STUDIES ON TRILOBITE MORPHOLOGY

Part III. The ventral cephalic structures with remarks on the zoological position of the trilobites.

BY

LEIF STØRMER

Abstract. The third and last part of the studies on trilobite morphology deals chiefly with certain grinding series through the cephalic region of specimens of Ceraurus pleurexanthemus Green, collected by the late Dr. Ch. D. Walcott from the Middle Ordovician Trenton Limestone in U. S. A. Information is obtained on the ventral cephalic structures, the appendages in particular. The appendages, with the exception of the antenna, are found to be constructed on the same pattern as those in thorax and pygidium and the cephalic coxae are not developed as true jaws such as generally assumed by the paleontologists. Criticism in connection with my previous descriptions and interpretation of the trilobitan appendage is met with. With regard to the zoological position of the Trilobita, the affinities to the Chelicerata are regarded as very probable. The Trilobita probably had a position not far from the ancestors of the Chelicerata, but whether they also stood near the ancestors of the Crustacea, still remains an open question.

Contents.

Introduction ...................................................... 109
Section series through the cephalic region of Ceraurus ....................... 110
Ser. H. ............................................................. 110
Ser. J. ............................................................. 116
Ser. K. ............................................................. 119
Ventral cephalic structures in trilobites ...................................... 120
General structures of the arthropod head ...................................... 125
Ventral cephalic structures in trilobites ...................................... 125
The labrum, mouth and postoral plate ...................................... 127
The appendages .................................................... 129
The feeding of the arthropods ............................................. 132
Remarks on the previously described section series of the thoracic appendages in Ceraurus .................................................. 134
Reconstructions of Ceraurus and Olenoides .................................. 141
Interpretations of the coxal region of the trilobite appendage .............. 141
The zoological position of the trilobites .................................... 150
Literature .......................................................... 155
Introduction.

Part I of the present studies (Stønner 1939) dealt with the thoracic appendages of trilobites, and discussed the probable affinities between the Trilobita and the Chelicerata. In part II (1942) the larval development as well as the segmentation and sutures of the shell were discussed. In the abstract of the last paper I indicated the appearance of a part III dealing with the cephalic appendages and presenting a general discussion of the trilobite affinities. During my studies it became apparent, however, that a general discussion of the trilobite affinities also involved a thorough study of several other fossils and recent arthropod groups. As the work proceeded, I found it appropriate to publish in a separate paper (1944) a general discussion of the affinities of a number of fossils and living arthropod groups, amongst them the trilobites, which I regarded as mutually related and belonging to one major group, the phylum Arachnomorpha.

Part III of the studies on trilobite morphology was therefore postponed, and the chapters on the affinities correspondingly abbreviated. The paper deals mainly with certain section series cutting through the head of Ceraurus pleurexanthemus Green from the Middle Ordovician Trenton Limestone, Trenton Falls, New York State, U.S.A. In connection with the description and discussion of the cephalic appendages it has become necessary to discuss some of my earlier described series and to meet certain criticism which has appeared since part I was published. In dealing with the affinities of the trilobites I have considered new evidence and new views published on the subject.

The material and methods applied are the same as those mentioned in part I (1939). The section series were carried out at Harvard University in U. S. A. in 1931—32, contemporaneously with those previously described. I wish also on this occasion to express my thanks to professor P. E. Raymond for his permission to use the collection and the facilities he offered me during the work. In connection with the studies and descriptions of the remaining series new glass- and wax models have been prepared.

In preparing the wax models I have had valuable assistance by Miss Lily Monsen. The photographs of the different models were taken by Miss Bergliot Mauritz and the drawings made by Miss Helga Lid, and Miss Lily Monsen under the supervision of the author.
**Section series through the cephalic region of Ceraurus.**

The section series are unfortunately not very complete and the preservation of the appendages is often less satisfactory. Nevertheless the remains give an impression of the original structures. The most complete series (H) comprises the frontal part of the head reaching backwards almost to the hind border of the labrum. Other series (J and K) demonstrate the remaining part of the head, but in these specimens the appendages are very fragmentarily preserved.

**Ser. H.**

(text-fig. 1—3 and pl. 1, 2).

Preliminary photographs of the wax model of this series have been published earlier (Størmer 1944, 1949).

The series comprises 64 sections. In preparing the magnified camera lucida drawings for the glass- and wax models it appeared that the magnification in the original photographs was not always quite the same. This had to be readjusted when preparing the magnified drawings. Succeeding drawings were compared and the adjustment of the magnification based on the known structures of the dorsal shell. As shown in the illustrations, the specimen appears to be slightly compressed at a right angle to the section-planes. This may be due to some inaccuracy in the magnification and in the measurements of the thicknesses of the sections.

The sections cut through an enrolled specimen. Best preserved are the sections through the anterior portion of the head. The sections are here almost vertical, forming an angle of 15° with the transversal plane. The most posterior section (no. 1) runs across the left lateral eye, cuts off the posterior border of the labrum and transverses the posterior margin of the cephalon just posterior to the right lateral eye, and crosses thoracic segments on the ventral side.

**The shell.** The sections give some information on the shell and its different sutures. The species *Ceraurus pleurexanthemus* was redescribed by Raymond and Barton (1913) and further morphological details were added by Whittington (1941) in his study of silicified trilobites from Trenton Limestone of Virginia. The morphology of the thoracic segments was treated in my earlier paper (1939).

As pointed out by the earlier authors the surface of the glabella is ornamented with larger and smaller tubercles. The larger ones
occur more or less symmetrically in two rows diverging forwards on the frontal lobe. Walcott mentions (1921, p. 440, pl. 96, fig. 4) that his sections show each tubercle to be pierced by a canal perpendicular to the shell. Similar canals have been described in caly­menids by Shirley (1936, p. 414) and in Ceraurus by Whittington (1941, p. 494).

The convex middle body of the labrum has numerous small tubercles and corresponding canals penetrating the test. This is well demonstrated in sections 40—55.

The canals of the test are concentrated chiefly on the convex exposed surfaces of the glabella and labrum and might have contained sensory or tactile hairs as suggested by Shirley (1936).

The sutures of the test are also indicated in the sections. The course of the facial sutures are well demonstrated in Whittingtons silicified specimens. Raymond (1920, p. 60) and later Whittington (1941, p. 499) did not actually find an epistoma or rostrum. Raymond assumed the epistoma either to be entirely absent or being so narrow as not to be seen in specimens in the ordinary state of pres­ervation. Whittington (1941, p. 499) did not recognize an epistoma in his material but assumed the presence of the plate from the shape of the head when placing specimens of cephalon and labrum in correct association to each other. An epistoma was demonstrated in Ceraurus aculeatus by Öpik (1937, pl. 17, figs. 2, 3).

As shown in text fig. 1 the cephalic sutures are well demonstrated in sections in the frontal portion of the head. The facial, epi­stomal and connective sutures appear in sec. 60. A transverse labral (hypostomal) suture appears in sec. 57 distinguishing a narrow epi­stoma in front of it. The epistoma, traceable on the left side down to sec. 46, thus forms a narrow transverse plate situated on the ventral part of the steep anterior border.

The appendages. The section-series cut through an enrolled specimen. Numerous sections of more or less fragmentarily preserved appendages are exposed in the photographs (pl. 1). The best preserved appendages occur in the cephalon on the right side of the labrum. The glass- and wax models prepared are confined to the cephalon and the appendages below it. The appendages below the thoracic test (opposite the labrum in the enrolled specimen on pl. 1) are too much dissolved to permit a closer identification. On the left side of the specimen (right side in photograph) a jointed appendage is demonstrated in sec. 1—6.
The cavity between the glabella and the labrum is filled with calcite. This probably means that this part of the body was kept intact, not filled by the surrounding mud. It is difficult, however, to trace a definite body wall (integument) on either side below the glabella. The first sections (pl. 1) illustrate the indistinct borders. Below the cheeks of the cephalon the integument must have been destroyed since no calcite fillings indicate the border of the original softer tissues between the test and the ventral integument.

The distal portions of the cephalic appendages preserved on the right side of the labrum, are broken off along the anterior margin of the cephalon. The appendages are to a great extent dissolved and foreign bodies or calcite fillings rather, disturb the general picture. In the model shown in text-fig. 2 a longitudinal body on the 3rd appendages is removed. In the following the different appendages are described, starting with the first one in front.

The antenna (a). Dorsal to the lateral ear of the labrum an appendage emerges from the more or less vertical body wall between the glabella and the labrum (text-figs. 1--3a). As mentioned above the body wall is not distinct, but the general structures leave little doubt as to this anterior attachment of the appendage. From the
base of the appendage an indication of two more or less plate-shaped formations extend backwards and unite with the body wall dorsal to the labrum. These formations do not seem to belong to the appendage or the primary structures at all.

From the body wall the appendage first has an antelateral direction, then turns anteriorly and slightly anteriomedially. The appendage has an elliptical almost constant cross-section, the smaller diameter being $1/2 - 2/3$ of the greater. The model indicates (text-fig. 2 and pl. 2) that the appendage is somewhat twisted round its axis at the point when it changes its direction. Slight thickenings before and after the bend of the appendage might suggest a division of the appendage into three separate joints. Dorsal to the presumed second joint, just below the dorsal test of the cephalon, a plate-shaped thickening unites this joint with the next appendage (I). This thickening also appears to be a secondary formation.

