

ON THE RELATIONSHIPS AND
PHYLOGENY OF FOSSIL AND RECENT
ARACHNOMORPHA

A COMPARATIVE STUDY ON
ARACHNIDA, XIPHOSURA, EURYPTERIDA, TRILOBITA,
AND OTHER FOSSIL ARTHROPODA

BY

LEIF STØRMER

WITH 30 FIGURES IN THE TEXT

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PREFACE

From time to time palaeontological research adds new material to our knowledge of the morphology and anatomy of extinct organisms. In studying fossil species the palaeontologist generally employs a working hypothesis concerning the affinities and descent of the fossil forms which are subject to his investigation. Such a preliminary working hypothesis is in most cases based on but few facts and will frequently be strongly modified or even abandoned as the work proceeds. At a certain stage in the investigation of an extinct group the knowledge may, however, be sufficient to permit a more detailed and more safe consideration of the relationships and phylogeny of the described forms.

During several years the present author has studied Palaeozoic Arthropoda, in particular Trilobita and Eurypterida, but also Xiphosura and certain peculiar Middle Cambrian Arthropoda described by the late Dr. Walcott. Well preserved arthropods with their highly differentiated exoskeleton offer good opportunities for comparative research. In recent years our knowledge of the morphology of these ancient groups is considerably extended and it seems possible at present to attempt a more detailed comparative study and discussion on their relationships and phylogeny.

New morphological studies have indicated several interesting characteristics common to the various groups, characteristics which seem to justify the assumption of a common ancestry to genera and species which generally are placed in quite different phyla or subphyla of the Arthropoda. Similar views have lately been strongly emphasized by some zoologists working on recent Xiphosura and Arachnida.

When I arrived at the general views set forth in the present paper it became more and more apparent that the results obtained in an essential way agreed with the far-reaching views expressed by Sir E. Ray Lankester in his *Limulus-theory* published already in 1881 and elaborated in later papers. Moreover the present more extensive knowledge also of the fossil forms seems to give the theory of Lankester a more general significance embracing a very great number of fossil and recent arthropods.

The scope of the present paper has been to offer a comparative study and discussion of several important Palaeozoic Arthropoda and their probable

relatives among fossil and recent Chelicerata. Naturally the limited extent of the present publication does not permit a detailed description of the various groups. In quoting earlier descriptions I have largely confined myself to the more general morphological papers. To the average biologist the literature on fossil Arthropoda is not easily accessible. The various descriptions are often disguised in papers on stratigraphy published in more local geological periodicals. Earlier illustrations are often little reliable, based as they in many cases are on incomplete material. For these reasons it has frequently been necessary not to quote and reproduce the original descriptions and illustrations, but as far as possible to prepare new drawings, or preferably reconstructions, of the more important species. To facilitate the comparison of different forms, numerous separate illustrations of one group are collected in one common figure. In most cases each major group is represented by one figure illustrating the morphological characters and one demonstrating the diversity in form, or what we might call the adaptive radiation of the group. On account of the present war much of the most recent literature has not been accessible.

The substance of the present paper was largely given as special lectures at the Oslo University in the spring of the year 1942.

During my earlier studies on fossil arthropods I have received the most valuable support from the late Prof. Dr. Johan Kiær. I am deeply indebted to him for his good advice and the interest shown towards my palaeontological work. I also wish to express my thanks to Prof. Dr. Olaf Holtedahl and Prof. Dr. A. Heintz for offering me the best facilities for my research at the University and the Palaeontological Museum. Further thanks are due to the trustees of the Fridtjof Nansen Fund. In Sweden I have received important assistance by Prof. Dr. E. A. Stensiö at the Riksmuseum in preparing wax models, and Dr. A. H. Westergård of the Swedish Geological Survey kindly informed me on trilobite structures. During a visit to the United States of America I was fortunate enough to be able to study trilobites and eurypterids with Prof. Dr. P. E. Raymond at the Museum of Comparative Zoology in Cambridge and with Dr. R. Ruedemann at the New York State University in Albany. I wish to express my gratitude for valuable advice and for the facilities set at my disposal. I am also indebted to Dr. Ch. Resser at the U. S. National Museum, the late Prof. Dr. Charles Schuchert and Prof. Ch. Dunbar of Yale University, New Haven, and to Prof. Dr. B. Bigelow of the Woods Hole Oceanographic Institution.

Dr. K. M. Strøm has kindly read through the present manuskript.

Finally my sincere thanks are due to Mrs. Kirsten Arneberg, Miss Bergliot Mauritz, and Miss Lily Monsen for valuable technical assistance in the preparation of the paper.

Palaeontological Museum of the Oslo University, March 1944.

INTRODUCTION

In recent years there is among biologists an increasing interest concerning the general features exhibited in the evolution of the larger animal groups. Some of the problems to be considered are the true relationships between major fossil groups, and the manner in which new morphological types, which signify major systematic units, emerge or evolve from previously established groups.

Naturally, since the days of Darwin, the demonstration of relationships and phylogeny has been one of the chief aims of the palaeontologist, but unfortunately the incompleteness of the fossil record has led to the establishment of too many different phylogenetic trees. The steadily increasing knowledge of fossil forms has made it necessary to abolish many of the more hazardous speculations and to return to the more solid ground of tangible facts.

Nevertheless it has been possible to arrive at fairly secure conceptions concerning the phylogenetic relations between the larger groups of the same phylum. One might mention the recent studies on fossil vertebrates. Fossil material has in a convincing way been able to shed new light on the affinities not only between fossil, but also between recent forms. It has become apparent that several common systematic units, chiefly based on recent material only, are more or less artificial, having a polyphyletic origin.

With invertebrates the fossil remains generally reveal but little of the internal organs and therefore are more difficult objects for more detailed comparative research. The conceptions on affinities and descent have to a great extent to be based on comparative, ontogenetic studies. In particular it has proved difficult to demonstrate the phylogenetic relationships between more remote groups within the same phylum. The demand for a clear demonstration of the origin and evolution of one separate group is recently expressed by the zoologists Garstang and Gurney (1938) in the *Essays on Evolution* presented to E. S. Goodrich: "If a case were known in which an existing class of animals with a metamorphic life-history could be traced back with absolute certainty to its origin in another class that preceded it geologically, and if the ontogenies of both classes were sufficiently well-known for comparison, we should have the most complete portrayal of the course of evolution that the heart of a biologist could desire."

It was expected that palaeontological finds gradually would fill the gap between the separate major groups. As pointed out by German authors in particular, the fossil record, however, has only to a smaller degree been able to demonstrate transitional forms such as would be naturally expected.

This leads us to the second problem, the manner in which greater systematic units branch off from older groups preceding them.

Schindewolf (1926) and Beurlen (1930) noticing the scarcity of transition forms, were inclined to conclude that the evolution at certain stages has a more explosive character, while at other stages the evolution went more slowly through a long chain of smaller changes. Studies on fossil animal groups have suggested that a new type, signifying a major systematic unit, apparently may develop rather suddenly from its progenitors. The essential feature of the new type is the new plan of construction. During the further evolution of the group this new plan of construction is strictly maintained. The more external characters may, however, be subject to multiple major changes illustrating the "adaptive radiation", the (non-Lamarckian) response to the environment. The flourishing of the group coincides with the development of these external specializations which ultimately may prove fatal and lead towards extinction. The great diversity in external form is beautifully illustrated in the numerous genera and species of the insects.

Evolution during the period of the adaptive radiation has been studied in detail in many cases. Among the invertebrates we might mention the investigations on ammonites by Brinkmann (1929) and on trilobites by Kaufmann (1933). Extensive material collected layer by layer in fossiliferous sequences, has indicated the gradual transformation of one species into another. Evolution may proceed along parallel trends illustrating what has been called "Programme evolution" (Bulman 1933).

From bio-stratigraphical studies on invertebrates, especially ammonites, Schindewolf (1926) arrived at conclusions which may elucidate the formation of new morphological types. It has become apparent from his studies that major changes in the type first appear in earlier ontogenetic stages only, and become obsolete in later growth stages of the same specimen. As evolution proceeds (demonstrated through collections from younger beds of the same geological sequence) the new morphological character is exhibited during a longer period of the ontogenetic series, and at last is prevailing also in the adult specimens. Schindewolf interprets the conditions mentioned as signifying a special evolutionary principle which he calls the "Frühontogenetische Typenbildung". According to this principle the major morphological changes take place in the earliest ontogenetic stages. A series of adult transition forms need not have existed. The new morphological characters are so to say foreshadowed in the early larva, but evidently subdued in later growth stages by the general characters inherited from the

predecessors. These views offer an explanation to the common scarcity of transition forms.

The demonstration of an early ontogenetic establishment of a new type has, however, to be founded on evolutionary series occurring in succeeding beds of stratigraphical sequences. Otherwise the structures might easily be misinterpreted the other way as signifying a manifestation of the biogenetic law of Haeckel. The important principle of ontogenetic recapitulation of descent, has been and will remain one of the chief means for determination of relationships and phylogeny of fossil forms. One might mention numerous cases in which a knowledge of larval stages of fossil species has thrown light on the relations to previous groups.

Another principle of evolution has also been of considerable importance to palaeontological research. The irreversibility in evolution, as demonstrated by Dollo, is evident in the phylogenetic development of morphological structures in various vertebrate and invertebrate groups. As already mentioned the "programme evolution" might also be significant. During the evolution of a certain group there is commonly an increasing differentiation (e. g. increasing spinosity of the shell), and at the same time an increase in size. American authors (Osborn and Fenton) have indicated several other features of the general evolution, but these will not be considered in this brief review.

In the present paper dealing with a very large group of fossil and recent Arthropoda, the general principles outlined above will be considered in connection with the evolution of the various separate groups. The major subject of the present studies has, however, been to discuss and possibly interpret the phylogenetic relations between the different forms. But at the same time it is of interest to investigate the general principles of evolution illustrated in the emergence and unfolding of the different groups.

Before we enter upon the discussion of the various Arthropod groups a brief review is given of the general structures and geological appearance of these forms, as well as a short account of previous views concerning the relationships and phylogeny of the Arthropoda.

GENERAL REMARKS ON RECENT AND FOSSIL ARTHROPODA

General Characters of the Arthropoda.

The Arthropoda form a vast and highly differentiated group of invertebrates playing an important part in the history of the earth from the earliest periods of fossil record up to recent time. Representatives of the Arthropoda are found in the sea and in fresh water, occupying both the bottom and the water-layers above. Subaërially they also live both on land and in the air above. In addition to this the Arthropoda are adapted to special modes of life such as a parasitism which is very elaborate in certain forms.

In the recent fauna the Arthropoda comprise the Crustacea, Arachnida, Xiphosura, Myriapoda, Insecta and Pantopoda (Pycnogonida). In addition to the typical arthropods mentioned we have the Onychophora which previously were included in the Arthropoda, but which one at present are more inclined to regard as belonging to a separate non-arthropod phylum. In the same way one notices a tendency of removing the Pentastomida, Tardigrada and Myzostomida from the true Arthropoda (comp. fig. 1).

We get an idea of the huge number of arthropod species when we learn, according to Metcalfe and Flint (1928) that in the recent fauna more than 675 000 species are described. If the total number of described recent animal species amounts to more than 840 000, the Arthropoda comprise about 80 % of the living forms. For comparison it might be mentioned that the vertebrates constitute about 4,3 %. The great number of arthropods is chiefly made up by the insects which form $\frac{9}{10}$ of the total amount, but other groups are also numerous, of spiders there are thus described about 20 000 species according to Kästner (1940 a).

The most characteristic feature in arthropod morphology is the presence of an external chitinous (or partly calcareous) skeleton which serves as a protective cover but at the same time gives an important support to the trunk and the appendages. The mobility of the body is facilitated by the exoskeleton being divided into numerous separate plates and rings which are connected by softer integument or by special joint mechanisms. The exoskeleton is of special importance to the further elaboration of the appendages which often are long, slender and powerful, thus deviating considerably from the parapodia of the Annelida.

On account of the solid exoskeleton the growth has to take place through numerous ecdyses. This is of importance to the palaeontologist because the empty sloughs seem to be rather easily preserved. During the ecdysis the skeleton splits along definite lines or sutures which may be of considerable systematic significance.

The arthropod body is divided into a number of distinct segments or somites. Only the anterior, preoral portion is possibly unsegmented, though certain features suggest a segmentation also of this portion of the body. The preoral portion (prostomium or acron) forms a separate cephalic lobe provided with the preoral antennae (a).

The primary segmentation is in general much disguised by an extensive differentiation of the body skeleton. The body is divided into separate divisions or tagmata (with more or less the same type of appendages) in which the somites might be anchylosed into a continuous plate or shield. In most cases the anterior somites form a separate head or headshield (cephalon or prosoma). The headshield may include a variable number of somites. According to Snodgrass (1938) one finds among the Crustacea certain Branchiopoda and Malacostraca which have a head comprising the cephalic lobe and one additional somite only, while other Branchiopoda have 3 postoral somites incorporated, among Amphipoda and Isopoda even 4. Many Malacostraca have a "cephalo-thorax" with up to 12 postoral somites. Myriapoda and Insecta have only 4 postoral somites included in the head and among the Arachnida and Xiphosura (= Chelicerata) we find a prosoma with 6—7 somites.

Also in the trunk the primary segmentation is sometimes less distinct. The mechanics of motion may have caused the joint-lines to cross the primary segmental division lines. Secondary segmental units are created which are very characteristic of the highly specialized insect thorax, but apparently also occur among the primitive trilobites.

The highly differentiated exoskeleton is of great importance to the muscles which are generally strongly developed and highly differentiated to very different functions. The muscles are often attached to the skeleton at special ingrowths, or apodemes of the shell. On fossil remains the apodemes give information as to the distribution of the muscles, but in certain cases also darker spots on the skeleton indicate the attachment of muscles.

The nervous system is centralized in the brain and the ventral nerve cord. The brain is normally divided into 3 parts, the Protocerebrum with the visual organs, the Deutocerebrum with the preoral antennae (antennules) (a) and the Tritocerebrum, the first postoral, typical somite, with the second antennae or chelicerae (I).

The other organ-complexes are of minor importance to the present comparative study.

Concerning the origin of the Arthropoda there seems to be hardly any doubt as to their derivation from Annelida. The Annelida, Onychophora and Arthropoda have many characters in common. The early ontogenetic stages (cp. Snodgrass 1938) exhibit the same closing of the middle portion of the blastopore and the same formation of the cephalic lobe, the mouth and the anal opening. The mesoderm originates on either side of

the blastopore in the posterior part of the embryo. During the ontogenetic development the mesoderm grows forward as mesodermal bands which afterwards become segmented and finally attain internal cavities or coeloms. Both the nervous system, the muscles, the blood vessels and the segmental organs show the same general features within the three groups.

The main difference between the Arthropoda, Onychophora and Annelida is found in the presence or lack of an exoskeleton and, in connection with this, the development of the locomotory appendages. The arthropod appendage deviates from the leg of the Onychophora which forms a conical outgrowth of the body, and outgrowth provided with numerous circular permanent folds in the integument instead of distinct joints. The typical arthropod appendage differs still more from the Annelidan parapodium which is merely a short lateral lobe of the body.

A certain difference is found also in the development of the segmental and the genital organs. The Arthropoda have a special development of the gonads with exit canals formed by the modification of coelom sacs (possibly extinct arthropod groups had more primitive structures).

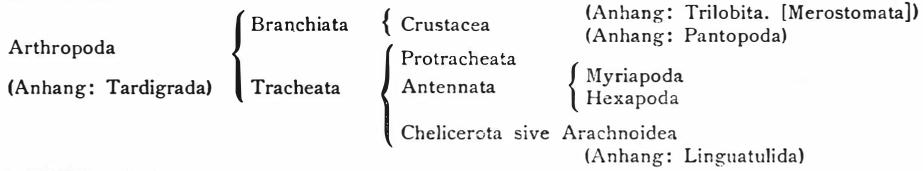
Evidently both the Arthropoda, Onychophora, Pentastomida, Tardigrada and Myzostomida evolved from Polychaeta, or more primitive Annelida.

Brief Account of Previous Views on Arthropod Classification.

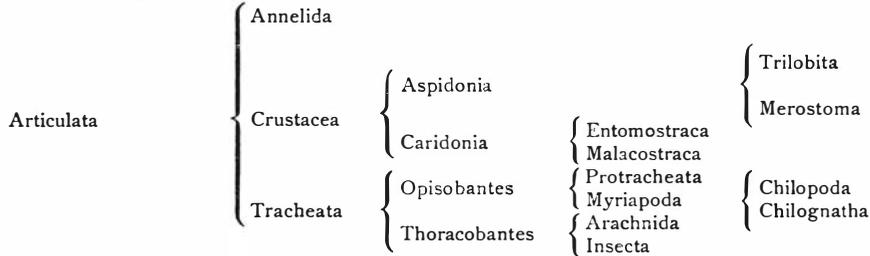
The phylum Arthropoda in our present conception corresponds exactly to the class Insecta established by Linné. The name Insecta, however, gradually became confined to signify only one group of the Arthropoda. Lamarck distinguished three major systematic units, the Crustacea, Arachnida and Insecta. The name Arthropoda is of more recent date being established by Siebold—Stanius in 1895 (cp. Lankester 1904, p. 524). Cuvier had previously placed the Annelida and Arthropoda in a common group for which he suggested the name Articulata.

Fig. 1 gives an idea of various attempts made to arrive at a natural classification of the Arthropoda. It appears that from time to time different morphological factors have been considered in connection with the classification. In the 19th century the main stress was laid upon the presence of either gills (branchiae) or trachea. It was particularly through the papers of Haeckel that this principle of classification attained such a dominant position. In his tracheate theory Haeckel strongly advocated a line of descent from Chaetopoda—Onychophora—Myriapoda, and from Myriapoda two separate branches to the Arachnida and Insecta. According to this theory the gill-bearing Crustacea and Xiphosura belong to a quite different line of development and have little to do with the tracheate forms. Haeckel even went so far as to regard the Crustacea and Tracheata as belonging to

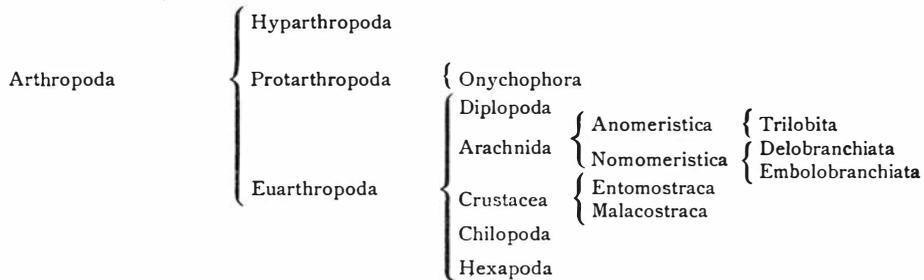
I. LANG 1888:



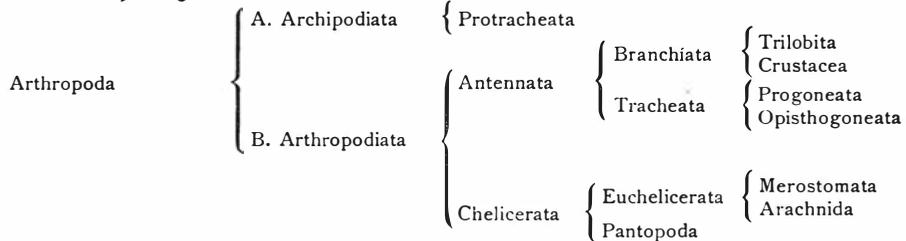
II. HAECKEL 1896



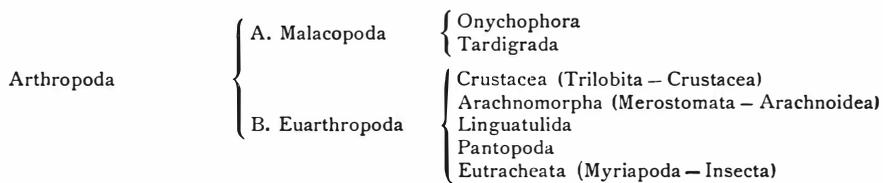
III. LANKASTER 1904 - 1905



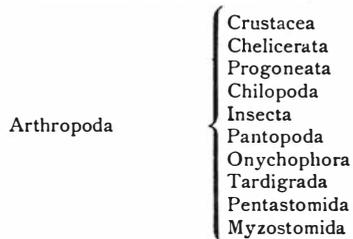
IV. BÖRNER 1912 - 32:



V. CLAUS-GROBEN-KÜHN 1932:



VI. HANDBUCH D. ZOOLOGIE 1926 - :



VII. BORRADAILE 1932:

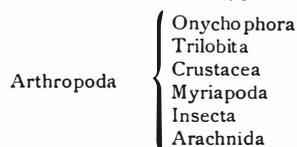


Fig. 1. Different classifications of the Arthropoda.

two separate branches arising independently from chaetopod annelids. To illustrate the mentioned branchiate-tracheate principle of classification, the systems of Lang (1888) and Haeckel (1896) are shown in fig. 1, I. II. As "Anhang" to the Crustacea, Lang regards the Xiphosura, Trilobita and Eurypterida, as well as the Pantopoda. Like Haeckel he interpretes the Onychophora or Protracheata as primitive Tracheata. Haeckel's division of the Crustacea into Aspidonia and Caredonia is based on the presence or absence of a nauplius, and the presence of one or two, assumed preoral (!), pairs of antennae. Among the Tracheata the Opisobantes is chiefly characterized by numerous, not differentiated metamers, while the Thoracobantes have few and strongly differentiated metamers.

The division of the Arthropoda into Branchiata (or Crustacea) and Tracheata largely corresponds to a division into water and land arthropods. A priori a classification coinciding with the mode of life of the two groups appears little reliable. The respiratory organs are hardly fit to serve as first rate morphological factors in establishing a major classification. It might in this connection be mentioned that among typical Crustacea certain terrestrial Isopoda have secondary lungs developed, and among the Insecta aquatic larvae have secondary gills.

It was the merit of Lankester to have broken through the generally adapted principle of Haeckel. In his important paper "Limulus an Arachnid", Lankester (1881) convincingly demonstrated the homology between the book-gills of *Limulus* and the lung-books of *Scorpio*. His scheme of classification (fig. 1, III) approaches the present conception on the relationships of the Arthropoda. He uses, however, the term Arachnida in a wider sense than other authors. The division into Anomeristica and Nomomeristica seems of minor importance according to more recent research. Lankester was supported by Oudmans (1885) who even advocated a polyphyletic origin of the Arthropoda, suggesting different origins of the major arthropod groups. A classification similar to that of Lankester was suggested by Heider (1913). This author separates three main branches of the Arthropoda: the Crustacea, the Arachnomorpha (including the Trilobita and Chelicerata) and the Antennata (comprising the Myriapoda, Insecta and Onychophora).

In more recent literature traces of the division into Branchiata--Tracheata may still be noticed. This is the case in the classification of Börner (1912—1932) (fig. 1, IV). A new principle is, however, introduced in these more recent classifications. Attention has been drawn to the fact that several groups, the Crustacea, Myriapoda and Insecta, have the frontal appendages developed as multijointed tactile organs or antennae, while in other groups, such as Arachnida, Xiphosura and Eurypterida, the frontal appendages consist of a pair of characteristic 2—3-jointed pincers, the so-called chelicera. The members of the former groups are included in one common unit, the Antennata, while the remaining are placed in another

group, the Chelicerata. Especially the Chelicerata seems to form a natural systematic group. The Xiphosura and Eurypterida (Gigantostroma) are included in the Merostomata (or Merostoma of Haeckel).

In the latest text-books one might trace a tendency towards more caution concerning the connection of major arthropod groups into larger systematical units. It has become apparent that the larger units (such as the Antennata) may be more or less artificial combinations of unrelated forms. Claus-Grobben-Kühn (1932) thus only coordinate a number of different arthropod groups, and similar divisions are found in a text-book of Borradaile (1932) and in the large "Handbuch der Zoologie" of Kükenthal (fig. I, V—VII). Divergences in opinion are noticeable as to the inclusion or exclusion of the Onychophora, Tardigrada, Pentastomida and Myzostomida from the true Arthropoda.

The tendency of separating the different major groups of Arthropoda has by some writers been carried so far as to regard (as did Oudmans) the phylum Arthropoda as an artificial group embracing different phylae descended from separate annelid groups.

Different Opinions on the Phylogeny.

Numerous theories or views have been offered to elucidate the problem of the phylogeny and relationship of the Arthropoda. The many different hypotheses, often rather speculative, generally agree on the assumption of a common ancestor for the various branches of the Arthropoda, this ancestor being a very primitive arthropod type, an archaic form or "Urarthropod". Certain writers, however, have more recently suggested a polyphylitic origin of the Arthropoda, emphasizing that the different arthropod branches descended from separate annelid groups.

In most theories considerable weight has been laid on the fossil record. In general only the more common fossil groups such as Trilobita and Eurypterida have been considered, but in certain cases also the more rare forms are taken into discussion. Unfortunately it appears that the hypotheses on the phylogeny are often based on rather incomplete knowledge of the fossil record. Only in few cases the fossil material is so satisfactorily preserved and described that it may be subject to a more detailed comparative research. Many of the early descriptions and illustrations are less reliable as to important details, and the original descriptions are often not easily accessible in special geological publications. To the zoologist it will therefore appear difficult to apply the palaeontological material in a satisfactory way.

By most writers the Trilobita have been regarded as a central group in the Arthropod phylogeny. The various theories have therefore been coloured by the conceptions on the zoological position of these extinct forms, conceptions which have changed from time to time. In order to obtain

an idea of the various theories on arthropod phylogeny it is therefore necessary briefly to mention the opinions on the position of the Trilobita.

One might largely separate three periods in the research and interpretation on the trilobite morphology.

In the first period the appendages of the trilobites were unknown. Dohrn (1871), Packard (1872) and others pointed out the general resemblance between Trilobita and Xiphosura. Packard demonstrated that the common characters in the dorsal shield, and particularly the so-called "Trilobite-larva" of *Limulus*, resembled the larval stages of trilobites and thus suggested a distinct relationship between the two groups.

The second period is influenced by the discovery of trilobite appendages. Already in 1870 Billings published a description on remains of trilobite legs (*Isotelus*), but more details were obtained through thin sections of Ordovician trilobites (*Ceraurus* and *Calymene*) by Walcott (1881). The sections did not, however, demonstrate the presence of antennae in the trilobites, and Walcott joined Dohrn and Packard in their views on relationship between Xiphosura and Trilobita. But then came the discovery of well-preserved appendages in the Ordovician genus *Triarthrus*. In a series of papers Beecher (1893, 1895 a, b, 1896, 1902) showed that the trilobites had one pair of long, multijointed and uniramous, preoral antennae and a series of uniform biramous appendages resembling the biramous appendages of crustaceans. Beecher, as well as Walcott (1894), Bernard (1894), and Carpenter (1903) therefore arrived at the conclusion that the trilobites were not related to the xiphosurs and arachnids, but were true crustaceans of a primitive type. Instead of being early relatives of Xiphosura and Arachnida the Trilobita were now regarded as "early offshoots from the line leading from the annelida to the crustacea". The structures found in *Triarthrus* were later confirmed by remains of other genera from Cambrian and Devonian strata. Palaeontologists working with fossil Arthropoda, Clarke and Ruedemann (1912), Pompeckj (1912), Walcott (1912, 1918, 1921), Raymond (1920), Richter (1926), Warburg (1925), Swinnerton (1930), Broili (1929 a, 1930 a), and Beurlen (1930, 1934), as well as zoologists such as Storch (1925, 1926) and Garstang and Gurney (1938) agree on the assumption of the crustacean nature of the Trilobita. Some writers place the Trilobita as a separate primitive crustacean group, others as more closely related to recent groups such as Branchiopoda and Copepoda.

A third period in trilobite studies is signified by a return largely to the earlier views on xiphosuran relationships. Already in 1881 Lankester had demonstrated the relationship between the gill-breathing Xiphosura and the trachea-breathing Arachnida. In spite of the discovery of the appendages in *Triarthrus*, Lankester maintained his views on the relationships between these groups and the primitive trilobites. In his well-known article in *Encyclopedia Britannica* (Lankester 1904, 1905) he places the groups mentioned in a common arachnid branch of the Arthropoda. More recently

Fedotov (1924) pointed out that the trilobites, in spite of their crustacean-like appendages, in the general plan of constructions appear to be related to the Chelicerata (Xiphosura + Arachnida). In his paper on the larval development of *Limulus* Ivanov (1933) convincingly demonstrated important common characters in the Xiphosura and Trilobita. The present author has arrived at the same conclusions from more detailed palaeontological studies especially on trilobite appendages (Størmer 1933, 1939, 1941). Arachnid affinities of the trilobites have been strongly emphasized also by Schulze (1936).

The position of the Eurypterida (or Gigantotraca) has been more clear. The scorpion-like body and the presence of characteristic chelicera as well as numerous other features decidedly express their affinities to the Xiphosura and Arachnida. The specialized Eurypterida cannot, however, be regarded as direct ancestors of these groups. Versluys and Demoll (1922) tried to show that terrestrial arachnids of the scorpion type might have been the ancestors of the non-marine eurypterids, not the other way as generally assumed. One of their arguments was the presence of true scorpions already in the Silurian. They emphasized the origin of the Chelicerata from terrestrial arthropods related to the Onychophora. This theory, elaborately presented in their stimulating paper on the "Limulus-theory", created considerable interest and received a certain support also from palaeontological quarters (Pompeckj 1923). It was particularly one point which was difficult to explain in their Limulus-theory. The abdominal feet of *Limulus* had to be merely modified sternites. Kästner (1929), Ivanov (1933) and Størmer (1934 a) showed that this view was hardly tenable. Especially Ivanov's embryological studies on *Limulus* clearly demonstrated the impossibility of the abdominal feet being modified sternites. If they were interpreted in that way the two last pairs of walking legs in the prosoma had to be interpreted in the same way (!). With our present knowledge the theory of Versluys and Demoll seems highly improbable.

Besides the trilobites and eurypterids other groups of Palaeozoic arthropods were also successively discovered and taken into consideration with regard to arthropod phylogeny. It was in particular the unique discovery by Walcott of well-preserved Middle Cambrian arthropods which gave new material to elucidate the nature of the oldest known arthropods. The highly interesting arthropod fauna is not yet described in full detail, but many excellent illustrations, especially by Walcott (1911 a, 1912, 1931) have furnished material for numerous discussions as to their zoological position (p. 80). In the great variation of the dorsal shield, these Middle Cambrian forms resemble both crustaceans, merostomes and trilobites. Some have a well-developed carapace just as typical crustaceans, while others show a trilobation of the body and a styliform telson such as in typical merostomes. The appendages are, however, of a pronounced trilobitan character.

Most authors regard these arthropods as belonging to different groups of Crustacea, particularly the Branchiopoda are presumed to be represented. The trilobitan appendages appeared to confirm the conception of a crustacean nature of the Trilobita. But certain merostome-like forms are also present, and they had also trilobite legs. Raymond (1920, 1935) therefore argued that the primitive Cambrian forms were the ancestors both of true crustaceans and typical merostomes and arachnids. Other writers such as Clarke and Ruedemann (1912), Versluys and Demoll (1922) would not admit that any of the merostome-like forms were related to true merostomes, the resemblance in their opinion was only due to convergence.

The zoologists Fedotov (1924) and Henriksen (1928) arrived at the conclusion that Walcott's arthropods include both Crustacea and Merostomata. Henriksen points out that the presence also of forms combining both crustacean (branchiopodan), merostome and trilobitan characters indicate that the trilobite stood near a common ancestor of both Crustacea and Chelicerata. Handlirsch (1926, 1927) has taken the consequence of this view. In his "Trilobite-theory" he assumes that all arthropods have developed from a kind of archaic arthropod, "Urarthropod" with biramous appendages, a form which was not much different from the trilobite. According to his theory Precambrian trilobites, or trilobite-like forms, gave rise to different lines of evolution leading to Crustacea, Chelicerata and Myriapoda—Insecta. The Trilobite theory has, however, been subject to considerable criticism. The relationship between trilobites and insects is only based on a certain similarity in the formation of pleurae and in the presence of cerci in Palaeozoic insects. The connection between Myriapoda and Insecta is more generally assumed, and their relationship to other arthropod groups is yet unknown. The fossil material gives no information on the subject.

In his discussion of the early Palaeozoic arthropods and the general phylogenetic problems, Fedotov (1925) suggests the possibility of the different arthropod branches having developed independently from different annelid groups. This would mean that the phylum Arthropoda had a polyphyletic origin and thus forms a more artificial systematic unit. These views are emphasized and more well founded in recent papers by Ivanov (1928, 1933). It is the merit of this author to have demonstrated two kinds of somites or segments in the body of the Annelida and Arthropoda. Fig. 2 illustrates the conception of Ivanov.

The early ontogenetic stages of Annelida give the best information as to the two types of somites. The mesoderm first appears as two large cells near the blastopore. From these cells, the mesodermal teloblasts, the mesoderm grows forwards. At the same time the blastopore is prolonged forward on the ventral side and its posterior portion becomes gradually closed. The frontal portion of the blastopore develops into the permanent mouth while the anal opening is formed secondarily. The present stage of development represents an unsegmented trochophore larva. At a next stage

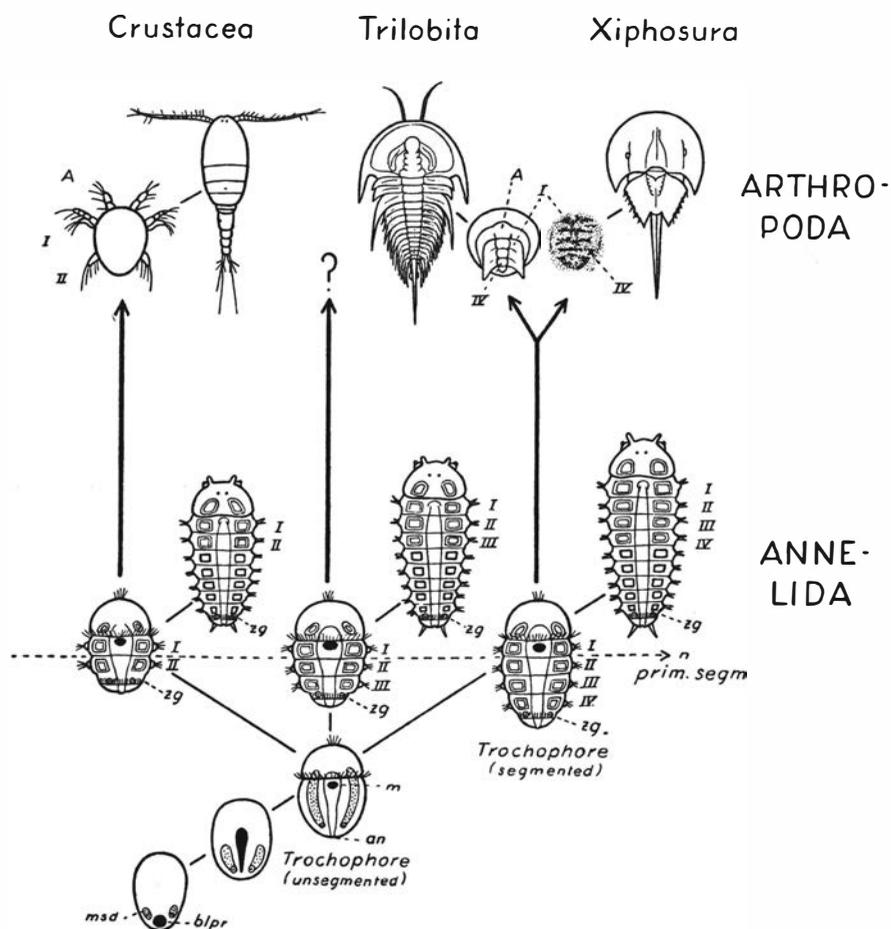


Fig. 2. An illustration of Ivanov's theory on a polyphyletic origin of the Arthropoda.

The schematic drawings of the Annelida are chiefly based on figures by Snodgrass (1938). I—IV = postoral somites, *a* = antennal segment, *an* = anus, *blpr* = blastopore, *msd* = mesoderm, *n* = number of primary or larval somites, *prim.segm.* = primary or larval somites, *zg* = zone of growth.

a segmentation or metamerism of the larva takes place. The segmentation, originating in the ectoderm (partly by the invagination of chaetal sacs), divides the mesoderm bands into a number of blocs which later develop internal coelomic cavities. These segments which develop simultaneously, or at least approximately so, form the primary or larval somites or segments. In later ontogenetic stages new somites are added, but these are formed by teloblastic growth from a vegetative zone (*zg*) in the posterior portion of the body. The new somites which are added one by one to the primary somites have thus another origin and are called the secondary

somites. The number of primary somites is in general quite small in comparison with the secondary somites.

The number of primary somites varies considerably within the polychaete Annelida, but seems to be distinct in separate families. Also among the Arthropoda it has been possible to distinguish primary and secondary somites. Ivanov has demonstrated the presence of 4 postoral primary somites in the Xiphosura and has given good reasons for the conception of the same number of primary somites in other Chelicerata and in Trilobita, while the Crustacea evidently have but 2 postoral, primary somites.

For these reasons Ivanov draws the conclusion that the two arthropod branches, the Crustacea and the Trilobita-Chelicerata, developed independently from two different annelid families. The number of primary somites is unknown in the Myriapoda—Insecta and uncertain in the Pantopoda, but the different number in the above mentioned groups may suggest a polyphyletic origin of the Arthropoda.

Ivanov's conception of primary and secondary somites has won approval among contemporary zoologists working on arthropod phylogeny. From comparative studies on Arachnida, Trilobita and certain other Palaeozoic Arthropoda, Schulze (1936, 1939) is inclined to regard the Trilobita and Chelicerata as belonging to a separate arthropod branch which might have developed, like the Crustacea, directly from a certain group of Annelida. Similar views have been presented by the present author (Størmer 1933, 1934, 1939, 1941) from comparative morphological studies on Trilobita, Merostomata, Arachnida and a number of other Palaeozoic arthropods. The present paper deals with these problems.

A valuable contribution to our knowledge on the relationship and phylogeny of the Annelida, Onychophora and Arthropoda was recently given by Snodgrass (1938). He believes that the Onychophora and Arthropoda have descended from primitive, more generalized "lobopod", not "chætopod" annelids, pointing out that there is reason to doubt that the polychaete parapodia are prototypes of the arthropod legs. Although Snodgrass lays weight on the distinction of primary and secondary somites, he believes in a monophyletic origin of the Arthropoda (including also the Onychophora). He assumes that the primitive "Protarthropoda" might have had a centipede-like form which is maintained in recent Chilopoda. According to his "Chilopod theory" the different arthropod branches developed from this primitive type and their chief characteristics were due to different cephalisation and the modification of certain appendages into mandibulate organs.

It is evident from the present brief review that the opinions on the relationship and phylogeny of the Arthropoda vary to a considerable extent. It seems, however, to be generally admitted that the Arthropoda descend from polychaete or more primitive, generalized Annelida. Most students imagine a monophyletic origin of the Arthropoda, but recently reasons have also been presented in favour of a polyphyletic origin.

Commonly the Trilobita are supposed to have been closely related to the progenitors, or progenitor, of the main arthropod branches. Opinions have, however, been subject to changes in connection with conflicting views on the systematical position of the Trilobita.

Preservation and Vertical Distribution of Palaeozoic Arthropoda.

Preservation. With their powerful chitinized exoskeleton the Arthropoda are well suited for preservation as fossils. The remains are generally confined to the thicker shell of the dorsal shield, but in certain cases also the more delicate test of the ventral surface and the appendages might be preserved. If the softer integument between the chitinous plates is easily destroyed, the separate plates may fall apart before the remains are imbedded in the sediment. Fortunately the main part of the body is often kept intact and we are able to get "complete specimens".

The dead arthropod remains are attacked and may be more or less destroyed by the bottom fauna. Where the bottom is more or less anaërobic conditions are more favourable.

The fossil remains of the arthropods are not, however, confined to the dead specimens. During the periodical ecdysis the empty sloughs are left on the bottom. These sloughs, lacking the internal softer parts, are less liable to destruction by the bottom fauna. In more primitive groups the arthropod leaves the slough through a frontal, marginal suture. After the ecdysis the suture might have closed and the empty slough remains as a "complete" fossil specimen, exhibiting all the finest morphological details of the exoskeleton. Probably the majority of fossil arthropods are represented by empty sloughs. In certain cases, however, traces of internal organs, such as imprints of the alimentary canal, indicate the remains of dead individuals.

The preservation is to some extent dependent on the chemical constitution of the skeleton. As shown by Richter (1931) the preservation may be selective. In sandy sediments, poor in lime, calcareous skeletons might have been dissolved while chitinous remains are well preserved. (This is probably the reason why the crustaceans of the Downtonian sandstone at Ringerike in Norway are so badly preserved compared with the eurypterids (Størmer 1934 b).)

The mode of preservation is also for other reasons subject to great variation. The skeleton either maintains its original plastic shape or is partly compressed or even flattened as a film. The skeleton may be but little altered, more or less replaced by various minerals, or even completely dissolved, leaving only the imprint of the external and the mould of the internal surface of the skeleton. In a very few cases remains of the

original colouring of the shell is indicated by the fossil. The preservation of internal organs such as the intestine requires special conditions. Certain fine-grained shales and limestones (waterlimes) have proved remarkable conditions for the preservation of the finest morphological details. We may mention the Middle Cambrian Burgess Shale, the Ordovician Utica Shale and Trenton Limestone, the Silurian waterlimes of New York State and Ösel (Saaremaa) in Esthonia, as well as the Devonian Hunsrück Shale and Siegener Shale of Germany. A unique preservation of fossil arthropods is found in the famous Rhynie Chert Bed of Scotland.

The investigation of the fossil material takes place after a thorough and careful cleansing of the specimens. In certain cases acids are applied. The finer structures are often profitably studied when immersed in alcohol or some fluid of high refraction. Serial grinding has more recently been applied to several more complicate structures. Thin sections have proved useful in particular to the study of special structures such as eye-lenses and other structures in the exoskeleton. When the fossil is preserved in pyrite or similar minerals, finer structures hidden in the matrix may be traced by x-ray photographs.

Vertical distribution of fossil Arthropoda. Before dealing with the separate groups of Palaeozoic Arthropoda, we shall briefly mention the appearance of the larger groups in the earlier geological formations.

Fossil Arthropoda are known from all fossiliferous formations. Even from the Precambrian, fossil remains are described which are interpreted as belonging to arthropods. Walcott (1911 a) described from Late Precambrian (Algonkian) strata in Alberta and Montana certain plates which by their characteristic outline and indication of sculpture possibly represent remains of arthropods, apparently tergites of eurypterid-like forms.

From late Proterozoic strata of Australia fossils are discovered and described as arthropod remains. A preliminary description was given by David (1929), but in recent years new material has been added. The fossils and their occurrence are treated in a paper by David and Tillyard (1936). Among the fragmentary fossils, which are interpreted as representing large Annelida and peculiar Arthropoda, Tillyard briefly describes a form which he regards as belonging to a new class of Arthropoda: the Arthrocephala. His description and more detailed reconstruction are commented upon by Schulze (1939) who remains sceptical as to his conclusions. The published photographs do not indicate a favourable preservation, and Tillyard does not give any separate description of the different specimens. It appears from the published material, that there is reason to doubt the reconstructions put forward by Tillyard. At present the important material is too incompletely known to be subject to more extensive comparative studies. One is anxious to obtain more information on these highly interesting arthropods and on the hitherto undescribed annelid remains.

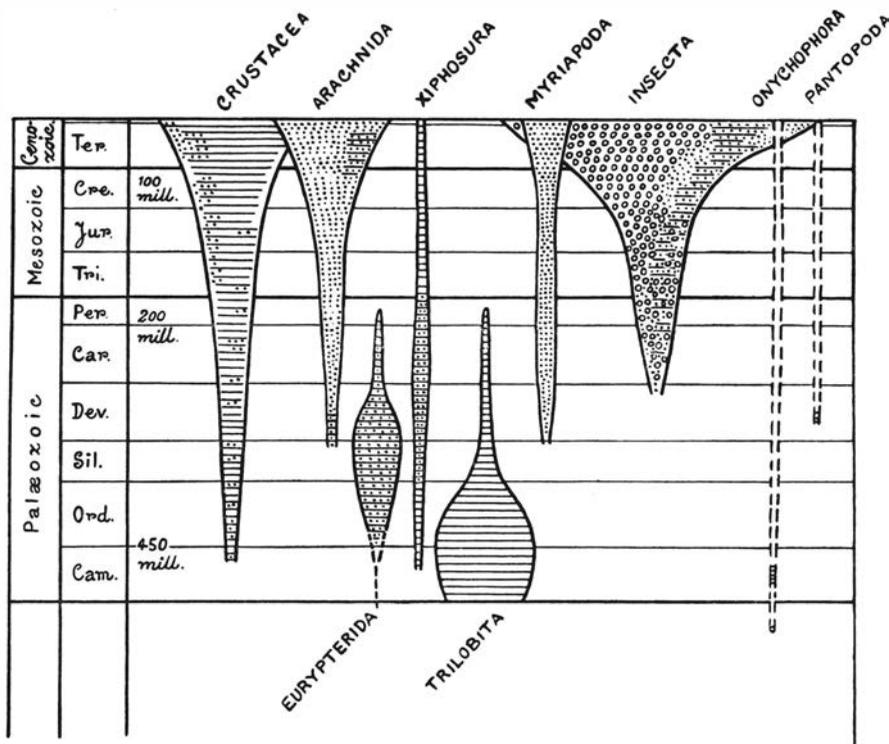


Fig. 3. Vertical distribution of the Arthropoda and Onychophora.

The width of the columns roughly suggests the frequency of the different groups at different geological times. Transverse lines indicate marine faunas, dots and transverse lines = freshwater faunas, dots = terrestrial faunas, and small circles = faunas with flying forms.

A third find has also created a certain sensation. Pompeckj (1927) described a fairly complete imprint of a form *Xenusion auerswaldi* which seems to be related to Middle Cambrian and recent Onychophora. The fossil which occurred in Quaternary deposits is regarded as belonging to the Precambrian, but the age appears to be uncertain according to verbal information by Prof. V. M. Goldschmidt who has examined the rock specimen.

We shall now consider the appearance of the Arthropoda in Palaeozoic and younger formations. Fig. 3 illustrates in a very schematic and general way the vertical distribution of the major arthropod groups. The width of the columns does not give a correct number of the species present at a certain time, but only intends to give a slight impression of the frequency of forms. In several formations the fossil material is very limited and certain fossil groups are confined to the less common continental deposits, facts which also impede our arriving at correct figures.

The Onychophora which, however, hardly belong to the typical Arthropoda, have possibly been found already in the Precambrian as above mentioned. In Walcott's excellently preserved material from the Burgess

Shale a form, *Aysheia pedunculata* Walcott occurs, which seems to belong to the Onychophora. The species was described by Walcott (1911) and has more recently been subject to new studies by the zoologist Hutchinson (1930). The genus has pronounced onychophorean characters in the external segmentation of the body and the presence of conical, annulate legs with claws. But at the same time the marine Cambrian species deviates considerably from the terrestrial recent ones. In contrast to recent forms *Aysheia* possesses a terminal mouth, a pair of frontal papillae anterior to the branched antennae, and the two first postoral appendages are not specialized into jaws and slime papillae. The differences are so considerable that if the Cambrian form belongs to the Onychophora at all, it has to be placed in a separate order, the Protonychophora, as suggested by Hutchinson.

The Crustacea, playing a very important part in the recent fauna, is well-known also in ancient formations. In spite of the great number of species described, our knowledge of the Palaeozoic species is fairly limited. In general only the more solid carapace is preserved. The appendages, of great importance to comparative research, are often destroyed. It is not until the later part of the Palaeozoic (and in younger formations) that we have a greater number of more complete specimens, and these forms are in general more or less closely related to recent Malacostraca.

In the Palaeozoic it is the Ostracoda and Archaeostraca that have made their impression on the crustacean faunas. The Ostracoda are very common in the Silurian and Devonian, but unfortunately only the bivalved shells are preserved. Muscular imprints on the shells indicate that they are from true Ostracoda (Triebel 1941). Silicified specimens in the Carboniferous demonstrate the structures of appendages and certain internal organs.

Besides the typical Ostracoda more thin-shelled forms occur already in the Lower Cambrian. These forms, which have a muscle scar in the frontal part of the shell, are regarded by Ulrich and Bassler (1931) to belong to the Conchostraca. It is possible that this group is more related to the Archaeostraca (cp. Raymond 1935).

The Archaeostraca, which are the forerunners of the typical Malacostraca, were mostly large forms related to the recent Leptostraca (*Nebalia*). The appendages of true Archaeostraca are incompletely known, but thanks to the brilliant preservation of the Lower Devonian Hunsrück Shale of Germany we know in detail the structure of an Archaeostraca-like form which on account of certain morphological characters is included in the Malacostraca by Broili (1928). *Nahecaris stürtzi* Broili has typical crustacean appendages, both antennules (*a*) and antenna (I) as well as thoracopods and pleopods.

