CYCLOIDEA

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MORPHOLOGY

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

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

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

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

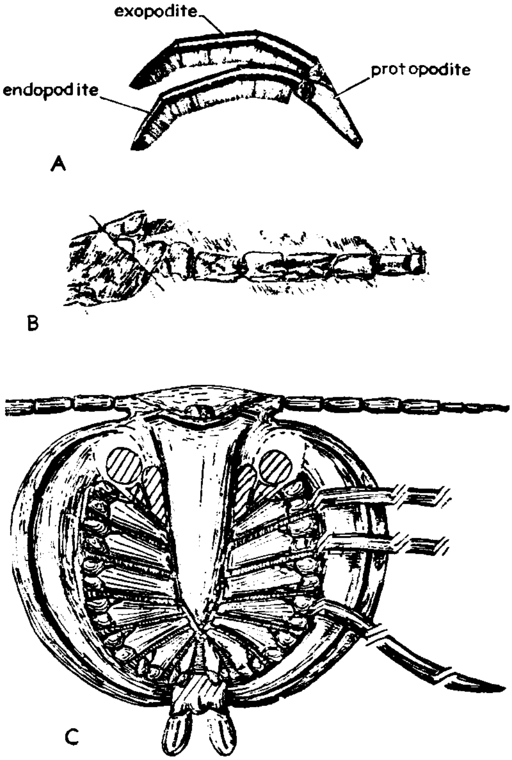

Fig. 363A. Morphology of Cycloidea.——*A*. Enlarged restoration of limb of Cycloidea, ×2.5(4).——*B*. *Cyclus (?) johnsoni* Woodward, base of antenna, ×2.5(4).——*C*. Reconstruction of the ventral side of Cycloidea, ×2 (referred to *Halicyne* by Hopwood) (4).

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

AFFINITIES

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

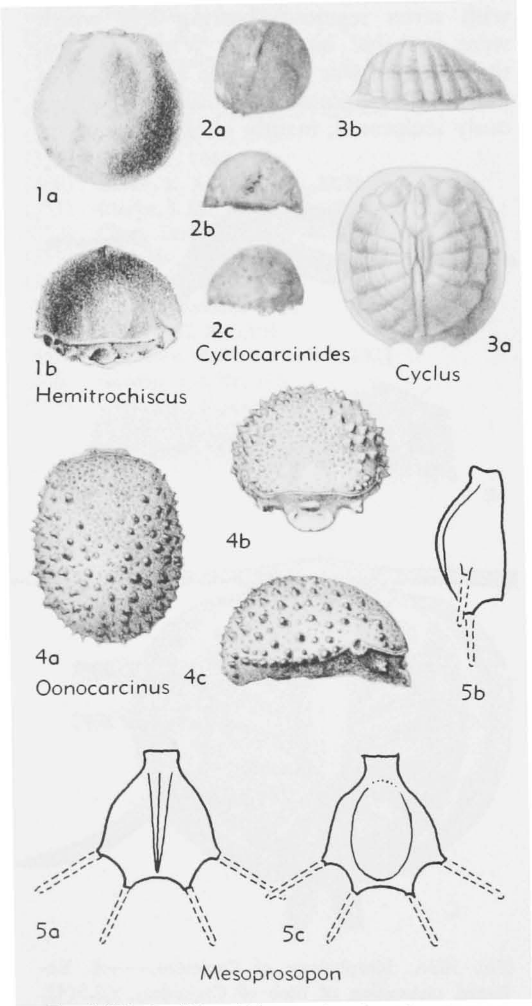

FIG. 363B. Cyclidae *(3)*; Hemitrochiscidae *(1-2,4)*; Mesoprosopidae *(5)* (p. *R*568-*R*569).

STRATIGRAPHIC AND GEOGRAPHIC DISTRIBUTION

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

SYSTEMATIC DESCRIPTIONS

Class and Order UNCERTAIN

Superfamily CYCLOIDEA Glaessner, 1928

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

Family CYCLIDAE Packard, 1885

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

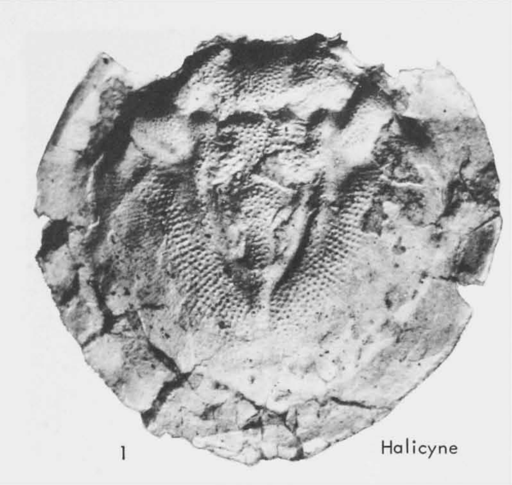

FIG. 363C. Cyclidae (p. *R*569).

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

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

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

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

Family HEMITROCHISCIDAE Trauth, 1918

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

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

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

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

Family MESOPROSOPIDAE Glaessner, 1928

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

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

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

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See Addendum to Cycloidea (p. R629).

BOSTRICHOPODIDA

By Gerhard Hahn

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

Class and Order UNCERTAIN

Order BOSTRICHOPODIDA Hahn, 1967

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

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

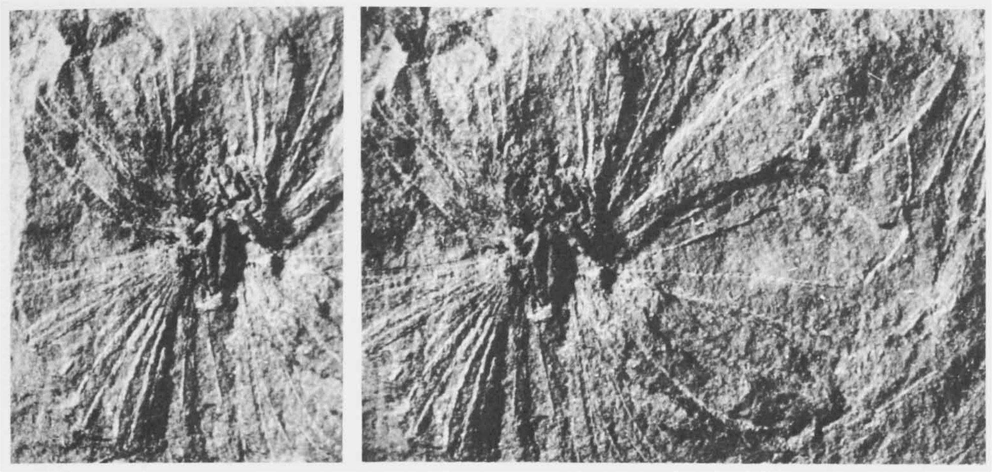

FIG. 363D. Bostrichopodidae (p. *R*571).

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

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

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

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

Family BOSTRICHOPODIDAE Hahn, 1967

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

Characters of order. *L.Carb.*

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

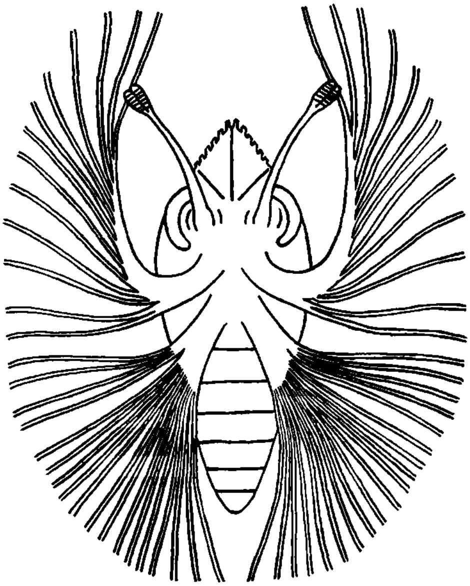

FIG. 363E. Bostrichopodidae (p. R572).

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

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MYRIAPODA, EXCLUSIVE OF INSECTA

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[Chapter submitted July, 1965]

CONTENTS

INTRODUCTION

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

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

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

Major Divisions of Myriapoda according to Pocock, 1893

Progoneata
    Class Pauropoda
    Class Diplopoda
    Class Symphyla

OPISTHOGONEATA
  Class Chilopoda
  Class Insecta

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

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

Major Divisions of Myriapoda according to Tiegs, 1947

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

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

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

Major Divisions of Myriapoda according to Fechter, 1963

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

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

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

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

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

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

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

GENERAL CHARACTERS OF MYRIAPODA

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

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

Major Divisions of Arthropoda

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

- Class Symphyla
- Class Chilopoda
- Class Insecta (or Hexapoda)

Subphylum Chelicerata (accorded this rank in *Treatise* Part P)

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

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

CLASSIFICATION

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

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

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

Major Divisions of Myriapoda

- Myriapoda *(superclass). U.Sil.-Rec.*
  - Archipolypoda *(class). U.Sil.-Penn.*
    - Euphoberiida *(order). U.Sil.-Penn.*
  - Diplopoda *(class). Penn.-Rec.*
    - Penicillata *(subclass). Oligo.-Rec.*
      - Polyxenida *(order). Oligo.-Rec.*
    - Pentazonia *(subclass). Penn.-Rec.*
      - Glomeridesmida *(order). Rec.*
      - Glomerida *(order). Oligo.-Rec.*
      - Amynilyspedida *(order). Penn.*
    - Helminthomorpha *(subclass). U.Penn.-Rec.*
      - Spirobolida *(order). U.Penn.-Rec.*
      - Stemmiulida *(order). Rec.*
      - Polyzoniida *(order). Oligo.-Rec.*
      - Siphonophorida *(order). Rec.*
      - Julida *(order). ?Eoc., Oligo.-Rec.*
      - Spirostreptida *(order). ?Penn., Rec.*
      - Callipodida *(order). Oligo.-Rec.*
      - Platydesmida *(order). Rec.*
      - Chordeumida *(order). Oligo.-Rec.*
      - Polydesmida *(order). Oligo.-Rec.*
  - Pauropoda *(class). Rec.*
    - Pauropodida *(order). Rec.*
  - Symphyla *(class). Oligo.-Rec.*
    - Scolopendrellida *(order). Oligo.-Rec.*
  - Chilopoda *(class). Cret.-Rec.*
    - Anamorpha *(subclass). Oligo.-Rec.*
      - Scutigerida *(order). Oligo.-Rec.*
      - Lithobiida *(order). Oligo.-Rec.*
    - Epimorpha *(subclass). Cret.-Rec.*
      - Geophilida *(order). Cret.-Rec.*
      - Scolopendrida *(order). Oligo.-Rec.*
  - Insecta *(class).*

SYSTEMATIC DESCRIPTIONS

Superclass MYRIAPODA Latreille, 1796

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

Class ARCHIPOLYPODA Scudder, 1882

[=Macrosterni Fritsch, 1899; Palaeocoxopleura Verhoeff, 1928]

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

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

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

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

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

Order EUPHOBERIIDA Hoffman, new order

[*nom. correct.* Hoffman, herein (*pro* Euphoberidae Scudder, 1882)]

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

Family EUPHOBERIIDAE Scudder, 1882

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

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

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

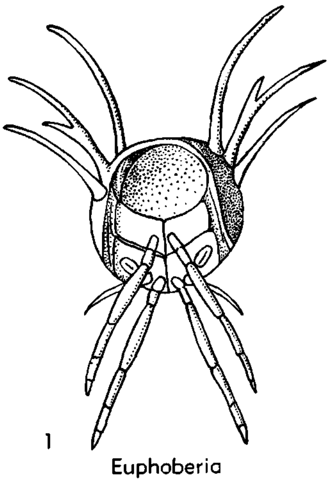


Fig. 364. Euphoberiidae (p. *R*577).