The appendage described, being uniramous, and apparently multijointed, and attached to the body wall far in front below the protecting antelateral ear of the labrum, evidently represents the antenna or antennule (or first antenna) in other arthropods. This appendage has previously not actually been recognized in this genus.
The first leg (I). This appendage is attached just behind the antenna (text-fig. 3, I), thus leaving hardly any space for a reduced "second antenna" such as suggested by some authors. As shown in text-fig. 1—3 and pl. 2, the first sections cut through the basal portion of the appendage. This basal portion communicates with the body wall, or more correctly the calcified space between the glabella and the labrum. This indicates that the appendage was attached dorsal to the postlateral portion of the labrum. The preservation does not permit a more detailed study of the basal structures.

A branchial ramus (preepipodite) is attached to the dorsal portion of the elongate basal body. The ramus is only fragmentarily preserved. The proximal joints seem hardly to have been reached by the section-series starting anterior to the posterior margin of the labrum. Judging from the more complete thoracic branchial rami earlier described (Størmer 1939), the first preserved joint might be the 3rd joint of the ramus. The 4th is almost completely dissolved and the 5th, forming the expanded distal joint, is but fragmentarily preserved. It forms a broader lobe with about 11 gills (text-fig. 3 l) directed anteriolaterally.

The coxa is narrow and slightly convex-concave with the concave side medially. The joint, which has a vertical position, is less tetrahedron-shaped than those described from the thorax (Størmer 1939, p. 177). The narrow basal portion might be due to the crowding up of the limbs round the mouth. Otherwise the coxa is much like those of the thorax. A basendite of the same type is present.

The first joint of the walking leg is separated from the coxa by a crossing furrow suggesting a jointline. The other joints of the walking leg are not distinct. Thickenings of the partly dissolved joints might suggest the positions of the articulating jointlines. Since the joints were partly telescoped one might assume that these portions were those least dissolved. Three transverse thickenings might suggest remnants of 3—4 joints, the fourth only represented by a very short basal fragment. The joints are flattened in a similar way as the coxa. The actual cross-section is, however, difficult to determine on account of the incomplete preservation. The first joint seems to be a little longer than broad, while the other ones seem to have a more equal length and width. A secondary cleft is seen in the second joint.

The second leg (II). This appendage has an extra body attached to the walking leg (pl. 2). In text-fig. 2 this is removed.
This leg (text-fig. 3 2) shows more of the fourth joint of the walking leg, but less of the basal portion of the coxal region and the branchial ramus. The sections comprise only parts of the two distal joints of the branchial ramus. The gills are fairly well preserved, the fringe lying in a plane ventral to the gills of the first leg. The number of gills preserved is here also about 11. The coxa is similar to that of the first leg. The convex-concave joint is almost vertical and tilted somewhat towards the labrum. The distal border of the coxa is suggested by a transverse furrow just as in the first leg.

The walking leg appears to be divided by three transverse thickenings into four joints. The outlines of the joints are, however, little distinct. The leg having a fairly constant width, is strongly flattened, the greatest width being about twice the smallest one or more. The greater axis in the cross-section forms an acute angle of about...
30°—40° with the horizontal plane, giving the walking legs the capacity of sliding over each other.

The third and fourth legs (III, IV). Only a small triangular portion of the coxa is included in the sections. Three fragmentary gills belonging to this appendage lie in a plane ventral to that of the gills in the second leg. The walking legs resemble those of the two anterior legs. Transverse thickenings indicate similar joints. A strong inclination of the leg at the third to fourth joints is indicated.

The last cephalic (IV) and the first thoracic leg (V) are much dissolved, but they appear to be similar to the three legs in front of them.

The section series described above has rendered valuable support to our general knowledge of the structures of the cephalic appendages in Ceraurus.

A pair of preoral uniramous antennae (or antennules) are attached to the body wall dorsal to the antelateral ears of the labrum. The 4 postoral appendages are built on the same pattern as those of the thorax, thus clearly demonstrating the uniformity of the appendages in different parts of the body. Only a slight specialization is indicated in the narrowness of the cephalic coxae. The first pair of postoral appendages (II) are situated on either side of the posterior portion of the labrum which probably just covered the most median portion of the coxa of these appendages. The basendites of the cephalic coxae are not developed as gnathites.

Ser. J.

Pl. 3 fig. 8, pl. 4, text-fig. 4.

This section series was partly dealt with in my previous paper in connection with the description of thoracic tergites (1938, text-fig. 6).

The 16 sections, running nearly parallel to the horizontal plane, cut through the dorsal portion of the cephalon and the main part of the thorax. In the cephalic region the most ventral section lies just dorsal to the posterior part of the labrum, the most dorsal section just above the right lateral eye and at the base of the left lateral eye.

The sections give some information on the structure and position of the posterior cephalic coxae, structures not demonstrated in the
Text-fig. 4. Ceraurus pleurexanthemus Green. Detail of wax model of Ser. J. Ventral view of middle portion of cephalon and two anterior tergites. Only the basal portions of the cephalic appendages are preserved (comp. pl. 4). \(ap\) = apodemes for the attachment of muscles to the appendages, \(m\) = probable position of the mouth, \(prpd\) = preepipodite, \(th_1, th_2\) = thoracic tergites. 

I—IV = postoral cephalic appendages.

above described H-series. A glass- and wax model have been prepared of ser. J (text-fig. 4 and pl. 4).

The space between the glabella and the labrum is also in this specimen filled with calcite. The vertical posterior wall of the calcite-filled portion has a dorsal position in relation to the labrum and might suggest the position of the mouth.

The appendages. The basal portion of the first walking leg (I) is apparently traced on both sides of the calcite-filled area. The portion preserved forms a longitudinal body attached to the body wall (?) along the median side and having an anteriolateral direction similar to that of the coxa of the posterior cephalic appendages. The pronounced anteriolateral position might at first sight suggest
a distinct preoral position, but one has to bear in mind that only the more dorsal portions of the cephalon is cut by the sections. The frontal portion including the antenna is not demonstrated in the series.

The second leg (II) is represented by the coxa preserved on both sides. Because of the oblique transverse section the appendage on the left side (right in photograph) appears to be stronger and reaches further back. The incomplete preservation does not permit a closer morphological study of the basal region. One notices, however, that the coxa forms an elongate, fairly narrow body attached to the postlateral portion of the body wall dorsal to the labrum. In ventral view the body appears to tilt slightly backwards. The median acute border of the coxae, the basendite, does not reach the median line.

The coxa of the third leg (III) is not connected with the calcite-filled central portion. The coxa is elongate with the long axis forming an angle about 60° with the median line and is tilted backwards (in ventral view) in the same way as the coxa of the second leg. Possible fragments of the basal joint of the branchial ramus is seen lateral to the coxa on the right side (left in ventral view). The coxa of the fourth appendage (IV) has a more transverse position than those in front, forming an angle of 80°—90° with the median line. The elongate coxa on the right side is nearly vertical, not tilted backwards as those in front. The median borders of the three posterior pairs of the coxa lie more or less on a line and those on the right and left side are well separated from each other. The coxae of the succeeding thoracic segments are not preserved.

The relation between the dorsal apodemes (gabellar furrows) and the cephalic coxae are demonstrated. The fourth coxa, or rather a precoxa dorsal to it, is attached just below the posterior glabellar apodeme (belonging to the occipital ring) just as the precoxa of the appendages of the thorax (Størmer 1939). The third coxa has a more posterior position than the corresponding apodeme or glabellar furrow. The tilting of the coxa might, however, be seen in connection with this. The same is the case, and more so, with the second coxa which is pushed backwards so that it has a position partly below the succeeding apodome. Since only parts of the first coxa is preserved, its connection with the dorsal test is less distinct.

The section series described illustrates the position of the cephalic coxae in relation to the dorsal test. Although the coxae are
incompletely preserved not permitting any closer study of the basal coxal region, they show that their basendites did not meet in the median line. The position of the coxa in relation to the corresponding apodemes on the glabella (glabellar furrows) indicates an inclination backwards of the basal portions of the appendages.

Ser. K.

(pl. 3, fig. 7, 9, text-fig. 5).

The specimen sectioned is not enrolled, but like many other specimens of Ceraurus in the Trenton Limestone, it shows a characteristic bend along the joint-line between cephalon and thorax. The 22 oblique transverse sections cut through this arched dorsal portion of the body. The most dorsal section (22) cuts off the median and left portions of the anterior tergites, while the most ventral one (1) runs through the posterior portion of the cephalon, from the left lateral eye across the glabella to the posterior margin just behind the genal angle on the right side, cutting through three tergites on the right side and four on the left.

The preservation is not satisfactory. The remnants of the appendages give little information of the morphological details. A glass- and wax model were prepared of the series, the former being stereographically photographed (text-fig. 5).

The shell. The sections through the posterior portion of the glabella show very well the larger tubercles penetrated by a central canal such as described above under ser. H. The deep apodemes of the two posterior glabellar furrows (the posterior one in the occipital furrow) are demonstrated. These structures are very distinct also in ser. J (pl. 4 gf) and in Wittington's silicified specimen (1941).

The ventral integument. In Triarthrus Beecher (1895) described the ventral integument which he found to be segmented below the axis (mesostegite). Similar structures are indicated in Walcott's sections of Ceraurus and Calymene from the Trenton Limestone (Walcott 1918, 1921).

In the specimen sectioned parts of the surface of the ventral integument seem to be preserved below the axis. Below the two posterior segments of the cephalon and the anterior tergite of the thorax, the integument is divided in segments, each forming a roll apparently on account of the bending of the body at this point.
The appendages. Also in this specimen the space below the glabella is filled with calcite. On the left side (right side in ventral view) the remnants of the coxa and basal part of walking legs of the posterior cephalic appendages (III and IV) are indicated. Anterior to the third coxa (III) a triangular portion probably belongs to the calcite-filled space rather than representing a dislocated anterior coxa. The fourth coxa has a concave anterior border and is tilted slightly forward probably on account of the crowding up of the coxa due to the inclination of the head. The slenderness of the coxae, at least those of the two anterior thoracic segments, may to some extent be due to incomplete preservation. The thicker basal portions with their blunt median border might suggest the presence of precoxae.