Another find has also illustrated the detailed structure of early fossil crustaceans. From the well-known Middle Devonian cherts of Rhynie in Scotland, Scourfield (1926) has described and reconstructed the small crustacean *Lepidocaris rhyniensis* Scourfield (fig. 4). Also in this case

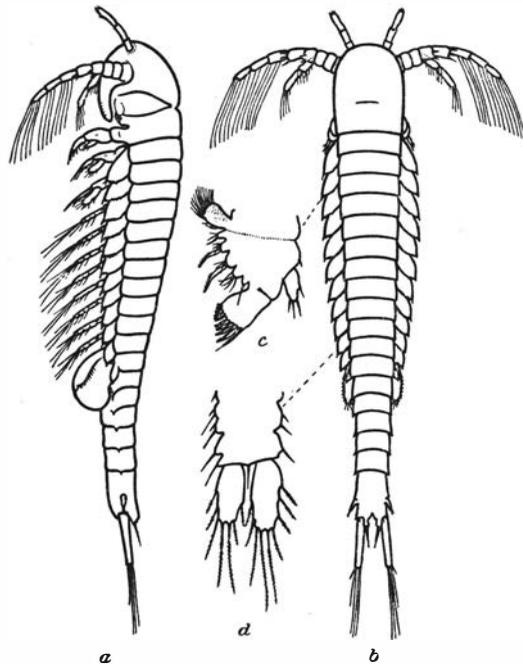


Fig. 4. Crustacean from the Middle Devonian.

Lepidocaris rhyniensis Scourfield. From the Rhynie Chert, Scotland. Length of body 3 mm. *a* = lateral view, *b* = dorsal view, *c*, *d* = appendages of the trunk. Reconstruction by Scourfield (1926).

we have a typical crustacean with two pairs of antennae and appendages which are partly phyllopodian and partly of the common biramous type. *Lepidocaris* known also in larval stages, represents a separate order of the Branchiopoda. We shall in this connection not consider the structures of these crustaceans in relation to the Trilobita and other Arthropoda. It is of importance to notice that a detailed knowledge of the earlier fossil crustaceans is very limited. No Predevonian species is known which demonstrates enough details to permit more extensive comparative considerations. As previously mentioned most authors regard many of the appendage-bearing arthropods from the Middle Cambrian as representing true crustaceans. But it will appear from later chapters that there are good reasons for believing that the resemblance is due to convergence only.

The Pantopoda or Pycnogonida form in the recent fauna a small group confined to marine waters. These peculiar arthropods have commonly been regarded as aberrant Chelicerata, especially on account of the presence of chelicer-like appendages. On the other hand the larva shows some resemblance to the crustacean nauplius (fig. 29 b). It seems most natural to regard the Pantopoda as a separate group of the Arthropoda. Fossil Pantopoda were completely unknown until Broili (1929 b, 1930 b, 1932 b) described two genera from the Lower Devonian Hunsrück Shale of Germany (fig. 29 a).

The fossil specimens are of particular interest in showing a well-developed segmented abdomen, and a segmentation also of the proboscis. Broili points out that the morphological characters of these ancient representatives suggest annelidan affinities.

The morphology of the fossil Myriapoda is imperfectly known. The earliest representatives of this group occur in the uppermost Silurian. Diplopoda from the Carboniferous indicate the structure of the legs. According to a reconstruction by Handlirsch (1926, 1927, p. 211), the appendages might have been biramous. In the Palaeozoic Diplopoda the tergum is often provided with integumental appendages.

Fossil insects are described in great numbers. Of particular interest are the Carboniferous—Permian forms with paranotal lobes (even with veins) suggesting rudimentary wings also on the first thoracic segment. The pleural lobes on the abdomen are possibly of phylogenetic significance as indicated by Handlirsch. The earliest insect remains are recorded from the Middle Devonian chert of Rhynie. These fragmentary remains are interpreted as true Collembola, but the structures are not very distinctly preserved. Our present knowledge of fossil insects has therefore little to say concerning the phylogenetic origin of this important and exceedingly numerous group. The earliest representative known, as well as the earliest better known fossil crustaceans, appear to be typical insects and typical crustaceans respectively.

The remaining groups, the Arachnida and Xiphosura, the Eurypterida and Trilobita, seem to be related in some way or other. The present paper is dealing especially with these groups which may be united in a common large group: the Arachnomorpha. In the following the different groups are treated more in detail and we begin with the important extant groups — the Trilobita and Eurypterida.

GENERAL DESCRIPTION OF FOSSIL ARTHROPODA PROBABLY BELONGING TO THE ARACHNOMORPHA

Trilobita.

More than any other fossil group the trilobites have dominated the Lower Palaeozoic marine faunas. It is difficult to give an exact figure of the great number of species hitherto described, but at least several thousand species, distributed on numerous genera and families, are known from different parts of the earth. The trilobites are described both from Arctic and Tropic regions and certain species have a great horizontal distribution. The trilobites had their acme of evolution already in Cambrian and Ordovician times. In the Silurian a distinct decline may be traced, but several genera live on to the close of the Palaeozoic, the last representatives

being known from the Permian. The literature on trilobites is very copious. In the present connection we need only keep to mind the classical memoirs of Barrande, Salter, Angelin, Schmidt, and Walcott.

The size of the trilobites ranges from about 1 cm to 70 cms, most species having a length from 3 to 10 cm. The trilobites had a powerful dorsal shield consisting of calcareous chitin. In thin sections well-preserved specimens may show the presence of different layers in the shell. An external, more pigmented layer is succeeded by a laminated inner layer and a more structureless basal layer (*Tretaspis* Størmer 1930). Numerous vertical canals of different size penetrate the shell. Especially on the doublure (the deflexed border) there are certain distinct, parallel lines (Terrassen-Linien) which may possibly represent some kind of infolding of the integument (Schulze 1936). Also traces of colour patterns have exceptionally been preserved in the shell of trilobites (Raymond 1922).

The dorsal shield is mostly broad and moderately vaulted. As expressed in the name Trilobita, the dorsal shield is divided by two longitudinal furrows, the axial furrows, into three parts, the median axis or rachis and the lateral plural areas on either side. A tripartition is also given by the transversal division of the dorsal shield into three tagmata, the head-shield (head) or cephalon, the thorax, and the tail-shield or pygidium. The lateral or pleural areas must to be interpreted as merely outgrowths of the main body. A cross-section of the body (fig. 5, 20) shows that the pleural areas of the body only form a thin, plate-shaped cover serving for protection of the appendages below. The strong development of the pleural area is very characteristic of the Trilobita. Along the outer borders of the dorsal shield the shell turns over and continues on the ventral surface as a deflexed border or doublure (fig. 5, 18).

The dorsal shield is divided into a number of segments of which a distinct number of the anterior ones coalesce into a cephalic shield and a variable number of the posterior ones fuse into a pygidium.

The cephalic shield, the head or cephalon, is usually rounded in front with the postlateral corners often prolonged into genal spines. The different segments building up the cephalic shield are best illustrated in the early larva with their annulated axes and sometimes also segmented lateral areas (fig. 5, 2, 3; fig. 7, 1—3). In the adult the cephalic axis or glabella generally shows remnants of the segmentation in the glabellar furrows (fig. 5, 1; fig. 6 *glf*; fig. 7, 9, 10, 12, 18).

The glabellar furrows serve as muscular apodemes and may therefore be secondarily deepened and modified in the adult. The posterior segment in the cephalon is commonly marked off as a nuchal ring which may be provided with median tubercle or nuchal spine.

The headshield has a pair of lateral eyes situated on the "cheeks" on either side of the glabella (*lat. eye* in fig. 5, 1, 7, 11, 16; fig. 6 and fig. 7). The sigmoid or kidney-shaped eyes might be more or less projecting, in

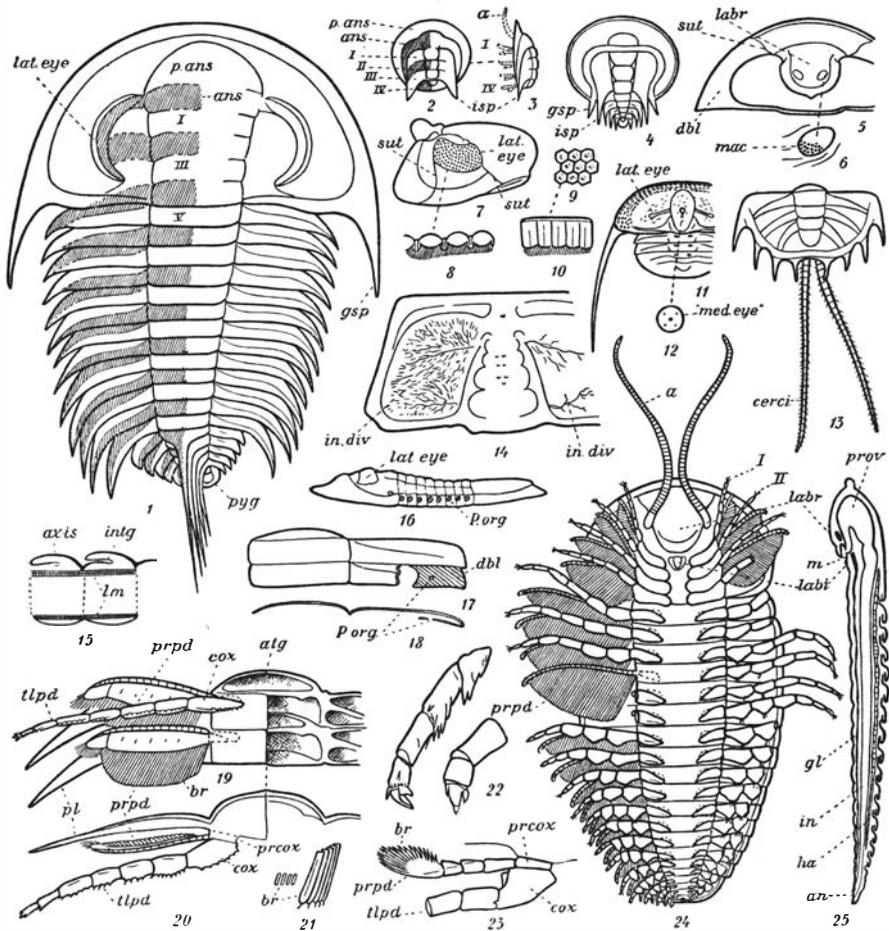


Fig. 5. Trilobita. General morphology.

1 = *Elliptocephalus asaphoides* (Emmons). (After Walcott 1890.) Somites indicated by hatching on the left side of the specimen. 2 = Anaprotaspis of the same species. Reconstruction based on illustrations by Walcott. 3 = The same in lateral view. Probable appendages dotted. 4 = Metaprotaspis of the species. Reconstruction. 5 = *Goldius* sp. Ventral view of cephalon (based on Barrande 1852 and Lindström 1901). 6 = Macula of labrum (after Lindström 1901). 7 = *Phacops* sp. lateral view of cephalon (after Barrande 1852). 8 = Vertical section of lateral eye (after Lindström 1901). 9, 10 = *Asaphus fallax* (Dalman(?)). Horizontal and vertical sections of lateral eye (after Lindström). 11, 12 = *Tretaspis seticornis* (Hisinger). Meraspide larva with median tubercle. 13 = *Neolenus serratus* (Rominger). Pygidium with cerci (based on Walcott 1918). 14 = *Elyx* sp. Probable impressions of intestinal diverticulae (after Jaekel 1901). 15 = *Ceraurus pleurexanthemus* Green. Median section of two thoracic segments (after Størmer 1939). 16 = *Isotelus gigas* DeKay. Lateral view (after Raymond 1920). 17, 18 = Asaphid. Diagram of tergites. Doubleure hatched. 19, 20 = *Neolenus serratus* (Rominger). Ventral and frontal view of thoracic appendages (after Størmer 1939). 21 = gill-blades of a trilobite. 22 = *Phacops* sp. Distal portion of telopodites (after Størmer). 23 = *Ceraurus pleurexanthemus* Green. Frontal view of thoracic appendage (after Størmer). 24 = *Triarthrus eatoni* (Hall). Ventral view. Reconstruction based on Raymond (1920). 25 = Median section of the same species. Internal organs suggested.

I—IV = postoral somites and corresponding appendages, a = preoral antenna, an = anus, ans = antennal somite or segment, axis = mesotergite or axis of thoracic tergite, br = branchiae or gills of appendages, cerci = caudal cerci, cox = coxa, gl = ganglion

certain species elevated on a long, fixed shaft (fig. 7, 20). The visual surface, generally fairly steep, is covered by a lobus palpebralis often connected with the glabella through an eye ridge. The visual surface of the eye contains a highly variable number (from 1 or 2—15 000) of lenses corresponding to separate eyes or facets (fig. 5, 7). In certain forms (Cryptolithidae) probably only one lens is present and numerous species appear to be blind. Richter (1932) demonstrates the successive reduction of the number of lenses in the eyes of Devonian Phacopida. In thin sections the lenses are ellipsoid or more or less prismatic, as shown by Lindström (1901) (fig. 5, 8—10).

Besides the lateral eyes certain writers (Ruedemann 1916 a and Størmer 1930) claimed the presence also of a median eye appearing as a small tubercle or knot on the top of the glabella. In the genus *Tretaspis* (fig. 5, 11, 12) the bottle-shaped glabella has a small pustule which in good preservation shows the presence of five, small pits arranged in a square with the larger one in the middle. The organ is well developed in the larva at a stage in which the lateral eyes appear to be rudimentary (11). In thin sections the shell above the median tubercle is much thinner than the shell around it — a feature also characteristic of the lateral eyes of this form. While the present author was inclined to interpret the median tubercle as a median eye, Hanström (1934), from recent studies on syncarid Crustacea, points out that the peculiar structure of the median tubercle in trilobites shows a striking resemblance to a combined dorsal organ, and four-celled sense organ occurring in these recent crustaceans. It might be mentioned that a dorsal organ is also found in certain Arachnida (Acari), though without the four-celled sense organ (Schulze 1936).

The headshield is intersected by certain lines of weakness, the so-called sutures, which open during the ecdysis and facilitate the shedding of the slough. The significance of the sutures has been subject to extensive discussion. As will be pointed out below, the course of the sutures seems to give a valid basis for a systematic division of the Trilobita. Without going into details concerning the morphology of the sutures, it might be mentioned that we have two major types of sutures, the marginal suture following largely the external margin, and the facial suture crossing the head-shield and running along the upper margin of the lateral eyes. The marginal suture is found in the primitive, Lower Cambrian Olenellida (fig. 5, 1—4 and fig. 7, 5, 10) and in certain peculiar, specialized forms such as the Agnostidae, Cryptolithidae and Harpedida (fig. 5, 11 and fig. 7, 18). The facial

of ventral nerve cord, *gsp* = genal spine, *ha* = heart, *in* = intestine, *in. div.* = intestinal diverticulae, *intg* = softer integument between tergites, *isp* = intergenal spine, *lab* = labrum or hypostoma, *labi* = labium or postoral plate, *lm* = longitudinal muscles, *lat. eye* = lateral eye, *m* = mouth, *mac* = macula, "*med. eye*" = median tubercle of the glabella, *pans* = preantennal somite or segment, *pl* = pleural spine, *P. org.* = Panderian organ, *prcox* = precoxa, *prov* = proventriculum of intestine, *prpd* = prepipodite, *pyg* = pygidium, *sut* = suture, *tlpd* = telopodite.

suture (*sut.* in fig. 5, 7) is found in the great majority of species (as an exception the facial suture may change into a marginal suture by the reduction of the lateral eyes). The facial suture divides the cephalon in a median piece, the cranidium, and two "free cheeks", which very often occur separately in the sediment. The facial sutures sometimes unite in front or continue across the doublure (*sut.* in fig. 5, 5). If a transverse marginal suture is present between the facial sutures in front, a rostral plate may be separated, abutting posteriorly to the transverse hypostomal suture bordering the labrum or hypostoma (*labr.*).

The thorax is covered by moveable tergites, the number of which can vary between 2 (*Agnostida*) (fig. 7, 8) and more than 40 (Olenellida, Menomonidae) (fig. 5, 1; fig. 7, 19 and fig. 15, 6). The tergites have a vaulted axial portion, the mesotergite, and more or less vaulted lateral portions, the pleurotergites. The pleurotergite, which in most cases has an oblique pleural furrow, is often prolonged into a pleural spine. The mesotergite has a frontal plate, the antetergite or articulating halfring (*atg* in fig. 5, 19) which in outstretched position of the body is hidden by the mesotergite in front. The antetergite serves as a sliding plate when the thorax is curved, particularly when the trilobite is enrolled (fig. 7, 15). The tergites are evidently connected by softer integument or membranes just as in other arthropods (fig. 5, 15). Accessory ball- and socket joints between succeeding tergites are indicated in some forms (*Ceraurus*). In the mesotergite the transverse articulating furrow (behind the antetergite) may be secondarily deepened to serve as apodemes (appendifers) for the attachment of muscles chiefly to the appendages. In most trilobites the tergites are mutually homogeneous, but among the Lower Cambrian Olenellida the third tergite may be strongly developed (fig. 7, 5, 10). In the members of the same family the posterior tergites, especially the pleura, may be rudimentarily, deviating distinctly from the tergites in front (fig. 21, 1—5). The mesotergites are often provided with dorsal spines of which one might be specially prominent, resembling a telson (fig. 7, 10, fig. 15, 6), particularly when the rudimentary tail-portion is not preserved.

From comparative studies of trilobite larvae and recent arthropods, especially Xiphosura, there are ample reasons to believe that the transverse joint-lines in the thorax do not coincide with the primary borders of the somites (Størmø 1942). The antetergite apparently belongs to the somite in front, and in the pleurotergite the pleural furrow probably marks the border between two succeeding somites as indicated in fig. 5, 1. The transverse secondary borders are more fit for mechanical hinge-lines than the oblique primary segmental borders.

The pygidium or tail-shield forms a terminal plate of variable size. In the early Olenellida and Paradoxidida the pygidium is very small including one or a few somites (*pyg* in fig. 5, 1; fig. 21, 1—5), but in most cases the plate is of greater size, obtaining in some species the size of the

cephalon and even exceeding it (fig. 5, 11, 13; fig. 7, 1—20). Remnants of the segmentation of the pygidium is seen in the annulated axis, the pleural furrows and "pleural spines" (fig. 5, 13).

With exception of the doublure and the upper lip, the ventral structures are generally destroyed in the preserved trilobites. The labrum or hypostoma (*labr.* fig. 5, 5, 24, 25) forms a vaulted plate which in front is attached to the doublure by a transverse (hypostomal) suture. In a number of species Lindström (1901) has demonstrated in the labrum, the presence of two maculae with a partly granulated surface recalling a vaulted visual surface (*mac.* fig. 5, 5, 6). Lindström was inclined to interpret the maculae as ventral eyes, and his results were supported by Hanström (1926), but other writers such as Jaekel (1901), Holmgren (1916), Richter (1932), and Johansson (1932) doubt their visual nature and describe them as muscle scars. The argument of Holmgren and Johansson postulating that proto-cerebral visual organs cannot occur in the labrum enerved from the tritocerebrum seems to be of minor value since the nerves, according to Snodgrass, are not restricted to primary somites (Snodgrass 1938). The true nature of the maculae is unknown.

Thanks to a few extraordinary finds of beautifully preserved trilobite specimens we are now able to obtain a fairly complete figure also of the other ventral structures in the trilobites. Especially four occurrences have yielded well preserved specimens showing the appendages. Walcott discovered remains of appendages in the genera *Ceraurus* and *Calymene* from the Trenton Limestone in New York State. The delicate structures are plastically preserved in the limestone and have to be studied in thin sections and by serial grindings (Walcott 1881, 1918, 1921, Raymond 1920, Størmer 1939). A wax model made from grinding series is shown in fig. 6. About ten years later new and important finds were made in the Ordovician Utica Shale in New York State. In a number of papers Beecher (1893, 1895 a, b, 1896, 1902) has described the beautifully pyritized appendages of *Triarthrus* and *Cryptolithus*. A magnificent and extensive description of the material was later given by Raymond (1920). The third important occurrence was also discovered by Walcott. The Middle Cambrian Burgess Shale of British Columbia contains excellently preserved specimens of the trilobites *Neolenus* and *Kootenia*. The ventral structures, which appear merely as imprints in the shale, were described by Walcott (1912, 1918, 1921) and supplementary descriptions were given by Raymond (1921) and Størmer (1933, 1939). Besides these American occurrences appendage-bearing trilobites have been found in the well-known Devonian Hunsrück Shale of Germany. Pyritized specimens of Phacops have been described by Broili (1929 a, 1930 a) and Størmer (1939).

The results obtained from the study of these fossils are of considerable general interest. It has become apparent that the morphological characters of the ventral structure in trilobites are essentially the same even in very

different genera belonging to different geological formations. This fact indicates the conservatism and evidently primitive character of the appendages in these old arthropods. In the sequel a general description of the structures is given without further attention to smaller generic divergences.

In a ventral view the posterior portion of the labrum evidently covers the mouth which has a central position on the ventral side of the headshield. Behind the mouth we notice a small plate forming a labium or postoral plate (*labi* in fig. 5, 24, 25). Beecher (1895) and Raymond (1920) mention it as a metastoma, but since it is hardly homologous with the metastoma of the Eurypterida, this name seems little appropriate. The postoral plate is probably a sternal formation and might rather be compared with the endostoma of the Eurypterida. The postoral plate is described in *Triarthrus* only, but in the U. S. National Museum collection in Washington I have noticed a specimen of *Neolenus* with the same type of postoral plate.

The ventral surface of the body was probably covered by a thinner and softer integument which laterally was connected with the doublure. Remains of the integument are preserved in a few specimens of *Triarthrus* and might be seen in thin sections of *Ceraurus* and *Calymene*. Only the portion below the mesotergite represents the sternites. Sections of the body (fig. 5, 15, 20) illustrate the position of the ventral integument.

On either side of the labrum we find the preoral antennae (*a*) which are uniramous, multi-jointed, flexible, tactile organs. The antennae are distinctly preoral and were for this reason evidently enerved from the deutocerebrum just as the antennules of crustaceans and the antennae of Myriapoda—Insecta.

Behind the antennae we notice a number of postoral appendages which are completely uniform as far as the general characters are concerned. This is of particular interest as showing very primitive features with a lack of a specialization of the appendages into distinct tagmata such as in all other known arthropods (except certain related Cambrian forms described in a later chapter). The primitive features recall the Annelida. A deviation from the mentioned uniformity is the presence of a pair of multi-jointed cerci (*cerci* fig. 5, 13) in the genus *Neolenus*. The appendages, which are known in this genus only, probably represent a specialization of the posterior pair of limbs. A slight specialization might also be seen in the somewhat more powerful coxa of the headshield in *Triarthrus* (fig. 5, 24). The headshield always has 4 pairs of postoral appendages.

The trilobite appendage is biramous, recalling the typical biramous feet of the Crustacea (fig. 22). Serial grindings of appendages in *Ceraurus* (Størmø 1939) show that the basal segment of the leg is attached to the ventral integument slightly inside the axial furrow, below the ventral apodeme (appendifer) of the mesotergite. The basal segment is quite short with a transverse extension (*prcox* in fig. 5, 23). Since this small segment is

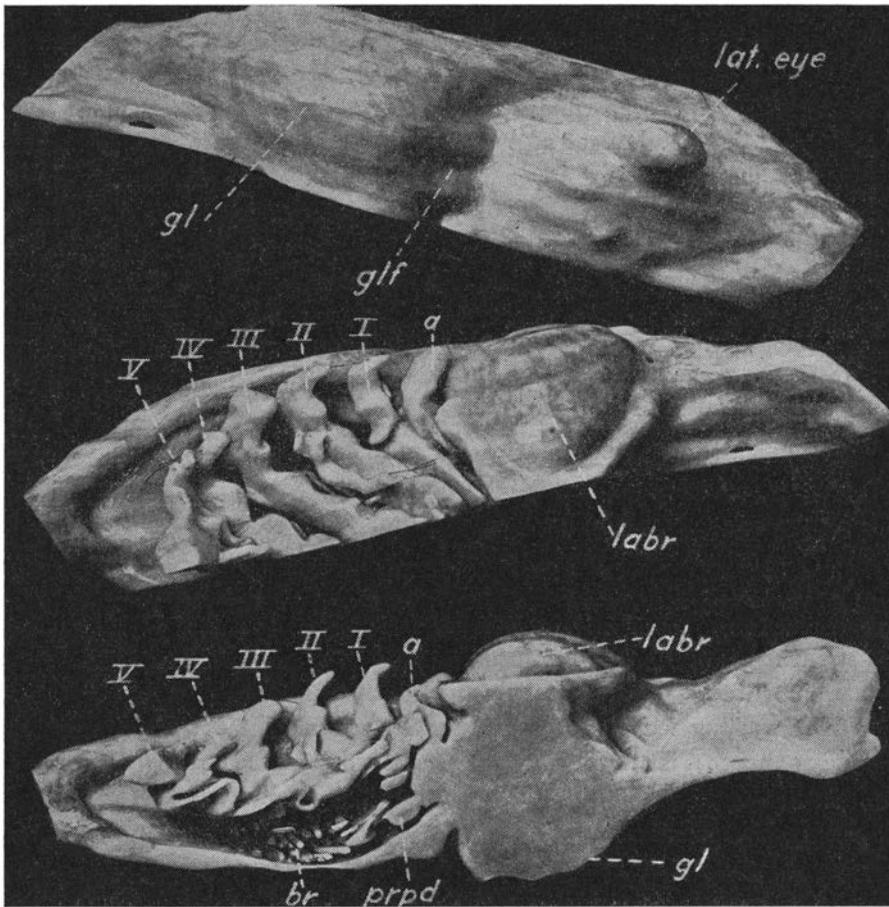


Fig. 6. Cephalic appendages of Ordovician trilobite.

Wax model of cephalon (part) of *Ceraurus pleurexanthemus* Green, made from grinding series. Dorsal, ventral and posterior view. (Specimen not yet described.)

I—V = Postoral appendages, *a* = antenna, *br* = branchiae or gills, *gl* = glabella, *glf* = glabellar furrow, *labr* = labrum or hypostoma, *prpd* = preepipodite.

succeeded by a larger triangular coxa it seems natural to interpret the former as a precoxa or subcoxa.

To the hind surface of the precoxa the gill-branch of the appendage is attached (*prpd* in fig. 5, 19, 20, 23, 24). The gill-branch was previously described as an exopodite or epipodite (erroneously interpreted as an endopodite by Storch (1925, 1926), but the present knowledge suggests it to be a preepipodite since it is attached to the precoxa (further discussion on the interpretation of the structures on p. 119). The gills of the preepipodite are attached to a long shaft which might contain a few joints (*Ceraurus*, 23) or be multi-jointed (*Cryptolithus* and *Triarthrus*, 24), or form a more flat lobe with a rudimentary segmentation (*Neolenus*, 19, 20). The shaft carries a fringe or fan of narrow, blade-shaped gills arranged like the teeth in a

comb (21). The gills are provided with setae at their distal ends. In all genera except *Ceraurus*, the shaft has a distal, spoon-shaped segment lacking gills, but carrying numerous setae. Normally the gills are directed backwards, but in certain specimens they are bent forward suggesting, in spite of a certain flexibility of the gills, some rotation of the shaft. When directed backwards the gills of one appendage are partly covered in ventral view by the succeeding preepipodite, a position which is different to that of the abdominal feet in recent Xiphosura. Evidently the gill-branch of the trilobite limb primarily functioned as a respiratory organ. The peculiar position of the appendages might, however, suggest that the gill-branches also served as a filamentous filter for catching small food particles. By an undulating movement of the gill-branches the particles might possibly have been transported forward to the mouth.

A plough-shaped coxa (*cox* in fig. 5, 19, 20, 23, 24) covers the smaller precoxa. The median point is but slightly projecting. In certain genera the medio-ventral margin is provided with short spines, but since similar spines also occur on the proximal segments of the walking leg or telopodite, they do not necessarily represent gnathal teeth such as indicated in previous reconstructions. Both in the cephalon and the rest of the body the coxae do not meet each other in the median line. This makes it unlikely that the coxae functioned as jaws such as commonly assumed.

The walking leg or telopodite, previously called the endopodite (exopodite of Storch), is attached to the lateral portion of the coxa (*tlpd* in fig. 5, 19, 20, 22—24; fig 6. I—V). This branch has six more or less cylindrical segments, the proximal ones being often projected into triangular endites, especially in the posterior portion of the body (24). The segments carry spines or denticles as demonstrated in *Neolenus* (19, 20) and *Phacops* (22). The six segments might possibly be interpreted as trochanter, prefemur, femur, patella, tibia and tarsus. In addition to these segments comes a distal claw (in *Phacops* apparently attached to a talon or pseudonychium) forming a seventh distal segment or pretarsus (22).

The fact that the trilobite limb is homogeneous in very different species from different formations, shows that the appendage is a characteristic and conservative structure. Moreover the uniformity of the trilobite appendages throughout the body strongly indicates their primitive nature.

Internal organs. Various impressions in the form of darker spots and markings on the dorsal shell have been interpreted as areas of muscle attachments (Moberg 1902, Richter 1923, Öpik 1929, Størmø 1930).

Traces of the intestine are probably seen in the Middle Cambrian species *Skania fragilis* described by Walcott (1931). The small form (5—17 mm), presumably representing a larval stage(?), shows an intestine expanded in front and extending backwards to the last segment. The position of the mouth in trilobites suggests that the oesophagus was directed forwards below a proventriculum occupying the space below the glabella

(*prov* in fig. 5, 25). According to Walcott's reconstruction of *Skania*, short and ramified intestinal diverticulae are observed in the cephalic region. Certain trilobites such as *Elyx* (fig. 5, 14), *Parabolina*, *Dionide*, *Eoharpes* and others, show characteristic, strongly ramified impressions on the cheeks of the cephalon. These structures, projecting as lateral branches from the glabella, are interpreted by Jaekel (1901) as impressions of intestinal diverticulae (*in.div*). The conditions in *Skania* and the structures in other Middle Cambrian Arthropoda (comp. fig. 17 and 19) seems to confirm this assumption. Richter (1932) also mentions the possibility of blood-sinuses or merely supporting structures of the shell.

The so-called Panderian organs are demonstrated in several species mostly belonging to the family Asaphidae (*P.org* in fig. 5, 16—18). The Asaphidae have a broad, dorsal shield with a well-developed doublure extending almost to the axis in certain forms. The Panderian organs appear as small, circular openings in the doublure of each tergite and in the nuchal segment of the cephalon. In accordance with the mentioned interpretation of the secondary segmentation of the pleurotergites, the openings are situated at the border between two primary somites. In certain species the apertures are not situated within the doublure, but only form a small invagination in its median border. The Panderian organs have been interpreted in many different ways, but recent studies by Öpik and Siegfried (Siegfried 1936) give reason to believe that they represent the apertures or primitive segmental organs. If that is the case, we have primitive conditions which recall the structures of the Onychophora in which the nephridiae have external openings in each of the segments. In the true arthropods the external openings are restricted to one or two segments (coxal, antennal, and maxillary glands).

Besides the internal organs mentioned only more indefinite impressions interpreted as vessels of some kind are described.

Ontogeny. In spite of the minute size of the early trilobite larvae, the fossil material has been able to demonstrate many important details of these highly interesting structures. Small oblong bodies have been interpreted as trilobite eggs, but their true nature is uncertain. Very small larvae are known in several trilobite species. The earliest stage, the so-called protaspis, has a continuous dorsal shield not divided by transverse joint-lines. The length of the protaspis varies from 0,24 to 1,3 mm, but was probably larger in certain Ordovician species of which the protaspis hitherto is unknown. The earliest protaspis stages are found in Cambrian species. Our present knowledge suggests that in higher (less primitive) trilobites the earliest protaspis stages were passed within the egg.

In Lower Cambrian Olenellida (fig. 5, 2, 3) the dorsal shield of the earliest protaspis forms a circular vaulted disc with a narrow axis. Not only the axis or glabella, but also the lateral portions of the disc show a distinct segmentation. This larva is evidently the most primitive arthropod larva

known. The frontal portion of the disc forms a broad rim which might be termed the preantennal segment (*p.ans*). The visual surface of the lateral eyes probably belongs to this segment. Behind the rim we notice a more vaulted segment with a median expansion corresponding to the frontal lobe of the glabella. This segment includes the lobus palpebralis (above the lateral eyes), and the antennae evidently belong to this segment. It may therefore be called the antennal segment (*ans*). Behind the antennal segment we find 4 more uniform segments corresponding to the 4 pairs of postoral, biramous appendages of the cephalon. Of these 4 segments the pleurae of the third one are prolonged into the so-called intergenal spines (*isp*) which are well-developed in later larval stages, but become rudimentary in the adult. The genal spines (*gsp*) appear later in the protaspis period and during the further growth they migrate outwards to the genal angles where they remain in the adult.

Early protaspids of *Olenus* in particular (fig. 7, 1), have indicated that the mentioned cephalic segments are formed more or less simultaneously (Størmø 1942). This makes it highly probable that they form primary or larval somites in the sense of Ivanov. This is confirmed by the fact that the succeeding segments are formed one by one in later larval stages and thus evidently represent secondary somites. As already pointed out by Ivanov (1933), Schulze (1936) and Snodgrass (1938) this indicates that the trilobites had 4 primary or larval postoral somites.

The apparent segmentation also of the frontal portion of the protaspis is of general interest. The morphological structures seem to indicate a segmentation of the preoral portion of the head, a portion which by recent authors such as Holmgren, Hanström, Sollaud, and Snodgrass is regarded as a primarily unsegmented archicephalon or acron corresponding to the annelid protostomium. One of the chief arguments in favour of an unsegmented preoral portion has been that: "There is never any external division of the acronal region into segmental areas" (Snodgrass 1938, p. 94). The conditions in the most primitive trilobites indicate, however, an external division which might suggest a primary segmentation also of this portion. The presence of coelomic sacs in the acronal region (pertaining to antennae, transitory preantennal appendages and in the labral region) appear to support this assumption.

With regard to the preantennal segment it is less prominent in the protaspis of less primitive trilobites (fig. 7, 1, 2). During the later ontogenetic development, however, the segment gradually becomes more significant. The ontogeny of different trilobite species suggests that the dorsal development of the preantennal segment has a tendency of being more and more delayed during the phylogenetic evolution of the Trilobita (Størmø 1942).

We may now return to the general ontogenetic development of the trilobite. In many species the larva passes through several protaspis stages

before the first secondary segments appear. The stages comprising only larval somites form the anaprotaspid period. When new, secondary segments are added we have the metaprotaspid period of the protaspis. At a certain stage in the metaprotaspid period (the number of secondary segments varies in different forms) a transverse suture or joint-line is formed which divides the dorsal shield into a head-shield and a preliminary, so-called transitory pygidium. The hinge-line, however, apparently crosses the original segmentation which has a more oblique (less effective) direction across the vaulted protaspis.

The transverse open suture introduces the meraspid stages comprising the period in which thoracic segments are released in front of the transitory pygidium. The secondary segments are formed at the posterior end of the body and pass forward through the transitory pygidium. When the complete number of thoracic segments is attained the trilobite passes into the holaspid period of growth. Numerous ecdyses remain until the larva reaches the adult stage.

Habitat and Adaptive Radiation of the Trilobita.

We shall not attempt to consider the special development of the many different trilobite families, but pay attention to certain morphological features which may be interpreted as expressing different modes of life. At the same time certain tendencies in the evolution of the trilobite stock are suggested.

Associating faunas have shown that the trilobites evidently were restricted to marine waters.

Fig. 7 illustrates some of the more different trilobite types. It plainly appears that the dorsal shield is subject to considerable variation. The shape of the dorsal shield gives us a clue to the understanding of the mode of life of the species. As pointed out by Richter (1919) one has to be cautious, however, not to apply too strictly the principles of Dollo (1910) on the relations between body and function.

The great majority of trilobites were evidently bottom dwellers. They crept and partly swam on and along the bottom and were evidently able to burrow in the mud or sand just as the horseshoe-crab nowadays. Typical benthic forms might be seen in species with a broad dorsal shield and a more central position of the lateral eyes. Some of these species (fig. 7, 12, 13, 19) have a spatulate rostral portion which might have served to shuffle in the mud. In the Cryptolithidae (fig. 5, 11) and Harpedidae (fig. 7, 18) the cephalon is provided with a peculiar broad perforated rim, the function of which is not understood. It is also difficult to interpret the strongly vaulted forms such as *Illaenus* (fig. 7, 16, 17). In many trilobites, both small and large forms, the shell is provided with knobs, tubercles and ribs. As pointed out by Richter (1923), these structures may to a large extent be interpreted as supporting structures serving to strengthen

the shell. But on the other hand a strong development of the shell-sculpture perhaps denotes a "racial senescence" such as indicated in the Eurypterida (p. 51). The sculpture could be more strongly developed into dorsal spines such as expressed in the Lichidae (fig. 7, 20). In this case the spines might serve as protective organs. A strong development of horizontal spines is characteristic of numerous trilobites. Chiefly the genal and pleural spines are prominent, but several species have also a projecting frontal spine (4) or show a strong development of the nuchal and dorsal spines of the axis (7, 10 and fig. 21). The strong development of horizontal spines is common in larvae and smaller trilobites. Probably these elaborate spines serve as floating or balance organs in more or less planktonic forms (fig. 7, 4, 5, 7, 10). The earliest larvae of trilobites were evidently planktonic forms, a fact which explains the considerable horizontal distribution of many species (Raymond, 1920).

Many trilobites were probably active swimming forms, but the structure of the appendages does not offer a clear demonstration of their swimming functions. It has been emphasized that narrow species with a more marginal position of the lateral eyes, were nectonic forms. *Triarthrus* (fig. 5, 24, 25, and fig. 7, 9) and *Phacops* with their appendages extending beyond the margin of the dorsal shield, might have been active swimmers.

The development and position of the lateral eyes are subject to considerable variation among the trilobites. Large visual surfaces are noticed in certain forms such as *Cyclopyge* (fig. 7, 14) and *Remopleurides*. From these types we find all transitions into very small and simple eyes such as in the Cryptolithidae (fig. 5, 11) and Harpedidae (fig. 7, 18). Even blind forms, such as the Agnostidae (8) and Raphiophoridae (4) occur. Dollo (1910) assumed that the large-eyed *Cyclopyge* lived in comparatively deeper waters. As shown in recent Crustacea, however, the size of the eyes is hardly a reliable indicator of the light conditions under which the arthropod lived. This is supported by the fact that in a coarse sediment, an interformational breccia indicating littoral facies, occurring in the Middle Ordovician (4a β) of Ringerike in Norway, a large-eyed *Remopleurides* is found together with species of *Trinucleus* with very small, apparently rudimentary lateral eyes.

Little is known as to the nourishment of the Trilobita. The lack of jaws suggests that most species were mudfeeders.

Concerning the general evolution of the trilobite stock, it might be mentioned that statistical, bio-stratigraphical research on Upper Cambrian Olenidae has indicated a gradual transition from one subspecies into another (Kaufmann 1933). Throughout the Upper Cambrian the evolution of the Olenidae takes place along different lines. One trend of development produces small forms with strongly developed horizontal spines suggesting planktonic habits (*Ctenopyge*, *Sphaerophthalmus*), while another line demonstrates the successive loss of spines (*Peltura*, *Acerocare*).

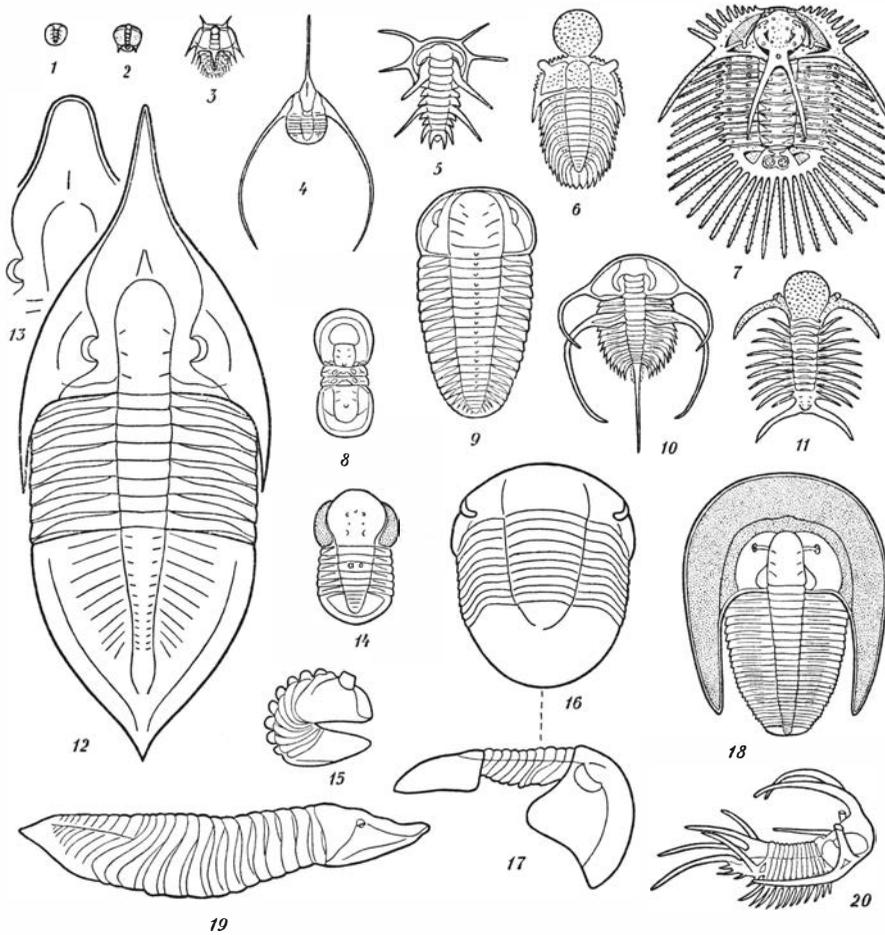


Fig. 7. Trilobita. Diversity in form.

1, 2 = *Olenus gibbosus* (Wahlenberg). Protaspis. Length 0,3, 0,5 mm. Upper Cambrian (after Størmer 1942). 3 = *Leptoplastus salteri* (Callaway). Meraspis larva. 1,1 mm. Upper Cambrian (slightly modified after Raw 1925). 4 = *Lonchodomas rostratus* (Sars). Med. length 31 mm, Ordovician. Reconstruction based on specimens from zone 4a β , Frierfjord, Norway. 5 = *Olenelloides armatus* Peach. Larva (?), 10 mm, Lower Cambrian (after Walcott 1908). 6 = *Steurocephalus purchisoni* Barrande, Silurian, 30 mm (after Salter 1864). 7 = *Radiaspis radiata* (Goldfuss). 17 mm, Devonian (after Richter 1919). 8 = *Condylopyge regia* (Sjögren). 8 mm, Middle Cambrian (after Westergård 1936). 9 = *Triarthrus eatoni* (Hall). About 25 mm, Ordovician. Reconstruction based on illustrations by Raymond and Walcott. 10 = *Olenellus fremonti* Walcott. 50 mm, Lower Cambrian (slightly modified after Walcott 1906). 11 = *Deiphon forbesi* Barrande. 28 mm, Silurian (after Barrande 1872). 12 = *Megalaspis acuticauda* Angelin. Up to 400 mm, Ordovician. Reconstruction based on Brøgger (1882) and Schmidt (1906). 13 = *Megalaspis acuticauda*, var. *obtusata* Schmidt. Ordovician. Frontal portion of cephalon (after Schmidt 1906). 14 = *Cyclopyge prisca* (Barrande). 11 mm, Ordovician (after Barrande 1872). 15 = *Asaphus expansus* Dalman. Normal length about 10 mm (after Schmidt 1901). 16, 17 = *Iliaenus sinuatus* Holm. 60 mm, Ordovician (after Holm 1886). 18 = *Harpes unguis* Sternberg. 32 mm, Silurian (after Barrande 1852). 19 = *Trimerus delphinoides* (Green). 155 mm, Silurian (after Salter 1864). 20 = *Ceratarges armatus* (Goldfuss). 35 mm, Devonian, Dorso-lateral view (after Richter 1919).

The development of the Asaphidae seems to indicate a more general principle in the evolution. The earliest representatives of typical Asaphids, *Promegaspides* and *Niobella*, are known from the Upper Cambrian *Peltura*-zones of Sweden (Westergård 1939). It is of interest to follow the genus, *Megalaspis*, in its development in the Lower Ordovician of the Scandinavian-Baltic regions. In the *Ceratopyge*-zones (3a β —3a γ) and in the Lower Didymograptus Shale (3 b), only small species occur (*M. intacta*, *M. stenorachis*). The further development is best studied in the Baltic section. It emerges from the description of Schmidt (1906) that the earliest species occurring in B₁, *M. pogrebowi* and *M. planilimbata*, are of moderate size. In B_{2a} *M. larvae* is of a similar size, while *M. limbata* and *M. polyphemus* are bigger. In the following zones, B_{2b}, B_{3a}, B_{3b}, we notice an increasing size of the Megalaspidae. Large forms such as *M. Hyorhina*, *M. acuticando* occur in the lower zone (together with the less imposing *M. extenuata*) and the upper zones are characterized by *M. gibba*, *M. lawrowi*, *M. centaurus* and *M. gigas* (the latter characteristic of the Scandinavian section). The development of the genus *Megalaspis* thus indicates a gradual increase in size during the evolution of the stock. Similar tendencies can possibly be traced in other groups of Asaphidae, at least it might be noticed that the largest species of *Asaphus* and *Isotelus* occur in the Middle and Upper Ordovician.

It is of interest to consider also another problem in connection with the general evolution of the Trilobita. Clarke (1913) mentions that the development of Devonian species indicate an increasing specialization leading towards "racial senescence". Richter (1932) has demonstrated the gradual reduction of lateral eyes, a reduction leading to blindness, in certain Devonian families. A successive specialization illustrating "racial senescence" has not been clearly demonstrated in fossil series of trilobites, but if we compare the Siluro-Devonian species with those of the older formations, we are inclined to conclude that a more pronounced specialization is indicated in the dorsal shield of the later representatives. The highly spiniferous species *Acidaspis* and *Lichas* (*Ceratarges*) (fig. 7, 7, 20) can probably be interpreted as exponents of "racial senescence" although the highly specialized spines also to a great extent might have served as floating and protecting organs.

We have seen that the trilobite stock was subject to considerable variation in shape and size, and was adapted to different modes of life in marine waters. But what is of particular interest to us is the fact that, in spite of the considerable variation, the dorsal shield and the ventral structures (as far as we know) have maintained the distinct plan of construction which is characteristic of the trilobite type. The conservatism of the general plan of construction in the trilobites, lead Pampeckj, Richter and others to the assumption that this group hardly gave rise to direct descendants.

Taxonomy.

It is beyond the scope of the present paper to deal with the systematic relations of the numerous trilobite families and genera. We might, however, briefly discuss the basis of a possible natural classification of the group. Several different morphological characters have been attributed systematic value, but no individual characters seem to warrant a natural classification into separate orders. Most authors abide by a division based on the course of the cephalic sutures. The Salter-Beecher system of classification, which more recently is discussed by Richter (1932) and Stubblefield (1936), in the main divides the trilobites into two major groups characterized by the course of the facial suture. In the order Opisthoparia the suture reaches the margin inside the genal spine, and in the Proparia the suture crosses the margin outside (in front of) the spine. Species with a distinct marginal suture (lacking the facial suture) were primarily included in the order Hypoparia, but more recent writers are generally inclined to regard the Hypoparia as an artificial group embracing more aberrant forms in which a facial suture is lost or has migrated to the margin. The ontogeny has demonstrated that the Opisthoparia passes through a proparian stage in their larval development. The geological appearance, however, does not agree very well with the assumption of the Proparia being ancestral to the Opisthoparia.

If the cephalic sutures had not empirically appeared to be useful in the classification, one would have been cautious in applying a "mechanic" structure such as the line of ecdysis as a basis for a natural classification. In many recent arthropods the shell breaks up along more indefinite lines although a marginal suture seems to be a primary feature in primitive forms (Henriksen 1931). In a recent paper (Størmer 1942) I have tried to show that a natural basis in classification is to be found in the combined development of the preantennal segment and the cephalic sutures. In the primitive Olenellida (certain authors claim this old group to be specialized) and probably also in the Hypoparia the preantennal segment (*p.ans.* in fig. 5, 1, 2) is well developed on the dorsal surface already in the protaspis stage. Among the Opisthoparia on the other hand (fig. 7, 1, 2) we notice a retarded development of the segment, and in the Proparia it is still more delayed, being incompletely developed even in the adult, at least in the lateral portions of the headshield. In the early larvae of all trilobites the cephalic sutures evidently first appear as a marginal, mechanical suture serving the ecdysis. During the further larval development the preantennal segment and the primarily marginal lateral eyes develop and migrate inwards on the dorsal surface. The previously marginal suture naturally follows the development of these structures, and is hence transformed into a facial suture. The reason why the suture does not remain marginal but runs along the eye is probably due to the difficulty in releasing the eyes during the ecdysis.