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

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

Family UNCERTAIN

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

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

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

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

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

Class DIPLOPODA Gervais, 1844

[=Chilognatha Latreille, 1802]

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

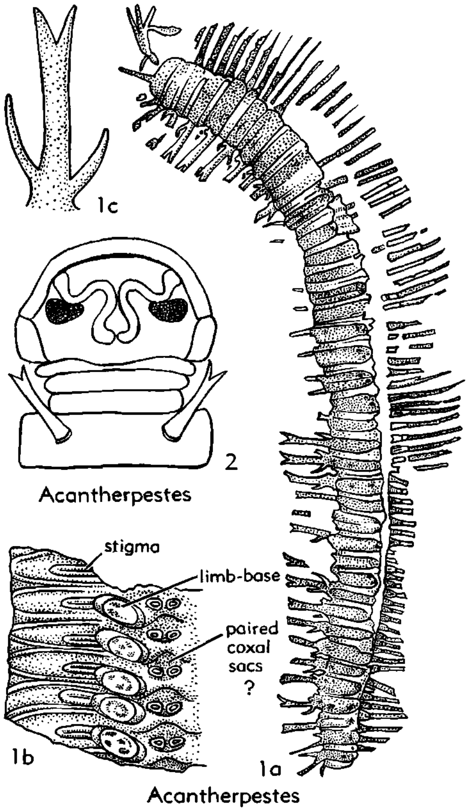


Fig. 365. Euphoberiidae (p. *R*577-*R*578).

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

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

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

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

EXTERNAL CHARACTERS

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

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

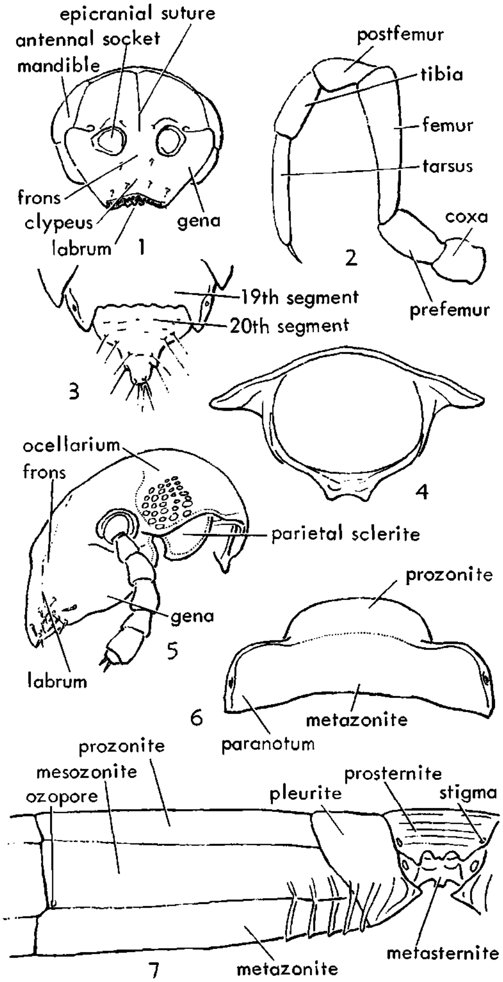


FIG. 366. External structural features used in classification of Diplopoda (Hoffman, n).——*1*. Head of generalized polydesmoid, anterior aspect, ×7.——*2*. Ambulatory leg of generalized polydesmoid, ×7.——*3*. Ultimate and penultimate segments of polydesmoid, dorsal aspect, showing modification of 20th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

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

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

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

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

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

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

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

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

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

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

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

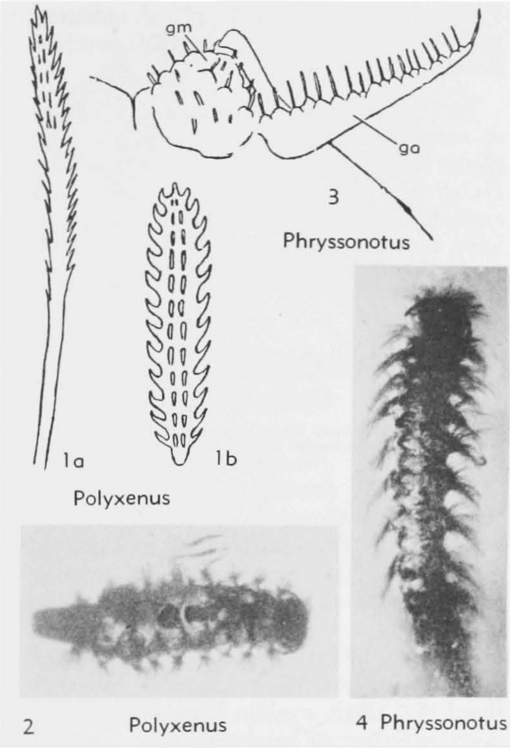


FIG. 367. Synxenidae *(3,4)*; Polyxenidae *(1,2)* (p. *R*583-*R*584).

Subclass PENICILLATA Latreille, 1827

[=Pselaphognatha LATZEL, 1884]

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

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

Order POLYXENIDA Chamberlin & Hoffman, 1958

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

Characters of subclass. *Oligo.-Rec.*

Family SYNXENIDAE Silvestri, 1923

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

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

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

Family POLYXENIDAE Gray, 1842

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

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

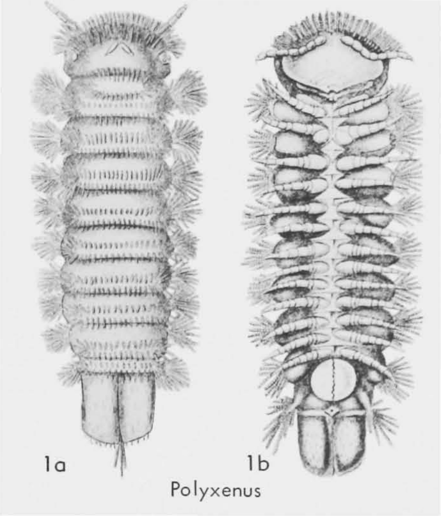


FIG. 368. Polyxenidae (p. *R*583-*R*584).

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

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

Subclass PENTAZONIA Brandt, 1833

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

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

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

Order GLOMERIDESMIDA Cook, 1895

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

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

Order GLOMERIDA Cook, 1895

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

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

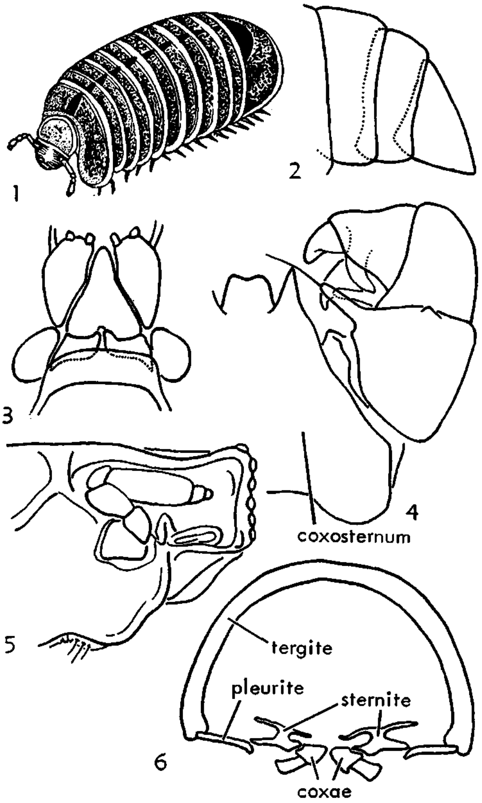


FIG. 369. External structural features used in classification of pentazoniate Diplopoda.——*1. Glomeris conspersa* (KOCH), lateral aspect of entire animal, ×3 (Koch).——*2.* Posterior segments of glomeroid, lateral aspect, ×10.——*3.* Generalized glomeroid gnathochilarium, ×18.——*4.* Pair of legs (18th)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

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

Family GLOMERIDIDAE Leach, 1815

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

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

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

Order AMYNILYSPEDIDA
Hoffman, new order

[=Palaeomorpha VERHOEFF, 1928]

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

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

Family AMYNILYSPEDIDAE Hoffman, new name

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

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

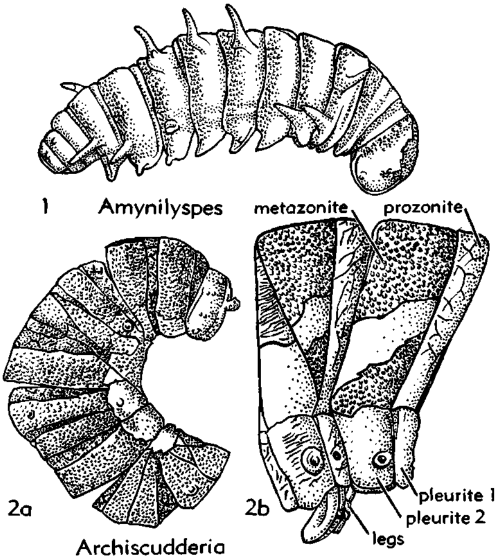


FIG. 370. Amynilyspedidae (p. *R*586).

