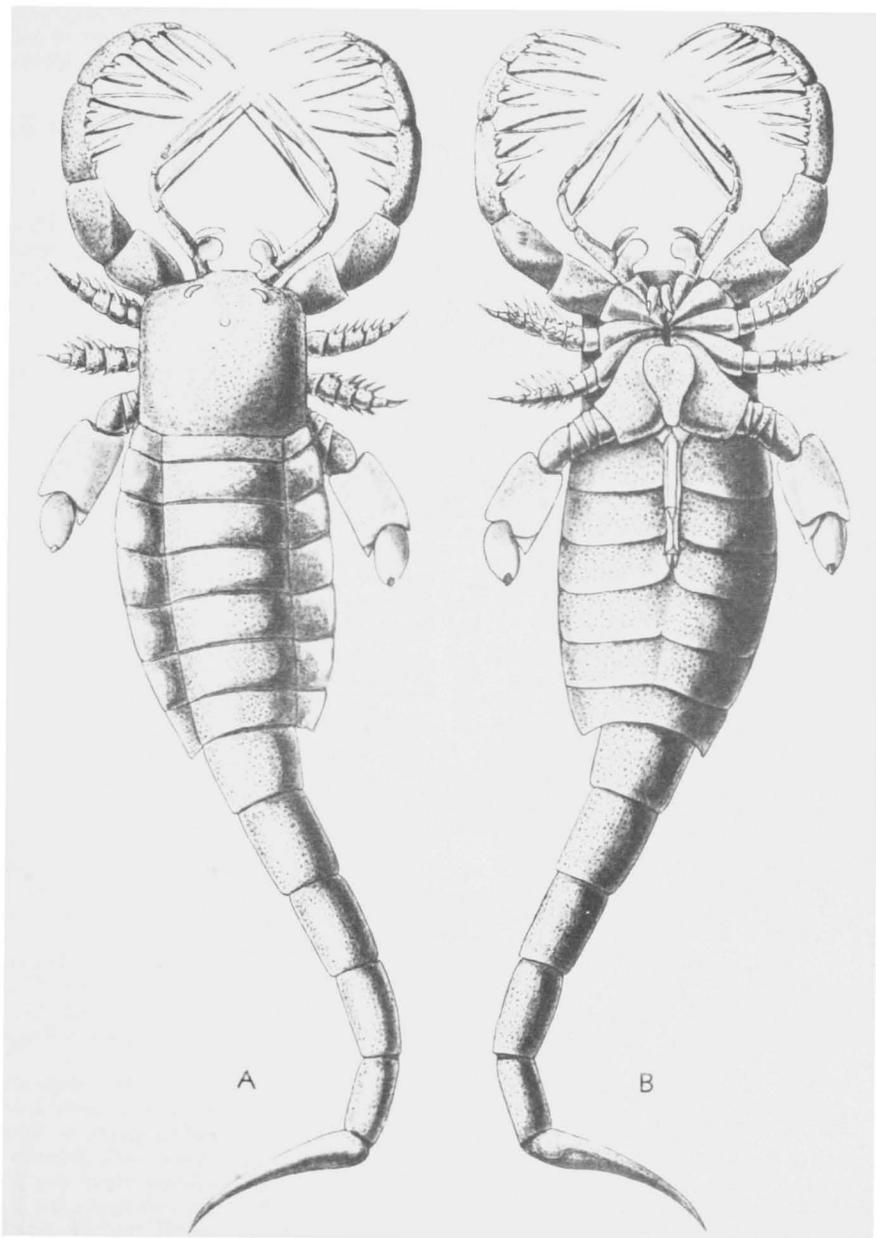


FIG. 25. *Mixopterus kjaeri* STØRMER, ?*L.Dev.*(Downton.), Norway. *A*, Dorsal view (reconstr.),  $\times 0.17$ .  
*B*, Ventral view (reconstr.), showing clasping organs on 1st walking legs,  $\times 0.17$  (64\*).