According to the present interpretation the proparian ontogenetic stage of the Opisthoparia need not indicate a deviation of the latter from the former, but might signify, in the sense of Schindewolf's principle on "Frühontogenetische Typenbildung", the introduction in the larva of a new character, in this case the retardation in the development of the preantennal segment. The present conception seems to justify the division of the Trilobita into four orders: The Protoparia, Hypoparia, Opisthoparia, and Proparia. The exact position of the Hypoparia is not certain on account of the lack of knowledge of the protaspis. The Proparia might probably be a polyphyletic group including separate families which are derived from different groups of Opisthoparia as suggested by Kobayashi (1935).

Eurypterida.

In contrast to the Trilobita the Eurypterida, or Gigantostraca as they have often been called, are known in a more restricted number of species. Only a little more than 200 species belonging to 22 genera and subgenera, and 4 families are described. The modest number of species is primarily due to the fact that these arthropods were not marine and their fossil remains therefore are confined to the less common continental sediments. The eurypterids are chiefly known from fresh-water and brackish-water sediments of the late Silurian and Devonian, but there are ample reasons to believe that these so-called sea-scorpions had a considerable development, possibly their acme of evolution, in the Ordovician and early part of the Silurian.

The eurypterids early attracted the attention of scientists and laymen. Their formidable size (up to at least 180 cm), and the excellently preserved specimens discovered from time to time, have made the eurypterids a favourite subject to the students of fossil arthropods. Well-preserved specimens were found in the Silurian waterlimes of New York State and described already in the earlier part of the last century by DeKay and Hall. British forms, including the giant "Seraphims" of Scotland, were described in detail by Huxley and Salter, and Woodward in the years from 1859—1878. Thanks to the excellently preserved specimens from Silurian waterlimes of Ösel (Saaremaa) in Esthonia, Schmidt (1883) and especially Holm (1898) succeeded in obtaining a detailed conception of the morphology of these extinct forms. The Baltic specimens have the primary chitinous skeleton largely preserved and Holm managed to dissolve the surrounding lime so that the "exuviae" could be studied imbedded in Canada Balsam like a recent object. Fig. 8 illustrates one of his specimens.

Our detailed knowledge of the external morphology of the Eurypterida is also due to the extensive studies by Clarke and Ruedeman (1912) on American forms, among others a number of species from the Ordovician. Additional knowledge is also obtained through the discovery by Kiær of a

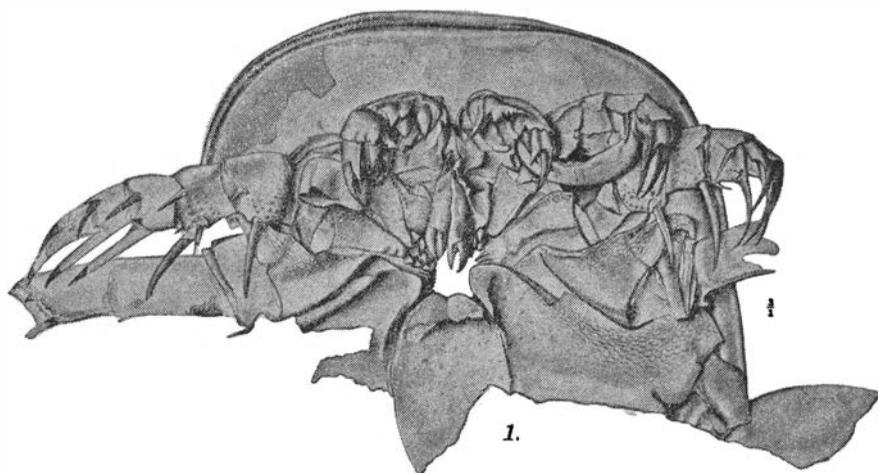


Fig. 8. Ventral surface of prosoma of Silurian eurypterid.

Etched specimen of *Eurypterus fischeri* Eichwald, from Esthonia. The small chelicerae are visible in the middle, in front of the mouth, (after Holm 1898, pl. 3 fig. 1).

rich eurypterid fauna from the Downtonian in Norway (Størmer 1934 a), and from well preserved Devonian forms from Germany (Størmer 1936).

The body of the eurypterid is covered by a chitinous skeleton which evidently contained less lime than was the case with the trilobite shell. The detailed structure of the shell has not been described, but in several cases numerous fine canals penetrating the shell have been demonstrated especially in the doublure of the abdominal appendages (Clarke and Ruedemann 1912, Størmer 1936).

The sculpture of the shell is very characteristic in the eurypterids. The beautiful scale- or feather-like sculpture of the big *Pterygotus* caused the workmen of the Scottish quarries in the old days to speak of these fossils as remains of giant petrified "seraphims". The most primitive type of sculpture is evidently demonstrated in the genus *Hughmilleria*. The shell is mostly smooth, but in front the prosoma is provided with numerous more or less parallel lines (folds in the integument) resembling closely the terrassic lines in the doublure of the trilobite shell. A further elaboration of this structure is to be seen in the rows of linguiform "scales" of the related genus *Pterygotus* (fig. 9, 20, 22). The scale-like sculpture is confined to distinct parts of the dorsal and ventral surface of the body (fig. 10, 1). In other genera, such as *Eurypterus* and *Stylomurus* the scales are more pointed (fig. 9, 16; fig. 10, 4, 5), and this type forms a transition to the round or oblong tubercles of *Carcinosoma* and *Mixopterus* (fig. 10, 2, 3). Carboniferous species often show a pronounced development of the sculpture. *Anthracopterus* is provided with coarse, pointed scales (Clarke and Ruedemann 1912) and *Glaucodes* has a special reticulate sculpture (Pruvost 1924).

In addition to the sculpture mentioned, the presence of fine hairs have been demonstrated in well-preserved Baltic and German eurypterids, particularly on the softer integument between the prosomal appendages (Holm 1898, Størmø 1936, Tobien 1937).

The elongate eurypterid body has a distinct scorpionid appearance. The body is divided into a headshield or prosoma, and an abdomen or opisthosoma comprising 12 segments and a terminal telson. In contrast to the conditions in the trilobites the number of segments is always the same. In several genera, particularly among the Carcinosomidae (fig. 10, 2, 3), (also in *Hughmilleria* in fig. 9, 1—3), the abdomen is divided into a broader 7-segmented preabdomen, and a more narrow postabdomen of 5 segments with telson. Another division of the abdomen or opisthosoma has been suggested. The 6 anterior appendage-bearing segments are included in a mesosoma, and the 6 posterior segments without appendages form the metasoma.

The prosoma is moderately convex with a semiparabolic to subquadratic outline. The prosoma is provided with two sets of visual organs, the lateral eyes and the median ocelli. The lateral eyes are generally kidney-shaped or ovate in outline (*lat. eye* in fig. 9, 1, 19). The visual surface contains numerous close set pits indicating the individual facets. The size and position of the lateral eyes are subject to considerable variation as shown in fig. 10.

The median ocelli (*m. oc.* in fig. 9, 1, 18) have a central position and are often slightly elevated on a median node.

The abdomen is covered by a number of movable tergites connected by a softer integument (demonstrated in *Rhenopterus*, Størmø 1936). The first tergite is attached to the prosoma by a special hinge formed by the doublure (Holm 1898). In most cases the frontal tergite is shorter than the posterior ones. This indicates a partial reduction of this segment which probably represents the frequently reduced pregenital segment of the Arachnida. (I. a. the carboniferous genus *Glaucodes* (Pruvost 1924) shows a very strong development of the first tergite.) As mentioned below it is hardly any reason to believe that the pregenital segment is completely reduced in the eurypterids just as in the scorpions.

In general the abdomen is not divided into axial and pleural portions such as the body of trilobites. Only *Mixopterus* (fig. 10, 3) has distinct axial furrows in the preabdomen. Occasionally the abdomen has short lateral "fins", especially in the seventh and twelfth segments. Each tergite has a lateral and posterior deflexed border or doublure. The six posterior tergites are fused with their respective sternites and form solid rings telescopically inserted into each other. Especially in the scorpion-like Carcinosomidae (fig. 10, 2, 3) the slender postabdomen might have had a great mobility.

The telson (*tel.* in fig. 9, 1—3) has commonly a lanceolate outline with a dorsal keel and a flat ventral surface. From this primary type is evidently derived the long styliiform telson of the Stylonuridae (fig. 10, 4) and the curved spine of the Carcinosomidae (fig. 10, 2, 3). The scorpionid tail-spine of the latter forms might have been poisonous. Also the broad spatulate telson of *Pterygotus* (fig. 10, 1) evidently developed from lanceolate types. The genus *Slimonia* (Woodward 1866—1878) illustrates a transitional stage in which the anterior portion of the lanceolate telson has broad fins similar to the telson of *Pterygotus*. Recent material of Devonian *Pterygotus* of Germany (Størmer 1936) has shown that the telson is provided with a median vertical crest giving the telson an appearance and function of a complete tail-rudder comparable to the rudder of an aeroplane or torpedo.

The ventral surface of the prosoma has a broad doublure (*dbl.* in fig. 9, 6) passing medially into a softer integument surrounding the appendages and the mouth. A marginal suture (or week line in the test) appears to be a constant feature in the Eurypterida. Additional sutures are seen crossing the doublure in front (*sut.* in fig. 9, 6). Two pairs of sutures seem to be present in *Hughmilleria*, and one pair, which is sometimes united into one median suture (*Eurypterus*, *Rhenopterus*), in other genera. The sutures outline a median plate (*ep.*) which probably corresponds to the rostral plate and parts of the labrum in trilobites. Certain impressions near the posterior border might suggest olfactory organs (*ol. o.?*).

The mouth has a central position surrounded by the prosomal appendages. A glance at the appendages readily shows a marked difference compared with the trilobite-structures. Instead of a number of uniform appendages we notice a pronounced specialization in the different pairs of legs. In front of the mouth the trilobitan antennae are replaced by a pair of pincers or chelicera. The 3-segmented appendage is generally quite small as might be seen in *Eurypterus* (fig. 8, fig. 9, 8 and fig. 10, 5). The chelicera are more prominent in *Hughmilleria* (fig. 9, 3) and attain a formidable size in *Pterygotus* (fig. 10, 1). In this genus the basal segment is greatly prolonged and the two distal segments forming the pincer are provided with long, powerful, flat, and striated teeth. As discussed in a later chapter (p. 118) the chelicera are evidently postoral appendages (*I*) and therefore not homologous with the preoral antennae (*a*) of the Trilobita and other arthropod groups.

Beyond the chelicera the prosoma of the Eurypterida has 5 pairs of uniramous appendages. The 4 anterior pairs are always developed as walking legs, more or less modified. Each leg has a large triangular coxa provided with teeth along the oral margin (fig. 9, 9—11). A small epicoxite (*epcox*) might be interpreted as a rudiment of a precoxa. The leg or telopodite has 7—8 segments (including the distal claw or pretarsus). The individual segments are more or less telescopically inserted into each

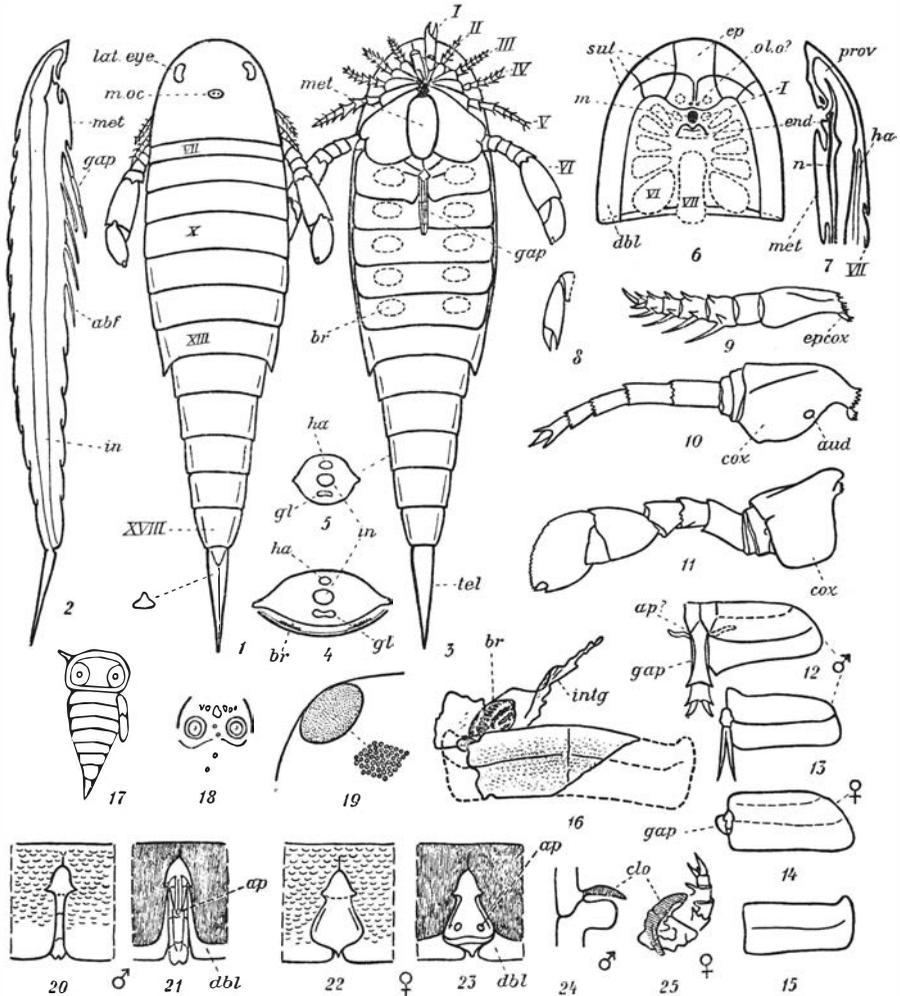


Fig. 9. Eurypterida. General morphology.

1—7 = *Hughmilleria norvegica* (Kiær). Length about 10 cm, Uppermost Silurian. 1 = dorsal view. 2 = median section with intestine suggested. 3 = ventral view. 4, 5 = cross-section of abdomen with internal organs indicated. 6 = ventral view of prosoma with appendages removed. 7 = median section of prosoma with assumed outline of intestine. 8—16 = *Eurypterus fischeri* Eichwald. Upper Silurian. (After Holm 1898). 8 = chelicera. 9 = walking leg (IV). 10 = walking leg (V). 11 = swimming leg (VI). 12 = Operculum (VIII). 13 = second abdominal gill-appendage (IX). 14 = Operculum (VIII). 15 = posterior gill-appendage. 16 = abdominal feet with gills or branchiae preserved. 17 = *Stylonurus myops* Clarke. Larva, length 1,8 mm, Silurian. (After Clarke and Ruedemann 1912.) 18 = *Eurypterus fischeri* Eichwald. Median ocelli. Upper Silurian. (After Holm 1898). 19 = *Pterygotus* sp. Lateral eye, with magnification of facets. Lower Devonian. 20—23 = *Pterygotus rhenaniae* Jaekel. Genital appendage of operculum. Lower Devonian. (After Størmer 1936). 20, 21 = ventral and dorsal view of male. 22, 23 = ventral and dorsal view of female. 24 = *Mixopterus kiari* Størmer. Clasp organ in first walking leg of male (II). Uppermost Silurian. (After Størmer 1934 a). 25 = *Eurypterus fischeri* Eichwald. Clasp organ in second walking leg (III) in female. Upper Silurian.

I—XVIII = postoral somites with corresponding appendages, *abf* = abdominal feet, *ap* = opening of genital duct, *aud* = auditory (?) organ, *br* = branchiae or gills,

other. The segments are commonly provided with a double set of ventral spines. In more specialized forms we notice a tendency of elaboration in these spines, as can be seen in the Carcinosomidae and Stylonuridae (fig. 10, 2—4). The leg segments might be interpreted as follows: precoxa?, coxa, a single or double trochanter, prefemur, femur, patella, tibia, tarsus, and pretarsus.

The fifth pair of legs (sixth pair of appendages) is in most species developed as a pair of swimming feet (*VI* in fig. 9, 1, 2, 11; fig. 10, 1—3, 5). Only in the Stylonuridae the last pair of legs is shaped as walking legs similar to those in front. In the typical swimming leg the distal segments of the telopodite are flattened out forming an oarblade-like palette analogous with the legs of the swimming crab. Interesting features are noticed in the hind legs of the Stylonurid genus *Dolichopterus*. In this genus described by Clarke and Ruedemann (1912) the sixth leg is evidently secondarily converted from a walking leg into a swimming leg. But in this case the ultimate segment forms the main part of the palette, not the penultimate as in other forms.

In spite of considerable variation in the development of the legs of different eurypterid species, it is of importance to notice that the general plan of construction is strictly maintained even in the strong development of the chelicera of *Pterygotus* and in the elaboration of the swimming leg of different genera.

The denticular oral margin of the coxa indicates that they to some extent acted as jaws.

In the coxa of the fourth walking leg of *Eurypterus*, Holm (1898) demonstrated a circular perforation apparently covered by a membrane, which he interprets as an auditory organ (*aud* in fig. 9, 10).

The mouth is bordered posteriorly by a small plate, the endostoma (*end* in fig. 9, 6, 7) which apparently is derived from anterior prosomal sternites and might be homologous with the labium or postoral plate in the Trilobita.

The endostoma is largely covered by a more prominent ovate plate, the metastoma (fig. 8; *met* in fig. 9, 2, 3, 7) which also covers parts of the large coxae of VI. From a comparison with the Xiphosura there is reason to believe that the metastoma represents the anchylosed appendages of the first abdominal segment (VII), the so-called pregenital segment.

The prosoma of the Eurypterida hence has 6 pairs of postoral appendages, and a modified seventh pair belonging to the abdomen seems to have been incorporated.

clo = clasping organ, *cox* = coxa, *dbl* = doublure or reflexed border, *end* = endostoma, *ep* = epistoma, *epcox* = epicoxite or precoxa(?), *gap* = genital appendage, *gl* = ganglion, *ha* = heart, *in* = intestine, *intg* = soft integument, *lat. eye* = lateral eye, *m* = mouth, *m.oc* = median ocelli, *met* = metastoma, *ol.o?* = possible olfactory organ, *prov* = proventriculum of intestine, *sut* = suture, *tel* = telson, *v.ol* = ventral olfactory organ(?).

The abdomen is covered by a series of plates which have the appearance of typical sternites. A more careful investigation, however, shows that the five anterior plates (mesosoma) differ distinctly from the typical sternites of the hind part (metasoma) of the body. The presumed sternites in front are loose plates only attached along the anterior border. The plates (*abf* in fig. 9, 2, 3, 12—16), overlapping each other backwards, are more or less separated along the median line. There is a division in the anterior plates, while the posterior ones are often united into one continuous plate. From a comparison with the abdominal appendages of the Xiphosura it is evident that the plates represent modified appendages. Transverse lines of pigmented scales seem to indicate traces of a rudimentary segmentation.

The plate-shaped appendages have a ventral doublure, and in the soft integument inside the doublure, the gills occur in special oblong areas (*br* in fig. 9, 3, 4, 16). The exact nature of the branchiae is unknown, but if they had been typical book-gills, one would certainly have found traces of them in the magnificently preserved eurypterids from the Baltic.

The first pair of abdominal plates is modified into an operculum (fig. 9, 3, 12, 14). The operculum forming the appendages of the eighth postoral somite has a median genital appendage (*gap* in fig. 9, 2, 3, 12, 14, 20—23) which occurs in two different modifications demonstrating a sexual dimorphism in the Eurypterida. In *Eurypterus* one of the sexual types (12) has a long 3-segmented appendage, while the other (14) merely has a short broader process. In the first type also a median process of the second pair of abdominal plates (13) takes part in the formation of the organ.

More details concerning the structures of the genital appendage are obtained from new material of well-preserved specimens of *Pterygotus* from Germany. In this form (Størmer 1936) the genital appendage is either narrowly lanceolate (20, 21) or of a broad pear-shaped type (22, 23). Both types consist of 3 segments. On the inside (dorsal side) of the pear-shaped form we notice in the basal segment the indications of two fairly large ovate openings (*ap*, 23) which probably represent the apertures of the oviducts. In the lanceolate type a small opening, probably a combined aperture of the vasa deferentia, occurs in the corresponding segment. Two parallel canals are indicated in front of the opening.

A sexual dimorphism is also indicated in the presence of clasping organs in certain forms. The male of *Mixopterus* has a clasping organ (resembling that in *Limulus*) on the basis of the first walking leg (*clo* in fig. 9, 24; fig. 10, 3). A female clasping organ is noticed in an oblong process on the second walking leg of *Eurypterus* (fig. 8, *clo* in fig. 9, 25).

The ventral plates of the posterior six segments (metasoma) are typical sternites united with the dorsal tergites into continuous rings (fig. 9, 5).

Internal organs. Very little is known of the internal structures. Only one specimen of *Carcinosoma* is described demonstrating imprints of

intestine (Ruedemann 1916 b). Probably most of the eurypterid specimens found are the empty exuviae from the numerous moultings.

Ontogeny. The earliest larval stages of the Eurypterida are unknown. Small larvae (2—3 mm), certainly not well-preserved, are described by Clarke and Ruedemann (1912) from the Silurian (fig. 9, 17). Characteristic of the youngest stages is the smaller number of abdominal segments, and that the lateral eyes seem to be situated on elevated nodes.

Habitat and Adaptive Radiation of the Eurypterida.

The absence of eurypterids in typical marine faunas, and their presence in continental sediments show that they lived in fresh or brackish water. Fig. 10 and fig. 9, 1 give an impression of the range of variation in the body of the Eurypterida. It seems possible from the morphological characters to draw certain conclusions as to the habits of the different types. The Stylonuridae (fig. 10, 4) with their 5 pairs of walking legs (the first pair hardly acted as effective legs) and the central position of the lateral eyes were evidently typical benthonic forms. They probably walked like terrestrial arachnids with the abdomen in an elevated position. Possibly some species occasionally might endure the life on land (the gills are well concealed below the abdominal appendages). Many of the other eurypterid genera were also bottom dwellers. The flat Eurypteridae (5) and the peculiar Carcinosomidae (2, 3) evidently belonged to the benthos, but at the same time the characteristic swimming legs indicate that they were actively swimming forms. The swimming legs might also have been useful balancing and steering organs during the swimming, and at the same time they seem well adapted to the digging in the mud and sand. The frontal position of the lateral eyes and the peculiar development of the anterior legs in *Carcinosoma* and *Mixopterus* suggest predaceous habits in these scorpion-like forms. The long spinous appendages probably served as tactile and catching organs. The tail with the possibly poisonous spine was probably able to bend forward above the body and sting just as in the terrestrial scorpions.

Typical nectonic species are seen in the Pterygotidae. The beautifully "stream-lined" *Hughmilleria* (fig. 9, 1—3) was well adapted for rapid movements through the water. Swimming was effected through movements of the swimming legs, but it is possible that rapid strokes of the abdominal appendages could result in a rapid shooting forward of the body (as indicated by the larvae of *Limulus*).

Concerning the nourishment of the eurypterids, the appendages and the powerful teeth-bearing coxae suggest that these forms were able to feed on larger objects, probably including animals with a solid external skeleton.

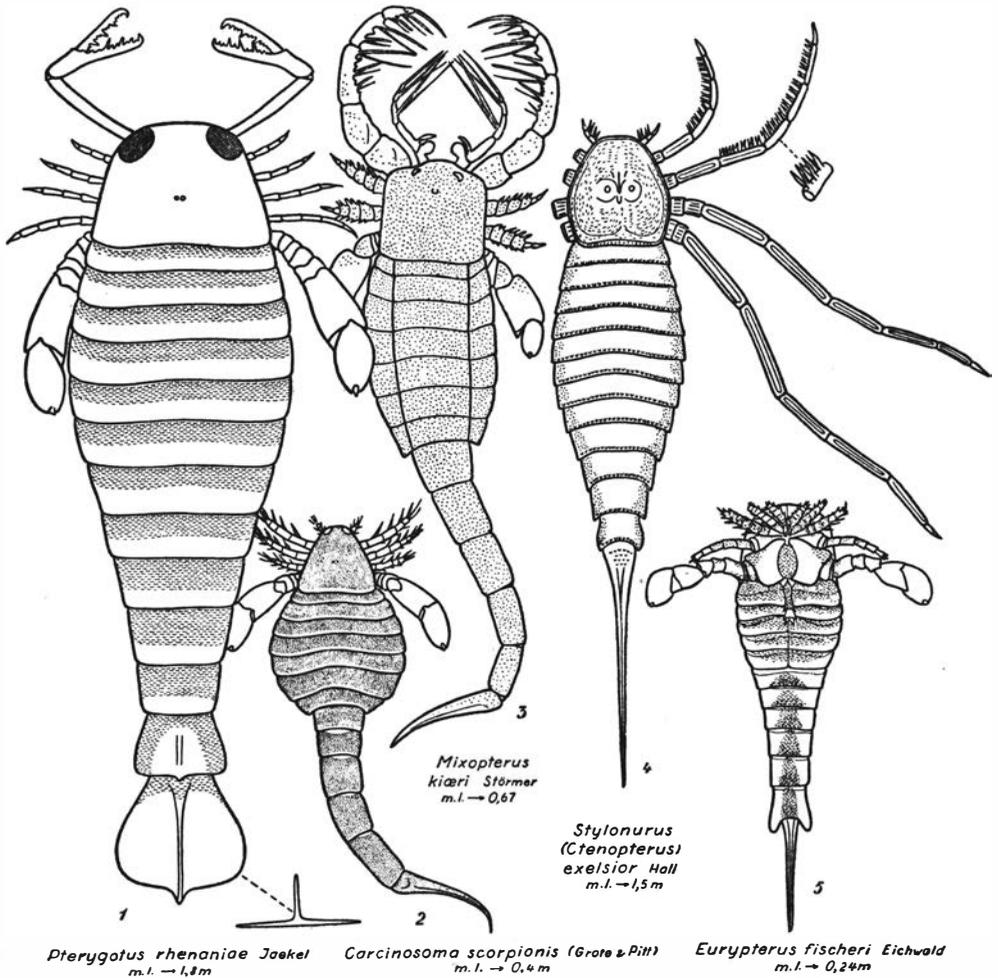


Fig. 10. Eurypterida. Diversity in form.

1 = *Pterygotus rhenaniae* Jaekel. Lower Devonian. Reconstruction. 2 = *Carcinosoma scorpionis* (Grote and Pitt). Upper Silurian (after Clarke and Ruedemann 1912). 3 = *Mixopterus kieri* Størmer. Uppermost Silurian (after Størmer 1934 a). 4 = *Stylonurus* (*Ctenopterus*) *excelsior* Hall. Middle Devonian (modified after Clarke and Ruedemann 1912). 5 = *Eurypterus fischeri* Eichwald. Upper Silurian.
Ventral view. (After Holm.)

Since very few non-marine fossiliferous sediments occur in the Cambrian and Ordovician, little is known of the early evolution of the Eurypterida. Ruedemann has shown that most genera were present already in the Ordovician. From the Cambrian, Beecher (Clarke and Ruedemann 1912) described *Strabops thacheri* (fig. 14, 13, 14) which by some authors is regarded as a true eurypterid. As shown below, however, recent studies of the genus rather indicate its belonging to an order of the Xiphosura.

In following the evolution of the Eurypterida, from the Ordovician through the Palaeozoic to their probable extinction in the Permian, we notice

certain characteristic features. The Ordovician species are generally comparatively small, and exception is formed by the genera *Megalograptus* and *Echinognathus*, the latter attaining a length of 1 m. In the Upper Silurian and particularly in the Devonian strata a larger number of very big forms occur. From Devonian sediments the largest known arthropods are described. *Stylonurus* (fig. 10, 4) measured 1—1,5 m in length, and several species of *Pterygotus* attained a length of at least up to 1,8 m. In the Carboniferous and the Permian the smaller "normal-sized" eurypterids (not of the same genera or sub-genera) prevail. The evidence suggests a gradual increase in size during the early evolution of the stock. It seems probable that the large forms of the Ordovician belong to genera which might have had their main development in the earliest part of the Ordovician.

Together with the increasing size we notice a tendency towards an elaboration of the sculpture. Clarke and Ruedemann (1912) point out that the strong development of the scales in *Anthraconectes* is significant of racial senescence.

We have seen that the Eurypterida form a very distinct arthropod group. Like the trilobites its members have a characteristic plan of construction which is maintained in spite of considerable external variation. The group has little in common with the contemporaneous trilobites, but we shall see that among the living members of the Chelicerata forms exist which may form a link between these two important fossil groups.

Taxonomy.

The four families are distinguished by differences in the development of the dorsal shield and the ventral appendages.

Arachnida.

It is difficult in a brief account to give an impression of the morphology of this large and highly differentiated group. In the following special stress is laid on the structures which are of interest in a comparison with fossil forms. The internal organs are but briefly mentioned or left out in the description. The present account is chiefly based on recent papers of Kästner.

The class Arachnida includes 4 extinct and 9 recent orders. With few exceptions the members of the class are terrestrial forms. Certain spiders and a number of mites are secondarily adapted to aquatic life and others live as parasites. Among recent arachnids the Araneae comprise a very great number of species, more than 20 000 are described. The Opiliones include more than 2000 species, and the Acari, of which only a part of the existing forms are described, amount to 6000 (Kästner 1940 a). The

number of scorpions is restricted to about 600 and certain rare groups such as the Ricinulei and Palpigradi (the latter discovered as late as 1885) have only 20 and 13 species respectively.

The size of the Arachnida is fairly modest, varying from about 0,1 mm to 180 mm.

The body is covered by a solid chitinous skeleton. In the Pedipalpi the shell consists of three layers: a thin, pigmented outer layer, an internal stratified layer and a basal hypodermic layer. This does not appear to be universal among the Arachnida since the scorpion has the pigmented layer below a lighter outer one. In the shell of the Ixodidae (Acari) Ruser (1933) found a distinct lamination pierced by numerous fine canals vertical to the surface. Schulze (1936) points out that the close-set canals in the exoskeleton differ from the structures in Crustacea, but show a marked resemblance to the trilobite shell (Størmer 1930).

The arachnid body is either elongate such as in the scorpions, or fairly short with a well-rounded hind portion such as is characteristic of the spiders.

In all arachnids except the Acari the body is distinctly divided in a prosoma and abdomen just as in the Eurypterida. The abdomen can be divided in a broader preabdomen and a more narrow postabdomen. The terms meso- and metastoma are generally used as synonyms of pre- and postabdomen. Börner's division based on the presence of rudimentary appendages in the mesosoma of the larva appears to be of little use.

The prosoma is generally covered by a continuous, slightly vaulted shield. In certain primitive groups, particularly the Palpigradi and Solifugae, the prosomal shield is divided into several segments (fig. 11, 6, 7). We have in front a larger plate, the propeltidium, and behind this a meso- and a metapeltidium. The propeltidium comprises the anterior prosomal portion with 4 pairs of postoral appendages. It is of special interest, as pointed out by Schulze, that this portion, the so-called proterosoma, corresponds to the cephalon of trilobites and also to the number of primary somites both in the Trilobita and Xiphosura (p. 110). In certain Acari the body might be divided into a proterosoma and a hind portion, a hysterosoma, formed by a combination of the abdomen and 2 segments of the prosoma. The Acari might, however, also have a distinct gnathosoma including only the 2 frontal postoral somites.

Schulze (1936) is inclined to see a trilobation of the scutum in the gnathosoma of the Ixodidae, a trilobation which he directly homologizes with the trilobation of the cephalon in trilobites. This homology, however, seems hardly convincing. (The comparison of *Haemaphysalis* and *Lichas* is based on the erroneous conception that the modified glabellar furrows of the latter are axial furrows.) Little evidence is also afforded concerning the comparison of the scutilateral furrows and the facial suture in trilobites. The facial suture is not a furrow and the muscles to the appendages were hardly attached to these regions in trilobites.

The prosoma of the Scorpionidae has 2 sets of eyes. The simple lateral eyes (*lat. eye* in fig. 11, 1) comprise 2—5 individual eyes on either side near the frontal margin of the prosoma. In the middle of the prosoma we find a pair of median ocelli (*m. oc* in fig. 11, 1).

In the abdomen the dorsal shield of the elongate forms are distinctly divided into a number of moveable tergites connected by softer intersegmental membranes. A certain trilobation of the abdomen occurs in the Ricinulei (fig. 11, 9), Ixodidae, Phalangidae (young specimens) and certain Araneae. In the scorpion and several other elongate forms the postabdomen has well defined tergites. In the shorter forms such as the Araneae on the other hand, the segmentation is more or less obliterated in the sac-formed abdomen. The Acari have the abdomen covered by a continuous shield which shows remnants of "pleurae" along the posterior and lateral borders.

The first, pregenital tergite shows a strong tendency to be reduced in the Arachnida. A rudimentary first tergite is only preserved in the Pedipalpi (fig. 11, 21) Palpidradi, and Araneae and is just indicated in the Solifugae. (The rudimentary sternite might be traced in the embryo of all arachnids (by VII in fig. 11, 5). The posterior abdominal segments are also sometimes reduced, especially the sternal portions (Araneae).

The number of abdominal segments is somewhat variable. The greatest number is found in the scorpions which, besides the completely reduced pregenital segment, have 18 distinct segments giving a total amount of 19 abdominal somites. (The posterior segment has no separate ganglion, but the ontogeny shows that a ganglion is primarily formed and afterwards unites with the ganglion of the penultimate somite.) Among the other arachnids a number of 18 abdominal somites (of which the first might be reduced) is the most common.

The scorpions have a narrow postabdomen with five segments just as in the eurypterids. Counting the number of tergites in the abdomen of an eurypterid we arrive at the same figure as in the scorpion. The resemblance is striking. Some writers (Kästner 1940 b) emphasize a homology between the 18 segments in both forms. The homology might seem very likely, the ventral surface, however, presents severe difficulties. The eurypterid operculum occurs in the sixth segment reckoned from the postabdomen. In the scorpion the same segment carries the pectines while the operculum belongs to the segment in front of it. If we maintain the homology suggested, we have to assume (with Kästner) that the operculum of the Eurypterida is formed by the combination of the appendages belonging to two succeeding segments. We are forced to regard the genital appendage (with the apertures of the genital ducts) as belonging to the genital segment (VIII) while the opercular plates are interpreted as the appendages of the following somite (IX). This is hardly possible because the eurypterid operculum corresponds in detail to the operculum of the Xiphosura (p. 70), and in these forms the ontogeny clearly demonstrates that the median (genital) appendage

and the lateral plates both represent the appendages of the genital (VIII) segment. I find it improbable that the pregenital segment is completely reduced in the ancient eurypterids (Størmer 1934). The eurypterid abdomen seems therefore to include 18 primary segments in contrast to the 19 of the scorpions, but in accordance with many other arachnids. The remarkable correspondence in the shape of the abdomen has to be interpreted as due to convergence. It may be noticed in this connection, that among the Arachnida several orders, the Pedipalpi, Palpigradi and Ricinulei, have only 3 segments in the postabdomen, and the preabdomen contains 9, 8 and 7 segments respectively.

The telson of the scorpions (*tel* in fig. II, 1, 2) is modified into a poisonous spine. The Pedipalpi (Uropygi) and Palpigradi have a more filiform, jointed telson. In the other groups the abdomen has a blunt hind border without a telson (8, 9).

On the ventral surface the comparatively small prosoma has a feebly developed doublure. According to Henriksen (1931) the marginal suture is evidently the most primitive ecdysial suture in the Arachnida. This suture is found in the Pseudoscorpionidae, Opiliones and Araneae. Particularly the presence of a marginal suture in the more vaulted prosoma of the Araneae would indicate a primitive and conservative structure.

The mouth has a frontal position, thus differing from the more central position in the Eurypterida. But it appears that the frontal position is secondarily acquired. At the end of the embryonic development the anterior portion of the body is bent dorsally backwards so that even the postoral sternites may advance as far as to form the frontal border of the body.

In front the mouth is bordered by an upper lip or labrum (*labr.* in fig. II, 7) which is specially developed in the Ricinulei. In this group the labrum forms a strong movable plate, the cucullus (*cu* in 9) which Schulze has compared with the labrum in trilobites. Posteriorly the mouth is bordered by a lower lip or labium (*labi* in 7) which by most authors is regarded as being composed of one or more postoral sternites. It is probable that the organ is homologous with the labium, or postoral plate, in trilobites and with the endostoma of the eurypterids. The sternites are preserved in forms with less prominent coxae of the prosomal appendages. In the primitive Palpigradi the individual sternites (*st* in 6, 7) are well exposed, only the II and III are anchylosed. (The fossil *Stenarthron* showing all separate sternites is apparently a dubious form.)

6 pairs of appendages are present in the prosoma of the Arachnida. The number and general development of appendages conform with that in the Eurypterida. Just as in the eurypterids the first pair of appendages is formed by short pincers or chelicera which have 2 or 3 segments (*I* in fig. II, 1, 2, 4—8, II, 15, 21). The ontogeny shows that the chelicera are primarily postoral and only lately in the ontogenetic development migrate forward in front of the mouth.

Of the remaining 5 pairs of limbs the first is often developed as powerful chelate appendages, the so-called pedipalpa (*II* in *1, 2*), or modified into tactile organs (*8*). Special modifications are seen in parasitic Acari. The 4 posterior pairs of appendages generally form more or less uniform walking legs. In the Pedipalpi it is of interest to notice that the first pair of walking legs (*III*) are modified into long tactile organs.

In comparison with the Insecta and Crustacea the appendages of the Arachnida show but little variation. The interpretation and names of the different segments of the arachnid leg have been subject to some discussion. In the present connection we shall only mention that in the general features of the leg we find considerable correspondence in Trilobita, Eurypterida, and primitive Arachnida (Størmer 1939). Traces of a preepipodite are not known in the prosomal appendages of the Arachnida, but rudiments of a precoxa (subcoxa) are described by Schulze (1932) (*prcox* in fig. *11, 8*), and, according to Neumann (1942), this basal segment might possibly be traced in certain other arachnids.

The coxae are in general strongly developed occupying most of the space below the prosoma. In most cases the coxae take part in the formation of the mouth. Kästner (1940a) has strongly pointed out that the Arachnida have no jaws. During the reception of food the prey is kept close to the mouth and is squirted by a liquid dissolving the object so that it might be drawn in by the suctorial pharynx. The lack of jaws seems also to have been characteristic of the Trilobita in which the coxae are not forming parts of the mouth opening. In the Eurypterida the powerful coxae were provided with teeth and hence had some gnathal functions, but a complete specialization of certain appendages into jaws, such as in the Crustacea, Myriapoda and Insecta (Mandibulata) has not taken place.

Below the prosomal tergum there are also frequently certain appendages actually belonging to the abdomen. Simultaneously with the forward migration of the prosomal sternites during the ontogeny, the frontal abdominal sternites with their appendages are inclined to attain a more anterior position below the prosoma. This is the case in the scorpion where the genital opening has migrated forward between the coxae of the last walking legs (fig. *11, 2*).

The abdomen has well-developed sternites, but the appendages are mostly absent being, however, indicated in the embryo (fig. *11, 5*). True appendages are seen in the pectines or combs of the scorpions (*comb* in fig. *11, 2, 3, 5*) and in the spinnerets of the spiders (*prpd?* in *23, 24*). The combs belonging to the 3rd abdominal, or 9th postoral somite, are attached to a median plate forming the rest of the 9th sternite. The appendages are composed of a dorso-ventrally compressed shaft divided by longitudinal and transverse furrows (representing softer integument between the plates) into a number of more or less defined segments. The segmentation is, however, sometimes different on the dorsal and ventral surface of the

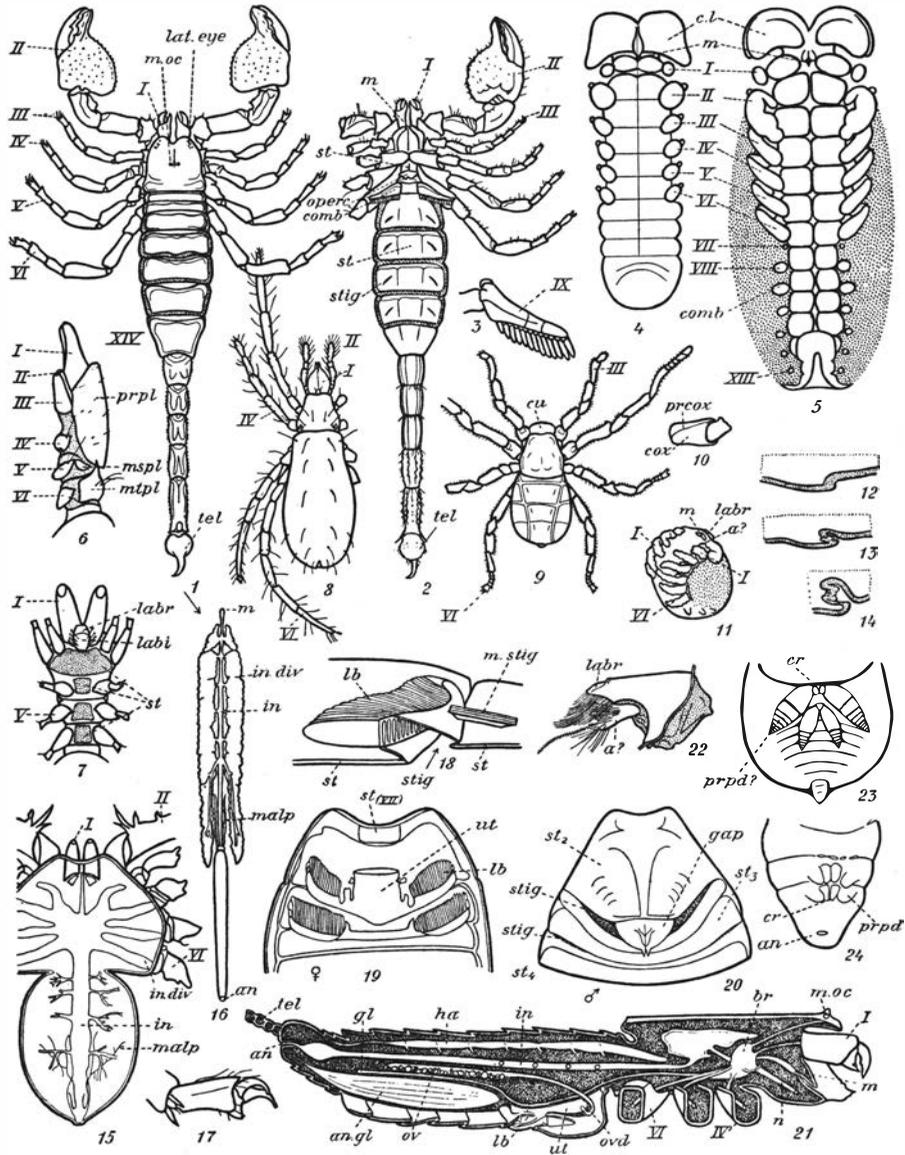


Fig. 11. Arachnida. General morphology.

1, 2 = Scorpionidea, *Pandinus* sp. Dorsal and ventral view (after Versluys and Demoll 1922). 3 = Scorpionidea, *Heterometrus* sp. Comb or pectine (after Størmer 1939). 4, 5 = Scorpionidea, *Euscorpilus* sp. Early ontogenetic stages (from Kästner 1940 b, after Brauer). 6, 7 = Paligradi, *Koenia* sp. Lateral and dorsal view of prosoma (from Kästner 1932 b, modified after Börner). 8 = Acari, Ixodida, *Rhagidia* sp. (from Schulze 1936, after Oudmans). 9 = Ricinulei, *Cryptocellus* sp. (from Kästner 1940 a, after Hansen and Sørensen). 10 = Acari, Ixodida. Basal portion of leg. (from Størmer 1939, after Schulze). 11 = Araneae, *Trochosa* sp. Embryo with possible rudiments of antennae (from Snodgrass 1938 after Jaworowski). 12—14 = Scorpionidea, *Euscorpilus* sp. Ontogenetic development of the lung-books (after Kästner 1940 b, from Brauer). 15 = Pedipalpi, *Tarantula* sp. Intestine with intestinal diverticulae and malpighian vessels. 16 = Scorpionidea, *Buthus* sp. Intestine with intestinal diverticulae and malpighian vessels (from Versluys and Demoll 1922, after Newport). 17 = Scorpionidea. Distal portion

shaft and varies greatly within the same genera. The posterior border of the shaft is provided with a variable number of close-set finger-shaped teeth, commonly with small conical fulcra intercalated at their bases. On the ventral surface the teeth have a more flattened sensitive area provided with close-set sensitive cells. The comb is furnished with a well-developed muscular system containing six muscles leading to the body and three kinds of internal muscles. Little is known of the actual functions of the pectines (Kästner 1940 b). A sexual dimorphism in the development of these appendages suggests their serving as sexual organs. This is supported by an observation according to which two scorpions were found with the ventral sides against each other and with the combs entangled. Observations also indicate that the appendages may be directed vertically towards the ground and act as chemically sensitive organs. A function as stridulatory organ is also substantiated in certain cases. The sound is created by the rubbing of the combs against the sculptured sternites above.

The evidence afforded shows that we cannot ascribe the combs one single definite function, but it appears that the organs have a certain sensitive function and are provided with a well-developed musculature. The pectines are only present in the scorpions, but in these forms they constitute a very conservative structure occurring already in the Silurian species (fig. 12, 3). As mentioned below also traces of a median process is found in the Silurian form, a process which possibly might be interpreted as rudiments of a median branch or telopodite in a primary biramous appendage (*tlpd?* in fig. 12, 4).

Concerning the origin and nature of the combs Lankester (1881, 1905) homologized these structures with the gill-bearing abdominal appendages of the Xiphosura. Calman (1919) questioned the possibility of a homology with the lateral branch of the trilobite limb. In earlier papers (Størmer 1933, 1939) I have pointed out the apparent correspondence in the morphology of the scorpion comb and the gill-branch or preepipodite of the trilobite appendage. It might be objected that the scorpion pectine is a highly

of leg. (after Hansen 1930). 18 = Pedipalpi. Diagram of lung-book (after Kästner 1932 a). 19 = Pedipalpi, *Thelyphonus* sp. Lung-books and uterus externus feminus in dorsal view (after Kästner 1932 a). 20 = Pedipalpi, *Tarantula* sp. Frontal abdominal sternites of male in ventral view (from Kästner 1932 a, after Börner). 21 = Pedipalpi, *Thelyphonus* sp. Diagram of left half of body (after Kästner 1932 a). 22 = Solifugae. Epistomal lobe with movable lateral appendage regarded by Snodgrass as possibly representing the antenna (after Snodgrass 1938). 23 = Araneae, *Heptathela* sp. Abdomen with appendages forming spinnerets (from Gerhardt and Kästner 1938, after Kishida). 24 = Araneae. Embryo with rudimentary appendages (spinnerets), (from Gerhardt and Kästner 1938, after Kishida).

I—XIII = postoral somites with corresponding appendages, *a?* = possible antenna, *an* = anus, *an.gl.* = anal gland, *br* = brain, *comb* = comb or pectine, *cox* = coxa, *cr* = cribellum, *cu* = cucullus, *gap* = genital appendage, *gl* = ganglion, *ha* = heart, *in* = intestine, *in.div.* = intestinal diverticulae, *labr* = labrum, *labi* = labium, *lat. eye* = lateral eye, *lb* = lung-book, *m* = mouth, *malp* = Malpighian vessel, *m.oc* = median ocelli, *m.stig* = muscle serving as stigma opener, *mspl* = mesopeltidium, *mtpl* = metapeltidium, *n* = nerve to appendage, *operc* = operculum, *ov* = ovarium, *ovd* = oviduct, *prcox* = precoxa, *prpd* = preepipodite(?), *prpl* = propeltidium, *st* = sternite, *stig* = stigma, *tel* = telson, *ut* = uterus.

specialized organ which therefore not easily is interpreted as a rudiment of a primitive respiratory branch of a limb. The present sensitive, not respiratory function of the comb need not, however, be an argument against the homology. In numerous cases a primary appendage is known to have acquired new functions and to have been correspondingly modified. In the Cumacea among the Crustacea, one of the epipodites of the maxilliped serves as a gill while the other, which apparently also had a primary respiratory function, is modified into a funnel-shaped cover of the former (Sars 1900).

The homology between the comb and the abdominal appendage of *Limulus* is discussed in a later chapter. Before we consider the homology also with the book-lungs of the scorpion we shall mention other kinds of distinct appendages in the arachnid abdomen.