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

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

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

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

Subclass HELMINTHOMORPHA Pocock, 1887

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

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

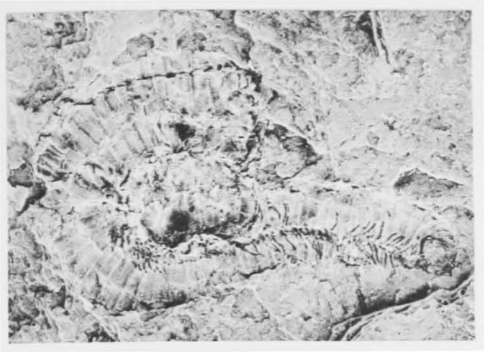


FIG. 371. Xyloiulidae (p. *R*587).

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

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

Order SPIROBOLIDA Cook, 1895

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

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

Family SPIROBOLIDAE Bollman, 1893

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

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

Family XYLOIULIDAE Cook, 1895

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

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

Family NYRANIIDAE Hoffman, new family

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

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

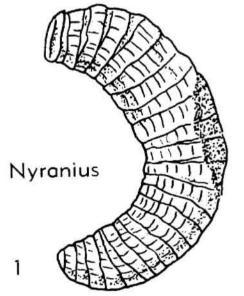


FIG. 372. Nyraniidae (p. *R*587-*R*588).

Family PLAGIASCETIDAE Hoffman, new family

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

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

Family ANTHRACOJULIDAE Hoffman, new family

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

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

Order STEMMIULIDA Cook, 1895

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

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

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

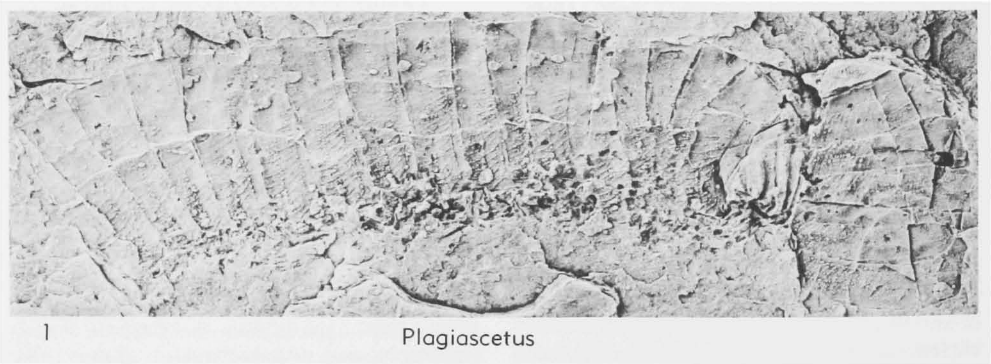
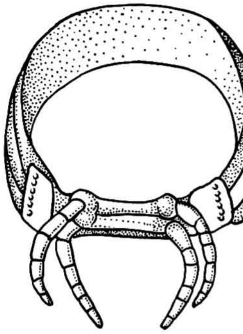


FIG. 373. Plagiascetidae (p. *R*588).



1 Anthracojulus

FIG. 374. Anthracojulidae (p. *R*588).

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

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

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

Order POLYZONIIDA Cook, 1895

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

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

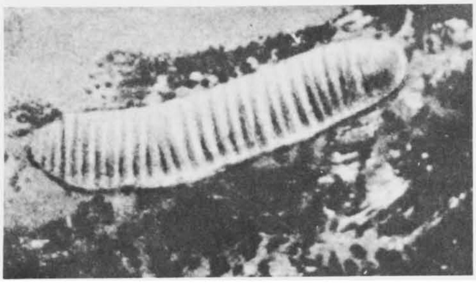
A basically Holarctic group most abundant today in western North America and east Asia; one family (Siphonotidae), however, is confined to the southern Hemisphere. One genus is known from the Baltic amber; this genus and probably the same species is still found in the same part of northern Europe.

Family POLYZONIIDAE Gervais, 1844

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

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

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



1 Polyzonium

FIG. 375. Polyzoniidae (p. *R*589).

Order SIPHONOPHORIDA Cook, 1895

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

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

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

Order JULIDA Brandt, 1833

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

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

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

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

Family JULIDAE Meinert, 1868

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

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

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

Family NEMASOMATIDAE Bollman, 1893

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

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

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

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

Family PARAJULIDAE Bollman, 1893

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

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

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

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

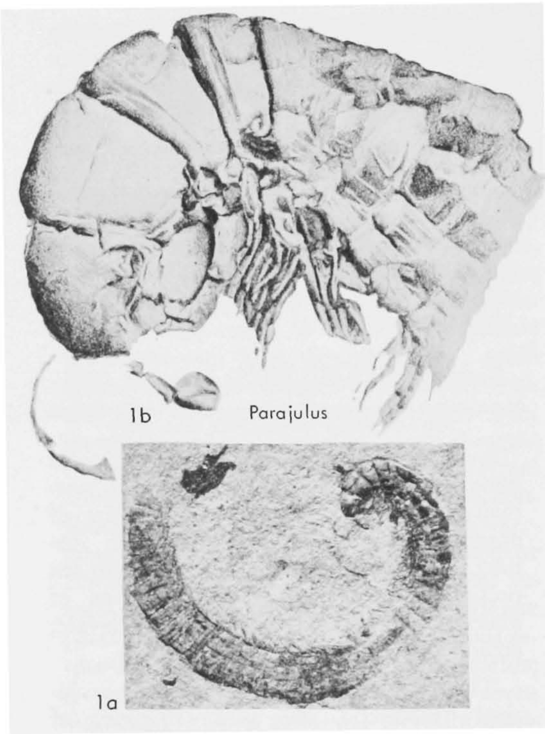


FIG. 376. Parajulidae (p. *R*591-*R*592).

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

Order SPIROSTREPTIDA
Cook, 1895

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

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

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

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

Order CALLIPODIDA
Bollman, 1893

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

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

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

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

?Family DORYPETALIDAE Verhoeff, 1900

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

Order PLATYDESMIDA Cook, 1895

[*nom. transl.* Chamberlin & Hoffman, 1958 (*ex* suborder Platydesmoidea Cook, 1895]

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

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

Order CHORDEUMIDA Cook, 1895

[*nom. transl. et correct.* Chamberlin, 1943 (*ex* suborder Chordeumoidea Cook, 1895)] [=Coelochaeta Cook, 1895; Ascospermophora Verhoeff, 1913]

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

?Family CRASPEDOSOMATIDAE Cook, 1895

[=Craspedosomidae Verhoeff, 1899]

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

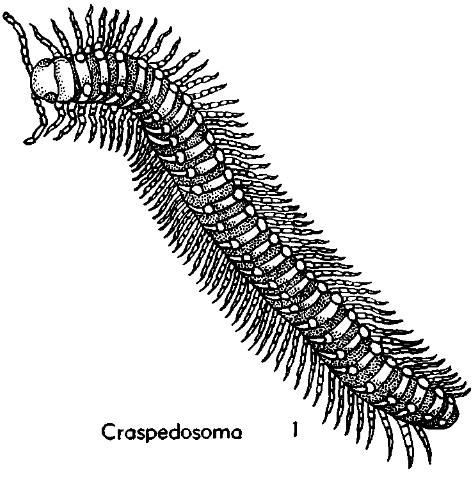


FIG. 377. Craspedosomatidae (p. R594).

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

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

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

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

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

Order POLYDESMIDA
Pocock, 1887

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

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

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

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

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

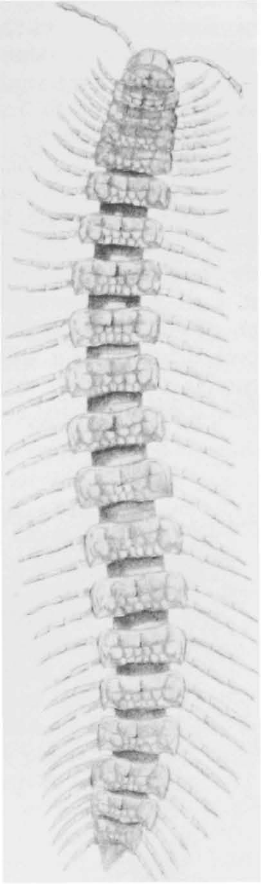


FIG. 378. Polydesmidae (p. *R*595).

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

Family POLYDESMIDAE Leach, 1815

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

Polydesmus LATREILLE, 1802 [**Julus complanatus* LINNÉ; OD, M]. Distinguishable from other genera of this family only by details of gonopod structure. Both sexes with 20 body segments. *Oligo.-Rec.*, Eu.——FIG. 378,*1*. *P. laurae* POCOCK, *Rec.*; entire animal, dorsal aspect, ×4.5 (after Attems).

Order and Family UNCERTAIN

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

Archicambala COOK, 1895, p. 6 [**Xylobius dawsoni* SCUDDER; OD]. Genus proposed by COOK without diagnosis and placed by him with *Archiulus* SCUDDER in family *Archiulidae*. This family-group in turn was aligned with several other families that make up the present suborder Cambalidea of the order Spirostreptida. Whether this placement is anywhere near being correct cannot even be guessed at present. *Oligo.*, N.Am.

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

Isojulus FRITSCH, 1899, p. 25 [**Julus constans* FRITSCH, 1879 (=*Archijulus constans* FRITSCH, 1894); SD HOFFMAN, herein]. *U.Carb.*, Eu. (Czech.).

Pleurojulus FRITSCH, 1899, p. 27 [**P. biornatus* FRITSCH; SD HOFFMAN, herein] [=*Pleuroiulus* VERHOEFF, 1928]. Juliform group with rounded ocellaria and antennae similar to those of Recent spirobolids. So-called "pleurites" are clearly nothing more than fractured lower ends of pleurotergites broken when animal was flattened, not an uncommon occurrence.] *U.Carb.*, Eu.——FIG. 379,*1*. *P. levis* FRITSCH, Czech.; entire animal, ×1.4 (from Müller).