On the right side (left side in ventral view) only the more dorsal portions of the appendages are demonstrated. While both the basal and more distal portions of the appendages on the left side were directed anteriolaterally, the basal joints on the right side are directed postlaterally and the more distal ones anteriolaterally. It is characteristic that the median basal portion of the coxal region is blunt transverse, not wedge-shaped such as in the typical coxa. The same is found in the thoracic appendages of ser. C (text-fig. 8) and in sections figured by Walcott (text-fig. 10). This basal portion I have interpreted as a precoxa (Størmer 1939). The branchial rami attached to the precoxae (?) of III—V, turn almost at a right angle forwards. The exact structure of the rami is not demonstrated, but a connection with fragments of branchiæ is indicated.

The described section-series demonstrates the segmental character of the ventral integument below the axis. It also furnishes some information on the structure and position of the posterior cephalic and the anterior thoracic appendages. The presence of a medially broader portion of the basal coxal region supports the assumption of the presence of a precoxa.

Ventral cephalic structures in trilobites.

General structure of the arthropod head.

The frontal portion of the arthropod body is covered by a continuous exoskeleton. This part of the body, the head, prosoma or cephalothorax, is separated from the rest of the body by a transverse joint-line. As pointed out particularly by Snodgrass (1938) the head
The segmentation of the frontal portion of the arthropod head is difficult to make out, but some information has been obtained by detailed studies of the nervous system. The arthropod brain is normally divided into three parts: the protocerebrum, deutocerebrum and tritocerebrum. The ganglia of the two first parts are preoesophageal (preoral), while the ganglia of the tritocerebrum are postoesophageal (postoral), belonging to the ventral nerve-cord, thus being of the same type as those enerving the somites (segments) of the rest of the body. We may easily distinguish a tritocerebral somite, but it is difficult to point out a division into separate somites of the preoral portion of the head. As pointed out in part II (1942, p. 120—123) the protaspis larva in primitive trilobites may suggest a division into two parts, the preantennal segmental complex and the antennal segment or somite. Also the presence in certain larvæ, of rudimentary preoral coelomic sacs and rudimentary antennæ in front of the antennæ enerved from the deutocerebrum, may suggest the presence of several segments in the preoral portion of the head. Studies on the arthropod brain have on the other hand lead to the conception that the preoral portion of the head was primarily undivided, differing considerably from the postoral portion of the body. Future studies, not the least on fossil forms, may settle this problem, but at present it seems useful to regard the frontal portion as one unit and apply the
A head consisting of the acron and 4 postoral somites is most common in the Arthropoda. It is found in trilobites, indicated in the embryo of the Xiphosura, occurs in most of the Entomostraca, and in the Leptostraca, Amphipoda and Isopoda among the Malacostraca, and is a constant feature in the head of Myriapoda—Insecta.

As pointed out by Snodgrass (1938, p. 107) this type of head hardly represents an early stage in the development of the Crustacea. A head composed of the acron and one postoral somite only, the so-called protocephalon, occurs in Anostracan Branchiopoda and in larval stages of many other forms. It is not certain whether the crustacean nauplius comprises the acron and two postoral somites, or possibly one or two more somites (Stønner 1944, Vandel 1949).

A head, or more correctly a prosoma composed of an acron and six postoral somites, is found in the Arachnida. In the Xiphosura the transverse joint-line between the prosoma and the metasoma or abdomen, crosses the primary more oblique segmentation, leaving a prosoma with six—seven postoral somites, the sixth and seventh belonging partly to the prosoma and partly to the metasoma.

The cephalo-thorax of the Malacostraca includes a considerable number of somites.

Turning now to the ventral side of the head, we find considerable variation in the development of the appendages and the structures connected with the mouth.

The mouth has a ventral position. A more frontal (terminal) position in the Arachnida is a secondary formation. In front the mouth is bordered by an upper lip or labrum (= hypostoma in trilobites) enervated from the tritocerebrum and therefore hardly representing a separate somite such as suggested by some authors. The ontogenetic development of the mouth and the labrum is recently demonstrated by Kästner (1948) in the Pedipalpi of the Arachnida (text-fig. 6). It appears that the labrum is primarily paired, being formed by the fusion of the two sides of the longitudinal mouth-slit. At the base (in front of) of the labrum a special plate, an epistoma, may be developed. The labrum forms a broad overhanging plate in certain arthropods such as in the Branchiopoda and particularly in the Trilobita, but in most groups it is reduced to a narrow plate between the appendages crowded around the mouth.
A lower lip or postoral plate may form the posterior border of the mouth. According to the ontogenetic development of the Pedipalpi (text-fig. 6) the lower lip develops as a swelling of the integument just behind the mouth. This would indicate that the lower lip is formed by tritosternum i.e. the sternum of the first postoral somite (I). Such a structure is indicated in the Palpigradi, but in other arachnids the lower lip (underlip) is formed either by more posterior sternites, or by the coxae of the cephalic appendages (Snodgrass 1948, p. 14). In the Acarina the structure is called hypostoma, a name which might easily be confused with the trilobite hypostoma meaning the labrum. The Xiphosura and the Eurypterida have an endostoma forming the posterior wall of the mouth opening. In the Eurypterida a larger ovate plate, the metastoma, forms a postoral plate below the endostoma. The metastoma is probably homologous with the chilaria of the Xiphosura, thus representing the rudimentary seventh postoral appendages. In the Myriapoda—Insecta the lower lip, the labium, is formed by the fusion of the bases of the second maxillae (IV).
It is evident that the lower lip in different groups of the Arthropoda is developed from very different structural elements. It is therefore difficult to apply one term such as the labium for all types of arthropods. The more neutral term lower lip or postoral plate seems appropriate until a common name is found.

The cephalic appendages vary considerably both with regard to position and structure. Primarily only the first antennæ or antennules (a) have a preoral position. The other appendages are attached to the sternum on the ventral surface of the transverse somites behind the mouth. This development is found more or less in the Crustacea and Insecta. In the Chelicerata on the other hand, a considerable displacement of the appendages in relation to the mouth has taken place. The preoral antennæ are completely reduced. The chelicerae forming the first appendages, belong to the tritocerebral somite and are thus primarily postoral, but in the Chelicerata these appendages (I) have a distinct preoral position. Even the second and third pair of primarily postoral appendages have a preoral position in the Xiphosura. Ontogenetic studies (text-fig. 6) have shown this to be due to a backwards migration of the labrum and then also the mouth in relation to the position of the appendages.

Primarily the appendages of the arthropod head were set well apart demonstrating the sternites in the middle between them. In many groups, however, a particular development of the coxæ reduces and conceals the sternites. Especially when the bases of the appendages form parts of the feeding organs, the structures differ considerably from the original one or the primitive conditions demonstrated in the larva.

The development of the feeding organs of the Arthropods depends on the kind of food they are consuming. The arachnids absorb liquid food only and have hence no jaws developed. Because of the liquid diet a special sucking apparatus and a preoral cavity formed by the coxæ develop in connection with the mouth.

Nor the Xiphosura have true jaws, but the powerful coxæ with their spiniferous median margins were probably able to serve to some extent as masticatory organs. The prey is seized by the legs and the chelicera, partly crushed by the spiniferous coxæ and the blunt median process of the sixth appendages (VI), but the chewing or grinding of the food take place in the proventricular gizzard. (Snodgrass 1948, Fage 1949).
In the Eurypterida the masticatory function of the prosomal coxae were somewhat more advanced. In the large forms in particular, the median border of the powerful flat coxae were provided with strong teeth and knobs. With their only partly masticatory function, the cephalic coxae of the Chelicerata cannot, however, be regarded as true jaws comparable to those in Crustacea, Myriapoda and Insecta.

In the Crustacea, Myriapoda and Insecta the second pair of postoral appendages (II) are transformed into powerful jaws, the so-called mandibles. Also the third and fourth pairs of appendages, the first and second maxillae (III, IV), serve as accessory feeding organs. In the maxillae the distal portion of the appendages are not reduced to the same degree as is the case in the mandibles.

The cephalic limbs are distinctly biramous in most Crustacea. Somewhat similar limbs are found in the Trilobitomorpha (trilobites and certain other extinct arthropods), but the limbstructures of these forms seem in my opinion hardly to be homologous with those of the Crustacea. A biramous appendage built on the same plan as in the Trilobitomorpha is indicated in the Xiphosura and probably in the Arachnida (Størmer 1939, 1944). A biramous appendage is not present in the Myriapoda—Insecta. Certain structures recalling biramous appendages exist in certain forms, but hardly significant (Størmer 1939, p. 258—261). The biramous legs of the Trilobitomorpha and Chelicerata are characterized particularly by the possible presence of a precoxal, a powerful coxa, a gill-branch with plate-shaped gills attached to the presumed precoxal, and a walking branch (telepod) normally with a patella intercalated between the femur and tibia. In the Crustacea, on the other hand, the two branches of the appendages are attached to a basal stem, the protopodite or sympod, the outer branch, exopodite, has setae, but no gills, the inner branch, the endopodite, has no patella.

After this general introduction we shall discuss the ventral cephalic structures of the trilobites.