The spinnerets of the Araneae form the appendages of the fourth and fifth somites (X, XI) of the abdomen. In most spiders the appendages are situated near the hind border on account of a reduction of the five posterior sternites. A primitive condition is found in the Liphistidae (Gerhardt u. Kästner 1938). The spinnerets (fig. 11, 23) are composed of a median plate, the cribellum (*cr*) and a lateral branch (*prpd?*) with a number of telescoped segments. The cribellum, appearing as a distinct median lobe in the early larval stages (*cr* in fig. 11, 24), forms in the adult a movable plate attached along a transverse frontal border. The spinnerets thus appear to be biramous, and the two branches have been described as endo- and exopodite. The position of the segmented lateral branch suggests a homology with the scorpionid comb. No teeth are, however, present on the spinneret. The median branch of the larvae shows at least an external resemblance to the median process in the combs of the ancient Silurian scorpion. This would imply that both the combs and spinnerets might be modified appendages of the trilobitan type. We shall see that this assumption is supported by the structures of the respiratory organs as well as with the development of the abdominal appendages of the Xiphosura described in a later chapter.

The respiratory organs of the Arachnida comprise three different types. We have the ventral sacs, the lung-books and the tracheae. The ventral sacs, occurring in the Pedipalpi and Palpigradi, form invaginations of the thin integument into a blood-sinus. The structures are of minor interest in our present connection.

The lung-books and the tracheae may occur simultaneously in the same species. In spite of considerable differences, investigations on the structures indicate that the two types might be derived from each other as mentioned below. In the scorpion the external openings of the lung-books form oblique slits or stigmata (*stig* in fig. 11, 2) in the fourth to seventh (X—XIII) abdominal segments. The Pedipalpi and Araneae on the other hand have no typical stigmata, the openings being found between succeeding sternites (*stig* in 18, 20). The external opening leads into a respiratory atrium into

which open numerous close-set narrow pockets. The flat respiratory pockets form the lung-books (*lb* in fig. 11, 18, 19, 21; fig. 23) and are placed in a common blood-sinus.

It was the merit of Lankester (1881) to demonstrate that the book-lungs were invaginated appendages homologous with the combs of the scorpion and with the gill-bearing abdominal feet of the Xiphosura. As shown in fig. 11, 12—14, the lung-books develop in the embryo as folds on the posterior side of the conical outgrowths forming the embryonic appendages (Kästner 1929, 1940 b). The folds and the rudimentary appendage gradually become invaginated in the body. The folds, corresponding to the gills in the Xiphosura and the teeth in the comb, are turned into pockets like the fingers of an everted glove. In its general morphology the invaginated appendage, such as it is demonstrated in the Scorpionidea, Araneae and Pedipalpi (*lb* in fig. 11, 18, 19) bears a considerable resemblance to the scorpion comb forming the appendage in front of it. In the lung-book the atrium might correspond to the shaft and the pockets to the teeth of the comb. It seems hardly doubtful that the mentioned appendages are homologous in structure. The homology with the xiphosuran and trilobitan appendage is discussed in later chapters.

The tracheae of the Arachnida appear in several different modifications. In some cases simple canals occur which might be interpreted as derived from prolonged cavities comparable to the atrium of the lung-books. In other types, bundles of tubuli open into a respiratory cavity or atrium in the same way as the pockets in the lung-book. As pointed out by Kästner (1940 a) the similar embryological development of both the trachea and the lung-books of the eighth and ninth somite (VIII and IX) in the Araneae substantiate the homology of these formations. This opens the interesting view that the trachea, composed of a respiratory atrium and a bundle of tubuli, once might have derived from appendages with gills which were not book-gills but more had the characters of a bundle of filaments. This is of interest with regard to the Eurypterida which apparently lack the typical book-gills (fig. 9, 16). Besides the mentioned types of trachea, others occur which evidently are derived from the mentioned forms.

Traces of a modified abdominal appendage can also be seen in the genital appendage of certain groups. It is characteristic of the Arachnida and other members of the Chelicerata that the genital ducts open in the 8th somite (VIII). Special genital appendages are found in many arachnids. In the female of the Pedipalpi (*Thelyphonus*) (fig. 11, 19, 20, 21) the integument between the 2nd and 3rd abdominal sternite (at the hind border of the genital segment VIII) is strongly invaginated forming a deep fold into which open both the lateral respiratory cavities (atrium) of the lung-books (*lb*), and a median cavity forming the uterus externus (*ut*). In the male of *Tarantula* the uterus externus is provided with a genital appendage, a so-called penis (*gap* in 20) which is composed of two elongate

bodies united at their base but separated by an internal median septum. The median appendage or penis projects from a cavity representing an uterus externus similar to that in the female (*ut* in 19). It is of interest to observe that both the lateral lung-books and the median uterus externus with the genital appendage, open into a common intersegmental fold at the hind border of the genital sternite. We have seen that the lateral lung-books evidently are homologous with the gill-bearing abdominal appendage of *Limulus* (fig. 13, 14, 15). The abdominal appendage of *Limulus* also contains a median branch which we interpret as a telopodite (*tlpd*). This telopodite is evidently homologous with the one half of the genital appendage in the Eurypterida (*gap* in fig. 9, 12). For these reasons it is highly probable that the genital appendage of the Pedipalpi (and other Arachnida) represents the rudiments of a median branch of a primary biramous appendage of which the lung-book constitutes the lateral branch. It is of interest to notice that while the base (*coxa*) and the lateral branch is completely invaginated in the body, the median branch is only partly invaginated, the distal portion not being invaginated and the invaginated basal portion being eversible. Börner (1904) also believed the genital appendage to be remnants of anchylosed appendages, while other writers express no definite opinion as to its origin.

Internal organs. Besides the external skeleton derived from the ectoderm, certain forms such as the scorpions have also an internal skeleton or entosternite of mesodermal origin.

The nervous system is unusually strongly concentrated. In correspondence with the lack of antennae the brain is not divided into a protocerebrum and deutocerebrum. The ganglia of the first postoral somite (cheliceral somite) migrate forward and unites with the brain forming the supraoesophageal ganglion or tritocerebrum.

The intestine has a narrow pharynx. One of the chief characteristics of the Arachnida is the very strong development of the intestinal diverticulæ (*in.div.* in fig. 11, 15, 16). The diverticulæ serving the digestion just as the main intestine, form either finger-shaped lateral sacs (15) or strongly ramified complex structures (16). The intestinal diverticulæ fill up the main part of the body in most arachnids. Embryologically these structures are formed by the ingrowth of the mesodermal septa into the yolk.

Excretory organs are seen in the Malpighian vessels opening into the posterior portion of the intestine (*malp* in fig. 11, 15), and in the well-developed coxal glands. The coxal glands, derived from the coelom, have one common opening at the base of the coxae of the II, III or V prosomal appendages.

Ontogeny. On the germ band of the egg the embryo develops with its convex ventral side almost embracing the egg (fig. 11, 11). The embryo is of the same type in all arachnids. As shown in fig. 11, 4, 5, the body has a distinct cephalic lobe (*c. l.*) and numerous uniform somites with

rudimentary appendages. The lobes representing the chelicera (I) have a distinctly postoral position. Indications of pre-cheliceral lobes in embryonic stages of the Araneae (*Trochosa* and *Pholcus*) were interpreted by Jaworski and Pokrowski (comp. Snodgrass 1938, p. 115) as rudimentary antennae (*a?* in fig. 11, 11). The structures are not very definite and the interpretation implies some conjecture. Snodgrass (l. c.) mentions that a small movable appendage near the labrum in the primitive solifugae possibly might represent the remnants of an antenna (*a?* in 22).

FOSSIL ARACHNIDA

Although a considerable number of fossil arachnids are described from different geological formations, the material throws but little light on the phylogeny of the class. The fossil material is chiefly confined to Carboniferous and Tertiary deposits, but true arachnids are discovered already in the Silurian. Since the Arachnida chiefly comprises terrestrial forms the faunas are restricted to the less common continental deposits. (By chance marine deposits include terrestrial forms which incidentally might have been swept into marine waters.) The often delicate chitinous shells contain little lime and are easily destroyed. For these reasons the palaeontological record of the Arachnida is very incomplete and at long intervals in the geological history remains of the group are lacking.

What is especially striking in the palaeontology of the Arachnida is the great conservatism of the group. In the Carboniferous we find most of the present arachnid orders and suborders, and even in the Silurian we meet true scorpions.

Most of the forms are of minor interest to our comparative considerations. We shall in the present connection deal more in detail only with the earliest fossil scorpions. Four different discoveries from the Upper Silurian of Sweden, Scotland and New York State have aroused considerable discussions especially as to the habitat of these early representatives of the Scorpionidae. Three of the species belong to the genus *Palaeophonus* (fig. 12, 1—4). As shown in the illustrations the body has the characteristic scorpionid form with the narrow postabdomen provided with a terminal spine. Median ocelli are seen in the Scottish specimens (Pocock 1901), but in the also well-preserved Swedish form only a median node (*m.oc*) without traces of the ocelli, is present (Thorell and Lindström 1885). In the American *Proscorpius* (5) Clarke and Ruedemann (1912) describe several different, more or less distinct eyes in the prosoma. On an anterior median lobe (*e. lob*) two distinct ocelli occur which the mentioned authors are inclined to interpret as belonging to lateral eyes, though of another group than those (*lat. eye*) near the antelateral angles of the prosoma (and possibly some along the border of the median lobe). A pair of larger ovate areas (*m.oc?*) near the posterior border are explained by Fritsch and Clarke

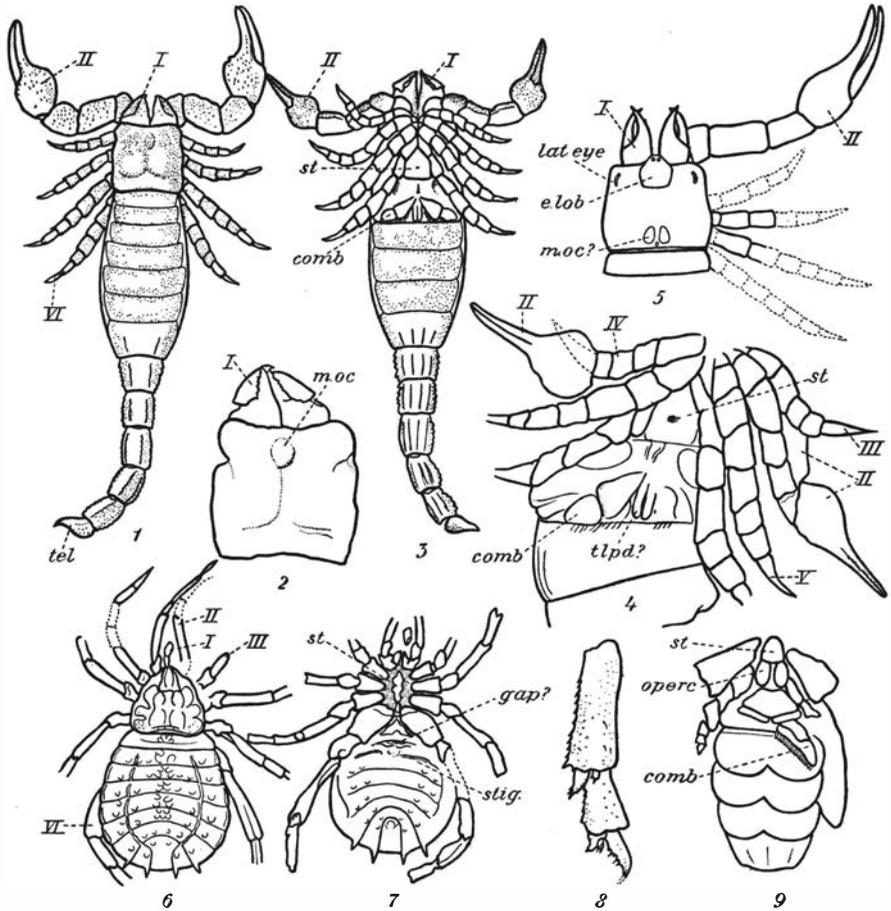


Fig. 12. Fossil Arachnida.

1—5, 8, 9 = Scorpionidea, 6, 7 = Anthracomarthi. 1 = *Palaeophonus nuncius* Thorell and Lindström. Upper Silurian. Reconstruction (from Pocock 1901, after Thorell). 2 = The same species. Detail of specimen (after Thorell and Lindström 1885). 3 = *Palaeophonus caledonicus* Hunter (= *P. hunteri* Pocock). Upper Silurian. Reconstruction of ventral side. Probably one more sternite was present in the abdomen (after Pocock 1901). 4 = The same species. Detail of specimen (after Pocock 1901). 5 = *Proscorpius osborni* Whitefield. Upper Silurian. Reconstruction of prosoma and first tergite (after Clarke and Ruedemann 1912). 6, 7 = *Eophrynus prestwichi* (Buckland). Carboniferous. Dorsal and ventral surface (after Pocock 1911). 8 = *Eobuthus* sp. Carboniferous. Distal portion of walking leg (after Wills 1925). 9 = *Eobuthus holti* Pocock. Carboniferous (after Pocock 1911).

I—IV = postoral appendage, comb = comb or pectine, e.lob = eye lobe, gap? = genital appendage(?), lat. eye = lateral eye, moc = median node probably provided with median ocelli, operc = operculum, st = sternite, stig = stigma, tel = telson, tlpd? = telopodite(?).

and Ruedemann as a pair of median eyes. The mentioned structures are not very distinct and the conception of their exact nature might therefore be subject to some conjecture.

Characteristic of the genus *Palaeophonus* is the presence of a very prominent sternum (*st* in 3, 4) in the prosoma. As pointed out by Versluys

and Demoll (1923) the number of sternites in the abdomen is too small in comparison with recent forms (3). This might probably be due to a secondary dislocation of the pectines in the Scottish specimen (4). In Pocock's (1901) reconstruction (3) a small number of sternites is, however, indicated.

The frontal appendages, the chelicers and pedipalps, are of the common scorpionid type, although the chelicers are more powerful than in recent forms. The walking legs deviate from the legs of recent species. They are much more of the eurypterid type, being composed of short and blunt, more cylindrical segments, and have a single terminal claw instead of two claws as in the typical scorpions. The comb is of particular interest in showing traces of a median lobe (*tlpd?* in 4) which possibly might be interpreted as a median branch, a telopodite of a biramous appendage.

The sternites show no traces of stigmata. The openings into the tracheae or gills must therefore have been situated behind the posterior border of each sternite. Certain writers have suggested that stigmata have been obliterated during the preservation of the specimens, but the presence of lobe-shaped, overlapping sternites (9) in the Carboniferous *Eobuthus* (Pocock 1911, Wills 1925) corroborates the assumption mentioned. The lobe-shaped plates in *Eobuthus* resemble the abdominal appendages in the eurypterids, but it seems yet probable that they form true sternites rather than modified abdominal appendages. In the walking leg of the genus mentioned the distal segments with the terminal singular claw (8) recall the structures in the walking leg of the trilobite *Phacops* (fig. 5, 22). (*Glyptoscorpium* with its comblike appendages was probably an eurypterid.)

It emerges from the evidence mentioned that the early scorpions possessed several primitive characters especially in the development of the prosomal and abdominal sternites, the walking legs and the combs. The structure of the walking legs suggests eurypterid (possibly trilobitan) affinities. (Pocock also compared the prosomal sternite with the eurypterid metastoma, but these structures are hardly homologous.)

The habitat of the early scorpions has been subject to much discussion. The Silurian specimens occur in association with eurypterid faunas indicating conditions other than marine. The blunt appendages and the lack of stigmatum might suggest an aquatic rather than terrestrial mode of life of these forms, but the problem can hardly be settled with our present knowledge.

Other groups of Arachnida are known already from the Devonian.

From the Carboniferous is also known four extinct orders of Arachnida: Kustarachnida, Haptopoda, Phalangiotarbi and Anthracomarti (fig. 12, 6, 7). The mentioned orders are related to recent groups. The Anthracomarti which are recorded also from the Devonian (Hirst 1923) played an

important part in the late Palaeozoic faunas. Schulze (1932) is inclined to regard the Anthracomarti as closely related to the ancestors of the Acari.

Tertiary deposits have provided a considerable material of fossil arachnids which are more or less closely related to recent species.

The fossil material has strongly confirmed the conception of the Arachnida as a really old group which very early acquired its distinct plan of construction, even with regard to the minor characteristics signifying the individual orders.

Habitat and Adaptive Radiation of the Arachnida.

With very few exceptions the Arachnida are confined to terrestrial forms. Only the Acari have been able to adapt themselves to many different modes of life (carnivorous, herbivorous, parasitic etc.). In this group we notice a strong adaptive radiation comparable to that found in Crustacea and Insecta. The bulk of the Arachnida, on the other hand, remained more or less unchanged as terrestrial carnivorous arthropods.

As already mentioned the different arachnid groups manifest their typical morphological characters already in their earliest representatives. Surveying the different groups it becomes apparent that no group can be distinguished as approaching a common progenitor of the class. Of the complex of characters distinguishing the Arachnida, one or two characters might be primitive in one order, while other primitive features prevail in another group. This variable development of the morphological characters also forms the basis of a taxonomic classification of the 4 extinct and 9 recent orders of the Arachnida.

The present description and discussion of the Arachnida have shown that these arthropods form a well defined group which, like the previously described Trilobita and Eurypterida, are characterized by a definite morphological plan of construction. In spite of the great numbers of recent representatives, the Arachnida appear to be a very old group. In most orders we notice a marked conservatism in the development of the morphological structures. Only in the Acari, which possibly might represent a younger group, we notice a tendency towards more extensive variation.

It emerges from the evidence afforded that the Arachnida show a distinct relationship to the Eurypterida. Affinities to the Trilobita are also suggested in certain characters, but several other recent and fossil forms may be used to support the affinities indicated. We shall primarily consider one recent and fossil group which has been subject to ardent discussions in connection with the problem of relationships between Trilobita, Eurypterida and Arachnida.

Xiphosura.

The recent representatives of this group are confined to a few species generally included in the genus *Limulus*. Pocock (1902) suggested, however, the establishment of three different genera (*Xiphosura*, *Tachypleus* and *Carcinoscorpius*), but this classification of the recent species is not generally adopted (Gravier 1929) and will not be used in the present comparative treatment.

The recent limulids, the horseshoe crabs, king-crabs or "Moluccen-Krebse", occur in marine waters off the Atlantic coast of North America from Maine to Yucatan, and along the south-eastern coast of Asia from India to the Malayan Archipelago and further north to Japan. They inhabit the shelf region of these waters and one of the Asiatic species migrates occasionally into the more or less fresh water of the estuaries. The females of the Atlantic species attain a length of more than 50 cm, while the males are smaller.

Limulus has a very powerful dorsal shield covering completely the ventral appendages (fig. 13). When creeping on the bottom the powerful shell gives a perfect protection to the ventral structures. The shape of the dorsal shield is typically "streamlined", offering little resistance to a forward movement through the water.

The broad dorsal shield shows a distinct trilobation. A pair of axial furrows separate the median axis from the broader pleural areas. In this respect the Xiphosura have much in common with the Trilobita. The division of the body by transverse joints is, however, not the same in the two groups. In both groups a headshield might be distinguished, but instead of a trilobitan thorax and pygidium, *Limulus* has an abdominal shield and a terminal telson of the eurypterid type.

The headshield or prosoma has a median axis (glabella) bordered by distinct axial furrows. Glabellar furrows similar to those in trilobites are not present, but muscle scars evidently indicate their place just as in many trilobites with smooth glabella (*Ampyx*). Muscle scars also occur laterally to the axial furrows (*ms* in fig. 13, 1).

A pair of median ocelli (*m.oc.*) have a more frontal position than in the Eurypterida. Demoll (cp. Versluys and Demoll 1922) has demonstrated the occurrence of one pair of rudimentary eyes below the shell in the same place as the median ocelli. The lateral eyes (*l. eye*) are situated on the broad cheeks just as in trilobites. A longitudinal crest, provided with spines in the younger stages, does not signify a rudimentary facial suture, but forms a segmental border as mentioned below. The lateral, kidney-shaped eyes are composite eyes, composed of numerous individual facets. The lateral eyes also have a rudimentary eye below the dorsal shell. According to Demoll both the median and lateral eyes, with their respective rudimentary parts, are apparently built on the same plan. In their particular

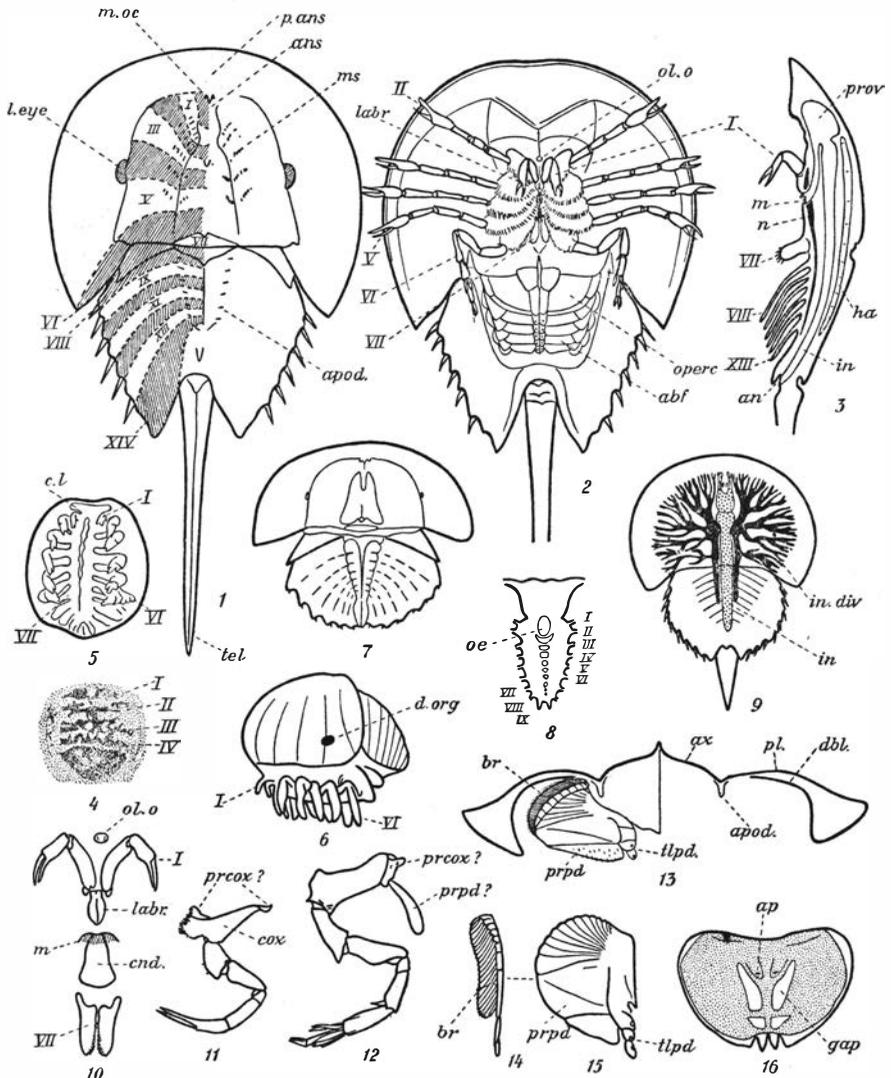


Fig. 13. Xiphosura. General morphology.

1—3, 6, 8—16 = *Limulus polyphemus* (Linnaeus) (= *Xiphosura polyphemus* (Linnaeus)).
 4, 5, 7 = *Limulus moluccanus* (Linnaeus) (= *Tachypleus gigas* Müller). 1, 2 = dorsal and ventral view. Somites indicated by hatching on the left side of specimen. (Based on Versluys and Demoll 1922.) 3 = median section. 4 = early embryological stage (after Ivanov 1933). 5, 6 = later embryological stages (after Ivanov 1933, and from Gerhardt 1935, after Watase). 7 = first free larva. 8 = central nerve cord of larva (from Gerhardt 1935, after Hanström). 9 = intestine (dotted) and intestinal diverticulae (black) in the larva (from Gerhardt 1935, after Watase). 10 = median structures near the mouth (after Lankester 1881). 11 = walking leg (from Størmer 1939). 12 = hind leg (VI) (after Størmer 1939). 13 = frontal view indicating position of gill-appendage in relation to dorsal shell. In the drawing the appendage should have been broader so that the telopodite practically reached the median line (after Størmer 1939). 14, 15 = lateral and ventral view of gill-appendage. 16 = dorsal view of operculum (VIII)

(after Størmer 1936).

I—XIV = postoral somites and corresponding appendages, abf = abdominal foot, an = anus, ans = antennal segment, ap = opening of genital duct, apod = apodeme for

structures the visual organs deviate both from the eyes in Crustacea and Arachnida. Concerning the lateral eyes of *Limulus* and *Scorpio*, however, Versluys and Demoll (1922, p. 250) postulate that a faceted eye might easily develop from a number of primitive ocelli, but the opposite development they find very improbable. Against the latter view might be put forward the fact that in trilobites Richter has clearly demonstrated a successive reduction in the number of facets in the lateral eyes, a reduction which might result in the presence of only a few individual facets appearing more or less as individual ocelli. Packard (1880) asserted the homology of the limulid and trilobite eye, but Lindström (1901), who specially studied the eyes of trilobites, concluded that the trilobite eyes, sometimes containing crystal cones(?), resembled those of the Crustacea, especially Isopoda.

The vaulted prosoma is separated from the abdomen or opisthosoma by a transverse joint or hinge-line. Extensive embryological studies on *Limulus moluccanus* Linnaeus (= *Tachypleus gigas* Müller) by Ivanov (1933) have shown that the hinge-line does not conform with the primary intersegmental borders. The structures are also complicated by the strong reduction (as in most arachnids) of the seventh somite (VII) of which only the mesotergite is preserved on the dorsal side. As shown by the segmental hatching of the left side of fig. 13, 1, the joint crosses the sixth pleurotergite and the seventh mesotergite, even a small portion of the eighth mesotergite takes part in the formation of the posterior portion of the hinge. The conditions are similar to that in the joint behind the cephalon in trilobites, although in this group the hinge intersects a more anterior segment (IV) (fig. 5, 1). In the prosoma the primary segmental borders are only indicated in the central portion. Ivanov (1933) and Schulze (1939) conceive the transverse borders of the somites to continue radially towards the lateral margin of the shield. Snodgrass (1938) on the other hand regards the marginal rim as belonging to a special acronal segment embracing the other segments in the central portion. The structures in trilobites support the interpretation of Snodgrass. As shown in fig. 13, 1 I find it probable that the preantennal (acronal) segment forms the broad rim and reaches as far backwards as to an oblique line running from the postlateral angles towards the transverse posterior line. This line is indicated in fossil Jurassic Limulida as shown by Ivanov (fig. 14, 2 a).

The segmentation as well as the number of ventral appendages show that the prosoma of *Limulus* is not homologous with the cephalon in a trilobite. While the former has 6—7 postoral somites in the headshield, the latter has only 4. Otherwise we notice a marked resemblance in the

muscles leading to the appendage, *ax* = axis, *br* = branchiae or gills, *cl* = cephalic lobe, *cox* = coxa, *dbl* = doublure or deflexed border, *end* = endostoma, *gap* = genital appendage, *ha* = heart, *in* = intestine, *in. div* = intestinal diverticulae, *labr.* = labrum, *l. eye* = lateral eye, *m* = mouth, *m. oc.* = median ocelli, *ms* = muscle scars, *oe* = oesophagus, *ol. o.* = olfactory organ, *operc* = operculum, *pl* = pleura, *prcox* = precoxa, *prov* = proventriculum, *prpd* = preepipodite, *tel* = telson, *tlpd* = telopodite.

general structures of the two groups. Affinities to the Eurypterida are also indicated, especially in the structure and position of the visual organs.

The abdomen or opisthosoma forms a solid, moderately vaulted plate with an axis distinguished by different convexity. In the shallow axial furrows we find a number of segmentally arranged tergal apodemes (or entapophyses) (*apod* in fig. 13, 1, 13) which have their counterparts in the apodemes of the mesotergites of many trilobites. The lateral margin of the abdomen is provided with movable spines corresponding in number to the coalesced segments.

The long styliiform telson (*tel*) is inserted into a posterior cleft of the abdominal shield. The tail-spine has a triangular cross-section with a flat ventral surface and a dorsal median crest. The telson articulates to the abdominal shield by means of a special T-shaped process. Schulze (1936) compares the T-shaped anterior process with the antetergite of the mesotergite in trilobites. The homology seems, however, little probable, because the invaginations in the articulating furrow in the trilobite *Ampyx* represent tergal apodemes, hardly comparable to the specialized structures in the telson. The particular structures in the anterior portion of the telson in *Limulus* enable movements of the spine to be made both in vertical and horizontal directions. The movements in the horizontal plane are accomplished by alternating contractions by the paired muscles (levators and depressors) of the telson (Gerhard 1935). The tail-spine probably serves more as a steering rod than as an implement for raising the body when turned on its back (Størmer 1936).

On the ventral side the prosoma has a very broad doublure with the more central portions passing into a softer integument or skin surrounding the appendages. The structures are similar to that of the trilobites and eurypterids. The mouth has a central position with a small and narrow plate forming the upper lip or labrum (*labr* in fig. 13, 10). In front of the labrum the skin is provided with two small pits (*olo* in 2, 10) which are interpreted as an olfactory organ. Patten and Hanström (1926) have been inclined to regard the olfactory organ as derived from a pair of primary ventral eyes apparently present in the larva. This conception is strongly opposed by Johansson (1937) who denies the presence of ventral eyes and interprets all the structures as parts of an olfactory organ.

Like the Eurypterida the Xiphosura have no antennae. In front of the mouth we find on either side of the labrum a 3-segmented pincer or chelicera (*I* in fig. 13, 2, 3, 10). Five pairs of legs are radially arranged around the mouth. Each appendage has a large oblong coxa (*cox* in 11) similar to those in the eurypterids and arachnids. A small median basal plate, the epicoxite (*prcox?* in 11), and lateral parts, especially in the hind leg, might be interpreted as remains of a precoxa (Coutière 1919, Størmer 1939). The median border of the coxa forms a gnathobase which is provided with spines in the frontal appendages, and forms a strong gnathal ridge

or plate in the hind leg. The hind leg (VI) has a club-shaped process, the flabellum (*prpd?* in 12) articulating to the presumed lateral rudiments of the precoxa. Ivanov (1933) has demonstrated that the flabellum develops independently from the rest of the appendages, a fact which shows that the process belongs to the very base of the appendage. It seems therefore probable that the flabellum represents a rudimentary preepipodite homologous to the lateral branch of the trilobite leg.¹

In the walking legs the telopodites contain 6 (II—V) or 7 (VI) segments. In the 4 anterior legs (II—V) the distal segments form a chela. In the posterior legs (VI) the same segments are provided with several spines and are well adapted for digging in the mud (fig. 13, 12). In the male the first walking leg, and in certain species also the second, has the distal segments modified into a special clasping organ.

The structure and number of prosomal appendages in *Limulus* clearly demonstrate the relationship between the Xiphosura, Eurypterida and Arachnida comprising the subphylum Chelicerata.

The mouth is bordered posteriorly by a small plate, the endostoma (*end* in fig. 13, 10), which probably corresponds to the same plate in the Eurypterida.

Beyond the mouth a pair of small, vertically situated plates, the chilaria (*VII* in fig. 13, 2, 3, 10), as shown by embryological investigations of Ivanov, represent the rudimentary appendages of the seventh somite (VII). Just as the frontal abdominal sternites of many arachnids secondarily have acquired a more frontal position below the prosoma, the chilaria forming the appendages of the pregenital segment in *Limulus* have migrated forward towards the mouth. The chilaria are probably homologous with the metastoma of the Eurypterida.

The abdominal shield has also a broad doublure (fig. 13, 2 and *dbl* in 13). The central portion is occupied by six overlapping plates concealing the gills below (in ventral view). Versluys and Demoll (1922) tried to interpret these plates as modified sternites, an assumption which has proved erroneous. Recent embryological studies by Ivanov (1933) have convincingly confirmed the previous views that they are true appendages. The general structure of the abdominal feet is best studied in the second pair of appendages. The plate-shaped feet are anchylosed along the median line. Each appendage is biramous in the distal portion. The short median branch is composed of several segments of which only the distal ones are free (*tlpd* in fig. 13, 13—15). The basal portion of the branch is separated from the prominent lateral branch by a distinct furrow. The lateral branch originates from the very base of the appendage. The proximal portion is divided into numerous short segments not demonstrated in the common illustrations. The distal segments are longer, the terminal one forming a

¹ Larval rudiments of the flabellum are present also in the 2nd—5th appendages of the Japanese *Limulus*. (Kishinouye, K.: On the Development of *Limulus Longispina*. Journ. College Sci. Imp. Univ. Japan. 5, 1893.)

triangular lobe. On the inside (dorsal side) the broad leaf-like branch is provided with the characteristic book-gills (*gills* in fig. 13, 14). The gills form a large number of close-set lamellae attached to the proximal portion of the appendage.

Lankester (1881) pointed out the probable homology of the book-gills of *Limulus* and the lung-books of the scorpion. This was in fact the cardinal point in his well-known *Limulus*-theory. As pointed out above, the embryological development of the lung-books in scorpions strongly corroborates his assumption on a homology between the two organs, and at present his conception is generally accepted.

The abdominal appendages of *Limulus* bear a close resemblance to the plate-shaped abdominal feet of the Eurypterida. It is, however, peculiar that in the ancient eurypterids the appendages seem to be more specialized than in the recent limulids.

Recent studies on trilobite appendages (Størmø 1933, 1939) have strongly indicated a homology also with the appendages of trilobites. Both in the Xiphosura and Trilobita we find, attached to the very base of the appendage, a lateral multi-segmented branch (a preepipodite) carrying numerous blade-shaped gills. The rudimentary median branch in *Limulus* is probably homologous with the walking leg or telopodite in the trilobite.

The operculum (fig. 13, 16, *operc* and *VIII* in 2, 3), forming the first pair of the plate-shaped appendages, has no gills and deviates in this respect from the operculum of the Eurypterida. The dorsal (inner) surface of the operculum (fig. 13, 16) is covered by softer integument except at the marginal doublure and near the median line, where 3 pairs of sclerites mark the outlines of the median branches of the appendages. At the base of these median appendages open the genital ducts, the openings differing in size in the female and the male. The structures are very similar to those in the Eurypterida (fig. 9, 22, 23). In the eurypterids the median branches of the appendage are completely anchylosed forming a specialized genital appendage (fig. 9, 20—23 and *gap* in 2, 3, 12, 14).

The abdominal appendages in *Limulus* are provided with powerful muscles partly attached to the apodemes of the dorsal furrows. The muscles enable the feet to be pulled up against the body, a movement applied by the larvae when swimming on their backs.

Internal organs. The nervous system is well developed (fig. 13, 8). The brain has been subject to detailed studies particularly by Swedish zoologists (Holmgren, Hanström and Johansson). In general the brain corresponds to the structures in the Arachnida. In a later chapter the relation of the brain to the frontal appendages is discussed.

The intestine has very characteristic, strongly ramified intestinal diverticulae (*in. div.* in fig. 13, 9). Similar structures were also very typical in the Arachnida and appear to be one of the specific characters of the Chelicerata.

The coxal glands show primitive features in being derived from six separate coelomic sacs (the first and sixth degenerate early) corresponding to the 6 postoral somites of the prosoma. Only the fifth vesicle is maintained as the coxal gland opening at the base of the fifth pair of appendages.

Ontogeny. The ontogeny of the *Xiphosura* is of particular interest to our comparative studies. Thanks to the elaborate studies by Ivanov (1933) on *Limulus moluccanus* (= *Tachypleus gigas*) we might follow in great detail the ontogenetic development of this form. In the early embryonic stages the ectoderm cells contain a great amount of yolk and the segmentation therefore first appears in the mesoderm. Four somites (fig. 13, 4) representing the 4 postoral segments (I—IV) are produced more or less simultaneously and thus form the primary or larval somites of the *Xiphosura* (comp. fig. 2). The following secondary somites are formed gradually, one by one, from a posterior generative zone. The preoral portion is not differentiated in the earliest stages, but develops later on, as cephalic lobes (*c. l.* in 5) without appendages.

The presence of 4 primary postoral somites in the *Xiphosura* is of great significance when compared with the conditions in the Trilobita. In the trilobites a larvatum with 4 postoral somites is demonstrated in the protaspis-larva and the same segments constitute the cephalon of the adult. A proterosoma with four postoral somites is also distinguishable in primitive arachnids as mentioned above. As pointed by Ivanov the correspondence in the development of the larval somites in the *Xiphosura* and Trilobita is of considerable importance and strongly corroborates the conception of a relationship between the two groups.

In following ontogenetic stages (fig. 13, 5, 6; fig. 15, 2, 3) the appendages develop and the dorsal surface becomes differentiated. A dorsal organ (*d. org.* in fig. 15, 3), apparently a sensitive organ of some kind, is present in the last embryonic stages.

The first free larva (fig. 13, 7; fig. 15, 4) is known in the zoological literature as the trilobite larva or trilobite stage of *Limulus*. With its broad headshield, lobe-shaped telson and the segments of the abdomen indicated by pigmented lines, the larva no doubt resembles a trilobite. The free thoracic segments are, however, not present and Packard (1872) pointed out the closer correspondence to certain trilobite larvae (first meraspid stage of *Cryptolithus*) which only has a free pygidium besides the cephalon. Remembering that the headshield of *Limulus* contains 2—3 somites more than the headshield of the trilobite, the name trilobite stage is hardly successful. The name was established before the cephalic appendages of trilobites were known. It would be more appropriate to apply the term to the early ontogenetic stage in which only the 4 primary somites are developed. In fig. 15, 1 this is suggested. As shown in the following the last embryonic stages exhibit several features in common with certain Palaeozoic forms

and might therefore be called the Synziphosuran stage (fig. 15, 2, 3). Already Oudemans (1885) pointed out that the first larva of *Limulus*, the so-called trilobite stage, rather should be termed the *Prestwichia* stage because of the greater resemblance to Late-Palaeozoic xiphosurans. The name, which has to be altered into *Prestwichianella*-stage because the name *Prestwichia* is preoccupied, seems to be correct and is applied in the present paper (fig. 15, 4).

In further larval stages the telson increases in length and the axis and the "pleurae" of the abdomen become less distinct.

The evidence afforded of the morphology and ontogeny of recent Xiphosura has proved to be of the greatest importance to the general understanding of the fossil groups previously described. The structures in *Limulus* in many respects fill the gap between the mutually rather remote Trilobita and Eurypterida of the Palaeozoic. The Xiphosura show a definite relationship with both groups, especially with the Eurypterida, which together with the Xiphosura are included in a common class, the Merostomata. As strongly emphasized by Lankester and pointed out also by certain previous authors, the Xiphosura, in spite of their aquatic habitat, are closely related to the Arachnida. The Merostomata and Arachnida are accordingly included in one larger group, the Chelicerata.

The great phylogenetic importance attached to the recent Xiphosura naturally demands an investigation also of the fossil representatives of the group.

FOSSIL XIPHOSURA

The fossil material is not copious, but yet it has been possible to follow the group very far back in the geological history. The fossil record is excellently suited to ascertain the broad features of the phylogenetic development of the interesting Xiphosura.

Instead of starting with the oldest representatives it seems more convenient to go the opposite way and start with the more recent species studying the gradual change backwards from the living forms. Fig. 14 illustrates some of the more characteristic genera and species from the Cambrian up to recent time. Recent discoveries, particularly in America and Russia, have considerably extended our knowledge of the earlier groups.

The recent *Limulus* (fig. 14, 1 a, 1 b) is depicted in order to show the great resemblance to the marine Jurassic species *Limulus walchi* Desmarest (2 a, 2 b) occurring abundantly in the lithographic shale of Solnhofen in Bavaria. The difference is restricted almost only to the presence of larger lateral spines in the abdomen and by the lines leading to the genal angles. The Jurassic form is referred to the genus *Limulus* but probably belongs to a separate genus or subgenus. Nevertheless the species illustrates the great

conservatism of the stock. The Mesozoic limulid form is one of the most striking examples of persistency in fossil forms. The often quoted *Lingula* is less significant because the more simple morphology of the shell might possibly be acquired by related brachiopods.

A typical limulid is described already from the Permian (Dunbar 1923) (fig. 14, 3 a, 3 b). The prosoma has, however, segmental lobes in the central portion, and the well marked annulated axis of the abdomen also recalls trilobitan features. Parts of the ventral surface is preserved demonstrating the characteristic chelate walking legs as well as the typical spinous distal portion of the hind leg.

Also from the Devonian a limulid form, *Protolimulus eriensis* Williams is described (Eller 1938), but since only the outline and the less distinct traces of the ventral structures are preserved, the exact nature and taxonomic position of the species cannot be decided. In a recent paper Caster (1938) has interpreted the supposed vertebrate tracks *Paramphibius* as the trails of *Protolimulus*.

We have hitherto dealt with the probable members of the family Limulidae. In the freshwater deposits of the Carboniferous and Permian other xiphosuran faunas prevailed. Small, nearly circular forms belonging to the genera *Euproops* (fig. 14, 5) and *Prestwichianella* (4) dominated these faunas and are known from many different localities in several continents. The broad prosomal shield is laterally prolonged into genal spines. The central portion of the prosoma varies in structure, but in several forms we can distinguish 6 lobes corresponding to the 6 postoral somites. The broad, rounded abdomen deviates from the limulids in having well marked segments which, however, are anchylosed into a continuous shield. The telson is much shorter than in the Limulidae.

In the Carboniferous also occur other types which evidently represent a lower stage in the phylogenetic line of development. The complex of forms chiefly belongs to the genus *Belinurus* which is known both from the Carboniferous and the Upper Devonian. *Belinurus* from fresh-water deposits of the Carboniferous comprises small forms with a very long styli-form telson (fig. 14, 6). Characteristic of the genus is the presence of well marked pleurae of which at least 4—5 anterior ones form free movable tergites. The posterior segments are anchylosed. The more recently described Devonian species *Neobelinuropsis rossicus* (Chernychev) (Chernychev 1933) and *Belinurus alleganyensis* Eller (Eller 1938) express primitive characters together with a general limulid appearance. In these earlier forms more "thoracic" segments seem to be free. The American species was apparently a marine form.

We will proceed further backwards in the geological time. The Xiphosura of the Upper Silurian and Lower Devonian brackish water (and partly marine) faunas belong to a separate order, the so-called Synziphosura (fig. 14, 9—12; fig. 15, 7—9). The Synziphosura comprise more elongate

forms in which we find a complete division of the abdomen into probably 10 separate segments (the sixth and seventh segment might be anchylosed in certain species). The prosoma is more or less limuloid in *Bunodes* (11) and *Hemiaspis* (12), but in other genera such as *Weinbergina* (Richter and Richter 1929) and *Pseudoniscus* (Clarke 1901) it forms a large apparently smooth shield. Ruedemann (1916) thought to be able to trace lateral eyes and facial sutures in the latter form, but the structures seem uncertain. In several genera a postabdomen of 3—4 segments is indicated (*Bunodes*, 11 and *Hemiaspis*, 12).

Only *Weinbergina* (fig. 14, 9) from the Lower Devonian of Germany has provided information on the structures of the appendages (Richter and Richter 1929). The presence of 5 pairs of walking legs indicate that the Synziphosura have the number of prosomal appendages characteristic of the Xiphosura. It is interesting to notice that the legs of the species closely resemble the last pair of legs in *Limulus*.

Weinbergina of the Hunsrück Shale might have been a marine form, but the other genera seem to belong to the eurypterid faunas. This offers some explanation to the scarcity of the synziphosuran finds. Very little is known of Silurian and older Xiphosura. The occurrence, in a Downtonian sandstone in Norway, of a large abdominal shield described as *Kiaria limuloides* Størmø (Størmø 1934 a), suggests the presence of unknown forms in the earlier formations.

In the Silurian and Devonian species we notice apparent trilobitan and eurypterid affinities in the general shape of the body, but in the Cambrian forms the resemblance is more striking

The Upper Cambrian *Strabops* was described and figured by Beecher (1901) (fig. 14, 13). Clarke and Ruedemann (1912), however, quoting that Beecher had no access to the counterpart of the specimen, arrived at another conception of the structures and position of the lateral eyes and of the number of abdominal segments (fig. 14, 14). Quite recently Raasch (1939) has reexamined the form and he fully agrees with the original description of Beecher. The lateral eyes are said to be too badly crushed to merit a detailed description as to shape and orientation. The body is elongate, strongly recalling the shape of the eurypterids. The semielliptical prosoma has antemedian lateral eyes. Traces of median ocelli are uncertain. The abdomen is composed of 11 (Clarke and Ruedemann believed them to be 12) segments and a terminal broad telson of unknown length. Clarke and Ruedemann interpreted the form as a primitive eurypterid and Gerhardt (1935) following these authors places the genus in a special suborder of the Eurypterida. Raasch (1939) on the other hand strongly advocates that the genus belong to the Aglaspida described below.

In late years important discoveries of well preserved fossil Xiphosura in the Cambrian of the United States have thrown new light on the early

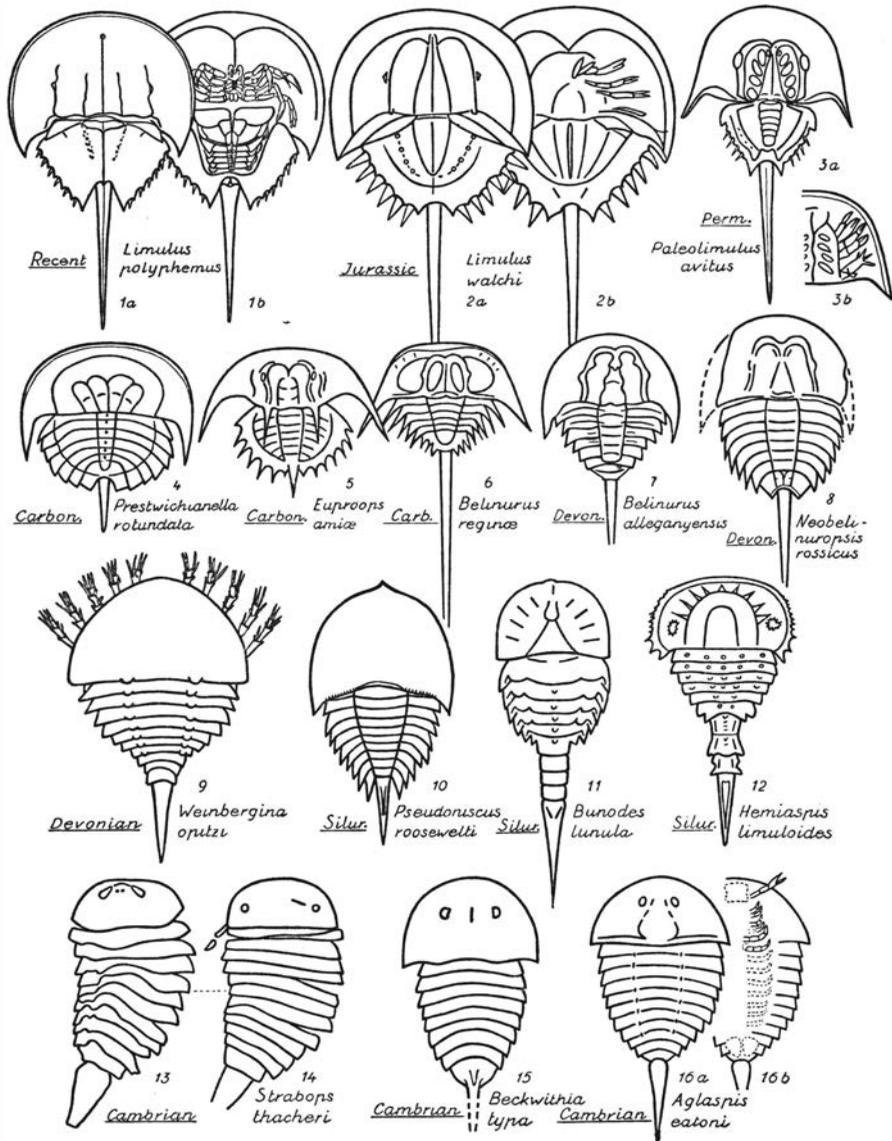


Fig. 14. Fossil Xiphosura.

1—8 = Limulida, 9—12 = Synziphosura, 13—16 = Aglaspida. (Figures reproduced after: 2 Zittel 1910, 3 Dunbar 1923, 4, 5, 6 Woodward (1868—1878), 7 Eller 1938, 8 Chernychev 1933, 9 Richter and Richter 1929, 10 Clarke 1901, 11 Störmer 1934 b, 12 Woodward 1868—1878, 13 Beecher 1901, 14 Clarke and Ruedemann 1912, 15 Resser 1931, 16 a Raasch in Twenhofel and Shrock 1935.)

representatives of the Merostomata. Thanks to the excellent finds by Raasch (1939) we know of 10 different genera (*Strabops* included) of primitive Xiphosura belonging to the order Aglaspida. The remains of these forms are confined to the Middle and Upper Cambrian. The size of the Aglaspida commonly ranges from 2—6 cm, but larger species, measuring 21.2 cm and

more, occur in the faunas. The integument of the exoskeleton appears to have been phosphatic rather than typically chitinous.