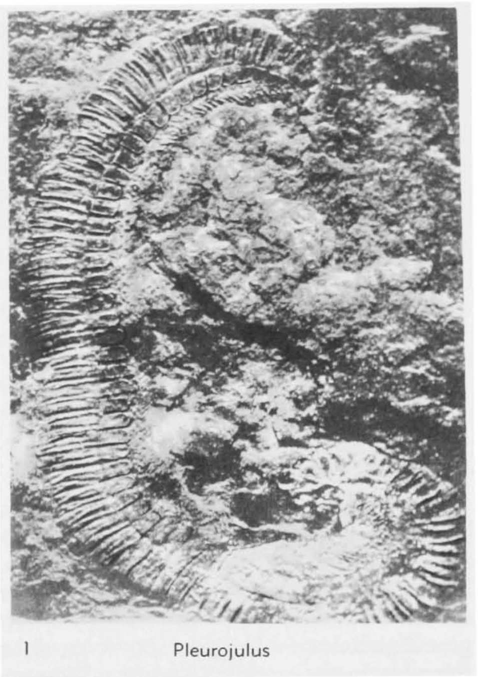


FIG. 379. Order and Family Uncertain (p. R595).

Class PAUROPODA Lubbock, 1866

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

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

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

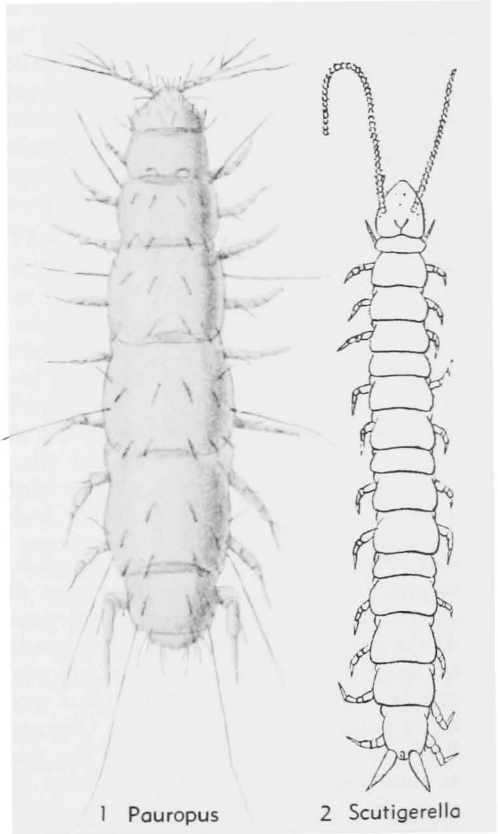


FIG. 380. Representatives of Pauropoda and Symphyla (Attems).——*1.* Pauropoda, Pauropodida, Pauropodidae, *Pauropus huxleyi* LUBBOCK, dorsal view of specimen, ×50.——*2.* Symphyla, Scolopendrellida, Scutigerellidae, *Scutigerella immaculata* (NEWPORT), dorsal view of specimen, ×15.

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

Order PAUROPODIDA
Lubbock, 1866

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

Characters of class. *Rec.*

Class SYMPHYLA Ryder, 1880

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

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

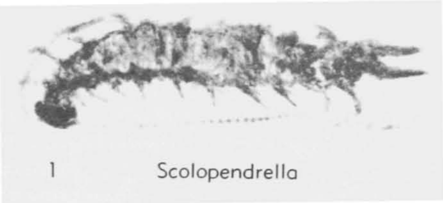


FIG. 381. Scolopendrellidae (p. *R*597-*R*598).

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

Order SCOLOPENDRELLIDA
Hoffman, new order

Characters of class. *Oligo.-Rec.*

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

Family SCOLOPENDRELLIDAE
Newport, 1845

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

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

Class CHILOPODA Latreille, 1817

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

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

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

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

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

CLASSIFICATION

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

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

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

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

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

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

EXTERNAL CHARACTERS

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

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

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

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

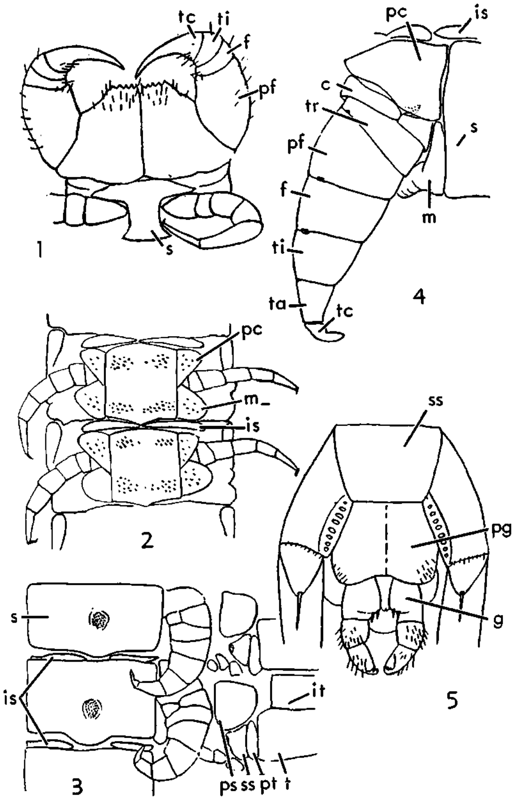


FIG. 382. External structural features used in classification of Chilopoda (Attems).——*1. Lithobius forficatus* (LINNÉ), prehensors and legs of 2nd body segment, ventral aspect, ×10.——*2. Pachymerium kervillei* ATTEMS, mid-body segments, ventral aspect, ×12.——*3. Himantarium gabrielis* (LINNÉ), mid-body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

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

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

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

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

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

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

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

Spur Distribution on Legs of Chilopoda

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

Subclass ANAMORPHA Haase, 1880

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

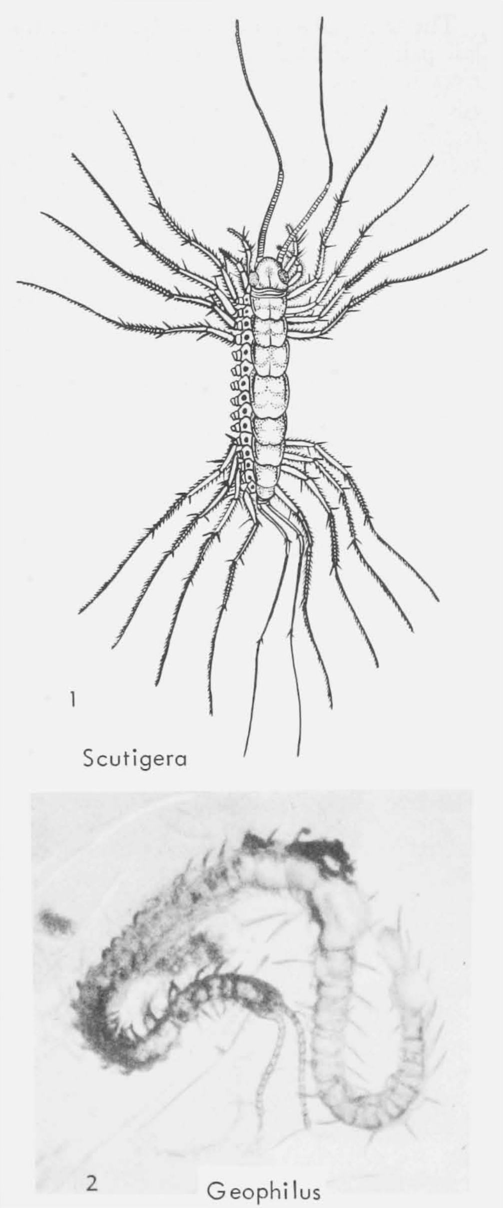


FIG. 383. Scutigeridae *(1)*; Geophilidae *(2)* (p. *R*602-*R*603).

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

Order SCUTIGERIDA Pocock, 1895

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

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

Family SCUTIGERIDAE Newport, 1844

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

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

Order LITHOBIIDA Pocock, 1895

[*nom. correct.* CHAMBERLIN, 1941 (*pro* Lithobiomorpha POCOCK, 1895)] [=Artiostigmata SILVESTRI, 1895; Unguipalpi BOLLMAN, 1893]

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

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

Family LITHOBIIDAE Leach, 1814

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

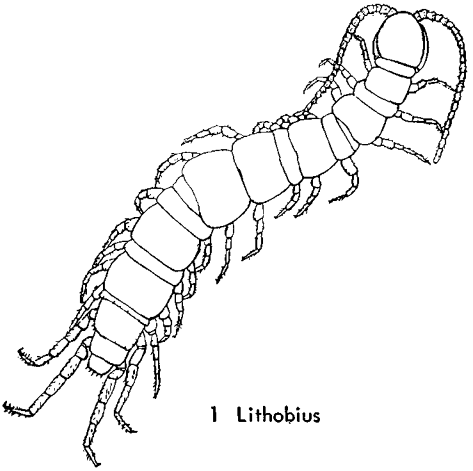


FIG. 384. Lithobiidae (p. *R*603).

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

Subclass EPIMORPHA Haase, 1880

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

Order GEOPHILIDA Pocock, 1895

[*nom. correct.* CHAMBERLIN, 1941 (*pro* Geophilomorpha POCOCK, 1895)] [=Pantastigmata SILVESTRI, 1895]

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

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

Family GEOPHILIDAE Newport, 1844

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

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

Family UNCERTAIN

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

Order SCOLOPENDRIDA Pocock, 1895

[*nom. correct.* CHAMBERLIN, 1941 (*pro* Scolopendromorpha POCOCK, 1895)] [=Oligostigmata SILVESTRI, 1895]