Family MEGALGRAPTIDAE Caster & Kjellesvig-Waering, 1955

Large exoskeleton with ovate to triangular scales; prosoma subquadrate, with tongue-like anterior process bearing marginal spines; compound eyes antemedian; preabdomen narrow, with axial furrows; postabdomen moderately narrow, with broad, curved and flat appendages; telson narrow lanceolate; epistoma short and broad; chelicerae small and short, 1st and 3rd walking legs short with diverging, or closely set spines, 2nd leg enormously developed, with long paired spines, 4th leg almost spineless, swimming leg with long 4th and 7th joints; metastoma subovate to cordate, with anterior cleft and with or without posterior indentation; genital appendage of female club-shaped, of male short and narrow. *Ord.*

*Megalograptus* MILLER, 1874 [*\*M. welchi*]. Third walking leg with rather short diverging spines; metastoma subovate, with posterior indentation.

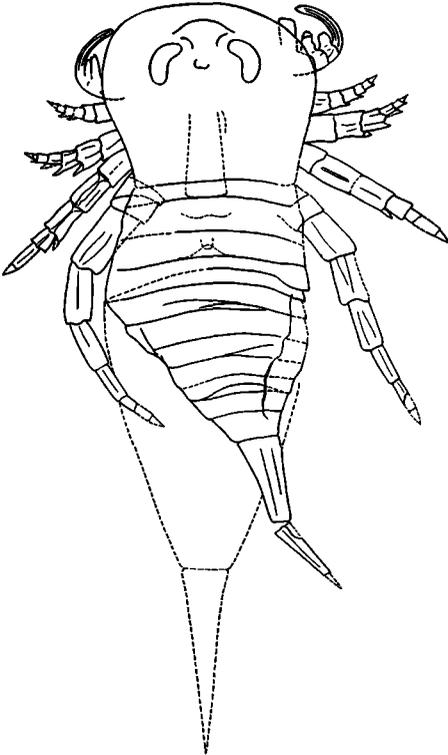


FIG. 26. *Brachyopterus stubblefieldi* STØRMER, *Ord.*, Wales, dorsal side,  $\times 1.5$  (64).

*Ord.*, N.Am.—FIG. 24. *M. ohioensis* CASTER & KJELLESVIG-WAERING, Ohio; reconstr., about  $\times 0.12$  (37\*).—FIG. 29,7. *\*M. welchi*, Ohio; walking leg, about  $\times 0.5$  (40).

*Echinognathus* WALC., 1882 [*\*Eurypterus clevelandi* WALC., 1882]. Third walking leg with long closely set spines; metastoma broadly cordate, without posterior indentation. *Ord.*, N.Am.—FIG. 29,5. *\*E. clevelandi* (WALC.), N.Y.; 5a, walking leg,  $\times 0.5$ ; 5b, probably spine of walking leg,  $\times 0.3$ ; 5c, metastoma,  $\times 0.3$ ; 5d, ornamentation,  $\times 0.75$  (40).

Superfamily STYLONURACEA  
Diener, 1924

[*nom. transl.* STØRMER, 1951 (*ex* Stylonuridae DIENER, 1924)]

Eurypterida with last prosomal legs developed as walking legs, or less commonly modified into swimming legs in which the paddle is formed by the 2 to 3 ultimate joints. *Ord.-L.Perm.*

Family STYLONURIDAE Diener, 1924

Small to very large exoskeleton with scales developing into tubercles and knobs; prosoma of variable outline with subcentral to more anterior arcuate compound eyes; abdomen slender, without or with lateral epimers; telson styliiform to clavate; prosomal doublure narrow, with epistoma; walking legs long and powerful, with or without spines; metastoma narrow; genital appendage of female short and broad, of male probably long. *Ord.-L.Perm.*

*Stylonurus* PAGE, 1856 [*\*S. powriei*]. Small to medium size; outer surface mostly smooth; prosoma semiovate to subrectangular, compound eyes with axes parallel or slightly converging forward; abdomen narrow, with long powerful styliiform telson; first 3 pairs of walking legs with spines, last 2 pairs of walking legs long, keeled, tapering slightly in width, last pair of legs reaching as far as telson; metastoma with deep anterior notch. ?*Ord.*, *Sil.-Dev.*, Eu.-N.Am.—FIG. 27,2b. *S. dolichopteroides* STØRMER, ?*L.Dev.* (Downton.), Norway; prosoma,  $\times 0.6$  (64).—FIG. 27,2c. *S. logani* WOODW., *Sil.*, Scot.; about  $\times 0.3$  (67).—FIG. 27,2a. *S. macrophthalmus* LAURIE, *Sil.*, Scot.; metastoma,  $\times 0.5$  (53).