**Ventral cephalic structures in Trilobites.**

As soon as the appendages of trilobites became known, particular interest was attached to the problem of the cephalic appendages, their structure, function and relation to the mouth.

Already Walcott's (1881) studies on thin sections of *Calymene* and *Ceraurus* gave some information, and the descriptions by Mickle-
borough (1883) and Walcott (1884) of appendages in *Isotelus* might also be mentioned.

Not until the discovery of the beautifully preserved specimens of *Triarthrus* a more detailed study of the cephalic appendages could be carried out. After having cleaned a considerable number of the pyrite specimens, Beecher (1895) was able to present a description and preliminary reconstruction of the cephalic appendages. In addition to the appendages he describes the ventral integument and postoral plate.

Beecher interpreted the cephalic appendages as antennules, antennae, mandibles and two pairs of maxillae, just as the appendages in the head of crustaceans. He assumed that the coxae of the cephalic appendages in trilobites served as gnathites, the inner edges on gnathobases of the coxae being “apparently finely denticulate”.

Beecher’s work was completed by Raymond (1920). He found the cephalic coxa of *Triarthrus* to be less like those of the thorax, otherwise his studies corroborated those of Beecher. Like Beecher, Raymond expressed the definite opinion that the cephalic coxae (coxopodites) served as gnathites. This opinion seems to a certain extent to have been influenced by the conception of a crustacean nature of the trilobites. As evidence in favour of a gnathic function of the coxae Raymond describes (1920, p. 152) the occurrence in one specimen (only) of the inner edges of the cephalic coxae as being “distinctly nodulose, and roughened for mastication”.

Valuable information on the structure of the cephalic appendage was presented by Walcott in two papers (1918, 1921) dealing chiefly with the appendages in *Olenoides*, *Calymene* and *Ceraurus*, but also describing other known forms. Concerning the structures of the cephalic appendages Walcott’s studies largely conform with those of Beecher and Raymond. Walcott also interprets the cephalic coxae as gnathites and meant to find traces of spines on the inner (median) margin of the coxa (1918, pl. 26, figs. 4, 15).

The works of Beecher, Walcott and Raymond are valuable not the least because of the many fine illustrations forming important sources of information.

---

1 As pointed out by Kobayashi (Journ. Fac. Sci. Imp. Univ. Tokyo, Sec. 2, 4, 2, p. 154. 1935) the name *Neolenus serratus* (Rominger) has to be replaced by *Olenoides serratus* (Rominger) since the genus *Neolenus* Matthew 1899 hardly differs from the genus *Olenoides* Meek 1877.
The labrum, mouth and postoral plate.

With its solid test the labrum or hypostoma is commonly preserved in the trilobite specimens. Numerous forms have been described belonging to many different genera. It might be mentioned that among certain families the labrum is rarely preserved. This is the case i.e. with the Cryptolithidae and Harpidae. In the appendage-bearing specimens of Cryptolithus the small labrum is only fragmentarily preserved (Raymond 1920, p. 62), indicating a less solid test.

The size and shape of the labrum vary considerably. In certain species, such as Ptychopyge angustifrons Dalman (Brøgger 1886 pl. 3, fig. 42) and Cheirurus (Crotalocephalus) gibbus (Barrande 1852) the labrum reaches almost to the hind border of the cephalon, in the case of the former, however, with a deep median cleft in the plate. The labrum is in front attached along the labral (hypostomal) suture. A possible independent movement of the labrum has been discussed by various authors (Brøgger 1886, Opik 1929, Stubblefield 1936. p. 410 and Whittington 1941, p. 514—515). Only a slight vertical movement and a possible vibration seems to have been able to have taken place.

The ontogenetic development of the labrum is little known. Whittington (1941, p. 496, pl. 72, fig. 2, text-fig. 1) has found a metaprotaspis of Flexicalymene senaria (Conrad) with a labrum provided with four pairs of short, thick spines.

The mouth has not actually been recognized in trilobites, but the ventral surface (the ventral membrane) of the cephalon as well as the position of the postoral plate might give some information of its location. Some of Walcott's sections of Calymene in particular (1921, pl. 101, figs. 1—4, pl. 105, fig. 2) show the ventral membrane curving in beneath the labrum, suggesting the position of the mouth slightly in front of the posterior margin of the labrum. Series J and K described above suggest a similar position. A backwards displacement of the mouth is discussed below in connection with the appendages.

The postoral plate, "metastoma" or labium was first described by Beecher (1895) in Triarthrus: "The metastoma is generally clearly shown as a convex arcuate plate just posterior to the extremity of the hypostoma. On each side, at the angles, are two small elevations, or lappets, which suggest similar structures in many higher
Crustacea, and apparently represent the entire metastoma in Apus and some other forms”. Raymond (1920, p. 42) remarks that the postoral plate (metastoma) is larger and more nearly circular than Beecher's earlier preparations led him to suppose.

In one of his thin sections of Ceraurus (not Calymene) Walcott (pl. 27, fig. 12) meant to trace a section of a postoral plate between the cephalic coxae. The structures are, however, little distinct and no trace of a postoral plate is found in the material sectioned by me.

Examining the collections of Olenoides serratus (Rominger) in U. S. National Museum in Washington, I noticed one specimen previously not described, which has the postoral plate fairly well preserved (text-fig. 7 and Størmer 1949 fig. 11 D). The dorsal test of the cephalon is broken off demonstrating the labrum, postoral plate and fragments of the appendages. Just behind the posterior margin of the labrum, the semicircular postoral plate is surrounded, except along the transverse frontal border, by a narrow rim. The lateral part of the plate lies ventrally in relation to one of the coxae, probably belonging to one of the third cephalic legs (III). This indicates that in ventral view the lateral portions of the postoral plate covered parts of the cephalic coxae.

Judging from the position of the postoral plate in trilobites it is natural to regard it as a sternal formation. Probably the main part of the frontal sternite (or sternites) is transformed into a postoral plate or lower lip with its lateral lappets covering to some extent the median portions of the coxae.

As mentioned above the postoral plate in trilobites is probably homologous with the lower lip in primitive arachnids and with the endostoma of the Xiphosura—Eurypterida. The postoral plate in trilobites has been described as a metastoma, but since this organ in the Eurypterida probably represents the modified appendages of the seventh postoral somite, this name is less appropriate (Størmer 1944, p. 32). In previous papers (1944 and 1949, p. 174) I have used the name labium for the postoral plate in trilobites. Since the term labium is a well known structure in the insects, meaning a lower lip formed by the second maxillæ, this term is hardly appropriate. Until more details are known concerning these structures in trilobites, I prefer provisionally to use the more neutral term postoral plate for the structures mentioned.
The appendages.

The antennæ are known more or less in species of the genera Olenellus, Olenoides, Kootenia, Ptychoparia, Cryptolithus, Triarthrus, Phacops, Asteropyge and Ceraurus (comp. Størmer 1939, p. 153—154). The antennæ have a preoral position, being attached to the bodywall on either side of the frontal portion of the labrum. The attachment of the antennæ is demonstrated in the sections of Ceraurus. The antenna is attached to the more vertical integument above the labrum and the point of attachment is evidently protected by the lateral ears of the labrum. Similar ears in the labrum of other trilobites may thus suggest the location of the antennæ in these forms. Special indentations in the lateral borders of the labrum, i. g. in Cheirurus fortis Barrande (Prantl and Pribyl 1947, pl. 2, fig. 1—2) probably indicate the position of the antennæ.

The uniramous, multijointed antennæ differ but slightly in the different genera known. Reconstructions of Triarthrus (Raymond 1920, text-fig. 10) indicate a comparatively long and strong basal joint of the antenna. In Ceraurus this seems hardly to be the case. The antennæ of Cryptolithus have longer joints than in other forms and the specimens preserved have the antennæ directed backwards.

The position and structure of the antennæ in trilobites strongly indicate these appendages to be homologous with the antennules.
(or first antennæ) in crustaceans and with the antennæ in insects, thus being preoral appendages enerved from the deutocerebrum.

There are no signs of a reduction of a second pair antennæ such as suggested by Öpik (1937).

The four biramous appendages occupy most of the space on the ventral side of the head. Beecher (1895) showed that the posterior pairs of appendages and apparently also the anterior ones in Triarthrus were biramous and built on the same pattern as those of the thorax and pygidium. The cephalic appendages in Olenoides are not well demonstrated. The present material of Ceraurus presents new information on the structures of the cephalic appendages in this genus. The sections demonstrate four pairs of legs mutually much alike. The frontal ones being only somewhat smaller than the pairs further back. The section series have shown that also the first and second pairs of cephalic appendages are provided with a branchial ramus (preepipodite) attached to the basal portion of the appendage.

The present studies verify the current conception of the trilobite head having one pair of preoral uniramous antennæ and four pairs of postoral biramous appendages built on the same pattern as those on the thorax and pygidium.

Raymond (1920 p. 42) found the cephalic coxa of Triarthrus to be distinctly different from the coxa of the thorax. He also assumed (l. c. p. 67) the two anterior pairs of cephalic appendages in Calymene and Ceraurus to be reduced because of a lack of function in connection with a backwards migration of the mouth in these genera. Concerning the last mentioned genera the present studies have shown this not to be the case as mentioned below.

With regard to the development of the cephalic coxae in Triarthrus, both Beecher’s and Raymond’s reconstructions are chiefly based on specimen 211 (Raymond 1920, pl. 2, fig. 5, and Walcott 1921, p. 104, fig. 15). In this specimen the coxae on either side are overlapping each other forwards, exposing their flat posterior surfaces. This give the impression of the cephalic coxae being considerably stronger than those on the thorax. As I pointed in part I (1939, p. 204), Raymond’s presumed difference in the development of the cephalic and thoracic coxae might to a large extent be due to
the thoracic coxæ having a more vertical position and therefore appearing more narrow and less strong in ventral view.