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

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

Family SCOLOPENDRIDAE Newport, 1844

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

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

Class, Order, and Family UNCERTAIN

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

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

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

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

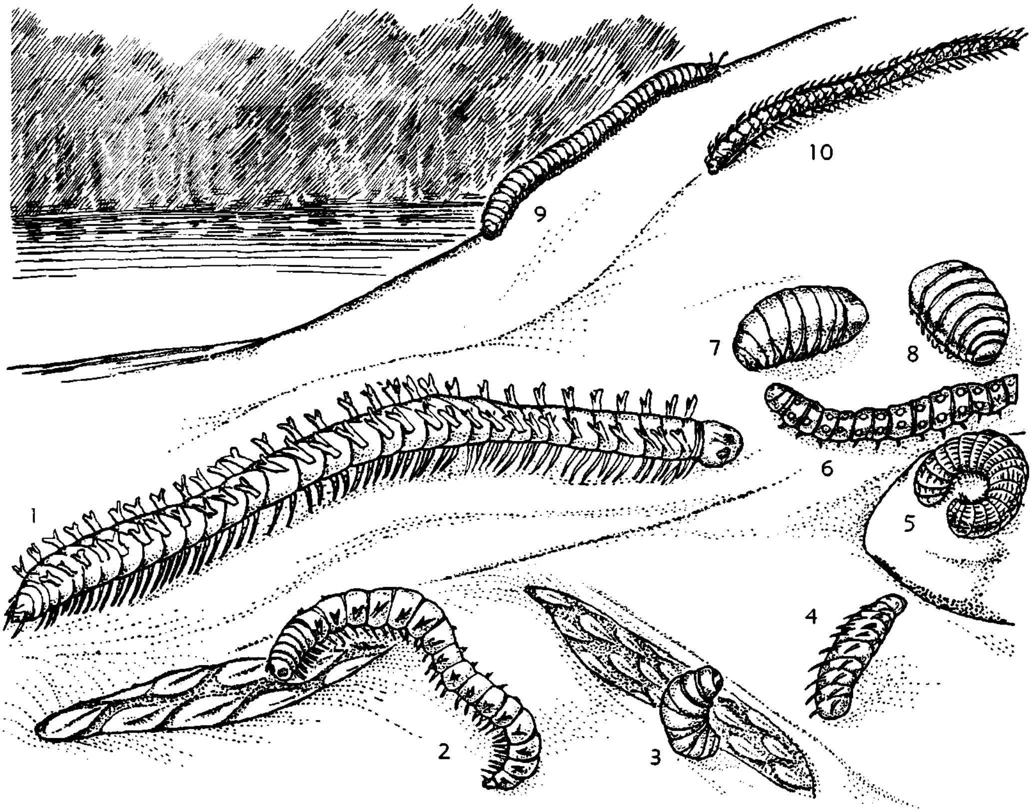


FIG. 385. Upper Carboniferous myriapod fauna from Bohemia (reconstr.), animals, ×0.7; (1) *Acantherpestes gigas;* (2) *Acantherpestes ornatus;* (3) *Archiscudderia paupera;* (4) *Amynilyspes typicus;* (5) *Xyloiulus pstrossi;* (6) *Sandtneria gemmata;* (7) *Glomeropsis ovalis;* (8) *Archiscudderia problematica;*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

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

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

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

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

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

GENERIC NAMES INCORRECTLY REFERRED TO MYRIAPODA

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

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

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

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

INVALIDLY PROPOSED FAMILY-GROUP NAMES FOR MYRIAPODS

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

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

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

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

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

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

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

RESTORATION OF CARBONIFEROUS MYRIAPODS

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

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ARTHROPLEURIDA

By W. D. Ian Rolfe

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

[Chapter submitted June, 1966]

CONTENTS

INTRODUCTION

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

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

MORPHOLOGY

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

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

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

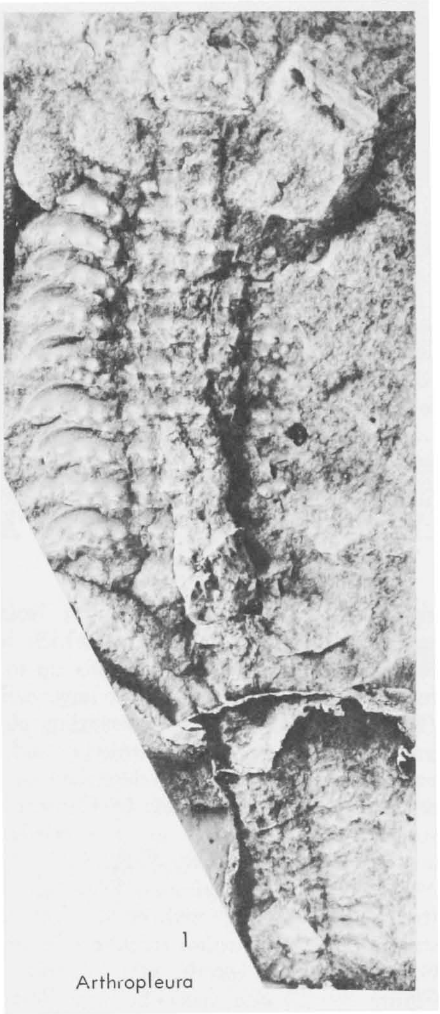

FIG. 386. Rubber cast from external mold of almost complete juvenile *Arthropleura armata* JORDAN & MEYER (holotype of *A. moyseyi* CALMAN), head slightly displaced, dorsal, U.Carb., Eng., ×2 (Rolfe, n).

HEAD

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

BODY

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

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

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

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

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

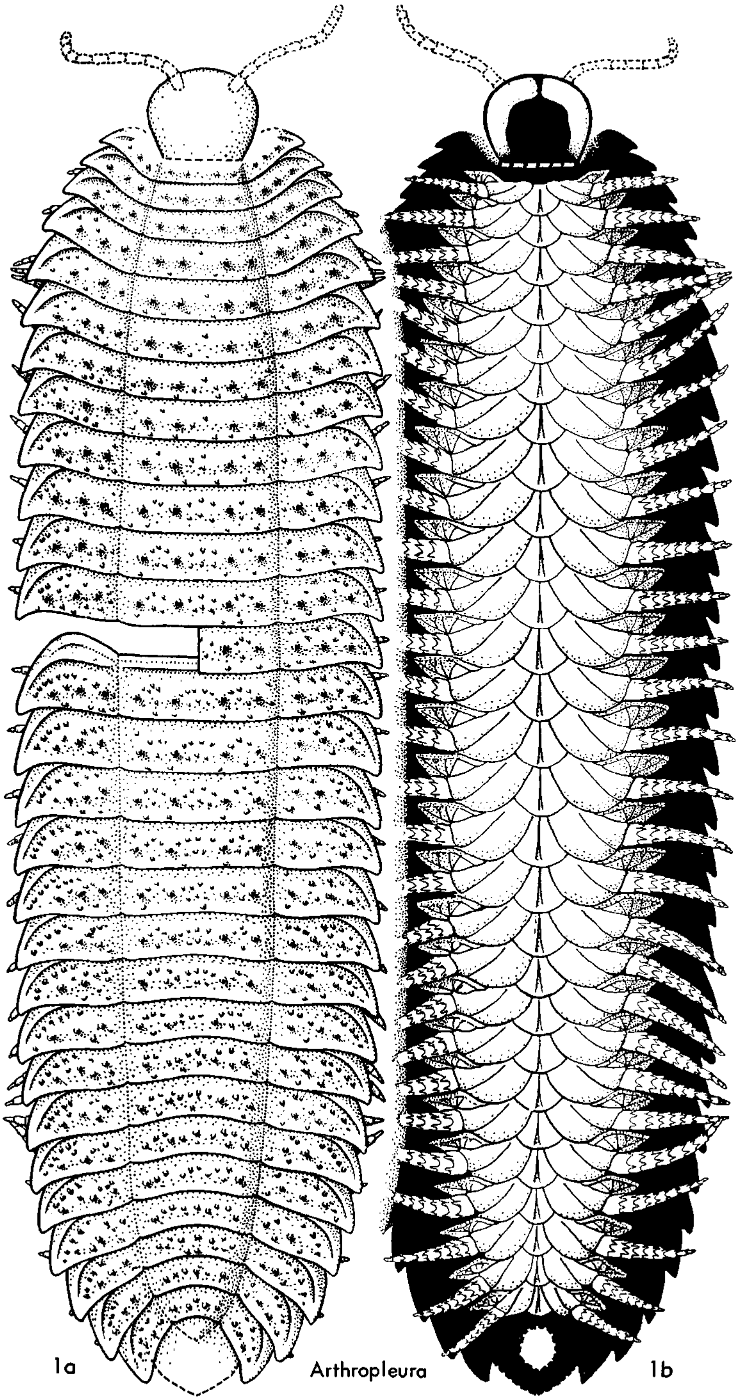

FIG. 387. Reconstruction of *Arthropleura armata* JORDAN & MEYER, dorsal, ventral. Half of one tergite removed to show anterior border of underlying tergite; no limbs shown on first trunk somite. Interrupted lines indicate restored regions of body, approx. ×0.1 *(16)*.

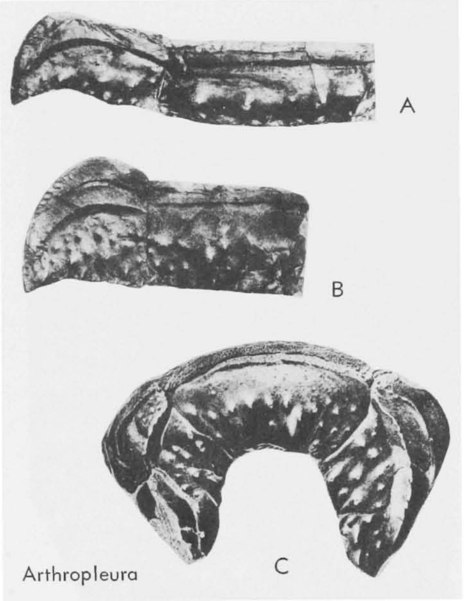

FIG. 388. Isolated tergites of *Arthropleura armata* JORDAN & MEYER, dorsal, Carb., Saar, ×0.5.——*A*. Axis and left paratergal fold from anterior body somite showing anteriorly directed paratergal fold and sparse tuberculation *(19)*.——*B*. Axis and left paratergal fold from middle body somite *(19)*.——*C*.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