*Drepanopterus* LAURIE, 1892 [*\*D. pentlandicus*]. Fairly large; outer surface with acute scales or tubercles; prosoma subrectangular to subovate, compound eyes with parallel axes; abdomen narrow, with styliiform to clavate telson; first 3 pairs of walking legs powerful, with spines, last 2 pairs moderate in length, smooth, tapering slightly in width toward strong curved terminal claw, last pair of legs reaching to penultimate abdominal

segment; metastoma unknown. *Sil.-U.Dev.*, Eu.-N.Am.—FIG. 27,1. *D. longicaudatus* CLARKE & RUEDEMANN, *Sil.*, Ind.; dorsal side (reconstr.,  $\times 0.25$  (40).

**Brachyopterus** STØRMER, 1951 [\**B. stubblefieldi*]. Small; outer surface probably smooth; prosoma large, subtrapezoid to subpentagonal; compound eyes slightly anterior in position, with axes converging anteriorly; abdomen narrow, with short styliform telson; first 3 walking legs short, with spines except when modified into clasp ing organ;

last 2 pairs moderate in length, keeled, tapering in width, last pair not reaching penultimate abdominal segment; metastoma narrow (29). *M.Ord.*, ?*L.Dev.*, Eu.—FIG. 26.\**B. stubblefieldi*, *M.Ord.*, Wales; dorsal side showing appendages, 1st walking legs modified into clasp ing organs,  $\times 1.5$  (64).—FIG. 27,7. *B.? pentagonalis* (STØRMER), ?*L.Dev.*(Downton.), Norway; 7a, ventral side of prosoma (reconstr.),  $\times 0.4$ ; 7b, dorsal side of prosoma,  $\times 0.4$  (64).