As mentioned above the cephalic appendages appear to be mutually alike showing no individual specialization. This is demonstrated in section series H of Ceraurus where the biramous first postoral appendage is preserved. The first coxa is considerably flattened and slightly concave-convex with the concave surface on the antemedian side. No postlateral process is apparently developed such as in the thoracic coxæ, but the short endobase appears to be of the same type as that found in the thorax. There is no sight of a long median “gnathite” provided with teeth. The lack of a spiniferous or nodolous median margin of the cephalic coxæ might to some extent be due to incomplete preservation, but on the other hand the general correspondance in structure with the coxæ of the thorax hardly speaks in favour of the presence of such structures. Walcott (1918, pl. 26, fig. 4, 15) figures and describes certain structures which he interprets as spines on the inner (median) margin of the coxæ. Having studied Walcott’s original sections of Ceraurus and Calymene I am little convinced, however, of the primary nature of the spine-like structures occurring particularly in his less well-preserved specimens. In several specimens the margins of the test are partly dissolved and drawn out into “threads”. The same was the case with the gills (Størmer 1939, p. 187—188).

Nor the other trilobite genera seem to show distinct traces of special teeth, denticles or knobs on the cephalic coxæ. The spines on the cephalic coxæ of Olenoides appear to be like those on the thoracic coxæ. In one specimen of Triarthrus, Raymond (1920, p. 152) describes the inner edges of the cephalic coxæ as “distinctly nodulose, and roughened for mastication”, but this single case, hardly represent any strong evidence in favour of the development of special gnathites.

As mentioned in part I (1939, p. 205—206) a faint indication of a transverse line across the base of the cephalic coxæ is suggested in specimens of Triarthrus figured by Raymond. The line might indicate the presence of a precoxa such as suggested in the thorax.

The position of the cephalic coxæ is not quite the same in the different trilobite genera. In Triarthrus the coxæ have an almost transverse position such as in the thorax, only the two frontal ones tend to have a more antelateral direction. In Ceraurus the cephalic
coxæ turn gradually forward when passing from the fourth to the first legs. Because of the change in the direction of the coxæ the median portions are crowded together leaving little space in between the individual coxæ. At the same time the coxæ of the frontal pairs of appendages are tilted backwards. The general structures suggest a backwards migration of the mouth in trilobites. The migration is less pronounced in Triarthrus where the coxæ are more transverse and tend to be tilted forwards instead of backwards. A posterior migration of the mouth is also suggested in the dorsal segmentation of the trilobite larva as pointed out in part II (1942, p. 122). A similar but more pronounced backwards migration of the mouth is characteristic of the Merostomata as mentioned above.

The cephalic coxæ just like the thoracic ones are set well apart, having, as discussed below, no possibility of meeting each other along the median line.

The feeding organs of the trilobites.

Having described the ventral cephalic structures in trilobites we might consider the relation between the mouth and the surrounding labrum, appendages and postoral plate in order to get some idea of the way of feeding in these primitive arthropods.

As mentioned above most authors have claimed a masticatory function of the cephalic coxa in trilobites. The coxæ have been regarded as acting powerful jaws (Richter 1932, p. 847) just like the mandibles in Crustacea and Insecta. Erikson (1934, p. 254) mentions that no decisive proof of the presence of a gnathobase in trilobites is presented in the published photographs, but since such a structure is demonstrated in Beecher's careful reconstruction he thinks they were evidently present. Erikson points out, however, that the elongate median endobase had to be very long because of the great distance between the rows of appendages. In part I (1938, p. 204) I doubt the presence of the long gnathobase (basendite) and at the same time Snodgrass (1938, p. 110) refers to the trilobites as non-mandibulate arthropods, a view also expressed by me (Størmer 1944, p. 34). More recently Snodgrass (1948, p. 2) points out that the leg bases in trilobites “could have had little use as feeding organs other than perhaps that of stirring up the mud from which the animals obtained their food”.
The present material gives further information on the function of the cephalic appendages. Because of the somewhat radial arrangement of the cephalic coxa, the frontal pairs of coxae probably were situated near the mouth. The coxae have no elongate gnathobase or basendite developed. The median border of the coxae is but slightly protruding forming a basendite of the same type as those in the thorax. The median border may have been provided with spines such as the coxae of the thorax, but there is no unmistakable evidence of a special development of teeth and nodules such as would be expected on the surface of true gnathites. At the same time the cephalic coxae, just like the thoracic ones, are set well apart making it impossible for the median margins of the coxae to meet each other along the median line. The structures mentioned make it very probable that the cephalic coxae in trilobites did not serve as jaws.

In order to comprehend the mode of feeding in trilobites it is useful to compare the trilobite structures with those in other arthropods particularly the Xiphosura. Neither the Xiphosura are true mandibulate arthropods. In the limulids the coxae are radially arranged round the mouth with the spiny median lobes almost meeting across the mouth. The food, consisting principally of worms and small molluscs, is caught by the pincers of the legs and placed between the coxae which with their spines push it forward to the mouth. The coxae are apparently to some extent able to crush the food, but the grinding is carried out in the proventricular gizzard into which the prey is ingested. (comp. Snodgrass 1948, p. 17). Larger, not assimilable pieces of food are gulped up and rejected (Fage 1949, p. 232).

In the Eurypterida the prosomal coxae might have formed a similar feeding organ. The eurypterid coxae seem, however, to have been more able to crush the food.

As mentioned above the Arachnida have no indication of jaws. These arthropods live on liquid food only, the food being ingested by means of an efficient sucking pump. As an exception it might be mentioned that the primitive Phalangida (Opiliones) also ingest fragments of their food besides the liquid (Snodgrass 1948, p. 50).
In the Arachnida the prey is brought by the chelicera into a specially developed intercoxal antechamber or preoral cavity.

Judging from the development of the cephalic coxae, the trilobites were hardly able to crush the food such as is the case in the Xiphosura and evidently even more so in the Eurypterida. Otherwise the feeding organs seem to have been much alike although no trace of a gizzard has been found even in the well preserved trilobite specimens from the Middle Cambrian Burgess Shale.

The strong development of the labrum in trilobites indicates the formation of a preoral cavity bordered laterally by the cephalic coxae and posteriorly by the postoral plate. In this preoral cavity the food was probably brought in by the legs (telopodites). By means of a sucking organ or pharynx the food might have been ingested and ground in some kind of a gizzard in the frontal portion of the head. As discussed in part I (1939, p. 224—227) the food might have been transported to the preoral cavity not only by means of the legs. The filamentous gills of the appendages might have served as filters holding back the food-particles from the water passing through them. By a certain undulating contraction of the gillbearing appendages the food particles might possibly have been pushed forward to the head region where they might have entered the preoral cavity in front of the coxae.

We may conclude by stating that the feeding organs of the Trilobita did not include true jaws such as in the Crustacea and the Myriapoda—Insecta. The food, consisting either of softer bodies, or finer food particles embedded in mud or extracted from it by means of filters, was probably brought into the preoral cavity from which it was ingested by means of a sucking organ and carried into a more or less developed gizzard lying in the frontal portion of the head. The trilobites seem thus to a large extent to have been mud feeders.

Remarks on the previously described section series of the thoracic appendage in Ceraurus.

In part I (1939) the general structures of the thoracic appendages in trilobites are discussed. From studies on Ceraurus in particular, I arrived at the conclusion that the trilobite appendage comprises a precoxal with two branches attached to it: a branchial ramus
(preepipodite), and a walking leg (telopodite) with a powerful basal joint forming a coxa.

In a paper not accessible to me until after the war, Garstang (1940) criticises my interpretations of the thoracic structures demonstrated in my section series. He publishes certain drawings based on small-size photographs reproduced in my paper. In order to meet his criticism I have reproduced in stronger magnification (pl. 3, fig. 1—6) certain details of the photographs, and prepared outline drawings of the sections series (text-fig. 8) and of the wax-model prepared from the series (text-fig. 9).

In Garstang's drawings, and also pointed out by him in the text (p. 62), there appears to be a great difference between sec. 39 and 40. As shown in text-fig. 8 this is not the case, but this may have been somewhat difficult to ascertain from the photographs reproduced in my paper. Garstang points out that while I claim the diameter of the precoxa to be 1.4 mm, the sections only show 0.8 mm. As shown in the drawings (text-fig. 8) the sections 45, 41 and 40 have a diameter of about 1.2 mm and the figure 1.4 mm was stipulated not from a single section, but from the dimension suggested in the wax model.

Garstang means to find a discrepancy in my treatment of the sections which in my opinion formed a transition between the presumed precoxa and the coxa. He indicates (p. 63) that in the text I treat the sections 36—39 as coxal, while in the lettering of the sections I draw the limit between coxa and precoxa at a higher level, viz., between 34 and 36. His argument is chiefly based on his assumption that in sections 36—39 the long backwards extension is identical with the postlateral process of the coxa described by me and shown in my wax models and reconstructions. This is not the case. As indicated in the drawing of the model in text-fig. 9, 2 (extended portion marked with an arrow and 39), this backwards extension was regarded by me as part of the branchial ramus, not as part of the coxa. In my description (l. c. p. 198, 181) I said that the postlateral margin of the coxa covered the first joint of the preepipodite (branchial ramus) and the proximal part of the second joint. Garstang evidently misunderstood this expression although the reconstructions (text-fig. 10 and pl. 11) showed that less than half of the second joint is covered by the postlateral process. In the sections 36—39 the backward extension may seem to be composed of two
bodies lying side by side as mentioned by Garstang, but a careful study of the photographs might suggest a further division as indicated in text-fig. 8 sec. 39, and pl. 3, fig. 5.