As shown in fig. 14, 16 *a* the body is trilobite-like, resembling the Lower Cambrian Olenellida (fig. 15, *o*). A median convex axis is indicated in the prosoma of many species. Median ocelli have not been traced, but lateral eyes of various sizes and positions are very characteristic. In several species the genal angles are produced into genal spines (the same species also have pleural spines in the abdomen, resembling the structures in trilobites). The abdomen is composed of 11 free segments. (Raasch mentions 12 segments, regarding the broad anterior portion of the telson as belonging to a twelfth segment, but there seems to be no real evidence in favour of this assumption.) Of the 11 segments the 2—3 posterior ones are frequently fused into a pygidial plate. A trilobation of the abdomen is more or less significant by relative convexity. The last segment is provided with a typical merostome telson. It is of considerable interest to ascertain that in the oldest genus, the Middle Cambrian *Beckwithia* (fig. 14, 15) (Resser 1931), the telson appears to be attached to the dorsal surface of the pygidial plate. This would imply that the telson spine represents a backwards directed dorsal spine of the last pygidial segment. There is no sign of a dislocation of the telson in the specimen, and the presence of a smaller spine on the first or second segment of the plate, corroborate the assumption of a dorsal spine. The presence of these telsonic structures in the earliest known representatives of the Merostomata, is of considerable interest in suggesting a connection between the merostome telson and the "telson-spine" of primitive trilobites such as the Olenellida. The telsonic structures (fig. 21) are discussed in detail in a later chapter.

In one species, *Aglaspis spinifer* Raasch, Raasch has been able to demonstrate the ventral structures. In fig. 14, 16 *b* an attempt is made to give an impression of the structures described which here are transferred to the related species *A. eatoni*, which probably had the same type of appendages. A median plate or epistoma may represent a median plate of the frontal doublure such as in the Pterygotidae of the Eurypterida. The prosoma is said to have, like that in other Merostomata, six pairs of appendages of which the frontal ones are developed as 4-jointed chelicera (fig. 24 d). The remaining appendages appear as short, curved walking legs. Four, more or less cylindrical segments are exposed, but since the distal one is fairly stout and long, one would expect a distal claw in addition to the segment preserved. As suggested by Raasch an extra proximal segment (or more) was probably present. In the abdomen quite similar walking legs or telopodites occur. It is of considerable interest to find well developed walking legs in the abdomen of these primitive merostomes. As shown in a later chapter it gives support to the conception that the abdominal feet in *Limulus* are derived from trilobite-like appendages. In recent Xiphosura the telopodites are strongly reduced.

A peculiar postventral plate is present below the postabdomen in the Aglaspida. The generally ovate plate is divided by a median cleft in two separate halves. The actual nature of the plate is unknown, but it seems most likely to interpret, as does Raasch, the structures as modified sternites serving to support the attachments of strong muscles from the powerful telson.

In the general shape of the body and in the structure of the 6 prosomal appendages, the Aglaspida show distinct morphological characters. The Aglaspida appear to approach both the ancestors of the Synziphosura and the Eurypterida. The number of abdominal segments in the Aglaspida seems to be intermediate between the numbers in the mentioned groups (10? and 12).

Comparing the Cambrian Aglaspida with the recent *Limulus* we notice considerable difference, but, thanks to the fossil material, it has been possible in an extraordinary way to follow the broad features of the gradual transition between the two types. The fossil record has to a great extent been able to illustrate the phylogenetic development of the Xiphosura through a space of time amounting to about 500 million years.

With our present knowledge of the phylogeny of the Xiphosura it would be of obvious interest to learn how this development conforms with the ontogenetic development of the recent representatives of the stock. One might expect that the established line of evolution could be traced in the ontogeny in late forms, thus offering an opportunity to test the biogenetic law of Haeckel.

In fig. 15 the ontogeny of recent Xiphosura is compared with adult fossil forms. The adult *Limulus* (5) differs but slightly from the Jurassic species (11). We might speak of a *Limulus*-stage in the phylogenetic development. The first free larva of *Limulus* (4), formerly called the "trilobite-stage", is very similar to late Palaeozoic forms such as *Prestwichianella* (10). (The special development of the central portion of the prosoma is of little significance because more "normal" characters are found in related forms.) As indicated by Oudmans already before the number of cephalic appendages in trilobites was known, the name "trilobite-stage" is not very appropriate and should rather be replaced by the term *Prestwichianella*-stage.

I have previously (Størmer 1934 b) pointed out that the embryo of *Limulus* (fig. 15, 2, 3) shows considerable resemblance to the Synziphosura. The convex abdomen has a 7-segmented preabdomen and an "unsegmented" postabdomen with a rudimentary telson. This might correspond to the 10-segmented abdomen of the Synziphosura. A postabdomen of 3—4(?) segments without pleurae are present in several genera. Possibly the dorsal organ (*d. org.* in 3) might be homologous with the lateral spots in *Hemiaspis* (9). It seems reasonable to call this ontogenetic stage of *Limulus* the Synziphosuran stage.

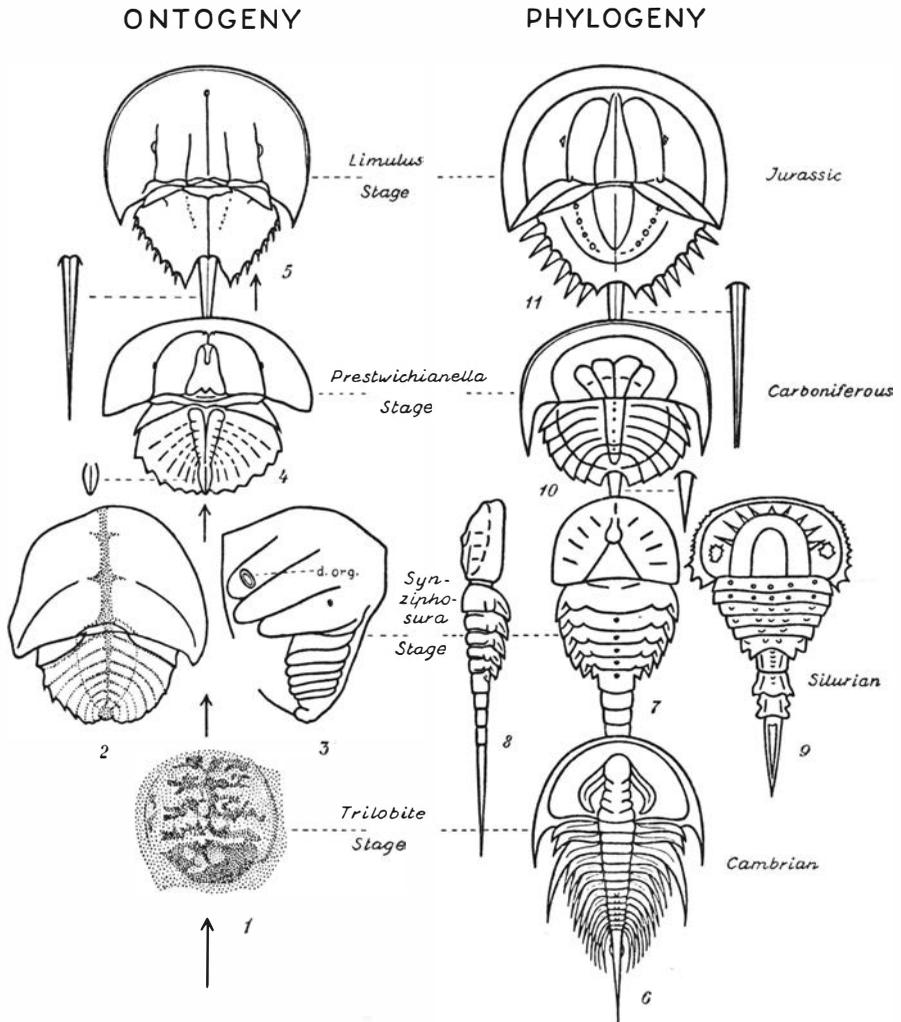


Fig. 15. Ontogenetic and phylogenetic development of the Xiphosura.

1-4 = *Limulus moluccanus* (Linnaeus) (= *Tachypleus gigas* Müller) (after Ivanov 1933).
 5 = *Limulus polyphemus* (Linnaeus) (= *Xiphosura polyphemus* (Linnaeus)). 6 = *Olenellus thomsoni* (Hall) (based on Walcott 1908). 7-8 = *Bunodes lunula* Eichwald (7 after Størmer 1934 b). 9 = *Hemiaspis limuloides* Woodward (after Woodward 1868-1878). 10 = *Prestwichianella rotundata* (Prestwich) (after Woodward 1868-1878).
 11 = *Limulus walchi* Desmarest (after Zittel 1910).

The very early embryonic stage (1) showing only 4 postoral somites indicates, as pointed out by Ivanov, the trilobite cephalon. This premerostome stage would seem reasonable to name the trilobite stage as suggested in fig. 15.

We have seen that the ontogeny of the recent *Limulus* in a striking manner agrees with the palaeontological record, and thus confirms the

biogenetic law of Haeckel. As is to be expected the correspondence is expressed only in the larger features.

The earliest ontogenetic stage also indicates trilobite-like progenitors of the Merostomata, a phylogenetic stage probably belonging to the earliest Cambrian or Precambrian period, since true Xiphosura already occur in the Middle Cambrian.

The fossil Xiphosura have also confirmed the eurypterid-xiphosuran affinities indicated in the structure of living Xiphosura.

Habitat and Adaptive Radiation of the Xiphosura.

The recent *Limulus* is a typical benthonic form crawling on the bottom and digging in the mud and sand. The same mode of life seems to be characteristic of the fossil species. It might be mentioned, however, that among the Aglaspida certain more convex forms, such as *U-arthrus* (Raasch 1939), might have been able to swim like the eurypterids.

The Cambrian representatives apparently had a 4-jointed chelicera in contrast to the 3-segmented one of more recent species. But already a Devonian species has prosomal appendages similar to recent ones, and a Permian form shows exactly the same modifications of all prosomal appendages. This confirms the assumption of a similar mode of life in the different Xiphosura. While the earlier forms both lived in salt and fresh water (particularly in brackish), the late palaeozoic species were confined to fresh water and the mesozoic and recent again to salt waters. (One of the recent species occasionally inhabits the fresh water of the estuaries.)

During their long phylogenetical development the Xiphosura show a tendency towards a shortening of the abdomen and a gradual fusion of the abdominal tergites into a solid continuous shield. This last tendency may have developed with different velocity in various evolutionary trends. A modification of the abdominal appendages into ventral plates apparently also took place during the phylogenetic development.

In spite of a gradual change in the morphology, the essential characters of the Xiphosura, the broad trilobate dorsal shield, the prominent prosoma with the 6—7 pairs of appendages, and the styliform telson, are fixed characters present in all types. Like the previously described groups the Xiphosura show a distinct plan of construction in their morphological characters, but the type seems not so settled as in the Trilobita and the Eurypterida. The primitive fossil Xiphosura probably are near to a common ancestor of both the Eurypterida and Xiphosura.

Taxonomy.

The classification of the subclass (or order) Xiphosura including the 3 orders (or suborders) Aglaspida, Synziphosura and Limulida is based chiefly on the different development of the abdomen.

The Aglaspida (Raasch 1939) have 11 abdominal segments of which the 2—3 last ones might be anchylosed. The group is also characterized by the presence of well-developed lateral eyes, the 4-segmented chelicera, the presence of walking legs also in the abdomen, and by the postventral plate.

The Synziphosura (Richter and Richter 1929, Størmøer 1934 b) have apparently 10 abdominal segments of which the 3—4 last ones might be anchylosed.

The Limulida (Richter and Richter 1929, Størmøer 1934 b) have a more or less anchylosed abdomen and chelate prosomal walking legs (unknown in earlier orders).

The living and fossil Xiphosura have provided valuable information and suggestions as to the relationships between the Xiphosura, Arachnida, Eurypterida and Trilobita. In several respects the Xiphosura form a central group combining both eurypterid and trilobitan characters. But although it has been possible, through the morphology of the Xiphosura, to approach the Trilobita, certain important characters remain, marking a distinct difference between the Chelicerata and Trilobita. The chief differences are the lack of antennae and the presence of chelicera and a total number of 6—7 postoral appendages in the prosoma in the Chelicerata.

But we shall see how a number of Cambrian and Devonian arthropods appear to be able to form a link between the Chelicerata and the Trilobita.

Cambrian and Devonian Arthropoda Related to the Trilobita and Chelicerata.

In 1909—10 the American palaeontologist Charles D. Walcott discovered a very rich and exceedingly well preserved fossil fauna in the Middle Cambrian Burgess Shale of the Stephen Formation in British Columbia, Canada. Although the fossils are more or less completely compressed in the silicious black shale, the structures are so well maintained that even the most minute morphological details and remains of the softer parts can be studied. Besides the shell-bearing forms the marine fauna comprises numerous impressions of algae, annelids, medusa-like forms and several other soft species. The arthropod material includes, besides the trilobites described above, a number of peculiar and unique forms which to a great extent have the appendages and even parts of the intestine preserved.

The valuable material was provisionally described by Walcott (1911 a, 1912, 1931). More especially in the posthumous paper (1931) edited by Resser, Walcott deals with the particular structures of the arthropods and presents reconstructions of the best known forms. His papers are provided with excellent photographs which to a certain extent permit a personal study of the material. Further descriptions are given chiefly by Hutchinson

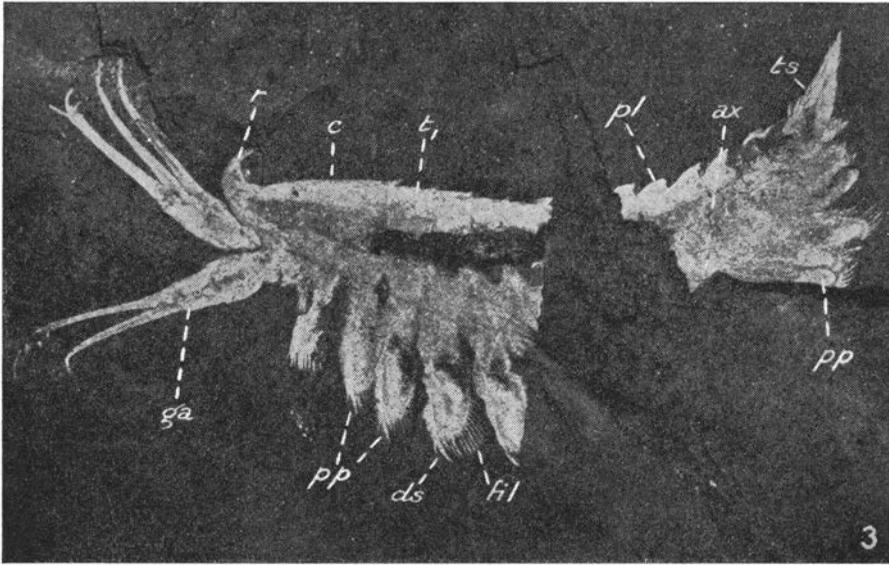


Fig. 16. Cambrian arthropod.

Leanchoilia superlata Walcott from the Middle Cambrian Burgess Shale, British Columbia, Canada. 1.5 X (after Størmer 1939).

ax = axis, *c* = cephalon, *ds* = distal segment of preepipodite, *fil* = gills, *ga* = "great appendage", *pl* = pleura, *pp* = preepipodite, *r* = rostrum, *t* = 1st tergite, *ts* = telson.

(1930), Ruedemann (1931), and Raymond (1935), the latter having collected new material in the type locality. In addition to these descriptions, students of fossil and recent arthropods, Raymond (1920, 1935), Versluys and Demoll (1922), Fedotov (1924), Warburg (1925), Henriksen (1928), Ivanov (1933), Størmer (1933, 1939) and Raasch (1939) have discussed the zoological position of the various forms. Personally I have had the opportunity, through the courtesy of Dr. Ch. Resser to study the type specimens of Walcott, and at the same time I have studied a collection belonging to the Palaeontological Museum in Oslo. As pointed out also by Walcott the arthropod material from the Burgess Shale is far from completely studied. It is to be hoped that the material will be subject to new detailed descriptions which certainly will throw new light on these interesting forms.

Since the zoological position of these Cambrian arthropods has been subject to considerable discussion and diversity of opinion, it is necessary in the following descriptions to treat separately the different genera and to discuss the various opinions concerning their relationships to other groups. After we have dealt with both these Cambrian forms and Devonian arthropods from Hunsrück Shale, we shall consider their mutual affinities and common characters as well as their habitat and adaptive radiation. The taxonomy, however, is more naturally dealt with in a later chapter.

Fig. 16—19 illustrate the more important Cambrian and Devonian species. The reconstructions of the Cambrian forms are chiefly reproduced

from Walcott's last paper (1931), but several figures are also based on published photographs and descriptions and on personal studies. The different genera are treated in a certain order, the first ones being those which apparently bear the closest resemblance to the fossil Xiphosura just described.

GENUS *LEANCHOILIA* WALCOTT

Fig. 16, fig. 17, 1, 2 and fig. 24 c.

In addition to Walcott's descriptions (1912, 1931), the genus has more recently been dealt with by Raymond (1935) in an important paper. Certain details in the structures of the appendages were furnished by the present author (1939).

The dorsal shield, somewhat laterally compressed, has a well marked headshield, an abdomen of 10 segments, and a short styliform telson. The dorsal shield is distinctly trilobate. The front of the headshield is turned up forming an acute rostrum. In a few specimens reniform areas are interpreted by Raymond as remains of lateral eyes, but since the structures are uncertain they are not indicated in the reconstruction figured. The tergites of the thorax-abdomen are not separated by distinctly transverse joint-lines such as in trilobites and in this respect more resemble the Aglaspidida. The telson has short lateral spines inserted in sockets. Raymond indicates that the ventral surface of the telson is not covered by a solid skeleton such as in the Xiphosura.

On the ventral surface remains of the appendages are known. In the headshield the presence of small (preoral) antennae is very uncertain, but is suggested by a pair of displaced appendages in front of the large appendages. Characteristic of the present genus is a pair of large branched appendages representing probably the first postoral appendages. As shown in fig. 16, fig. 17, 1, 2, and fig. 24 c the appendage is composed of a probably 5 or 6-segmented shaft, of which the third and fourth(?) segments each are provided with a long internal spine. The distal portion of the spine is modified into a multi-segmented tactile organ. The fifth(?) segment of the shaft forms an elongate spine provided with two short claw-like spines at the distal, slightly enlarged, portion. Besides the mentioned appendages several specimens have demonstrated at least two more pairs of prosomal feet. The exact number is not substantiated, but Raymond suggests the presence of 4 pairs of cephalic appendages in addition to the uncertain antennae. The prosomal limbs behind the "great appendage" are of the same type as those found in the abdomen. The appendages (*prpd* in fig. 17, 2; fig. 22) are closely similar to the gill-branch or preepipodite of the trilobite *Neolenus* (*prpd* in fig. 5, 19, 20). A broad shaft, with a segmented frontal rim, bears a row of filaments. The many well preserved specimens show no distinct traces of telopodites. Raymond is inclined to

assume their presence, but the "long, slender terminal spine with two subordinate ones" rather appear to belong to the frontal rim of the gill-branch (Størmer 1939). It seems probable that the telopodites are lacking or at least considerably reduced.

Remains of the mud-filled, segmented(?) intestine occur in several specimens.

The zoological position of *Leanchoilia* has been subject to much discussion. Walcott (1912) found it to be a typical branchiopod crustacean (Anostraca) evidently on account of the shape of the body and the great appendages comparable to the second antennae in the male of *Branchipus*. Fedotov (1924) suggested affinities to the Amphipoda, but Henriksen (1928), on the other hand, denies the crustacean nature of the genus, pointing out that the prominent pleurae and the telson plainly argue the merostome character of *Leanchoilia*. His conclusions are approved by Hutchinson (1930). It is interesting to notice that Henriksen asserts that "the curious, big antennae may very well be interpreted as primitive chelicerae". Størmer (1933) also advocated merostome affinities of this and other Middle Cambrian arthropods with trilobitan limbs. Raymond (1935), who has specially studied the genus, advocates, however, its crustacean nature because of the presence of tactile antennae and biramous limbs, characters which he regards as outstanding features of the Crustacea. On the other hand he admits that the trilobitan limbs point at a relationship to the Trilobita (which he considers as crustaceans) and the Xiphosura. He suggests that the Xiphosura might have descended from some group of trilobites or Mid-Cambrian arthropods, a group which thus is regarded as ancestral to both Chelicerata and Crustacea. In a recent paper the present author (1939) has emphasized, from studies of the appendages, the affinities of *Leanchoilia* to the Trilobita and Xiphosura, and the difference from the Crustacea.

In judging the position of the genus *Leanchoilia* we might bear in mind the general resemblance to the Cambrian Aglaspida described above (fig. 14, 13—16). The general shape of the body is very much the same. The headshield of *Leanchoilia* certainly contains less segments than in the the Xiphosura, but otherwise there is a general resemblance. The lateral spines and lack of a ventral plate in the telson might be of minor importance. The chelicera of *Aglaspis* is possibly comparable to the great appendage as discussed in a later chapter. Lateral branches of the appendages are not preserved in the described specimens of Aglaspida. Concerning the relationship to the Trilobita this is manifested in the structure of the gill-appendages.

It might be concluded that *Leanchoilia* in the general habitus of the dorsal shield expresses typical xiphosuran characters, particularly in the trilobation, the abdominal tergites and the telson. Trilobitan characters are exhibited in the structure of the appendages. The possible crustacean affinities are chiefly confined to the presence of 2(?) pairs of tactile organs.

The species *Emeraldella micrura* Walcott (1912) is probably synonymous with *Leanchoilia superlata* as suggested by Henriksen (1928).

The genus *Bidentia* (Walcott 1912) is possibly also synonymous with *Leanchoilia*. The figured specimens, which are not well preserved, show a general resemblance to this genus. The number of abdominal segments are reported to be 12 instead of 11, but this may be due to preservation. The great appendage in front has the particular characters of *Leanchoilia*, but seems to have more segments according to the considerably retouched photograph. Until more specimens are described it is hardly possible to decide whether *Bidentia* represents a separate genus or is synonymous with *Leanchoilia*.

GENUS *EMERALDELLA* WALCOTT

Fig. 17, 3.

This slender form bears considerable resemblance to the primitive Merostomata. The distinctly trilobate dorsal shield has a small cephalon, a thorax-preabdomen of 10 segments with curved pleurae, and a 3-segmented postabdomen without pleurae, but provided with a long styliform telson. It is of interest to notice that the telson has an expanded anterior portion just as in the Aglaspida, in which it was interpreted by Raasch as a separate segment.

On the ventral side of the head is a prominent labrum. The appendages are not well known. Walcott (1918) has, however, stated that some appendage-bearing specimens previously (1911 a) referred to the species *Sidneya inexpectans* Walcott, in fact belong to the present genus. The headshield has a pair of long, multi-segmented and setiform antennae which are quite similar to those of the Trilobita. The number of postoral cephalic appendages is probably 4. The remains preserved indicate trilobitan telopodites with strong ventral spines, and preepipodites of the *Neolenus*-type. The post-cephalic appendages are of the biramous trilobitan type. The actual gill-blades are not satisfactorily determined according to Walcott, but personal studies of the original material have convinced me of their presence.

An alimentary canal can be traced from the head backwards to the last segment.

Walcott (1912) referred *Emeraldella* to the Aglaspina (Aglaspida) of the Merostomata. He is inclined to regard the genus as filling the gap between the Branchiopoda and Merostomata. Raymond (1920) mentions the merostome characters of the dorsal shield, but yet finds the crustacean features to dominate. Also Fedotov (1924) claims a crustacean nature (Isopoda) of *Emeraldella*, but this is strongly opposed by Henriksen (1928) who, like Walcott, points out the relationship to the Xiphosura. A similar view is expressed by the present author (1933, 1939). In his more recent paper Raymond (1935) includes *Emeraldella* in a group of Crustacea "leading to the Merostomata".

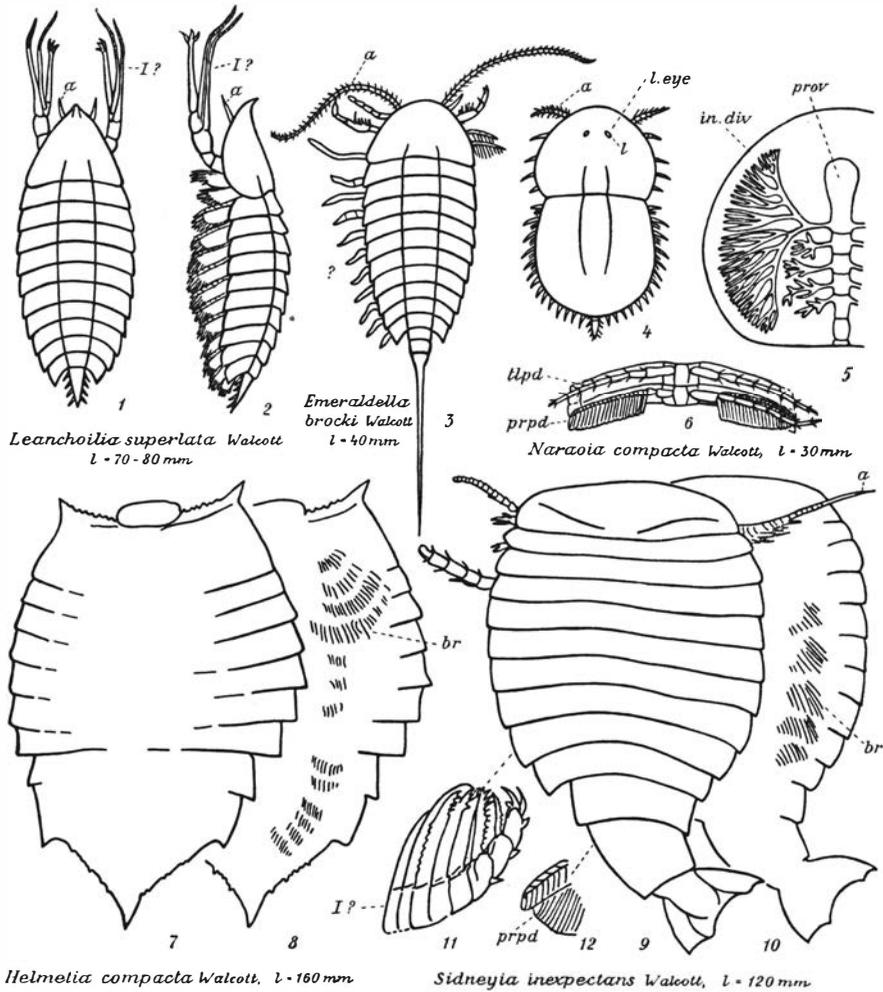


Fig. 17. Cambrian Arthropoda. Merostome-like forms from the Middle Cambrian Burgess Shale.

(2 modified after Raymond 1920, 3—10 after Walcott 1911 a, 1912, 1931.)

I = first postoral appendage, *a* = antenna (preoral), *br* = branchiae or gills, *in.div.* = intestinal diverticulae, *l. eye* = lateral eye, *prov* = proventriculum of the intestine, *prpd* = preopodite, *tlpd* = telopodite.

The evidence offered strongly indicates a relationship to the Xiphosura and the Trilobita. The trilobate body and the long, segmented abdomen with a narrow postabdomen provided with a styliform telson expanded in its anterior portion, are characters typical of the Aglaspida. The chief difference is found in the smaller cephalon comprising less appendages than in the Xiphosura, and in the general structure of the appendages. The trilobitan affinities are demonstrated in the trilobate body and particularly in the morphology of the appendages.

GENUS *MOLARIA* WALCOTT AND GENUS *HABELIA* WALCOTT

These small forms are probably related to *Emeraldella* and seem to belong to the same group. The dorsal shield has the same aglaspid habitus with a distinct trilobation also of the head. In *Molaria* the postabdomen has narrow pleurae. The little known appendages are of the trilobitan type. According to Walcott (1912) one specimen of *Habelia* shows two pairs of antennae, but it seems probable that the smaller of the two might represent telopodites projecting forward below the head. The number of postoral cephalic appendages (*Habelia*) appears to have been 4 according to Raymond.

Traces of the intestine is preserved in several specimens of *Molaria*. Of special interest are the vestiges of branched intestinal diverticulae in one specimen (Walcott 1912, pl. 29, fig. 3).

With regard to the position of the genera *Molaria* and *Habelia*, Walcott, Fedotov and Henriksen claim their relationships to *Emeraldella*, while Raymond, although grouping them with the xiphosuran *Aglaaspis*, regards them as crustacean forms leading to the Xiphosura(?). As discussed in a later chapter Raymond refers the forms leading to the Xiphosura(?) as belonging to a subclass different from those leading to the Merostomata(?). This conception is difficult to maintain as long as the Xiphosura are regarded as a part of the Merostomata.

There seems to be little doubt that *Molaria* and *Habelia* are related to *Emeraldella* and hence approach the Trilobita and primitive Xiphosura.

GENUS *NARAOIA* WALCOTT

Fig. 17, 4—6.

A new and detailed description of this interesting form was given in the last paper of Walcott (1931). As shown in fig. 17, 4 the dorsal shield is strongly developed, forming a large, but apparently thin-shelled, head-shield, and a similar more oblong thoracic-abdominal shield at the posterior end of which a short postabdomen with the telson projects. The broad cephalic shield is according to Raymond (1935) distinctly trilobate just as the rest of the body and this is therefore indicated in the reconstruction. Traces of small lateral eyes are recognized. The visible portion of the apparently 2-segmented postabdomen is formed by a single anal segment and a short triangular telson provided with lateral spines just as in *Leancoilia*.

From the ventral surface nothing has been obtained concerning the labrum, and but slight knowledge of the cephalic appendages. A pair of short multi-segmented antennae are present. Of the remaining cephalic appendages only the distal portions of the telopodites are known. The number of postoral pairs of cephalic limbs is not determined, but was hardly more than 4 (3 are suggested in Walcott's reconstruction of the ventral surface).

The thoracic-abdominal appendages are distinctly of the trilobitan type. Walcott's reconstruction (detail in fig. 17, *b*) even suggests a pre-coxa dorsal to the longer coxa. The narrow jointed shaft of the gill-branch or pre-epipodite recalls the *Triarthrus*-type of the trilobitan appendages (cp. fig. 5, 24).

Of particular interest is the wonderful preservation of the intestinal diverticulae in this "kidney crab". The intestine extends backwards as far as to the anal segment. In a diagrammatic reconstruction by Walcott (fig. 17, 5) the alimentary canal is supposed to have a frontal lobe which may represent a proventriculum (*prov*) such as in *Limulus*. In the posterior half of the cephalon the alimentary canal appears to be segmented. (In the drawing the hind segments belong to the thorax which is partly covered by the headshield.) Anterior to the first segmental division-line we notice the first pair of strongly ramified intestinal diverticulae (*in. div.*) In the following 4 segments similar, but smaller and less ramified diverticulae occur.

As discussed in a later chapter the intestinal diverticulae bear a striking resemblance to the structures in recent Xiphosura and Arachnida and probably also Trilobita.

Walcott (1912) placed the genus *Naraoia* in the Branchiopoda because of its resemblance to *Burgessia* described below (fig. 19, 1—4) which has similar intestinal diverticulae and a headshield overlapping the thorax. The genus *Naraoia* plays an important part in Raymond's (1920) theory on the origin of the Trilobita. On account of the absence of free thoracic tergites in the protaspis-larva of trilobites, Raymond assumes that the trilobites differentiated from forms without free thoracic segments. Accordingly he interprets *Naraoia* as a primitive trilobite representing an intermediate form between the typical trilobites and their ancestors. Fedotov strongly objects to the views expressed by Raymond. Primarily the numerous segments in the "pygidium" of the genus show that it cannot be regarded as a few-segmented form, and secondarily the genus is not a trilobite because the presence of a postabdomen substantiates that the thorax-abdominal shield is not a true pygidium.

Henriksen (1928) points out the resemblance to *Limulus* and regards *Naraoia* as a primitive xiphosuran belonging to the ancestry of *Limulus*. Walcott (1931) expresses his belief in trilobitan affinities, and at the same time suggests relationship to the crustacean-like forms *Marrella*, *Burgessia* and *Waptia* described below.

With its broad, trilobate dorsal shield the genus *Naraoia* shows a distinct resemblance to the Xiphosura and Trilobita. The large thoracic-abdominal shield, not including the telson, indicates xiphosuran affinities. As pointed out by Fedotov and Henriksen (1928) a coalescence of the thoracic segments is quite unknown in the Crustacea. A relationship with the Trilobita is expressed in the presence of antennae and in the characteristic structure of the appendages. The intestinal diverticulae suggest affinities to the Chelicerata and to the crustacean-like Cambrian forms described below.

GENUS *HELMETIA* WALCOTT

Fig. 17, 7, 8.

This large and imposing form (fig. 17, 7, 8) was never described by Walcott, but an excellent photograph is published (Walcott 1917, 1931) of the single (?) specimen which I have seen in the collections in Washington.

The flat, expanded dorsal shield is divided into a trapezoid headshield, a thorax with apparently 6 tergites, and a large pygidium with an acute distal point. A median axis seems to have been present, but the preservation gives no certain evidence. The headshield has pointed antelateral corners, a median frontal lobe may belong to a somewhat dislocated labrum.

Impressions of rows of filaments indicate that *Helmetia* had fringes of gill-blades similar to the preepipodites in trilobites.

The present genus shows affinities to the Trilobita in the presence of a pygidium and in the structure of the appendages.

The genera *Mollisonia* and *Tontoia* Walcott (1912, 1931) seem to be related to the described form. The known species, however, are quite small, but possibly represent larval stages since the cephalon is divided into 5 transverse lobes. Cephalon and pygidium are of equal size and the thorax is composed of 7 and 4 segments respectively. The thoracic pleurae are quite narrow. The appendages are unknown.

Mollisonia and *Tontoia* may be related to trilobites such as *Agnostus* (claimed by Fedotov 1924), but their position is open to question. The presence of a pygidium points in the direction of *Helmetia* and possibly to *Marrella* as suggested by Warburg (1925).

GENUS *SIDNEYA* WALCOTT

Fig. 17, 9—12.

This is perhaps the most striking form discovered by Walcott. It was also the first to be found and described (Walcott 1911 a). Quite a few specimens have been collected, but yet the knowledge of the ventral structures of this comparatively large form leaves much to be desired. New investigations of the original material would probably reveal new and important morphological details. In judging the morphology of *Sidneya* one has to bear in mind that some of Walcott's illustrations (1911 a, pl. 2, fig. 2, 3, and textfig. 10) later were stated to represent the above described genus *Emeraldella* (Walcott 1918, p. 118).

The broad and flat dorsal shield, tapering in width backwards to the flat caudal "fins" has a distinct eurypterid appearance. A trilobation is not indicated. The prosoma is very short and is, according to the description, provided with lateral eyes at the lateral margins. The abdomen (a thorax-abdomen) has a preabdomen of 9 segments and a postabdomen of 2 or 3 segments. The caudal fan might represent a third segment or a telson.

In two specimens figured (Walcott 1911, pl. 3, fig. 3, and pl. 5, fig. 2) the intestine does not seem to invade the median lobe of the caudal fan, but in another specimen (l. c. pl. 3, fig. 2) the probable filling of the intestine is traced to the distal point of the lobe. The postabdomen is composed of longer and more narrow segments than the preabdomen. The tenth and eleventh segments probably form simple annular rings such as in the eurypterids. Walcott describes the caudal fan as consisting of a central axis with two wing-like posterior pleural extensions, and attached to the anterior portion of this axis a pair of lateral swimmerets which more or less overlap the pleural extensions. The lateral portions of the caudal fan are thus interpreted as appendages of a terminal segment in front of the telson. In order to decide whether the lateral portions of the caudal fan are modified appendages (cerci) or merely lateral extensions of a telson, I have examined two specimens belonging to the collections of the Palaeontological Museum in Oslo. In these specimens the caudal fan appears to belong to one plate rather than being formed by an appendage-bearing twelfth segment and a posterior telson. An examination of more specimens is, however, necessary to solve the problem.

On the ventral surface a well developed labrum seems to have been present. The appendages are incompletely known. As shown in fig. 17, 9 a pair of multi-segmented, partly setiferous antennae (*a*) evidently represents the preoral appendages. On the left side of the figured specimen the terminal portions of a segmented limb provided with three distal claws was interpreted by Walcott as belonging to the second pair of appendages (first postoral pair). This terminal portion may, however, just as well represent one of the other telopodites of the prosoma.

It seems more likely that a peculiar big appendage (fig. 17, 11) belongs to the first pair of postoral appendages. As discussed below it bears a certain resemblance to the great appendage of *Leanchoilia* (fig. 24) and there appears to be reason to believe that the specialized limb of *Sidneya* also represents the first postoral appendages in front of the more unspecialized telopodites. The appendages are composed of a 9—10(?)—segmented leg with a terminal claw flanked by two similar short spines. The inside (primarily ventral side) of the leg is provided with a number of long and flat spines carrying close-set spines along their margins. The left and right leg, with their long blade-shaped spines, might together have formed a special organ which partly could have served as a catching implement comparable to the large appendages in the eurypterid *Mixopterus* (fig. 10, 3).

The remaining prosomal appendages are little known, but jointed legs suggest telopodites of the trilobitan type. The presence of spinous gnathobases on the appendages does not seem substantiated. The number of prosomal appendages cannot be decided (previous accounts were erroneously based on specimens of *Emeraldella*).

Imprints of the abdominal appendages are seen in the figured specimen (*br* in fig. 17, 10) and individual appendages are also described (12). The preabdominal segments have large gill-appendages consisting of a narrow jointed shaft and a broad fringe of apparently blade-shaped gills just as in the gill-branch of the trilobite *Triarthrus* (fig. 5, 24). A jointed telopodite lateral to the third tergite (fig. 17, 9) may appear to belong to the trunk, but the lack of similar legs further back suggests that this branch of the appendages was reduced in the trunk, such as was probably the case in *Leanchoilia*.

Concerning the zoological position of the present genus Walcott (1911 a, 1912) is inclined to interpret it as a transitional form between the Trilobita and Eurypterida. In their eurypterid memoir Clarke and Ruedemann (1912) concluded that *Sidneya* is not a eurypterid, but a primitive form demonstrating remarkable adaptive features. They conclude that the genus possibly belong to the Merostomata, "but is distinctly allied to the crustaceans in such important characters as the structures of the legs and telson". Kassianov (1914) was inclined to agree with Walcott. Similar views are also expressed by Raymond pointing out that the trilobitan abdominal legs of *Sidneya* suggest its origin from the same ancestral stock as the Trilobita which he considers as being primitive Crustacea. Versluys and Demoll (1922) very strongly emphasize the crustacean, not arachnid, nature of the genus, basing their argument on the non-eurypterid type of appendages. (They were not aware of Walcott's correction as to some specimens belonging to *Emeraldella*.) Fedotov (1924), on the other hand, shares the opinion of Walcott in stating that "*Sidneya* possesses features of *Merostomata*, but in the differentiation of the appendages is not so far remote from the trilobites as the other representatives of *Merostomata*". Henriksen (1928) also lays stress on the general merostome habitus of the genus, but asserts that the *Merostomata* "possess a telson (styliform) but miss cerci, whereas cerci are typically found among the Crustaceans". Henriksen also points out the trilobitan features and concludes that the present genus distinctly demonstrates characters of both *Merostomata*, Trilobita and Cambrian forms which he refers to the Branchiopoda of the Crustacea.

We have seen that most authors dealing with the present form have expressed its affinities both to the *Merostomata* and Trilobita. Others have claimed a relationship also to the Crustacea, and some have even argued that it represents a true crustacean having no relations among the other groups.

Considering the morphology of *Sidneya*, as far as it is known at present, we may conclude that the general habitus, the headshield with the segmented thorax-abdomen, exhibits distinct merostome features. The general correspondence must, however, not be taken too literally. The headshield, just as in *Leanchoilia* and *Emeraldella*, evidently comprises a smaller number of segments than the prosoma of the *Merostomata*. A narrow postabdomen

is characteristic of both primitive Xiphosura and Eurypterida. In *Sidneya* the telson, or may be a combination of a telson and a last segment, differs from the styliform telson of typical Merostomata. But also among the Eurypterida the telson is sometimes expanded and forms a caudal fan (*Pterygotus* fig. 10, 1). If the lateral portion of the caudal fan is a pair of cerci, the structures no doubt resemble the tail of certain Crustacea. But even if they were true cerci, it is not unlikely that modified cerci might occur in forms related to the Trilobita among which one genus (*Neolenus* fig. 5, 13) is known to possess a pair of caudal cerci evidently representing modified appendages.

Turning now to the appendage, both the antennae, the common telopodites and the branchial appendages are distinctly of a trilobitan type. Antennae of this type are also characteristic of the Crustacea, and the specialized first (?) pair of postoral appendages (1) also resembles certain crustacean appendages. The presence of maxillae in *Sidneya* is, however, highly problematic. Spinous gnathites might as well be the margins of proximal spinous segments of the limbs just as in the trilobite *Neolenus*. It seems more natural to compare the specialized first(?) pair of postoral appendages in *Sidneya* with the "great appendage" in *Leancoilia* (fig. 17, 1, 2, fig. 24 c). In both cases a modified telopodite is provided with long internal spines. As discussed in a later chapter the specialized appendage in *Sidneya* can be interpreted as suggesting evolutionary tendencies towards the formation of chelicerae. At the same time it may be noticed that a peculiar development of the internal spines of these cephalic telopodites is characteristic of the Merostomata (*Mixopterus* and *Stylonurus*, fig. 10, 3, 4).

From this discussion it appears that *Sidneya* exhibits merostome characters in the general morphology of the dorsal shield, and in the development of the appendages shows relationship to the Trilobita and to the merostome-like Cambrian Arthropoda described above. The typical crustacean characters (not counting characters common both to the Crustacea and Trilobita) are restricted to the more uncertain expanded cerci, but even the presence of such cerci might be expected among representatives of the Trilobita—Merostomata. In the author's opinion the evidence offered indicates affinities to the Merostomata and Trilobita, but not necessarily to the Crustacea.

The apparently allied genus *Amiella* (Walcott 1911) is too imperfectly known to be considered in the present connection.

The Cambrian forms hitherto dealt with have clearly demonstrated their relationship both to the Merostomata and Trilobita, and thus fill the gap between the large groups previously described and discussed. We are now going to consider another group of Cambrian Arthropoda which exhibit features more in common with the Crustacea, but still have distinct trilobitan characteristics.

GENUS *OPABINIA* WALCOTT

Fig. 19, 10.

This form (Walcott 1912) has been regarded by most authors as a typical representative of the Branchiopoda. The species *Opabinia regalis* Walcott was restudied by the zoologist Hutchinson (1930) and additional knowledge was presented by Raymond (1935).

The body is narrowly elongate, the dorsal shield being laterally compressed. The cephalon is provided with well developed pedunculate eyes (*l. eye* in fig. 19, 10). Behind the small head the trunk (thorax-abdomen) apparently comprises 16 segments and a small terminal anal plate(?) or telson. As pointed out by Raymond the dorsal shield of the trunk is distinctly trilobate with pleural lobes sufficiently wide to cover the appendages when in their natural position. (Indicated in the present reconstruction, fig. 19, 10.) As suggested by Raymond, Hutchinson probably misinterpreted remains of the pleurae as parts of foliaceous appendages. The last abdominal segment apparently had no pleurae.

The ventral structures of the head are little known. The outstanding feature is the remarkable frontal process (*frpr* in fig. 19, 10) projecting from the front of the head. The frontal process or proboscis forms an elongate flexible tube without traces of segmentation, but with a wrinkled external surface. The distal portion is somewhat expanded with a distal cleft provided with short spines or denticles. The process, which probably was erectile, has a median canal. The organ has been compared with the frontal organ in the male of the Anostraca among the Branchiopoda. In this group the organ, which is coalesced only at the base, is formed by the internal branches of the second antennae (*I*). The correspondence is not very convincing and it might be mentioned that a certain resemblance also is noticed to the erected alimentary canal of several annelids belonging to the same Cambrian fauna (Walcott 1911 *b*, 1931). It seems, however, difficult to assume the presence of an erectile enteric canal in the Arthropoda. A ventral postlateral lobe of the head is interpreted by Hutchinson as parts of the postoral antennae, but the structures are not clear.

As shown by Raymond the postcephalic appendages are distinctly trilobitan, and apparently correspond to the gill-branch in *Neolenus* (fig. 5, 19, 20). I have seen gill-blades in the Washington specimens. Hutchinson claims a foliaceous shape of the appendages, but this interpretation is evidently due to a misinterpretation of the specially preserved (compressed) structures (Raymond 1935). Only the last pairs of appendages might have had a more foliaceous appearance and have served as a pair of expanded cerci taking part in the formation of tail fan.

All previous authors, except Raymond in his last paper, are unanimous in regarding *Opabinia* as a true branchiopod. (As discussed below the present author (1933) has suggested the arachnid affinities of all the

crustacean-like forms here described.) The branchiopod characters are chiefly pointed out in the general shape of the body, the pedunculate eyes, the frontal process, and in the flat blade-shaped cerci. Foliaceous appendages have also been attributed to the present form, but actually these are of the trilobitan type. For this reason Raymond is inclined to place *Opabinia* in a special crustacean order leading to the Anostraca.

With our present knowledge of the genus it may be concluded that a resemblance to the Crustacea (Anostraca) is expressed in the pedunculate eyes, possibly in the peculiar frontal process, and in the possession of cerci forming a tail fan. The general shape of the body, however, is not necessarily crustacean. On the contrary the distinctly trilobate dorsal shield is significant of the Trilobita — Merostomata, and is unknown in the Branchiopoda. The gill-appendages obviously indicate affinities to the Trilobita and the above described Cambrian Arthropoda. Concerning the tail fan a similar structure might have occurred in *Sidneya*. *Opabinia* deviates from the mentioned forms by the absence of antennae (their presence is uncertain in *Leanchoilia*).

We arrive at the conclusion that *Opabinia* expresses definite trilobitan characters, but at the same time has certain non-trilobitan features which are characteristic of the Crustacea.

Hutchinson has paid attention to the probable affinities of *Opabinia* to the carboniferous genus *Rochdalia* described from England by Woodward (1913).

GENUS *YOHIOA* WALCOTT

Fig. 18, a—d.

This small form described by Walcott (1912) is of a certain interest in forming some kind of link between the Trilobita and the more crustacean-like Cambrian Arthropoda. The illustrations in fig. 18 are based on photographs reproduced by Walcott. Unfortunately the material is too scanty to permit a closer morphological study of the genus. It seems doubtful whether the specimen in fig. 18 *b* actually belongs to the present genus.

The very slender body is distinctly trilobate, but the pleurae are quite narrow. An axis is also distinguished in the cephalon. The headshield has a marked trilobitan appearance with five segments expressed by transverse furrows. The lateral eyes are, however, described as pedunculate. On the 12 postcephalic segments the pleurae seem to be absent on the 4 posterior ones. According to the description the abdomen has a pair of expanded caudal rami (cerci), but in the specimens figured (except the one reproduced in fig. 18 *b*) only one terminal plate is demonstrated. The presence of either cerci or a broad telson does not seem satisfactorily decided.

Five pairs of appendages are said to belong to the cephalon, but the published photographs give but little information of the structures. The short and blunt frontal processes interpreted as preoral antennae (fig. 18 *d*)

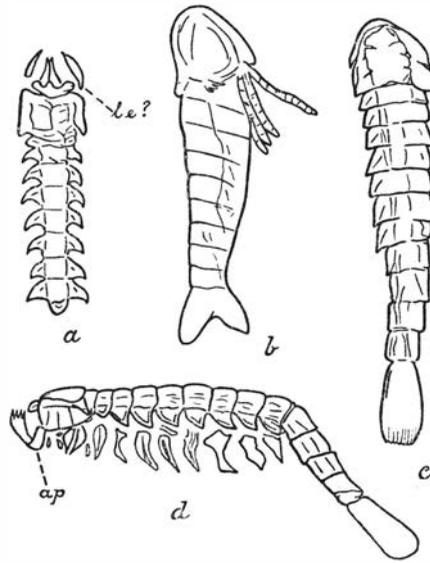


Fig. 18. Cambrian Arthropods.

a, c, d = *Yohoia tenuis* Walcott, 2 x. *b* = *Yohoia plena* Walcott 3 x. From the Middle Cambrian Burgess Shale. *ap* = first postoral appendage(?), *l. e.* = lateral eye(?).

are very dubious. The first postoral(?) appendages seem to be comparatively large and provided with distal spines (*ap* in fig. 18 *d*). A certain resemblance to the frontal process in *Opabinia* might be noticed. The postcephalic limbs were probably similar to the gill-branch of the trilobitan appendage.

Walcott (1912) considered the present genus as belonging to the Branchiopoda and related to *Waptia* (see below) on account of the shape of the body and the presence of caudal rami. Fedotov (1924) is inclined to agree with Walcott. Henriksen (1928) suggests that the genus belongs to a separate family with possible affinities to the below described *Marrella*. Hutchinson (1931) indicates relationship to *Opabinia* and Raymond (1935) groups the genus *Yohoia* with *Opabinia* and *Leancoilia* in an order leading to the Anostraca of the Branchiopoda.