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

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

LIMBS AND ASSOCIATED STRUCTURES

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

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

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

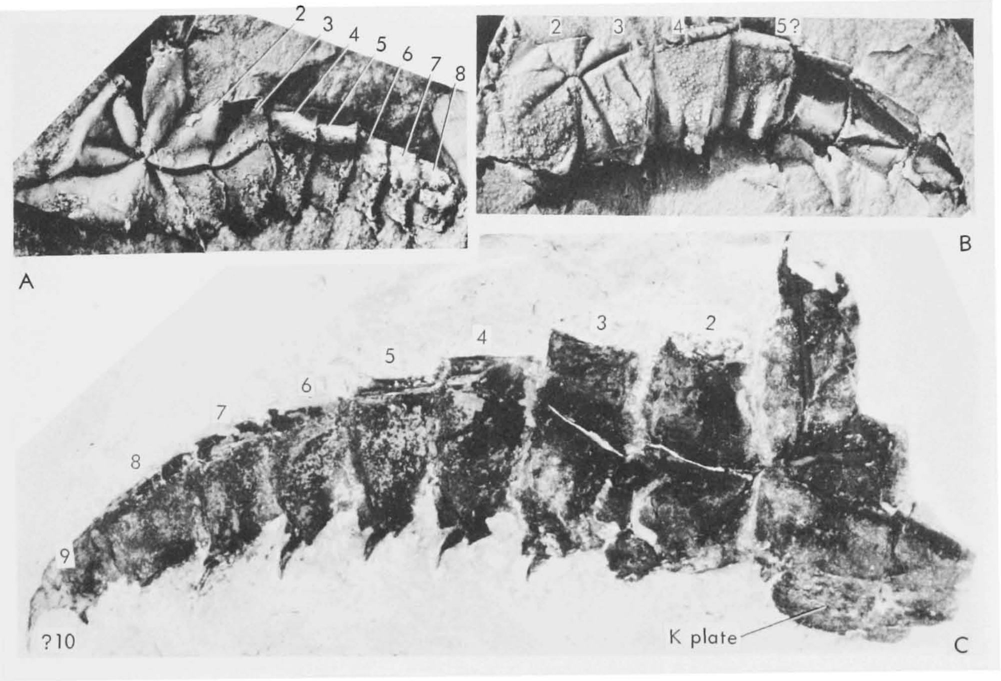

FIG. 389. Limbs of *Arthropleura.*——*A.* Rubber cast from external mold of anterior face of left leg of young individual showing *B* and rosette plates and segments *2-8,* Carb., Eng., ×2.3.——*B.* Right leg, showing internal mold of posterior face of segments *2-5?* and external mold of anterior and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

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

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

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

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

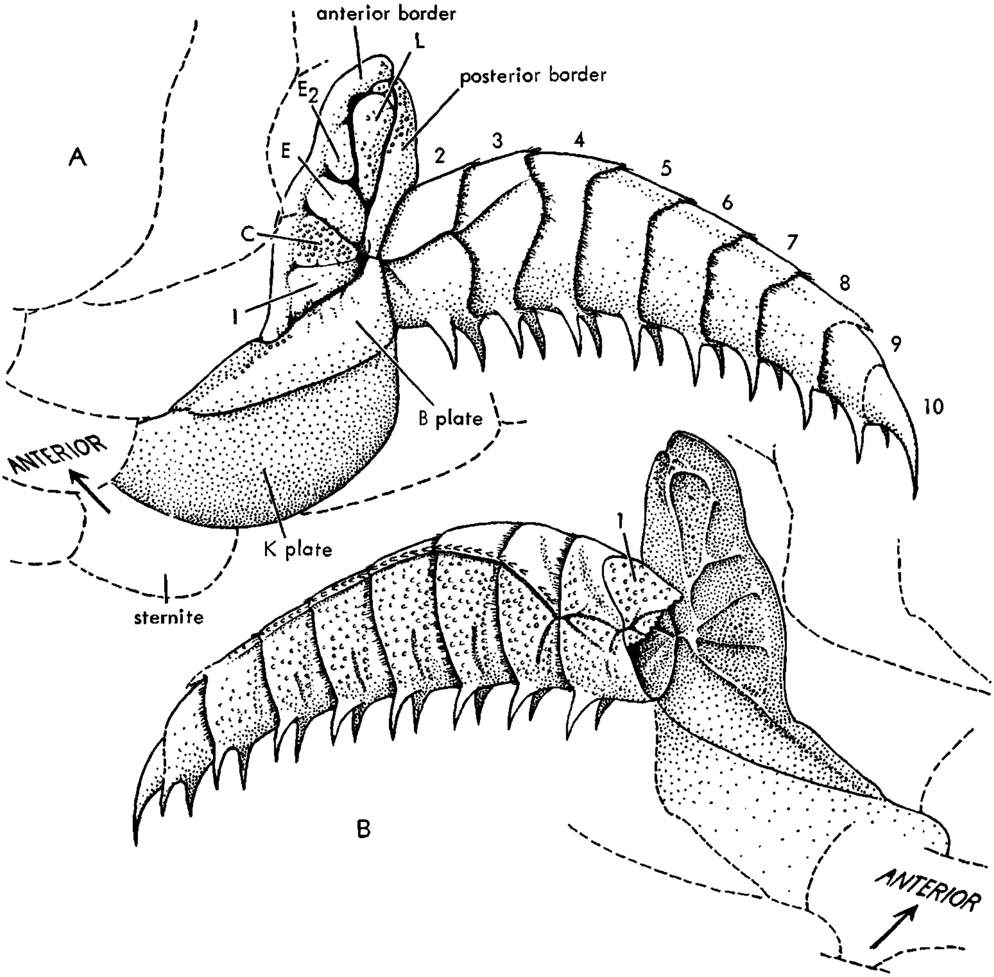

FIG. 390. Reconstruction of left leg of medium-sized adult *Arthropleura.* Both views are taken obliquely to emphasize the morphology and the limb is thus slightly foreshortened. Interrupted lines indicate most of sternite, *K, B,* and rosette plates of body somite immediately in front and posterior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

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

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

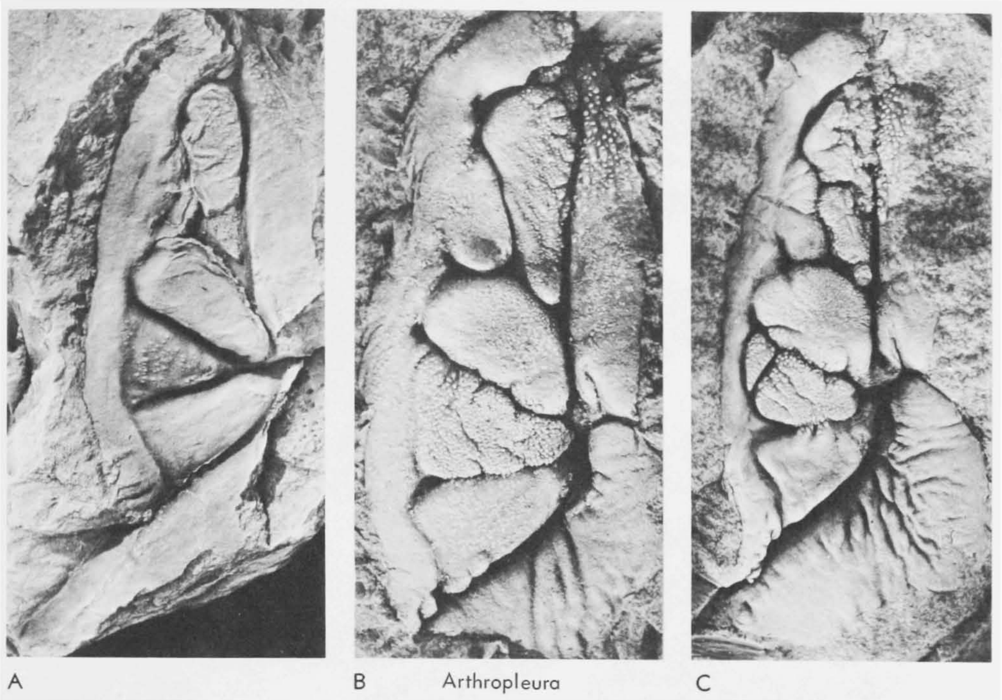

FIG. 391. Left rosette plates with portion of *B* plate attached of *Arthropleura* to show increase in tuberculation and number of adventitious lobes with size (i.e., age).——*A*. Westphal., Neth., ×1.8.——*B*. Penn., USA(Ill.), ×1.5.——*C*. Penn., USA(Ill.), ×1 (Rolfe, n).

brane between these plates and limb segment *2*.

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

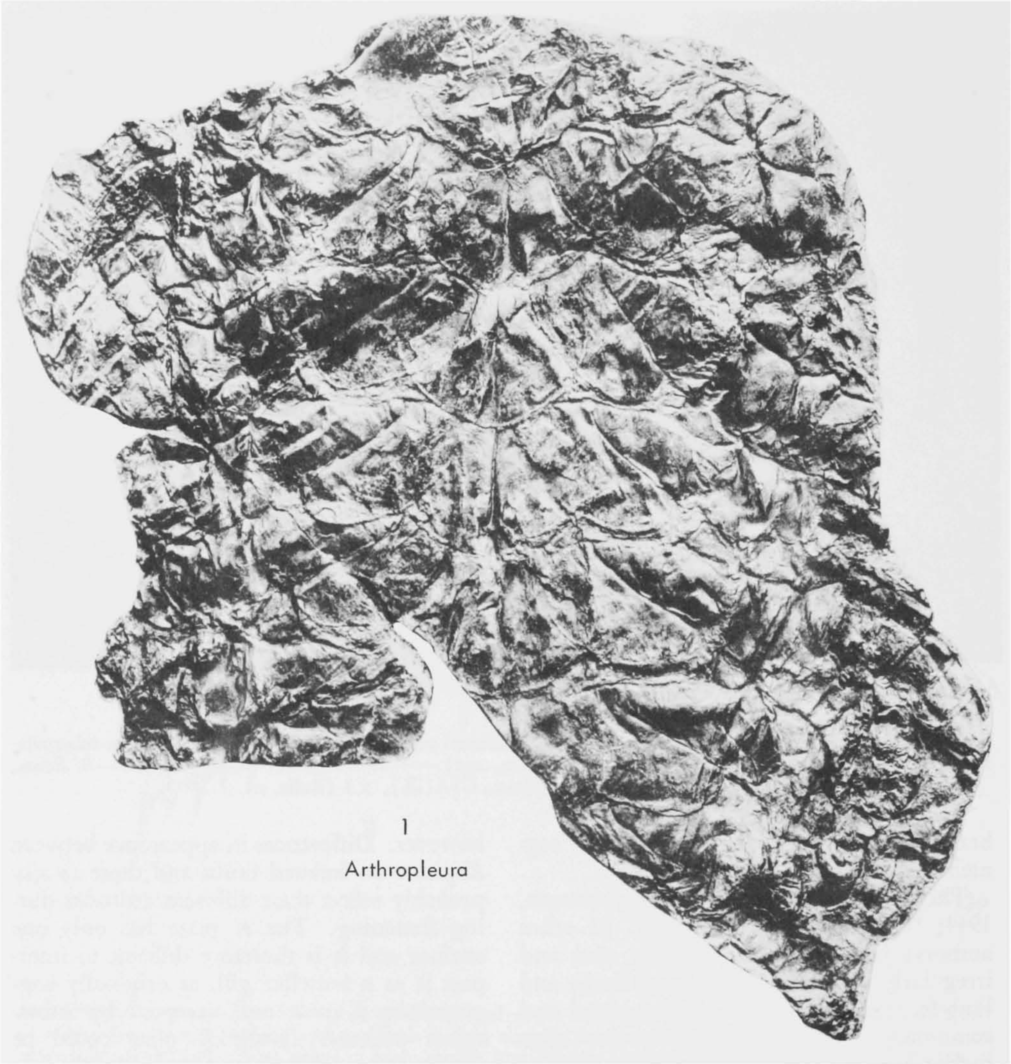

FIG. 392. Pedigerous ventral surface of small specimen of *Arthropleura armata* JORDAN & MEYER. This specimen, which is only half of an originally larger specimen, shows 7 pairs of limbs flattened *in situ* onto 6 sternites. Most of the rosette plates are concealed beneath limbs of the somite immediately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

could be everted to function as gills when in water.