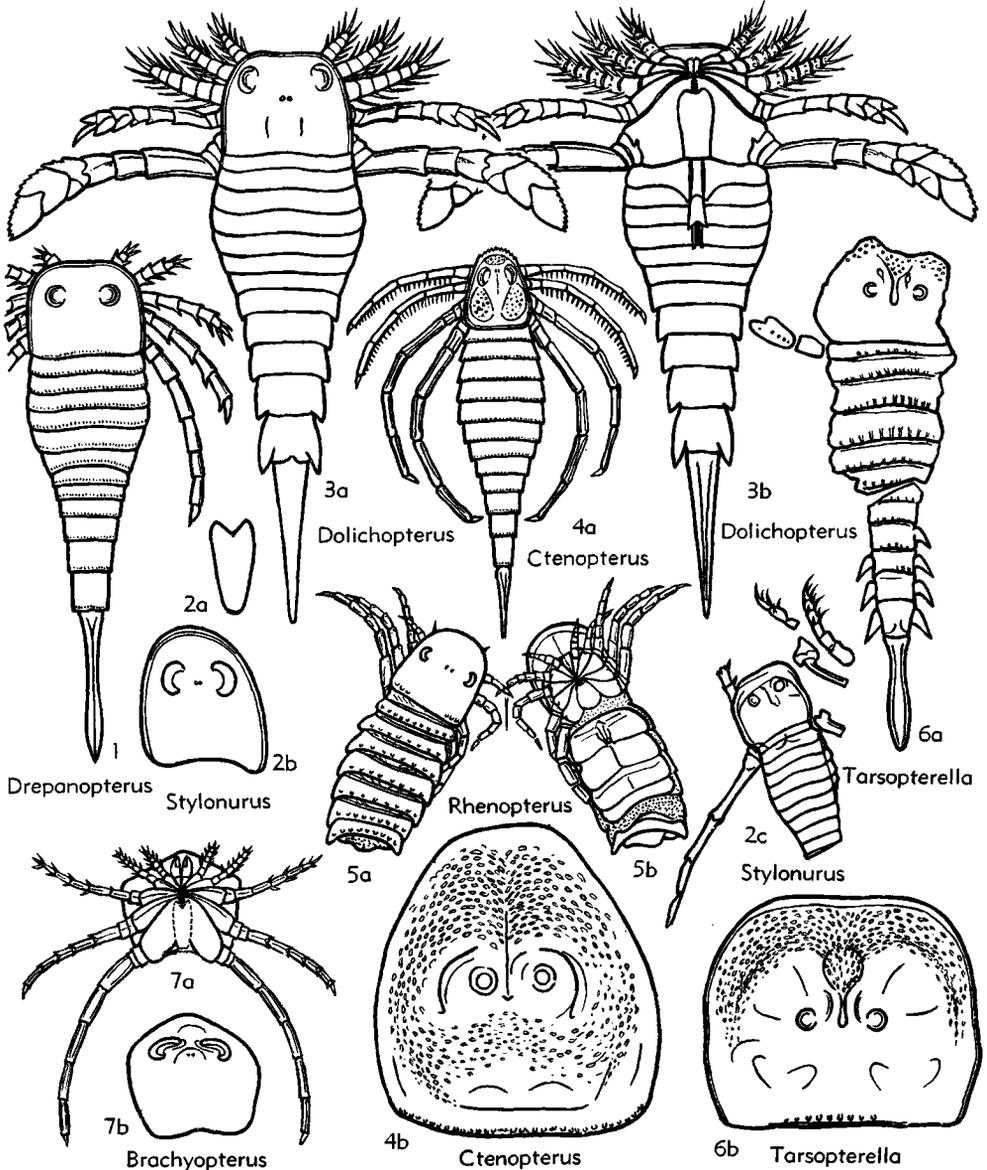


FIG. 27. Stylonuricae (p. P36-P38).

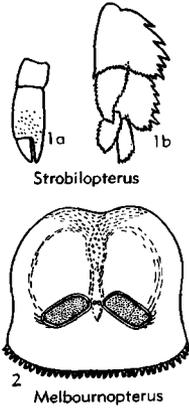


FIG. 28. Stylonuricae (p. P39).

*Ctenopterius* CLARKE & RUEDEMANN, 1912 [*Eurypterius cestrotus* CLARKE, 1907] [= ?*Dolichocephala* CLAYPOLE, 1883 (non MACQUART, 1823)]. Small to very large; outer surface with numerous tubercles and scales; prosoma narrow in front, 2nd and 3rd pairs of walking legs strongly developed with double row of numerous flat spines, last pair of legs long, without spines (5). *Sil.-Dev.*, N.Am.-Eu.—FIG. 27,4a. \**C. cestrotus* (CLARKE), *Sil.*, N.Y.; dorsal side,  $\times 0.5$  (40).—FIG. 27,4b. *C.? lucoana* (CLAYPOLE), *U.Dev.*, N.Y.; dorsal side of prosoma,  $\times 0.17$  (40).

*Tarsopterella* STØRMER, 1951 [*pro Tarsopterius* CLARKE & RUEDEMANN, 1912 (non REINHARDT & LUTKEN, 1862)] [*Stylonurus scoticus* WOODWARD, 1864]. Medium to large; outer surface with strongly developed knobs and scales; prosoma broadly subrectangular, slightly concave in front; compound eyes small; abdomen with pronounced lateral epimers, telson clavate; prosomal legs prob-