It appears that these authors regard the genus *Yohoia* as belonging to the Branchiopoda, or to ancestors of this crustacean group. The crustacean characters are chiefly confined to the probable pedunculate eyes and the somewhat uncertain caudal cerci. Trilobitan characters are on the other hand expressed in the trilobate body, particularly in the cephalon, and evidently in the type of appendages. At the same time the present genus demonstrates distinct affinities to other Cambrian Arthropods from the same fauna. In the general shape of the body, except the telson, *Yohoia* bears resemblance to the more merostome-like *Molaria*, and in the structure of the eyes and

caudal fan it shows affinities to crustacean-like forms such as *Opabinia* and *Waptia*. The importance of *Yohoia*, so far as is known at present, lies in its linking together the trilobites and merostome-like forms with the crustacean-like arthropods of the Cambrian.

GENUS *MARRELLA* WALCOTT

Fig. 19, 5, 6.

The Burgess Shale has yielded a great number of specimens of this beautiful and most extraordinary form. The small "lace crab", so called in the explorers camp because of its very delicate test, was evidently a planktonic form. The single species *M. splendens* Walcott is well illustrated by numerous photographed specimens (Walcott 1912, 1931, and Ruedemann 1931). Reconstructions of the species have previously been attempted by Raymond (1920), Beurlen (1930), Walcott (1931) and Richter (1932).

The dorsal shield of *Marrella* consists of a peculiar 4-horned cephalon, a thorax-abdomen of 24 segments, and a small terminal telson or pygidium. The lateral and posterior borders of the plate-shaped, not trilobate, head-shield are prolonged into flat spines directed backwards. The margins of the posterior spines show a distinct denticulation. Lateral eyes (*l. eye* in fig. 19, 5, 6) are situated at the frontal margin. It is of interest to notice the presence of facial sutures crossing the base of the frontal horns. The presence of facial sutures, such as in trilobites, suggests that the frontal horns may be interpreted as genal spines of trilobites. The thorax-abdomen has a very delicate test. A median axis is distinct, but it is difficult to decide whether pleurae were present or not. The pleurae are not indicated in Walcott's reconstruction (1931), but suggested in those of Beurlen (1930) and Ruedemann (1931). In the present reconstruction (fig. 19, 5) dotted lines suggest the outline of the more doubtful pleurae. The apparently unsegmented pygidium or telson forms a terminal lobe.

The ventral surface with the appendages is known to a certain extent (Walcott 1931). An elongate labrum (*labr*) is attached to the doublure in front just as in trilobites. The mouth has probably a more central position at the posterior margin of the labrum. The preoral antenna (*a*) is long and flexible with numerous segments provided with few, short setae. The second appendage, evidently belonging to the first postoral somite (*I*), is also developed as an uniramous tactile organ. This telopodite is composed of 9 elongate segments which are almost covered by fine setae giving a plumose appearance to the appendage. The two following appendages are not well known, but are probably similar to the limbs of the thorax-abdomen (the telopodites might possibly have more segments). Walcott assumes that only three postoral appendages belong to the cephalon. The determination of the exact number involves, however, a great amount of conjecture,

and it does not seem excluded that an extra appendage might be present in the cephalon such as in trilobites.

The appendages of the thorax-abdomen are exactly of the trilobitan type resembling the limbs of *Triarthrus* (fig. 5, 24). Even a precoxa seems to be indicated above the coxae (Størmer 1939). The posterior telopodites have triangular endites just as in *Triarthrus*. The gill-blades of the pre-epipodites form a broad fringe. According to Walcott the base of the appendage has a more lateral position than in trilobites.

The intestine is, according to Walcott, traced from the labrum backwards to the telson.

When Walcott published his first description of the genus *Marrella* he placed it near the Trilobita, a conception also shared by Raymond (1920) and Warburg (1925). Fedotov (1925) misinterpreted the often indistinct fringes of gills as the remains of a delicate, transparent valve of a crustacean belonging to the Conchostraca or Cladocera. Henriksen (1928) points out that the prolonged cephalic spines are not to be interpreted as representing a carapace, and he corrected Walcott's primary conception of the frontal horns as modified antennae and the plumose second appendages being mandibles. Henriksen is inclined to regard *Marrella* as a primitive branchiopod. Gürich (1931 a) and Beurlin (1930, 1934) assume an intermediate position between the Branchiopoda and Trilobita, a view largely similar to that held by Walcott, Raymond and Warburg:

In his last paper Walcott (1931) discusses the affinities of *Marrella*. The following characters are regarded as trilobitan: A cephalon supporting a labrum with the proximal points of the cephalic limbs gathered at its posterior end, sessile eyes on proximal end of a free cheek, and biramous limbs of the trilobite type. The characters dissimilar to trilobites are said to be: The absence of a thoracic dorsal shield, almost total absence of a pygidium, posterior position of the proximal joint of antennae, a large second (by a mistake he mentions it as third) cephalic appendage (mandible), and the lateral attachment and lack of gnathobases in the trunk limbs.

With regard to the dissimilarities, the absence of pleurae (thoracic dorsal shield) is doubtful, and the small pygidium or telson is not very different from the 1 or 2-segmented pygidium in primitive trilobites such as the Olenellida. The posterior position of the antennae seems to be of minor significance. The lack of gnathobases on the coxae represents no difference according to recent studies on trilobite limbs. The lateral position of the appendages seems largely conjectural since the absence of pleurae is not decided. There chiefly remains the possible lack of postcephalic pleurae, and the special development of the second cephalic appendage. To this might be added the peculiar development of the non-trilobate cephalon.

On the other hand Walcott points out branchiopod characters in the presence of a true carapace arising from a fold in the integument, a labrum attached to the doublure, and a large mandible serving as a jaw. As pointed

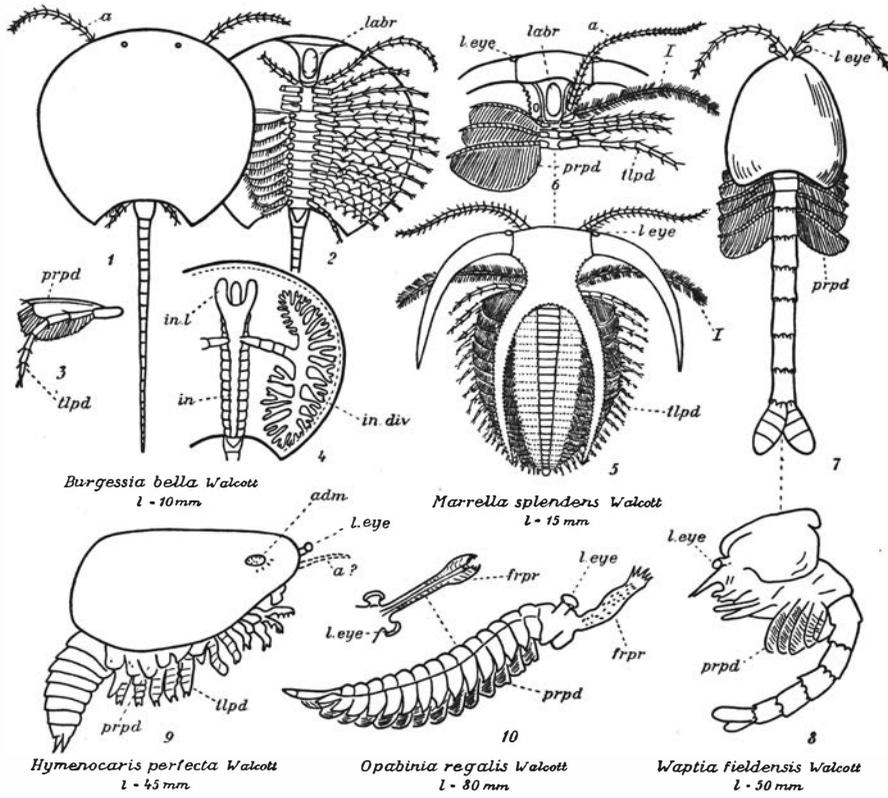


Fig. 19. Cambrian Arthropoda. Crustacean-like forms from the Middle Cambrian Burgess Shale.

1, 2, 4, 7—9 after Walcott 1912, 1931; 3, 5, 6, 10 based partly on description and illustrations by Walcott 1912, 1931, Hutchinson 1930 and Raymond 1935.

I = first postoral appendage, a = antenna (preoral), adm = adductor muscle, frpr = frontal process, in = intestine, in. div. = intestinal diverticulae, in. l. = intestinal lobe, labr. = labrum, l. eye = lateral eye, prpd = prepedipodite, tlpd = telopodite.

out by Henriksen, however, *Marrella* has no carapax in the sense of being “a backwards directed, free duplication from the hind edge of the head”. The so-called mandible evidently had no gnathous function and would correspond to the second antenna in the Branchiopoda. Since a labrum of the mentioned type is typical also of trilobites, the arguments in favour of branchiopod affinities seem to be of no value. *Marrella* is said to differ from the Branchiopoda in the absence of foliaceous trunk limbs and cerci or caudal rami, and by the presence of appendages on each segment back to the telson.

In Walcott's opinion *Marrella* is less primitive than the Apodida of the Branchiopoda and at the same time more primitive than the Trilobita. He assumes that both *Marrella* and the *Trilobita* in the earlier phylogenetic development passed through a stage with foliaceous limbs, an assumption which would involve a secondary nature of the characteristic trilobitan limb.

Our conclusion with regard to the position of *Marrella* must be that it shows distinct affinities to the Trilobita in the presence of free cheeks with lateral sessile eyes, and by the trilobitan appendages. The genus differs from the Trilobita chiefly in the peculiar development of the cephalic shield, the possible lack of pleurae in the trunk, and in the tactile, uniramous second cephalic appendage. Crustacean characters are only suggested by the presence of two pairs of antennae.

Marrella has a unique position among the Cambrian Arthropoda, but a related form seems to occur in the Devonian (*Mimetaster* described below) and possibly in younger formations (Pygaspidae).

GENUS *BURGESSIA* WALCOTT

Fig. 19, 1—4.

Another beautiful little arthropod occurs abundantly in the Burgess Shale. Owing to the very delicate test we are ignorant of many morphological characters of *Burgessia*, but still there are certain well preserved structures which prove to be of great importance to a general conception of the zoological position of the Cambrian Arthropoda.

The body is almost covered by a large, subcircular, plate-shaped carapace. A pair of small lateral eyes are said to occur near the frontal margin. The trunk contains, according to Walcott, 8 limb-bearing segments and an ultimate segment to which a long multi-jointed telson is attached.

On the ventral side a labrum of the trilobitan type is attached to the doublure in front. A multi-segmented, evidently preoral, antenna is succeeded by 3(?) more or less uniform telopodites. Gill-branches are not observed, but might have been present just as in the trunk. In Walcott's reconstruction (fig. 19, 2) the first telopodite is shown to be composed of 10 segments, but, according to the description in the text, very little is known of this appendage. The limbs of the trunk are distinctly of the trilobitan type with a preepipodite more of the *Neolenus*-type (Størmer 1939).

Of particular interest is the wonderful preservation of the intestine with the intestinal diverticulae (fig. 19, 4). The alimentary canal (*in*) has a frontal stomach apparently forked anteriorly into two lobes (*in. l*). From the stomach the intestine runs backwards to the anus in front of the jointed telson. Near the hind border of the head the intestine on either side has a powerful segmented(?) tube leading to the strongly ramified intestinal diverticulae (*in.div.*). The structures are similar to those demonstrated in the merostome-like *Naraoia* (fig. 17, 5) and are evidently homologous with the same organs in the Chelicerata and probably Trilobita.

The *Lepidurus*-like carapace has been the major reason for including the genus *Burgessia* in the Notostraca of the Branchiopoda. Several authors have also placed the genus near the Branchiopoda, stating that the trilobitan

appendage differs from the foliaceous one of *Lepidurus* (Raymond 1920, 1935). Fedotov (1925) and Henriksen (1928) are inclined to regard the numerous segments of the telson as representing true abdominal segments, an assumption which seems hardly possible since the intestine does not invade this jointed portion. A jointed telson is known in the Palpigradi among the Arachnida. In his last paper Walcott (1931) places *Burgessia* near *Marrella* and the Trilobita.

We might conclude that the large carapace and the lack of trilobation point towards the Crustacea. On the other hand the trilobitan labrum and appendages, the styliform telson, and the intestinal diverticulae clearly demonstrate affinities to the Trilobita and merostome-like Cambrian arthropods, as well as to the Chelicerata.

GENUS *WAPTIA* WALCOTT

Fig. 19, 7—8.

Even more crustacean-like is the present form which in its general habitus and size might recall a recent shrimp.

The narrow body has a laterally compressed carapace covering the head, the thorax, and the frontal portion of the abdomen. No trilobation is traced in the body and the trunk which lack the pleurae. According to Walcott's descriptions (1912, 1931) the thorax contains 5—7 short segments, the preabdomen(?) 8, also short, and the postabdomen 6 long cylindrical segments. A small rostral plate (or process?) is located in front between the pedunculate lateral eyes (*l. eye* in fig. 19, 7, 8).

The exact position of the mouth is unknown. A pair of flexible antennae, composed of comparatively long segments, have a frontal position. Indications of two small lobes near the rostrum have been interpreted by Walcott as antennules, but the structures are too indefinite and the determination of the structures seems highly conjectural. The conception of Walcott would involve that the antennae represented the first postoral appendages, an assumption which is strongly opposed by the frontal position of these tactile organs and by the evidently preoral nature of similar antennae in related forms. Walcott mentions the possible presence of 3 pairs of cephalic appendages behind the antennae. The thoracic appendages are also unsatisfactorily known, but trilobitan telopodites appear to be present. The preabdomen has typical trilobitan preepipodites (*prpd* in fig. 19, 7, 8) of the *Triarthrus*—*Marrella* type. The broad fringe of gill-blades is attached to a narrow jointed shaft. The telopodites were evidently reduced such as in *Leancoilia*. (In the thorax the preepipodites are possibly reduced and the telopodites maintained.) The last segment of the postabdomen is provided with a pair of flat, segmented cerci forming a caudal fan.

Traces of the intestine are described, but the "shell glands" of Walcott seem doubtful.

While Walcott (1912) originally regarded *Waptia* as a transition form between the Branchiopoda and Malacostraca, Fedotov (1925) and Henriksen (1928) believed the genus to belong to the Leptostraca. (Fedotov also suggested larval stages of Malacostraca). Raymond on the other hand primarily referred the genus to the Branchiopoda, together with *Burgessia* and *Yohoia*, and later on (1935) placed it in a group leading to the Notostraca among the Branchiopoda. In 1933 the present author suggested the non-crustacean nature of *Waptia* on account of the trilobitan appendages. For the same reason Raymond (1935) objects to the placing of the genus in a higher group of Crustacea.

The evidence afforded from the present knowledge of the morphology of *Waptia* demonstrates several crustacean features. The major crustacean characters are the carapace, the rostrum, the pedunculate eyes projecting from below the carapace, the absence of pleurae in the trunk, and the presence of expanded cerci. Of these characters the carapace and the lack of pleurae were common also to *Burgessia*. The pedunculate eyes and probably also the expanded cerci (though not jointed) are also found in *Yohoia*, which on the other hand demonstrates merostome and trilobitan features in the distinct trilobation of the body. The relationship to the Trilobita, and the other above described Cambrian Arthropoda of the Burgess Shale, is demonstrated in the trilobitan appendages.

? GENUS *HYMENOCARIS* SALTER

Fig. 19, 9.

Still more crustacean-like is the present form described by Walcott (1912) as *Hymenocaris perfecta* Walcott. The appendage-bearing species of the Burgess Shale has been referred to genus *Hymenocaris*, known from the European Cambrian, but the generic identity is not convincingly demonstrated.

The laterally compressed carapace covers a considerable portion of the body. The carapace has on either side a muscle scar (*adm* in fig. 19, 9) evidently distinguishing the area of attachment of a strong adductor muscle.

The pedunculate eyes (*l. eye*) project in front from below the carapace just as in *Waptia* and probably in *Yohoia*. The trunk is narrow without pleurae. The thorax, or thorax-preabdomen, is said to include 8 segments. The abdomen or postabdomen is composed of 7 annulate segments without appendages, except the terminal segment which is provided with a pair of cerci (cercopods). Walcott mentions the presence of from 2 to 6 cerci, but according to the published photographs only 2 cerci are present, the other ones are evidently formed by the serrate hind margin of the last segment.

Besides the uniramous and multi-segmented antennae (*a*), Walcott suggests the presence of minute, jointed antennules. It seems more probable that these appendages represent distorted cephalic telopodites. The other

cephalic appendages are said to comprise 2 pairs of slender walking legs and one pair of more powerful legs with short stout segments. The determination of the cephalic appendages apparently involves a certain amount of conjecture. It is of importance to substantiate that the 8 pairs of trunk-limbs are of the trilobitan type with a distinct telopodite and a preepipodite with gill-blades.

The intestine is traced back to the hind border of the last abdominal segment.

Walcott (1912), Raymond (1920), and Henriksen (1928) referred the genus to the Archaeostraca (Phyllocarida or Leptostraca). Fedotov (1925), on the other hand, suggests the Branchiopoda or Ostracoda. In his last paper Raymond (1935) questions the placing of *Hymenocaris perfecta* in the Archaeostraca on account of the trilobitan, not at all malacostracan, limbs of the trunk. He refers the genus to the same subclass as *Marrella*, *Leanchoilia*, *Burgessia*, *Waptia* and certain other genera.

The trilobitan appendages clearly show that the present form is related to the Trilobita and the other above described genera of Middle Cambrian Arthropoda. But at the same time the crustacean features are striking. Crustacean characters are expressed in the large carapace with the adductor muscle scar, the pedunculate eyes, the lack of trilobation of the body, and to a certain extent in the presence of caudal cerci. The muscle scar is particularly crustacean, but, on the other hand, a development of this structure might be expected as a consequence of the elaboration of the large, laterally compressed carapace. In the other crustacean features the present form bears relationship to *Waptia* and *Burgessia* and in several respects also to the more merostome-like *Yohoia*.

It cannot be denied that *Hymenocaris perfecta* in its general habitus closely resembles the Palaeozoic Archaeostraca. The Burgess Shale genera *Hurdia*, *Fieldia*, *Carnarvonina*, *Tuzoia*, and *Odaria* have apparently an archaeostracan carapace, but might yet have had trilobitan appendages such as the present form. *Protocaris* Walcott (Resser 1929) resembles *Hymenocaris*, but has a trunk with numerous short segments of which the anterior ones are appendiferous with trilobitan(?) limbs. In the collection in Washington I have examined a specimen of the genus *Portalia* (similar to *Protocaris*) which has indications of gill-blades on the appendages.

Before we discuss the habitats and adaptive radiation of the described Cambrian forms, we shall mention two Lower Devonian genera which appear to be related to the Middle Cambrian arthropods.

GENUS *CHELONIELLON* BROILI

Fig. 20.

The famous Lower Devonian Hunsrück Shale of Bundenbach in Germany has yielded two arthropod genera, *Cheloniellon* and *Mimetaster*, which seem to be related to the mentioned Cambrian form. The genus *Cheloniellon*, with its single species *C. calmani* Broili, was described by Broili (1932 a, 1933) and its zoological position is more recently discussed by Schulze (1939) and Størmer (1939).

The comparatively large form (10,5 cm without furca) has a broad, almost circular, flattened dorsal shield. The shield is distinctly trilobate and the segmentation is more or less radial with the pleurae of the hind segments embracing the narrow postabdomen with the furca. An examination of the appendages shows that the dorsal segmental division also comprises the cephalic region.

As pointed out by Broili the headshield includes only the first postoral somite. The next tergite comprises the 2 following segments, while the following cephalic tergites represent one segment each. In accordance with Snodgrass (1938), Schulze (1939) interprets the headshield as a protocephalon which Snodgrass believes to be the primitive head of all the mandibulate arthropods. A functional protocephalon is also to be seen in the Anostraca of the Branchiopoda. The division of the cephalic region of *Cheloniellon* into separate movable segments, or combinations of segments, might, however, be of minor phylogenetic importance as asserted by Schulze. It is to be remembered that in the Annelida the 2 first postoral somites are united into a peristomium, and in the Arachnida the prosoma might be divided in many different ways. The functional cephalon of *Cheloniellon* (based on the structures of the coxae) comprises one more segment than the cephalon in the Trilobita.

The headshield has a pair of lateral eyes with a central position. The postabdomen (or abdomen) has a pair of long furca attached to the dorsal surface of the last segment. The probable lack of segmentation, and particularly the point of attachment of these appendages, indicate that the furcae are neither modified ventral appendages such as the cerci of the trilobites and several Cambrian Arthropoda, nor identical with the crustacean furca forming a terminal prolongation of a telson. I am inclined to agree with Schulze in interpreting the structures as tergal outgrowths of the last segment, homologous with the telson of *Limulus* and the dorsal spines on the hind segments of certain trilobites (Olenellida) as shown by Ivanov (1933).

The ventral surface with the appendages is well demonstrable in the excellently preserved specimens. Behind a narrow frontal doublure the long, multi-jointed and uniramous antenna is attached. With its frontal position the antenna evidently represents a preoral appendage. Between

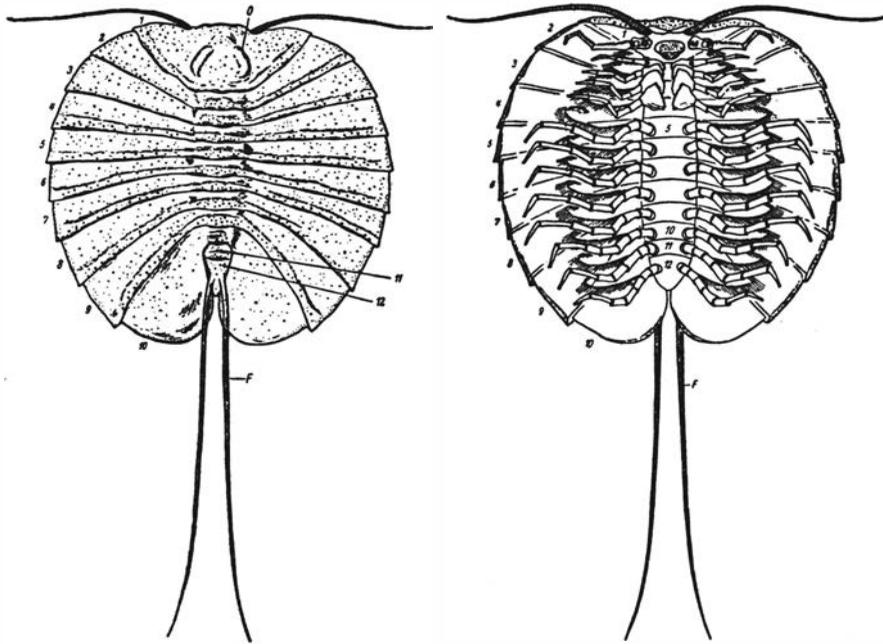


Fig. 20. Devonian arthropod.

Cheloniellon calmani Broili. Med. length 105 mm. Dorsal and ventral side. From the Lower Devonian Hunsrück Shale of Bundenbach, Germany. (After Broili 1933.)

the next pair of appendages, not in front of it, is situated a subtriangular plate which Broili interprets as a labrum (hypostoma) comparable to the labrum in trilobites. The plate differs, however, from the trilobite labrum in being covered by rows of tubercles which in the posterior portion of the plate are prolonged into short spines directed backwards. Similar spines occur on the coxa of the surrounding appendages (I and II). The plate is neither attached to the frontal doublure such as would be the case with a labrum of the trilobite type. From our knowledge of the mouth region in trilobites it seems possible to regard the small sclerite as homologous with the labium or postoral plate in trilobites (*labi* in fig. 5, 24) and to assume that a labrum has escaped preservation in the described specimen. Also the posterior position of the plate, compared with the position of the frontal appendages, might support this view. The spinous ventral surface of the plate suggests a more "internal" position of it, and recalls the similar endostoma in the Eurypterida (*end* in fig. 9, 6, 7) and Xiphosura (*end* in fig. 13, 10).

The first postoral appendage is probably uniramous. A pit on the coxa is explained by Broili as the opening of antennal glands, similar to the excretory glands in Crustacea. Although an opening in the first postoral somite is unknown in the Chelicerata, as indicated by Schulze, the diagnostic importance of this structure seems to be of minor value.

The remaining appendages are of the trilobitan type (Størmø 1939). The preepipodite, with the fringe of filaments, is very delicate, suggesting some reduction of the gill-branch. The coxae of the cephalic appendages are well-developed with spiniferous endites. Their position partly far beyond the mouth suggests that they hardly served as true jaws, but chiefly served to keep and to carry the prey to the mouth. The thoracic-abdominal limbs are uniform, without a prominent coxa. A precoxa is suggested.

Concerning the zoological position of the present genus, Broili points out the relationship to the Trilobita and at the same time mentions several characters in which *Cheloniellon* represents a more advanced stage. Regarding the Trilobita as belonging to the Crustacea he introduces a new crustacean subclass for the present genus. Schulze (1939), on the other hand, interprets the genus, as well as the trilobites, as being related to the Chelicerata.

The structure of the appendages in particular shows that *Cheloniellon* is related to the Trilobita and the merostomid Cambrian Arthropoda. Affinities to the primitive Merostomata are suggested in the broad trilobate dorsal shield and the narrow postabdomen (or abdomen). A paired telson is unknown in the Merostomata, but, since a paired nuchal spine might occur in the Trilobita (fig. 7, 7), this difference probably is of minor importance. The Ordovician genus *Duslia* is probably related to *Cheloniellon* as mentioned by Broili and Schulze, but the appendages of this form are unknown.

GENUS *MIMETASTER* GÜRICH

Synonyme: Genus *Mimaster* Gürich.

Another peculiar arthropod is described from the Lower Devonian Hunsrück Shale. The structures are not sufficiently clear to attempt a reconstruction of the genus, but the numerous good photographs published by Gürich (1931 a, 1931 b), and the detailed descriptions presented by the same author, give many interesting details of this most extraordinary form. The single species, *M. hexagonalis* Gürich, measures only 2—3 cm in length.

The subtriangular headshield has 6 strong radiating spines giving to the cephalon a starfish-like appearance. The spines, which exhibit a bilateral rather than radial arrangement, have numerous cross-bars and muscular fibres(?) indicating that the spines and bars acted as frames supporting a flat disc or umbrella composed of softer integument. Below the posterior "interradius" a wedge-shaped trunk occurs, projecting backwards but not so far as to a line between the distal points of the posterior spines of the umbrella. *Mimetaster* is thus composed of a large cephalic disc and a comparatively small and narrow thorax-abdomen. The central portion of the headshield shows indications of 5 transverse lobes. Stalked, sessile eyes were possibly present on the dorsal surface. The trunk has a segmented axis

and probably lateral pleurae. The axis consists of 24 segments and a small terminal knot or plate forming a pygidium or telson.

The appendages are also peculiar. A pair of more delicate, uniramous antennae projects in front. The most outstanding appendages are the "second antennae" (I) which evidently are biramous. The largest branch, considerably exceeding the length of the body, is segmented and strongly curved. The smaller branch is similar, but less than half the length. The following cephalic appendages, being of the same type, diminish in size backwards towards the trunk. Of considerable interest is the structure of the trunk-appendages. The limbs are evidently composed of a narrow jointed shaft to which a broad fringe of filaments, probably gill-blades, are attached. The appendage seems to correspond closely to the gill-branch of the trilobite limb.

Gürich compared the present genus to the Cambrian arthropod *Marrella* (fig. 19, 5, 6) which also has some kind of a cephalic disc. Both forms have a multisegmented trunk with a small plate-shaped pygidium or telson, and the appendages are largely of the same type, although the telopodites apparently are absent in the trunk of *Mimetaster*. The relationship is also argued by Beurlen (1934) who placed the two genera in a common larger group, the Marrellomorpha. In the same group he also places the late Palaeozoic Pygaspidae. These forms are, however, little known, particularly with regard to the structure of the appendages. *Pygaspis* has an arachnid appearance (certain circular spots on the abdomen might possibly suggest ventral gills such as in the eurypterids).

Concerning the position of *Mimetaster*, its relationship to the Cambrian *Marrella* seems comparatively well founded. In addition to the common characters mentioned by the previous authors, we might add the presence of a small plate-shaped pygidium or telson in both forms. The structures of the appendages of *Mimetaster* indicate that this genus belongs to the same chain of forms as do the Trilobita and the Cambrian Burgess Shale forms as well as *Cheloniellon*. The present genus might also have been related to the Carboniferous—Permian Pygaspidae, but these forms are not sufficiently known to permit a closer comparison.

Habitat and Adaptive Radiation of the Cambrian and Devonian Arthropoda Described in the Present Chapter.

From the preceding account it is apparent that already in the Middle Cambrian a highly differentiated arthropod fauna occurred. In spite of the great diversities in form the above described genera possess certain common morphological characters that force us to conclude that these forms are mutually related and represent different trends of development leading back to a common ancestor, or at least to closely related forms. The diversity in form appears to be due, to a great extent, to different modes

of life, but yet one gets the impression that among these forms the morphological type or general plan of construction is less constant or conservative than in the previously described groups, particularly the Trilobita and Eurypterida.

Only a small number of genera and species are known of the different types. The adaptive radiation of the various stocks is therefore difficult to demonstrate, but certain characters might be considered.

The merostome-like forms were evidently bottom inhabitants. Most characteristic is the broad *Cheloniellon* with its centrally situated lateral eyes. Among the Cambrian genera, the broad-shielded *Naraoia* and *Helmetia* are to be mentioned. *Leanchoilia* and *Sidneya* might have been swimmers also, as suggested by the lack of distinct walking legs in the thorax-abdomen, and by the presence of a tail fan in *Sidneya*. Also *Opabinia* seems to have been adapted to a more nectonic mode of life. The function of the peculiar frontal appendage is unknown.

More pronounced nectonic forms are seen in the shrimp-like *Waptia* and *Hymenocaris*.

Typical planktonic forms also occur among the described genera. Characteristic of the planktonic forms are the small size and the development of special floating organs. *Marrella*, with its expanded cephalic horns, is evidently a planktonic genus. The apparently related *Mimetaster* from the Devonian is claimed by Gürich to have been benthonic because of the occurrence of one specimen in which the antenna is embracing an arm of a star-fish. The small size and the elaborate cephalic disc seem, however, rather to indicate a planktonic habitat also of this form. The small *Burgessia* apparently was a free-swimming, more or less planktonic genus. If the remains described by Ruedemann (1931) under the generic name *Marrria* are correctly interpreted, this form represents a highly specialized planktonic arthropod.

Regarding the merostome-like genera with trilobitan appendages (such as *Emeraldella*) as the more primitive types, we may notice in other genera certain evolutionary tendencies leading away from this primary plan of construction. In the cephalon the hind border of the headshield might develop into a carapace. An initial indication of such a structure is possibly seen in the overlapping headshield of *Naraoia*. The well developed carapace of the crustacean-like forms is either flat, as in the branchiopod *Lepidurus* (*Burgessia*), or laterally compressed such as in the archaeostracans (*Waptia* and *Hymenocaris*). Along with the formation of a carapace the sessile lateral eyes show a tendency to leave the dorsal shield and become pedunculate, apparently movable eyes in front below the carapace (both sessile and pedunculate eyes occur in typical Crustacea).

In the trunk the pleural areas might be more or less reduced. Smaller or larger portions of thoracic-abdominal tergites might be ankylosed into one shield (*Helmetia*, *Naraoia*).

The trilobitan appendages are subject to modifications. In several forms (*Leancoilia*, *Opabinia*, *Waptia*) the telopodites of the trunk appear to be reduced. The antennae are strongly reduced in *Leancoilia*. The frontal postoral appendages are specially modified in several genera (*Leancoilia*, *Sidneya*, *Marrella*), and in later forms we notice an elaboration also of the succeeding cephalic appendages (*Cheloniellon*, *Mimetaster*). The caudal cerci often develop into flat expanded lobes forming a tail fan.

This differentiation of the primitive characters develop variously in the separate trends. A strong development of a carapace takes place practically without any modification of the trilobitan appendages (*Burgessia*, *Hymenocaris*?). In *Yohoia* apparent pedunculate eyes and expanded cerci occur together with a trilobitan cephalon and pleurae in the trunk. The merostome-like *Leancoilia* has modified frontal appendages.

We have now dealt with a number of well preserved Cambrian and Devonian arthropods showing relationships to the previously described fossil and recent forms. It has become apparent that these highly interesting forms to a great extent have filled the gap between the Trilobita and the Xiphosura, and at the same time some of these early Palaeozoic genera demonstrate morphological features pointing in the direction of the Crustacea. The crustacean affinities may, however, only be due to convergence, signifying a common mode of life rather than true relationships.

After having described and discussed in detail the Cambro-Devonian forms, we shall in the sequel consider the common characters linking together all the fossil and recent arthropod groups treated above.

GENERAL COMPARISON OF DESCRIBED FORMS

In the previous chapter we have described and discussed the morphology of a number of fossil and recent arthropod groups. It has been attempted to demonstrate the material available and to illustrate the development of the more important morphological characters. The affinities of the various groups have also been touched upon, but a comparison of the separate organs has only been dealt with in special cases.

In the following we shall try to consider the development of the separate morphological characters within the different groups. We shall attempt to point out the common structures and thereby endeavour to arrive at a decision concerning the relationships and phylogeny. When pointing out the common characteristics of such a large and in many ways heterogeneous collection of groups, we arrive into the same difficulties as when attempting to present a definition of a large systematic unit. The definition is apt to be vague, comprising but a few morphological features.

But although it might be difficult to point out a number of morphological characters common to all the above described arthropods, a more detailed consideration of the various organs in the different forms will enable us to link together forms which in many respects are strongly differentiated and apparently different.

Among the groups described, certain classes and orders distinctly show their mutual relationship. This is the case with the Eurypterida, Xiphosura and Arachnida, which obviously belong to a separate subphylum. Other groups, such as the Trilobita and the Cambro-Devonian Arthropoda, also manifest their common origin, but the relationship is not so striking as in the mentioned members of the Chelicerata.

The major problem presented to us is to consider the relationship between the Chelicerata and the Trilobita with allied Arthropoda. This involves an investigation also of the possible affinities to the Crustacea, affinities which are advocated by most biologists.

In discussing the common characters we shall confine ourselves to the more essential features, the development of the dorsal shield, the appendages and the intestine.

THE DORSAL SHIELD

The different groups to be considered comprise both aquatic and terrestrial forms. The solid exoskeleton, forming the dorsal shield, is divided into a well marked headshield and a thorax-abdomen composed of a number of segments of free or anchylosed tergites. Only in certain crustacean-like Cambrian arthropods the headshield is not well distinguished on account of the presence of a carapace.

As pointed out by Fedotov (1924) a flat shape of the body is characteristic of the Trilobita and Merostomata.

The outstanding feature in the body of the Trilobita, Xiphosura and many Cambro-Devonian forms is the distinct trilobation of the dorsal shield. The dorsal shield is divided by two longitudinal furrows into a median axis and lateral pleural areas. The pleurae are merely lateral out-growths of the axial tergum which covers the vital portions of the body.

Among the Eurypterida and Arachnida, which undoubtedly are related to the Xiphosura, the trilobation is less distinct. In the former group it is expressed in the preabdomen of the genus *Mixopterus* (fig. 10, 3), and among the Arachnida it is traced in the abdomen of the Palaeozoic *Anthracomarthi*, the recent *Opiliones* (larvae) and to some extent in the *Ixodidae* (Schulze 1936).

A distinct trilobation occurs in most of the Cambrian Burgess Shale arthropods, especially in the merostome-like genera *Leancoilia*, *Emeraldella* and *Naraoia* (fig. 17, 1—4), but also in more crustacean-like forms such as *Opabinia* (fig. 19, 10) and *Yohoia* (fig. 18). Like the Eurypterida,

Sidneya (fig. 17, 9) apparently lacks a trilobation, and the same might be the case with *Helmetia* (fig. 17, 7). It deserves to be remembered that also among the Trilobita the trilobation might be more or less obsolete as demonstrated in the Homolonotidae (fig. 7, 19) and Bumastidae.

The typical carapace-bearing forms such as *Burgessia*, *Waptia* and *Hymenocaris* (fig. 19, 1, 7, 8, 9) have apparently no pleurae. This may be due to a reduction of the pleurae below the carapace (a reduction of the postabdominal pleurae is common also in the Merostomata). A partial reduction of the pleurae is indicated in *Yohoia* (fig. 18).

The trunk of the Devonian *Cheloniellon* and *Mimetaster* is trilobate (not so distinct in the latter form).

The trilobation of the dorsal shield is not characteristic of the Crustacea. Indications of such structures are found among the Isopoda and Decapoda, but are not typical of these groups. Larvae of insects might exhibit a distinct trilobate dorsum. Characteristic is the larva of cockroaches which represent a primitive insect group. Heymonds (1901, p. 69) from a study on the ontogeny of *Scolopendra*, suggests that probably all arthropods primarily possessed a trilobate tergite, but this is at least not characteristic of the Crustacean nauplius.

Fedotov (1924), Hanström (1926b), Ivanov (1933), and Schulze (1936) have strongly pointed out the importance of the trilobation of the Trilobita and Xiphosura (and according to Schulze also the Arachnida). The authors mentioned regard this character as a more or less decisive proof of the relationships between these groups. The presence of a trilobate dorsal shield in the Trilobita, Xiphosura and a number of Cambro-Devonian arthropods, and indications of the same features in the Eurypterida and Arachnida, at least form a strong indication of a mutual relationship among these groups.

The Headshield.

In the different groups the frontal segments are anchylosed into a headshield, a cephalon or prosoma. A large and broad headshield is very characteristic of the Trilobita and Xiphosura, but also in the other forms a prominent headshield is characteristic. An expanded, flat cephalic shield is not typical of the Crustacea. In certain Cambrian crustacean-like genera, however, the headshield is less distinct. The hind portion of the shield is prolonged into a carapace, forming a free duplicature covering larger parts of the trunk. This crustacean feature has been the chief reason for including these forms in the Crustacea. It deserves to be mentioned that in the merostome-like *Naraoia* the overlapping of the cephalic shield over the abdominal shield behind might possibly be interpreted as the initial formation of a carapace. Because of the many structures common to *Naraoia* and *Burgessia* the present author is inclined to regard the formation of a crustacean carapace in the described Cambrian forms as a special feature not necessarily indicating affinities to the Crustacea.

The number of segments included in the headshield differs in the different groups. At the same time the hind border of the headshield does not necessarily conform with the borders of the original segments. In *Limulus* it has become apparent that the transverse joint between the prosoma and the abdomen to a certain extent crosses the primary segmentation (Ivanov 1933), and therefore is to be regarded as a more artificial hinge-line independent of the segmental borders. In the Trilobita the ontogeny has indicated a similar secondary hinge-line between the cephalon and the thorax and between the different pleurae (Størmer 1942).

The trilobite cephalon is composed of a preoral portion with 4 postoral somites attached. In the protaspis-larva an antennal segment is indicated in the preoral complex (acron), but whether the preantennal portion includes a preantennal somite cannot definitely be decided from the morphological structures.

In the Cambrian Arthropoda of the Burgess Shale a number of 4 postoral somites seems to have been characteristic of the headshield. The exact number is, however, difficult to establish in spite of the good preservation.

In contrast to the Trilobita the prosoma of the Chelicerata (Merostomata and Arachnida) comprises 6—7 postoral somites. In certain primitive Arachnida, however, there occurs a proterosoma with 4 postoral somites. Particularly the Palpigradi and Solifugae have the prosoma divided into a pro-, meso-, and metapeltidium. The propeltidium, representing a proterosoma, has 4 postoral somites and thus corresponds to the trilobite cephalon. Certain Acari have the body divided into a proterosoma and a so-called hysterosoma, the latter forming a thorax-abdomen comparable to the thorax-abdomen in Cambrian arthropods and to the thorax-pygidium in trilobites.

Ivanov's studies on the ontogeny of *Limulus* are of considerable interest in the present connection. While the adult xiphosuran has 6—7 postoral somites included in the prosoma, the earliest embryo shows only 4 postoral somites, representing, according to the interpretation of Ivanov, the larval or primary somites. The extra 2—3 somites of the prosoma are secondary segments added to the primary ones by teloblastic growth. As pointed out by the mentioned author (1933) and emphasized also by Schulze (1936, 1939) and Snodgrass (1938), this strongly suggests a common ancestor of the Trilobita and Xiphosura. The earliest larva of the Trilobita also indicates that the 4 postoral somites are more or less simultaneously developed, such as are characteristic of the primary somites (Størmer 1942). In the Trilobita the primary somites constitute the cephalon, while in the Xiphosura (and Eurypterida) a few secondary somites are included in the headshield forming a prosoma.

The presence of a larvatum (Schulze) with 4 postoral somites both in the Trilobita and Xiphosura indicates that these groups descended from

Annelida with a similar larvatum (Ivanov). The crustaceans, on the other hand, apparently have a larvatum with only 2 postoral somites as expressed in the nauplius-larva with its 3 pairs of appendages (of which the first pair represents the preoral antennules). It deserves to be mentioned, however, that complete agreement concerning the larvatum of the Crustacea does not seem to have been established. As pointed out by Snodgrass (1938), Sollaud (1923) claims to have found that in the palaemonid *Leander* the antennae, the mandibles and the two pairs of maxillae are formed before the activity of the teloblast takes place. This would involve that all these segments are primary, belonging to a larvatum. Manton (1928), on the other hand, includes the two maxillary somites in the part produced by the teloblast, thus the larvatum should possess 2 postoral somites. In a recent paper Garstang and Gurney (1938) point out that the nauplius of certain copepods shows a prolonged hind portion of the body which might suggest the presence of more than 2 postoral somites. The mentioned authors are inclined to interpret the presence of two long setae in the genus *Longipedia* as rudiments of maxillules. The evidence offered is hardly sufficient to decide the question on the number of postoral primary somites. Our present knowledge of the ontogeny of the Crustacea seems to the present writer rather to favour the conception of a larvatum with 2 postoral somites in this group.

The visual organs are probably of minor value for the determination of the relationship between the different groups. Among the Chelicerata the aquatic Xiphosura and the terrestrial Arachnida have apparently very different median and lateral eyes. Versluys and Demoll (1922) assert that the median eye (Hauptauge) of the scorpion has no homologon in the *Limulus* eyes.

Concerning the lateral eyes, Hanström (1926 b) and Schulze (1936) believe the lateral eyes of the Trilobita to be homologous with those of the Chelicerata. A disintegration of the complex lateral eyes is seen in certain trilobites (Richter 1932), and a similar reduction of the lateral eyes might possibly have taken place when the Arachnida, or rather their ancestors, changed from an aquatic to a terrestrial mode of life (Schulze 1936).

The median ocelli, which are differently developed in the Arachnida and Merostomata, are not found in the Trilobita. In the trilobite *Tretaspis*, particularly in the larva, a median pustule occurs, which is provided with 5 small pits (Størmer 1930). Hanström (1934) points out that these structures bear a striking resemblance to a combined dorsal organ and four-celled sense organ in certain primitive crustaceans (*Anaspides*). On account of the affinities suggested by these structures he is cautious in giving up the possibility of a relationship between the Trilobita and Crustacea. Although the correspondence in structures seems very distinct the actual nature of the organ in the trilobite is unknown. Schulze (1936) mentions the presence in certain arachnid larvae of a dorsal plate which might correspond to the dorsal organ in the Crustacea.

The maculae of the labrum (hypostoma) of trilobites have by several authors been interpreted as ventral eyes homologous with the "ventral eyes" of *Limulus*. The nature of the maculae is, however, doubtful and the "ventral eyes" of *Limulus* might only be parts of a primary olfactory organ, as suggested by Johansson (1932).

The labrum of the Trilobita (and Cambrian Arthropoda) has often been regarded as a crustacean character. A similar plate is, however, developed in the cucullus of the Ricinulei, and traces of a trilobitan labrum might also be seen in the smaller labrum of *Limulus*.

The presence of a postoral plate or labium also appears to be of minor significance because this organ occurs in most arthropods.

The Trunk.

The trunk comprises the postcephalic or postprosomal portion of the body. A division of the trunk into a thorax and abdomen is less distinct. In the Chelicerata the postprosomal portion represents an abdomen, but in forms possessing a cephalon (comprising a smaller number of segments) we might speak of the trunk as forming a thorax-abdomen. In most cases, however, a thorax is distinguishable neither in the development of the dorsal shield nor in the structure of the appendages. In the Trilobita the trunk is divided into a thorax and a pygidium, but the thorax is not distinguished by special appendages, and comprises a very variable number of segments in the different forms. Among the Chelicerata the abdomen is often divided in a preabdomen and postabdomen, a feature also found in Cambrian arthropods with a cephalon instead of a prosoma.

Particular stress has been laid on the fact that the number of thoracic segments is subject to great variation in the Trilobita. Since the number of segments included in the pygidium also is subject to considerable variation, it is necessary, in order to obtain a correct impression of the variation, to consider the total number of postcephalic segments. In spite of the different development of the pygidium, the total number of segments in the trunk is subject to extensive variation in the Trilobita. The inconstancy in number has been compared with the conditions in primitive Crustacea, particularly the Branchiopoda. Lankester applied these circumstances in a classification of his Arachnida (Trilobita — Chelicerata). The Trilobita with their variable number of segments were included in the Anomomeristica and separated from the other groups belonging to the Nomomeristica, characterized by more constant number of segments (fig. 1).

According to more recent studies on fossil and living forms, this distinction seems less successful. Among the forms related to the Trilobita (Anomomeristica) we notice a tendency towards a more fixed number of segments, and among the primitive Chelicerata (Nomomeristica) the number varies to a certain extent.

Concerning the number of segments in the trunk, a large number is found in certain trilobites and in the Cambrian genera *Marrella*, *Naraoia* and *Waptia* as well as in the Devonian *Mimetaster*. A smaller number is possessed by the Cambrian *Leancoilia* and in the Devonian *Cheloniella* (total number of postoral segments = 13 and 14 respectively). It is of interest to notice that in the merostomoid genera *Sidneya* and *Emeraldella* the total number of postcephalic segments amounts to 15—16 and 16(?). This closely approaches conditions in the Xiphosura where the Aglaspida and Limulida apparently have 17 (more or less abortive in the Limulidae) and (16?) in the Synziphosura. The Eurypterida and most Arachnida have a number of 18 (the posterior segments are secondarily reduced in certain groups). 19 are present in the Scorpionidea. It is therefore of importance to notice in the merostome-like Cambrian Arthropoda and the various groups of the Chelicerata, a tendency towards a more fixed number (about 17—18) of postcephalic segments. It might in this connection be mentioned that in the primitive Olenellida of the Trilobita the number of thoracic segments between the cephalon and the telsonic dorsal spine (when present) amounts to 15 (the segment with the spines regarded as the terminal one). Behind the telsonic spine only rudimentary segments occur (see below). With the 4 cephalic segments the number of well developed postoral segments thus is a total of 19, a number which corresponds fairly well to the conditions in the Chelicerata.

A tendency towards the establishment of about 17—19 postoral segments is thus traced in certain trilobites, in the merostomes and in merostome-like Cambrian forms. The common tendency might suggest a certain relationship between these groups.

In *Limulus* and the Arachnida the first abdominal tergite, representing the 7th postoral somite, is generally more or less reduced. Among the Eurypterida the same segment is shorter than the succeeding, in certain genera (fig. 9, 1; fig. 10, 2, 3), but in other forms this is less significant, and in one genus (*Glaucodes*) the first tergite is even very strongly developed.

The partial reduction of the first tergite in the Chelicerata probably has something to do with the formation of a prosoma. A reduction of the somite is not indicated in the early embryological stages of *Limulus*, and it is therefore possible that the reduction is a consequence rather than a cause of the formation of a prosoma.

As pointed out above the trilobation of the body is characteristic of most forms. The pleurae of the trunk form lateral outgrowths of the mesotergites. In a recent paper Garstang and Gurney (1938) try to homologize the pleurae of trilobites with the lateral scales in the trunk of crustacean *Lepidocaris* (fig. 4) from the Devonian. According to Scourfield, Calman and Borradaile these scales are evidently homologous with the proximal exites (prepipodites) of the Anostraca. Garstang and Gurney claim the

homology of the trilobitan pleurae with these scales because of their apparent "pinching-off" from lateral folds of the bodying in *Lepidocaris*. The assumption involves that the trilobitan pleura is transformed into a pre-pipodite, a part of a central appendage. The authors mentioned quote this as "an example of momentous evolutionary change wrought by very simple means — practically nothing more than the introduction of a dorsal line of articulation". This hypothesis is highly conjectural, lacking any evidence from other fossil forms.

Characteristic of many forms is the presence of an abdominal shield formed by the fusion of a variable number of tergites.