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

PALEOECOLOGY

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

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

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

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

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

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

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

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

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

AFFINITIES AND CLASSIFICATION

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

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

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

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

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

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

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

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

SYSTEMATIC DESCRIPTIONS

Class ARTHROPLEURIDA Waterlot, 1934

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

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

Family ARTHROPLEURIDAE Zittel, 1885

Characters of class. *U.Carb.*

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

TAXA DOUBTFULLY CLASSIFIABLE AS ARTHROPLEURIDA

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

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

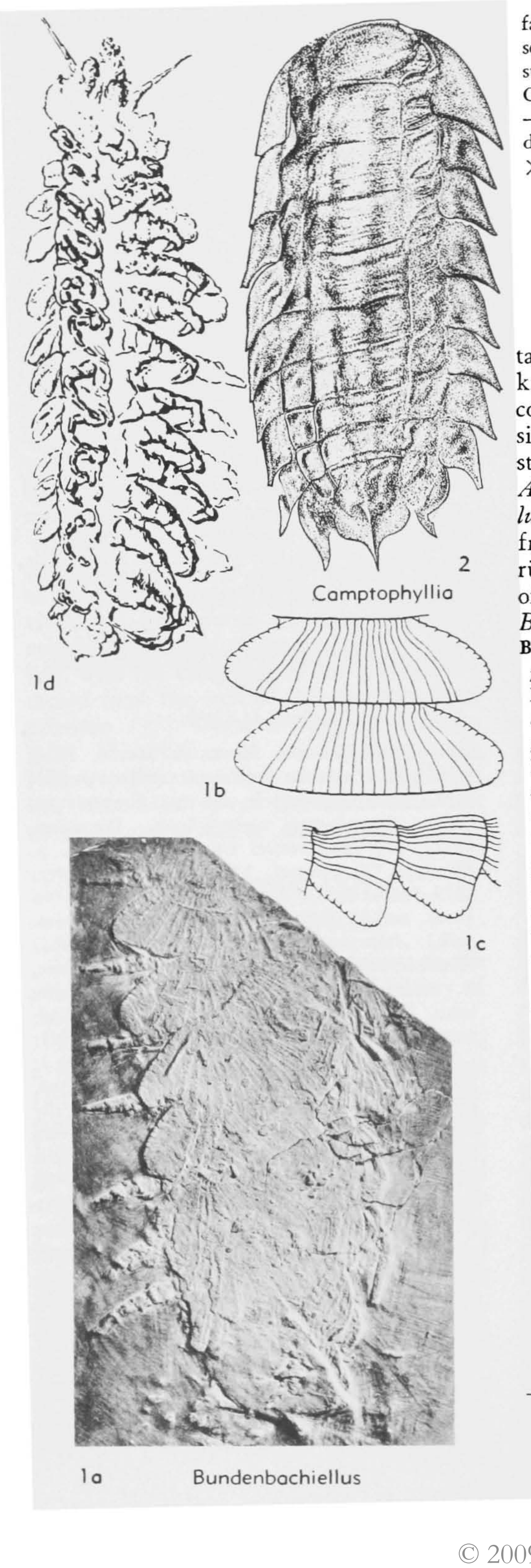

FIG. 393. Doubtful taxa, Arthropleurida (p. *R*618-*R*619).

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

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ARTHROPODA INCERTAE SEDIS

By W. D. Ian Rolfe

[Hunterian Museum, University of Glasgow]

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

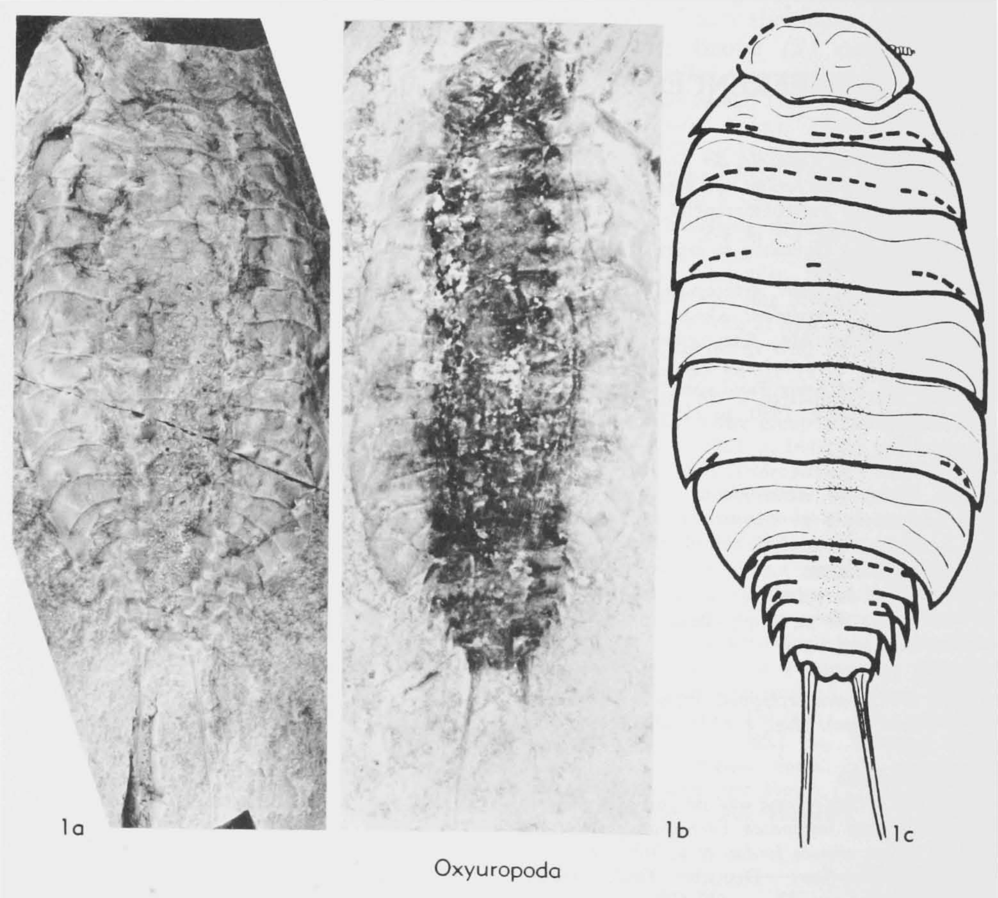


FIG. 394. Doubtful taxa formerly attributed to Arthropleurida (p. *R*621).

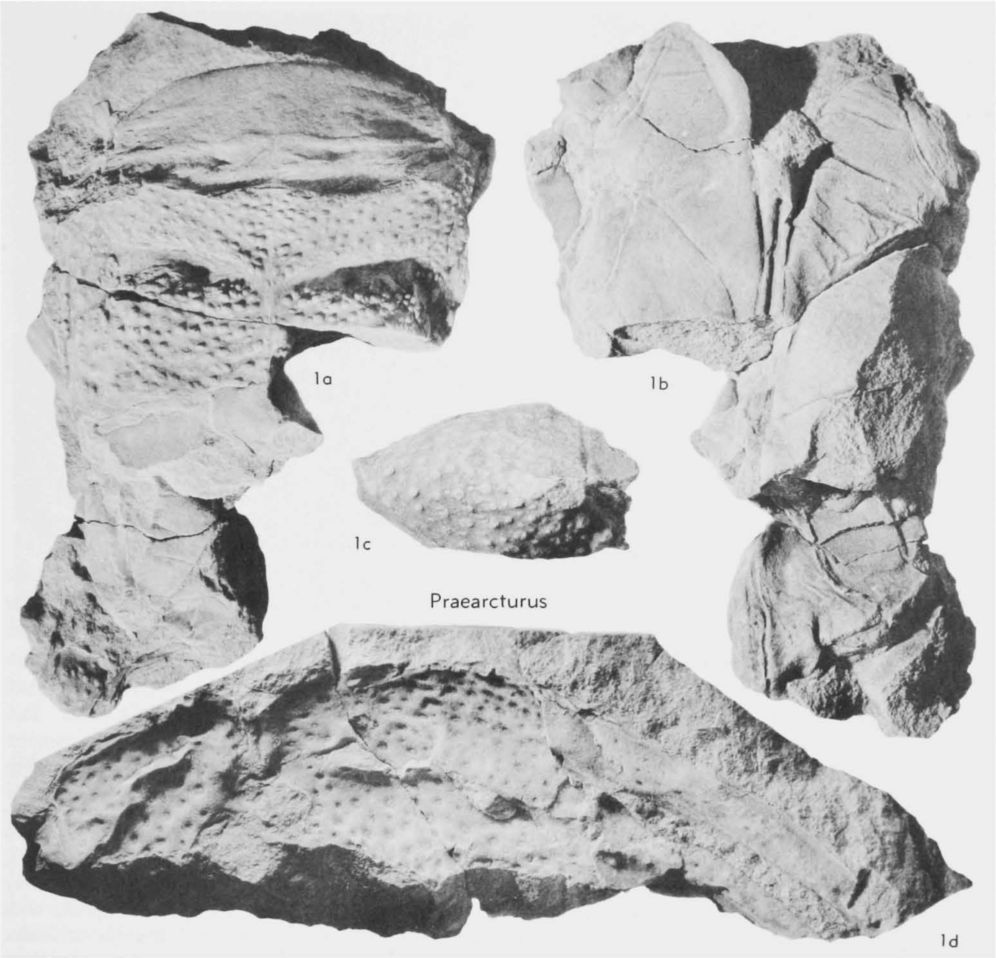


FIG. 395. Doubtful taxa formerly attributed to Arthropleurida (p. *R*622).