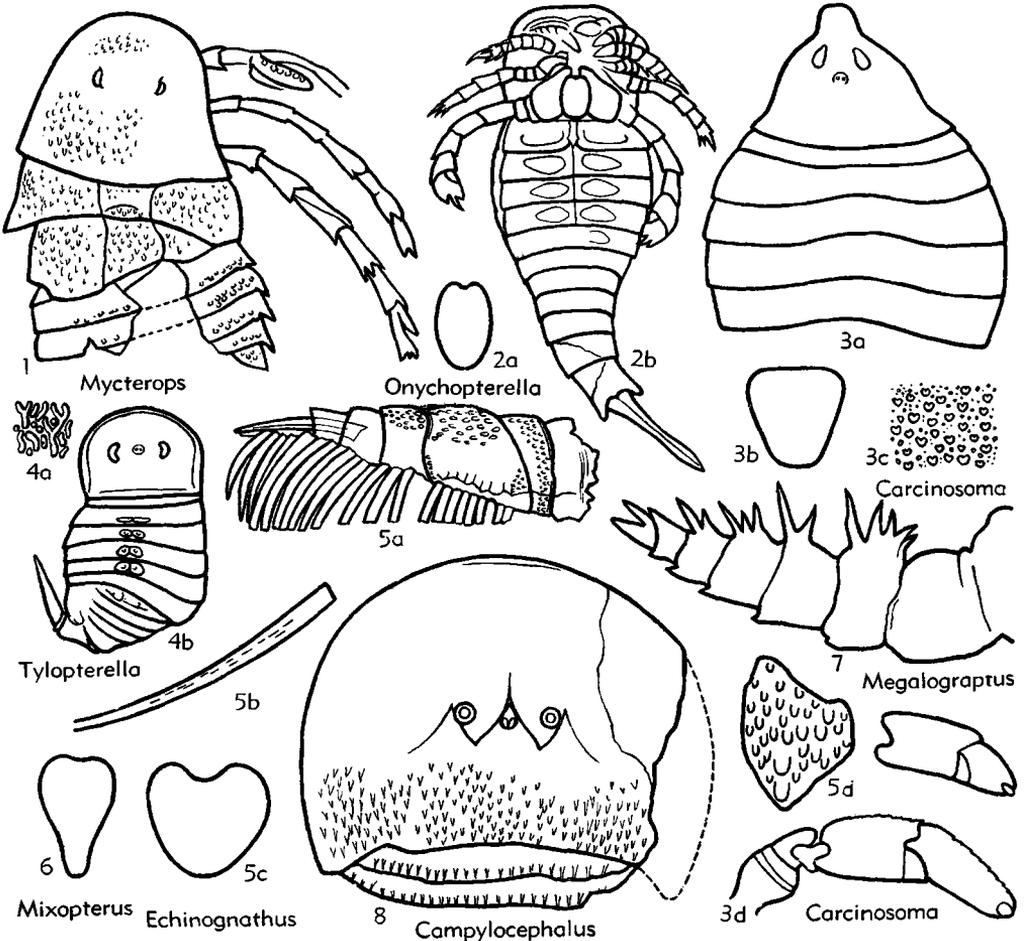


FIG. 29. Eurypterida (p. P34-P39).

ably stylonurid (29). *L.Dev.*, Eu.—FIG. 27,6. \**T. scoticus* (WOODW.), L. Old Red Sandstone, Scot.; 6a, dorsal side,  $\times 0.07$ ; 6b, prosoma,  $\times 0.2$  (67).

**Melbournopterus** CASTER & KJELLESVIG-WAERING, 1953 [\**M. crossotus*]. Small; prosoma bell-shaped, emarginate in front; subrectangular compound eyes in posterior half of prosoma, with axes strongly converging anteriorly; abdomen and appendages unknown (2). *U.Sil.*, Austral.—FIG. 28,2. \**M. crossotus*, Vict.; prosoma,  $\times 1$  (37).

**Campylocephalus** EICHW., 1860 [\**Limulus oculatus* KUTORGA, 1852] [= *Eidothea* SCOULER, 1831 (non RISSO, 1826; nec CHAMBERS, 1873)]. Large; outer surface with arcuate scales; prosoma subsemicircular, strongly convex; compound eyes subcentral, with inflated posteriorly acute lobes between them; abdominal tergites convex, with articular processes; appendages almost unknown. *L.Carb.-L.Perm.*, Eu.—FIG. 29,8. *C. scouleri* (HIBBERT), L.Carb., Scot.; prosoma and 2 abdominal tergites,  $\times 0.25$  (67).