In my description of the precoxal region (36—48) I say: “we notice a distinct line of division between the two elongated segments lying side by side”. Garstang finds that this reference, “though not explicit, can only be the two dark strips in the coxal shield of sections 36—39”, and therefore is of the opinion that I have called the same thing coxa in one place and precoxapreepipodite in another connection and thus have no real grounds for my views. To this I want to point out: 1. that Garstang’s criticism evidently is based on his erroneous conception of the postlateral process on the coxa (sec. 39), and 2. when mentioning “two elongated segments lying side by side”, I meant, as pointed out in the text, the segments demonstrated in sections 36—48, not only those in sections 36—39. I admit that the expression “lying side by side” might be somewhat inaccurate as long as the two segments are actually separated from each other in several sections.

To summarise briefly, my opinion on the basal portion of the appendages was that the subcoxal membrane was limited to the sections below (dorsal) to sec. 49 (?). In the sections following (from 49 to about 36) the two proximal points were interpreted as precoxapreepipodite and basal segment of the branchial ramus or preepipodite attached to it. The border-line between the precoxapreepipodite and the overlying (ventral) coxa was not actually demonstrated but indicated by the general shape and direction of the basal portion of the appendage.

Garstang interprets my precoxapreepipodite (as far up as to section 40—41) as the collapsed subcoxal membrane (l. c. p. 62). The other proximal joint or body is interpreted by him as the basal joint of the branchial ramus, but since my precoxapreepipodite is interpreted as a subcoxal membrane he has to have the basal segment of the branchial ramus attached to the inner surface of the coxal shield (l. c. p. 64). He points out that the mentioned basal joint of the branchial ramus exactly underlies a part of the coxa.

In the text-fig. 8 it is possible to follow the first joint of the branchial ramus from sec. 49 and upwards (ventrally) through the series. The joint lies close to the precoxapreepipodite in sec. 47, but is more or less separated from this joint upwards through the series. The first
joint of the branchial ramus is easily separable from the precoxa and also from the second joint of the ramus in all sections up to 39. Here the second joint of the branchial ramus seems to be more closely connected, both with the precoxa and the first joint of the ramus, a fact which led Garstang to the erroneous conception that the whole backwards extension belonged to the coxa. As shown in the text-fig. 8 it seems possible to trace the first joint of the ramus up to sec. 34. The structure is illustrated in the drawings of the wax model (text-fig. 9, c, d). If we follow Garstang's view assuming a collapsed subcoxal membrane up to sections 40—41, only a very small portion of the first segment of the branchial ramus abuts to the coxa. Garstang's definite conclusion that the branchial ramus is an outgrowth from the inner surface of the coxal shield, seems therefore most unlikely.

Garstang's interpretation of one of the basal bodies being a collapsed subcoxal membrane seems also improbable for other reasons. It is hardly likely that of two well-preserved basal bodies, one should represent a collapsed membrane and the other a solid joint. With the assumed height of the membrane (a height which seems to have been the same in appendage II of the same series) no articulation could have taken place between the body and the appendage.

To me it hardly seems doubtful that the branchial ramus was attached to the very basal portion of the appendage, i.e. to the portion interpreted by me as the precoxa. The fact that the basal joint of the branchial ramus and the presumed coxa are separated from each other in many sections does not contradict this explanation. The intersegmental membrane might have been destroyed so that the mud penetrated in between the joints. Concerning the presence of a separate distinct precoxa, it must be admitted that the proximal and distal border lines are not distinctly demonstrated in the section series. It has, however, to be remembered that such a line may not have been distinguishable in sections more or less parallel to the joints. The evidence which led to the assumption of such a joint is the general difference in shape and direction of this joint compared with the coxa (text-fig. 9, l).

As pointed out above I do not agree with Garstangs criticism and interpretation of the sections. I may admit, however, that some of my expressions might have been more accurate, and with regard
to the presence of a separate precoxa the opinion expressed by me might have been a somewhat less conclusive.

The section series described in the present paper do not, on account of the incomplete preservation, give any decisive evidence in favour of the presence of a precoxa. A blunt median margin on the basal portion of the appendages in series K, however, suggests structures similar to those described in part I (1939).

One of Walcott's slides (text-fig. 10 a) also shows the blunt median margins of the basal portion of the appendages. The coxae on the other hand, have an acute median margin. Walcott (1921, p. 397
and p. 401) also considered the possibility of a precoxal in *Calymene* and *Ceraurus*. In certain specimens of *Calymene* and *Ceraurus* (text-fig. 10 b) he found suggestions of a small very short joint between the coxopodite and the ventral surface. It deserves to be mentioned, however, that he also ventilated another interpretation suggesting the narrow connection between the coxopodite and the ventral side to be “a cross section of the space occupied by the muscles connecting the ventral integument and the axial processes and mesoskeleton of the dorsal test”. Walcott probably meant a proximal portion surrounded by a subcoxal membrane.

Judging from the structures demonstrated in *Calymene* and *Ceraurus* we arrive at the following conclusions concerning the appendages of these forms:

The biramous appendages have a prominent coxal region. Whether the elongate basal portion of this region represents a separate joint, a precoxal, is not decisively determined as long as the actual jointline is only indicated in one of Walcott’s slides. The presence of a separate joint is, however, suggested by the difference in shape and direction of the basal elongate portion in comparison with the typical coxa. The branchial ramus is attached to the basal body (a small portion seems to abut to the lateral base of the coxal body).
Reconstructions of Ceraurus and Olenoides.

Reconstructions of these genera have been published by Walcott (1918, p. 30 and 1921, pl. 94) and Raymond (1920, text-fig. 8 and pl. 11). Since new informations have been obtained since then, I have found it appropriate to present new reconstructions of the two genera.

In the reconstruction of Ceraurus (text-fig. 11) the gills are directed backwards such as demonstrated in Olenoides and Triarthrus. In fact specimens of Ceraurus often show the gills turned forwards (Størmer 1939, text-fig. 8, 9 and text-fig. 3 of the present paper). The position of the gills may therefore have been somewhat different from what is suggested in the reconstruction. The tuberculation of the dorsal test is somewhat schematic. Probably each tubercle was provided with one sensory hair not indicated in the reconstruction. Hairs or setæ were probably also present on the antennæ and other appendages. A lower lip was present, but since it is not actually found, the probable outline is just suggested.

The reconstruction of Olenoides (pl. 12) is to a large extent based on Walcott’s figures and descriptions. The structure of the gill-branches (Størmer 1933) and the find of a lower lip furnish the new evidence.

In both reconstructions the ventral integument is dotted.

Interpretations of the coxal region of the trilobite appendage.

Different opinions have been expressed in connection with the interpretation of the basal structures of the trilobite appendages. Calman (1939) is inclined to regard the short precoxa as a protopodite (sympod or peduncle) with the branchial ramus representing the exopodite. A similar view has more recently been advocated by Heegaard (1945, 1947) and suggested by Vandel (1949, p. 90).

When Calman interprets the basal joint as a protopodite it is apparently because he is convinced that the trilobites are crustaceans and because an unjointed protopodite (peduncle) occurs in not a few crustaceans.

I have previously (1944, p. 121) pointed out that Calman’s interpretation meets with considerable difficulties. It involves among others a peculiar rather unique development of the ischiopodite and
Text-fig. 11. Reconstruction of *Ceraurus pleurexanthemus* Green from the Middle Ordovician of U.S.A.
Text-fig. 12. Reconstruction of *Olenoides serratus* (Rominger) from the Middle Cambrian of U.S.A.
necessitates the presence of eight (possibly seven) segments in the endopodite, structure apparently unknown in the Crustacea. I also pointed out that since primitive Crustacea, according to Hansen (1925, 1930) and others, had a sympod of three separate joints, a short undivided protopodite in the very primitive Trilobita was most unlikely.

Heegaard (1945, 1947) has questioned Hansen's conception of a primary three-jointed sympod, a conception which Hansen arrived at from his extensive comparative studies on recent Arthropoda. Heegaard believes the unsegmented sympod to be the primitive structure. The division into three joints is thought to be a secondary formation. He bases his opinion on ontogenetic studies on copepods, parasitic in particular. The crustacean appendage first develops as a bud which becomes bifurcate before any articulation appears. In the nauplius the endo- and exopodites contain several joints while the sympod is still undivided. According to Heegaard the division of the sympod appears later in the ontogeny and is therefore believed by him to be a secondary formation. As an example of this he mentions the late appearance of a middle joint in the sympod of Calanus tonsus (Campbell 1934).

But does this ontogenetic development give any real clue to the phylogenetic development? When Heegaard puts such weight on the lack of separate joints in the sympod of the ontogenetic stages I think he is carrying the biogenetic law a little too far. Even if the primitive arthropods had a threejointed sympod one would hardly expect to find the early, imperfectly developed bifurcate appendage in later forms divided into a complete number of segments. Lang (1946, 1948) strongly criticises Heegaard's conclusions which he finds not well founded. Lang mentions (1946, p. 8) that although he at first was very sceptically inclined towards Hansen's theory on the threejointed sympods, he afterwards changed his mind: "I was, therefore, very astonished after an extremely careful examination of the extremities of the harpacticides, to find myself convinced that Hansen is right after all".