In the Trilobita the pygidium includes a variable number of segments. (During the ontogenetic development the secondary segments, formed by teloblastic growth at the end of the body, pass forward through the pygidium and are released as movable tergites in front of it.) A pygidium is also found in the Cambrian *Helmetia* (fig. 17, 7), *Mollisonia*, *Tontoia*(?) and possibly in *Marrella* (fig. 19, 5) and the Devonian *Mimetaster*.

Another type of abdominal (or thoracic-abdominal) shield occurs in the Chelicerata and in the Cambrian *Naraoia*. In these forms the shield is found in front of a movable telson. *Naraoia* (fig. 17, 4) has a large thoracic-abdominal shield covering the whole trunk except the telson and 1—2 postabdominal segments. Among the primitive Xiphosura in certain genera, such as *Beckwithia* (fig. 14, 14), the posterior segments form a small abdominal shield, a feature also indicated in the ontogeny of *Limulus* (fig. 15, 2, 3). A similar tendency is seen in the Belinuridae (fig. 14, 6—8). In younger Limulidae, however, we notice an increasing development of the abdominal shield (fig. 14, 1—5). In the Synziphosura a possible coalescence of the 6th and 7th abdominal segment is suggested in some genera (fig. 14, 11, 12). The formation of an abdominal shield is observed already in the xiphosuran *Kieria* (Størmø 1934a) from the uppermost Silurian. Arachnida have free as well as anchylosed abdominal segments (e. g. Scorpionidae and Ixodida).

In general we notice, in many of the groups considered in the present paper, a tendency towards the formation of an abdominal or thoracic-abdominal shield, a common tendency which might suggest a certain relationship between these forms.

The Telson.

A very characteristic feature of the Eurypterida and the fossil and recent Xiphosura is the presence of a more or less styliform telson at the end of the body. A similar telson is also significant of certain Arachnida and most of the merostome-like Cambrian arthropods. A segmented telson occurs in the arachnid order Palpigradi and in the crustacean-like *Burgessia* (fig. 19, 1) from the Cambrian.

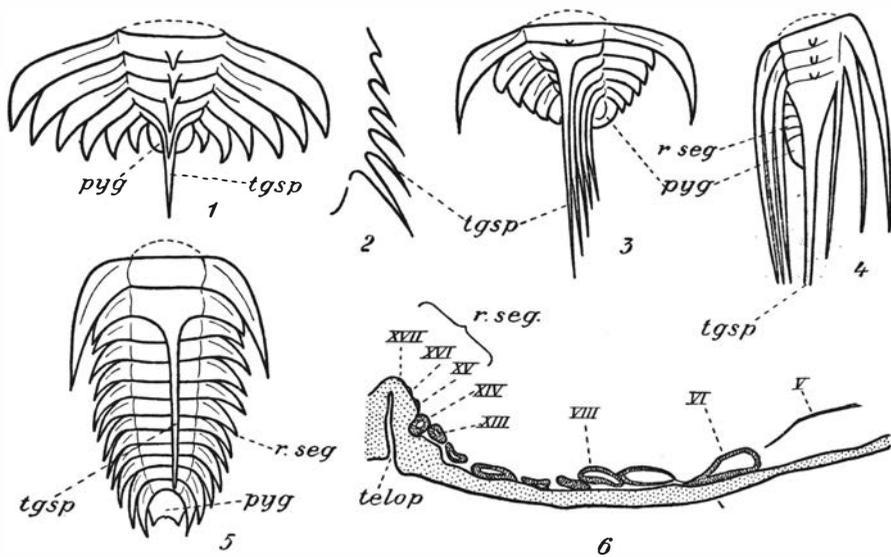


Fig. 21. Telsonic structures in Trilobita and Xiphosura.

1, 2 = *Kjerulfia lata* Kiær (after Kiær 1916). 3 = *Elliptocephalus asaphoides* (Emmons) (after Walcott 1908). 4 = *Olenellus thomsoni* Hall (after Walcott 1908). 5 = *Olenellus vermontana* Hall (after Walcott 1890). 6 = *Limulus moluccanus* (Linnaeus) (= *Tachypleus gigas* (Linnaeus) (after Ivanov 1933).

V—XVII = postoral somites, pyg = pygidium, r. seg = rudimentary segments, telop = telopore, tgsp = dorsal tergal spine.

In the Trilobita, on the other hand, the pygidium occupies the hind portion of the body. In certain genera (s. g. *Dalmanites*) the pygidium has a terminal spine, but this is not articulated to the abdomen and cannot directly be homologized with a telson.

Concerning the origin and nature of the telson the embryological studies on *Limulus* by Ivanov (1933) are of considerable interest. Ivanov was able to demonstrate the development of the limulid telson from tergal portions of the rudimentary, posterior abdominal segments. As shown in fig. 21, 6 a number of rudimentary somites are traced round the telopore behind and below the last segments forming the dorsal abdominal shield in front of the telson. Consequently Ivanov points out that the telson of *Limulus* evidently is homologous with the median dorsal spines in primitive trilobites. In the Lower Cambrian genus *Holmia* (fig. 21, 1, 2) the mesotergites of the thorax have short spines directed backwards and increasing in length towards the small terminal pygidium. In *Callavia* (fig. 21, 3), another member of the Olenellida, the 5 posterior tergites have long spines. *Olenellus* (including the synonymous genus *Mesonacis*) (fig. 21, 4, 5) has only one tergite provided with a dorsal spine. This spine is, however, very long and resembles to a great extent the telson of the Merostomata. Behind this tergite we find a number of rudimentary tergites in front of the small pygidium. The number of rudimentary segments varies from a few up to

about 30 (*O. robsonensis*). In earlier descriptions of the Olenellida the "posttelsonic" tergites and pygidium escaped notice in most cases on account of unsatisfactory preservation.

Comparing the powerful dorsal spine and the posterior rudimentary tergites in Olenellida with the telson and the posterior rudimentary segments in *Limulus*, it seems evident that Ivanov is right in homologizing the dorsal spine of the primitive Olenellida with the telson of the Merostomata. It is significant that in primitive Merostomata (Aglaspida, fig. 14, 15, 16) the telson has a broad base just as when typically developed in the Olenellida (fig. 21, 4).

In most trilobites the evolution took a course different to that in the Merostomata. The dorsal spine or spines became reduced and the posterior segments united into a continuous shield, the pygidium. Raymond (1920) has statistically demonstrated how the number of segments in the pygidium increases throughout the Palaeozoic.

The two terminal dorsal appendages of the Devonian genus *Cheloniellon* (fig. 21, fig. 20) are interpreted by Schulze (1939) as derived from tergal portions just as the telson in *Limulus*. A paired telson of the trilobite-chelicerate type is rather unusual, but the presence of a paired nuchal spine is known in the Trilobita (fig. 7, 7).

Comparing the Trilobita and the Merostomata we conclude that the formation of a merostome telson is indicated already in the primitive Lower Cambrian trilobites. During the development of the two groups, however, the evolutionary trends evidently diverged. The Trilobita maintained and developed the rudimentary posttelsonic segments which gradually became incorporated in a pygidium, while in the Merostomata the posttelsonic segments became reduced and the pretelsonic ones gradually became united into a pretelsonic abdominal shield.

THE APPENDAGES

We now arrive at a point which has played an important part in the discussion on the zoological position of the Trilobita. As previously mentioned (p. 16) the discovery of the antennae and biramous limbs of the trilobites commonly was regarded as a proof of the crustacean nature of the group.

In possessing uniform appendages, apart from the preoral antennae (and in one case a pair of cerci), the trilobites distinctly show primitive characteristics. Similar characteristics, though less primitive, are found in the Cambrian and Devonian arthropods described. The Chelicerata, on the other hand, have specialized appendages, differently developed in the various parts of the body. The antennae are lacking in this group and replaced by the chelicerae.

We shall first consider the preoral appendages and afterwards deal with the postoral limbs.

The Preoral Appendages.

When comparing the appendages in the different arthropod groups the problem on the homology of the frontal appendages forms a decisive point. Of special importance is the relation between the preoral antennae and the chelicerae. Are the apparently preoral chelicerae homologous with the preoral antennae in trilobites, or with the first postoral limbs of this group? Although most recent writers appear to agree in regarding the chelicerae as homologous with the first postoral appendages in other arthropods, the other conception is put forward in several text-books also of recent date.

In deciding the present problem it is necessary to consider researches on the brain of the Chelicerata (a review on the subject was lately given by Johansson 1932).

The arthropod brain is normally divided in a protocerebrum, deutocerebrum and tritocerebrum (Viallenes). The protocerebrum comprises the frontal portion of the brain, containing among others the visual ganglia. The deutocerebrum contains the gangliae of the preoral antennae (antennules). These two parts form the preoral, or prostomial, portion of the brain, the so-called archicerebrum. A division of the archicerebrum into a proto- and deutocerebrum is expressed in the mandibulate arthropods, but in the Chelicerata the division is not clear. The tritocerebrum, derived from the ventral nerve cord, innervates the first pair of postoral appendages.

From their studies on the *Limulus*-brain Owen (1872) and Viallenes (1893) arrived at the conclusion that the nerves leading to the chelicerae were homologous with the nerves to the antennules of the Crustacea and thus belonged to the deutocerebrum. Milne-Edwards (1893), on the other hand, found the nerves of the chelicerae to belong to the ventral nerve cord sooner than to the brain, and therefore expressed the opinion that the preoral appendages are absent in *Limulus*. Brauer (1894--1895) and McLendon (1904) found, however, a preoesophageal chelicer-commissure in the scorpion, a structure which seemed to confirm the view of Owen and Viallenes.

A more extensive comparative study on the brain of the Annelida, Onychophora and Arthropoda was carried out by Holmgren (1916). From his thorough research Holmgren concludes that the chelicer-ganglion is postoesophageal, its commissure running below the stomodaeum. The preoesophageal commissure described by McLendon and Brauer in the scorpion, and noticed also by Viallenes in *Limulus*, is interpreted as derived from the stomodaeum, a conception which is verified by later studies by Holmgren (1920) on the larva of the spider *Trochosa*. In the *Limulus*-brain he found antennal lobes connected by an antennal commissure and consequently concluded that the ancestors of the Xiphosura once had preoral antennae (antennules). The deutocerebral portion, representing the antennae, is largely reduced in the *Limulus*-brain.

Hanström's (1928) elaborate studies on the brains of arthropods corroborate the general results of Holmgren. Hanström regards the homology of the chelicer-ganglion of the Chelicerata and the tritocerebrum of the Mandibulata as a completely established fact. He assumes, like Holmgren, that the progenitors of the Chelicerata possessed antennae, but regards the deutocerebrum as completely reduced, doubting the presence of the antennae-glomeruli described by Holmgren. From his embryological studies on the brain in *Limulus*, Johansson (1938) combines the mentioned views in finding the antennal region, the deutocerebrum, not to be quite reduced.

Recent works by Kästner, Snodgrass and others also clearly emphasize the postoral, tritocerebral nature of the chelicera.

The ontogeny of the Chelicerata demonstrates the forward migration of the primarily postoral chelicerae. In the adults the chelicerae attain a distinctly preoral position. Also the corresponding ganglia migrate forwards and unite with the preoral brain.

It appears obvious from the present review that the chelicerae of the Chelicerata represent the first pair of postoral appendages and are hence not homologous with the preoral antennae of the Trilobita, Crustacea and Myriapoda—Insecta. Studies on the *Limulus*-brain also make it probable that the Xiphosura evolved from antennate forms. During the evolution of the stock the preoral antennae became completely reduced and were replaced, as far as their position is concerned, by the first pair of postoral appendages. As pointed out by Ivanov (1933), Størmer (1933), Schulze (1936), Snodgrass (1938), and Kästner (1940a) the absence of the antennae in the Chelicerata therefore forms no major difficulty in deriving this group from trilobite-like ancestors provided with well developed preoral antennae.

Among the described forms a preoral, uniramous and multi-jointed antenna occurs in the Trilobita and the described groups of Cambro-Devonian Arthropoda. In the merostome-like *Leancoilia* (fig. 17, 1, 2) the antennae appear to be strongly reduced, their function being to some extent taken over by the specially developed first pair of postoral appendages. A complete reduction of the antennae seems to have taken place in the genus *Opabinia* (fig. 19, 10).

The Postoral Appendages.

At first sight there seems to be but few relations between the appendages of the many different and highly modified forms described in the previous chapters. The biramous limbs of the trilobites appear to have little in common with the uniramous walking legs of the Arachnida, or the plate-shaped abdominal feet of the Merostomata. On the other hand, a less detailed study of the biramous trilobitan limbs would suggest distinct affinities to the Crustacea, among which the biramous limb is one of the most characteristic features. In fact the presence of a biramous appendage in the Trilobita has generally been emphasized as a strong indication of a

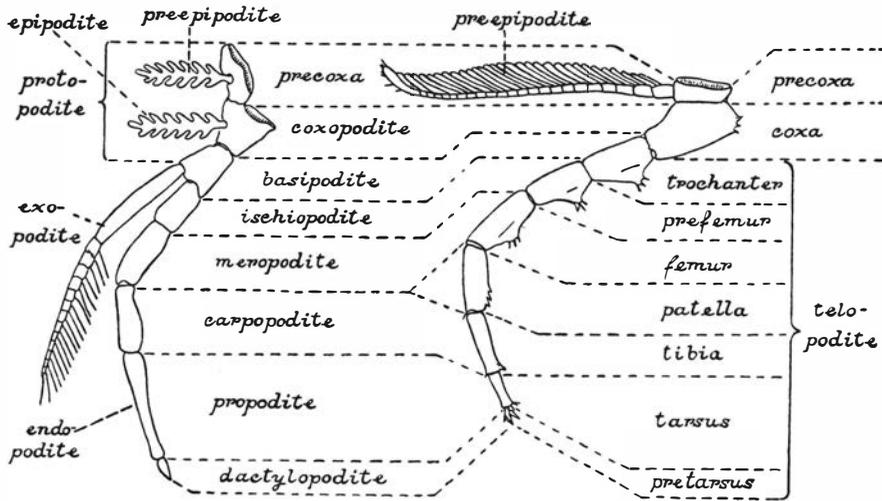


Fig. 22. Crustacean and trilobite appendage. A comparison. (After Størmer 1939.)

relationship between the two groups. Recent studies on the trilobite appendages give reasons, however, to alter this view.

Before we consider the development of the appendages in the various groups described, we shall briefly recapitulate the general structure of the trilobite appendage and compare it with the limb of the Crustacea.

Recent studies on trilobite limbs, chiefly carried out through serial grindings (fig. 6), have demonstrated the structure of the basal portion of the appendage (Størmer 1939). As shown in fig. 22 the appendage has a short basal segment above the more prominent coxa. To the basal segment, interpreted as a precoxa, a lateral branch representing a preepipodite is attached. The preepipodite has a multi-segmented or more leaf-like shaft to which is attached a number of narrow gill-blades, distinctly different from common setae. Setae of the ordinary type are present on the gill-blades and on the shaft, especially on the distal spoon-like segment (the segment is absent in *Ceraurus*). The coxa is more or less plough-shaped, lacking the pronounced endite demonstrated in previous reconstructions. A walking leg or telopodite articulates to the lateral portion of the coxa. The telopodite is composed of 7 segments of which the distal one forms a claw (probably attached to a small pretarsal talon). Triangular endites and spines occur on the inside of the telopodites.

When the appendages of the trilobite *Triarthrus* became known in 1890—1900, the different authors (Beecher, Matthew, Walcott, Bernard and Carpenter) unanimously interpreted them as typical crustacean biramous legs. Jaekel (1901) compared the trilobite limb with the legs of schizopods, while Carpenter (1903) and Raymond (1920) suggested copepodan affinities. Walcott (1918) indicated a relationship to the primitive malacostracan Syncarida and Storch (1925, 1926) claimed a phyllopodan nature of the

trilobite limb, an assumption which, however, was based on an incorrect interpretation of the biramous limb in the fossil form.

Borradaile (1917) and Snodgrass (1935) paid attention to the fact (according to the information available at that time) that the gill-branch was attached to the coxopodite, and therefore should be interpreted as an epipodite rather than an exopodite, which must be attached to a basipodite forming the next segment of the telopodite.

More recently Garstang and Gurney (1938) have strongly advocated the crustacean nature of the trilobite appendage. They base their arguments to a large extent upon the structures demonstrated in the Devonian crustacean *Lepidocaris* (Scourfield 1926). As shown in fig. 4 and mentioned above, this form has lateral scales forming preepipodites (exites) of the appendages. The authors, who are well acquainted with recent Crustacea, suggest a new interpretation of the trilobite limb. The powerful segment, generally regarded as the coxa or coxopodite, is interpreted as a basipodite because of the presence of a strong gnathic process in the maxillule throughout the Malacostraca. In support of this view the writers point out, quoting Coutière and Hansen, that the endopodite of primitive Malacostraca has 6 instead of 5 segments.

With our present knowledge of the trilobitan appendage serious objections might be raised against the opinion of Garstang and Gurney. The trilobitan coxa interpreted by these authors has no distinct gnathic process. The gill-branch is not attached to this segment, but to a small segment proximal to it. The telopodite (interpreted as an endopodite) has 7 segments, not 6 as in primitive Crustacea.

It deserves to be noticed, however, that Calman, with his extensive knowledge of crustacean morphology, apparently is inclined to regard the trilobitan gill-branch as a true exopodite, and the short precoxa as representing the protopodite or peduncle. In his comments upon my paper on trilobite appendages, Calman (1939) states: "To anyone with a sense of morphological values, however, the flagelliform preoral antennules, the five pairs of biramous gnathobase-bearing head appendages following them, and the furcal filaments (of *Neolenus*) far outweigh the fact that the peduncle of the biramous limbs is unsegmented, as it is, by the way, in not a few Crustacea."

To the present writer the interpretation of Calman seems very difficult to maintain. If the trilobite appendage is considered a crustacean limb, it is unexpected to find the protopodite reduced to a single, almost rudimentary segment. Calman hints that this condition occurs in not a few crustaceans, but, according to comparative research by Hansen (1925, 1930) the primitive crustaceans appear to have a well developed protopodite or peduncle composed of 3 separate segments. Garstang and Gurney (1938) have tried to explain the 3-segmented protopodite as due to a secondary development, caused by a reduction of the pleurae, but this hypothesis is contradicted by

the fact that typical trilobitan limbs, or at least parts of them, occur in Cambrian arthropods (more or less without pleurae in the trunk). The trilobite appendage is no doubt a primitive structure in which one would expect to find a 3-segmented protopodite, in case the limb belonged to a crustacean. The conception of Calman would involve an interpretation of the prominent coxa as an ischiopodite, a segment which in recent crustaceans (as far as I know) never attains a similar development. Calman's interpretation also necessitates the presence of an endopodite with 8 segments, 2 more than in any known crustacean group. A difference might also be seen in the particular gill-blades of the trilobitan appendage, a structure different from the setae of the crustacean exopodites. Raymond (1935) tried to explain this feature by assuming that the exopodite was formed by degeneration of the gill-branch, so that only parts of the primitive shaft remained.

One might also consider another "crustacean" interpretation of the trilobite limb. Following Garstang and Gurney regarding the coxa as a basipodite, the precoxa (not known by these authors) would represent a coxopodite and the gill-branch an epipodite. In this case we also get too great a number (7) of segments in the endopodite, and at the same time have to imagine a complete reduction of the exopodite, a feature not probable in a primitive crustacean.

The interpretation suggested by the present author (fig. 22) seems to be more in accordance with the general structure of the arthropod limb. The powerful second segment is naturally regarded as a coxa, an assumption which is also supported by the mode of articulation of the proximal segments. As in primitive Crustacea and other primitive Arthropoda the 3 basal segments are present. The 6 succeeding segments correspond in number to the crustacean endopodite and to the corresponding portion of the telopodite in other arthropods. The gill-branch has to be interpreted as a preepipodite; both epipodites and the exopodite are absent.

From the evidence presented it seems obvious that a homologization between trilobitan and crustacean appendage meets with great difficulties. We are forced to conclude that little relation appears to exist between the two types of limbs.

Calman laid considerable stress on the presence of preoral antennae (antennules) in the trilobites. As mentioned above, this indication of affinities is of little value as long as the ancestors of the Chelicerata apparently also possessed such appendages. Concerning the presence of "the five pairs of biramous gnathobase-bearing head appendages", it is to be remembered that true gnathobases hardly existed in the 4 (not 5) cephalic limbs of trilobites, and even if they were present they would, with their unreduced telopodites, be more of the xiphosuran than the crustacean type. Calman also points out the crustacean nature indicated in the presence of "furcal filaments". These organs in *Neolenus* emerge, however, from below the

dorsal shield, and it seems more likely to interpret them as a pair of cerci representing modified ventral appendages.

A non-crustacean nature of the trilobite appendage has been advocated by Ivanov (1933), Størmøer (1933, 1939) and Snodgrass (1935). The present author paid attention to the common features demonstrated in the trilobite limb and the abdominal foot of *Limulus*. As described in a previous chapter the plate-shaped gill-appendage of *Limulus* has a rudimentary median branch (developed as a short walking leg in Cambrian Xiphosura) and a very broad lateral branch, evidently attached to the very base of the limb. Like the trilobitan preepipodite the lateral branch (fig. 13, 14, 15) is divided into numerous short segments, and bears numerous blade-shaped gills, which in *Limulus*, however, are very broad just as the shaft is broader than that of the trilobite. A distal segment without gills, but provided with setae or hairs, is similar to the distal spoon-like segment of the preepipodite in most trilobites. The abdominal appendages of *Limulus* are situated below the axial furrows which are provided with tergal apodemes serving as attachments of muscles leading to the appendages. The apodemes correspond closely to the apodemes (appendifers) of the mesotergite in trilobites.

The comparison of the trilobite limb with the abdominal appendages of the Xiphosura strongly indicate a homology of these structures. From being the major objection to a relationship between the Trilobita and Xiphosura, the appendages on the contrary speak in favour of such affinities.

Having established the relation between the trilobitan and chelicerate appendages, we shall consider the development of the trilobitan appendages in all the various groups described.

Among the Trilobita the typical trilobite limb shows little variation within the different orders and within forms of very different geological age (Cambrian — Devonian). The small variation observed is mainly confined to the shaft of the gill-branch.

Strangely enough the trilobite appendage, or part of it, apparently occurs in all the Cambro-Devonian arthropods described above. It is found in very different, both merostome-like and crustacean-like forms, in forms which either had the appendages freely exposed or well concealed below a carapace or broad pleurae. This clearly shows that the trilobite limb is a primitive and at the same time conservative structure, which maintains its characteristic plan of construction in spite of considerable changes in the morphology of the dorsal shield.

Fig. 23 illustrates the modification of the trilobite limb in some of the groups described.

In the trilobites all the postoral appendages are more or less uniform in shape. A slight specialization appears to occur in the cephalic coxae of *Triarthrus*. These coxae seem to be stronger than those in the postcephalic portion, but the apparent difference might to a certain extent be due to a

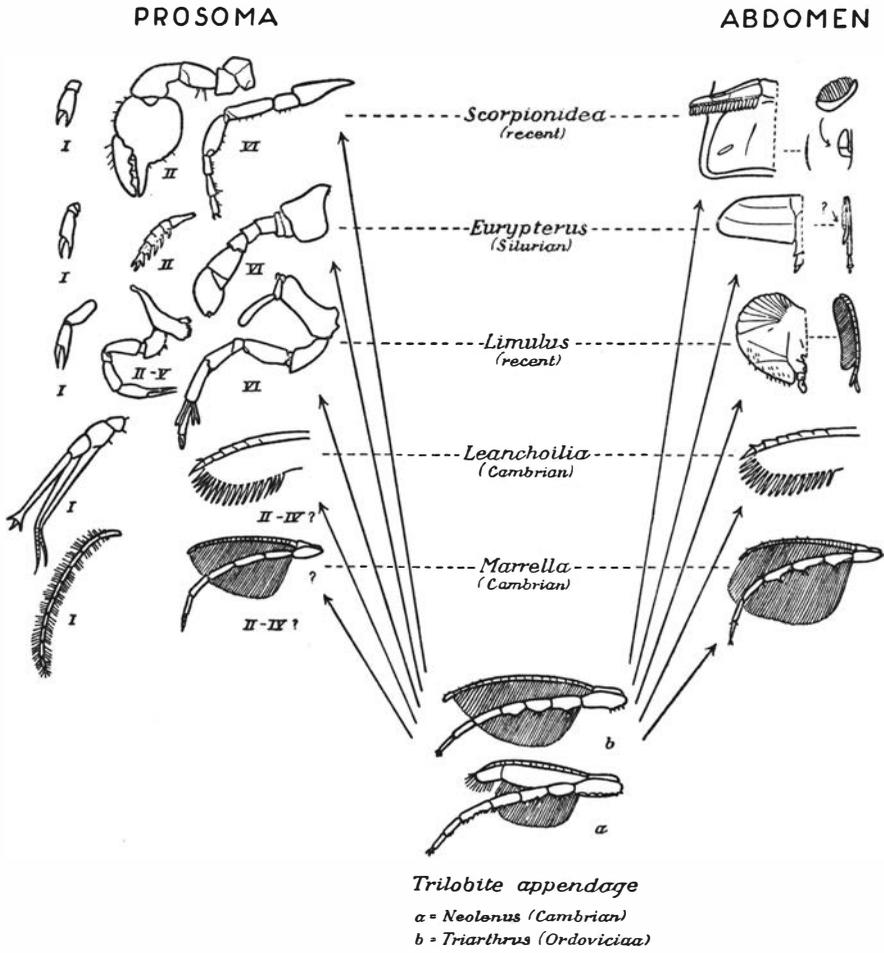


Fig. 23. Modifications of the trilobitan appendages in different fossil and recent groups.

turning forward of the more narrow coxae, a condition which offers better possibilities for preservation during the cleaning of the specimens. In one genus (*Neolenus*) we find a pair of multi-jointed cerci which belongs to the ventral structures and probably represents modified appendages rather than caudal furca.

The trilobitan limb is found also in the Cambrian Arthropoda of the Burgess Shale, and in certain Devonian genera from the Hunsrück Shale. We notice both the *Triarthrus* and the *Neolenus* type of gill-branch in the appendages. The former is characteristic of *Marrella* (fig. 23), *Naraoia*, *Sidneya* and *Waptia*, especially, and the latter is significant of *Leanchoilia* (fig. 23) and *Burgessia*.

The trilobitan appendages are, however, partly reduced or even modified in certain genera.

In *Emeraldella* and *Naraoia* the biramous postcephalic appendages seem to be uniform in all segments just as in the Trilobita. In several genera, such as *Leancoilia* (fig. 23), *Helmetia*, *Sidneya*, *Opabinia* and *Waptia* the telopodite of the appendages in the trunk appears to be more or less completely reduced, only the gill-branch is maintained. A complete reduction of the appendages is found in the abdomen (or postabdomen) of *Waptia* and *Hymenocaris* and probably in the postabdomen of *Emeraldella* and *Sidneya*.

A modification of the trilobite appendage into special organs is of considerable interest.

In *Marrella* (fig. 23) the typical trilobitan limb is present in all postoral segments, except the first (a certain modification of the cephalic telopodites might also have taken place). The first postoral appendage (*I*) is especially developed forming a uniramous tactile appendage, densely covered by setae. The telopodite of the first appendage is thus evidently altered into second antennae, and the corresponding gill-branch is apparently completely reduced.

A specialization of the first postoral appendage is characteristic also of other genera. The peculiar "great appendage" of *Leancoilia* (fig. 23) evidently represents the first postoral pair of limbs. The organ, which is discussed below, apparently forms a modified telopodite in which certain long spines secondarily have been transformed into a segmented tactile organ or second antenna. Also in *Sidneya* (fig. 24 *b*) we notice a special development of the same(?) appendage. The powerful limb, provided with numerous flat spines, evidently represents a modified telopodite. As in the previous genera the preepipodite is apparently reduced.

The posterior pairs of appendages tend to develop as flat cerci forming a caudal fan (*Yohoia*(?), *Opabinia* and *Waptia*).

The Devonian *Cheloniellon* (fig. 20) has trilobitan appendages. The telopodite of the first postoral appendage is somewhat modified and the preepipodite probably reduced. The coxa of following four pairs of limbs (*II—VI*) are strongly developed, deviating from those on posterior segments. A certain specialization of cephalic segments is seen in *Mimetaster*.

A more extensive modification of the appendages is found in the Chelicerata. As mentioned above, the abdominal feet of the Xiphosura (fig. 23) are evidently derived from a trilobitan type of limbs. It is of considerable interest that the Cambrian Aglaspida have much less reduced telopodites than the later representatives (fig. 14, 16 *b*). The prosomal limbs are, however, strongly modified, having little in common with trilobitan telopodites. A rudiment of the preepipodite is probably seen in the flabellum of the last pair of appendages (*VI*) in *Limulus* (fig. 23). The large coxae have a basal portion which possibly corresponds to the precoxa of the trilobite limb.

The Eurypterida, which antedate the Limulida, are in certain features more specialized. The plate-shaped abdominal feet are in the posterior segment completely anchylosed along the median line, and hardly show any trace of being modified appendages. The operculum (VIII) (fig. 23) is, however, similar to the operculum of *Limulus*. The genital appendage is evidently formed by fusion of the two telopodites, and the broad lateral plates, practically without signs of segmentation, are gill-bearing and correspond to the trilobitan preepipodites. The prosomal appendages (fig. 23) are similar to those of *Limulus*, but no rudiments of preepipodites are found. On the other hand, the walking legs exhibit primitive features in the development of 9 segments (counting a precoxa suggested by the epicoxite), except in *V* and *VI* where a double trochanter makes a total of 10. The strongest modification of the appendages is seen in the pregenital segment (*VII*) where the metastoma is evidently homologous with the chilaria of the Limulida.

Only in the Merostomata the prosomal coxae seems to form true gnathites approaching the conditions in the Mandibulata.

In the terrestrial Arachnida one would expect to find a still further modification of the primary trilobitan limb. Lankester (1881) demonstrated the homology between the book-gills of *Limulus* and the lung-books of *Scorpio*. Embryological studies by more recent authors have fully confirmed his results. The scorpionid lung-books evidently developed by invagination of xiphosuran-like gill-appendages (fig. 23). This type of modified appendages occurs in the Scorpionidea, Pedipalpi and Araneae, and other types of arachnid tracheae might be related to these lung-books. Especially in the Pedipalpi (fig. 11, 18) the more narrow pockets of the lung-book recall the gill-blades of the trilobitan preepipodite. Of particular interest is the combined median genital appendage and the lateral lung-books in the genital somite of the male in the Pedipalpi. The cavities leading into the lung-books communicate with a median cavity forming an uterus externus. The uterus externus contains an erectile bilobed genital appendage. This semi-invaginated appendage might be interpreted as being formed by the rudimentary telopodites of the same pair of limb as to which belongs the completely invaginated lung-books, representing the preepipodites. The genital segment of the Pedipalpi thus indicates the presence of a more or less invaginated biramous appendage of the trilobitan type.

In the scorpion the combs or pectines represent rudimentary limbs, and it seems natural to homologize them, as did Lankester, with the book-lungs and with the gill-bearing abdominal feet of *Limulus*. One might also compare the combs with the preepipodite of the trilobitan limb. In the abdomen of the Scorpionidea the trilobite-like appendages of their ancestors probably develop in two directions (fig. 23). In the appendage of the 9th somite the telopodite is completely reduced, while the gill-branch has evidently maintained its general morphology, but acquired new functions. In the

following limbs the telopodites are completely reduced, while the gill-branches have become invaginated and modified, but have maintained a respiratory function.

Remnants of the trilobitan preepipodites are possibly seen in the spinnerets of the Araneae.

The prosomal appendages of the Arachnida are strongly modified, but the walking legs (telopodites) of primitive forms, both fossil and recent, show several characters in common with the walking leg of the trilobites. A precoxa is found in certain forms.

We have thus been able to trace the trilobite appendage through a great number of forms from the Cambrian up to the present time. The evidence offered makes it obvious that the characteristic and conservative trilobitan limb-structure can be maintained even through major changes in the function of the appendage. Finally we shall again point out the difference in the development of the frontal appendages of the Trilobita (and related forms) and the Chelicerata. The former have well developed preoral antenna, while the latter lack these appendages, but have the secondarily preoral chelicerae evidently representing the first pair of postoral appendages.

We have learnt from the brain-studies on the Chelicerata that these forms might have had ancestors with preoral antennae. The absence of the antennae in the Chelicerata therefore is a minor obstacle to a relationship between them and the Trilobita.

The chelicerae are very characteristic of the Chelicerata. It is of interest to find out whether the frontal appendages in any of the Cambrian forms tend to form cheliceral structures.

In the 3-segmented chelicerae the 3rd segment forms the movable finger and the fixed finger is formed by a spinous prolongation of the second segment. The formation of powerful spines on the segments of the telopodites is characteristic of many representatives of the Chelicerata, particularly the Eurypterida (*Mixopterus*, *Stylonurus*), but also in the Trilobita the telopodites are often provided with spines or endites on the ventral side (fig. 24 a).

Turning to the groups of Cambrian Arthropoda, we notice a special development of the frontal postoral appendages (probably I) in the merostome-like genus *Sidneya* (fig. 24 b). The strong telopodite is provided with a number of long, flat spines, one on each segment except the distal ones.

In *Leanchoilia*, another merostome-like form, the first postoral appendage is also developed as a powerful, modified telopodite with long spines on certain segments (fig. 24 c). In contrast to *Sidneya* this genus has only two segments provided with long spines. The spines have a multi-segmented flagelliform distal portion, suggesting a tactile function of these organs. As suggested by Henriksen (1928) the "great appendage" of *Leanchoilia* might be interpreted as a primitive chelicera in which the reduction of segments and spines is not so pronounced as in the pincer of the Chelicerata.

Fig. 24. Possible stages in the development of the chelicera.
a = trilobite, *b* = *Sidneya inexpectans* Walcott, *c* =
Leanchoilia superlata Walcott, *d* = *Aglaspis spinifer*
 Raasch, *e* = eurypterid.

The 4-segmented(?) chelicera of the Cambrian Xiphosura (Aglaspida) (fig. 24 *d*) aids to bridge the gap between the "great appendage" in *Leanchoilia* and the typical 3-segmented chelicera of younger Chelicerata (fig. 24 *c*).

The structure of the forms mentioned seem to indicate a line of development leading to the formation of the characteristic chelicerae. It is significant that the preoral antennae, so well developed in the trilobite and in *Sidneya*, are apparently considerably reduced in *Leanchoilia* and are lacking in the Aglaspida and more recent members of the Chelicerata.

These observations seem at least to minimize the importance of the marked difference in the development in the frontal appendages of Trilobita and Chelicerata.

THE INTESTINE

Naturally the internal organs of fossil arthropods are rarely preserved, but a few fortunate cases are of considerable phylogenetic interest.

A common character to the many different members of the Arachnida is the enormous development of the intestinal diverticulae. Kästner (1940 *a*) regards this as an important character which separates the Arachnida (or rather the Chelicerata) from the other arthropod groups. (The Pantopoda have also pronounced intestinal diverticulae.) Fig. 11, 15, 16 illustrate the development of these organs in the arachnid orders Pedipalpi and Scorpionidea.

In the Xiphosura a similar strong development of the intestinal diverticulae is characteristic. Fig. 12, 9 demonstrates the highly branched structures presented in the larva of *Limulus*.

Strongly ramified impressions on the cephalic cheeks of certain trilobites have been interpreted by Jaekel (1901) as similar organs (fig. 5, 14). The exact nature of these impressions, which seem to branch off from the axial portion of the cephalon, is not known, but the interpretation of Jaekel seems probable. Traces of branched organs in the Cambrian trilobite *Skania* appear to corroborate this view.

Of particular interest is the occurrence of an excellently preserved intestine with lateral diverticulae in certain Cambrian Arthropoda from the

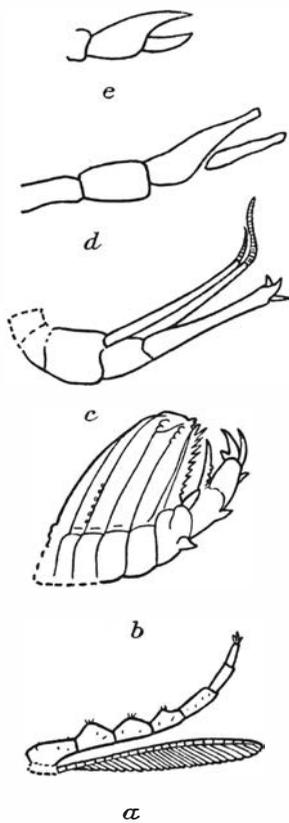


Fig. 24.

Burgess Shale. Both in the merostome-like *Naraoia* (fig. 17, 5) and in the crustacean-like *Burgessia* (fig. 19, 4) the alimentary canal has powerful lateral tubes branching strongly towards the cephalic margin. The five, segmentally arranged tubes in *Naraoia* apparently are a more primitive feature than the one tube in *Burgessia*, but otherwise the structures are distinctly homologous.

The presence of strongly developed intestinal diverticulae both in the Chelicerata and in the Cambrian Arthropoda related to the Trilobita, and probably also in the Trilobita, strongly suggests a relationship between these groups. The common structures in *Naraoia* and *Burgessia* are of special interest in linking together the merostome-like and crustacean-like Cambrian arthropods. Strongly developed intestinal diverticulae are not characteristic of the Crustacea.

CONCLUSIONS

A morphological comparison of the various groups described in the previous chapters has revealed the presence of a number of common characters which form a base for regarding these groups as belonging to a separate branch of the Arthropoda. The major common characters might be summarized as follows:

1. The trilobation of the dorsal shield, the presence of a well defined headshield, and the tendency to develop a styliform telson.
2. The presence of 4 postoral larval or primary somites.
3. The appendages of the postoral somites being either trilobitan limbs or modifications of this type of appendages.
4. The intestinal diverticulae being very strongly developed.

Of these four points the second and fourth are not to be found in many groups, but their occurrence in widely separated representatives confirms their general significance. The first point is not satisfied in the described crustacean-like forms of the Cambrian. But this group, on the other hand, completely possesses the third and fourth points, and therefore obviously is related to the other groups. The crustacean-like forms might possibly have some connection with the Crustacea, but the present author is more inclined, as pointed out below, to interpret the common characters as a matter of convergence.

The present comparative research strongly indicates the relationships of the Trilobita, Arachnida, Xiphosura and the Cambro-Devonian Arthropoda related to the Trilobita. All these groups evidently belong to one common branch of the Arthropoda.

TAXONOMIC RELATIONS

The large groups comprising the Chelicerata, Trilobita and trilobite-like Palaeozoic Arthropoda, seems to form a natural systematic unit which might be defined as a special phylum or subphylum of the Arthropoda.

Lankester (1904, 1905) applied the term Arachnida to embrace not only the true Arachnida, but also the Pantopoda, Merostomata and Trilobita. With exception of the Pantopoda the group is practically the same as the the group indicated above. The name Arachnida, however, is hardly a good one, because it has been and is generally used to designate a minor systematic group, the true Arachnida. More recent writers who share the general view of Lankester as to the relationships between the Trilobita and Chelicerata (Fedotov, Ivanov, Størmer, Schulze and Snodgrass) have not suggested a special name for this large group.

It seems reasonable to include the Chelicerata, Trilobita and trilobite-like forms in a common arthropod phylum (or subphylum) which we may call the ARACHNOMORPHA. The name was applied by Heider (1913) to comprise the Trilobita and Chelicerata. It seems appropriate to extend this designation to a larger group including also the Palaeozoic Arthropoda related to the Trilobita.

The subphylum CHELICERATA seems to form a natural group comprising the two classes Arachnida and Merostomata. Dahl (1913) also included the Tardigrada, Linguatulida, Pentastomida and Pantopoda, but these appear to belong to other branches of the Articulata and Arthropoda.

The Eurypterida and Xiphosura are generally regarded as two different orders of the class Merostomata. The Eurypterida seem, however, to form a limited, well defined group differing distinctly from the related Xiphosura and approaching the Arachnida in certain characters. I would therefore prefer to place the Eurypterida and Xiphosura in two different subclasses of the Merostomata. Concerning the Xiphosura this subclass may be divided into three orders, the Aglaspida, Synziphosura and Limulida. Raasch (1939) has suggested another division, regarding the Eurypterida, Aglaspida, Synziphosura and Xiphosura as equal groups of the Merostomata. The more ancestral Aglaspida possibly represent a separate subclass, but the Synziphosura are at least intimately connected with the Limulida.

With their absence of the preoral antennae and the presence of the characteristic chelicerae, the subphylum Chelicerata is well delimited from the Trilobita and related forms. The latter forms, which are characterized by the presence of preoral antennae and trilobitan appendages, appear to constitute another subphylum of the Arachnomorpha. This group I suggest to call the subphylum TRILOBITOMORPHA, with regard to the trilobitan characters. A definition of the group is given below.

Among the Trilobitomorpha the Trilobita form a very distinct, limited group. The Trilobita are generally distinguished as a separate subclass, class or even subphylum (Borradaile 1932). In the taxonomy suggested in the present paper the Trilobita are given the rank of class.

More difficult appears the taxonomy of the many different Cambrian and Devonian arthropods which in my opinion belong to the Trilobitomorpha. Palaeontologists have previously placed them together with the Trilobita, as members of the Crustacea. Walcott chiefly referred them to recent subclasses or orders of the Crustacea, and two orders, the Aglaspina and Limulava, were referred to the Merostomata.

Among the recent authors dealing with the Palaeozoic Arthropoda, only Raymond (1920, 1935) has suggested a more detailed taxonomy of the Cambrian Arthropoda mentioned. He separates 3 subclasses: the Trilobita (including *Naraoia*), the Homopoda (synonymous with the preoccupied name Haplopoda) and the Xenopoda.

The subclass Homopoda is defined as: "Crustacea with two pairs of tactile organs, the other appendages trilobitan. Biramous appendages on some or all the trunk segments. Carapace present or absent. No facial sutures." (Raymond 1935.)

The subclass Xenopoda is defined as: "Crustacea with more or less eurypterid-like form, one pair of uniramous antennae, biramous appendages on anterior part of the trunk, modified endopodites on cephalon." (Raymond 1920.) (According to the text (1935) Raymond evidently means trilobitan appendages rather than the more indifferent term "biramous appendages".)

The systematic division of Raymond can be presented as follows:

- I. Subcl. Trilobita Walch.
- II. Subcl. Homopoda Raymond.
 1. Ord. Marrellina Raymond (*Marrella*).
 2. Ord. Pseudanostraca Raymond (*Opabinia*, *Leanchoilia*, *Yohoia*, *Bidentia*).
 3. Ord. Pseudonotostraca Raymond (*Burgessia*, *Waptia*, *Protocaris*).
 4. Ord. Hymenocarina Clarke (*Hymenocaris*, *Anomalocaris*, *Tuzoia*).
 5. Ord. Aglaspina Walcott (*Aglaspis*, *Molaria*, *Habelia*).
- III. Subcl. Xenopoda Raymond.
 1. Ord. Limulava Walcott (*Sidneya*, *Amiella*, *Emeraldella*).

The major difference between the Homopoda and Xenopoda is said to be the presence of two tactile organs in the former and only one in the latter which is also distinguished by a more or less eurypterid form.

The number of tactile organs is not exactly determined in several species. Two pairs of tactile organs are obvious in *Marrella* and are probably present in *Leanchoilia*. In the latter form the postoral tactile organ is not a typical antenniform appendage such as in *Marrella*. Two pairs of tactile organs

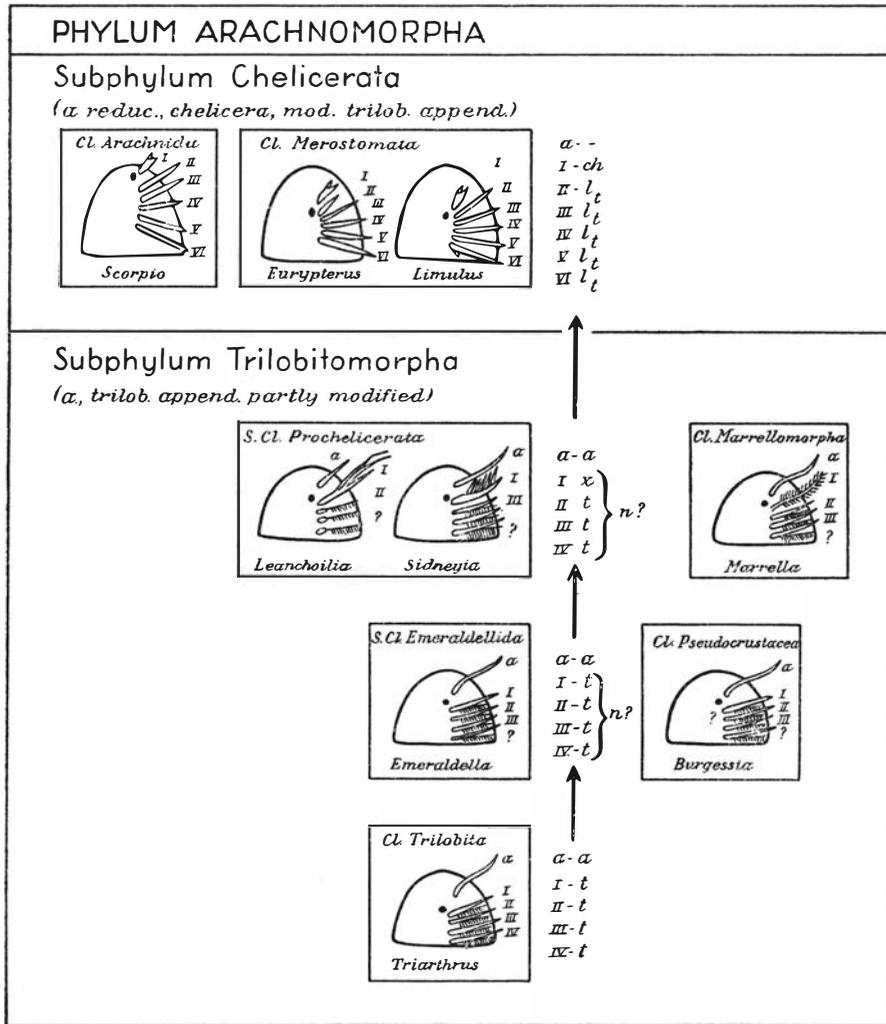


Fig. 25. A classification based on the development of the cephalic appendages. I—VI = postoral appendages, α = preoral antenna, *ch* = chelicera, *lt* = modified trilobitan limb, *t* = trilobitan limb, *x* = modified antenniform trilobitan limb.

cannot be said to have been demonstrated with certainty in the other forms. The structures of *Burgessia*, according to the material presented by Walcott, would rather favour the assumption of one pair of tactile organs such as in trilobites. Recent research on Aglaspida demonstrates the lack of typical tactile organs in these forms (the chelicerae certainly have some tactile function, but are not typical tactile organs). The Aglaspida (Aglaspina of Raymond) evidently belong to the Chelicerata.

With regard to the "eurypterid form" certain members of the Homopoda (*Aglaspina*, *Molaria* and *Leanchoilia*) also have a shape of the body approaching this form, or at least have a merostome-like shape of the body.

According to Raymond's interpretation of the taxonomic relations, the orders Pseudanostraca and Pseudonotostraca lead to (evolve into) the recent orders Anostraca and Notostraca of the Branchiopoda. The order Aglaspina is with doubt regarded as leading to the Xiphosura, and the Limulava (belonging to the Xenopoda) as leading to the Merostomata. Representatives of the two different subclasses Homopoda and Xenopoda are both supposed to have given rise to members of the Merostomata. The opinion of Raymond would involve the descendance of the Chelicerata from crustacean ancestors, a view which does not seem probable. A division into the two subclasses Homopoda and Xenopoda seems also difficult to maintain because of its separation of apparently closely related forms. The genus *Leancoilia* belongs to the Homopoda, while the apparently related genera *Emeraldella* and *Sidneya* are placed in the Xenopoda.

In addition to the taxonomy suggested by Raymond, Hutchinson (1930) has introduced a new suborder, Palaeanostraca to comprise the Opabinidae and Rochdaliidae. Beurlen (1934) establishes the group Marrellomorpha including the genera *Marrella*, *Mimetaster* and *Pygaspis*. He also suggests another group containing the genus *Marrria* Ruedemann, a somewhat problematic form not considered in the present paper.

Our knowledge of the Trilobitomorpha, the Trilobita excepted, is limited to a comparatively small number of species chiefly confined to one single occurrence. It is therefore premature to establish a taxonomy with claims to finality, but one may, along the lines of the present comparative research, attempt to establish a preliminary system.

A systematic division may be based on one or more morphological characters. The chief characters to be considered are the development of the headshield and the differentiation of the trilobitan appendages. In the dorsal shield the presence or absence of pleurae, and the formation of a telson or pygidium might also be of some importance.

Regarding the Trilobita as the most primitive group, it seems fruitful in the classification, to lay stress on the gradual modification of the primary trilobitan structures.

The headshield of the Trilobita and apparently many Cambrian Arthropoda from the Burgess Shale includes 4 postoral somites, while 6—7 are present in the Chelicerata. Exceptional structures are found in *Cheloniellon* with only 1 postoral somite in the headshield.