#### Family DOLICHOPTERIDAE Kjellesvig-Waering & Størmer, 1952

Outer surface smooth or with pustules and semilunar scales; compound eyes arcuate, located anteriorly, axes nearly parallel; abdomen commonly with epimers, telson lanceolate; chelicerae small, 1st 3 walking legs stout, with powerful spines, last pairs with supplementary lobes, last legs with ultimate joint enlarged to form part of paddle; metastoma narrow, male genital appendage long. *Sil.-Dev.*

**Dolichopterus** HALL, 1859 [\**Eurypterus (Dolichopterus) macrocheirus*]. Medium size; outer surface almost smooth; prosoma subquadrate; last legs with slightly serrate margin on distal joints and lobes. *Sil.*, N.Am.—FIG. 27,3. \**D. machocheirus*, N.Y.; 3a,b, dorsal and ventral side of male, reconstr.,  $\times 0.3$  (40).

**Strobilopterus** RUEDEMANN, 1935 [\**S. princetoni*]. Medium size; outer surface with pustules and semilunar scales; prosoma semioval; compound eyes submarginal; last legs with strongly serrate margin on distal joints and lobes. *L.Dev.*, N.Am.—FIG. 28,1. \**S. princetoni*, Va.; 1a, chelicera,  $\times 1$ ; 1b, distal end of swimming leg,  $\times 1$  (51).

#### Family RHENOPTERIDAE Størmer, 1951

Small; outer surface with scattered tubercles and knobs; prosoma subtrapezoid, prosomal doublure with median suture, no epistoma; first 2 (or ?3) pairs of walking legs with spines, last 2 pairs long and powerful, without spines; metastoma pear-

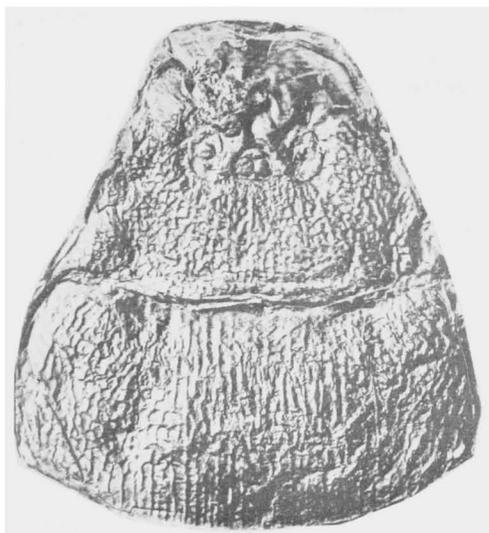


FIG. 30. *Mycterops mathiewi* (PRUVOST), U.Carb., Belg.; prosoma with large 1st abdominal tergite,  $\times 0.5$  (58).

shaped, with slightly concave anterior margin; genital appendages of male short, with 2 distal spines. *L.Dev.*

**Rhenopterus** STØRMER, 1936 [\**R. diensii*]. *L.Dev.*, Eu.-?N.Am.—FIG. 27,5. *R. diensii*, Ger.; 5a,b, dorsal and ventral side of prosoma and preabdomen of ?male,  $\times 0.75$  (64).

#### Family MYCTEROPIDAE Størmer, 1951

[*nom. correct.* STØRMER, herein (pro Mycteropteridae STØRMER, 1951)]

Medium to fairly large forms; outer surface with numerous scales and reticulate ornamentation; prosoma subtrapezoid, 1st and ?2nd tergite of abdomen strongly developed; prosomal legs of stylonurid type. *U.Carb.*

**Mycterops** COPE, 1886 [\**M. ornatus*] [= *Glaucodes* PRUVOST, 1923]. *Carb.*, N.Am.-Eu.—FIG. 29,1. *M.?* *scabrosus* (H.WOODWARD), L.Carb., Scot.;  $\times 0.5$  (67).—FIG. 30. *M. mathiewi* (PRUVOST), Belg.; prosoma with large 1st tergite of abdomen, about  $\times 0.5$  (30\*).

#### Class UNCERTAIN

**Glyptoscorpis** PEACH, 1882 [\**G. perornatus*]. Very large arachnids or merostomes possibly belonging with eurypterids, exoskeleton provided with tongue- or V-shaped scales; distal part of legs with 2 claws, scorpion-like; comb organs with 2 rows of numerous flattened filaments. *L.Carb.*, Scot.

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## Incertae Sedis

*Belinuropsis* MATTHEW, 1909 [*B. wigodensis*].  
Little-known form. *U.Sil.*, Can.—FIG. 11.8. \**B. wigodensis*, ×1 (after MATTHEW).