Only the fossil material is able to decide whether or not the larger number of joints in the appendage is the primitive character. Unfortunately the fossil record on early primitive crustaceans is rather incomplete as far as the appendages are concerned. It might be mentioned that in the Middle Devonian Lepidocaris rhyniensis (Scour-
field 1926) the sympod of the second antenna (I) is divided into 3 distinct joints, the precoxa, coxa and basis (basipodite). This division is even indicated in the small larva (text-fig. 14), although the separation of the two basal joints is not quite distinct (Scourfield 1940). This one case is not conclusive, but it shows at least that a three-jointed sympod occurs already in early and apparently primitive crustaceans.

Among the Chelicerata we are more able to follow the development of the joints in fossil and recent forms. In earlier papers (Størmer 1936, 1939, 1944) I have pointed out the presence of a larger number of joints in the appendages of early and primitive members of the Chelicerata. This has been emphasized also by Vachon (1944-45, 1945). He points to the fact that in the Lower Devonian *Weinbergina* (Richter and Richter 1929), a primitive Xiphosuran (Synziphosura), the five prosomal legs (II—VI) appears to have a larger number of joints than the same legs in the recent *Xiphosura* (*Limulus*). In *Weinbergina* all the prosomal legs appear to have the same number of joints as the last pair (VI) in *Xiphosura*. In the four frontal legs of the recent form the number of joints is reduced both in the larva and the adult. Since the more primitive *Xiphosura* evidently had more joints in these appendages it is hardly doubtful that a reduction in the number has taken place. This impairs in my opinion Heegaard’s arguments against a primary three-jointed sympod in the Crustacea.

Vachon explains the reduction of joints as a case of partial neoteny or merostasis (1945, p. 175). The division into several joints was postponed or never accomplished. The same view might be applied on the conditions in the Crustacea. The late appearance of the division of the sympod or protopodite into two or three joints might be explained as due to partial neoteny rather than signifying a one-jointed sympod in primitive forms such as advocated by Heegaard. The fossil record seems to support Hansen's conception of a reduction rather than an increase in the number of joints in the arthropod appendage during the phylogenetic development.

It thus appears to be but slight evidence in favour of interpreting the short basal portion of the trilobite appendage as a protopodite or sympod.

We shall now consider my arachnomorph interpretation of the trilobite appendage (Størmer 1939, 1944).
Among the Chelicerata Vachon finds it possible to refer the joints of the appendages to four primary groups: the protocoxa, protofemur, prototibia and prototarsus. The fossil arachnids show more joints than the related recent ones. In its complete development the appendage is supposed by him to have had 9 joints composed of $3 + 2 + 2 + 2$ joints. The trilobite appendage (in my interpretation) would according to Vachon just demonstrate the primitive chelicerate appendage such as it would be expected.

The interpretation of the trilobite appendage as composed of a precoxa, coxa and a seven-jointed walking leg finds its chief support in the identification of the coxa. A prominent coxa similar to that in trilobites, is found in the Xiphosura which have so many other characteristics in common with the Trilobita.

The interpretation of the powerful plough-shaped joint in the trilobite appendage as a coxa involves the identification of the basal joint as a precoxa (or possibly as a basal portion of the coxa) and the branchial ramus attached to it as a preepipodite (or possibly an epipodite).

Among the Chelicerata a precoxa is not at all a common structure and its presence is not unanimously accepted. The presence of a precoxa in the five posterior prosomal appendages (II—VI) of the Xiphosura is suggested by Coutière (1919), Størmer (1939, 1944) and Fage (1949). The muscles of the joints present, however, no evidence for or against this assumption which is based on certain lines on the test (Vachon 1945, p. 292). (Another in my opinion less probable interpretation of the coxal region in Xiphosura has been suggested by Heegaard 1947, p. 184—185).

An unjointed appendage, the flabellum, is attached to the lateral, possibly precoxal, portion of the coxal region. In the Japanese xiphosuran *Tachypleus tridentatus* the lay outs of such appendages are found also on the other prosomal legs. It seems natural to homologize these organs with the branchial ramus of the trilobites (Størmer, 1939). In the abdomen of the Xiphosura a prominent gillbranch similar to that in trilobites, is present and it is of importance to notice that it is attached to the very base of the appendage just as in trilobites.

In the Arachnida a rudimentary precoxa has been demonstrated in the Acarina by Schulze (1932) and by Ruser (1933). Neumann (1941, p. 619) shows, by the attachment and course of the muscles,
that the basal portion of the syncoxa represents a real precoxa. The same author (1942) has also meant to trace rudiments of a precoxa or corresponding muscles in primitive arachnids such as the Solifugae, Araneae and Pseudoscorpionidea.

In part I (1939, p. 249) I suggest the possibility that a certain organ, the cymatium, in the syncoxa of the Acarina may be interpreted as a rudiment of a preepipodite of the type found in the trilobites.

Certain lateral sterno-coxal processes in the embryo of Euscorpius are regarded by Dawydoff (1949, p. 348) as without doubt homologous with the flabellum on the sixth prosomal appendage of Xiphosura (Limulus). Median processes in the prosomal appendages of the embryo of Araneae have been interpreted in the same way, but I find it more probable that these processes are rudimentary coxal endites such as explained by Schimkewitsch who originally described them (Schimkewitsch 1911, p. 691—692, pl. 1, fig. 28).

Ecdysial teeth are a common feature in the embryo of the Arachnida. The teeth serve to puncture the cuticle during the ecdysis. In the primitive Pedipalpi Kästner (1949) has demonstrated the ontogenetic development of the organ. Already in an early ontogenetic stage (text-fig. 6) a small bud (et) on the lateral basal portion of the pedipalps (II) indicates the ecdysial tooth. In a later stage (text-fig. 13) the lateral processes forming the ecdysial teeth are very distinct. In this stage the shape and position of the coxae in relation to the mouth are much more trilobite-like than in later stages where the coxae form larger plates meeting along the median line. The general appearance and position of the ecdysial teeth in the Pedipalpi might suggest these organs to be remnants of the lateral branch (pre-epipodite) in the appendages of the Trilobitomorpha. Other ecdysial teeth may, however, have had an other origin.

As pointed out in earlier papers (Størmer 1939, 1944) the walking leg (telopodite) of the trilobite appendage corresponds well with the legs of primitive Chelicerata.

In general we may state that the appendages of the Trilobitomorpha on one side and the appendages of the Chelicerata on the other side demonstrate so many common features that it seems very probable that the latter type is derived from the former.
Remnants of the characteristic trilobitan appendage are recognized in many different groups of the Chelicerata. The remnants are preserved also in terrestrial forms having a mode life very different from the marine trilobites.

It is possible also to trace a distinct connection between the trilobitan and crustacean appendage? As mentioned above some recent authors such as Garstang and Gurney (1938), Calman (1939, Garstang (1940) and Heegaard (1945, 1947) have interpreted the trilobitan appendage as homologous with the appendage of the Crustacea. An essential feature in the crustacean appendage is the bifurcation, the two branches (the endopodite and exopodite) attached to a basal sympodite or protopodite. The bifurcation also of the trilobitan appendage is taken as a strong suggestion of homology of the two types of appendages. The trilobitan “exopodite” is attached to the very base of the appendage and differs in this respect from the crustacean exopodite which is attached to the distal end of a sympodite. The sympodite may be short and consisting of one joint only, but yet the attachment of the exopodite is different. The “exopodite” of the Trilobitomorpha is normally provided with gills, an organ which in the crustacean appendage is connected with the preepipodite and epipodite, not the exopodite.

Of course a transition from the trilobitan to the crustacean type of appendage may theoretically have taken place. It was assumed by Raymond (1935) and by the more recent authors cited above. The “crustacean” interpretation of the trilobite appendage meets, however, with certain difficulties (p. 141). Since the gillbranch is attached to the
very base of the appendage, this portion has to be interpreted as the sympodite or protopodite, an explanation which involves the presence of eight or at least seven joints in the “endopodite” (seven joints if the coxa is regarded as belonging to the same joint as the basal one). This number exceeds the five to six joints in the crustacean endopodite (Størmer 1944, p. 121).

In spite of the difficulties the possibility of a transition from the trilobitan to the crustacean appendage may not be excluded. But why do we not find any distinct signs of such transition? The trilobitan appendage is traced among numbers of the Chelicerata, particularly in the aquatic ones, but apparently also in forms having attained a terrestrial mode of life. My previous studies (1939) have shown the trilobitan appendage to be a very conservative structure which is maintained in very different form of Middle Cambrian Trilobitomorpha, forms belonging both to the benthos, necton and plankton. It might be objected that some of the mentioned Middle Cambrian arthropods in fact were crustacean, but even if this should turn out to be the case, it is difficult to understand why no existing crustacean shows distinct traces of the trilobitan appendage. As mentioned above the Middle Devonian *Lepidocaris* (text-fig. 14) has typical crustacean legs. Garstang and Gurneys (1938) and Garstang (1940) explain the elongate sympodite in the Crustacea as being formed when the appendage developed from a less movable appendage confined to the sub-pleural chamber, into a free swimming organ. This development has not been demonstrated in the fossil record and it might be mentioned that nor are any signs of elongate sympodites found in Middle Cambrian Trilobitomorpha with more or less freely exposed appendages (Størmer 1939, p. 239). The mentioned authors also state that the pleural “scales” which overlap the bases of the appendages in *Lepidocaris* on one side are clearly foreruners of the pre-epipodites (proepipodites) of the Anostraca and on the other side no less clearly homologous with the pleura of Trilobites. If we consider homologies of this, in my opinion rather far-fetched type, any transition may be possible. It seems, however, more safe to confine ourselves to the observed facts.