Concerning the development of the appendages, we find the most primitive conditions in the Trilobita with their preoral antennae and uniform postoral appendages (except the cerci). Fig. 25 illustrates the gradual modification of the appendages in the headshield. The typical trilobitan feature, a cephalon with preoral antenna and 4 postoral, typical trilobitan appendages, appears to be preserved in the merostome-like *Emeraldella*. A similar

structure might have been present in the crustacean-like *Burgessia* (the cephalic appendages are, however, little known).

A stronger modification of the trilobitan limb seems first to take place in the first postoral somite. (A modification of the last legs into cerci occurs already in the trilobites.)

This further step in the phylogeny of the Trilobitomorpha is demonstrated in *Marrella* where the first telopodite is evidently modified into a second antenna. A similar evolutionary stage is noticed in *Leancoilia* in which the same appendage is modified into a tactile organ bearing some resemblance to the chelicera of the Chelicerata.

In the Chelicerata the antennae are completely reduced and the trilobitan appendages are strongly modified. At the same time 2 (3) extra somites are included in the headshield forming a prosoma.

The following suggestion of a classification of the Arachnomorpha is chiefly based on the lines indicated above. Only brief diagnoses are given of the different orders.

A TENTATIVE CLASSIFICATION OF THE ARACHNOMORPHA

Phylum Arachnomorpha Heider, emend.

Arthropoda with a more or less trilobate dorsal shield. Frontal somites united into a cephalon or prosoma. Trunk terminating in a mostly styliform telson, or a pygidium composed of variable number of anchylosed tergites. Appendages trilobitan, or modifications of this type. Preoral antennae present or more or less completely reduced. Intestinal diverticulae strongly developed. 4 postoral larval somites.

A. Subphylum Trilobitomorpha nov.

Aquatic Arachnomorpha with a cephalon provided mostly with 4 postoral somites. Preoral antennae present, other appendages of trilobitan type. Parts of trilobitan appendages may be reduced, those of anterior and posterior somites may be more strongly modified.

I. Class Trilobita Walch.

Trilobitomorpha with distinctly trilobate dorsal shield. Cephalon with 4 postoral somites. Thorax and pygidium with variable numbers of somites. Postoral appendages of characteristic trilobitan type, except last ones which may be modified into multi-jointed cerci.

1. Order Protoparia Swinnerton (emend. Størmer).

Primitive trilobites with marginal suture. Rudimentary intergenal spines may occur besides genal spines. Preantennal segment well developed on dorsal side in protaspis.

2. Order Hypoparia Beecher.

Trilobites with marginal suture and more or less reduced lateral eyes. Intergenal spines absent. Preantennal segment probably well developed on dorsal side in protaspis.

3. Order Opisthoparia Beecher.

Trilobites with facial suture crossing margin behind genal angles. Intergenal spines absent in adult. Preantennal segment but slightly developed on dorsal side in protaspis.

4. Order Proparia Beecher.
Trilobites with facial suture crossing margin in front of genal angles. Intergenal spines present, genal spines absent. Preantennal segment not developed on dorsal side in protaspis.
- II. Class Merostomoidea nov.
Trilobitomorpha with distinctly trilobate dorsal shield. Cephalon mostly with 4 postoral somites. Tergites of trunk free or anchylosed into a continuous shield. Telson mostly styliform. First and last pair of trilobitan appendages may be modified, others partly reduced.
- II a. Subclass Emeraldellida nov.
Merostomoidea with practically unaltered trilobitan appendages.
 1. Order Emeraldellida nov.
Emeraldellida with 12 free tergites in an elongate trunk.
 2. Order Naraoidea nov.
Emeraldellidae with trunk covered by a continuous dorsal shield.
- II b. Subclass Cheloniellida Broili.
Merostomoidea with cephalic region divided into movable tergal portions, frontal one including one postoral somite. Telson(?) bifurcate. Postoral appendages trilobitan, first one somewhat modified.
 1. Order Cheloniellonida Broili.
- II c. Subclass Prochelicera nov.
Merostomoidea with frontal postoral appendages more or less chelicera-like, other limbs trilobitan with reduced telopodites.
 1. Order Limulava Walcott (emend.).
Prochelicera with eurypterid body, expanded telson. Frontal(?) postoral appendage provided with numerous flat spines (*Sidneya*, *Amiella*).
 2. Order Leancoilida nov.
Prochelicera with merostome-like body, styliform telson. Preoral antenna much reduced. Frontal postoral appendage provided with 2 spines, modified into tactile organs. (*Leancoilia*, *Bidentia*).
- III. Class Marrellomorpha Beurlen.
Trilobitomorpha with cephalic shield prolonged into flat horns or forming large disc. Trunk with numerous, free tergites and small telsonic plate, or with abdominal tergites anchylosed.
 1. Order Marrellina Raymond.
Marrellomorpha with cephalic shield prolonged into 4 flat horns. First postoral appendage antenniform, other of trilobitan type.
 2. Order Mimetasterida Beurlen.
Marrellomorpha with expanded cephalic disc. Telopodites of frontal postoral appendages modified into tactile organs. Trunk-limbs probably trilobitan with reduced(?) telopodites.
 3. Order Pygaspida Beurlen.
Marrellomorpha with cephalic shield prolonged into 2 long postlateral horns. Trunk with free thoracic and anchylosed abdominal tergites. Appendages practically unknown.
- IV. Class Pseudocrustacea nov.
Trilobitomorpha with well developed carapace, sessile or pedunculate lateral eyes. Pleurae absent in trunk, telson styliform or plate-shaped with flat or styliform cerci. Postoral appendages trilobitan, may be partly reduced, but apparently little modified.
 1. Order Burgessida nov.
Pseudocrustacea with flat expanded carapace, sessile eyes and jointed styliform telson.

2. Order Waptida nov.
Pseudocrustacea with laterally compressed carapace with pedunculate eyes. Flat cerci.
3. Order Hymenocarina Clarke, Raymond.
Pseudocrustacea with laterally compressed carapace, pedunculate eyes, adductor muscle scar. Styliform cerci. (*Hymenocaris*, *Protocaris*, *Portalia*, ? *Hurdia*, ? *Fieldia*, ? *Carnarvonina*, ? *Tuzoia*, ? *Odaria*).

Trilobitomorpha incertae sedis.

Genus *Mollisonia* Walcott, genus *Tontoia* Walcott.

Trilobitomorpha with equally sized cephalon and pygidium. Thorax with narrow pleurae and 4—7 segments.

Remarks: Possibly larval forms. May form, together with the next genus, a separate group related to the Trilobita.

Genus *Helmgia* Walcott.

Trilobitomorpha with expanded dorsal shield and prominent pygidium. Trilobitan appendages of trunk, probably with telopodites reduced.

Order Opabinida nov. (Palaeanostraca Hutchinson).

Trilobitomorpha with distinctly trilobate trunk. Cephalon with pedunculate eyes and large frontal organ. Cephalic appendages unknown, trunk-limbs trilobitan with reduced telopodites. (*Opabinia*, *Rochdalia*, ? *Yohoia*).

B. Subphylum Chelicerata.

Arachnomorpha with 6—7 frontal postoral somites incorporated into a prosoma. Preoral antennae completely reduced. First postoral appendage, secondarily preoral, developed as 2—4(?)—segmented chelicera. Strongly modified appendages. Genital ducts opening in 8th somite.

I. Class Merostomata Woodward.

Aquatic Chelicerata with variable number of abdominal somites. Tergites free, or more or less anchylosed into an abdominal shield. Telson styliform or secondarily expanded. Large prosomal coxae partly acting as jaws. Abdomen with gill-bearing appendages of modified trilobitan type.

Ia. Subclass Xiphosura nov.

Merostomata with distinctly trilobate dorsal shield. Prosoma large, abdomen with variable number of segments and long styliform telson. Abdominal appendages biramous.

1. Order Aglaspida Raasch.

Xiphosura with 11-segmented elongate abdomen. Posterior tergites may be anchylosed. Chelicera 4-segmented(?), abdominal telopodites but slightly reduced. Pretelsonic ventral plate present.

2. Order Synziphosura Packard.

Xiphosura with 10-segmented(?), more or less elongate abdomen. 6th and 7th tergites may be anchylosed. Prosoma without lateral eyes. Chelicera unknown, prosomal telopodites provided with flat spines.

3. Order Limulida Rud. et E. Richter.

Xiphosura with large headshield and short abdomen. Posterior somites of abdomen rudimentary. All, or at least a few of abdominal tergites anchylosed into an abdominal shield. Chelicera 3-segmented, prosomal legs chelate.

Ib. Subclass Euryptera (Burmeister).

Merostomata with elongate, rarely trilobate, body. Abdomen with 12 segments and styliform to spatulate telson. Chelicera 3-segmented, 6th prosomal leg generally

developed as swimming-foot. Appendages of pregenital somite evidently forming metastoma. Operculum with median genital appendage.

1. Order Eurypterida Burmeister.

II. Class Arachnida.

Chiefly terrestrial Chelicerata with prosoma occasionally divided in minor units (pro-, meso- and metapeltidium). Abdomen normally 12—13-segmented, either elongate with free tergites and telson, or short with less distinct segmentation and without telson. Chelicera 2—3-segmented. Prosomal appendages not acting as jaws. Abdominal appendages mostly reduced or modified into lung-books, combs, spinnerets or genital appendages.

1. Order Scorpionidae.¹
2. Order Pedipalpi.
3. Order Palpigradi.
4. Order Ricinulei.
5. Order Pseudoscorpionidea.
6. Order Solifugae.
7. Order Opiliones.
8. Order Araneae.
9. Order Acari.
10. Order Anthracomarti.²
11. Order Kustarachnida.
12. Order Haptopoda.
13. Order Phalangiotarbi.

Arachnomorpha incertae sedis?³

1. ? Order Arthropleurides Waterlot.
Arthropoda with distinctly trilobate, multi-segmented trunk. Headshield and telson(?) unknown. Trunk-appendages probably uniramous with medio-ventral lobe and dorsal "rosette"-organ.
2. ? Genus *Oxyuropoda* Carpenter and Swain.
Arthropoda with distinctly trilobate body. Trunk with alternating single and double segments. Postabdomen with cerci, other appendages practically unknown.

The tentative classification indicated above has certain weak points. Particularly it has been difficult to arrive at a satisfactory division of the Trilobitomorpha. It has been necessary to introduce a number of coordinate classes covering different genera which seem to be more closely related than suggested in this classification. The difference between genera belonging to different classes may appear to be smaller than between various crustacean groups, generally referred to one common class.

The size of the systematic groups has, however, to be based on a coordination with the more natural groups already existing. The conception of the Arachnida and Merostomata as two separate classes of the subphylum Chelicerata appears to be well founded. Similarly the Trilobitomorpha seem to form another subphylum of the Arachnomorpha. As long as the Trilobita

¹ For definition see Kästner 1940 a.

² For definition see Petrunkevitch (1913).

³ Described in the following chapter.

are regarded as a separate class of this group, this necessitate the introduction of other classes embracing the other groups of the subphylum Trilobitomorpha. Among these primitive members of the Arachnomorpha it is not unreasonable to expect that forms of different classes might seem more related than is the case among the more specialized members of the phylum. The present division of the Trilobitomorpha into a number of classes and subclasses may, however, have to be changed when new material emerges.

The present classification, comprising 2 subphyla with 6 classes, gives an idea of the importance of the phylum Arachnomorpha. In fig. 28 the phylum evidently forms one of the 4 phyla constituting the Arthropoda. It appears from the figure that most groups of the Arachnomorpha are extinct. Compared with the other large phyla, the Crustacea and Myriapoda—Insecta, the Arachnomorpha represent a very old group. Already in the Cambro-Silurian most of the major classes are represented. The extensive differentiation of the stock probably took place already in Precambrian time. One of the subphyla, the Trilobitomorpha, became extinct, as far as we know, already at the close of the Palaeozoic (about 200 mill. years ago). Among the Chelicerata one of the 2 classes, the Merostomata, is practically extinct, having only one recent order represented by a few species.

Only the Arachnida have maintained a leading position also in more recent faunas. One reason for this is probably the early adaptation of the Arachnida to terrestrial mode of life. It seems probable that the decline and extinction of the aquatic forms, so abundant in the early Palaeozoic, to a considerable extent might have been due to the increasing development of the Crustacea. In later periods the Crustacea fill the same places as previously occupied by the different aquatic members of the Arachnomorpha (Størmer 1933).

OTHER FOSSIL ARTHROPODA POSSIBLY BELONGING TO THE ARACHNOMORPHA

I. ORDER *ARTHROPLEURIDES* WATERLOT

In the Carboniferous (Coal Measures) of many European countries a peculiar arthropod occurs which has attracted considerable attention especially because of its great size. According to Guthörl (1936) the length possibly amounted to $1\frac{1}{8}$ m.

The fragments of this giant arthropod have been described as belonging to both Crustacea and Eurypterida. In more recent time important contributions to the knowledge of the genus *Arthropleura* have been presented by Waterlot (1934) and Guthörl (1936). Unfortunately the head and telson(?) remain unknown, but on the other hand new finds have made known the structures of the trunk and its appendages.

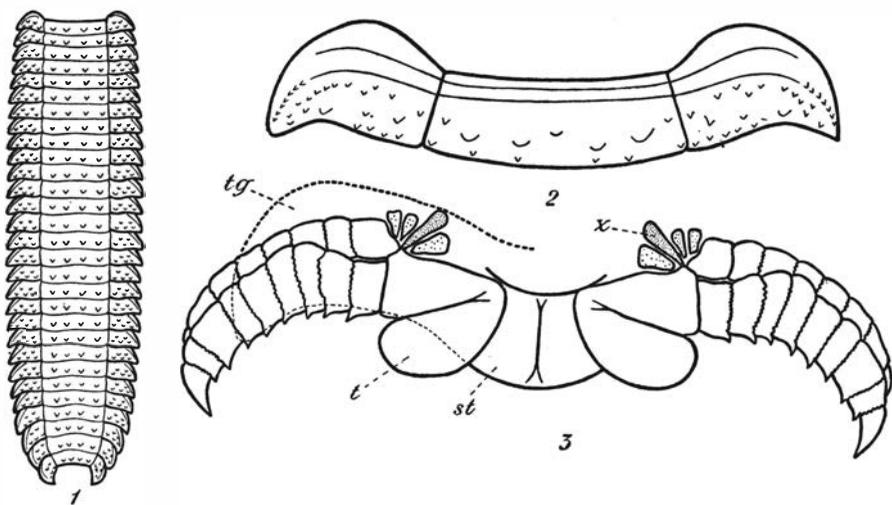


Fig. 26. Carboniferous arthropod.

Arthropleura armata Jordan. Reconstruction of trunk. Length up to $1\frac{3}{4}$ m (?). (After Guthörl 1936). 2 = anterior tergite. 3 = reconstruction of one pair of appendages in the trunk. (2, 3 after Waterlot 1934).

st = sternite, t = ventral lobe, tg = tergite, x = "rosette"-organ.

As shown in fig. 26 the distinctly trilobate body has about 20—30 uniform segments. Each tergite (2) with its pleurae resembles the thoracic tergites of trilobites. The appendages, on the other hand, differ from the typical trilobitan limb. In his reconstruction of the ventral surface with the appendages, Waterlot (1934) presents a biramous leg in which both branches are alike. The basal, common segment has a prominent ventral lobe (t in fig. 26, 3) which is interpreted as a gill. The dorsal side of the basal segment is provided with 4 small, radially arranged plates, the so-called "rosette"-organ. The 2 branches attached to the basal segment have each 9 short segments, the last one forming a distal claw.

Studying the numerous instructive photographs and drawings by Waterlot of the two branches of the appendages, one is struck by the fact that the 2 branches always lie close together, only separated by a well marked line (fig. 26, 3). The joints can even be traced from one branch to another. These features give the impression that only one branch is present. After more careful study of the published illustrations I am inclined to interpret the presumed 2 branches as only parts of the dorsal and ventral surface of one single branch. The supposed division line might be a sharp edge between the upper and lower surface (fig. 26, 3). Assuming only one segmented branch in the appendage, the structure appears to have little in common with the trilobite appendage. If the 9-segmented leg is compared with the trilobitan telopodite the "rosette"-organ and the ventral lobe find no counterpart in the trilobitan limb. It is not impossible, how-

ever, that the segmented limb of *Arthropleura* should be interpreted as a modified preepipodite. The limb has a distinct lateral position and the "rosette"-organ possibly represents modified basal segments similar to those of the gill-appendages in *Limulus*. In this case the ventral lobe would be the modified coxa or rudiment of the telopodite. The explanation is, however, highly conjectural, and, until knowledge of the cephalic appendages is obtained, it is hardly possible to decide the homologies mentioned.

As far as known trilobitan affinities are only expressed in the trilobation of the tergites. The belonging of the order to the Arachnomorpha (such as emphasized by Schulze, 1939) is therefore still very doubtful. The order Arthropleurides probably belongs to a separate class which may be called the Arthropleurida.

2. GENUS *OXYUROPODA* CARPENTER AND SWAIN

The species *Oxyuropoda ligioides* was described by Carpenter and Swain (1908) from Upper Devonian freshwater-deposits in Ireland. As indicated in the specific name, the form was referred to the Isopoda (denied by Calman), but recently Schulze (1939) has claimed affinities to the Chelicerata.

The possibly arachnomorph characters are the trilobate dorsal shield and to some extent the limuloid axis of the cephalon. Schulze tries to homologize the cephalic structures with the gnathosoma of the Acari, but as long as the appendages are practically unknown, this homology seems to be hypothetical.

Like the preceding form, *Oxyuropoda* may with doubt be referred to the Arachnomorpha.

REMARKS ON THE RELATIONSHIPS BETWEEN THE ARACHNOMORPHA AND OTHER PHYLA OF THE ARTICULATA

The group Articulata of Cuvier includes the Annelida as well as the Onychophora, Tardigrada, Pentastomida and Myzostomida. It is generally accepted that the Arthropoda have developed from polychaetous or more primitive annelids.

In the previous chapters we have pointed out the affinities between the different groups referred to the Arachnomorpha. There is strong evidence of a closer relationship between the various groups. The chief problem to be touched upon in the present paper is the relation of the Arachnomorpha to other phyla of the Arthropoda. Primarily we shall consider the relations to the Annelida.

ANNELIDA

The studies of Ivanov (fig. 2) have strongly suggested that the arthropod phyla descended from annelid groups with the same number of larval somites. Accordingly the Arachnomorpha should be derived from annelids with 4 postoral somites.

It has been attempted to homologize the arthropod limb with the parapodium of the Annelida. In the present case it would imply a homology between the trilobitan limb and the parapodium of a polychaetous annelid. A closer study of the development of the parapodium gives, however, little support to an assumption of a homology. Snodgrass (1938) mentions that during the ontogeny the cirri and the chaetal sacs are first developed. Not until afterwards these morphological structures "are carried outwards on an outgrowth of the body wall that becomes the principal part of the appendage" (Snodgrass l. c. p. 37). There is reason to believe that the apparently biramous parapodium of the Polychaeta is formed by the union of a dorsolateral and ventrolateral cirrus and chaetal sac.

The Middle Cambrian Burgess Shale has also yielded numerous excellently preserved specimens of Annelida. Fig. 27 shows one of the interesting forms described by Walcott (1911 b, 1931). As I have previously (1933) pointed out, the blade-shaped setae of the genus *Canadia* recall the gill-blades of the gill-branch in the trilobitan limb. In the fossil polychaete the setae are attached to uniramous lobes or parapodia. Whether these lobes and setae are homologous with the trilobitan appendages is not possible to decide with our present knowledge of the fossil worms. The correspondence in structure may be due to convergence, or signify a common origin. (Possibly the appendages of these Annelida may also be considered as secondarily reduced appendages of the trilobitan(?) type.)

Several Gephyrea-like annelids (*Selkirkia* and *Ottoia*) have a spinous erectile proboscis not unlike the frontal process in *Opabinia* (fig. 19, 10). It is not possible to decide whether the resemblance is of any phylogenetic significance.

Concerning these peculiar Cambrian Annelida I wish to point out that these forms bear considerable resemblance to the class Priapulida, a rare bipolar group of recent Annelida. According to published illustrations of the Priapulida (Baltzer 1928—1934) the proboscis is very similar. Of particular interest is the presence of an "armoured" larva in the recent worms, a feature strongly suggesting the structures of *Selkirkia*.

CRUSTACEA

It is of particular importance to consider the relationships of the Arachnomorpha to the other phyla of the Arthropoda. Fig. 28 indicates the four main branches of the Arthropoda. The two large phyla, the Crustacea and Myriapoda—Insecta, are often placed in a common group,



Fig. 27. Cambrian annelid.

Canadia spinosa Walcott. Med. length about 50 mm. From the Middle Cambrian Burgess Shale, British Columbia, Canada. (After Walcott 1931.)

the Mandibulata. The name indicates the presence of special masticatory organs in the cephalon round the mouth. The masticatory organs are formed by strongly modified appendages. Particularly in the mandibulae (the 2nd pair of postoral appendages) the uniramous basal portion of the limb is modified into strong gnathites, while the distal branches are more or less completely reduced.

This development is practically unknown in the Arachnomorpha. Only among the larger forms, the Eurypterida and Limulida (and possibly Cheloniellonida), the coxae of the prosomal appendages appear to have some masticatory function. The telopodites of these appendages are, however, not reduced and it seems probable that the spinous oral margins of the coxae to a great extent also serve the keeping and transport of the food at and into the mouth. In *Limulus* the mastication of the food actually takes place also in the intestinal proventriculum which has folds of hard cuticula provided with prickles.

In the fossil *Cheloniellon* the coxae of the cephalic appendages are developed into "gnathites" which, however, neither are concentrated round the mouth nor meet their counterpart in the median line, and therefore rather served the seizing and transport of the food to the mouth than acted as true jaws.

Recent studies of the Arachnida have made it evident that the coxae of these forms never are developed as jaws.

In general we might conclude that the Arachnomorpha differ from the Mandibulata in the absence of true jaws. The presence of some kind of jaws in the Merostomata might probably be regarded as a special development not necessarily suggesting affinities to the Mandibulata.

The characteristic development of the intestinal diverticulae of the Arachnomorpha, in contrast to the Mandibulata, may have something to do with the lack of masticatory organs, a feature probably acquiring a more extensive digestive surface of the intestine.

In the discussion of the zoological position of trilobites the possible affinities to the Crustacea have formed the essential point. Most authors have claimed a relationship between both groups. Quite recently Calman (1939) points out the striking resemblances between trilobites and isopods and quotes several important characters which in his opinion are common to the Trilobita and Crustacea. The trilobites are generally regarded as primitive crustaceans from which both the Chelicerata and the more recent Crustacea evolved.

The problems to be considered are on one side the amount of relationship between the Arachnomorpha and Crustacea, and on the other side the possibility of the Crustacea being derived from primitive Arachnomorpha, i. e. members of the Trilobitomorpha.

In a previous chapter we have discussed the morphology of the Arachnomorpha in comparison with the Crustacea, particularly with regard to the structures of the appendages. Concerning the development of the dorsal shield it cannot be denied that certain benthonic crustaceans bear a close resemblance to the Trilobitomorpha, but on the other hand the characteristic features of the latter, the trilobation and the tendency towards the formation of a styliform telson, are not characteristic of the Crustacea.

Calman (1939) mentions as decisive characters proving the relationship between the two groups, the "preoral antennae, the five pairs of biramous gnathobase-bearing head appendages following them, and the furcal filaments". As discussed above (p. 120) the mentioned characters appear to be of minor value, some of them being hardly correctly interpreted (the number of biramous head appendages is 4, not 5).

A detailed comparison of the trilobitan and crustacean appendages shows but little correspondence. Already Lower and Middle Devonian crustaceans have typical appendages deviating decidedly from the trilobitan limb. Raymond and others have postulated the derivation of the character-

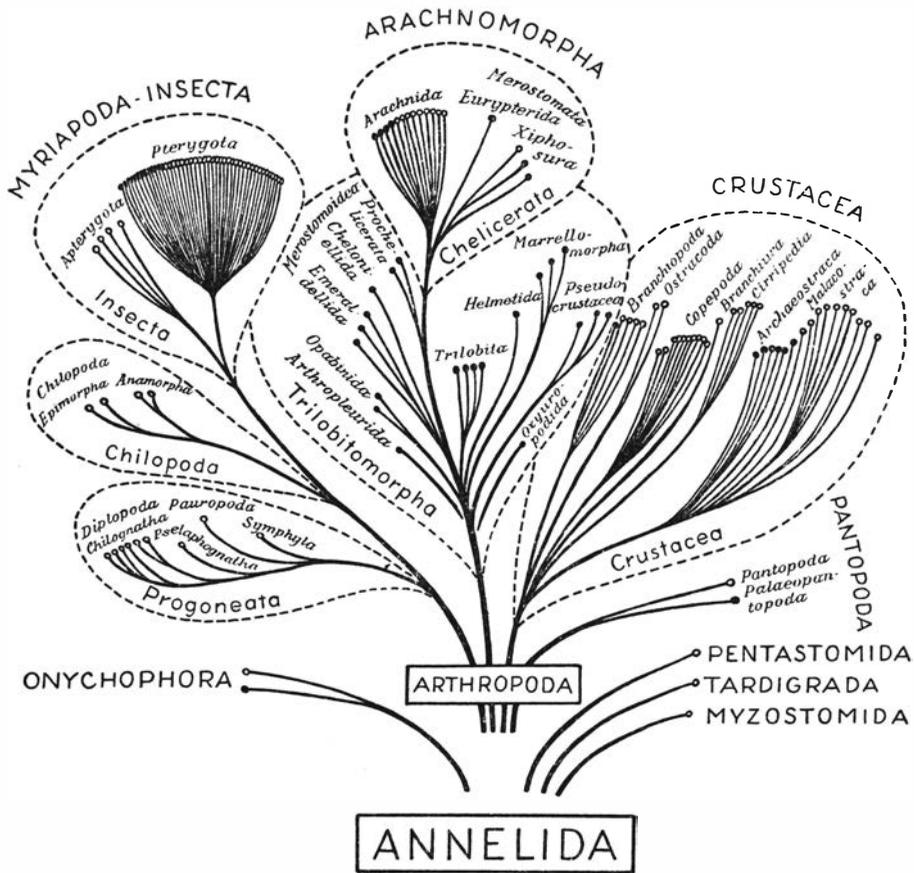


Fig. 28. A tentative scheme of the relationships and phylogeny of the Arthropoda. Orders from the smallest groups indicated. Branches terminating in an open ring have living representatives, other branches represent extinct orders.

istic biramous limb of the Crustacea, from the biramous limb of the Trilobita. This conception, however, is quite hypothetical, not based on any fossil evidence. We cannot completely exclude the possibility, but with our present knowledge of the appendages we are forced to conclude that the trilobitan and crustacean limbs differ in most essential characters.

Taking into account also the differences demonstrated in the morphology of the dorsal shield, the intestinal diverticulae and the number of larval somites, it seems reasonable to assume that the Arachnomorpha and the Crustacea belong to two different branches of the Arthropoda, branches which possibly have developed independently from different annelid ancestors.

With our present knowledge of the fossil forms it is difficult, however, definitely to exclude the possibility of crustaceans being derived from members of the Trilobitomorpha. The crustacean-like arthropods of the

Cambrian, no doubt, demonstrate crustacean characters. Biologists discussing these forms have been unanimous (with one exception of the present writer) in regarding them as true crustaceans, as progenitors of recent species. In their morphology they show distinct crustacean tendencies in the development of a carapace, pedunculate eyes and flat cerci, and it cannot be denied that the archaeostracan-like *Hymenocaris* (fig. 19, 9) bears considerable resemblance to other, still more archaeostracan-like forms (represented by carapaces only) in the same fossil layers (*Hurdia*, *Tuzoia*). A conception of a non-crustacean nature of the described crustacean-like arthropods would involve that the apparent close resemblance of *Hymenocaris* and true members of the Archaeostraca (known from the Silurian and Devonian), is only due to convergence.

It is, however, evident that the crustacean-like arthropods from the Middle Cambrian are closely related to the Trilobita and to the merostome-like form of the same beds. They conform exactly in the structure of the limbs and the intestinal diverticulae. It seems therefore reasonable to assume that also the crustacean-like forms belong to the Arachnomorpha such as indicated in the present classification.

Shall we presume that crustacean-like members of the Arachnomorpha gave rise to the Crustacea? The problem can hardly be definitely solved with our present knowledge of the fossil forms. In spite of the crustacean characters exhibited in certain genera the present author is not inclined to assume an evolution of the Crustacea from groups related to the Trilobita. The chief objection to such a relationship is the complete lack of trilobitan appendages in the Crustacea. Calman is obviously right in warning against putting too much weight on more isolated coincidences, or lack of coincidences in structure, but the presence of the characteristic trilobitan limb in many different groups of the Arachnomorpha can hardly be regarded as an isolated coincidence. We have seen how the primitive trilobitan limb is found, more or less modified, in very different groups and traced even in terrestrial forms. It seems therefore difficult to understand why this conservative structure evidently is not preserved in any of the numerous aquatic Crustacea, not even in Devonian representatives. The peculiar development of the intestinal diverticulae is, with the exception of a few parasitic copepods, apparently unknown in the Crustacea. Perhaps the most important difference between the Crustacea and Arachnomorpha is the probably different number of larval somites in the two groups.

For these reasons the present author is preliminarily inclined to regard the crustacean-like members of the Trilobitomorpha as not related to the Crustacea. The resemblance in structures must consequently be interpreted as due to convergence, an adaption to a common mode of life. As suggested in a previous paper (Størmer 1933) the Trilobitomorpha of the early Palaeozoic seas might have occupied the same place, and to some extent have

been "dressed" in the same way as the Crustacea which replace them in the more recent marine faunas.

In fig. 28 the different subclasses and orders of the Crustacea are indicated. The classification is based chiefly on the system of Calman and with regard to the extinct groups a division suggested by Raymond (1935) is applied. In establishing the different orders or suborders, I have to a considerable extent also followed the classification presented in Kükenthal's *Handbuch der Zoologie*. In the figure the subclass Branchiopoda includes the orders: Lipostraca, Anostraca, Notostraca, Conchostraca and Cladocera; the Ostracoda: Myodocopa, and Podocopa; the Copepoda: Gymnoplea, Podoplea, Philichtyes, Dichelestia, Caligi, Chondracanthi, Lernaeae, Lernaeopoda, Choniostomata and Herpyllobii; the Cirripedia: Thoracica, Acrothoracica, Ascothoracica and Apoda; Archaeostraca: Bradorina, Ceratocarina, Rhinocarina and Discinocarina and ?Nahecarida (referred by some authors to the Malacostraca); Malacostraca: group Leptostraca with order Leptostraca, group Syncarida with order Anaspidacea, group Peracarida with order Mysidacea, Cumacea, Tanaidaea, Isopoda and Amphipoda, group Eucarida with order Euphausiacea and Decapoda, and group Hoplocarida with order Stomatopoda. Raymond (1935) places the Lipostraca in the Malacostraca, but I have followed Scourfield (1926) in regarding this order as belonging to the Branchiopoda.

MYRIAPODA — INSECTA

This large arthropod phylum comprises, with a few exceptions, only terrestrial forms. As mentioned in the introduction, Handlirsch (1926, 1927) strongly argues the derivation of the Myriapoda—Insecta from the Trilobita. The evidence in favour of such a relationship is, however, very vague. The mentioned author particularly points out the presence of pleurae on the abdomen of the primitive Carboniferous Palaeodictyoptera. The present author (1939) has mentioned that the structures of the abdominal appendages of certain insects to some extent recall the trilobitan appendage. The possible homology is, however, hypothetical and may well be due to convergence.

Handlirsch (1926, 1927, fig. 211) illustrates an appendage-bearing, double segment of a diplopod from the Carboniferous. According to this reconstruction the biramous appendages, with the lateral branch attached to the very base of the limb, is not unlike the trilobitan appendage. It is not apparent whether the reconstruction is based upon sufficient material. In general the Palaeozoic diplopods show but few details of the appendages.

We may conclude that our present knowledge of fossil and recent Insecta and "Myriapoda" shows very little evidence in favour of a closer relationship to the Arachnomorpha.

In fig. 28 the branching of the Myriapoda—Insecta is based directly on recent articles in Kükenthal's *Handbuch der Zoologie*. It seems therefore hardly necessary to name the many different orders. The subphylum Progoneata is divided in 3 classes, the Symphyla, Pauropoda and Diplopoda, the latter including 2 subclasses, the Pselaphognatha and Chilognatha.

In the subphylum Insecta the class Pterygota comprises, according to Handlirsch (cp. Twenhofel and Shrock 1935, p. 452) more than 40 orders of which 13 are extinct.

PANTOPODA

The Pantopoda or Pycnogonida form a peculiar group of marine arthropods. Fossil remains of this group were unknown until Broili (1929 *b*, 1930 *b*, 1932 *b*) described well preserved species from the Lower Devonian Hunsrück Shale (fig. 29 *a*).

The Pantopoda have a narrow body provided with a long frontal proboscis and normally 7—8 pairs of preabdominal appendages. The first pair of appendages resembles the chelicerae of the Chelicerata. In the fossil genus *Palaeoisopus* only the 4 posterior pairs of limbs are developed. In this form we find a distinct segmentation also of the proboscis, suggesting the presence of 8 segments between the rostrum and the abdomen which in this extinct form is bulbous and segmented, not rudimentary as in recent species. The intestine of recent forms has strongly developed intestinal diverticulae penetrating into the appendages. Very characteristic of the Pantopoda is the protonymphon-larva, provided with 3 pairs of appendages (fig. 29 *b*).

The zoological position of the Pantopoda has been subject to much discussion. The group has frequently been classed with the Chelicerata. The chief characters suggesting this relationship are: 1. The chelicera-like frontal appendages, 2. the dorsal (Araneae-like) eyes situated between the bases of the third pairs of appendages, 3. the large number of preabdominal appendages, 4. the intestinal diverticulae, and 5. the manner of ecdysis. Snodgrass (1938) also adds the presence of a patella in the legs, but this character seems less significant at least in the fossil form. The author mentioned points out that 8 somites also occur in the Xiphosura, but although a small part of the eighth somite is medially incorporated in the headshield of *Limulus*, the typical prosoma of the Merostoma primarily seems to contain only 6 postoral somites. In contrast to the Chelicerata the Pantopoda have multiple genital openings.

Several authors have suggested crustacean affinities of the Pantopoda. The chief argument has been the apparently close resemblance between the protonymphon and the nauplius. Both have a short body with 3 pairs of appendages. Biramous legs are, however, not present in the protonymphon-larva. In comparing the two larvae it is necessary to know the nature of the frontal appendages in the Pantopoda. From the literature I have not been able to find out whether the frontal appendages belong to

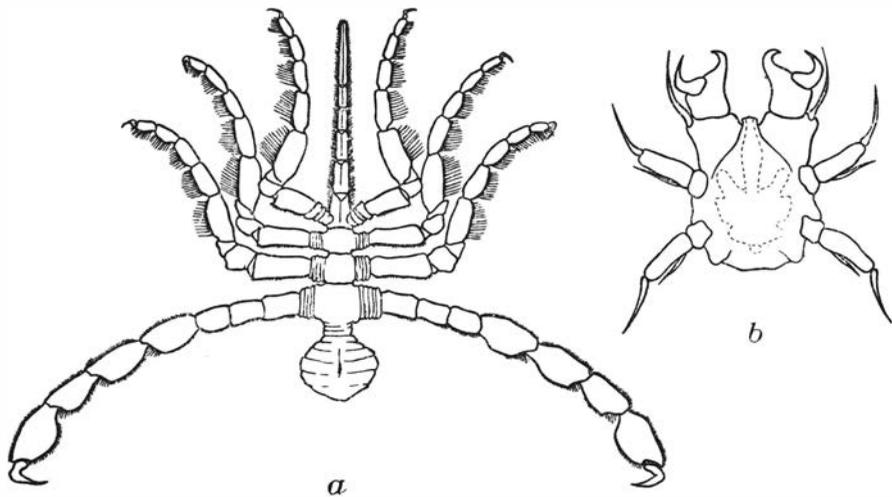


Fig. 29. Pantopoda. Fossil form and recent larva.

a = *Palaeoisopus problematicus* Broili. Med. length 124 mm. From the lower Devonian Hunsrück Shale, Bundenbach, Germany. (After Broili 1932 *b*.) *b* = Protonymphon larva of recent form (*Ammonothea*). (From Meisenheimer 1912, after Meisenheimer.)

the preoral portion of the head (innerved from a deutocerebrum) or belong to the postoral somites (innerved from the tritocerebrum). In the first case the frontal appendages may be homologized with the antennules of the crustacean nauplius, in the other case the resemblance between the two larvae is only superficial and must be interpreted as a matter of convergence.

The chelicera-like character of the first appendage may suggest a postoral appendage. According to this conception the Pantopoda have a larva, probably a larvatum, with 3 postoral somites. This would imply that the Pantopoda have a larvatum or 3 somites in contrast to 4 in the Arachnomorpha and probably 2 in the Crustacea.

The morphology of fossil and recent Pantopoda shows little resemblance to that of the Arachnomorpha.

With our present knowledge it seems natural to place the Pantopoda in a special phylum besides the Arachnomorpha, Crustacea and Myriapoda—Insecta (fig. 28, 30).

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These groups have also been referred to the Chelicerata. Most recent authors, however, are not inclined to regard them as true arthropods, but as independent phyla directly derived from annelid ancestors just at the Onychophora.

The present comparisons indicate that the phylum Arachnomorpha shows little affinities to the other phyla of the Arthropoda. It must be

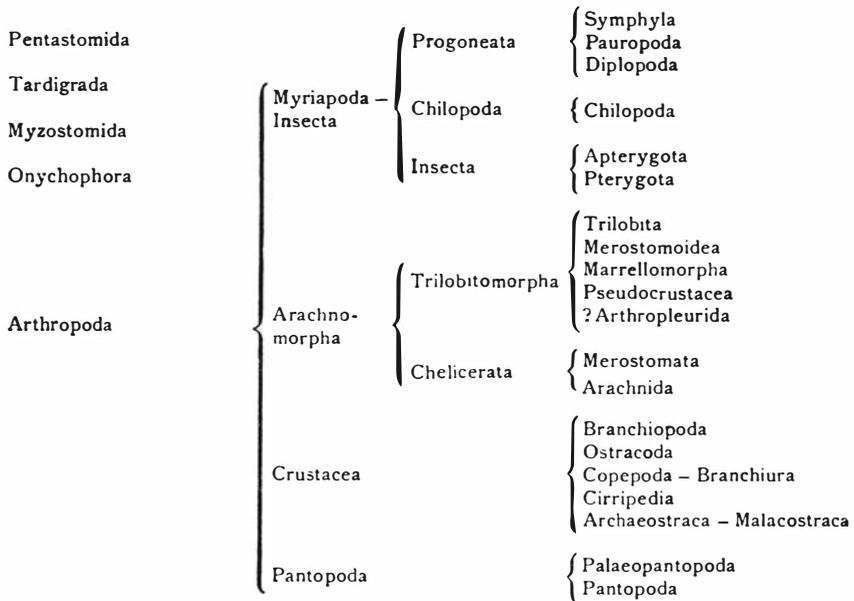


Fig. 30. A suggestion for a classification of the Arthropoda. (Cp. fig. 1.)

admitted that the possibility of a certain connection with the Crustacea is not quite excluded, but seems hardly probable to the present author.

Returning to the general classification of the Arthropoda, such as briefly discussed in the introduction (fig. 1), the present author arrives at a conception of a classification as suggested in fig. 30.

As mentioned in the introduction many zoologists believe in a monophyletic origin of the Arthropoda. Recently this view has been advocated by Snodgrass (1938). The studies of Ivanov (1933), on the other hand, give good reasons to believe that each arthropod phylum possesses a characteristic number of larval somites suggesting a derivation from different annelids with a similar larvatum. Unfortunately we are ignorant as to the number of larval somites in the Myriapoda—Insecta and very uncertain as to the Pantopoda. To the present author a polyphyletic origin of the Arthropoda seems to be most in accordance with the fossil record.

Finally we may conclude that the Arachnomorpha appear to constitute a distinct major group of the Arthropoda, a phylum which may have evolved directly from a special group of polychaete annelids.

REMARKS ON SOME EVOLUTIONARY PRINCIPLES INDICATED IN THE DEVELOPMENT OF THE ARACHNOMORPHA

In the introduction to the present paper it is pointed out that the chief problems to be considered were the true relationships between the major fossil groups, and the manner in which new morphological types, which signify larger systematic units, branch off or evolve from previous groups. The first problem has been dealt with in the previous chapters. The results of these studies lead to a conception of a near relationship between the many different groups constituting the Arachnomorpha according to the present definition of the term.

It remains to consider the general development of the phylum and to investigate the manner in which the separate groups evolve from their more primitive progenitors. It is worth while also to consider the development within one separate group, a development taking place after the morphological type has become established.

We know nothing definite as to the origin of the Trilobitomorpha, the most primitive representatives of the phylum, but it is generally assumed that these forms evolved from polychaete or more primitive annelids. Future detailed studies of the excellently preserved Cambrian annelids from the Burgess Shale may perhaps throw new light on the connection between the Annelida and the early members of the Arachnomorpha.

Among the Trilobitomorpha the Trilobita appear as a well established, stable group already in the Lower Cambrian. In spite of the great bulk of genera and species, and the considerable adaptive radiation, the trilobites maintain a strict and conservative plan of construction. They appear as a fixed stable type which hardly gave rise to the more advanced subphylum Chelicerata.

Besides the trilobites the Cambrian seas were occupied by other members of the Trilobitomorpha, members which were less numerous, but nevertheless were subject to extensive adaptive radiation. These forms were evidently related inter se, but their plan of construction appears to be less distinctive. The type was evidently more labile, tending to attain new characters through a modification of the dorsal shield and the ventral appendages. Among these groups or related forms it seems natural to look for possible ancestors of the Chelicerata, the other subphylum of the Arachnomorpha.

The Chelicerata differ definitely from the Trilobitomorpha by the lack of antennae and by the presence of the characteristic chelicerae. This might indicate a sudden, more explosive development of the Chelicerata. The fossil record, however, seems yet to warrant a connection between the two groups. Representatives of the Merostomoidea possess certain characters which point to a line of evolution leading to the Merostomata, the most

primitive class of the Chelicerata. The formation of the chelicera appears to be foreshadowed in certain members of the Merostomoidea. In one genus (*Leancoilia*) the development of chelicera-like appendages occurs coincidentally with a partial(?) reduction of the preoral antennae. Recent discoveries of primitive Merostomata (Aglaspida) have corroborated the assumption of a connection between the Merostomoidea and the Merostomata. These primitive merostomes show affinities to the Trilobitomorpha both in the general structure of the dorsal shield and by having an apparently 4-segmented chelicera. The abdominal walking legs show only a partial reduction such as would be expected in more intermediate forms. By having chelicerae and apparently 2 extra somites incorporated in the headshield, these forms are true members of the Chelicerata. Resembling both the Eurypterida and Limulida, this primitive merostome group probably represents an early offshot from the line of evolution leading from the Trilobitomorpha to the Chelicerata.

The fossil material thus suggests a development from one subphylum to another. With the evidence offered it seems hardly necessary to take into account an explosive development of the new subphylum. It must be admitted, however, that our knowledge of the primitive representatives is very limited. A more spontaneous appearance of certain new characters (prosoma?) cannot be excluded.

We have pointed out the constancy and conservatism of the morphological plan of construction in the members of the major groups such as the Trilobita, Eurypterida, Xiphosura and Arachnida. This feature is perhaps most typical in the Eurypterida and Arachnida, groups in which we are ignorant of the earliest representatives. In the Trilobita we notice among the earliest forms slight merostome tendencies in the development of a dorsal telsonic spine and rudimentary caudal segments. In the Xiphosura the oldest known representatives (Aglaspida) possess morphological characters recalling previous ancestors.

Although a more intimate knowledge of the primitive members of a group may prove these forms to be less characteristic, the fossil evidence seems to corroborate the general assumption importing that during the evolution a new, favourable type may appear which afterwards maintains its characteristic plan of construction during a flowering period characterized by extensive adaptive radiation.

Concerning the development of genera and species within one well defined group, studies on trilobites have suggested a gradual transition from species to species. Statistical investigations of Olenidae from succeeding beds of the Upper Cambrian have demonstrated the gradual transformation of the dorsal shield from subspecies to subspecies (Kaufmann 1933).

The biogenetic law of Haeckel has proved to be of great value in establishing the evolutionary trends in different animal groups. With regard to the fossil arthropods this principle has not frequently been possible to

apply because of our limited knowledge of the ontogeny of most groups. Two cases might, however, be mentioned. In trilobites larval series (*Leptoplastus*, Raw 1925) have indicated the phylogenetic relationships of families and genera, and from the early ontogenetic stages (protaspis) of certain forms one has been able to demonstrate the number of larval somites in the Trilobita. The ontogeny of *Limulus* corresponds very well with the successive geological appearance of the different groups of the Xiphosura. A comparison of the ontogeny and phylogeny appears to give a valuable confirmation to the biogenetic law.

Having considered the general evolution of the Arachnomorpha we may now briefly examine the evolutionary principles suggested in the development of the phylum.

We have already mentioned that a more explosive development of the major groups may not necessarily have occurred. The speed of development and the duration of existence of the various genera and species differ considerably within the different groups. In the Trilobita certain families are subject to rapid development or generic divergence within relatively short geological periods ((Asaphidae in the Lower Ordovician). Other families (Proetidae) have a slow development covering a long space of time, but pronouncedly persistent forms are not very characteristic. Persistent forms are in evidence in the Xiphosura where the living *Limulus* differs but slightly from its Jurassic relatives.

Parallel development within different evolutionary trends is indicated in trilobites. We may mention the studies of Kaufmann (1933) according to which the development of certain morphological characters (e. g. the tapering in width of the pygidium) proceeds along similar, parallel lines in different evolutionary trends. Similar features may be traced in other trilobite groups. The demonstration of parallel trends, suggesting an orthogenetic(?) development, is, however, difficult to decide upon unless an extensive and stratigraphically well determined material is at hand.

A convergent development of the morphological structures is often observed in the Arachnomorpha, but this is not to be confused with the parallel evolution mentioned. Among the Eurypterida the specialized body and appendages are subject to convergent development. It is demonstrable in the family Pterygotidae where species of the genus *Hughmilleria* may be very similar to species of the genus *Eurypterus* belonging to another family. It is of interest to notice that in the genus *Dolichopterus*, belonging to the family Stylonuridae, a secondary swimming palette is developed, which, however, is composed of segments different from those in the similar swimming palette of the hindmost legs in *Eurypterus*.

"Racial senescence" is a term which has been applied in connection with the special development of late representatives of certain arachnomorph groups. Particularly in the Eurypterida, but also in certain groups of the Trilobita, we notice an increase in size when the extinction of the

genus or family approaches. This is not to be understood as a general rule. In many genera it is not in evidence, and in groups where such a tendency is observed smaller species may coincidentally occur and even survive the giant representatives.

Characteristic of the late representatives of a stock is also an increased spinosity of the exoskeleton. This feature occurs in trilobites and eurypterids. One has, however, to be cautious not to confuse protective structures with those probably signifying racial senescence.

Dollo's principle on the irreversibility in evolution should also be mentioned in connection with the development of the Arachnomorpha.

The members of the Trilobitomorpha possess one pair of preoral and multi-segmented tactile antennae. In the merostome-like genus *Leancoilia* the antennae seem to be much reduced and the tactile function is taken over by the multi-segmented slender spines of the chelicera-like postoral appendages (fig. 17, 1, 2). In the true Chelicerata, however, the antennae are completely lost nor are the chelicerae developed as tactile organs. Being formed by the reduction of a primary telopodite the chelicera has retained only a few segments. Fossil and recent forms indicate that during the evolution of the Chelicerata, the chelicera has neither been able to regain the primary larger number of segments, nor been able to regain a pronounced tactile function. In the eurypterid *Pterygotus* (fig. 10, 1) the long pincers have thus maintained its few segments, although this evidently hampered the mobility of these prominent organs. Tactile organs are secondarily developed in the Pedipalpi, but in these arachnids it is neither the reduced preoral antenna, nor the chelicera, but the first walking leg (III) that has developed such an organ.

The mentioned cases, demonstrating the constancy in structure and function of the specialized chelicera, appear to illustrate the principle of irreversibility in evolution.

Finally the principle of Schindewolf, that an early ontogenetic appearance of a new morphological character signifies a new type, should be considered. As mentioned in the chapter on the taxonomy of the Trilobita, this principle may be applied in a more abstract sense concerning an arrested dorsal development of the preantennal segment in the cephalon. In the phylogenetically most advanced forms (Proparia) the preantennal segment is only developed to a small degree on the dorsal surface. This reduced dorsal development of the preantennal segment is found only in the early larval stages of more primitive trilobite groups (Opisthoparia), and thus appears to corroborate the principle suggested by Schindewolf.

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