DOUBTFUL TAXA FORMERLY ATTRIBUTED TO ARTHROPLEURIDA

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

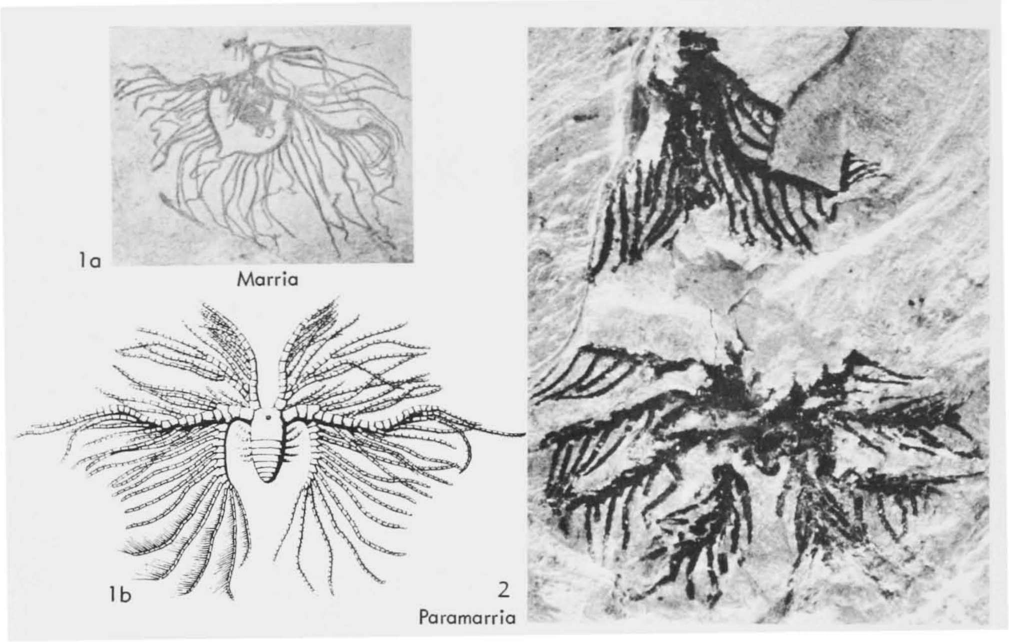


FIG. 396. "Marriocarida" (p. *R622-R623*).

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

Praearcturus WOODWARD, 1871, p. 266 [**P. gigas;* M]. Tergite large; smooth anterior? semicircular articulating half ring; low median keel and pair of transverse lateral furrows, each furrow deepening to a pit under halfway from median keel to edge of tergite; covered with large rounded tubercles except in furrow. Limb bases deeply inserted on ventral surface, anteriorly? directed, separated by median, longitudinally grooved sternite. Each limb with subtriangular basal segment and up to 2 short segments preserved distally; dorsal surface tuberculate, ventral smooth. [Known only from specimen preserving one tergite with 2 pairs of ventral limb bases and from a number of isolated cheliform appendages. Supposed chelation of appendages may be due to fracture along deep invaginations of cuticle. Referred by WOODWARD to Isopoda and by ZITTEL (1885) to Arthropleuridae, although presence of 2 pairs of limbs per somite excludes it from either of these groups.] *L.Dev.(Gedinn.),* Eng.——FIG. 395,*1.* **P. gigas,* Ditton. (I_9), Hereford(Rowlstone); *1a,b,* lectotype, dorsal, ventral, ×0.54; *1c,d,* paralectotypes, fragments of supposed chelate appendages, ×0.54 *(10).*

"MARRIOCARIDA"

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

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

MIMETASTER

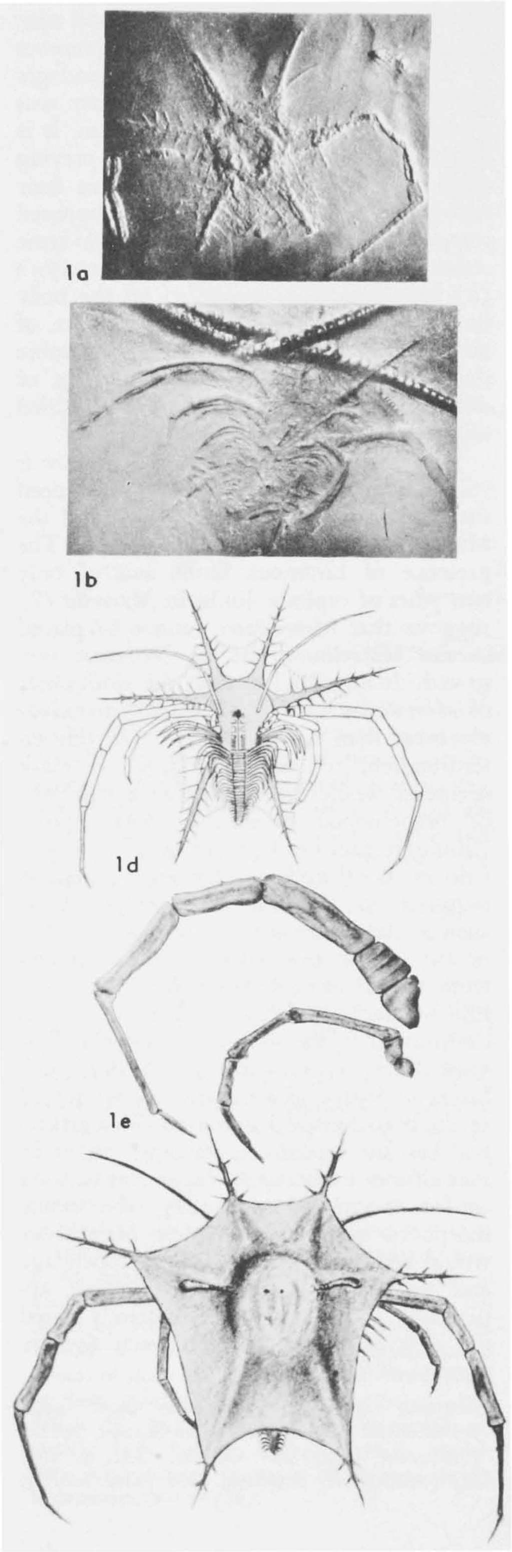
This remarkable arthropod was originally thought by Abel and Broili not to be a single animal but to comprise two symbionts. The six-rayed dorsal headshield has suggested a starfish body to all workers, and the name *Mimetaster* was given in the belief that this was an arthropod which mimetically resembled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

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

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

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

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



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

KABLIKIA

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

[The unique specimen occurs on a slab with the equally unique *Dalmaniopsis kablikae* GEINITZ (p. O525); both specimens were destroyed in Dresden during the war on 13/14 February 1945. The slab did not come from the Semily Formation, Stephanian, Upper Carboniferous of Dolní Stěpanice, near Vrchlabi, Czechoslovakia, as originally recorded and subsequently cited (Richter & Richter, 1955; *Treatise,* p. O525), but from the Dobrotivá Shales, Osek and Kvan Beds, Llandeilian, Ordovician, as corrected by GEINITZ in 1863. *D. kablikae* was shown by GEINITZ (1863) (*cf.* Richter & Richter, 1955) to be a synonym of *Placoparia zippei* (BOECK). In the absence of any specimens, it is impossible to be sure of the affinities of *Kablikia,* but it may be a poorly preserved dalmanitid trilobite, possibly even *Ormathops* which is known from these beds.]

FIG. 397,*1*. *Mimetaster hexagonalis* (GÜRICH), L.Dev. (Hunsrück Sh.), Ger.; *1a-c,* ×1; *1d,* ×0.7; *1e,* ×2 (*1a, 1b; 1b-e,2*) (p. *R623-R624*).

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ADDITIONAL SOURCES OF ILLUSTRATIONS

(10) **British Museum (Natural History)**

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

ADDENDUM TO DECAPODA

By M. F. Glaessner

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

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

Infraorder CARIDEA Dana, 1852

Family UNCERTAIN

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

Infraorder ASTACIDEA Latreille, 1802

Family ERYMIDAE Van Straelen, 1924

Subfamily ERYMINAE Van Straelen, 1924

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

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

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

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

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

Family PLATYCHELIDAE Glaessner

(see p. *R*458)

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

Infraorder PALINURA Latreille, 1802

Family GLYPHEIDAE Winckler, 1883

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

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

Family MECOCHIRIDAE Van Straelen, 1925

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

Infraorder BRACHYURA Latreille, 1802

Superfamily DROMIOIDEA de Haan, 1833

Family PROSOPIDAE von Meyer, 1860

Subfamily GONIODROMITINAE Beurlen, 1932

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

Subfamily PROSOPINAE von Meyer, 1860

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

Family DROMIIDAE de Haan, 1833

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

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

Family DYNOMENIDAE Ortmann, 1892

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

Superfamily DORIPPOIDEA de Haan, 1841

Family CYMONOMIDAE Ihle, 1916

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

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

Superfamily CALAPPOIDEA de Haan, 1833

Family CALAPPIDAE de Haan, 1833

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

Superfamily RANINOIDEA de Haan, 1841

Family RANINIDAE de Haan, 1841

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

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

Superfamily PORTUNOIDEA Rafinesque, 1815

Family PORTUNIDAE Rafinesque, 1815

Subfamily POLYBIINAE Ortmann, 1893

[=Macropipinae STEPHENSON & CAMPBELL, 1960]

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

Superfamily XANTHOIDEA Dana, 1851

Family PINNOTHERIDAE de Haan, 1833

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

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

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

DECAPODA

of uncertain systematic position or validity

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

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ADDENDUM TO CIRRIPEDIA

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

MORPHOLOGY OF THORACICA

(see p. *R*217)

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

ADDITIONAL RHIZOCEPHALAN GENERA

(see p. *R*272)

PELTOGASTRIDAE

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

SACCULINIDAE

Drepanorchis, Heterosaccus, Loxothylacus, Ptychascus, Sesarmaxenos.

LERNAEODISCIDAE

Parthenopea, Septodiscus, Triangulopsis, Triangulus.

ADDITIONAL THORACICAN SUBGENUS (BALANIDAE)

(see p. *R*285)

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

ADDENDUM TO CYCLOIDEA

By M. F. GLAESSNER

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

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