With our present knowledge it seems to me less probable, though not impossible, that the crustacean appendage evolved from the appendage of trilobitomorph ancestors.
The zoological position of trilobites.

In part I (1939, p. 147—152) I give a brief review of the various conceptions of the zoological position of the trilobites. It appears that the opinions have changed considerably from time to time. Referring to my previous review of the literature, I am in the present connection dealing only with the more recent literature.

In my paper on the Arachnomorpha (1944) I have treated the problem on the probable relationship between the Trilobita, Chelicerata and other groups of Arthropoda. I arrived at the conclusion that the
Trilobita and the Chelicerata and certain other extinct arthropods were mutually related forming one larger taxonomic unit for which I adopted the name Arachnomorpha, a name primarily introduced by Heider. The forms provided with preoral antennæ and trilobitan appendages were included in the new subphylum Trilobitomorpha corresponding in rank to the Chelicerata characterized by the lack of antennæ and the presence of chelicera.

I found it less probable that the Crustacea were derived from the Trilobitomorpha, but could on the other hand not definitely exclude the possibility of a relationship (p. 143).

As characteristic of the Arachnomorpha I pointed out (p. 128):

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.

Within one large taxonomic group, comprising many different genera, it is of course difficult to demonstrate particular characters which are present in all genera and at the same time confined to this one group only. In many cases the significant characters may be traced to a small extent also in other groups, and it is more or less a matter of judgement to which degree this occurrence means affinities or merely coincidence. Although the trilobation is found in other groups it is rather characteristic of the Arachnomorpha.

Heegaard (1945, p. 10) and Linder (1945, p. 22) question the importance of the trilobation in the Trilobitomorpha and the Chelicerata. Heegaard explains it as “being mainly based on biology”, and Linder points out that the trilobation among the Crustacea is not confined to members of the Isopoda and Decapoda, but occurs also in the Branchiopoda.

The value of the four postoral larval or primary somites has also been discussed. Their presence in the Trilobita and the Xiphosura seems to indicate a relationship between these groups, but since we do not know for certain whether the crustaceans have two or four larval somites, this character cannot be used as a decisive character separating the Arachnomorpha and the Crustacea.
Linder (1945, p. 21) points out that among the Crustacea strongly developed intestinal diverticulae are not confined to a few parasitic copepods only, but are characteristic also of the head of most branchiopods. This impairs somewhat the importance of the intestinal diverticulae as significant characters of the Chelicerata such as urged by Kästner (1940) and maintained by me.

Tiegs (1947, p. 318) discusses the relationship between the different groups of the Arthropoda. He is inclined to regard the affinities between Trilobita and Arachnida as closer than with the Crustacea and finds that the primitive fossil Xiphosura shows a most remarkable resemblance to trilobites. (The articulated telson spine is thought to form an exception, but as I have previously pointed out (Størmer 1944, p. 115) Ivanov's (1933) studies on the ontogeny of Limulus (Xiphosura) rather supports the resemblance). Tiegs assumes that both the Chelicerata and the Crustacea evolved from the trilobite stem.

The affinities of trilobites are discussed recently in Volume VI of Traité de Zoologie edited by P. P. Grasse (Vandel 1949, Waterlot 1949, Fage 1949 and Størmer 1949).

In his general review of the Arthropoda (Vandel 1949, p. 147) arrives at the conclusion that the Trilobita cannot be placed in any of the recent classes of the Arthropoda. The Trilobita are regarded as a very primitive group which Vandel prefers to place in a separate subphylum for which he proposes the name Proarthropoda. Following Heegaard and others before him he figures the trilobites to be closely related to a presumed common ancestor of both the Chelicerata and the Crustacea. He is not inclined to attach much importance to the trilobation, the number of primary somites or the non-crustacean interpretation of the trilobitan appendage. At the same time (l. c. p. 146) he is primarily disinclined to place the Trilobita and Chelicerata in one taxonomic group as long as the former have antennæ and labrum and lack the chelicera characteristic of the latter group. The value of these arguments are discussed below, but in this place I want to point out the labrum is not alien to the Chelicerata. A narrow labrum is distinct in the Xiphosura and a labrum is also found in the larval stages of the Arachnida. In the adult arachnids the organ is surpressed in connection with the special development of the preoral cavity.
In his treatment of the Merostomata Fage (1949, p. 246–247) strongly stresses the close affinities of the Trilobita and Xiphosura (in spite of the lack of the antennæ in the latter). He writes: “En réalité les rapport qui unissent les Trilobites et les Xiphosures sont si étroites qu'il existe toute une série de formes que l'on hesite à classer ici ou là’.”

Waterlot (1949, p. 215) emphasizes the relationship between the Trilobita and the peculiar giant arthropod Arthropleura from the Carboniferous.

In my article on the Trilobita (Størmer 1949, p. 186; 187) I give a brief review of the different opinions on the systematic position of the group.

We have now considered the more recent evidence and views on the affinities of the trilobites. It has become apparent that certain features, such as the number of the primary or larval somites, are yet too little known to be able to give decisive evidence. Future ontogenetic studies in particular, may solve or at least throw new light on these important question.

The general phylogenetic and taxonomic problems to be considered may be summarized in two points: 1. Are the Trilobitomorpha related to the Chelicerata? 2. Are the Trilobitomorpha related both to the Chelicerata and the Crustacea, thus being more or less ancestral to both groups?

Concerning the affinities between the Trilobitomorpha and the Chelicerata, recent research seems to confirm the existence of a closer relationship between these groups. Most recent authors seem to have adopted this view. Among the characters common to most members of the two groups may be mentioned:

1. A distinct trilobation representing a strong development of the pleural area of the dorsal shield, a distinct head-shield or prosoma, and the tendency to develop a styliform telson.
2. The lack of true jaws.
3. The postoral appendages being either trilobitan limbs or modifications of this type of appendages.

In addition to these we may mention two extra points which are characteristic of both groups, but which at the same time may pos-
sibly be more or less characteristic also of members of other groups e. g. the Crustacea:

4. The presence of four postoral larval or primary somites.
5. A strong development of the intestinal diverticulae.

With our present knowledge of fossil and recent forms it is considerably more difficult to answer the question whether or not the trilobites also are related to the Crustacea. It is tempting to regard the primitive trilobites as being closely related to the ancestor of both the Chelicerata and the Crustacea. But do we have enough evidence in favour of such a relationship? As I have previously pointed out (Størmer 1944, p. 144) certain Middle Cambrian Trilobitomorpha are very crustacean-like and have in fact been looked upon as true crustaceans by most authors. If the crustacean-like features of these forms are true crustacean characters and not merely matters of convergence, these arthropods must be regarded as transition forms demonstrating direct affinities between the Trilobitomorpha and the Crustacea.

When I doubt the relationship between the Trilobitomorpha and the Crustacea it is chiefly because of the difference in the structure of the postoral appendages. In a previous chapter I have paid attention to the fact that satisfactory transition stages between the trilobitan and crustacean appendages have not been demonstrated as far as I can make out. Traces of the characteristic trilobitan appendages ought in my opinion to have been found in the many types of fossil and recent crustacean appendages. The lack of true jaws in the trilobitomorpha may not exclude the possibility of a relationship between the trilobites and crustaceans, but also here we might have expected to find certain distinct transition stages in the larval or adult stages of fossil or recent forms. In my paper from 1944 I proposed, like did Heider, to include the Trilobitomorpha and the Chelicerata into one phylum the Arachnomorpha, thereby suggesting that the Trilobita were not phylogenetically connected with the Crustacea. Although I am still inclined to hold this view, more recent contributions from zoologists in particular, have shown that a definite decision of the problem is still somewhat premature.

The conclusions to be drawn from the present discussion might be summarized as follows: Recent research indicates the relationship between the Trilobitomorpha
and the Chelicerata. The Chelicerata evidently evolved from ancestors not much different from the Trilobita. It still remains an open question, however, whether the Crustacea evolved from the same ancestors and thus also are more closely related to the Trilobita.

Literature.

Beecher, C. E., 1895: Further observations on the ventral structures of Triarthrus. Amer. Geol. 47.


— u. Richter, E., 1929: Weinbergina opitzi n.g.n.sp. ein Schwerträger (Merost. Xiphos.) aus dem Devon (Rheinland). Senckenbergiana. 11.


Snoddgrass, R. E., 1948: The feeding organs of Arachnida, including mites and ticks. Smiths. misc. coll. 110.


— 1884: The appendages of the trilobite. Science. 3.


Explanation of Plates.

*Ceraurus pleurexanthemus* Green from the Middle Ordovician Trenton Limestone, Trenton Falls, New York State, U.S.A.; Wallcott's collection. Photographs not retouched.

*Pl. 1.* Samples of section series H, 5 ×, (comp. pl. 2).

*Pl. 2.* Wax model of ser. H. Fig. 1 = dorsal view of cephalon, fig. 2 = antero-ventral view, fig. 3 = ventral view and fig. 4 = posterior view. *a* = antenna, *br* = gills of branchial ramus, *eye* = eye, *cox* = coxa, *gl* = glabella, *glf* = glabellar furrow, *lab* = labrum, *prpd* = branchial ramus (preepipodite), *−IV* = postoral cephalic appendages.

*Pl. 3.* Figs. 1–6 = details of ser. C, Nos. 34–37, 39–40 (comp. text-fig. 8). Fig. 7 = Wax model of ser. K. Ventral view of posterior portion of cephalon and anterior portion of thorax.

Fig 8 = Sample of section series J (comp. pl. 4).


Pl. I

1

2

3